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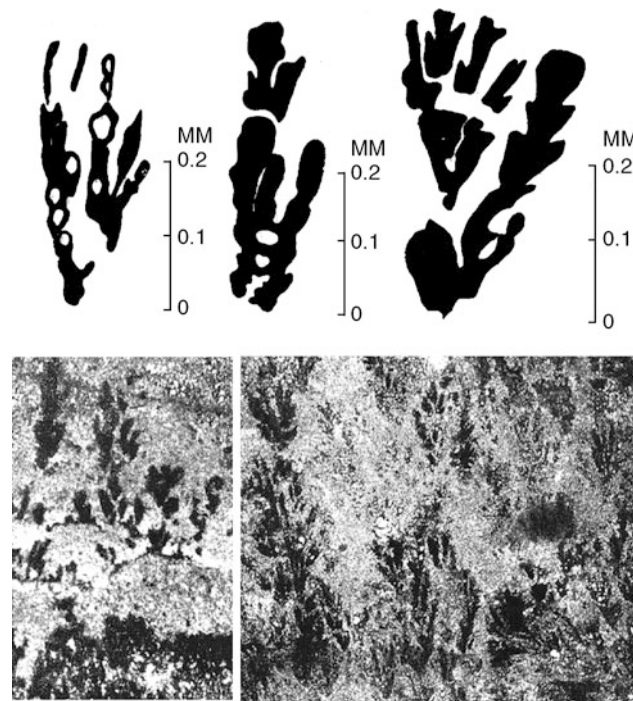
Algae (Eukaryotic)
 Bioerosion
 Carbonate Environments
 Carbonates
 Chemolithotrophy
 Divalent Earth Alkaline Cations in Seawater
 Isotopes and Geobiology
 Protozoa (Heterotroph, Eukaryotic)
 Symbiosis

FRUTEXITES

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Synonyms

Colloform limonitic crusts; Frutexites crusts; Frutexites-like forms; Frutexites microstromatolite; Frutexites tuffs; Haematitic/ferruginous/iron microstromatolites; Iron dendritic aggregates; Iron shrubs; Pillar-shaped microstromatolites



Frutexites, Figure 1 Original figures of genus of *Frutexites* described by Maslov (1960).

Definition

Frutexites is a problematic microfossil rich in iron. From a taxonomic point of view, only five species have been figured (*Frutexites arboriformis*, Maslov, 1960; *F. microstroma*, Walter and Awramik, 1979; *Frutexites* sp. 1, *Frutexites* sp. 2, and *New gen.* 3, Tsien, 1979), although the authors mostly use the term *Frutexites sensu lato*. The genus *Frutexites* was coined by Maslov (1960) in order to describe submillimeter-sized, iron-rich, and subordinate calcite microfossils (Figure 1). *Frutexites* have a dendritic shape formed by divergently branched microcolumns. The height and width of microcolumns as well as their composition and microstructure can vary (Table 1). The preservation of microstructure is strongly controlled by its dominant mono- or polymineral

character. Microstructure is formed by convex-upward laminae, which sometimes show radially arranged fibers.

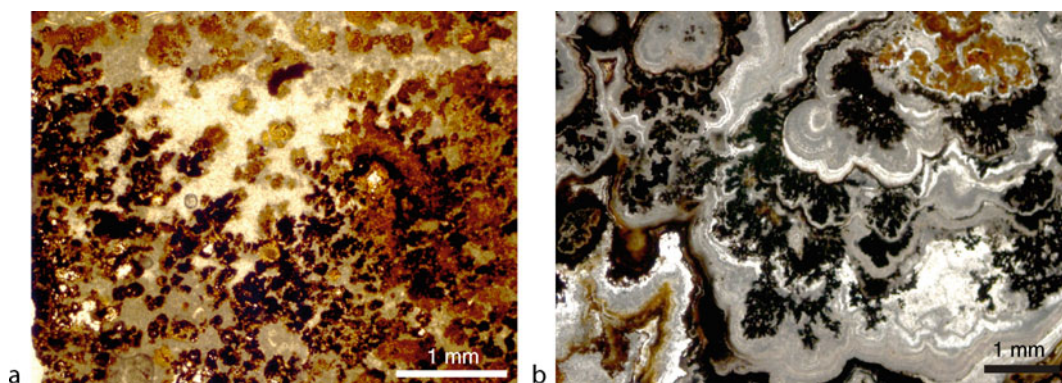
Frutexites can occur mainly as monomineral as well as polymineral structures with: iron-rich and/or manganese-rich (hematites, iron hydroxides, Fe-Mn oxyhydroxides), and/or carbonate-rich (calcite, ferroan calcite, dolomite), and/or siliciclastic-rich (argillite, microquartz), and/or phosphatic-rich zones.

Depositional environmental occurrences

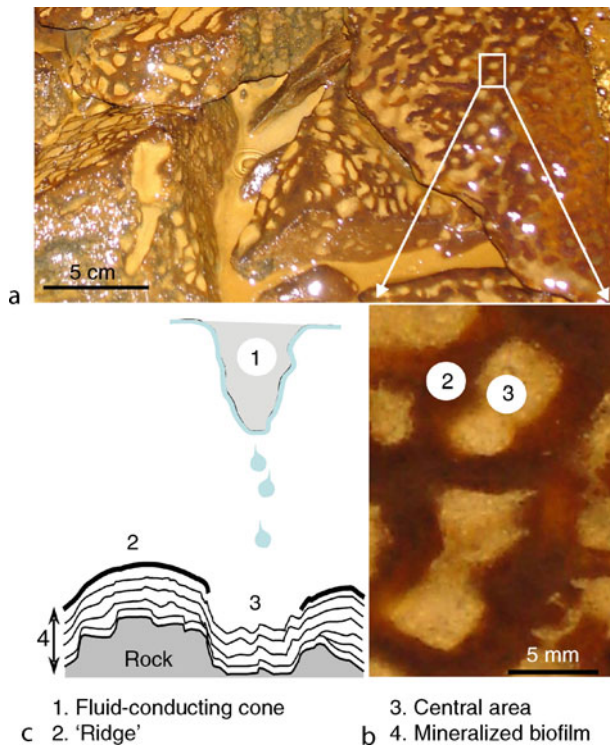
Frutexites has been described in marine environments such as shallow and deep water stromatolites, microbial limestones, hardgrounds, and condensed pelagic limestones as well as in cavities, sheet-cracks, veins, and Neptunian dikes. However, comparisons with

Frutexites, Table 1 Sizes, morphological and compositional parameters of *Frutexites* according to different authors

Authors	Height	Width	Microstructure	Morphology	Composition
Maslov (1960)	Up to 400 μm (see Figure 1)	25–30 μm , more of 50 μm	Sheets with occasionally circular spaces	Radially diverging and branched sheets	Iron hydroxide and carbonate
Horodyski (1975)	20–500 μm	10–200 μm	2–10 μm convex-upward laminae	Pillar-shaped branched and not	Hematite, calcite, and argillite
Walter and Awramik (1979)	Up to 450 μm	5–120 μm	0.7–2.7 μm convex upward laminae and axial tube (trichome?)	Undulose layers, laminae with protruding pustules and erect branching microcolumns	Organic matter permineralized by silica
Myrow and Coniglio (1991)	250 μm –4 mm, most <1 mm	75–600 μm , 250 μm average	Chambers, laminae, fibers, and projections	Unbranching and branching columns	Calcite, ferroan calcite, hematite, and microquartz
Böhm and Brachert (1993)	Up to 5 mm, average 1–2 mm		Convex laminae with radially arranged fibers		Fe-Mn oxides, calcite, and phosphates
Woods and Baud (2008)	Up to 800 μm	50–200 μm	Lighter and darker colored layers resulting chambered appearance		Hematite and/or Fe-Mn minerals, and calcite



Frutexites, Figure 2 (a) Marine Upper Cenomanian/Lower Turonian *Frutexites* colonies from a deepwater hardground environment (Liencrees coast, northern Spain; Reitner et al., 1995). The *Frutexites* facies is located on top of the hardground sequence and marks a fundamental change of the oceanographic conditions. (b) Deep subterranean *Frutexites* colonies growing on calcareous microstromatolites from tectonic fractures in the so-called “sole dolomite” at the base of the Naukluft Nappe Complex (NNC) in southern Namibia. The colonies are growing upside down from the fracture ceiling. The black ones are rich in manganese oxides, the ochre parts are enriched in iron oxides.

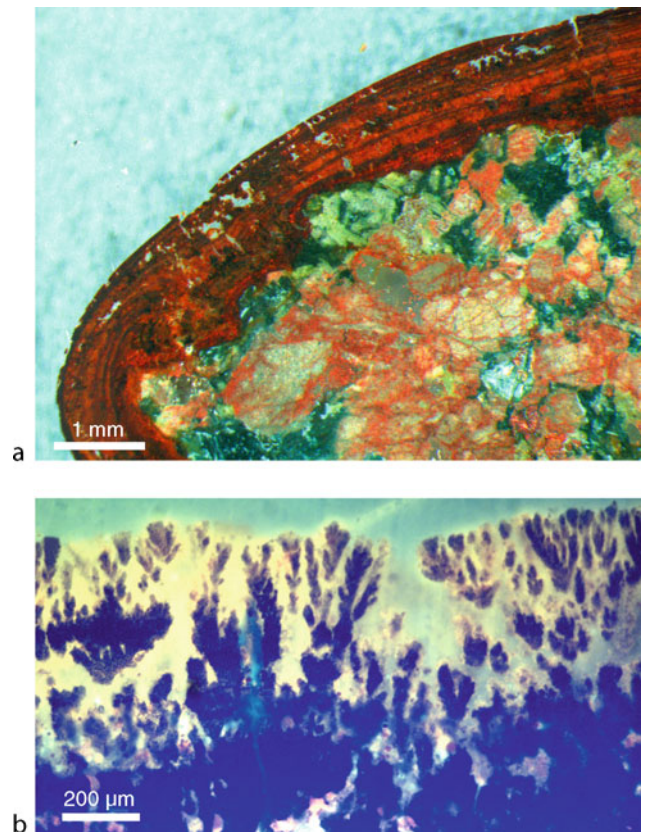


Frutexites, Figure 3 (a) Net-like, mineralized microbial mat covering the surface of granitic rocks (Åspö Hard Rock Laboratory, Sweden). (b) Close-up of the net-like, mineralized microbial mat, pointing to the dark mineralized ridge (2) and the bright central area (4) according to scheme b.

continental black shrubs are common, too. *Frutexites* structures are also frequently found in veins and fractures of deep subterranean environments (Figures 2b, 3, and 4).

Stromatolites

The main record of *Frutexites* has commonly been recognized from shallow to deep calcareous stromatolites from Proterozoic to recent examples (see Caldera lake stromatolites at Tonga, by Kazmierczak and Kempe, 2006). *Frutexites* structures grow upward perpendicular to the stromatolite laminae; however, they can sometimes cross them (Horodyski, 1975) and even destroy them. For this reason, Böhm and Brachert (1993) interpreted that stromatolite accretion was independent of *Frutexites*, which would act as dweller or secondary binder in the Jurassic deep water stromatolites from Germany and Austria. Descriptions about the associated macro- and microfauna in the *Frutexites*-bearing stromatolites are not



Frutexites, Figure 4 (a) Thick section of the mineralized, net-like, recent biofilm from the tunnel of Åspö (Sweden) under reflected light, revealing the typical laminated structure. These laminae predominantly consist of iron oxides and hydroxides. (b) UV-fluorescence microphotography exhibits *Frutexites*-like colonies within the laminae of the mineralized biofilm.

abundant. In the Canning Basin, the late Devonian *Frutexites*-bearing stromatolites show abundant meta-zoans in life position as crinoids and coral holdfasts encrusting the successive laminae (Playford et al., 1976), which would indicate normal oxygenated water conditions (Nicoll and Playford, 1993). In Jurassic stromatolites, *Frutexites* occur with shells of *Bositra* and *Lenticulina* foraminifers.

Cavities, sheet cracks, veins, and Neptunian dikes

The second most frequent occurrence of *Frutexites* in the geologic record is related to cavity walls and fissures. On the horizontal surfaces *Frutexites* could display a dominant upward growth, but, in general, their growth is normally perpendicular to the substrate where they were nucleated. *Frutexites* occur interbedded with fibrous calcite cements as well as with internal sediment. The oldest described record of *Frutexites* is in the Paleoproterozoic Gunflint chert (Walter and Awramik, 1979) and from sheet

cracks within stromatolites of the Upper Vendian to Lower Cambrian Chapel Island Formation, Canada (Myrow and Coniglio, 1991). *Frutexites* have been found in cavities of Devonian deep water mud mounds and grouped with *Renalcis-Epiphyton* calcimicrobes, and with deep water stromatolites assemblage (Tsien, 1979) as well as in stromatactoid cavities from Viséan microbial limestones where they occur interbedded with marine isopachous crusts of fibrous and botryoidal calcite cements (Gischler, 1996). The presence of *Frutexites* in Neptunian dikes has been described only in Devonian records from the Harz Mountains in Germany (Gischler, 1996) and mud mounds of the Hamar Laghdad Ridge in Morocco (Cavalazzi et al., 2007). Similar structures as *Frutexites* have also been described in voids from Toarcian Mn-rich layer at Tatra Mountains in Poland (Jach and Dudek, 2005) as well as in synsedimentary karstic cavities in Pleistocene travertines in Germany (Koban and Schweigert, 1993).

Condensed pelagic limestones and hardgrounds

The last most extended occurrence of *Frutexites* is associated with condensed hemipelagic and pelagic red to grey limestones like Griotte and Hallstatt Limestone as well as Rosso Ammonitico facies from Devonian up to Jurassic. These facies occur during very low sedimentation rates, from deep to relatively shallow water depths, during fast transgressive and/or drowning episodes. Nektonic organisms are the dominant fauna (goniatites, nautiloids, ammonoids) and *Frutexites* occur in (a) water-sediment interfaces colonizing sessile fauna, reworked bioclasts as well as ferromanganese hardgrounds (see below) and (b) within the micritic sediment. The first type of *Frutexites* growth in condensed pelagic limestones was described in Matagne Formation (Devonian of Belgium) by Tsien (1979) and in current-swept shallow pelagic ridge (Tafilalt Platform, Devonian of Morocco) by Wendt (1988). No less representative examples have been shown from the Triassic Hallstatt facies of Austria (Wendt, 1969; Rodríguez-Martínez et al., in press) and Oman Mountains (Woods and Baud, 2008). In the Oman Mountains, the sea-floor was directly colonized by *Frutexites*-bearing microbialites and synsedimentary cements. However, in the Northern Calcareous Alps, multiple ferromanganese crusts were colonized by epibenthonic sessile agglutinated foraminifers which were successively encrusted by *Frutexites* forming pillar-like structures above the seawater-sediment interface.

A similar situation has been described from deep-water hardgrounds during Mid-Cretaceous times in Spain (Reitner et al., 1995) (Figure 2). In this case, a previous benthic community dominated by coralline sponges was replaced by thick limonitic stromatolites with encrusting foraminifera and colonies of *Frutexites*.

The growth of *Frutexites* within the sediment was firstly pointed out by Böhm and Brachert (1993). They described the changes in composition and shapes of

Frutexites as a result of their growth in open spaces or in interstitial environments. Mamet and Pr at (2006) found *Frutexites* associated to other hematite microstructures in condensed Griotte facies (Coumiac Limestones, Montagne Noire, Baleas Limestone Spain) and Rosso Ammonitico Limestone (Subbetic Cordillera Spain).

Continental environments

Some authors (Myrow and Coniglio, 1991; B hm and Brachert, 1993) have compared the marine records of *Frutexites* with similar arborescent, dendritic forms found in speleothems, desert varnish, and travertines. Also, continental manganese and iron-rich black shrubs have been compared with the marine *Frutexites* records (Koban and Schweigert, 1993; Chafetz et al., 1998). Shapes, sizes, and polymineral character are similar in both marine and continental records.

Subterranean environments

Frutexites structures are sometimes common in light-independent, deep continental caves, fractures, and veins forming small microbial crusts often associated with calcareous stromatolitic structures. A characteristic representative was found by J. Reitner in southern Namibia (Figure 2b) at the base of the Naukluft Nappe Complex (NNC), which is part of the early Cambrian Damara orogeny (Miller, 2008). The deep base of the NNC is formed by the so-called "Sole Dolomite" (Korn and Martin, 1959) which is often heavily fractured. Within these cryptic fractures *Frutexites* is very common and intergrows with calcareous stromatolitic structures. Thin-shelled freshwater type ostracodes are also abundant in this fracture system.

A modern example of *Frutexites* structures has been found in the deep tunnel of  sp  in southern Sweden (Heim et al., 2007), as part of a highly oxygenated system. Wherever groundwater drops from the tunnel ceiling, a net-like, mineralized micro-system is formed on any rock surface beneath (Figure 3). In general, the dropping system is associated to pending mineral cones which are dominated by the iron-oxidizing, chemolithotrophic bacterium *Gallionella ferruginea*.

The evolving net-like structures feature semi-solid ridges, harboring a particular, highly diverse microbial community. The cross-section of this mineralized biofilm shows laminae with *Frutexites*-like structures (Figure 4). These are mainly composed of iron hydroxides, iron oxides, and less abundant manganese oxides. Small amounts of siderite, calcite, and siliceous material occur side by side with iron and manganese oxides.

Interpretation

Holotypes of *Frutexites* spp. (*Frutexites arboriformis*, Maslov, 1960; *Frutexites microstroma*, Walter and Awramik, 1979) were originally described from stromatolites; thus, they were genetically linked to different types of cyanobacteria (Playford et al., 1976, 1984; Scytonematacean – Walter and Awramik, 1979;

Rivulariacean – Hofmann and Grotzinger, 1985; Angulocellularia group – Riding, 1991). Hofmann and Grotzinger (1985) discussed the affinity of *Frutexites* to different cyanobacteria and proposed further alternatives (purely physicochemical accretion and/or iron bacteria due to the ferruginous character of stromatolite). The occurrence of *Frutexites* in cavities, fissures, and dykes was interpreted as a cryptobiont role (Myrow and Coniglio, 1991). However, Tsien (1979) was the first suggesting a non-phototrophic character, sometimes linked to chemoheterotrophic cyanobacteria (Gischler, 1996) or to chemohetero and autotrophic bacteria (Cavalazzi et al, 2007). Böhm and Brachert (1993) emphasized the roles of *Frutexites* as a cryptobiontic as well as a cryptoendopelitic organisms (living in interstitial habitats). Based on these aspects, the authors proposed the preference of *Frutexites* for oxygen-deficient environments (dysaerobic to anaerobic conditions). Furthermore, they suggested a bacterial precursor for the formation of *Frutexites* but did not exclude a possible fungal and/or physicochemical origin. According to previous publications (Maslov, 1960; Myrow and Coniglio, 1991), Böhm and Brachert (1993) explained the ferromanganese or phosphate mineralogy of *Frutexites* as a replacement of primary carbonate mineralogy. However, a primary iron mineralization of *Frutexites* was postulated by Horodyski (1975) and Hurley and Van der Voo (1990). Others like Hofmann and Grotzinger (1985) believed that microbiota involved in *Frutexites* could regulate the local water chemistry and iron oxyhydroxides as well as aragonite could coprecipitate.

Finally, the occurrence of *Frutexites* in condensed pelagic limestones and hardgrounds has been linked to a physicochemical origin (Wendt, 1969) as well as to iron bacteria (Reitner et al., 1995; Mamet and Pr eat, 2006). Reitner et al. (1995) interpreted the *Frutexites*–foraminifer assemblage as an R-strategic community which replaced the previous K-strategic community (sponges–microbes) due to fundamental changes in oceanographic conditions (from oligotrophic to more eutrophic conditions). Mamet and Pr eat discussed the origin of red pigmentation in some Phanerozoic limestones, where some condensed pelagic limestones with *Frutexites* are included. They argued that under anoxic to dysoxic conditions, ferrous iron may be available for oxidation by microaerophilic iron microbes growing at the sediment–water interface. In contrast, the recent *Frutexites*-like structures found in the deep biosphere in fact grow in air-exposed environments under aerobic conditions. However, the presence of different mineral phases within these structures could be associated to changing redox conditions and/or to a different microbial community composition at micrometer-range.

Conclusions

The different modes of growth of *Frutexites* have been recognized within shallow to deep water stromatolites,

on the seawater–sediment interface, marine micritic sediments, continental cavities, and fractures of deep subterranean environments. Such wider environmental distribution has been taken into consideration for paleoecological interpretations. According to the occurrence of *Frutexites*, some general aspects can be summarized: (a) its distribution does not show bathymetric control (although the dominant record is in deep waters facies), (b) it is formed in environments with very low sedimentation rate (in quiet as well as in agitated waters), (c) in marine environments, *Frutexites* mainly encrusts heterozoan assemblages (crinoids, sponges, solitary corals, and foraminifers), and finally, (d) there is no proof for an exclusive occurrence of *Frutexites* under anoxic and aphotic conditions.

Most of the authors considered a bacterially induced origin for *Frutexites*, but the final assessment strongly depends on which mineralogical composition they interpreted as primary (timing of iron mineralization) as well as its *loci* of growth.

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Cross-references

[Bacteria](#)
[Calcified Cyanobacteria](#)
[Cyanobacteria](#)
[Fe\(II\)-Oxidizing Prokaryotes](#)
[Gallionella](#)
[Microbial Biomineralization](#)
[Microbialites, Modern](#)
[Microbialites, Stromatolites, and Thrombolites](#)
[Stromatactis](#)
[Stromatolites](#)

FUNGI AND LICHENS

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Definition

Fungi. Saprophytic, parasitic, or symbiotic living organisms, mainly filamentous (hyphae), rarely unicellular. Cell walls are of chitin or other non-cellulose compounds.

Lichens. Symbiotic organisms composed of a fungal partner, the mycobiont, and one or more photosynthetic partners, the photobiont.

Characteristics

Fungi

Fungi are a group of eukaryotic, heterotrophic organisms with their thallus on or in the substratum. The thallus can be unicellular (rarely) or filamentous (mostly), the latter being either composed of septate or nonseptate hyphae and often forming a more or less defined web of filaments (mycelium). The cell wall is typically chitinized or composed of other non-cellulose compounds. The spore forming thallus (sporocarp) can be microscopic or macroscopic with limited tissue differentiation. Fungi are cosmopolitan and ubiquitous, saprotrophic, mutualistic (mycorrhizal, lichen-forming), or parasitic. A number of rock-inhabiting fungi belong to the Deuteromycetes, a heterogenic group of fungi that develop no or only asexual sporocarp types. The vast majority of rock fungi are dark brown to blackish pigmented and are filamentous or forming microcolonies (B del et al., 2000).

Lichens

Symbiotic mode of living

Lichens are mutualistic organisms consisting of a fungal partner, the mycobiont, and of one or more photosynthetic partners, the photobiont. Taxonomically speaking, they belong to the kingdom of fungi and represent here a special group, the lichenized fungi (Honegger, 1996). The lichen-forming fungi are polyphyletic, meaning that they have developed several times during the evolution of fungi. This brought about a taxonomically heterogeneous group with the large majority of them belonging to the Ascomycetes and only few Basidiomycetes and Deuteromycetes (= Fungi Imperfecti; Nash III, 1996a, Miadlikowska et al., 2006).

As photobiont of lichens, green algae with the most frequent genera *Trebouxia* and *Trentepohlia* make up about 90% of the photosynthetic partners, whereas cyanobacteria with the prevalent genus *Nostoc* account for the remaining 10%. The green algae, also referred to as “chlorobionts” (Lange and Wagenitz, 2003), belong to the eucaryotic algae which share many cytological features and their pigmentation (e.g., chlorophylls a and b) with land plants (Bold and Wynne, 1985; van den Hoek et al., 1993). Cyanobacteria (“cyanobionts”) are of