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Abstract: Ancient microbial activity in volcanic glass creates micron-sized cavities that can be regarded as trace fossils. These are common in glassy rims of oceanic pillow lavas and volcanic breccias. Morphologically comparable mineralized traces are also found in (meta)-volcanic glasses from ophiolites and Precambrian greenstone belts. Multiple lines of evidence indicate microbial formation of these borings, although the affinity of the trace maker(s) is poorly constrained. Two broad morphological types have been previously recognized and termed 'granular' and 'tubular' bioalteration textures. Here optical microscopy and SEM observations are used to erect two new ichnogenera: *Granulohyalichnus* igen. nov. and *Tubulohyalichnus* igen. nov. Five ichnospecies are also defined: *Granulohyalichnus vulgaris* isp. nov., a granular species; *Tubulohyalichnus simplus* isp. nov., an unornamented tubular species; *Tubulohyalichnus annularis* isp. nov., an annulated tubular species; *Tubulohyalichnus spiralis* isp. nov., a helicoidal tubular species; *Tubulohyalichnus stipes* isp. nov., a branched tubular species. This systematic taxonomy is advanced to allow reliable comparisons to be made between new and existing reports of these microbial borings. Moreover, the adoption of a taxonomic framework will aid the development of these ichnofossils as palaeoenvironmental indicators and tracers of microbial evolution.

A trace fossil is defined as 'a morphologically recurrent structure resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate' (Bertling *et al.* 2006). This definition encompasses both macroscopic and microscopic traces that are found in substrates such as rock, unlithified sediment, shell, bones and wood. Familiar examples include burrows, tracks and trails in soft sediments, and, our focus here, borings in marine substrates (Bromley 2004). Less well-known than microborings in marine carbonate substrates are borings found in the volcanic glass of pillow lava rims and volcanic breccias. These micro-textures have now been recognized for over 20 years (Ross & Fisher 1986), during which time multiple lines of evidence have come together to support their biogenicity, and these are briefly reviewed below (see also Staudigel *et al.* 2006; Furnes *et al.* 2008). We formally propose herein that these textures should be considered as trace fossils. Microborings are widespread in marine pillow lavas and have been described from all of the major oceanic basins back to the oldest (*c.* 170 Ma) *in situ* oceanic crust (e.g. Fisk *et al.* 1998). Comparable mineralized micro-textures have also been reported from ancient fragments of oceanic crust preserved in Phanerozoic ophiolites and Precambrian greenstone belts, to as early perhaps as the Early Archaean (Furnes *et al.* 2004; Banerjee *et al.* 2006, 2007; Furnes *et al.* 2007). The idea that these micro-textures are trace fossils has been implicit in many earlier reports and explicit in some recent studies that used the term ichnofossil (e.g. Walton 2005; Banerjee *et al.* 2007; Cockell & Herrera 2008; Staudigel *et al.* 2008); however, to date only a preliminary ichnological description using open nomenclature has been attempted (McLoughlin *et al.* 2008).

Here the first systematic description of microbial ichnofossils from volcanic glass is presented, and the novel ichnogenera

Granulohyalichnus igen. nov. and *Tubulohyalichnus* igen. nov. are defined. Their occurrence in volcanic glass substrates is the principal criterion or ichnotaxobase that underpins the establishment of these novel ichnogenera, and to emphasize this *hyalo* from the Greek *hyaleos* for glassy is incorporated into their name. These new ichnotaxa show some morphological similarities to trace fossils previously described from carbonate substrates and further details are given below. We argue that they deserve to be treated as separate ichnotaxa however, because their occurrence in volcanic glass requires markedly different bioerosion mechanisms and opens up a novel, globally extensive ichnofossil habitat. (A parallel situation exists for borings in lithic and woody substrates that exhibit similar morphologies but form two exclusive ichnofossil groups with separate ichnotaxonomies; Bertling *et al.* 2006.) In this study we focus on examples obtained from the *in situ* oceanic crust and Phanerozoic ophiolites that are relatively well preserved and exhibit intricate morphological details that allow the establishment of five new ichnotaxa.

The principal motivation for erecting these trace fossils and providing distinguishing features for the different taxa is to allow reliable comparisons to be made between new and existing reports from *in situ* oceanic crust, ophiolites and greenstone belts. The second reason is that trace fossils can be used as palaeoenvironmental indicators, and systematic taxonomy will aid the development of trace fossils in volcanic glass as indicators of, for instance, palaeo-redox conditions, fluid flow and microbial evolution (e.g. Furnes & Staudigel 1999). Third, trace fossils often provide information concerning the behaviour of the constructing organism, and we here draw attention to some of the key morphological and textural relationships observed in volcanic glass that may encode behavioural information (see also

Walton 2008). Hence, the overall aim of this paper is to provide an ichnological framework that will facilitate the future study of microbial trace fossils in volcanic glass. In comparison with the study of trace fossils in sedimentary and biological substrates this is a fledgling branch of ichnology. Below we briefly review what is currently known about the micro-organisms thought to be responsible, the distribution of these trace fossils in the oceanic crust and their fossil record (see Furnes *et al.* 2008, for a detailed review). Table 1 of Staudigel *et al.* (2008) gives the most up-to-date summary of (meta)-volcanic glass sample sites investigated for ichnofossils by the authors of this paper.

Review of work to date

Microbial bioerosion of volcanic glass was first recognized by Ross & Fisher (1986), who reported grooves on the surface of glass shards from a Miocene tephra that they likened to fungal borings found in carbonate grains. Some years later, the investigation of sub-glacial volcanic breccias from Iceland led Thorseth *et al.* (1992) to propose a mechanism for the microbial dissolution of volcanic glass leading to the creation of etch pits. Since that early work, it has been argued in global surveys of volcanic glass from the oceanic crust that microbial bioerosion is a widespread phenomenon that produces conspicuous granular and tubular cavities (e.g. Fisk *et al.* 1998; Furnes *et al.* 2001*c*). Moreover, these microbial bioerosion traces or ichnofossils can be distinguished from abiotic processes of glass alteration that produce a smooth interface between the fresh glass and altered products (e.g. Furnes *et al.* 2007, fig. 13). This altered material is termed palagonite and is a fine-grained and often banded mixture of clays, iron-oxyhydroxides and zeolites (Stroncik & Schmincke 2001). In contrast, the granular and tubular textures produced by microbial alteration form a much more irregular and ramified interface between the fresh glass and alteration products. The complex morphology of the tubular textures, in particular their often curved, twisted and sometimes branched paths, which are described in detail below, led to their investigation as biogenic structures.

Trace fossils in volcanic glass substrates have been documented in the rims of pillow lavas and hyaloclastites from submarine environments (e.g. Furnes *et al.* 2001*c*), with the majority of known examples occurring in basaltic glasses. Subterranean microbial activity in continental flood basalts has also been reported (e.g. Stevens & McKinley 1995) but no trace fossils have been described from these environments. There are four main lines of evidence that support a biological origin for tubular and granular microborings found in pillow lavas. (1) The application of biological stains has shown that DNA is concentrated at the interface between fresh and altered glass, especially on the margins of granular and tubular structures (e.g. Giovannoni *et al.* 1996; Torsvik *et al.* 1998, fig. 2; Banerjee & Muehlenbachs 2003, fig. 14; Walton & Schiffman 2003, fig. 8.). (2) Thin linings less than 1 μm wide of carbon, nitrogen and phosphorus have been detected by electron probe mapping of modern and ancient bioalteration textures (e.g. Giovannoni *et al.* 1996; Torsvik *et al.* 1998; Furnes & Muehlenbachs 2003). These linings are independent of the distribution of calcium, thereby confirming that the carbon occurs in an organic phase that is interpreted to be decayed cellular material (e.g. Torsvik *et al.* 1998; Banerjee & Muehlenbachs 2003). (3) Carbon isotope values measured upon volcanic glasses from pillow lava rims that contain candidate ichnofossils show a marked shift relative to the pillow cores that lack ichnofossils, and this shift is consistent with biological activity (further explanation has been given by

Furnes *et al.* 2001*b*). (4) Partially fossilized, mineral encrusted microbial cells have been observed in or near etch pits on altered glass surfaces and, crucially, these pits show forms and sizes that resemble the microbes, suggesting that they are responsible for pit formation (e.g. Thorseth *et al.* 1992, 2001, 2003). Taken together, this morphological and chemical mapping, combined with the carbon isotopic shifts in the host glass, strongly points towards a microbial origin for these ichnofossils.

A consortium of endolithic (i.e. rock dwelling) micro-organisms including heterotrophs and chemolithoautotrophs is involved in the bioalteration of volcanic glass. Culture-independent molecular profiling studies have found that basaltic glass is colonized by micro-organisms that are distinct from those found in both seawater and sea-floor sediments (Mason *et al.* 2007, and references therein). For example, one study found that indigenous microbial sequences obtained from the Arctic sea floor were affiliated to eight main phylogenetic groups of bacteria and a single marine Crenarchaeota group (Lysnes *et al.* 2004). In contrast, another study found a predominance of archeal over bacterial nucleic acid sequences in submarine oceanic island hyaloclastites from Hawaii (Fisk *et al.* 2003). It is envisaged that these micro-organisms include heterotrophs, which use organic carbon from circulating seawater as a carbon source (Staudigel *et al.* 2008). The microbial consortia also likely include chemolithoautotrophs that use oxidized compounds such as Fe^{3+}, Mn^{4+}, SO_4^{2-} and CO_2 in the glass and/or circulating seawater as electron acceptors coupled to electron donors such as reduced Fe and Mn in the glass (e.g. Bach & Edwards 2003; Templeton *et al.* 2005). The suggestion that iron oxidation is employed by microbes that bioerode volcanic glass is consistent with the resemblance of bacterial moulds found on glass to the branched and twisted filaments of iron-oxidizing bacteria such as *Gallionella* and *Mariprofundus ferrooxydans* (e.g. Thorseth *et al.* 2001; Emerson *et al.* 2007). Volcanic glass substrates may also provide a source of key nutrients, especially phosphorus, which is otherwise scarce in oligotrophic sub-sea-floor environments, and it has been confirmed experimentally that micro-organisms preferentially colonize both phosphorus- and iron-bearing silicate glass (Roberts-Rogers & Bennett 2004). In the oceanic crust prokaryotic micro-organisms occur as a dispersed biomass and apparently have long generation times that may explain why it has not yet been possible to cultivate any of these micro-organisms in the laboratory (Einen *et al.* 2006). There are even reports of eukaryotes from within the oceanic crust, with putative marine fungi described from carbonate-filled vesicles in Eocene sea-floor basalts (Schumann *et al.* 2004). These findings may be significant, because fungi produce hyphae that are known to produce tubular cavities in silicate minerals (see Smits 2006).

Controlled laboratory experiments in which seawater microbial populations are cultivated on volcanic glass have produced etch pits and alteration rinds on glass fragments (e.g. Thorseth *et al.* 1995*a*). Moreover, it has been shown that micro-organisms enhance the production of authigenic mineral phases relative to purely abiotic experiments and, in particular, cause marked Sr exchange between seawater and volcanic glass (Staudigel *et al.* 1998). These types of laboratory experiments have failed to produce extended micro-tubular cavities, however, and it has been speculated that this again may be due to the long microbial generation times involved. None the less, it has been demonstrated that micro-organisms contribute to enhanced, localized dissolution of volcanic glass, and thus a conceptual model of how they create granular and tubular bioerosion traces has been advanced and refined in a series of papers (e.g. Thorseth *et al.* 1992, 1995*a*; Staudigel *et al.* 1995, 1998, 2008; Furnes *et al.*

2008). This process begins when circulating fluids introduce micro-organisms into pore spaces in the rock such as fractures or vesicles and along the rims of glass fragments. These microbes progressively etch the fresh glass, creating the trace fossil cavities, which radiate away from the surface of initiation and form a ramified interface comprising tubes and coalesced granular cavities, thereby increasing the surface area of fresh glass available for dissolution (Staudigel *et al*. 2004). Dissolution may also be accompanied by precipitation of fine-grained authigenic minerals such as clays, iron-oxyhydroxides and zeolites within the ichnofossils and fractures. These may entomb decayed organic remains, creating the localized enrichment in carbon, nitrogen and phosphorus along the margins of the bioalteration textures. The exact biochemical mechanisms of dissolution of the glass by micro-organisms are only partially understood and might conceivably include the secretion of organic acids, or the production of siderophores and complexing agents (Staudigel *et al*. 2008).

Systematic ichnology and methods

In this paper we erect two novel ichnogenera *Granulohyalichnus* igen. nov. and *Tubulohyalichnus* igen. nov., which correspond to the previously recognized granular and tubular bioalteration textures found in volcanic glass. We provide below a systematic description of the morphological features that characterize both ichnogenera. We then further subdivide these into five ichnospecies on the basis of morphological variations in their form: *Granulohyalichnus vulgaris* isp. nov., a granular form; *Tubulohyalichnus simplus* isp. nov., an unornamented tubular form; *Tubulohyalichnus annularis* isp. nov., an annulated tubular form; *Tubulohyalichnus spiralis* isp. nov., a helicoidal tubular form; *Tubulohyalichnus stipes* isp. nov., a branched tubular form. All of these ichnotaxa are summarized in the line drawing Figure 1, and optical and scanning electron microscopy images are shown in Figures 2–6. The helicoidal and branched morphologies, in particular, have not previously been illustrated in such detail and these images provide new constraints, discussed below, on the microbial origins of these structures. A previous study by Fisk *et al*. (1998) stated that 'putative microbial weathering, produces at least eight styles of pits, channels tunnels and voids'. A survey of the material available to us and examination of previous illustrations (detailed synonym lists are given below) provided us with ichnotaxobases for proposing five ichnospecies at present. We hope and intend that this ichnotaxonomy will be adopted by future studies of microboring in volcanic glass and will be extended and refined to include new morphologies that may come to light.

The trace makers responsible for each of these ichnotaxa have not yet been positively identified, and we suspect that homomorphic production of these traces (i.e. different organisms creating the same traces), especially in case of the more simple granular forms, is highly likely. Conversely, it is also probable that the same micro-organisms may produce different ichnofossil morphologies in volcanic glass with different substrate geochemistries and environmental conditions. It is therefore unlikely that there is a one-to-one relationship between ichnofossil morphology and the constructing micro-organisms.

The optical images shown here were obtained using a Nikon LV100Pol Polarizing microscope at the Centre for Geobiology in Bergen, and the images denoted edf are extended depth of focus images. These are composite images created by stacking an aligned series of images collected in the *z*-direction. This allows 3D structures such as microborings that curve in and out of the
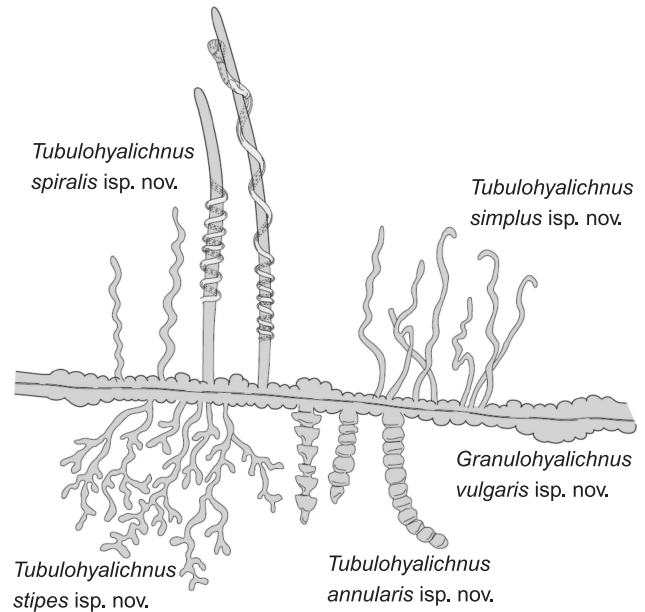

Fig. 1. Line drawing showing the novel ichnotaxa erected in this study radiating from a central fracture. From left to right these are: helical-shaped or coiled *Tubulohyalichnus spiralis* isp. nov.; simple unornamented and unbranched *Tubulohyalichnus simplus* isp. nov.; on the lower side of the fracture, branched *Tubulohyalichnus stipes* isp. nov.; annulated *Tubulohyalichnus annularis* isp. nov.; on both sides of the fracture, *Granulohyalichnus vulgaris* isp. nov. (Note: this is a schematic juxtaposition of the ichnotaxa; all five have not been observed alongside one another in natural samples; approximate relative scales are illustrated.)

plane of the section to be shown entirely in focus at high magnification. The three slides containing type material (collection numbers: TS-3419, TS-3420, TS-3421) are lodged with the Natural History Museum in Bergen, Norway.

Ichnogenus *Granulohyalichnus* igen. nov. McLoughlin & Furnes 2008
Type ichnospecies. Granulohyalichnus vulgaris isp. nov.

Diagnosis. Spherical structures found along fractures, on vesicle walls and around the margins of volcanic glass fragments. Occur as isolated granules, or irregular clusters of granules that can coalesce to form bands of granular textures.

Differential diagnosis. Isolated granules that may coalesce to form larger, irregular clusters and or bands. The granules are equidimensional and can be distinguished from *Tubulohyalichnus* igen. nov., which shows much greater length-to-width ratios. *Granulohyalichnus* igen. nov. is comparable with the ichnotaxon *Planobola* isp. (Schmidt 1992) found in carbonate substrates, which is thought to include the initial microborings of various trace makers, especially cyanobacteria and green algae, as well as the mature traces of unicellular or globular–multicellular cyanobacteria such as *Cyanosaccus piriformis* (Lukas & Golubic 1981). However, *Planobola* isp. traces are significantly larger in diameter than *Granulohyalichnus* igen. nov., typically 10–30 μm, and are sometimes connected to the surface by a single, thick stalk that is not seen in the *Granulohyalichnus* igen. nov.

Etymology. *Granulum* (Latin, a small particle; this follows previous terminology used to describe these structures), *ichnos*
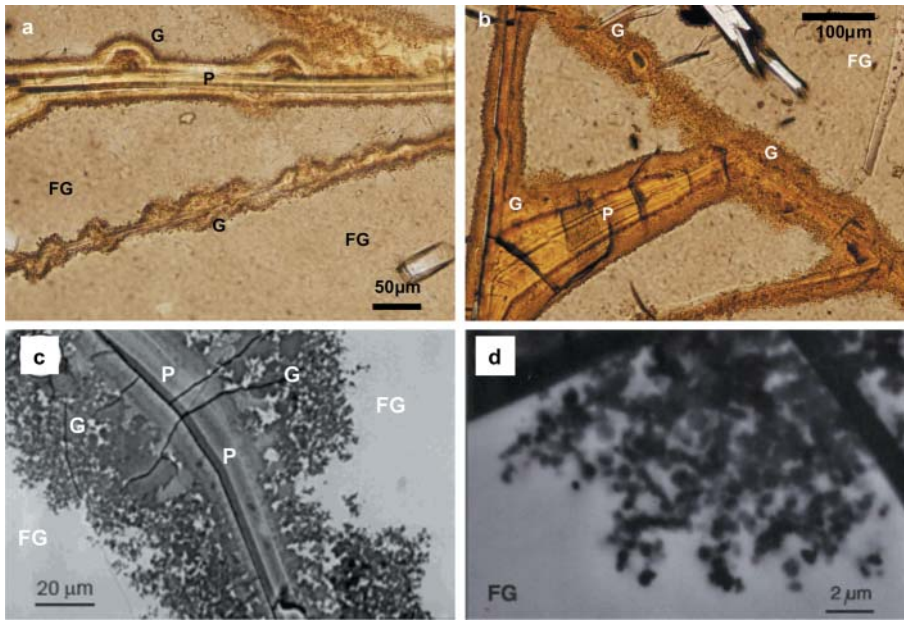
Fig. 2. Images of the *Granulohyalichnus* igen. nov. (G) in fresh glass (FG) with banded palagonite (P). (**a**) Transmitted light image with a fracture in the upper part of the image containing banded palagonite and *Granulohyalichnus vulgaris* isp. nov. on the outer margins; in the lower part of the image is a fracture with less advanced alteration and patchily distributed *Granulohyalichnus vulgaris* isp. nov. (**b**) Transmitted light image of a fracture network, with some fractures containing banded palagonite (P) in the centre and with *Granulohyalichnus vulgaris* isp. nov. on the outer margins with the fresh glass. (**c**) Back-scattered electron image of a fracture containing banded palagonite and *Granulohyalichnus vulgaris* isp. nov. at the interface with the fresh glass. (**d**) Back-scattered electron image showing clusters of *Granulohyalichnus vulgaris* isp. nov. at the junction of two fractures. (**a**) and (**c**) are from ODP–DSDP sample 418A-62-4, 64–70, and (**b**) from ODP–DSDP sample 418, 56-5, 129–132, from the Bermuda Rise; (**d**) from DSDP sample 69-504B, 4-2, 0–20.
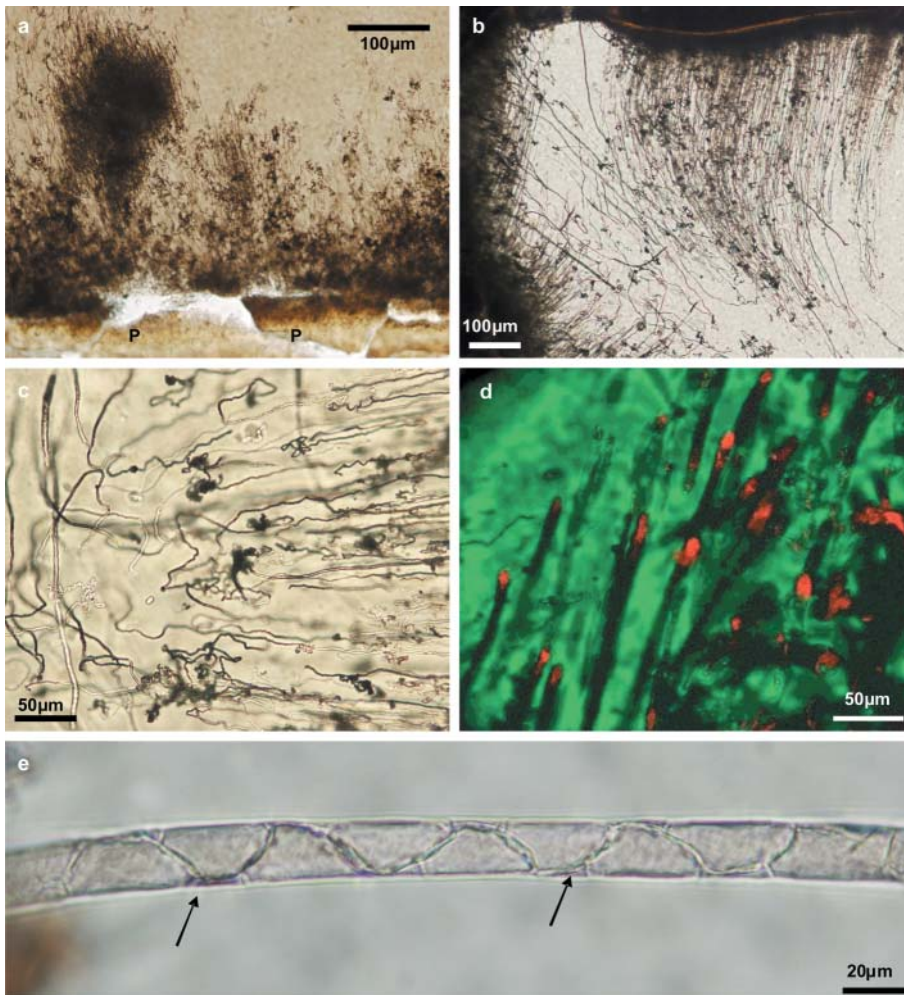

Fig. 3. Images of the *Tubulohyalichnus* igen. nov. (**a**) Transmitted light image showing a palagonite-filled fracture (P) in the lower part of the image with a dense intergrowth of *Tubulohyalichnus simplus* isp. nov. above. (**b**) Transmitted light image of dense clusters of *Tubulohyalichnus simplus* isp. nov. radiating inwards from the margins of a volcanic glass fragment in a felsic tuff. (**c**) Higher magnification image showing the anastamosing paths of *Tubulohyalichnus simplus* isp. nov. It should be noted that some form loose tangles towards their ends (edf image). (**d**) Differential interference contrast image showing *Tubulohyalichnus simplus* isp. nov. overlain by a laser confocal scanning microscopy image showing fluorescence EtBr dye locally bound to cellular material along the margins of the *Tubulohyalichnus simplus* isp. nov. (**e**) *Tubulohyalichnus simplus* isp. nov. with a fine ornament on the tube wall (arrowed); this is discontinuous in some examples, with portions of the tube wall being smooth. (**a**) From ODP–DSPD sample 418A-62-4, 64–70, from the Bermuda Rise; (**b**)–(**d**) from ODP sample 1184A-13R-3-4, from the Ontong–Java Plateau (see also Banerjee & Muehlenbachs 2003); (**e**) from sample CY-1-34 from the Troodos ophiolite.
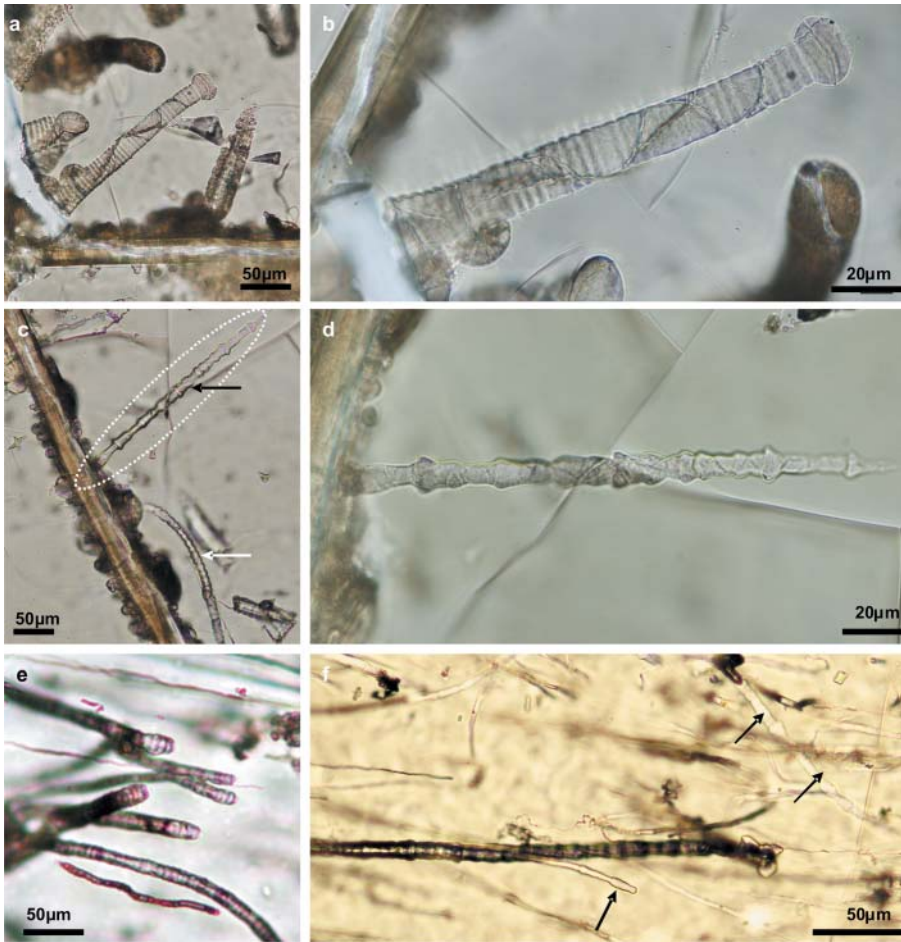
Fig. 4. Transmitted light images of the *Tubulohyalichnus annularis* isp. nov. (**a**) and (**b**) *Tubulohyalichnus annularis* isp. nov. on the edge of a glass fragment, showing uniformly spaced annulations along the length of the tube and a terminal swelling. (**c**) Fracture with *Granulohyalichnus vulgaris* isp. nov. on the margins and two examples of *Tubulohyalichnus annularis* isp. nov. arrowed. (**d**) Enlarged image showing an example of *Tubulohyalichnus annularis* isp. nov. that has unevenly spaced annulations along its length that define changes in diameter of the tube. (**e**) and (**f**) several examples of *Tubulohyalichnus annularis* isp. nov.; some examples are infilled with mineral phases, giving them a dark brown coloration, whereas other examples in (**f**) are hollow (arrowed). (**a**–**c**) from sample CY-1-30 from the Troodos ophiolite; (**e**) and (**f**) are from the ODP Ontong–Java Plateau sample 1184A-13R-3-4.

(Greek, trace) and *hyaleos* (Greek, glass), referring to the sole substrate bearing this ichnogenus and species.

Ichnospecies. Granulohyalichnus vulgaris isp. nov.
(Fig. 2)
1992 'pit textures', Thorseth *et al.* (1992, pp. 845–849, figs 1 and 2)
1995*b* 'etching marks', Thorseth *et al.* (1995*b*, pp. 146–152, fig. 4)
1996 'micropits ... small to large spherical bodies (types 1, 2, 3 subdivided by size)', Furnes *et al.* (1996, p. 192, figs 1–3)
1998 'spherical structures', Torsvik *et al.* (1998, p. 167, figs 2 and 3)
1999 'spherical alteration', Furnes *et al.* (1999, pp. 229–230, figs 2 and 3)
1999 'isolated and/or ... continuous zones of coalescing spherical patches', Furnes & Staudigel (1999, p. 98, fig. 1)
2000 'spherulitic bodies', Alt & Mata (2000, pp. 303–305, fig. 1)
2001*c* 'granular alteration', Furnes *et al.* (2001*c*, pp. 5–16, figs 3 and 7)
2001 'etch marks', Thorseth *et al.* (2001, pp. 33–35, fig. 1 especially 1e)
2001a 'spherical bodies', Furnes *et al.* (2001*a*, pp. 76–77, fig. 2)
2002a 'granular textures', Furnes *et al.* (2002*a*, pp. 408–411, figs 1, 2 and 6)
2003 'granular alteration ... individual and/or coalesced spherical bodies', Banerjee & Muehlenbachs (2003, pp. 4–5, fig. 4)
2007 'granular alteration', Furnes *et al.* (2007, pp. 159–160, figs 9A and 10)

2008 'granular alteration', Furnes *et al.* (2008, pp. 1–68, fig. 1)
2008 'granular alteration', McLoughlin *et al.* (2008, pp. 392–393, fig. 5)

Diagnosis. Spherical structures found along fractures, on vesicle walls and around the margins of volcanic glass fragments. Occur as isolated granules, or irregular clusters of granules that can coalesce to form bands of granular textures.

Etymology. Granulum (Latin, a small particle), *hyaleos* (Greek, glass), *ichnos* (Greek, trace) and *vulgaris* (Latin, common), chosen because of the abundance of this ichnospecies.

Description. Individual spherical bodies may be partly hollow or filled with very fine-grained phyllosilicates, zeolites and iron-oxyhydroxides and perhaps also titanite ($CaTiSiO_4$). The diameter of the granules, regardless of age, location and depth in the oceanic crust, varies from around 0.1 μm to rare examples that are 1.5 μm across, with the most common size around half a micron (data presented by Furnes *et al.* 2007, fig. 6). In the initial stages of bioerosion the granules occur as isolated spherical bodies along fresh surfaces in the glass; as the bioalteration proceeds they become more numerous and coalesce into aggregates, and then continuous bands of granular material.

Type material, locality and horizon. Sample 418A-62-4, 64–70 from Ocean Drilling Program–Deep Sea Drilling Project (ODP–DSDP) hole 418A on the Bermuda Rise in the Atlantic Ocean (25°02.10′N, 68°03.44′W). The oceanic crust has an age of 110 Ma at this location and the sample was collected 366.1 m into the volcanic basement (Furnes *et al.* 2001*c*). This sample

Fig. 5. Transmitted light images of the *Tubulohyalichnus spiralis* isp. nov.; all images are from the Troodos ophiolite. (**a**) *Tubulohyalichnus spiralis* isp. nov. showing a central tube with an outer helix; eight whorls are visible. (**b**) *Tubulohyalichnus spiralis* isp. nov. central tube with an outer helix, occurring alongside simple unbranched *Tubulohyalichnus simplus* isp. nov. (partly out of focus). (**c**) Low-magnification image showing two examples of *Tubulohyalichnus spiralis* isp. nov. enlarged in (**d**) and (**e**); these occur in a glass matrix that contains a fine angular fracture network and pyroxene microphenocrysts. (**d**) *Tubulohyalichnus spiralis* isp. nov., showing an outer helix with very uneven spacing of the whorls (edf image). (**e**) *Tubulohyalichnus spiralis* isp. nov.; the change in spacing of the outer whorls and the terminal swelling at the end of the outer helix (arrowed) should be noted. (**f**) Single-stranded helical *Tubulohyalichnus spiralis* isp. nov. Samples CY-1-34 (**a**, **b**) and CY-1-34 (**c**–**f**) from the Troodos ophiolite.

also contains the type example of *Tubulohyalichnus simplus* isp. nov. Bergen Natural History Museum collection number TS-3419.

Distribution. *Granulohyalichnus vulgaris* isp. nov. has been reported from numerous *in situ* oceanic crust sites worldwide. These include the Atlantic Ocean ODP–DSDP holes 648B, 409, 411, 559, 561, 410A, 396B, 407, 417D and 418A; and the Pacific holes 504B, 896A, 834B and 1184A. A map of these has been given by Furnes *et al.* (2008, fig. 4) and lithological logs for each site have been given by Furnes *et al.* (2008, fig. 5). Examples described from ophiolites include the 92 Ma Troodos ophiolite from Cyprus (Furnes *et al.* 2001*a*) and the 160 Ma Mirdita ophiolite from Albania (Furnes *et al.* 2007). The only putative examples documented to date from meta-volcanic glass in Precambrian greenstone belts come from the Barberton Greenstone Belt of South Africa (Banerjee *et al.* 2006).

Remarks. *Granulohyalichnus vulgaris* isp. nov. is by far the most abundant ichnofossil found in recent volcanic glass. Their relatively small size, however, means that they are highly susceptible to recrystallization of volcanic glass during metamorphism, and as a consequence their geological record is less extensive

than that of *Tubulohyalichnus* igen. nov. As a note of caution, the relative simple morphology of *Granulohyalichnus vulgaris* isp. nov. demands that putative examples must be carefully distinguished from abiotic, chemical etch pits that may form in the absence of microbes. For example, geochemical support for microbial involvement, such as enrichments in carbon and nitrogen associated with *Granulohyalichnus vulgaris* isp. nov. and the attachment of biological stains in sub-recent material, must be sought.

Ichnogenus *Tubulohyalichnus* igen. nov. McLoughlin & Furnes 2008

Type ichnospecies. Tubulohyalichnus simplus isp. nov.

Diagnosis. Tubular structures that radiate away from fractures, vesicle walls and inwards from the margins of volcanic glass fragments. Tubes range in diameter between *c*. 0.4 μm and *c*. 6 μm with an average diameter of 1.4 μm and the mineralized tubes being higher in this range (data presented by Furnes *et al.* 2007, fig. 6). Their lengths are highly variable, from a few microns to several hundred microns, with only limited variation in diameters along their lengths. Tubes may be straight, curved, branched or helical, and may exhibit annulations along their
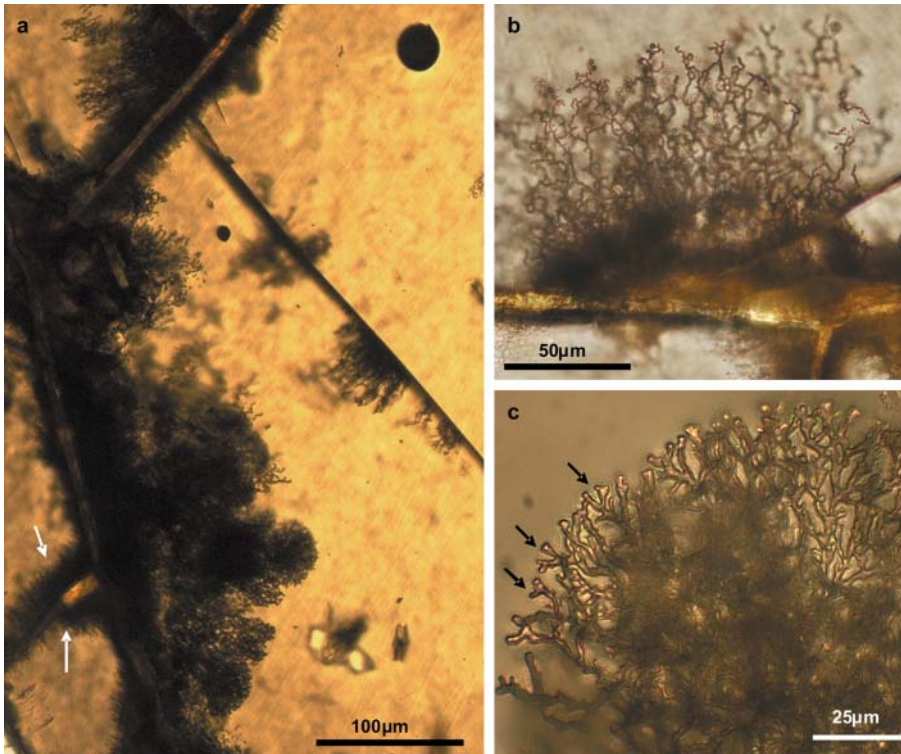
Fig. 6. Images of the *Tubulohyalichnus stipes* isp. nov. (**a**) Linear fracture network in volcanic glass with dark brown–black microbial alteration consisting of intergrown branched *Tubulohyalichnus stipes* isp. nov. on the right and unbranched *Tubulohyalichnus simplus* isp. nov. (arrowed). (**b**) Dendritic cluster of *Tubulohyalichnus stipes* isp. nov. on the margin of a fine fracture filled with palagonite (yellow). (**c**) Cluster of *Tubulohyalichnus stipes* isp. nov. showing bifurcating branches, which are most clearly seen on the outer margins (arrowed) (edf image). Sample 396B-20R-3, 108–112 from ODP hole 396B in the Mid-Atlantic.

walls. They occur as isolated tubes or dense clusters of subparallel tubes that may be hollow, partially or wholly infilled with mineral phase(s).

Differential diagnosis. Extended tubular structures that propagate away from fresh surfaces along fractures, vesicle walls and the rims of volcanic glass fragments. They can be distinguished from *Granulohyalichnus* igen. nov. by their much greater length-to-width ratio. *Tubulohyalichnus* igen. nov. is comparable with the ichnogenus *Fascichnus* ispp. found in carbonate substrates (Radtke & Golubic 2005), which is produced by cyanobacteria, and, in particular, ichnotaxa such as *Fasciculus dactylus*, first described by Radtke (1991). This trace is characterized by a carpet or radiating bundle of tubes up to 150 μm long and 3–8 μm in diameter that show only rare bifurcations (e.g. Wisshak *et al*. 2005, fig. 6A). These tubes are of constant diameter except sometimes for slight thickening seen towards their distal ends. This ichnotaxon is known to be produced homeomorphologically and at least three cyanobacteria species are capable of forming this trace (see Wisshak *et al*. 2005).

Etymology. Tubulus (Latin, a small tube; this follows previous terminology used to describe these structures), *hyaleos* (Greek, glass) and *ichnos* (Greek, trace).

Ichnospecies. Tubulohyalichnus simplus isp. nov.
(Fig. 3)
1996 'micro-channels, vermicular (type 4)', Furnes *et al*. (1996, p. 192, figs 1–3)
1998 'tube-like structures', Torsvik *et al*. (1998, p. 167, figs 2 and 3)
1998 'channels ... septate channels ... bulbous channels ... irregular branching channels', Fisk *et al*. (1998, pp. 978–979, fig. 1)
1999 'irregular tubular features', Furnes & Staudigel (1999, p. 98, fig. 1)

1999 'irregular vermicular bodies', Furnes *et al*. (1999, pp. 2–4, figs 2 and 3)
2000 'irregular or vermicular tubes and channels', Alt & Mata (2000, pp. 303–305, fig. 1)
2001c 'tubular alteration', Furnes *et al*. (2001c, pp. 5–16, figs 4 and 7)
2001a 'tubular bodies', Furnes *et al*. (2001a, pp. 76–77, fig. 2)
2002a 'tubular textures', Furnes *et al*. (2002a, pp. 408–411, figs 3–5, 7 (fig. 3b shows projections termed buds on the sides of the tubes))
2003 'tubes', Fisk *et al*. (2003, pp. 3–4, figs 2 and 4)
2003 'tubules, curving and villiform', Walton & Schiffman (2003, pp. 10–11, figs 4, 7 and 8)
2003 'tubular to vermicular, channel-like features ... straight and curved ... highly convoluted ... bifurcate, numerous branches ... scalloped walls', Banerjee & Muehlenbachs (2003, pp. 4–8, fig. 4)
2004 'tubules and zones of microbial alteration', Storrie-Lombardi & Fisk (2004, p. 3, fig. 1)
2007 'tubular alteration, straight to curved ... budding, branching', Furnes *et al*. (2007, pp. 159–160, figs 2–5, 9b, c and 10b)
2008 'tubular projections', Furnes *et al*. (2008, pp. 1–68, fig. 25g and h)
2008 'tubular alteration', McLoughlin *et al*. (2008, pp. 393–396, figs 6 and 7)
2008 'simple tubes', Walton (2008, pp. 351–364, figs 1–5)

Diagnosis. Simple unbranched, tubular structures that lack ornamentation on their walls and may be hollow or partially infilled with mineral phase(s). Are of near-uniform diameter, except towards their terminations, where they may taper or swell. The majority, however, simply end or pass out of the plane of section, although some show more complex terminal morphologies (Walton 2008, and below).

Differential diagnosis. Unbranched, unornamented tubes with a straight to curvilinear growth axis. These are the simplest morphological form of the genus *Tubulohyalichnus* igen. nov.

Etymology. Simplus (Latin, simple), emphasizing that this is the simple, unornamented species.

Description. The borings are unbranched and occur as isolated tubes or dense clusters and 'fringing' bands of subparallel tubes that propagate away from fractures, vesicle walls and the rims of glass fragments (e.g. Fig. 3). In some examples the tubes show an anastamosing path that can curve back on itself and form loose tangles towards their ends (e.g. Fig. 3b; also Walton 2008, fig. 5A). More typically, however, the tubes show a strong directionality, propagating in a linear to curvilinear path at high angles to the surface from which they originate. Some examples from the Troodos ophiolite show a very fine ornament, often discontinuous on the wall (e.g. Fig. 3c); the origin of this is uncertain but we hypothesize that the desiccation of fluids once present inside the tubes may be responsible. Microtubes described from the Hawaii Scientific Drilling Project exhibit an especially wide range of terminal morphologies including 'finials, nail heads, numerous branches . . . mushroom shapes' (Walton 2008).

Type material, locality and horizon. Sample 418A-62-4, 64–70 from ODP–DSDP hole 418A on the Bermuda Rise in the Atlantic Ocean (25°02.10'N, 68°03.44'W). The oceanic crust is 110 Ma old at this location and the sample was collected 366.1 m into the volcanic basement (Furnes *et al.* 2001c). This sample also contains the type example of *G. vulgaris* isp. nov. Bergen Natural History Museum collection number TS-3419.

Distribution. These are widely reported from *in situ* oceanic crust, including the North to central Atlantic Ocean, the Lau Basin in the SW Pacific and the Costa Rica Rift in the western Pacific (Furnes *et al.* 2008, fig. 4), the Hawaiian seamount chain (e.g. Walton & Schiffman 2003; Walton 2008) and the Ontong–Java Plateau (Banerjee & Muehlenbachs 2003). Examples described from ophiolites include the 92 Ma Troodos ophiolite from Cyprus (Furnes *et al.* 2001a, fig. 6F and G), the 160 Ma Mirdita ophiolite from Albania (Furnes *et al.* 2007, fig. 7B) and the 443 Ma Solund–Stavfjord Ophiolite in Norway (Furnes *et al.* 2002b). Mineralized examples described from greenstone belts include the *c.* 2.5 Ga Wutai Greenstone Belt of China, the *c.* 2.7 Ga Abitibi Greenstone Belt of Canada (Bridge *et al.* 2007), the *c.* 3.5 Ga Barberton Greenstone Belt of South Africa (Furnes *et al.* 2004; Banerjee *et al.* 2006, 2007) and the *c.* 3.5 Ga Pilbara Craton of Western Australia (Banerjee *et al.* 2007; Furnes *et al.* 2007).

Remarks. The simple unbranched tubular forms lacking ornamentation are the most abundant of all the tubular forms. Scanning electron microscopy investigation has found examples containing fine, sub-micron wide filaments that are suggested to be of biological origin (Banerjee & Muehlenbachs 2003, Figs 6–8).

Ichnospecies. Tubulohyalichnus annularis isp. nov.
(Fig. 4)
1998 'septate channels . . . string-of-bead shapes', Fisk *et al.* (1998, pp. 978–979, fig. 1f and g)
2001 'segmented tubes', Furnes *et al.* (2001a, pp. 76–77, fig. 2f)
2002a 'segmented tubes', Furnes *et al.* (2002a, pp. 408–411, fig. 4)
2003 'anastamosing channels with dark walls and segmented appearance', Banerjee & Muehlenbachs (2003, pp. 4–8, fig. 4e)
2008 'annulated tubular', McLoughlin *et al.* (2008, pp. 393–396, fig. 6B)

Diagnosis. Tubes with regularly or irregularly spaced annulations or constrictions along their length that confer a septate appearance.

Differential diagnosis. Only species that exhibits annulations.

Etymology. Annulatus (Latin, ringed) referring to the diagnostic morphological annulations.

Description. Most commonly, tubes are of near-uniform diameter with regularly spaced annulations (e.g. Fig. 4a and b). Less common are examples with irregularly spaced annulations and variations in tube diameter, especially towards their ends (e.g. Fig. 4c and d). These can be compared with the 'string-of-beads' form previously described by Fisk *et al.* (1998), which shows irregularly spaced bulbous swellings along the length of the tubes. *T. annularis* isp. nov. has a larger diameter than *T. simplus* isp. nov., being up to 15 μm across.

Type material, locality and horizon. Sample CY-1-30 from drill core CY-1 in the Akaki River section (35°02'54"N, 33°10'46"E) through the Troodos ophiolite, Cyprus (location map and lithological log of the drill core and sample heights have been given by Furnes *et al.* 2001a, fig. 1). This partially altered volcanic glass fragment, with an age of *c.* 92 Ma, is of zeolite to prehnite–pumpellyite grade and also contains the type example of *T. spiralis* isp. nov. Bergen Natural History Museum collection number TS-3420.

Distribution. From the *in situ* oceanic crust, *Tubulohyalichnus annularis* isp. nov. is reported from the Ontong–Java Plateau (Banerjee & Muehlenbachs 2003) and in pillow lavas from the Indian Ocean (Fisk *et al.* 1998). The only examples described to date (four samples) from an ophiolite come from the Troodos ophiolite of Cyprus (Furnes *et al.* 2001a).

Remarks. The annulations are an intrinsic feature of the tube, as their orientation and spacing are independent of glass substrate; that is, they do not change when the tubes curve, as would be predicted if this reflected some structural control or imprint from the host glass. It has been suggested that the annulations are a result of stepwise or pulsed dissolution by the euendolithic micro-organisms that created the tube (Staudigel *et al.* 2008). Such features are well known from ichnotaxa in calcareous substrates; for instance, *Podichnus centrifugalis* as reported by Bromley (2005, fig. 6).

Ichnospecies. Tubulohyalichnus spiralis isp. nov.
(Fig. 5)
1998 'helical channels', Fisk *et al.* (1998, p. 979, no illustration)
2001 'spiral structures', Furnes *et al.* (2001a, pp. 76–77, fig. 2c)
2002a 'spiral tubes', Furnes *et al.* (2002a, pp. 408–411, fig. 2b)
2008 'tubular', McLoughlin *et al.* (2008, pp. 393–396, fig. 6f and g)

Diagnosis. Unbranched tubes with a coiled or helical axis (Fig. 5), with up to 12 whorls (i.e. complete rotations), but they normally show fewer than this and may be either sinistrally or dextrally coiled. *Tubulohyalichnus spiralis* isp. nov. may show a linear or curved growth axis with the spacing and diameter of the whorls changing along its length.

Differential diagnosis. The only tubular ichnotaxa in volcanic glass that has a helical axis.

Etymology. Spiralis (Latin, a coil) referring to the diagnostic helical form.

Description. These are coiled or helical-shaped tubes that penetrate into the glass away from the margins of glass

fragments, analogous to the cavity made by a corkscrew driven into the cork of a wine bottle. The tubular helix may change along its length, most typically with the diameter decreasing towards the termination of the tube and the whorls becoming more closely spaced. Occasionally, *T. spiralis* isp. nov. is seen to wrap around a single-stranded tube of *T. simplus* isp. nov. (e.g. Fig. 5a–e).

Type material, locality and horizon. Sample CY-1-30 from drill core CY-1 in the Akaki River section (35°02'54"N, 33°10'46"E) of the Troodos ophiolite of Cyprus (location map and lithological log of the drill core and sample heights have been given by Furnes *et al*. (2001*a*, fig. 1). This partially altered volcanic glass fragment, with an age of *c*. 92 Ma, is of zeolite to prenhite–pumpellyite grade and also contains the type example of *T. annularis* isp. nov. Bergen Natural History Museum collection number TS-3420.

Distribution. All examples known to date (four samples) come from the Troodos ophiolite of Cyprus (Furnes *et al*. 2001*a*).

Remarks. This sophisticated helical morphology strongly supports a biogenic origin for these structures. The functional significance of the helical shape is uncertain but might reflect a growth and/or feeding strategy developed by a hypha-like process within the tube. The documentation of *Tubulohyalichnus spiralis* isp. nov. wrapping around a simple *Tubulohyalichnus simplus* isp. nov. is also suggestive of biological behaviour.

Ichnospecies. Tubulohyalichnus stipes isp. nov.
(Fig. 6)
1998 'radiating, irregular branching channels', Fisk *et al*. (1998, pp. 978–979, fig. 1e)
2002*a* 'curved tubes sometimes branching', Furnes *et al*. (2002*a*, pp. 410–411, fig. 3b)
2008 'branched tubes', McLoughlin *et al*. (2008, pp. 393–396, fig. 6d and e)
2008 'fine branching channels', Cockell & Herrera (2008, p. 105, fig. 1 (M. Fisk, unpublished material from the Mid-Atlantic Ridge; the tubes and branching are more widely separated in comparison with the example shown here)
2008 'branching microtubules', Walton (2008, pp. 351–364, fig. 3a and c)

Diagnosis. Dichotomously branching tubes in which the diameters of the daughter branches are equal to those of the parent branches.

Differential diagnosis. The only tubular ichnotaxa in volcanic glass that exhibits branching.

Etymology. *Stipe* (Latin, branch), referring to the diagnostic branching of this ichnospecies.

Description. Dense intergrowths of branching tubes that may occur in hemispherical-shaped clusters or more irregular bands that radiate away from fractures in the glass, vesicle walls and the rims of glass fragments. The tubes are of similar diameter to *T. simplus* isp. nov., being typically less than 3 μm across.

Type material, locality and horizon. Sample 396B-20R-3, 108–112 from ODP hole 396B located 150 km east of the Mid-Atlantic Ridge (22°59.14' N, 43°30.90'W). The oceanic crust has an age of 10 Ma at this location and the sample was collected 140.1 m into the volcanic basement (Furnes *et al*. 2001*c*). Bergen Natural History Museum collection number TS-3421.

Distribution. Only a small number of *Tubulohyalichnus stipes* isp. nov. have been described to date compared with the abundance and widespread distribution of *Tubulohyalichnus simplus* isp. nov. The sample locations include a Pacific seamount (sample CD-1-6, Fisk *et al*. 1998), DSDP site 504B on the Costa Rica Rift (Furnes *et al*. 2002*a*), ODP site 396B in the mid-Atlantic (McLoughlin *et al*. 2008) and the Mid-Atlantic (M. Fisk, unpubl. data, illustrated by Cockell & Herrera (2008)).

Remarks. Short projections on the margins of tubular textures have previously been illustrated and termed buds (e.g. Furnes *et al*. 2002*a*, fig. 3b). It is suggested that these may represent incipient branching. We suspect that as new material comes to light additional branching morphologies may be found in microborings within volcanic glass.

Discussion

This paper systematically describes the range of morphological features known to date from microbial ichnofossils in volcanic glass and uses these to erect the ichnotaxa illustrated in Figure 1. This has highlighted key morphological attributes that further strengthen the case for a biogenic origin of these micro-textures and that also encode behavioural information. First, the complex helicoidal morphology of *Tubulohyalichnus spiralis* isp. nov. is very suggestive of a biological origin, especially examples in which the spacing and diameter of the helix changes along the length of the tube. These features cannot be explained by the migration of mineral inclusions through the glass under elevated fluid pressures, a phenomenon known as ambient inclusion trails that has previously been highlighted by some workers as capable of generating hollow tubular structures in chert substrates (Barghoorn & Tyler 1965; Brasier *et al*. 2006). Rather, we tentatively compare *Tubulohyalichnus spiralis* isp. nov. to helical fungal hyphae, like those exhibited by some laboratory cultures of dermatophytes (e.g. *Trichophyton mentagrophytes* var. *Mentagrophytes*; Ellis & Hermanis 2006). This is a tentative comparison, as morphological similarities alone cannot be used to demonstrate a fungal origin. Second, a putative biological growth relationship is recorded by the intertwining of *Tubulohyalichnus spiralis* isp. nov. and *Tubulohyalichnus simplus* isp. nov. in which the spiralled tube wraps around a central linear tube and is comparable in shape and size with the coiling of parasitic fungal hyphae around the hyphae of a host fungus (e.g. Nordbring-Hertz 2004, fig. 8). Third, it is conspicuous that the tubular borings do not intersect; rather, subparallel *Tubulohyalichnus simplus* isp. nov. are sometimes seen to abruptly change growth direction by up to 180° when they meet another tube or fracture (as previously recognized by Furnes *et al*. 2007, fig. 4C; Walton 2008, fig. 5A). This is argued to reflect adjacent micro-organisms sharing the substrate (i.e. 'not invading one another's patch'), whereas abiotic tubular structures might be expected to intersect. This sharing of the substrate may also explain why in areas with a high density of microborings the tubes are subparallel to avoid intersecting, whereas in areas of lower density microboring the tubes show more anastamosing paths. Lastly, it has been argued that microborings show evidence of mining behaviour in volcanic glass, with their sometimes anastamosing paths being designed to systematically exploit the substrate and extract useful material (Walton 2008). Moreover, tubular microborings sometimes appear to seek olivine phenocrysts, which are a rich source of iron in the glass, and to avoid plagioclase (Walton 2008). Microborings in volcanic glass are thus more than dwelling traces and represent feeding traces, created by microbes harvesting chemical energy in the glass. This is a strong argument for establishing microborings in volcanic glass as a separate taxonomic group

from borings in marine carbonates that may show some morphological similarities but are largely dwelling traces.

There have only been a small number of systematic studies to date that have investigated the controls on the distribution of ichnofossils in volcanic glass. Preliminary studies have been undertaken to estimate the per cent abundance of microbial ichnofossils in volcanic glass with depth, temperature, permeability and porosity in the oceanic crust (e.g. Furnes *et al*. 2001*c*, and references therein). These studies have found that *Granulohyalichnus* igen. nov. is by far the most abundant trace fossil and can be found at all depths into the oceanic crust where fresh glass is preserved down to *c*. 550 m. In the upper *c*. 350 m of the oceanic crust *Granulohyalichnus* igen. nov. is the most abundant trace fossil, decreasing steadily to become scarce at temperatures of *c*. 115 °C near the currently known upper limits of hyperthermophilic life. In contrast, the ichnogenera *Tubulohyalichnus* igen. nov. constitute only a minor fraction of the total microbial alteration, at most *c*. 20%, and show an abundance maxima at *c*. 120–130 m depth. In the whole oceanic volcanic pile, the total percentage of microbial alteration increases with permeability and also with the presence of celadonite, which is suggestive of oxygenated waters (e.g. Furnes & Staudigel 1999; Furnes *et al*. 2001*c*). With respect to the timing of microboring in the oceanic crust it is noteworthy that both the 5.9 Ma Costa Rica Rift and the 110 Ma western Atlantic oceanic sections show a similar maxima in the amount of microbial alteration as a percentage of the total alteration, despite their very different ages (Furnes *et al*. 2001*c*, fig. 11). This suggests that a substantial portion of the microboring occurs early in crustal history, but it is thought to persist within the crust as long as hydrothermal fluid circulation continues (Staudigel *et al*. 2008). It should also be borne in mind that taphonomic variables such as changes in fluid flow and authigenic mineral precipitation will modify the preservation potential of the microbial trace fossils in different parts of the oceanic volcanic pile. In summary, the development of an ichnofabric index for volcanic glass substrates, or in other words, a semi-quantitative measure of the textural products of microbial activity in volcanic glass, could help to further elucidate the controls on the distribution of microbial activity in the oceanic crust. This ichnofabric approach is well established for sedimentary substrates (see Droser & Bottjer 1993) and initial attempts have been made to apply and adapt this to volcanic glass substrates (e.g. Montague *et al*. 2007).

Concluding remarks

Microbial borings in volcanic glass are ubiquitous in the modern oceanic crust. They represent a valuable potential archive of information concerning the activities of euendolithic microorganisms in the sub-sea-floor, given that as much as 10–20% of the upper oceanic crust may comprise volcanic glass (Staudigel & Hart 1983). Continuing work suggests that microbial activity is also recognizable in meta-volcanic glasses, with a fossil record that is extensive and may include some of the earliest forms on life on Earth (e.g. Furnes *et al*. 2004; Banerjee *et al*. 2006, 2007). We therefore formally propose herein an ichnofossil taxonomy for these conspicuous features that have previously been loosely termed tubular and granular bioalteration textures. The new ichnogenera *Granulohyalichnus* igen. nov. and *Tubulohyalichnus* igen. nov. are defined and subdivided into the ichnospecies *G. vulgaris* isp. nov., *T. simplus* isp. nov., *T. annularis* isp. nov., *T. spiralis* isp. nov. and *T. stipes* isp. nov. (Figs 1–6). It is hoped that this ichnotaxonomy will aid the comparison of new and existing reports of microbial bioerosion textures in volcanic glass and that this 'common language' will aid communication between geobiologists, palaeontologists and igneous petrologists investigating these features. Lastly, the acceptance of an ichnotaxonomic framework, such as that proposed here, will facilitate future efforts to develop the use of microbial borings in volcanic glass as both palaeoenvironmental indicators and recorders of microbial evolution.

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