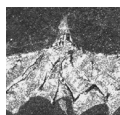


Hemichordata (Enteropneusta & Pterobranchia, incl. Graptolithina): A review of their fossil preservation as organic material

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Hemichordata and especially the Pterobranchia (Cephalodiscida and Graptolithina) can be regarded as useful examples to understand the fossil preservation of organically preservable (non-mineralized) fossils through geological history due to the commonality of their fossils in Palaeozoic sediments. The organisms consist of organic materials of three different types, the zooids (cellular tissues), the stolon system (recalcitrant matter) and the tubaria (recalcitrant matter). These materials differ considerably in their taphonomical changes and final preservational potential. While the soft-bodied zooidal or cellular tissues, similar to the bodies of the phylogenetically related enteropneust worms, are nearly impossible to preserve, the recalcitrant material of pterobranch tubaria is extremely common in the early Palaeozoic fossil record. The durable stolon systems of benthic graptolites are largely found in residues from the dissolution of carbonate rocks. Diagenesis, metamorphism and tectonics modify pterobranch tubaria within the sediment. Tectonic distortion and subsequent weathering may have the largest influence on the destruction or preservation of these fossils. Graptolite reflectance is used commonly in Palaeozoic sediments to determine the thermal maturity of the encasing sediments. These maturity investigations and comparisons show that organic materials of animals and plants behave similarly when subjected to geological modifications and, thus, can be used to interpret taphonomical changes of fossil preservation in a consistent way. The review includes also an overview on fossil lagerstätten with important graptolite components in their faunal associations and the preservational interpretations derived from these. In this respect, it is important to determine preservational aspects carefully and to use precise terminology to describe the fossil material, to recognize fossil modifications and replacements, both in originally organically preserved fossils and in mineralic remains like shells or skeletons. • Key words: Hemichordata, graptolites, taphonomy, preservation, organic material, lagerstätten.

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Fossil preservation has been discussed at length in numerous publications, but still many details are unclear or have not been considered. It is usually discussed in relation to individual fossil groups (e.g. bacteria, brachiopods, graptolites, plants, trilobites, vertebrates) or types of fossil lagerstätten (cf. Seilacher 1970). In the Hemichordata, the preservation of the fossils is especially important, as the involved materials differ considerably between the two groups, the Enteropneusta (Fig. 1A) and the Pterobranchia (Fig. 1B–D).

The results found in the fossil preservation are often interpreted from the visual aspects of the fossils only, and without consideration of the composition and reaction of the various materials involved in the decay processes and the subsequent fossilization processes over millions of years. Also a differentiation of originally preserved organic material and replacement of this due to later processes is

often not considered. Briggs (2003) suggested replication of the morphology by rapid in situ growth of minerals as essential to preserve labile tissues, which means the loss of the original organic material through geological processes and replacement by secondarily formed minerals.

Decay-retardation during early biostratinomic processes may increase the potential for the preservation of fossils, not just in organically preserved material, but also in mineralic skeletons or shells. Important changes, however, modify the fossils considerably during later geological processes. To gain insight into the preservation of fossils it is necessary to consider the changes through these geological processes and to understand the various paths necessary to produce the final results, to see what happens to materials during numerous geological processes in Earth history. The fossilization of the Hemichordata may serve as a very important and useful example here.

In recent years, theoretical considerations and mineralogical interpretations (e.g. Page *et al.* 2008, Wilson *et al.* 2016, Kloss *et al.* 2017, Parry *et al.* 2017) have been considered more important than experimental methods like decay experiments with extant taxa (e.g. Darroch *et al.* 2012; Schiffbauer *et al.* 2012; Murdock *et al.* 2014, 2016; Butler *et al.* 2015; Nanglu *et al.* 2015; Sansom 2016; Beli *et al.* 2017) and the comparison of these results with actual fossil preservation. Parry *et al.* (2017) even considered decay experiments of extant taxa a poor guide to fossilization by stating that ‘in some cases, features that are decay resistant do not survive diagenesis, while others that are decay-prone preserve readily’. The authors (Parry *et al.* 2017, p. 2) state that organic material can be preserved in various ways as carbonaceous compressions, via early (authigenic) mineralization in iron sulphide (pyrite) and apatite (calcium phosphate), and by early cementation or entombment, such as in concretions or within amber. These modes of preservation are based on very different pathways and processes during the often long time interval the fossilization process takes. Thus, primary preservation of organic material and subsequent secondary replacement and preservation as mineralic phases during diagenesis, metamorphism and weathering have to be differentiated to understand the fossilisation process.

Purnell *et al.* (2018) considered taphonomic experiments as an important aspect of fossil investigations and differentiated between fossilization and preservation, but used the terms soft tissues and non-biomineralized tissues interchangeably and even included sclerotized tissues, thus, essentially all organic or non-mineralized materials to describe organic preservation of fossils. The here presented research shows, however, that we need to be more careful in our observations and interpretations and use a precise terminology.

The various materials found in organisms lead to differences in their preservational potential and appearance of the fossils in the rocks. Also the type of sediment in which the organisms are buried leads to modifications of the fossil remains. Compaction, diagenetic changes and tectonic overprint alter the fossil remains subsequently and often the original organism is not recognizable any more or at least is difficult to interpret. This becomes more and more obvious the older the fossils are.

Interpretations of fossils of organisms not relatable to modern ones, such as the planktic graptoloids, are often based on a pre-existing focus of palaeontologists and were commonly misleading (Fig. 1E–G). The most prominent example of misleading interpretations in graptolite research may be the extrathecal tissue concept of Nancy Kirk (Fig. 1G). Even though the idea is now regarded as erroneous (see discussion in Rigby 1993a), it had a considerable positive impact, as it stimulated an enormous amount of research and led to the understanding of *Rhabdopleura* zooids as

useful models for graptolite zooids (Crowther 1981) and finally of the extant *Rhabdopleura* as a living graptolite (Mitchell *et al.* 2013). Also the early interpretation of graptolite colonies by Hall (1865) and Ruedemann (1895) (Fig. 1E) or the interpretation of muscle scars in graptolites by Habermehl (1933) must be regarded as erroneous. They were based on genuine research, but incomplete understanding of graptolites at an early stage in their investigation (Maletz 2015). Ulrich & Ruedemann (1931) even provided a detailed reconstruction of graptolite zooids (Fig. 1F) based on the assumption that graptolites were bryozoans and used their interpretation of supposed muscle scars in climacograptid graptolites as an argument. In this light it is understandable, that early palaeontologists even misinterpreted fossil material as graptolites, that were later recognized to represent eurypterids (*Megalograptus*: Miller 1874, Caster & Kjellesvig-Waering 1955), phyllocarids (*Coronagraptus*: Hundt 1951, *Dawsonia*: Nicholson 1873) or trace fossils (*Protovirgularia*: M’Coy 1850, *Nereograptus*: Geinitz 1852, *Triplograptus*: Richter 1871). Modern interpretations of fossil graptolites (Fig. 1H, I) focus on the phylogenetic connection to the extant Pterobranchia and use the *Rhabdopleura* zooid (Fig. 1J) as a model for their interpretations (e.g. Crowther & Rickards 1977, Melchin & DeMont 1995, Rigby & Sudbury 1995, Maletz 2015).

An interesting story of misidentification of graptolites also led to the name Graptolite Island for a small island in the South Orkney Island complex close to Antarctica (Dalziel 1979). The fossil material was initially identified as Ordovician graptolites by Gertrude Elles and published by Pirie (1905). The name for the island still exists and can be found even on Google Earth, but the fossils were later identified as Triassic plants.

Terminology

A serious problem in fossil preservation and taphonomy is the used terminology. Terms like ‘soft-body preservation’ and ‘soft-tissue preservation’ are used interchangeably and even the general term ‘soft-body’ would need a more precise definition. A typical example of the supposed ‘soft body preservation’ is the Herefordshire Lagerstätte, in which cuticularized fossils are preserved in three dimensions, filled with calcite (Briggs *et al.* 1996, Orr *et al.* 2000a, Siveter *et al.* 2007). None of the described taxa shows any preservation of cellular tissues, and Orr *et al.* (2000b) described even the most recalcitrant biological tissues as having been lost through decay. The specimens are external casts of the decayed specimens, filled with secondary sparitic calcite. Thus, no organic material is preserved and the term ‘soft-body preservation’ is completely misleading.

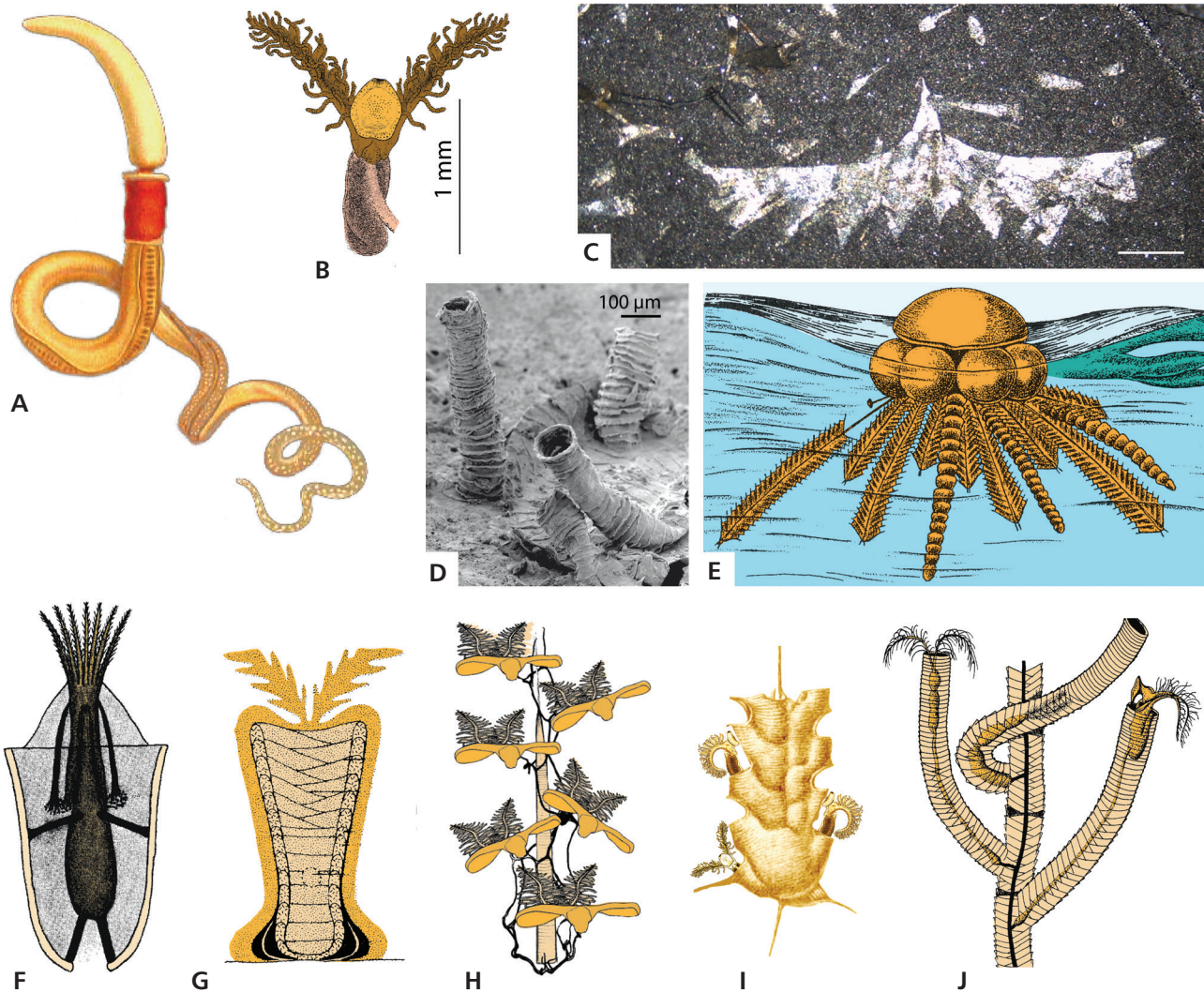


Figure 1. Preservation and interpretation of fossil and extant Hemichordata. • A – *Saccoglossus kowalevskii* (Agassiz, 1873), extant, drawing of specimen (adapted from Spengel 1893, pl. 1, fig. 10). • B, D – *Rhabdopleura* sp., zooid, soft tissues; B – drawing of specimen (after Sars 1874); D – SEM photo of tubarium, SMF 75727. • C – *Expansograptus hirundo* (Salter, 1863), NRM-PZ Cn 42824, Slemmestad, Oslo Region, Norway, Middle Ordovician, Dapingian. • E – graptolite colony with gonangia and pneumatophore (interpretation after Ruedemann 1895). • F – interpretation of graptolite zooids by Ulrich & Ruedemann (1931). • G – extrathecal tissue model of Kirk (1979, fig. 3). • H – *Neogothograptus* sp. with zooids following Melchin & DeMont (1995), based on Kozłowska-Dawidziuk (2004). • I – *Pseudamplexograptus distichus*, small colony with zooids (based on Maletz 2015). • J – part of *Rhabdopleura* colony with zooids (after Dawydoff 1948, fig. 78). Illustrations not to scale.

A discussion on fossil preservation needs to separate between preservation of the original material, its somewhat geochemically modified remains (organic tissues and other organic matter; see hydrocarbons, *etc.*), or the replacement of tissues and other fossil material by secondary mineralisations. It is here suggested to use the term ‘soft-tissue preservation’ only for the preservation of cellular tissues and not for any replacement of these. The term tissues actually already indicates a cellular development (see Cambridge Academic Content Dictionary online). Thus, non-cellular materials should not be termed tissues. Following this guide, the carapace of arthropods cannot be called tissue, as it is an extracellular development as are

clam and brachiopod shells, or – as a matter of fact – the tubaria of the Pterobranchia. These extracellular organic materials may be termed recalcitrant matter or recalcitrant material instead, as they represent more durable organic materials.

The general term or attribute ‘soft’ is misleading as the exoskeletons of arthropods can be quite soft during moulting stages, but harden later on and robust organisms may have much harder and thicker carapaces. Can these be called ‘soft matter’ or not is not a question. If any material of organisms can be called ‘soft’, it should be the cellular tissues. Cellular tissues however, are not preserved in most Palaeozoic fossil lagerstätten. It may even be questioned,

whether the famous Precambrian embryos from China and other regions should be identified as soft. Steiner (2018, p. 96) discussed the preservation in soft-bodied fossil lagerstätten and considered that ‘many Burgess Shale-type fossils may be considered as “soft-bodied” due to the weak state of cuticularization, but rarely preserve soft tissues’.

Hemichordate preservation potential

The hemichordates include two main groups, the Enteropneusta, worm-like animals and the often colony-forming Pterobranchia (Cephalodiscida and Graptolithina). The Enteropneusta are barely known in the fossil record (Cameron 2016, 2018) as they are represented essentially by soft-bodied, worm-like organisms and do not produce any durable (recalcitrant) materials. The Pterobranchia are a group of largely Palaeozoic organisms usually preserved as flattened films of organic material in mudstones and often in full relief in limestones. They include one of the most important groups of marine fossils in the early Palaeozoic, the planktic graptolites (Maletz 2014a, b, 2019a). Already Suess (1851, p. 88) discussed the preservation of graptolites and noted that they are not made of carbonate, but of organic material (‘bituminöse Stoffe’). Maletz & Steiner (2015), Maletz (2017, 2019a) and Beli *et al.* (2017) discussed the preservation of fossil and extant pterobranchs and differentiated three different materials, the organic tissue (cellular tissue; soft tissue) of the zooids (Fig. 2A, B), the stolon system (Fig. 2C) and the housing

secretion or tubarium (non-cellular, recalcitrant matter, the fusellum and cortex of Maletz *et al.* 2014) (Fig. 2D, E), all having quite different propensity to decay. These, together with the entombing sediments, diagenesis, metamorphism and tectonics influence the preservation and interpretation of the fossils considerably. Thus, a general concept for the differentiation and preservation potential of these various organic materials needs to be established, that can be applied to all graptolites and compared to other organically preserved fossils. It is unlikely that different organically preserved fossils go through vastly different pathways of taphonomical change as the comparison of arthropod cuticle and graptolite fusellum indicates. Importantly, Gupta & Briggs (2011) discussed the composition of fossil arthropod cuticles and graptolite tubaria, stating that both change considerably from their original composition and that these organic materials converge in composition during fossilisation towards aliphatic hydrocarbons due to maturation of the organic material (*cf.* Hartkopf-Fröder *et al.* 2015).

Cellular tissues (Enteropneusts/Pterobranch zooids)

Enteropneusts and pterobranch zooids consist of cellular tissues and their fossil preservation may be termed soft body preservation. The enteropneusts are soft-bodied animals and are extremely rare in the fossil record (Boulter 2003, Caron *et al.* 2013, Maletz 2014b, Nanglu *et al.* 2016). They are found in a few fossil lagerstätten like the Burgess

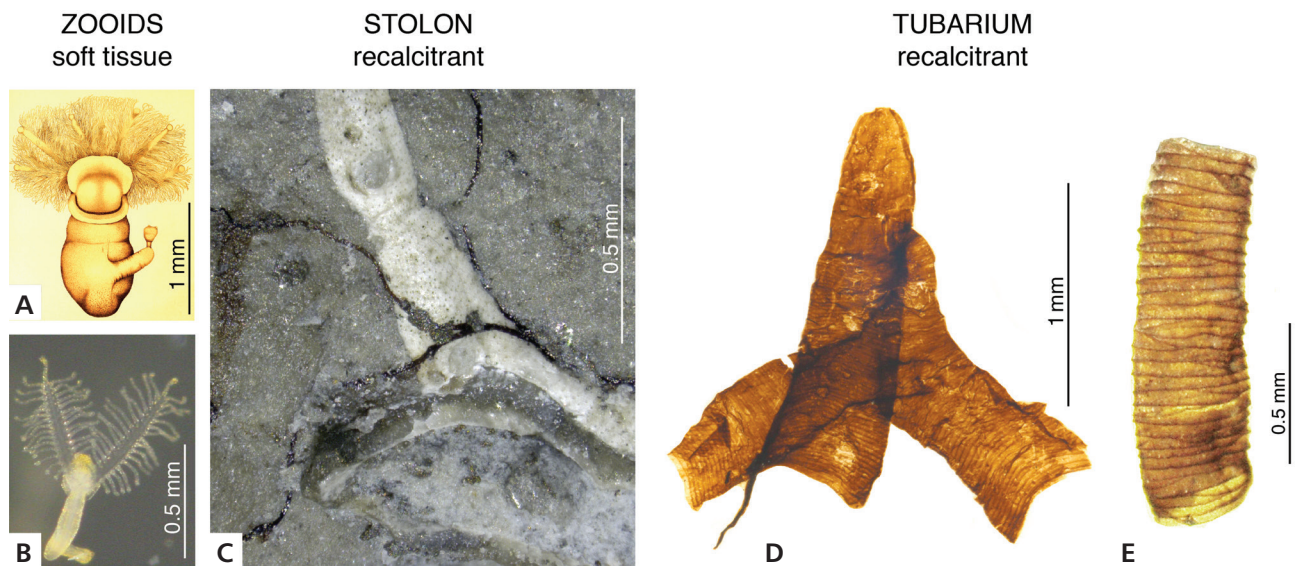


Figure 2. The organic materials of the Pterobranchia. • A – *Cephalodiscus* sp., zooid, drawing (after M’Intosh 1887, pl. 2). • B – *Rhabdopleura* sp., zooid (Sato 2008). • C – rhabdopleurid stolon (black lines) on hardground with bryozoan colony (white) (Keupp *et al.* 2016). • D – *Didymograptellus cowheadensis* Maletz, 2010b, GSC 133396, bleached, showing fusellar construction. • E – *Rhabdopleura* sp., SMF 75776, partially translucent, brown tube showing fuselli, Ordovician, Öland, Sweden.

Shale and the Mazon Creek fauna, but the preserved fossil remains usually lack detail of their anatomy. Extant enteropneusts are quite fragile and often break during the recovery as can be estimated through modern descriptions (e.g. Holland *et al.* 2012, 2013; Cameron & Ostiguy 2013). This may indicate that even transport of the organisms through currents or in a sediment load may inflict considerable damage and makes their fossil preservation unlikely. The precise mode of preservation of the organic remains in the fossil enteropneusts from the Burgess Shale (e.g. Caron *et al.* 2013, Nanglu *et al.* 2016) is uncertain. Caron *et al.* (2013, supplementary information) indicated a carbonaceous preservation of *Spartobranchus tenuis* (Walcott, 1911), but did not prove it through an analysis. Arduini *et al.* (1981) indicated the preservation of *Megaderaion sinemuriense* as an organic film, but did not provide more detail. Information on the preservational aspects of the enteropneusts from the Mazon Creek fauna (Maletz 2014b, Cameron 2016) are not available, but the material is preserved in weathered concretions and outlined by colour differences to the surrounding sediment. There is no evidence of the preservation of organic material in the pterobranch material, supported by the notion of Baird *et al.* (1986) that many Mazon Creek fossils are preserved as molds and composite impressions within siderite concretions. There are, however, also fossils in the Mazon Creek fauna, in which recalcitrant organic material is preserved (Clements *et al.* 2018). *Megaderaion callovianum* from the Callovian (Jurassic) of France (Alessandrello *et al.* 2004) is preserved as a pyritic relief specimen in most parts and the authors suggested that the trunk was covered by a segmented cuticle, a feature not known from extant Enteropneusta. *Mesobalanoglossus buergeri* from the Solnhofen Limestone is preserved in partial relief with a sediment fill of the gut (Frickhinger 1999), but details of the preservation are not available. There is no evidence of the preservation of organic material in the specimen. Thus, the preservation of fossil enteropneusts is quite variable and strongly depended on the sediments in which the material is found.

The zooids of the Pterobranchia are not known in organic preservation from the fossil record. Their bodies consist of various tissues including muscles, the nervous system, the skin and the intestines among others. None of these tissues is especially decay resistant and Beli *et al.* (2017) indicated that the zooids are completely decayed within 3–7 days (64–168 hours), supporting earlier information from Briggs *et al.* (1995). Obviously, the fast decay is also supported by the small size of the zooids, measuring a few millimetres at maximum (Fig. 2A, B). Durman & Sennikov (1993) and Sennikov (2016) showed evidence of zooidal preservation in the middle Cambrian *Sphenoecium obuti* (Durman & Sennikov, 1993), but anatomical details are not available. There is

also no information on the (?)minerals involved in the mode of preservation of the putative zooids as no further investigation is available. Lower Ordovician specimens of the genus *Psigraptus* (see Rickards & Stait 1984) have been indicated to show zooidal preservation, but the information is inconclusive. The stolons and zooids are apparently preserved as goethite infills or replacements (Rickards *et al.* 1991), probably originally formed from pyrite. Also the X-ray investigations of Bjerreskov (1978) of Silurian monograptids are inconclusive, as they show only vague and cloudy patches of minute pyrite crystals inside and around the apertures of the tubaria, but no evidence of zooidal anatomy. None of the supposed zooidal preservation in fossil graptolites preserves any traces of organic material. However, pterobranch zooids are well known from extant taxa and their anatomy has long been established (see compilation in Maletz & Cameron 2016).

The graptolite stolon system

The stolon system (Fig. 2C) is a thickened and hardened cover of the gymnocaulus and forms the stolon system of the colonial pterobranchs (Graptolithina). It is probably secreted from the surface of the gymnocaulus, but the precise development mode is unclear even in extant taxa (Schepotieff 1904, Urbanek & Dilly 2000). The stolon system is well known from the extant *Rhabdopleura* (Sars 1874, Lankester 1884, Schepotieff 1906, Maletz & Cameron 2016), but has also been found in the fossil state and has been described under a number of taxonomic names (cf. Mierzejewski 1986, Maletz & Beli 2018). The stolon is the part of the benthic graptolite that is most decay resistant. Even after an eight-month investigation interval, the stolon pieces of the extant *Rhabdopleura recondita* investigated by Beli *et al.* (2017) were fully intact. Stolon material is commonly preserved in dendroid graptolites (e.g. Mierzejewski 1986, Saunders *et al.* 2009, Maletz 2014a, Maletz & Beli 2018) but appears to be lacking in most planktic taxa, probably evolutionarily absent or at least is not preserved and thus, taphonomically absent. An extremely wide stolon system appears to be present in the stem of the Middle Ordovician genus *Mastigograptus* (Bates & Urbanek 2002). Jackson (1967) and Rickards & Stait (1984) described remains of a (?)pyritized stolon system in the Tremadocian, Lower Ordovician genus *Psigraptus*. Hutt (1974) illustrated the stolon system in the early planktic *Adelograptus tenellus* from chemically isolated material as line drawings, but it has not been further investigated. A stolon system is not preserved in isolated specimens of the planktic *Rhabdinopora flabelliformis* described by Legrand (1974), suggesting that it may have been only weakly, if at all, sclerotized and was not preserved.

Zalasiewicz *et al.* (2013) discussed a ‘stolon-like system’ in the planktic graptoloid *Dicranograptus* aff. *ramosus* as an abnormal recalcitrant pectocaulus or a stolon-like system. As an alternative interpretation, the authors suggested an infestation of colonial xenobionts. The investigation with the backscatter method at the scanning electron microscope (SEM BSE method) (Fig. 3A) shows that there is very little organic material left in this specimen. Unfortunately, a counterpart specimen was not available in which the complementary remains of the graptolite tubarium may have been found. It can be seen in many places along the specimen that the black fusellum covers pressure shadow minerals and this is visible only when the fusellum disappeared through splitting of the rock slab. Zalasiewicz *et al.* (2013, fig. 3) indicated this in a photo, stating that the original carbon flaked away and provided an unobstructed view onto the ‘clay mineral template’, herein interpreted as pressure shadow minerals, following Underwood (1992) and Page *et al.* (2008). The described hour-glass structures and other features do not represent a stolon system. As a stolon system, they should be preserved as a complete and un-interrupted strand of organic material, broken only in places where the organic material disappeared (see nema in proximal end of Fig. 3A), as it was connecting the zooids of the colony. The recognizable structures are preserved partly as clay minerals (as is normal for graptolites in the Southern Uplands), and partly as remains of organic material in the nema in the center of the biserial tubarium and as curved or ‘hour-glass’ like small organic remains that represent thickened parts of the thecal apertures and genicular rims. Associated specimens of *Nanograptus phylloides* (Fig. 3D, F, G) show the organic remains of their tubaria strongly affected by parallel fractures indicating considerable tectonic deformation. The majority of the fossil described by Zalasiewicz *et al.* (2013) represents remains of pressure shadow minerals (*cf.* Underwood 1992) in a poorly preserved and strongly tectonized graptolite. Thickened genicular rims are clearly visible in a specimen of *Dicranograptus spinifer* investigated with IR-photography (Fig. 3E) and can be used to explain the described ‘hour-glass’ like structures as preserved organic material and remains of pressure shadow minerals accumulated around these. These details are not visible in relief specimens of *Dicranograptus* (*cf.* Fig. 3C).

Loydell *et al.* (2004) illustrated specimens of *Rastrites geinitzii* (Törnquist, 1907) and ?*Neolagarograptus* sp. from the Llandovery of Latvia containing presumed parts of the contractile stalks (gymnocaulus). The remains are preserved as a two-dimensional film of organic carbon residues, surrounded by an early diagenetic pyrite fill of the thecal tubes. This is the only fossil evidence for the possible presence of a zooidal stalk in Silurian graptoloids, but not of the stolon system (see Maletz & Cameron 2016).

The pterobranch tubarium

As the graptolite tubarium is the most commonly preserved fossil material known in graptolites, its construction (*cf.* Bulman 1970, Maletz *et al.* 2016) is not discussed in detail here. The tubarium is formed from individual halfrings or full rings, the fuselli, and may be covered by a secondary material, the cortex or cortical tissue (*e.g.* Andres 1977, 1980; Crowther 1981). Its biochemical composition is still unclear (Foucart *et al.* 1965, Florkin 1969, Sewera 2011, Gupta 2013). Towe & Urbanek (1972) suggested formation of the tubaria from polysaccharide-associated collagen-fibres on the basis of electron microscopic studies. It is generally found as a dark brown to black film of organic (carbonaceous) material, either flattened or in partial or full relief showing the complex shapes of the graptolite colonies. The presence of fuselli may be recognizable in specimens with thin fusellum or through the SEM BSE investigation and used to identify fossils as pterobranchs (Fig. 3B) (Zhang & Erdtmann 2004a, b; Maletz *et al.* 2005; Maletz & Steiner 2015). In chemically isolated graptolite material, the fuselli can be made visible through chemical bleaching (*e.g.* Maletz 1994) or through IR-microphotography (Melchin & Anderson 1998), important measures to recognize questionable fossils as pterobranch remains (see Maletz *et al.* 2005, Maletz 2019a).

The decay of the fuselli of the pterobranch tubarium (Fig. 2D, E) is considerably slower than the decay of the zooids and leads to a much higher preservation potential of the graptolite tubaria. Indications of decay may be seen after a few days, but even after eight months, the tubes were largely intact. The tubes, however, became thinner and the fusellar rings were more pronounced, while aperturally some fusellar rings may have separated (Beli *et al.* 2017). Fuselli are still prominent in some well-preserved middle Cambrian pterobranchs, while in other specimens they cannot be recognized even though the general shape of the tubaria is preserved (see Sennikov 2016).

Biostratinomy (Pre-burial modifications)

Biostratinomy involves the early changes of organisms, death and mechanical changes in the distribution of the remains (Weigelt 1927), but the boundary to fossil diagenesis is difficult to define (Fernández-López & Fernández-Jalvo 2002) and both may easily be combined (*cf.* Cai *et al.* 2010). Biostratinomy represents the earliest stages of fossil formation before the organism is buried in the sediment. Decay experiments (*e.g.* Sansom 2014, 2016; Butler *et al.* 2015; Nanglu *et al.* 2015; Beli *et al.* 2017) mimic this part of geological fossil alteration to understand fossil formation. Even the modification of

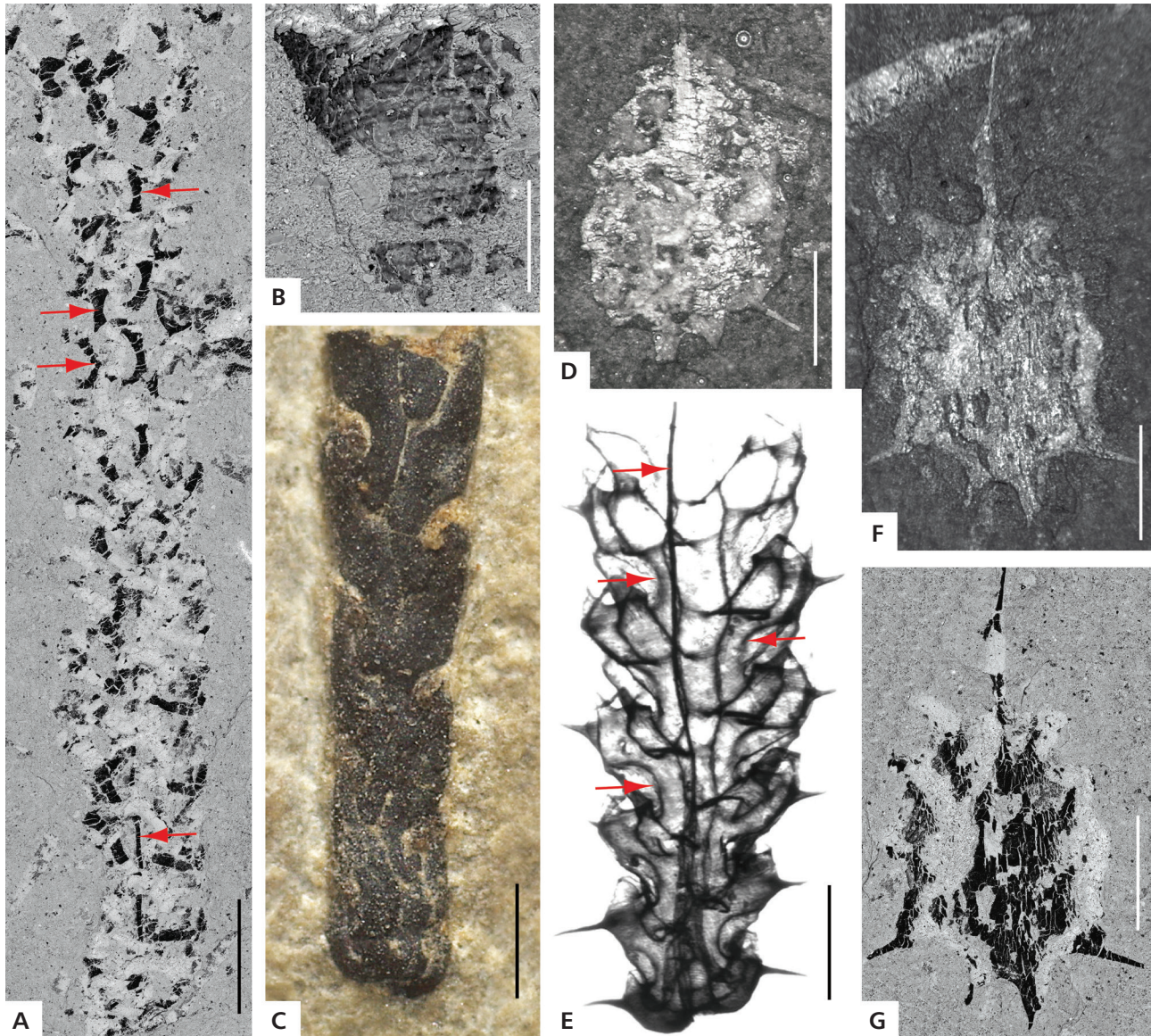


Figure 3. Graptolite preservation and investigation. • A – *Dicranograptus* cf. *ramosus*, GSE 5495, SEM-BSE photo showing remains of organic material, fusellum in black, pressure shadow minerals in light grey, sediment darker grey. • B – *Archaeocryptolaria longicornis* Chapman, 1919, NMVP 13114, fragment showing fuselli, SEM-BSE photo (Maletz & Steiner 2015, fig. 4g). • C – *Dicranograptus ramosus* (Hall, 1847), NIGP 106259b, internal cast, relief specimen in reverse view (counterpart of Ge *et al.* 1990, pl. 18, fig. 11). • D, F, G – *Nanograptus phylloides* (Elles & Wood, 1908); D – GSE 5496, lectotype, light photo; F, G – light photo (F) and SEM-BSE photo (G) showing preservation of organic material (black) and tectonic fractures. • E – *Dicranograptus spinifer* Elles & Wood, 1904, IR-photo. Scale bars indicate 1 mm in each photo, except for (B), where it is 100 µm. Red arrows in (A) and (E) indicate preservation of thickened thecal apertural and genicular rims and nema in the specimens.

organic materials like cuticle and graptolite fusellum cannot be regarded as the result of decay resistance, but represents a diagenetic transformation within the sediment (*cf.* Gupta *et al.* 2006, Gupta & Briggs 2011, Gupta & Summons 2011).

Maletz (2017) discussed the biostratinomy of the pterobranchs in some detail and showed them to be useful for palaeoecological interpretations. Pterobranchs may be differentiated into benthic and planktic taxa. While the benthic taxa lived largely in shallow water regions

and may be transported as fragments into deeper water settings, planktic taxa were more widely distributed and can be found in various sediment types. Fragments of benthic and planktic tubaria may have been transported for long distances before settling on the sea floor due to their durability. Depending on the sedimentation rates, they may have resided on the sea floor for some time before they were embedded in the sediment (Maletz 2017). Post-mortem transport can be seen in often highly fragmented benthic taxa as they are found in deeper water successions,

far from their living environment, but rarely *in situ* in places where they lived. Planktic taxa are commonly current oriented indicating the transport direction through their alignment (Maletz 2017, fig. 5.5). Information on the decay during this time is not available, but it may be noted that the zooids are not preserved. Cooper *et al.* (2012) discussed death assemblages of planktic graptolites, providing information on living associations and possible accumulations as indication of time averaging (*cf.* Kowalewski 1996). Thus, not all graptolite tubaria found in a single layer of sediment may have been deposited at the same time instant, but may have accumulated during a longer time interval during which considerable changes may already have occurred to earlier deposited specimens (see also discussions in Rigby 1993b, Underwood 1998). Jones *et al.* (2002) interpreted clingfilm preservation in spiraliform monograptids as encasement of the graptolites by marine snow or microbial mats, indicating that graptolite tubaria may survive destruction for considerable time spans prior to burial and compaction.

Diagenesis (Post-burial modifications)

The material of the graptolite tubaria will be flattened into an organic film in most specimens, but sometimes early diagenetic processes or sediment fill prevent the flattening and the specimens may be preserved in full relief showing their original shapes. Most graptolites are preserved as flattened films and subsequently may have been modified by diagenesis, metamorphism and tectonics. All these changes may be independent of each other, but follow a directional path (Fig. 4). Two main paths of modification of graptolite tubaria can be differentiated: (1) preservation as uncompacted mineral-filled relief specimens and (2) post-compaction preservation as flattened films of organic material. Relief specimens (Fig. 4A, B, D, F, H) show early diagenetic mineral fills (Fig. 4B) before the entombing sediments are compacted, indicating an empty space in which the zooids may have decayed leaving space for the diagenetic mineral growth. At any time, these relief specimens may have been affected by maturation (Fig. 4D), deformation (Fig. 4F) or weathering (Fig. 4H), modifying the specimens, but these aspects act independently and are not mutually connected. Thus, for example specimens modified through deformation or weathering do not need to have been affected by diagenesis or maturation at an earlier stage.

The (now) compacted specimens also must have had an empty space inside initially (Fig. 4A), that was compressed during the compaction of the sediment, as there is no mineral or sediment fill in the tubaria. Their modifications follow the same paths seen in relief specimens (Fig. 4A, C, E, G, I). The two different paths in modification of

the tubaria strongly affect the taxonomic identification of the graptolites. Flattened material often does not show the necessary details for a proper taxonomic identification at the species level as does the preservation in full relief in shale or limestones, but in relief specimens preserved in the rock, certain details may be covered in the sediment and, thus, not visible either. If the tubaria are later exposed on the sediment surface, they may easily be destroyed by weathering or even by bacterial degradation, but the latter has not been demonstrated so far even though Radzevicius *et al.* (2013) showed possible bacterial epibionts on Silurian monograptids.

Tanning

Wilson & Butterfield (2014) hypothesized a process they called taphonomic tanning, the enhancement of recalcitrance of organic material due to cross-linking of structural biomolecules in arthropods, enhancing their preservation potential. They differentiated biological and abiological (taphonomic) tanning and noted a distinct effect of the sediment composition on the preservation of the cuticle of the polychaete *Nereis*. It is unknown whether this process might also enhance the preservation of pterobranch fossils. The dark colour of fossil graptolite tubaria may indicate that taphonomic tanning had a distinct effect on the pterobranch fusellum, as the tubaria of extant pterobranchs are usually colourless to light brownish (Maletz & Beli 2018, fig. 3.4). Fossil graptolites often show a dark brown to black colour of the tubarium (Fig. 4B, C) and the original translucence is lost. However, it is unclear whether this may be called tanning or is simply an effect of early diagenetic coalification of the organic material. The Burgess Shale-type preservation (BST), discussed by Wilson & Butterfield (2014) as an example of biological and also sediment-induced taphonomic tanning, may alternatively be referred to a metamorphosis induced coalification due to the well-known greenschist metamorphosis of the Burgess Shale localities (see Powell 2003).

Sediment and mineral fills

A sediment fill of graptolites as it occurs in turbidite layers can prevent compaction of the specimens through the coarser-grained material being less susceptible to compaction. Thus, specimens of *Levisograptus primus* (Legg, 1976) from the Lower Head Sandstone of western Newfoundland (Maletz 2017, fig. 5.6) show full three-dimensional preservation as do many Silurian monograptids preserved in carbonates (Maletz 2017, pl. 15). More common, however, is the preservation of relief

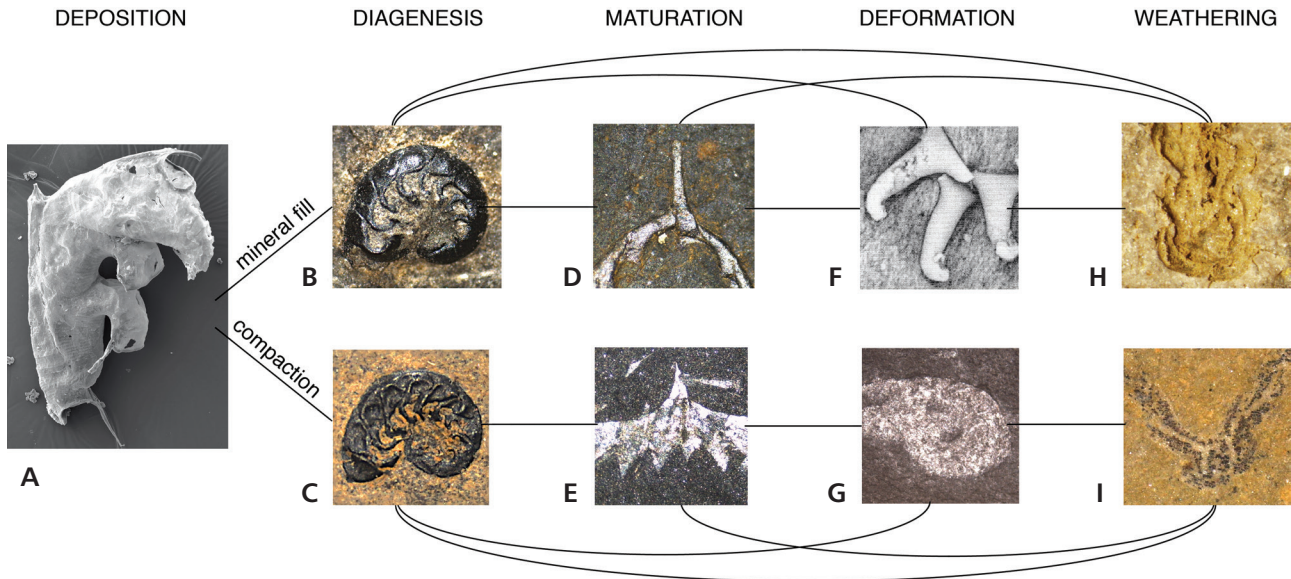


Figure 4. Taphonomical changes in graptolites. • A – *Cochlograptus veles* (Richter, 1871), PMU 31876, chemically isolated specimen, Dalarna, Sweden. • B, C, G – *Cochlograptus veles*; B – LO 1071t, relief specimen with surrounding pyritic halo, Kalholn, Dalarna, Sweden (Törnquist 1892, pl. 3, fig. 27); C – LO 1527t, flattened specimen, Röstånga, Scania, Sweden (Törnquist 1899, pl. 4, fig. 25); G – SMF XXIV 301, flattened, tectonized, showing parallel fractures and pressure shadow minerals, Raitzhain, Thuringia. • D – *Didymograptus artus* Elles & Wood, 1901, PMO 234.062, coalified relief specimen, Slemmestad, Norway. • E – *Expansograptus hirundo* (Salter, 1863), NRM-PZ Cn 42824, flattened and coalified specimen, Slemmestad, Norway. • F – *Demirastrites triangulatus* (Harkness, 1851), showing displaced, pyrite-filled thecae, central Wales (Palmer & Rickards 1991, pl. 74). • H – *Pseudoclimacograptus formosus* var. *nana* Ge & Yin in Mu *et al.*, 1962, NIGP 10856, relief specimen, partly weathered tubarium fill, Chilianshan, China. • I – *Jiangxigraptus inculus* Ge in Ge *et al.*, 1990, NIGP 106213a, Ningxia, China, flattened, fractured specimen (see Ge *et al.* 1990, pl. 27, fig. 7). Specimens not to scale.

specimens in mudstones, the so-called ‘Graptolite Shales’. In these cases, the specimens must have been filled with early diagenetic minerals before the compaction of the surrounding shales (Figs 4B, 5A). In most cases, this mineral is pyrite (Fig. 5F, H) and pyrite-filled graptolites are quite common, but often the pyrite is weathered to limonite or iron hydroxide (Fig. 5I) due to subsequent surface weathering and the original composition of the cast might be difficult to establish. Sometimes even the fusellar construction can be visible on the surface of the internal pyritic molds (Fig. 5H). Underwood & Botrell (1994) discussed the pyrite formation of graptolites in some detail and Blackett *et al.* (2009) illustrated steinkerns of graptolites, comparable to the ones previously investigated by Törnquist (1893) (Fig. 5F).

Bjerreskov (1978, 1991, 1994) discussed the pyrite fill of Silurian (Llandovery) graptolites of Bornholm as early diagenetic and found that pyrite was rare on the outside of the tubaria. Cavities within the graptolites also included stalactite-like forms of pyrite suspended from the roof of the tubaria. These and geopetal layering of pyrite framboids indicates the very early formation of the pyrite within the graptolite tubaria. Törnquist (1893) illustrated a number of beautiful specimens of biserial graptolites from the Silurian shales of southern Sweden as drawings. His material was preserved in full relief filled

with pyrite (Fig. 5F) with the fusellum preserved as a thin mantle around the mineral fill and inside as the interthecal septa, the median septum and the nema. He sectioned the specimens and polished them to show the internal parts. Very good preservation can be seen in graptolites covered by a thin layer of pyrite in carbonates (Fig. 5D, E), which may be invisible in non-isolated material.

As a rare example of mineral fills in graptolite tubaria, phosphate was discussed by Goldman & Bergström (1997) forming molds of *Climacograptus putillus* (Hall, 1865) and *Rectograptus peosta* (Hall, 1861) at Graf, Iowa. The specimens are found in the brown shale facies of the Elgin Member of the Maquoketa Formation. In fresh material, the black fusellum of the specimens is still preserved, but quickly disappears through weathering.

Maletz (2009) described Middle Ordovician graptolites chemically isolated from limestones of the Quebec Appalachians. The specimens were preserved in three dimensions, but in part covered by irregularly grown silica crystals, protecting them from destruction. It is apparent that the specimens were already broken in part due to tectonic distortion, but the parts of their organic tubaria were kept together by the silica overgrowth (Fig. 5M). Even better preserved are the Silurian graptolites from cherts described by German scientists (Hundt 1934, 1946, 1957; Horstig 1952; Richter 1948, 1951; Münch 1951).

Silurian chert pebbles with graptolites were found in a number of secondary deposits of glacial or glacio-fluvial origin in Germany. A detailed investigation shows a thin inner and outer cover of the preserved organic tubaria with white silica (Greiling 1958). Even though originally described as silicified, the material clearly shows that the tubaria were covered or coated by early diagenetic silica (Fig. 5G) before any compaction happened and the organic material is well preserved. The tubaria may in part be filled with sediment, but also specimens completely filled with white silica have been discovered.

The early formation of carbonate concretions as in the Silurian Kallholn Shale Formation of Dalarna, Sweden, can preserve graptolites in three dimensions (Hutt *et al.* 1970; Loydell 1991; Loydell & Maletz 2004, 2009), while in the surrounding mudstones, the same graptolite species are completely flattened (see Walasek *et al.* 2019). The same effect appears to be responsible for the beautiful preservation of graptolites in glacial boulders of northern Germany and Poland (*e.g.* Heidenhain 1869; Eisenack 1951; Kozłowski 1962; Urbanek 1958; Maletz 2008, 2010a; Maletz & Schöning 2017; and many more) or the beautiful retiolitids and other graptolites described from Arctic Canada (*e.g.* Lenz & Melchin 1987, Lenz & Kozłowska 2006). This material is generally so well preserved that it is possible to chemically isolate the specimens from the sediments and investigate them in three dimensions to understand their construction.

Compaction

Burial may not have altered graptolite morphologies considerably, unless the tubaria are compacted. Due to the compaction of most sediments, the specimens have been flattened into a double layer of organic material without much change of the outline of the specimens. As the graptolite tubaria were made from flexible organic material, the compaction led to wrinkle effects (Fig. 5K), not noticeable on flattened specimens in mudstones, but more recognizable in material chemically isolated from the sediment. These wrinkles can easily be differentiated from the fusellar construction by their irregular position

and short lengths. Wrinkles are common also in other organically preserved, flattened fossils as the example of a Silurian naraoid from Canada (Caron *et al.* 2004) shows.

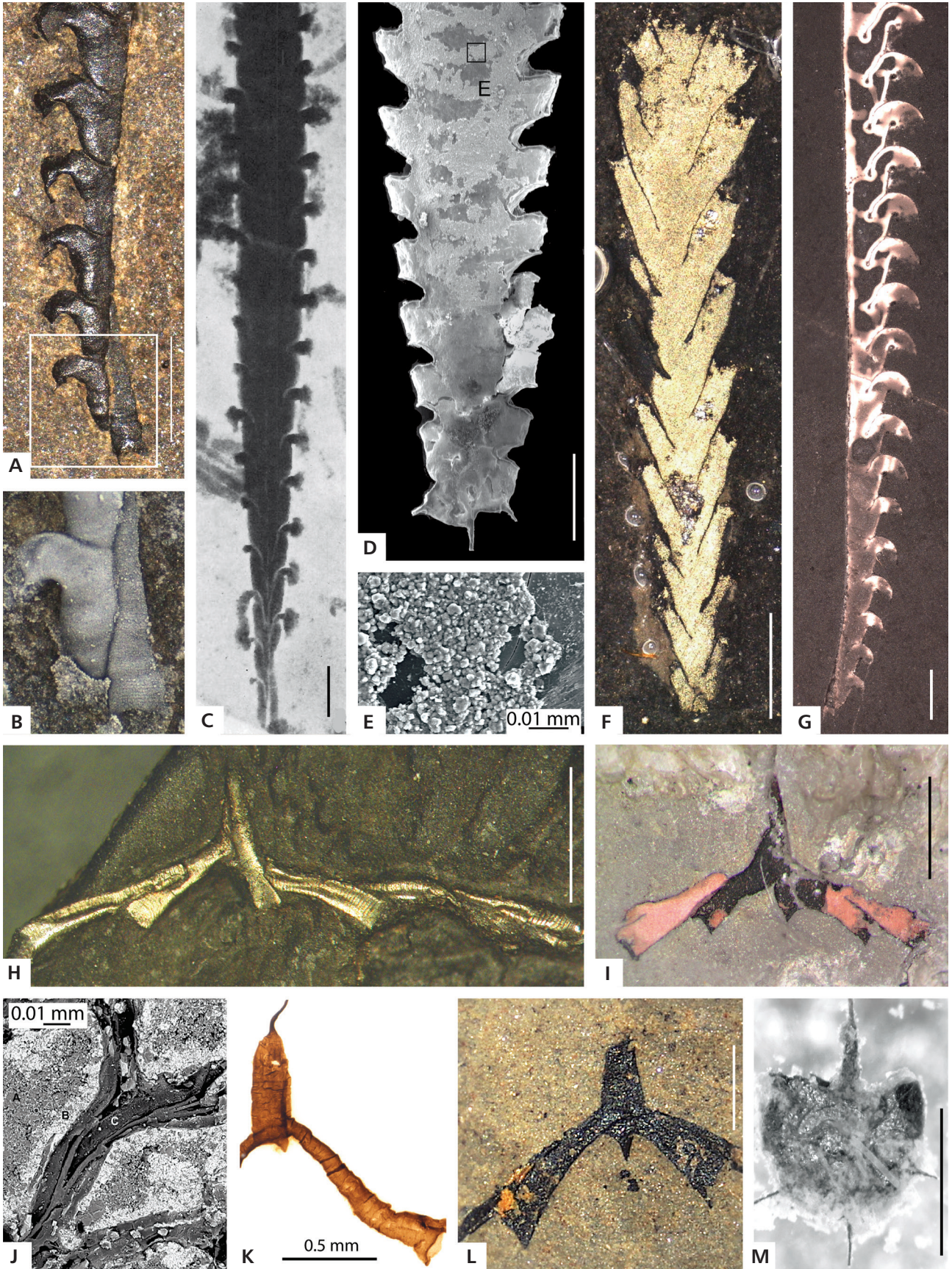
There appears to be no significant lateral expansion of the tubaria (see Briggs & Williams 1981, Williams *et al.* 1982) due to the pressure of the sediment from all sides on the entombed specimens. Changes in the dimensions are generally been attributed to tectonic deformation and no analysis exists to show with certainty lateral extension of undeformed material. Flattening of graptolite colonies (Fig. 5K) leads to the projection of several layers of the fusellum (incl. intertheical septa and median septa) into a single plane. Therefore, the three-dimensional development of the tubarium is difficult to reconstruct or it might be impossible to recognize certain important taxonomic features. It might even be impossible to identify dextral and sinistral development in these specimens. However, in cases when the fusellum is thick, some details may still be recognizable (Fig. 5L).

Coalification (maturation)

Coalification or maturation of the graptolite fusellum, or graptolite reflectance, has been investigated thoroughly due to the interest of the oil industries (Figs 6, 7). Coalification is achieved through heating of the organic material within the sediment, usually by an increasing depth gradient through deposition of sediments in a subsiding basin during regional metamorphism, or through contact metamorphism from magmatic intrusions and associated heating of the host sediment. Both can happen without the effects of tectonic action such as folding and faulting, but often is associated with these and it may be difficult to separate the real cause of some of the metamorphic changes in the fossil material.

Graptolite reflectance is used commonly in Palaeozoic sediments to determine the thermal maturity of sediments and can be correlated with other maturity parameters, especially the vitrinite reflectance used commonly in coal geology. The thermal alteration of the graptolite fusellum follows closely the alteration of other organic materials

Figure 5. Diagenetic effects on graptolites. • A, B, G – *Monograptus priodon* (Bronn, 1835); A – SMF 75780, relief specimen, filled with pyrite, glacial boulder, Germany; B – SMF 75780, coated with ammonium chlorite to show fuselli; G – SMF XXIV 401, relief, coated by silica in chert (see Greiling 1958, fig. 7). • C – *Rhaphidograptus toernquisti* (Elles & Wood, 1906), Bornholm, x-ray photo, showing pyritic clouds at thecal apertures (from Bjerreskov 1978, pl. 21, fig. 3). • D, E – *Amplexograptus perexcavatus* (Lapworth, 1876) SMF 75778, isolated specimen showing pyrite overgrowth (detail in E). • F – *Rivagraptus bellulus* (Törnquist, 1890), LO 1128t, pyrite fill, sectioned. • H – *Adelograptus tenellus* (Linnarsson, 1871), LO 2257t, Scania, pyritic internal cast showing fuselli (see Westergård 1909, pl. 5, fig. 20). • I – *Cymatograptus bidextro* Toro & Maletz, 2008, IANIGLA-PI 1810, pink mineral fill (Toro & Maletz 2008, fig. 7.6). • J – *Desmograptus micronematodes* (Spencer, 1884a), stolon system in relief (from Saunders *et al.* 2009, fig. 3). • K – *Holmograptus* sp., GSC 140108, bed WBS 52, Cow Head Group, flattened, chemically isolated, showing wrinkles due to flattening. • L – *Acrograptus* sp., NRM-PZ Cn 2191, nearly flattened specimen in green shale, Dalarna, Sweden. • M – *Archiclimacograptus decoratus* (Harris & Thomas, 1935), proximal end covered in silica, GSC 133529, Les Méchins, Quebec, Canada. Scale bars indicate 1 mm unless differently indicated.



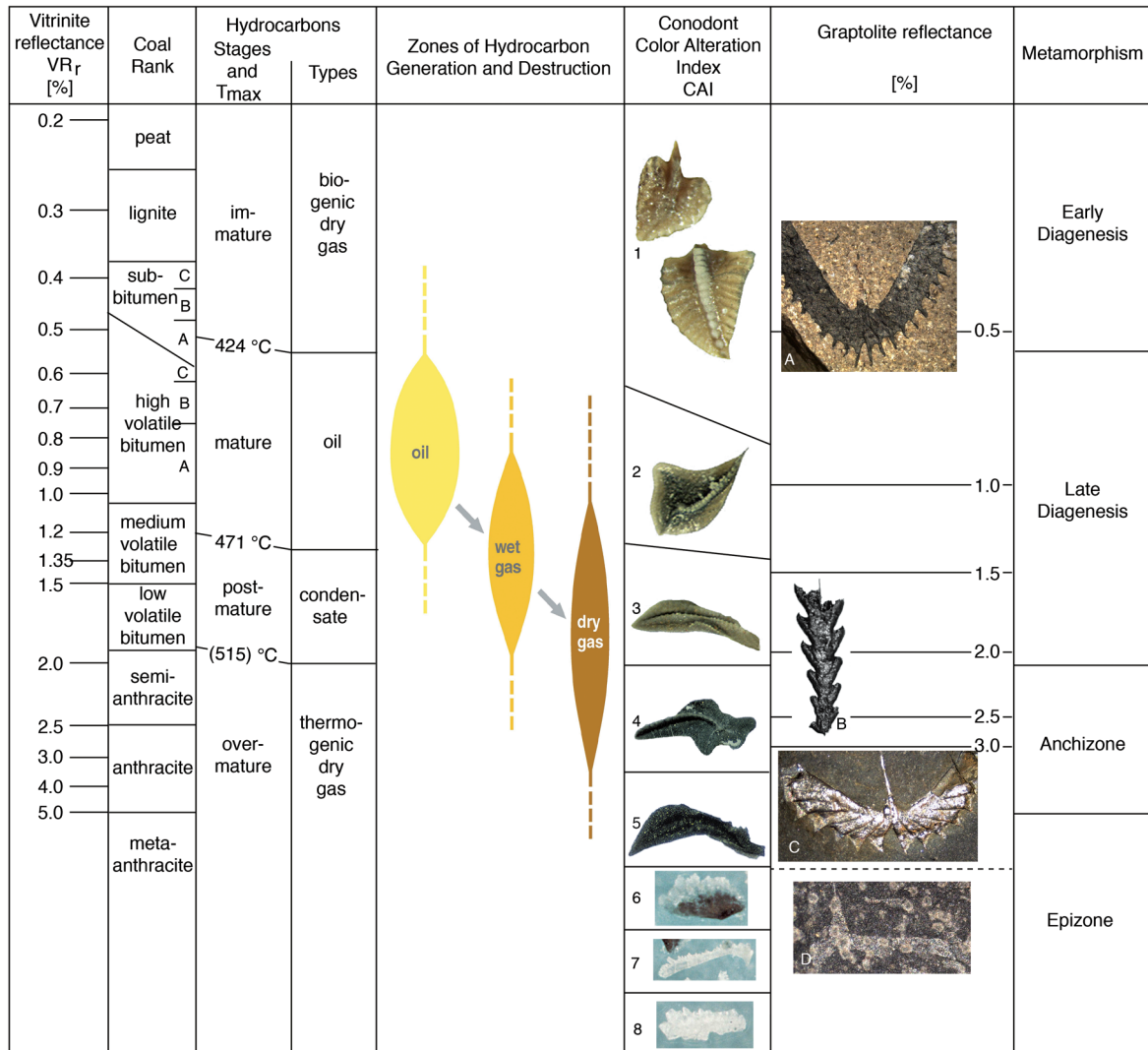
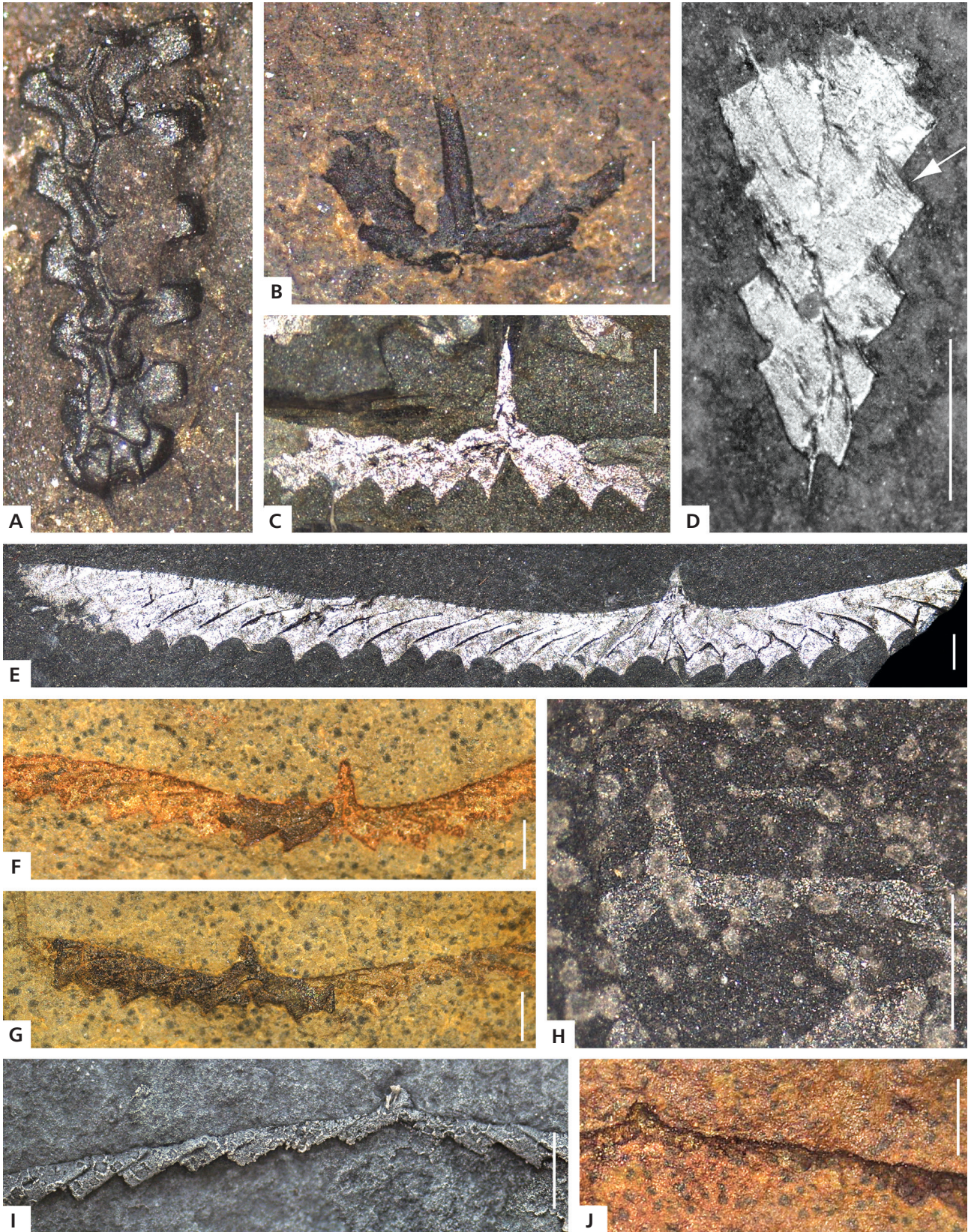


Figure 6. Diagram showing correlation of vitrinite reflectance with other thermal maturity parameters including graptolite reflectance and metamorphic stages (based on Hartkopf-Fröder *et al.* 2015, fig. 26; Voldman *et al.* 2008). Conodont specimens from Hartkopf-Fröder *et al.* (2015) to demonstrate CAI values. Graptolites: A – *Parisograptus imitatus* (Harris, 1933), GSC 139246, Cow Head Group, western Newfoundland; B – *Orthograptus apiculatus* Elles & Wood, 1907, PMU 35732, Gullhögen Quarry, Billingen, Västergötland, Sweden; C – *Isograptus rigidus* Maletz, 2011, PMO 234.063, Slemmestad, Oslo Region, Norway; D – *Baltograptus geometricus* (Törnquist, 1901), LO 1585T, lectotype, Diabasbrottet, Hunneberg, Sweden. Specimens not to scale.

and its investigation is valued for the understanding of oil and gas generation in graptolite bearing rocks. The effect of thermal alteration is very similar to the coalification of plant material and even arthropod cuticles and other organic material (Hartkopf-Fröder *et al.* 2015). The optical properties of the graptolite fusellum change considerably

with increasing temperature (Teichmüller 1978, Goodarzi 1990, Hoffknecht 1991, Inan *et al.* 2016, Schmidt-Mumm & Inan 2016). Progressive colour changes as are apparent in conodonts (CAI – Colour alteration index: Epstein *et al.* 1977, Königshof 2003, Hartkopf-Fröder *et al.* 2015), in ostracods (Ainsworth *et al.* 1990) and other, mostly

Figure 7. Maturation of graptolite fusellum. • A – *Haddingograptus eurystoma* (Jaanusson, 1960), NIGP 157476, full relief, Saergan Fm., NW China (see Chen *et al.* 2016). • B – *Dicellograptus johnstrupi* (Hadding, 1915), PMU 35733, Bestorp, Västergötland, coll. Törnquist, relief in obverse view. • C – *Cymatograptus undulatus* (Törnquist, 1901), NRM-PZ Cn 1207, Norway, flattened. • D – *Parapetalolithus conicus* (Bouček, 1932), SMF 68214, G-14 borehole, flattened, thick fusellum, highly coalified, showing indications of fuselli (Maletz 1997, fig. 5f). • E – *Expansograptus hirundo* (Salter, 1863), PMO 234.064, low relief, highly coalified, Slemmestad, Norway. • F, G – *Expansograptus* sp., PMU 31878/1, 2, preserved part as cast, part as imprint, showing mineral growth (greenish dots) in contact metamorphous sediment, Diabasbrottet, Västergötland. • H – *Baltograptus geometricus*



(Törnquist, 1901), LO 1585T, holotype, showing metamorphous minerals in sediment, Diabasbrottet, Hunneberg, Sweden. • I, J – *Baltograptus* sp., PMU 23163B, latex cast (I) and mold (J) of highly contact metamorphosed specimen showing poor preservation and preserved mineral imprints on latex cast, Diabasbrottet, Hunneberg, Sweden. Scale bar indicates 1 mm in each photo.

organic fossils, have not been established for graptolites, even though some changes are easily recognizable in the field. A general trend can be seen in graptolite samples from low reflectance typically found in the Cow Head Group of western Newfoundland to high reflectance typical for the Oslo Region of Norway. It can easily be correlated with the CAI of the conodonts in associated sediments (Figs 6, 7).

Unaltered or weakly altered fossil graptolite material is dark brown to black in colour as specimens from many regions indicate (Fig. 7A, B). These graptolites consist of supposedly thermally unaltered fusellum as typically found in the Cow Head Group of western Newfoundland (Williams & Stevens 1988), where the CAI of the sediments is between 1.0 and 1.5 (Stouge 1986, Nowlan & Barnes 1987). It changes to an intense silvery shine as examples from the G-14 drill core N of the island of Rügen, Baltic Sea (Fig. 7D) and the Ordovician of the Oslo Region, Norway show. The Norwegian graptolites from the Tøyen Shale Formation and Elnes Formation show a strong silvery shine of the fusellum (Fig. 7C, E), while conodonts associated in the succession have a CAI of 5 (Bergström 1980). This colour in the graptolites can easily be mistaken for a pyritization (and has been), especially in relief specimens filled with pyrite. In these specimens, the construction of the tubarium may still be recognizable through the presence of interthecal septa and crossing canals (Fig. 7E), but in many specimens only the outline may be seen (Fig. 7C). Sometimes even the fuselli are preserved, especially in specimens or species with robust thecal walls and little cortical overgrowth (arrow in Fig. 7D).

At higher temperatures, mineral growth in the sediments may partly destroy the graptolites, but the remains of the fusellum can be recognized and the outline reconstructed even in flattened specimens (Fig. 7H). In this flattened specimen from Mt. Hunneberg, the growth of metamorphic minerals in the sediment is clearly visible. Graptolites, thus, still preserve their fusellum in early epizone metamorphism, but at higher temperatures, the fusellum might disappear. With increasing temperatures,

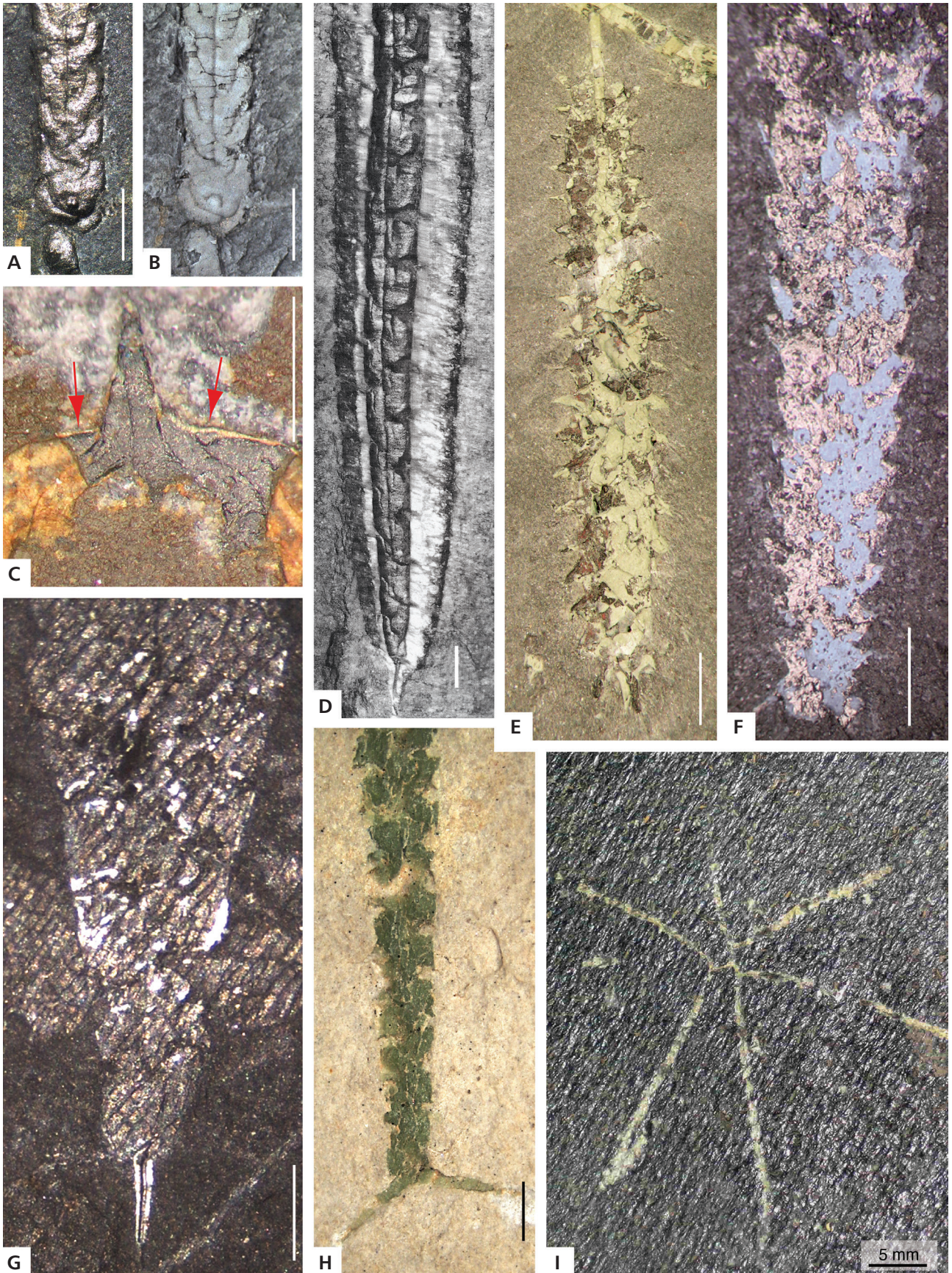
the dark mudstones get lighter, the graptolite fusellum darkens to a brownish colour and starts to disappear (Fig. 7F, G). At this point, the specimens may appear like faint imprints. Only in parts of the tubaria filled with pyrite, the full outline and shape may be discernable (Fig. 7G) before the fossils disappear completely. In partial relief specimens, the relief part may be preserved and in higher metamorphic grades even imprinted outlines of metamorphic minerals may be found on the graptolite casts (Fig. 7I, J). Hoffknecht (1991) indicated values of CAI 6 for samples close to the contact of a dolerite dyke at Mt. Hunneberg, Sweden, where poorly preserved graptolites were still present (see section in Egenhoff & Maletz 2007, fig. 3). The exact temperature of the disappearance of the graptolite fusellum has not been estimated and would need more research. It is not clear whether there are differences in preservation between contact metamorphosed and regionally metamorphosed material.

Dieni *et al.* (2005) reported well-preserved graptolites from greenschist metamorphic facies in the southalpine metamorphic basement and stated that the fusellum is heavily cracked, but undeformed. A thin section shows the relief specimens filled with (?)silica. The documented fracturing of the tubaria, however, should indicate a certain degree of deformation that might be difficult to see with the naked eye. Considerable resistance of graptolite tubaria to contact metamorphism and deformation was demonstrated by Štorch & Kraft (2009, fig. 3), showing that graptolite specimens can be assigned to a genus even in chialstolitic porphyroblastic slates.

Tectonic deformation

Tectonic deformation of graptolites is often easy to recognize (Figs 8, 9) and was described quite early in graptolite research, as the examples of Richter (1853) and Eisel (1908) show. In pyritic relief specimens, however, it may be difficult to detect (Fig. 8A, B). Tectonic deformation can be quite severe and specimens stretched in different directions may appear to belong to separate

Figure 8. Tectonic deformation. • A, B – *Archiclimacograptus wilsoni* (Elles & Wood, 1906), SMA 19619, Dob’s Linn, Scotland, showing coalified fusellum (silvery in A) with parallel fractures (more easily visible in B, coated) indicating low tectonic deformation. • C – *Baltograptus jacksoni* Rushton, 2011, BGS Ht 1260a, holotype, showing pressure shadow minerals (orange) and complete, apparently undistorted fusellum in partial relief proximal end, arrows indicate largely covered pressure shadow minerals in proximal end. • D – *Normalograptus normalis* (Lapworth, 1877) relief specimen, filled with pyrite, surrounded by strong pressure shadow minerals, Llandoverly, Wales (from Palmer & Rickards 1991, pl. 30). • E – *Cryptograptus* sp., Korpa, Bolivia, showing dark fusellum and high amount of yellowish pressure shadow minerals, Nordenskjöld collection, Riksmuseet, Stockholm (photo by E.D. Brussa, Cordoba, Argentina). • F – *Orthograptus* sp., drill core, New York State, silvery shining fusellum and blue pressure shadow minerals. • G – *?Rickardsograptus thuringiacus* (Kirste, 1919), SMF XXIV 222, Raitzhain, Thuringia, coll. Hemmann, specimen with thick fusellum showing parallel fractures, some white pressure shadow minerals visible. • H – *Diplacanthograptus spiniferus* (Ruedemann, 1912) showing green mineralization, Agort Chert, plate E, HD Range, Nevada, coll. J. Riva; Quebec City, Canada (see Riva 1970, p. 2712). • I – *Anomalograptus reliquus* (Clark, 1924), SMF-JOS 23.1a, Sandia Region, Peru, strongly tectonically distorted specimen, see tectonic wrinkles in mudstone. Scale bars indicate 1 mm in each photo, unless indicated otherwise.



species (e.g. Gortani 1922, Schauer 1971, Maletz *et al.* 1998). Eisel (1908) showed this especially well from specimens bent or curved at various degrees. He warned against identifying graptolite specimens without the understanding of the effects of tectonic deformation. In many strongly deformed specimens the deformation can be seen through the parallel fractures in the fusellum (Fig. 8G) as discussed by Mitchell *et al.* (2008) for material from Bolivia. This fracturing may appear only in more strongly deformed specimens and is related to the thickness of the fusellum.

Richter (1853) described the graptolites of Thuringia as often preserved as fibrous, silvery white to greenish minerals, that Geinitz (1852) had already identified as talcum. Gumbel (1868) identified the mineral as a pyrophyllite and compared it with the minerals surrounding many Carboniferous plants. Kobell (1870) described the mineral as gumbelite, but the name has rarely been used outside of Germany. Underwood (1992) compared the preservation of graptolites with the preservation of plant fossils from the Carboniferous of Hartland Quay. The same preservation can be seen in the Carboniferous flora from Piesberg, Germany (e.g. Krings & Kerp 2006) and gumbelite preservation was recently noted in associated insect fossils from this locality (Brauckmann & Herd 2002, Dunlop *et al.* 2008).

These chloritic minerals were identified as pressure shadow minerals by Underwood (1992), formed around the organic material during tectonic deformation (Fig. 8C–F) of the sediments due to the differences in the composition and reactivity of the sediment and the organic material of the fossils. The colour of these chloritic minerals may vary considerably and range from white to yellow (Fig. 8E, I), reddish (Fig. 8C), blue (Fig. 8F) and green (Fig. 8H). These pressure shadow minerals can be regarded as the most important feature for recognizing tectonically deformed graptolites. They often show the direction of tectonic deformation through the lineation (Fig. 8D, G) in the fibrous minerals (see Mitchell *et al.* 2008). The deformation may also be seen in fracturing of the graptolite fusellum (Fig. 8G) and the lineation in strongly deformed rocks (Fig. 8I) when the graptolites are barely identifiable (see Schauer 1971). Thus, deformed graptolites can be used to measure finite strain and volume loss in sedimentary rocks (e.g. Hills & Thomas 1944, Wright & Platt 1982, Jenkins 1987, Goldstein *et al.* 1998). Sherlock *et al.* (2003) even used pressure shadows (strain fringes) around pyritic casts of basal Silurian graptolites to date the Acadian orogeny in the Welsh Basin.

The graptolites from the Upper Ordovician of Dob's Linn, Scotland show a 'striking white preservation' as pressure shadow minerals (Underwood 1992, p. 183), as can easily be seen also in the illustrations of Williams (1982). Williams (1981, pl. 2, fig. 4) indicated considerable

tectonic deformation of graptolites from Dob's Linn, but did not describe the tectonic lineation of the fusellum in this material. Page (2007) and Page *et al.* (2008) discussed the preservation of the graptolites from Dob's Linn and compared the preservation with the Burgess Shale. The low-grade metamorphic rocks of Dob's Linn and the Burgess Shale show the close association of fossils with distinct phyllosilicates interpreted by Page (2007) as clay templates. A closer look at the geology of the regions shows that the geological history includes not just heat related metamorphism, but also considerable tectonic deformation, folding and faulting of the rocks that modified the fossil appearance. The Dob's Linn locality shows imbricate-thrust slices of the upper Ordovician Moffat Shale Formation in a terrane composed largely of the Silurian Gala Greywacke Group in which the Ordovician/Silurian GSSP with its important graptolite faunas can be investigated (e.g. McKerrow *et al.* 1977; Williams 1979, 1982).

Meyer *et al.* (2018) discussed 'exceptionally preserved soft-bodied problematica' from the Martinsburg Formation of Pennsylvania and showed the strong tectonic deformation of the associated graptolites. The graptolite fusellum is preserved as organic films, but is heavily fractured (Meyer *et al.* 2018, fig. 3). The associated problematica are largely found as poor remains of fractured organic particles (Meyer *et al.* 2018, fig. 4) surrounded by pressure shadow minerals. The rocks are of anchizone metamorphic grade, as the illite crystallinity and the CAI of 4.5 indicate. Thus, the preservation of the Martinsburg succession demonstrates strong thermal alteration and tectonic deformation of the included graptolites.

It has not been investigated when the formation of pressure shadow minerals starts around the graptolites or can be recognized with the naked eye, but pressure shadow minerals already appear in sediments when the organic tubaria of the graptolites do not yet show any tectonic deformation through cracks in the fusellum, especially in relief or partial relief specimens filled with pyrite. The holotype of *Baltograptus jacksoni* Rushton, 2011 shows an undeformed proximal end in partial relief with preserved fusellum. The distal parts of the stipes are lost and the surrounding pressure shadow minerals are visible. These also surround the proximal end as a thin line (Fig. 8C, arrows). The pressure shadow minerals can reach considerable thicknesses in relief specimens (Fig. 8D). Only at a higher degree of deformation is the development of pressure shadow minerals associated with fracturing of the fusellum, at least in flattened specimens.

Robust relief specimens of biserial graptolites filled with pyrite may resist the tectonic deformation more easily, while monograptid forms with slender prothecae may be broken into individual, slightly displaced thecae (see Sudbury 1958; Palmer & Rickards 1991, pl. 74).

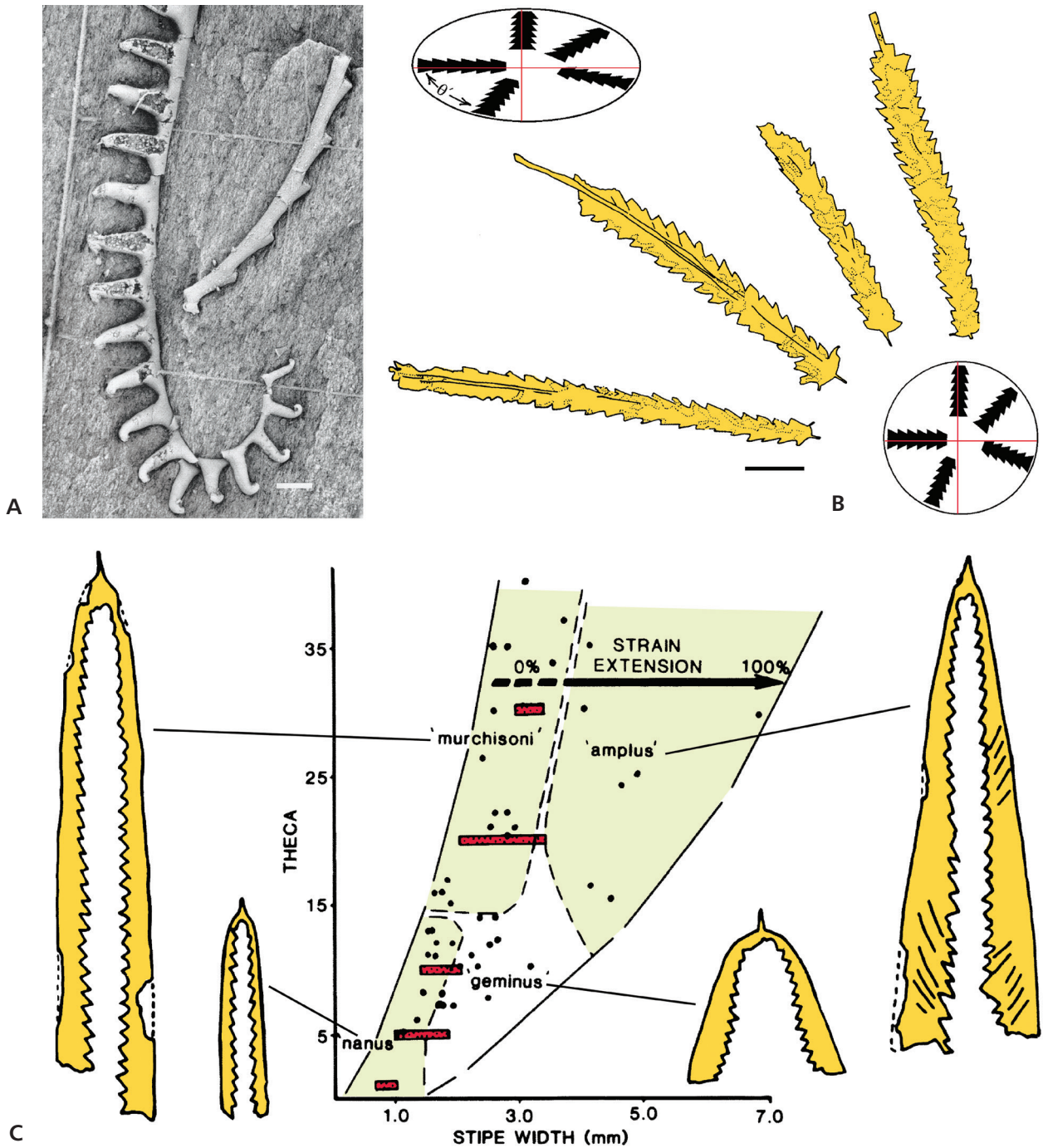


Figure 9. Deformation and strain. • A – *Demirastrites triangulatus* (Harkness, 1851), central Wales, showing deformation of a relief specimen, note thecal displacement in lowermost part of colony, *Coronograptus gregarius* (Lapworth, 1876), apparently undeformed specimen (after Palmer & Rickards 1991, pl. 74). • B – deformation of *Levisograptus shelvensis* (Bulman, 1963) in relation to direction of deformation (black line), after Jenkins (1980) and Goldstein *et al.* (1998). • C – *Didymograptus murchisoni* (Beck in Murchison 1839), interpretation of deformation at Aberiddi Bay, red boxes represent variation of undeformed types from Gelli Hill (after Jenkins 1987, fig. 4).

A specimen of *Demirastrites triangulatus* in full relief clearly shows the displacement of the individual thecae, while an associated fragment of *Coronograptus gregarius* appears to be undistorted (Fig. 9A). Deformation and pressure shadow mineralization may produce considerable

problems for the identification of graptolites. Jenkins (1987) demonstrated deformation of flattened graptolites at Aberiddi Bay, where numerous specimens of pendent didymograptids may be explained as preservational morphs of a single species (Fig. 9C). Also the angle between

a specimen and the direction of deformation may influence the identification considerably. Several specimens described by Bulman (1963) as separate axonophoran (biserical) graptolite species were interpreted by Jenkins (1980) as representing the same taxon (Fig. 9B).

Weathering

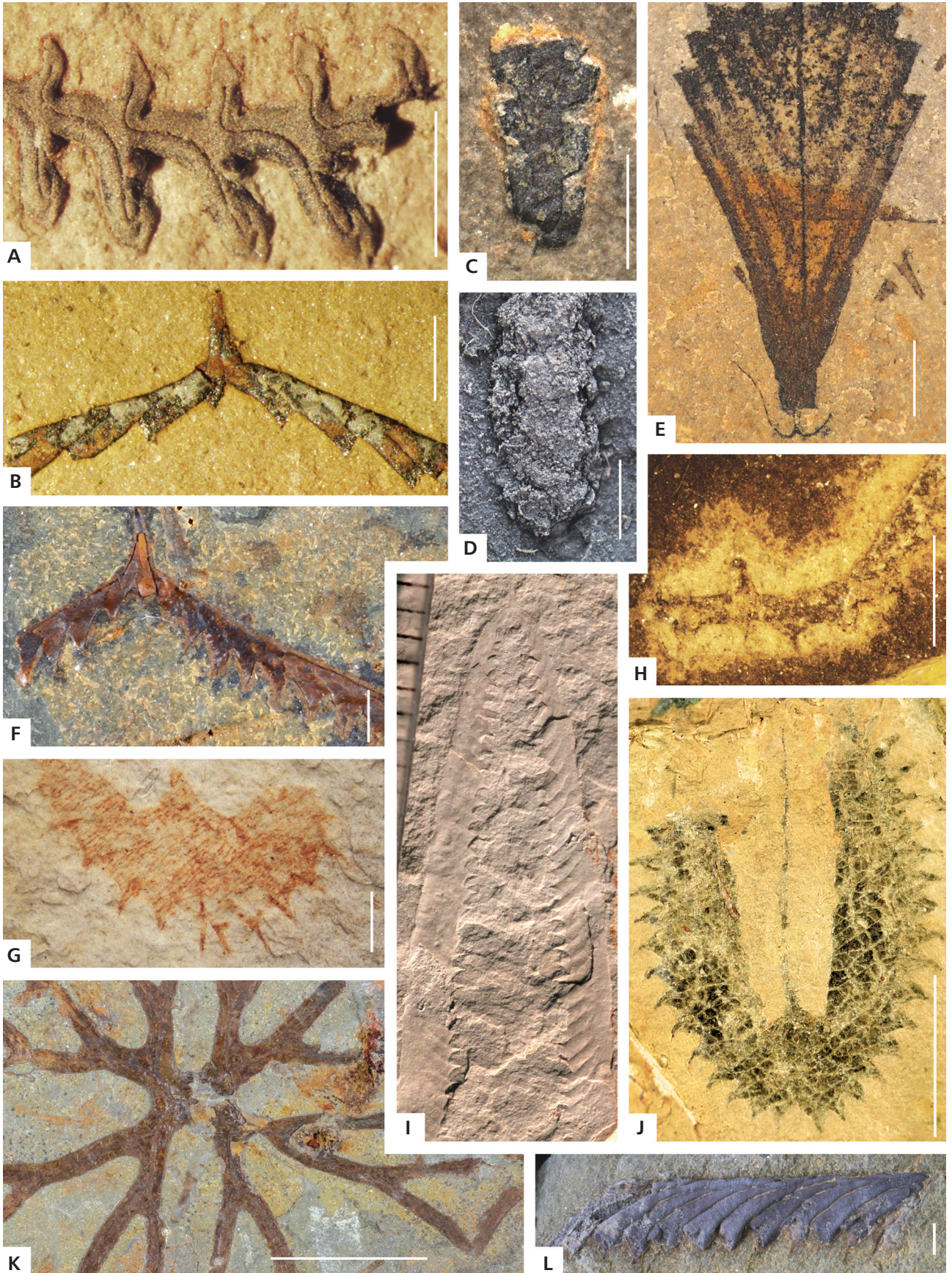
Surface weathering affects most of the fossils we collect (Fig. 10) and only material from drill cores or fresh material from active quarries may be unmodified by weathering. Thus, it is an important aspect we need to consider when we look at graptolites and try to identify their preservational conditions. The effects of weathering might be quite variable, as weathering can affect organisms in any stage of the fossilization process, in fresh material, compacted specimens, thermally altered material and tectonically distorted ones. However, the effects of weathering do not attract much attention during identification of the material. Dark shales and mudstones may weather to light coloured, often yellow to whitish sediments (*e.g.* Victoria, Australia; Yangtze Platform, China; North America; North Africa), where often the fossils remain visible as darker outlines of carbon or faint imprints when the organic material has decayed. Similarly preserved material also exists in other regions, for example in the Czech Republic (Štorch 1998, 2015; Štorch *et al.* 2016; Manda *et al.* 2019).

The typical Australian graptolite material from Victoria consists often largely of pressure shadow minerals (Fig. 10G), but sometimes remains of the organic material are preserved, especially in less strongly weathered material. Light coloured halos around the darker fossils (Fig. 10H) in a dark mudstone can be found commonly indicating partial weathering and disappearance of organic material (see many examples in Rickards & Chapman 1991). This preservation is commonly found in flattened material, but may be found also in relief specimens. In extreme cases, the weathering leaves only faint imprints in the weathered sediments without any hints of preserved organic material (Fig. 10I).

The originally often pyritic fill of relief specimens of graptolites may be modified into limonite or other minerals through weathering effects, but the full three-dimensional shapes may be preserved even when the organic material of the fusellum has disappeared (Fig. 10A, L). Through partial compaction others only retain some of the constructional details (Fig. 10B). Pyrite filled tubaria may weather due to the decay of the pyrite and yellow to red colours of resulting iron hydroxide minerals may appear (Fig. 10C). A special development of this preservation is the white and pink colour (Fig. 5I) of the tubarium fills of Lower Ordovician graptolites from Argentina (Toro & Maletz 2008). Unfortunately, it was not possible due to the limited material to figure out the composition of this mineral fill. Pyrite fills of graptolites may be relatively stable and are unchanged even after decades in collections, but in other cases quickly decay through pyrite disease (Fig. 10D), a factor that is important for many fossil collections (Birker & Kaylor 1986, Newman 1998) as it can destroy important fossils very quickly.

Weathering may enhance the visibility of flattened specimens due to the combined presence of dark iron hydroxide minerals from pyrite degradation and remains of organic material (Fig. 10E) and also the tectonic deformation of graptolites. In the case of low deformational values, little may be seen in the organic fabric, but stronger deformation forms more or less parallel fractures. These may be enhanced by the dyeing of the pressure shadow minerals through iron mineralization (Fig. 10G). In certain localities, more than one direction of deformation can be recognized through these fractures (Fig. 10J). Various staining of the preserved organic films or the preserved pressure shadow minerals may alter the original colour of the pressure shadow minerals often to yellowish or reddish colours (Fig. 10C, F, G). The lack of organic material in some specimens of *Sphenoecium wheelerensis* Maletz & Steiner, 2015 (Fig. 11H) may also be due to weathering and subsequent mineralization of the fossil. The material shows imprints of fuselli, but the dark film suggestive of organic material was identified as Fe- and Mg- rich aluminosilicates (Maletz & Steiner 2015, p. 1083).

Figure 10. Weathering of graptolites. • A – *Sinograptus typicalis* Mu, 1957, NIGP 8909, holotype, pyritic internal cast, China. • B – *Baltograptus geometricus* (Törnquist, 1901), NIGP 31987, low relief cast with part of fusellum (dark), weathered pyrite fill red, China. • C – *Normalograptus mohawkensis* (Ruedemann, 1912), GSC 139252, Quebec, Canada, slightly weathered specimen, fusellum black, orange weathering of iron minerals. • D – *Pseudorthograptus cyperoides* (Törnquist, 1897), LO 1294T, syntype, Tommarp, Scania, Sweden, decayed pyritic internal cast. • E – *Petalolithus folium* (Hisinger, 1837), PS730, flattened, Tmaň, Czech Republic. • F – (?) *Kiaerograptus supremus* Lindholm, 1991, internal cast, see gaps indicating decay of organic material. • G – *Arienigraptus angulatus* (Mu, Geh & Yin in Mu *et al.*, 1962), SMF 75825, Victoria, Australia, strongly tectonized and weathered specimen, lineation shown by pressure shadow minerals dyed orange by iron oxides. • H – *Eotetragraptus arcuatus* (Hall, 1865), NIGP 10643, China, flattened and weathered specimen, showing preservation of some organic material in black, note halo of weathering (illustrated in Mu *et al.* 1962, pl. 7, fig. 1). • I – *Didymograptus artus* (Elles & Wood, 1901), TU Bergakademie Freiberg Nr. FG-667-1, Darriwilian, Jordan, imprint of flattened specimen in weathered, originally black shale. • J – *Pseudisograptus manubriatus* (Harris, 1933), NMVP 30513, Victoria, Australia, tectonized, showing greenish pressure shadow minerals and some preservation of fusellum (in black). • K – *Paradelograptus norvegicus* (Monsen, 1937), AA-JTZ-OI-10, Fezouata, Morocco, flattened specimen, weathered. • L – *Paratemnograptus magnificus* (Pritchard, 1892), AA-BIZ13-OI-14, Fezouata, Morocco, internal cast, originally pyritic, no organic material preserved. Scale bar indicates 1 mm in each photo, except J, where it is 10 mm.



Palaeozoic fossil Lagerstätten and graptolites

Muscente *et al.* (2017) discussed the concept of Konservat-Lagerstätten and considered these to be geological deposits containing fossils with remains of non-bio-mineralized tissues (*e.g.* organic or carbonaceous material). The authors stated that ‘hemichordates include clades with planktonic and cosmopolitan lifestyles that influence the preservation and geospatial distributions’ as an argument to exclude them from their investigation of ‘exceptionally preserved fossil assemblages’, even though they illustrated the pterobranch *Yuknessia* (*Sphenoecium wheelerensis* in Maletz & Steiner 2015) as an important example (Muscente *et al.* 2017, fig. 2i). Thus, graptolitic successions are not included, even though they represent a common occurrence of organically preserved fossils in the Palaeozoic and in many lagerstätten. They can provide essential information on preservational aspects of the fossils in these lagerstätten. While many graptolitic successions include a variety of other fossils (*e.g.* Hall 1865, Schauer 1971), these additional fossil groups are generally ignored and not described due to the special focus of the investigators. More and more lagerstätten have become known that include graptolites, however (*e.g.* Young *et al.* 2012, Baliński & Sun 2015, Gutiérrez-Marco & Martin 2016). The Burgess Shale itself is not an exception as the record of benthic graptolites in this lagerstätte indicates (*e.g.* Walcott 1919, Ruedemann 1931, Ramírez Guerrero 2019). Thus, a few examples are provided here showing the general preservation of this material and the consistent interpretation possible.

Burgess Shale (Cambrian)

The Burgess Shale (overviews in Gould 1989, Briggs *et al.* 1994) is one of the most treasured fossil lagerstätten in the world and the mechanism of the preservation of its fossils is still debated (*cf.* Powell 2003; Gaines *et al.* 2012a, b; Wilson & Butterfield 2014). The Burgess Shale is regarded as the standard for the Burgess Shale-type preservation (BST) of many authors (*e.g.* Butterfield 1995, 2003; MacGabhán 2014; Gaines *et al.* 2012b). It has been seen as a special and unique (exceptional) type of preservation restricted to the lower and middle Cambrian (Zhang *et al.* 2008, Parry *et al.* 2017, Van Roy *et al.* 2015). Briggs & Kear (1993) and Butterfield (2003) discussed the organic remains of Burgess Shale fossils and postulated a rapid degradation and collapse of cellular tissue, leaving a residue of resistant recalcitrant extracellular structures, largely the preservation of cuticular material. Thus, these authors were aware of the differences of the various organic materials to be preserved in the fossil record.

Sedimentology, diagenesis, metamorphism and tectonics have been incorporated in the interpretation of this ‘preservational window’ (*cf.* Butterfield *et al.* 2007, Gaines *et al.* 2008, Gaines 2014), but may play a larger role in its fossil preservation and interpretation than anticipated. A geological interpretation (*cf.* Powell 2003, Powell *et al.* 2003, Collom *et al.* 2009, and others) may provide a more differentiated insight into the fossilization processes and resulting modifications of the Burgess Shale and provide a better understanding of its fauna.

As graptolite tubaria are preserved as carbonaceous films, they should be understood in terms of Burgess Shale-type preservation. A number of Burgess Shale fossils may be identified as graptolites, even though this identity is not proven in all cases (Maletz 2019a, Ramírez Guerrero 2019). The Burgess Shale fossil *Dalyia* Walcott, 1919 was identified as a possible graptolithine by Maletz & Beli (2018), but the inclusion is problematic due to the unusual construction of the specimens. Ruedemann (1931) described the encrusting graptolite *Chaunograptus scandens* associated with a specimen of the sponge *Tuponia lineata* Walcott, 1920 from the Burgess Shale. Maletz & Steiner (2015) and Maletz & Cameron (2016) identified the problematic Burgess Shale genus *Yuknessia* Walcott, 1919 (Fig. 11F) as a possible pterobranch. LoDuca *et al.* (2015) documented the presence of fuselli in *Yuknessia* material from the Burgess Shale (the specimen is identified as *Sphenoecium* by Maletz & Steiner 2015).

Erect growing, bushy benthic graptolites are present in another Burgess Shale-type deposit not far from the original site (Johnston *et al.* 2009a, b). The material includes large specimens of a dithecodendrid graptolite, identified as Graptolithina gen. et sp. nov. The fusellar construction can be seen from imprints in the sediment, but the original organic material of the graptolites is not preserved.

Chengjiang (Cambrian)

The Chengjiang fauna of China (*cf.* Zhang & Hou 1985; Hou *et al.* 1991, 2004), a lower Cambrian fossil assemblage of originally organically preserved and mineralized organisms appears to be deeply weathered, but still contains some amounts of preserved organic material (see Forchielli *et al.* 2012, 2014). The fossils are strongly affected by sub-recent to recent weathering and oxidation of organic material and diagenetic clay mineral formation (Fig. 11A). Phosphatization and pyritization played a key role in the preservation of the fossils. Interestingly, Forchielli *et al.* (2012, 2014) show that iron mineral precipitation is confined to later diagenetic processes and is not crucial for the preservation of volatile tissues. Fossils in grey shales, interpreted as least altered, lack evidence of pyrite or any other iron minerals replacing tissues. The

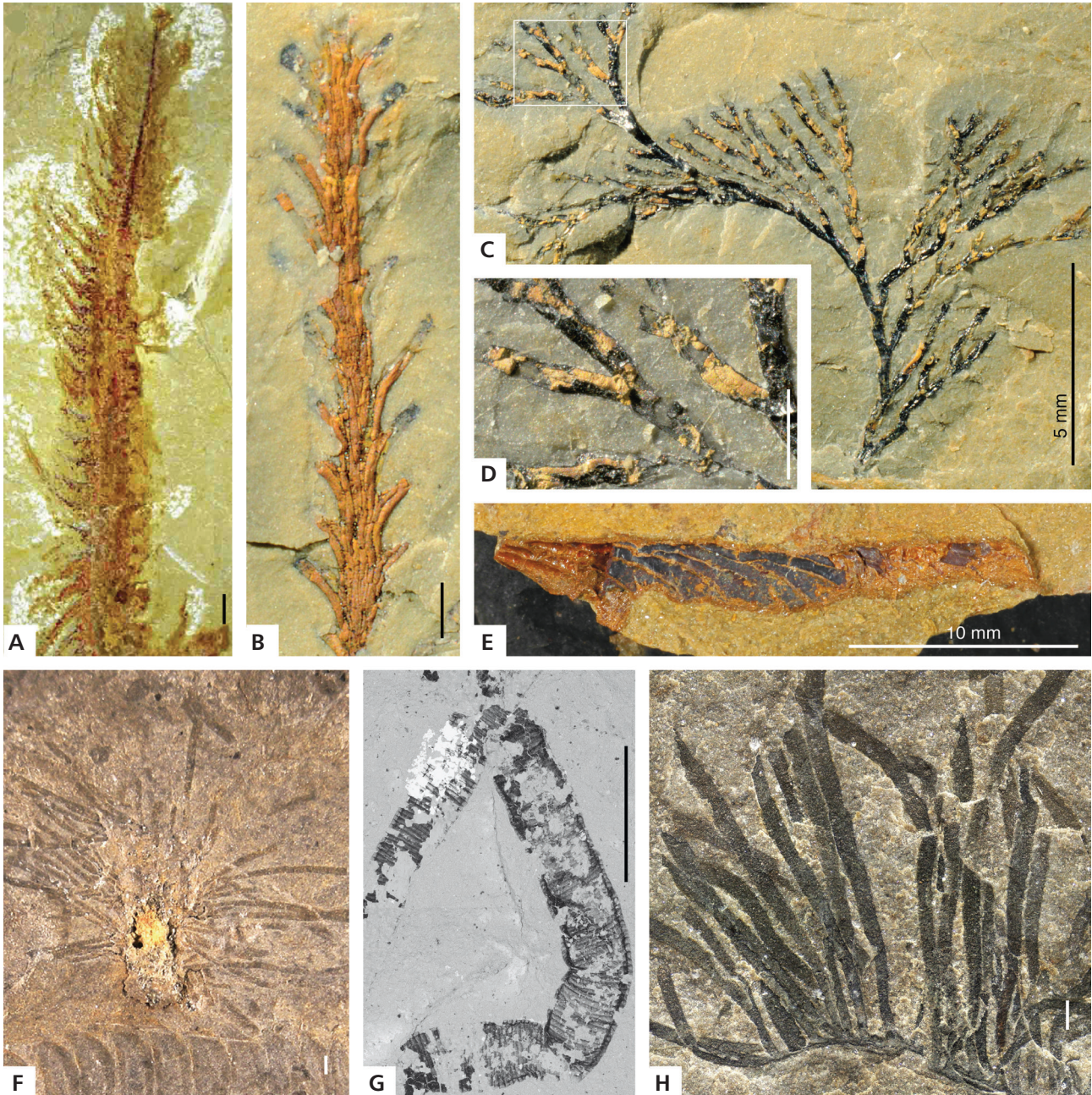


Figure 11. Graptolites and Palaeozoic Lagerstätten. • A – *Galeaplumosus abilus* Hou *et al.*, 2011, holotype, flattened, no preservation of organic material, Chengjiang, China, now identified as part of *Xianguangia sinica* Chen & Erdtmann, 1991 (Hou *et al.* 2011, fig. 1e). • B – ?*Acanthograptus sinicus* Hsü & Ma, 1948, limonitic fill, weathered from pyrite, Fenxiang Biota, China (Maletz & Kozłowska, 2013, fig. 1). • C, D – (?)*Aspidograptus uniflexilis* Yu *et al.*, 1985, limonitic fill with fusellum in black, Fenxiang Biota, China (Maletz & Kozłowska, 2013, fig. 4). • E – *Paratemnograptus magnificus* (Pritchard, 1892), weathered pyrite fill surrounded by iron oxides, Fezouata, Morocco. • F – *Yuknesia simplex* Walcott, 1919, USNM 35406, holotype, notice pyrite concretion in center, imprint, no organic material preserved, Burgess Shale, Canada. • G – *Spenoecium wheelerensis* Maletz & Steiner, 2015, holotype, part, SEM-BSE photo to show fusellar construction, House Range, Utah, white colour indicates pyrite (see Maletz & Steiner 2015, fig. 17b). • H – *Spenoecium wheelerensis* Maletz & Steiner, 2015, specimen showing dark mineralization, organic material of fusellum is not preserved, House Range, Utah (Maletz & Steiner 2015, fig. 7a). Scale bar is 1 mm unless stated otherwise.

late stage chemical alteration and weathering was linked to intense post-Cretaceous faulting.

The preservation of the Chengjiang fauna (e.g. *Gabbot* *et al.* 2008) represents a situation similar to the Bur-

gess Shale fauna. The succession is less strongly metamorphosed and apparently not tectonized. Hemichordates (pterobranchs) have been claimed to exist at Chengjiang, but *Ou et al.* (2017) identified the supposed hemichordate

Galeaplumosus abilus Hou *et al.*, 2011 as an isolated tentacle of the possible cnidarian *Xianguangia sinica* Chen & Erdtmann, 1991 (Fig. 11A). The precise mode of preservation of this material has not been determined, unfortunately. Pterobranch remains have been discovered in the slightly older Kaili Biota (Harvey *et al.* 2012) and in the lower Cambrian of Greenland (Slater *et al.* 2017), showing indications of fusellar construction, preserved as chemically isolated small pieces of organic material. Maletz (2014b, 2019a), Maletz & Steiner (2015) and Maletz & Beli (2018) demonstrated that pterobranch remains are found in the early Cambrian and predate the Chengjiang Biota, and thus, could be present in the Chengjiang fauna.

Fenxiang (Ordovician, Tremadoc)

Baliński & Sun (2015) described the early Ordovician shallow-water Fenxiang Biota of China as an Ordovician Burgess Shale-type fauna. While mixing this term with a Burgess Shale-type preservation, the authors stressed the much wider temporal distribution of this type of preservation in the Ordovician. Baliński & Sun (2015) illustrated a range of organisms. The supposed soft parts are often preserved as weathered, pyritized remains of the organisms in three dimensions (Baliński *et al.* 2014), but the original composition of the material is unclear. Others are phosphatized like the antipatharian coral remains (Baliński *et al.* 2012, Baliński & Sun 2017) and phosphatic brachiopods in which the long pedicle is preserved in three dimensions in pyrite, now weathered to limonite (Baliński & Sun 2013). Maletz & Kozłowska (2013) described a small fauna of dendroid graptolites from the Fenxiang Biota, including *Acanthograptus*, *Aspidograptus*, *Dendrograptus* and *Koremagraptus* (Fig. 11B–D). The material is preserved in partial relief, probably pyrite filled originally, and shows some organically preserved fusellum, but also shows extensive weathering and limonitization of the fills. In many relief specimens the internal limonitic casts may be exposed through the splitting of the shale (Fig. 11B, D), separating the covering by the fusellum on the counterpart slabs. There is no information available on the thermal history and tectonic distortion of the succession, but the preservation of the graptolites as dark to black, often massive looking fusellum may indicate a low grade of metamorphism at maximum. There is no evidence in the specimens for a tectonic overprint.

Fezouata (Ordovician, Tremadoc)

The Fezouata Biota (Van Roy *et al.* 2010, 2015) were characterized as typical of Burgess Shale-type assemblages.

Van Roy *et al.* (2010) compared the preservation to the Chengjiang fauna of China. Graptolites are prominent in this early Ordovician fauna from Morocco and have been used to precisely date the succession (Gutiérrez-Marco & Martin 2016). Therefore the Fezouata Biota are discussed in more detail here. Saleh *et al.* (2020a) discussed the preservation of the Fezouata fossils and stated that ‘entirely soft non-cuticularized organisms are absent’, but suggested that ‘partly mineralized and sclerotized tissues’ may have protected the soft tissues. Saleh *et al.* (2020b) demonstrated that the soft-tissues described from echinoderms are the results of recent weathering and fossil preparation, probably also negating the claim of the presence of soft tissue preservation in the specimens of Lefebvre *et al.* (2019). Based on these interpretations, it appears that there is no real soft tissue preservation or preservation of carbonaceous material in the Fezouata Biota, which is supported by the graptolite fauna.

The graptolite fauna includes largely flattened specimens from the Tremadocian and lower Floian (Lower Ordovician). More rarely, fragments are preserved in partial to full relief as internal casts. Van Roy *et al.* (2010, suppl. info fig. s2i) even mentioned preserved zooids in a tuboid graptolite, but these were never described. Illustrations of the graptolite faunas from the Fezouata Lagerstätte (Martin *et al.* 2016) show that the specimens are actually poorly preserved and largely do not retain any organic material. The preservation, often as reddish outlines implying lack of organic material, may indicate late stage weathering impregnation with iron minerals. Some specimens are preserved in relief as originally pyritic internal casts (Fig. 11E), but are clearly modified by subsequent mineralization and weathering. However, there is much more to the geological history of the material that has not been considered so far in connection with the fossil record, but can easily be understood from a closer look at the regional geology.

The Fezouata lagerstätte of the Anti-Atlas is found in a mountain chain showing considerable tectonic deformation (Caritg *et al.* 2004, Helg *et al.* 2004, Burkhard *et al.* 2006, Robert-Charrue & Burkhard 2008, Ruiz *et al.* 2008). Apart from gentle folding, probably already starting in the late Carboniferous, considerable thermal influence can be seen in the strata. Soulaimani *et al.* (1997) discussed the deformation and thus formed schistosity of Cambrian to Silurian rocks of the Anti-Atlas and noted the presence of chloritic mineralizations. Ruiz *et al.* (2008) used the illite crystallinity to determine the palaeo-thermal gradient and recognized a considerable burial metamorphism. While the boundary between epizone and anchizone metamorphism (at *ca.* 300 °C) was found approximately at the Cambrian–Ordovician boundary in the western Anti-Atlas, it is found in the middle–upper Cambrian in the central Anti-Atlas. The diagenesis/ anchizone boundary (*ca.* 200 °C)

would be found probably in the Silurian, while the Devonian strata are clearly in the diagenetic zone (see Ruiz *et al.* 2008, fig. 4). The final exhumation of the Anti-Atlas happened in the Mesozoic–Cenozoic (Ruiz *et al.* 2011, Oukassou *et al.* 2012) as zircon and apatite fission-track data and thermochronological analysis suggest. These data indicate that the early Ordovician graptolites and accompanying fossils are considerably thermally altered and tectonized. Due to surficial weathering, the material is also poorly preserved, altered and dyed through iron minerals, enhancing the contrast between the specimens and the surrounding sediment. This may have led to the reddish colour many graptolites (and also other fossils) show (see Van Roy *et al.* 2010, Martin *et al.* 2016). Specimens preserved originally as pyritic internal casts would have to be converted into limonite or other iron minerals due to the weathering. Tectonic deformation of the Fezouata fossils has not been documented so far, but may be difficult to recognize in the material, even though it has to be expected from the tectonic history of the region. Conodont faunas from the Fezouata Biota are too poorly preserved to gain insight into the thermal history of the material, as the specimens are largely recrystallized to fluorite due to the extraction method used (Lehnert *et al.* 2016).

Lower Ordovician faunas from a number of drill cores in the Algerian Sahara, outside the Anti-Atlas (*e.g.* Legrand 1964a, b; 1974) show much better preservation of graptolite fusellum in chemically isolatable material. Legrand (1974) for the first time demonstrated the quadriserial development of the proximal end in *Rhabdinopora flabelliformis* ssp. from this material. The preservation is restricted to the tubaria showing all details of the fusellar construction. It does not include remains of the stolon system and remains of the zooids have not been discovered. This material did not experience higher metamorphic coalification or tectonic deformation, even though some fractures are visible in the material. This fracturing, however, may be due to the method of preparation.

Eramosa (Silurian, Wenlock)

The Eramosa Lagerstätte (Tetreault 2001) is one of the Silurian lagerstätten on the Bruce Peninsula of Ontario, Canada. According to von Bitter *et al.* (2007), the Eramosa Lagerstätte is restricted to only four localities, producing three different biotas. LoDuca & Tetreault (2017) termed it an ‘algal-Lagerstätte’ due to the domination of algae in the fossil composition. The fossils are found in the Eramosa Formation (Brett *et al.* 1995, Brunton 2009) of Sheinwoodian, Wenlock age (Bancroft *et al.* 2016), preserved as calcium phosphate and as carbon films.

The Eramosa Formation is widely distributed in the region as part of the Lockport Group. The Lockport Group

includes several formations and the correlation is often difficult, especially with old fossil records as various informal names are used in the region and fossil faunas are not too well located (see Brett *et al.* 1995). Organic preservation of fossil faunas has previously been described from the Lockport Group of western New York and southern Ontario. Dendroid graptolites are common in the so-called ‘Gasport Lens’ of the Lockport limestone (*e.g.* Ruedemann 1925, 1947, p. 127) and in the Lockport Dolomite at Hamilton, Ontario (Spencer 1884b, Bassler 1909), also including taxa now referred to as dasycladacean algae (LoDuca 1990). It is to be expected that this type of preservation is distributed much more widely in the region, but has not been investigated in detail. Comparable graptolite faunas from the Rochester Shale of the Clinton Group (see Brett *et al.* 1995 for lithostratigraphy) are preserved as thick, black organic films of flattened tubaria, sometimes even showing partial relief, as in the type material of *Dictyonema retiforme* (Hall, 1843) redescribed by Maletz (2019b).

LoDuca & Brett (1991) discussed the *Medusaegraptus* epibole from the Niagara Falls Member of the Goat Island Formation, described first by Ruedemann (1925), as an exceptional biota with non-calcified organisms such as marine algae, annelids, and possible land plants. The fossils include a diverse fauna of dendroid graptolites that in part may have been found in life position as the completeness of the material indicates (*cf.* large specimen of *Dictyonema crassibasale*: Ruedemann 1925, pl. 1). Also the specimens of the noncalcified dasycladacean alga *Medusaegraptus mirabilis* (Fig. 12A) are considered to be preserved *in situ* in the sediment in a normal marine environment (LoDuca 1990). The preservation of the *Medusaegraptus* epibole is closely comparable with that of the Eramosa Formation in the same region.

Dendroid graptolites from an equivalent of the Lockport Group of New York State and Ontario can also be found in inter-reef facies of Huntington, Indiana (Erdtmann & Przebindowski 1974, Erdtmann 1976) and a number of further localities referred to as Konservat-Lagerstätten (Kluessendorf 1994). The material of the Mississinewa Shale was originally described by Shrock (1928). Erdtmann & Przebindowski (1974) described and illustrated the fossils and remarked on the preservation of organic material in many specimens found in life position preserved *in situ* in the shale. Apart from a number of dendroid and graptoloid graptolites, remains of echinoderms, worms and other undetermined fossils were found, but never described in detail.

Little is known about the preservation of the fossils in the Eramosa Lagerstätte and related strata, even though preservation as carbonaceous films is generally understood for the pterobranch and algal material in the region. Collette & Rudkin (2010) described phyllocarids

from the Eramosa Formation in some detail, but did not provide detailed information on the preservation of the material, which is apparently preserved as low relief molds of the specimens not bearing any organic material. Waddington *et al.* (2015) discussed marine scorpions and showed them to be preserved either as low imprints or films of dark material (not necessarily organic). There is no information on the CAI of the conodont faunas available for the discussed sections. Thus, information on the thermal history of the faunas is not available. The Eramosa Formation and related units may represent the typical preservation of the shallow water marine biota in the region including numerous organically preserved taxa.

Mazon Creek (Carboniferous)

The Mazon Creek fauna does not include any graptolites or pterobranchs, but two species of enteropneusts have been described (Cameron 2016). Apart from the long-known *Mazoglossus ramsdelli* Bardack, 1997 (Maletz 2014b), *Saccoglossus testa* Cameron, 2016 was referred to the extant genus *Saccoglossus* and represents the second oldest enteropneust known from the fossil record. Even though the preservation of the Mazon Creek fossils is often considered to be good, the completely preserved outlines of the enteropneust specimens do not show the preservation of any organic material (Fig. 12B). They are found as light colour stains contrasting with the slightly darker matrix of the siderite concretions, probably the result of oxidation of pyritic replacements or weathering of the organic components of the original specimens (Murdock *et al.* 2016), lacking anatomical details. Baird *et al.* (1986) discussed the taphonomy of the lagerstätte and considered rapid burial prior to significant decomposition and subsequent concretion formation as the main reason for the preservation of these molds and impression fossils. The whitish mineralization is considered as a secondary calcite precipitation on the fossils by Baird *et al.* (1986), but was identified as caolinite by Murdock *et al.* (2016) (see Fig. 12B). It is unclear, whether organic material is preserved in most specimens. Nitecki & Schramm (1976) described the problematicum *Etacystis communis* as a possibly colonial organism in which the individuals are connected with a stolon system and compared it with the pterobranch hemichordates.

Graptolites and the understanding of organically preserved fossils

As palaeontologists, we often pick the best and ignore the poor in our fossil hunting. The identification of tapho-

nomic windows and the supposed special or exceptional preservations in certain deposits (*e.g.* Orr *et al.* 2003, Porter 2004, Zhao *et al.* 2005, Cherns *et al.* 2008, LaFlamme *et al.* 2014, Baliński & Sun 2015, Bienkowska-Wasiluk *et al.* 2015, Tarhan *et al.* 2016, Cunningham *et al.* 2017, Eldijk *et al.* 2018) has sometimes been considered as more important than a holistic approach comparing the preservation of the various tissues and materials in fossils and understanding their preservational potential in connection to other geological factors (Purnell *et al.* 2018).

In understanding the preservational aspects of fossil pterobranchs, it has to be recognized that the preservation of organic material *per se* cannot be regarded as exceptional preservation. What appears to be exceptional in many Konservat-Lagerstätten is the presence of complete cuticularized animals (*e.g.* arthropods in the Burgess Shale and Chengjiang Biota), which are usually preserved as fragments and moulting remains in other sediments. The actual composition of the preservable or preserved material of a fossil has to be analyzed to evaluate the preservational potential of certain lagerstätten. While we are excited about the presence of fossils, it is often unclear how they are actually formed. Thus, we miss to investigate and analyse the chemical (biogeochemical) composition of the remains in order to recognize features that are unlikely to be preserved.

Biom mineralized and organically preserved fossils

In terms of body fossils, we have to consider the main preservable aspects, the biomineralized skeletons and shells and other, organic material, be it skeletons or tissues. The original composition of an organism may lead to certain parts being preserved more readily, whereas other portions will decay within a short time, as we have seen in the examples of the Hemichordata. So we find the bones of vertebrate skeletons (biomineralized), but rarely, as in the feathered dinosaurs and early birds of the Jehol Biota (*e.g.* Hou *et al.* 1995, Ji & Ji 1996), we have remains of their organic bodies (cellular tissues) or coverings of their skin, feathers or hair (extracellular or recalcitrant material) formed under special preservational conditions. Thus, the situation is closely comparable to that of the preservation in the Hemichordata discussed earlier. Yang *et al.* (2020) discussed the preservation of some of the supposedly earliest biomineralizing metazoan, the cloudinids, as originally organic, formed from chitinous or collagenous material, showing the interdependence of preservational aspects.

The preservation of the soft tissues or cellular tissues, sometimes also called labile tissues, might be extremely difficult in the fossil record (Butterfield 1990, Briggs & Kear 1993) and in invertebrate fossils is based largely on

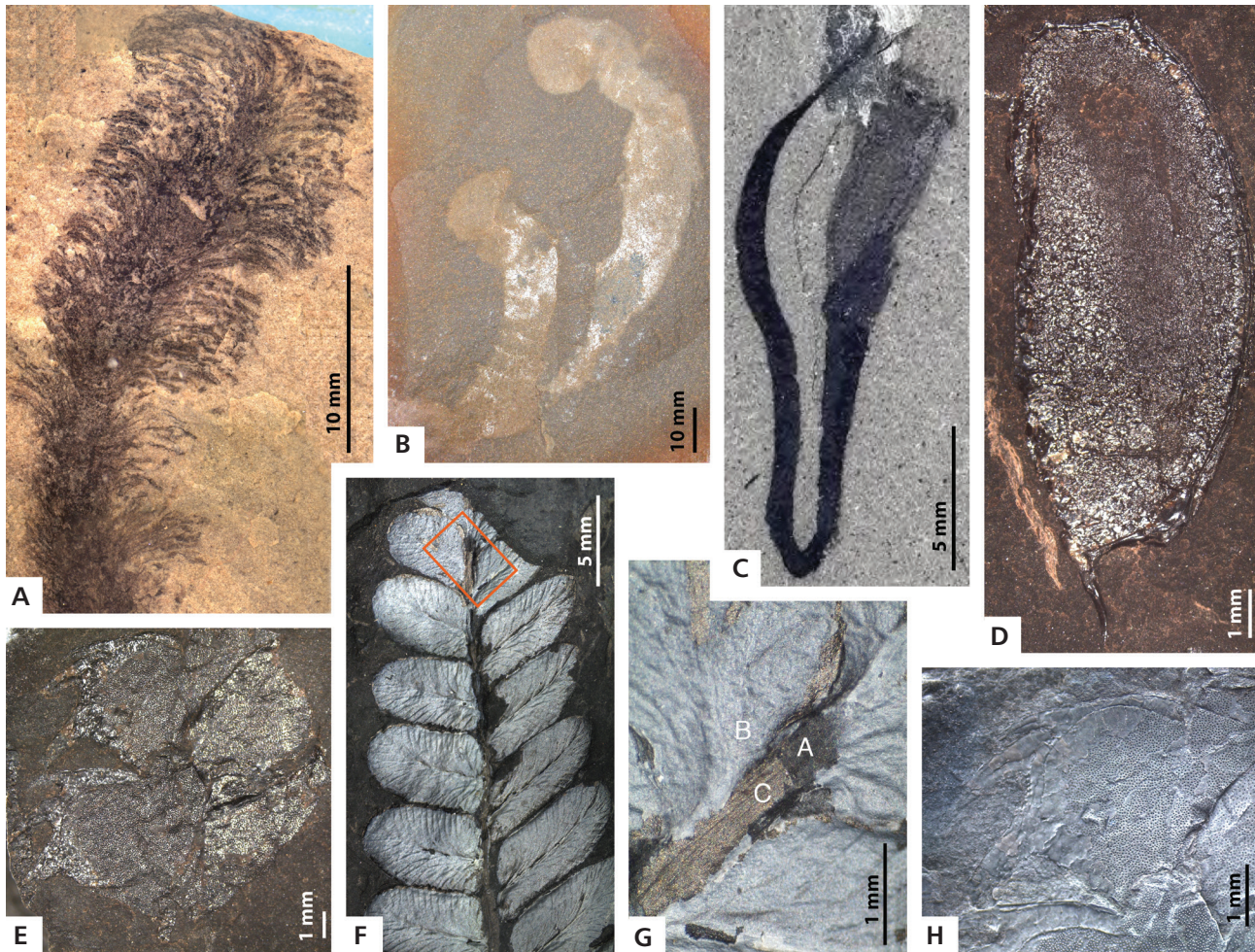


Figure 12. Organic preservation in fossils. • A – *Medusaegraptus mirabilis* Ruedemann, 1925, SMF 75806, showing organic preservation, Lockport Formation, Ontario, Canada. • B – *Mazoglossus ramsdelli* Bardack, 1997, FMNH 45207, holotype. Francis Creek Shale, Illinois, Will, Kanakee or Grundy County, Mazon Creek Region. • C – *Spartobranchus tenuis* (Walcott, 1911), USNM 108494, lectotype, polarized light, Burgess Shale, Canada. • D – phyllocarid carapace, GSC 140106, late Tremadoc, Cow Head Group, Martin Point, western Newfoundland, Canada. • E, H – undetermined arthropod fragment, GSC 140107, late Tremadoc, Cow Head Group, Martin Point, western Newfoundland, Canada; H – detail showing surface ornamentation, specimen coated with ammonium chlorite. • F, G – *Neuropteris attenuata*, SM.B.22105, specimen coated with white pressure shadow minerals (B), some pyrite (C) and organic material (A) is visible, Piesberg near Osnabrück, Germany, Carboniferous.

interpretation of the outlines of the specimens. Typical examples are the enteropneust worms described from the Burgess Shale (Caron *et al.* 2013, Cameron 2016, Nanglu *et al.* 2016). Most preserved materials in the Burgess Shale (*cf.* Gould 1989, Briggs *et al.* 1994) may, however, be regarded as remains of cuticles, either of worms or of arthropods and has to be identified as recalcitrant material. Even in the Burgess Shale, the preservation of soft tissues or cellular tissues is rare in most taxa, but may be found in ctenophores or in some completely preserved sponges (Botting 2012). The preservation of organ systems and neurological tissues in Chengjiang fossils has recently been challenged and explained as possible microbial biofilm remains following the decomposition of the original tissues (Liu *et al.* 2018). Thus, in many cases of

supposed soft body preservation, actually the preservation only includes recalcitrant tissues, and true cellular tissues such as organs, skin or muscles are not preserved at all, as Steiner (2018) suggested.

All extracellular materials are here identified as recalcitrant materials, formed as secretions from special glands of the organisms. The cuticle is a tough, recalcitrant material covering the outside of many organisms (Fig. 12E, H), animals and plants (Fig. 12F, G: *Neuropteris attenuata*, Carboniferous), which prevents loss of fluids and provides protection. It may be variable in thickness, thus also variable in its preservational potential and can break into smaller pieces due to robustness of involved material and the differentiation or segmentation of the involved organisms (*e.g.* Wilson & Butterfield 2014).

Briggs & Kear (1993) described the decay of the extant polychaete *Nereis* in some detail. They recognized that all muscles were broken down after eight days, while the recalcitrant cuticle lasted much longer. Only the most durable parts, the jaws and setae were retained much longer. Sansom (2016, fig. 2) provided information on the extant priapulid *Priapulid*, in which basically all non-cuticular tissue was lost after six days. Cuticular tissue was still present after 224 days.

Arthropod cuticles, especially of phyllocarids (Fig. 12D), are often found associated with graptolites in Palaeozoic shales, and their remains behave similarly during fossilization (Gupta & Briggs 2011, Hartkopf-Fröder *et al.* 2015). They are part of what is now identified as ‘small carbonaceous fossils’ or SCF’s (Butterfield & Harvey 2012) but are very difficult to relate to a specific organism. Arthropod cuticles are quite common in the fossil record and it is known from extant taxa, that the foregut and the hindgut are also outlined by a cuticular development, and thus may be responsible for the interpretation of intestinal remains (Chapman 1985, Steiner 2018). The cuticle may be thin and difficult to preserve (caryocaridids: Vannier *et al.* 2003), but certain parts like the feeding apparatus of arrow worms are heavily cuticularized and easily preservable (*e.g.* Vannier *et al.* 2007). A similar situation can be seen in the scolecodonts where only the jaw apparatuses are preserved, while we know little about the rest of the organisms from the fossil record (*e.g.* Kielan-Jaworowska 1966; Eriksson *et al.* 2004, 2017). The development of the black stolon system of the Pterobranchia (Schepotieff 1906, Maletz & Cameron 2016) may be more easily related to a cuticular development as it represents the hardened surface of the gymnocaulus, connecting the individual zooids of the graptolite colony. Both, the graptolite tubaria and the stolon system, are durable organic materials and especially the tubaria are common in the fossil record. Therefore, they can be investigated in some detail and represent a key to understand the preservation and modifications of organic materials in geological history.

What is exceptional preservation?

In general, exceptional preservation appears to describe the preservation of more or less complete fossil specimens and not as fragmented remains, largely as organic films (*e.g.* Burgess Shale, Chengjiang Biota, *etc.*). The preservation as organic material, however, may lead to a more precise question: Does exceptional preservation of fossils also invariably means carbonaceous preservation and how can we interpret this? Certainly, it is exceptional when we find fossil organisms that show the preservation of features we consider to be non-preserved (*e.g.* preservation of

cellular material), but there may be a better interpretation when we understand the differences between materials, sediments, diagenesis and tectonics; when we understand all the things that can happen to a dead organism during the process of taphonomy, and the preservation of graptolite remains may provide a useful key to our understanding of organically preserved fossils. Features may have a different explanation (*cf.* Liu *et al.* 2018) and what we see may not be exceptional preservation, but represent different and sometimes exceptional circumstances under which certain materials are preserved, modified or replaced.

The preservation of complete carbonaceous carapaces of arthropods, as in the Burgess Shale or the Herefordshire lagerstätten for example, is as spectacular and special, as it is rare, as is the preservation of complete vertebrate skeletons. Altogether excellent preservation of fossils is rare and what we now often call Konservat-Lagerstätten (*cf.* Seilacher 1970) may include complete carapaces of animals – at least their outlines – the interpretation is only due our lack of understanding of the real preservational conditions. Even in these Konservat-Lagerstätten, the preservation of soft tissues or cellular tissues is extremely rare. The lax use of the term soft-bodied preservation may mislead us, so we do not look in enough detail at the preservational aspects. Recalcitrant material may be far more common and already provides us with a lot of otherwise unavailable anatomical information, but should not invariably be called exceptional.

(?)*Kiaerograptus supremus* Lindholm, 1991 (Fig. 13) is a common and widely distributed late Tremadocian graptolite species and a good example to compare various preservational aspects of a single taxon to understand the challenges to interpret and recognize an organically preserved fossil. The holotype of this species is preserved in full relief in a black shale in a drill core from southern Sweden (Fig. 13A, B). Many details of the tubarium are only visible when coated with ammonium chlorite (Fig. 13B), but information on the fusellar construction is not available at all. The specimen shows no tectonic distortion and little maturation of the well-preserved fusellum. A low relief specimen from Fezouata (Fig. 13C–E) is preserved as an internal cast, now probably made from limonite, but originally supposedly formed as a pyritic internal cast. It shows parts of the proximal development in obverse view including the presence of a sicular bitheca (Fig. 13E, arrow). Distally, the thecae are less well preserved and in the distal end, the cast is lost (Fig. 13D, red arrow). There is no preservation of organic material as the fine gap between the cast and the surrounding sediment shows (Fig. 13E: red arrows). This loss may have happened during the weathering of the sediment, shown through the red color of the iron staining. The preservation of this material is quite poor, as is the flattened and metamorphosed or coalified material from the Fågelsång 3 drill core of southern Swe-

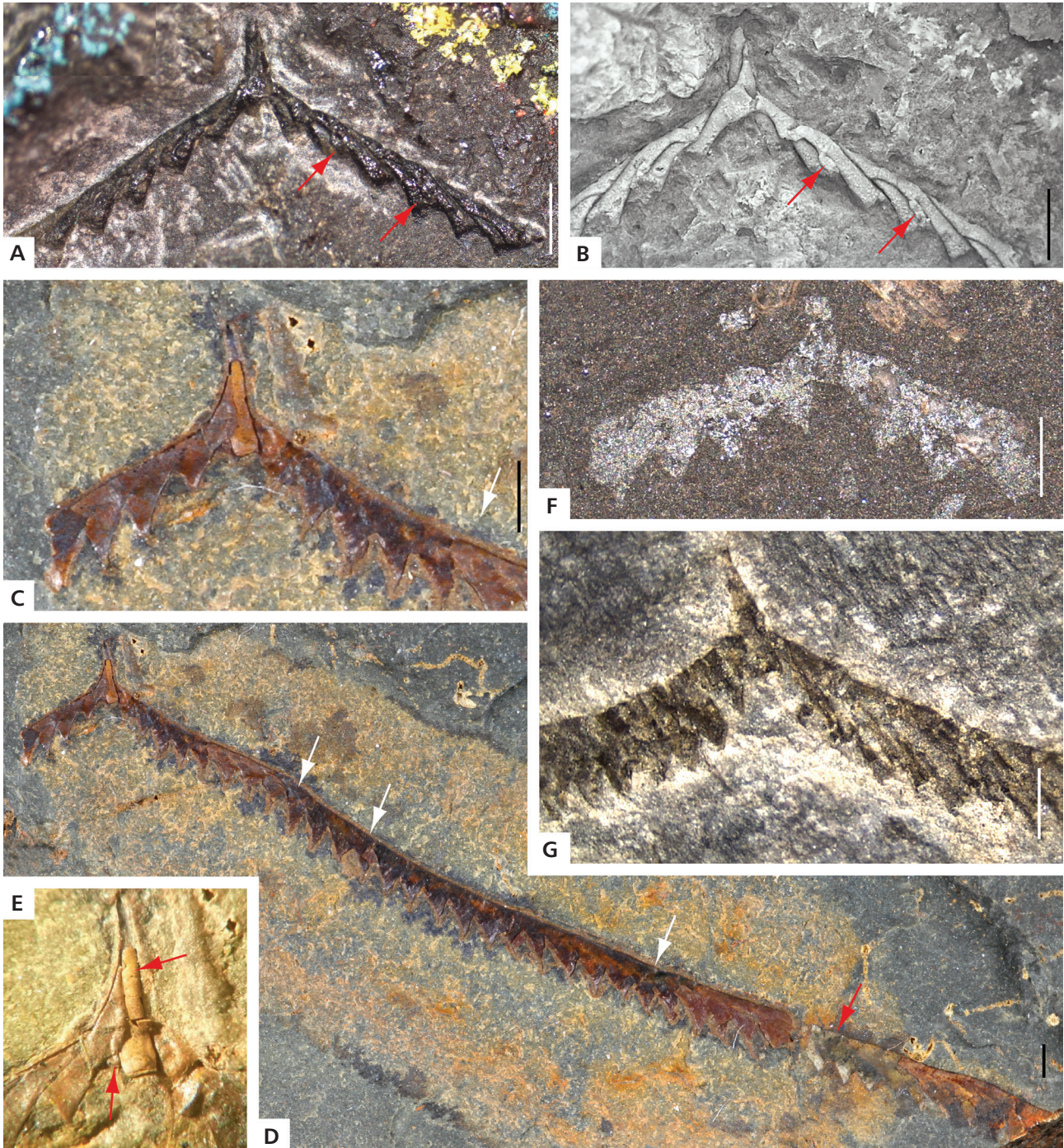


Figure 13. (?)*Kiaerograptus supremus* Lindholm, 1991 in various preservational aspects; A – LO 5970T, holotype, relief in black shale, Krapperup drill core at 151.46–151.50m depth; B – LO 5970T, coated with ammonium chlorite to show details of tubarium construction; C – E – AA-BGF2-OI-6, specimen preserved in partial relief as an internal cast, Fezouata, Morocco (see Martin *et al.* 2016, fig. 5); F – PMU 31719/3, flattened, poor specimen, highly coalified, Fågelsång 3 drill core, 64.7–64.75 m, Scania, Sweden; G – SMF-BO CUL 8-042, Culpina, Bolivia, strongly tectonized and weathered specimen preserved as dark green pressure shadow minerals, no organic material preserved. Red arrows in A, B indicate bithecae. Scale bars indicate 1 mm in each photo.

den, showing a silvery shine (Fig. 13F). Specimens from the early Ordovician of Culpina, Bolivia are preserved as greenish pressure shadow minerals lacking the organic material of the original specimens (Fig. 13G). This material

is strongly tectonized, as the asymmetrical outlines and the tectonic lineation of the rock indicate and show the effects of recent weathering. The comparison of the various specimens of (?)*Kiaerograptus supremus* shows the

importance of understanding of late stage taphonomical changes for the proper identification of taxa and also to estimate the quality of preservation.

We need to investigate fossils in a geological context by using our knowledge on preservation and modification through geological history and not describing fossil preservation in narrow limits as exceptional. Thus, the change of the organic material through geological processes as documented here for graptolite faunas (Fig. 13) may help also to understand other ‘exceptional’ preservations. There are certainly differences between the organic material of the graptolite tubaria and the cuticles of arthropods or plants or even the microfossils like acritarchs and chitinozoans. However, many similarities also exist and show patterns in the taphonomy of organically preserved fossils that can easily be compared.

Conclusions

(1) The Pterobranchia can be regarded to provide typical examples of organic preservation in the fossil record and used as a guide to interpret the taphonomy of organically preserved fossils.

(2) Taphonomy includes all modifications of an organism from death to the discovery as a fossil.

(3) Organic preservation of fossils is in general nothing special, but may be found everywhere in suitable sediments and can only be regarded as an alternative to the preservation of biomineralized fossils.

(4) Thermal maturity investigations show that the geological modifications of the organic materials of fossils follow similar paths in the various groups of organisms, including both, animals and plants.

(5) Two types of organic material of fossils can be differentiated, cellular or soft tissues and non-cellular or recalcitrant materials (not tissues). These two types need to be differentiated carefully, as their preservational potential differs considerably.

(6) Metamorphism and tectonics change the fossil appearance considerably through coalification (heating) and the formation of pressure shadow minerals (tectonic deformation).

(7) Many ‘exceptional’ faunas actually represent poorly preserved fossils (e.g. Burgess, Chengjiang, Fezouata) in which the fossil recognition is enhanced by later taphonomic processes (diagenesis, metamorphism, tectonics, weathering).

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Fossil Repositories

Illustrated material originates from the following institutions: AA – Faculty of Sciences and Technics, Cadi-Ayyad University, Marrakesh, Morocco; FMNH – The Field Museum, Department of Geology, Chicago, USA; GSC – Geological Survey of Canada, Ottawa, Canada; GSE – British Geological Survey, Keyworth, Nottingham, UK; IANIGLA – CONICET Mendoza, Argentina; LO – Department of Geology, Lund University, Sweden; NIGP – Nanjing Institute of Geology and Palaeontology, Nanjing, China; NMVP – Museum Victoria, Australia; NRM PZ – Naturhistoriska Riksmuseet, Stockholm, Sweden; PMO – Natural History Museum, University of Oslo, Norway; PMU – Museum of Evolution, Uppsala, Sweden; PŠ – Petr Štorch collection, Czech Geological Survey, Prague; SGU – Sveriges Geologiska Undersökning, Uppsala, Sweden; SM – Sedgwick Museum of Earth Sciences, Cambridge, UK; SMF – Senckenberg Naturmuseum, Frankfurt/Main, Germany; USNM – US National Museum, Washington, USA.

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