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Citation for final published version:

Edwards, Dianne , Axe, Lindsey and Honegger, Rosmarie 2013. Contributions to the diversity in cryptogamic covers in the mid-Palaeozoic: 'Nematothallus' revisited. Botanical Journal of the Linnean Society 173 (4) , pp. 505-534. 10.1111/boj.12119

Publishers page: http://dx.doi.org/10.1111/boj.12119

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Contributions to the diversity in cryptogamic covers in the mid-Palaeozoic: *Nematothallus* Lang revisited

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Running head : Lower Devonian *Nematothallus* and *Cosmochlaina* anatomy

Compression fossils from the Silurian and Devonian of southern Britain, composed of cuticles and tubes, were described by W.H. Lang as genus *Nematothallus* and placed, together with *Prototaxites,* in the Nematophytales, related neither to algae nor tracheophytes. Dispersed cuticles of *Nematothallus* and perforated forms assigned to *Cosmochlaina* were frequently recovered in macerates, their affinities being unresolved. New collections from a Lochkovian locality in the Welsh Borderland permitted the reconstruction of the stratified thalli of these nematophytes; they comprise a superficial cortex (which produced the cuticles) overlying a palisade zone composed of septate, parallel tubes, presumed hyphae, and a basal zone comprising wefts of randomly interwoven hyphae. Excellent three -dimensional preservation allows the erection of a new

species of *Nematothallus, N. williamii*. A similar anatomy is seen in a new group of fossils with either circular incisions in the cortex or complete separation of thickened cortical cells, presumably comprising a developmental sequence. By their stratified organization the nematophytes differ from extant and extinct algae and bryophytes and the enigmatic *Spongiophyton*. A complex anatomy and septate tubes suggest affinity with lichenized fungi. Limited data support a fungal rather than embryophyte chemistry, but a photobiont is missing. Nematophytes, globally wide spread in cryptogamic covers from mid-Ordovician times, added to the biodiversity in early terrestrial ecosystems and enhanced chemical weathering.

ADDITIONAL KEY WORDS: algae - bryophytes - *Cosmochlaina* - embryophytes - fungi - lichens – Lochkovian - *Prototaxites* - weathering – Welsh Borderland.

INTRODUCTION

W.H. Lang's work on the Prídolí (Upper Silurian) and basal Lochkovian (lowermost Devonian) assemblages of southern Britain were seminal not only in demonstrating the vascular status of *Cooksonia*, since considered the iconic archetypal tracheophyte, but also in drawing attention to non-vascular components of pioneering terrestrial ecosystems (Lang, 1937). He created a new class (sic), the Nematophytales, for plants, including *Prototaxites* Dawson,

that he considered neither algae nor higher plants and a new genus, *Nematothallus,* for thalloid, coalified compressions. Similar fossils, but lacking anatomy, had been earlier recorded in the Silurian (e.g. Murchison, 1839; Dixon, 1921) and frequently considered plant debris, but Lang, employing film pulls and transfers, showed that they comprised an outer cuticle with reticulate patterning covering associations of wide, sometimes banded, tubes, and wefts of small tubes. Spores were recorded intermingled with tissues. In such compression fossils the spatial relationships between the layers could not be determined, nor indeed their organic connection, leading to some controversy as to what tissues the name *Nematothallus* should be applied (e.g. Strother, 1988, 1993). Edwards, in a series of investigations using both Lang's techniques and material from bulk maceration, so named the cuticles initially (Edwards, 1982) and divided them into a number of categories based on size and shape of the 'units' comprising the reticulum and on further cuticular characteristics (e.g. Edwards & Rose, 1984) and erected a new genus, *Cosmochlaina*, for perforated and ornamented forms (Edwards, 1986). By contrast Strother (1988, 1993, 2010), after failing to find organic connection between the cuticles and tubes, restricted the use of *Nematothallus* to the latter and erected three species based on thallus outlines in compression fossils and to a lesser extent their filamentous construction (Strother, 1988).

Fragments of cuticle and, less frequently, associations of tubes have been recorded in dispersed spore assemblages recovered from Middle Ordovician (O) to basal Lower Devonian (D) rocks (e.g. Caradocian (O): Gray & Boucot, 1982;

Llandovery (Silurian): Pratt *et al*., 1978; Wenlock (O): Burgess, 1991, Wellman, 1995; Ludlow (S): Hagström, 1997; Emsian-basal Eifelian (D): Filipiak & Zaton, 2010) from geographically widespread localities (e.g. Viet Nam (Lower D.) – Janvier *et al*., 1987; Canada (Upper Silurian) – McGregor & Narbonne, 1978; U.S.A. (Lower S): Johnson, 1985; Libya (O-S**):**--Al-Ameri, 1983, as well as Britain (S-Lower D**).** This is of particular interest because in older rocks they co-occur with spores derived from basal embryophytes. The latter were members of pioneering land plant vegetation and, because these nematophyte cuticles were thought to reduce drought stress as do the cuticles of extant vascular plants, the producers have long been considered remains of a non-embryophytic component of land vegetation (e.g. Banks, 1975; Gray & Boucot, 1982; Gray, 1984; Strother, 2010). However Jonker (1979) postulated that mid-Pragian *Nematothallus pseudovasculosa* thalli were phylloids attached to *Prototaxites* (cauloids), and interpreted the organism as allied to the red algae, a relationship recently revived by Smith and Butterfield (2013) but in this case to a non-calcified coralline form. Affinities with embryophytes and particularly bryophytes have been suggested based on similarities of the cellular patterning on *Nematothallus* cuticles with acetolysis resistant cells in sporangial walls of bryophytes, including the peat-moss (*Sphagnum*) and hepatics (*Conocephalum*, *Lophocolea* (Kroken *et al*., 1996) and *Sphaerocarpos* (Graham & Gray, 2001) and the lower epidermal cells of marchantialean liverwort thalli (Graham *et al*., 2004). By contrast, Steur and Van der Brugghen (1998) illustrated similar surface patterning produced by the plectenchymatous cortex of the lichen, *Leptogium*

tenuissimum. Lichen affinities had also been suggested by Wellman and Gray (2001), a relationship that has some support from geochemical evidence from *Nematothallus* cuticles (Edwards *et al.,* 1996), which led to speculation relating to possible functional similarities with the superficial layers of lichens rather than those of vascular plants (Gray, 1984).

The production of the cuticular reticulate patterning and its relationship to underlying tissues was addressed by Lang (1937), who initially but tentatively concluded that it could have indicated contact points between the wefts of small tubes and the cuticle. In 1945, following sectioning of coalified material, he recorded the presence of a superficial layer of cells. This would explain the occasional records of sheets of cells with similar surface patterning (e.g. Gray & Boucot, 1982). A further hypothesis that the pattern was produced by tubes stacked at right angles to the cuticle (Lang, 1937), as seen in some algae and fungi, has some support from a specimen attributed to *Prototaxites taitii* (Kidston & Lang, 1921, figs 113-114) where such organization is seen in superficial tissues.

Here we report numerous examples of three dimensionally preserved, sometimes charcoalified, material below cuticles of both *Nematothallus* and *Cosmochlaina* from the Lochkovian of the Welsh Borderland, that allow more reasoned speculation on the nature of the original organisms and their affinities.

GEOLOGY, MATERIAL AND TECHNIQUES

The fossiliferous fluvial strata occur in a stream-side exposure of the Ditton Formation on the northern side of Brown Clee Hill, Shropshire (Ball & Dineley, 1961). Spores recovered from the same horizon belong to the middle sub-biozone of the *micrornatus-newportensis* Sporomorph Assemblage Biozone (Richardson & McGregor, 1986; Richardson, unpublished data) and indicate an early Lochkovian (Early Devonian) age. Charcoalified (three-dimensionally preserved) and coalified (compressed) fragments recovered after conventional bulk maceration using HCl and HF, but no centrifugation, were air dried and promising material of nematophytes, readily distinguished from the axes and fertile material described in previous studies (e.g. Edwards, 1996; Edwards *et al*., 2012a, b; Morris *et al*., 2011; Morris *et al*., 2012 a) was picked out, mounted on stubs and coated with gold/palladium followed by scanning electron microscopy (FEI (Philips) XL30 ESEM FEG). After initial SEM examination, selected specimens were turned over and dissected before further SEM studies. Some specimens were removed from the stubs, treated with Schultze's solution for up to five hours, washed, dried and mounted in Aquamount for light microscopy.

All figured specimens are housed at the National Museum

BACKGROUND TO SYSTEMATICS

The acquisition of three dimensionally preserved specimens of *Nematothallus* Lang allows emendation of the genus, but we are reluctant to assign the specimens described here to Lang's *N. pseudo-vasculosa* and *N*. (?) *radiata* nor to those of Strother (1988). Differences in preservation, viz. coalified compressions comprising smooth or differentially thickened tubes with or without 'cuticles' v. three dimensionally preserved coalified and charcoalified material prevent unequivocal synonymies. We agree with Lang and demonstrated by Strother (1988) that the genus encompasses a number of species, the majority of examples too fragmentary to warrant naming. We make no mention of differentially thickened (banded) tubes (included by Lang (1937) in the type species) in the emended diagnosis as we consider these, as well as the variously sized spores, as contaminants. Thus the new species described here, based on a single specimen, lacks banded tubes.

The genus, *Cosmochlaina*, based on dispersed cuticles (Edwards, 1986)**,** is here emended to include internal zones. Edwards used an artificial classification for dispersed cuticles (Roselt & Schneider, 1969) when naming it, but here we recognize a close relationship with *Nematothallus* based on similarities in anatomy and place it in the Nematothallaceae (Strother,1993) as part of Lang's Nematophytales, although we remain uncertain about its affinities, be they with non-lichenized or lichenized fungi. With this in mind we use the term hyphae rather than tubes, although evidence of a septate construction is very limited. We noted certain similarities between Edwards' species of *Cosmochlaina* and some

of the new specimens, but are not sufficiently confident, bearing in mind the differing forms of preservation, to assign the new material to her species.

Initially we were inclined to place the specimens with incised cortices in a new genus, but evidence of examples where surface features intergrade with those of *Nematothallus* prompted reconsideration, and we leave them as a developmental form. A similar argument might be used to unite *Nematothallus* with *Cosmochlaina,* but because there are differences in the emergence of cortical hyphae through the cuticle, we propose to retain the latter genus for the moment. Alternatively, there are some specimens comprising only regularly porate 'cuticles' that might have derived from arthropods.

SYSTEMATICS

Order Nematophytales Lang 1937

Class Nematophytina Strother 1993

Family Nematothallaceae Strother 1993

Genus *Nematothallus* Lang1937

Original diagnosis: Flat leaf-like expansions of no great thickness, composed of a system of i**n**terlacing tubes, often of two distinct orders of size; usually covered by a cuticle with a pseudo-cellular pattern; and producing among the tubes and within the cuticle firm-walled (cuticularised) spores of various sizes

Emended diagnosis: Thalloid organism with stratified dorsiventral organization comprising two systems of hyphae with two distinct orders of size and a cortex of at least one layer of cells. Wider hyphae aligned in parallel at right angles to upper surface with cortex; smaller hyphae, infrequently branched, form randomly orientated wefts in a basal zone.

Notes. Outer wall of cortex may be detached and bear an inner raised reticulum of anticlinal walls and thus be represented in the dispersed spore record as 'cuticles'. Isolated wefts of small hyphae are less confidently assigned. The nature of the wall in the wider tubes is not specified in the emended diagnosis which could thus embrace species with both smooth and differentially thickened walls.

Lectotype: (designated by Strother**,**1993): *N. pseudo-vasculosa.*

Prídolí (Uppermost Silurian), Freshwater East, Pembrokeshire, Wales. Lang 1937, plate12, figs 71, 7-80, 82. Film pull, V54851 (Natural History Museum, London.)

Notes: Strother in his emended diagnosis of the lectotype excluded the covering cuticles, although they were present in similar associations of tubes at the same locality. Narrow tubes are c. 2.5m; wider tubes with thickenings are c. 25µm (Strother, 1988)

Nematothallus williamii Edwards, Axe & Honegger **sp nov**.

Derivation: In honour of William H. Lang

Diagnosis: As for genus. Wider sparsely branched hyphae septate and smooth walled; narrower hyphae occasionally branched. Cortical cells 5-16µm diameter in surface view. Wider hyphae, 11-28µm diameter, narrower hyphae 3-5µm.

Type: Holotype NMW2013.39G.1(now on stub).

Illustrations: Fig. 1A-E.

Locality: Stream section on north side of Brown Clee Hill, near Monkton, Shropshire, England.

Stratigraphy: Ditton Group, lower middle part of *micrornatus-newportensis* Sporomorph Assemblage Biozone, Lochkovian Stage, Lower Devonian.

Notes. Dimensions in diagnosis are based on the holotype.Other species, all from the upper Silurian Bloomsburg Formation, included in the genus by Strother (1988) are compressions with one size of smooth hyphae , species delimitation being based on thallus morphology and hyphal size. They are :

N. elliptica, hyphal diameter 5-13µm

N. lobata, hyphal diameter 2.5-8.5µm

N.taenia, hyphal diameter 6-10µm

Genus *Cosmochlaina* Edwards 1986.

Original diagnosis: Cuticle with inwardly directed flanges, units randomly orientated. Stomata absent. Projections (?trichomes) always present on outer surface, sometimes on inner. Surface of cuticle itself smooth on both surfaces.

Type species: Cosmochlaina verrucosa

Holotype: NMW85.20G.1. Lochkovian. North side of M50 motorway In Herefordshire, near 29.5 marker post just south of Exit 3.

Emended diagnosis: Thalloid organism with stratified organization comprising two systems of hyphae with two distinct orders of size and peripheral cortex at least one layer thick. Wider hyphae aligned in parallel at right angles to upper surface; smaller hyphae infrequently branched form randomly arranged basal wefts. Cortex occasionally porate, partly with apically emergent, ovoid cortical cells and perforated by hyphae.

Notes. Outer wall of cortex may be detached and show an inner raised reticulum of anticlinal walls and perforations or outgrowths. When recovered from rock such fragments are usually called cuticles. In that we are unable to isolate these structures from the new material, we cannot assign these coalified fragments to the cuticle-based species erected by Edwards (1986) with any confidence. We therefore await better preserved specimens that will allow erection of new species or assignation to existing ones.

DESCRIPTIONS

The usually irregularly shaped fragments were divided into three broad groups based on surface characteristics. A well preserved superficial layer covers two further layers, which are preserved to varying extents. Where complete they comprise two systems of hyphae, one below the superficial layer composed of hyphae aligned perpendicular to the surface and thus reminiscent of leaf palisade tissue, and a basal one of usually randomly arranged wefts of smaller hyphae. The covering layer is usually represented by a 'cuticle' with inwardly directed flanges but occasionally appears as a sheet of cells, here termed a cortex. In one group the surface is smooth or hummocky. It lacks perforations and hence belongs to *Nematothallus*. The second group shows some projections and/or perforations and corresponds to *Cosmochlaina*. The third group is new, with the surface showing circular to oval incisions, projections or voids. In stereo light microscopy studies before chemical oxidation, the surface layer of all groups may appear black, either matt or glossy, and the underlying tissue, brown. Such variation, while possibly reflecting differences in chemistry, also indicates differences in preservation related to degrees of charcoalification and coalification.

Nematothallus (Figs 1, 2; NMW2013.39G.1-6)

The most complete, three dimensionally preserved, charcoalified specimen is c. 1.5mm in maximum diameter and c. 400µm thick (Fig. 1A). It comprises three zones, the *Nematothallus*-type cortex, overlying a well preserved zone (here termed palisade zone) of plectenchymatic hyphae, perpendicular to the surface (Fig. 1B) and less well preserved basal wefts of fused small hyphae (Fig. 1D). The upper surface is grossly very irregular, and shows a reticulum of depressions enclosing slightly raised polygonal cells, some of which are centrally depressed (Fig. 1B). Small areas may be flatter. Less well preserved areas are associated with smooth hyphae and banded tubes (Fig.1C). Where the outermost layer of the cortex is detached, a network of fused anticlinal walls is revealed beneath. There is some evidence of burning from crater-shaped elevations on the surface. The flanges typical of isolated *Nematothallus* 'cuticles' are only occasionally seen. Dimensions of the cortical cell outlines fall into the range of those taken from the inside of other specimens (see Table 1). Most of the palisade hyphae are collapsed fragments and thus impossible to measure, but a few have retained their three dimensional shape, are septate (Fig. 1C) and show crater-shaped lateral outgrowths (Fig. 1B) that are interpreted as either the bases of branches or remains of contact sites with photobiont cells or colonies. The hyphae range between 15 and 18µm in diameter and are considerably wider than the cells of the cortex. The nature of the junction between the two zones remains unknown. The basal zone is poorly preserved. Small hyphae, between

3 and 5µm in diameter, are barely distinguishable (Fig. 1D) and are intermingled and possibly continuous with occasional wider branched hyphae (11-15µm) although these, as well as short lengths of unevenly thickened tubes, may be contaminants. The fractured example in Figure 1E shows an ultrastructure very similar to that in the cords of *Nematasketum* (Edwards & Axe, 2012).

No two fragments in this group are identical, although all have typical *Nematothallus* cellular patterning, usually obscured by underlying zones. Exposed areas show the typical arrangement of flanges, previously described for dispersed *Nematotallus* 'cuticles' (Edwards, 1982) but here are interpreted as the outer periclinal and anticlinal walls of a cortex with, in some specimens, an additional further acellular outer covering. Anticlinal walls may be short (Fig. 2A), more extensive (Fig. 2B) or retain vestiges of internal hyphae (Fig. 2C). The outer surface of the cortex is usually hummocky, reflecting the topography of the cortical cells (Fig. 2F), but the latter are clearer where the fused outer periclinal walls have become detached as a film (Fig. 2D, E) or partially removed during charring (Fig. 2I). This outermost layer is sometimes associated with and penetrated by smooth or internally irregularly thickened tubes (Fig. 2F, G).

Figure 1F, G illustrates a unique fragment where a roughly rectangular, slightly depressed area with a smooth surface contains four oval regions delimited by a ridge and enclosing circular to oval structures limited by indentations. The latter are larger than those described in one specimen with incised surface and emergent hyphal protrusions (see below) and far more variable in size.

Vertically fractured thalli reveal the thickness of the cortical outer periclinal walls and extent of anticlinal walls (Fig. 2F), but inner periclinal walls are very rarely seen. Information on the junctions between cortex and palisade zone remains elusive. Almost all specimens show preservation of the palisade zone that ranges from fragments of individual hyphae to a more condensed plectenchymatous zone, demonstrating the orientation of hyphae perpendicular to the surface but rarely intact individual elements (Fig. 2H). Hyphae are usually of variable diameter, twisted and collapsed, and lack convincing evidence of septa in such preservation.

The basal wefts of hyphae may show more distinct outlines (Fig. 2J) with occasional branching. In other specimens this zone may be completely homogenised. Dimensions are given in Table 1. Widths range from 2 to 5.5µm (confidence in measurements is low, but they are definitely much narrower than the palisade hyphae). Banded tubes are frequently found within this zone, interpreted as either symptomless, parasitic, or even mutualistic endobionts of *Nematothallus* thalli, although Lang considered them an integral part of the organism.

Cosmochlaina (Figs 3, 4, 5, 6A-G; NMW2013.39G.7-21)

The fragments in this group are united in possessing a superficial layer that, because there are projections, sometimes accompanied by perforations and an

inwardly directed reticulum of flanges, would on ‘cuticular’ features be placed in the dispersed genus *Cosmochlaina* (Edwards, 1986). Edwards used the suffix, chlaina, rather than cutis, to emphasise differences from vascular plants in cellular patterning. The fragments also possess two further thallus layers, viz. a palisade zone and an innermost layer of predominantly small tubes. As in *Nematothallus,* preservation is variable, but even so there are at least five types based on differences in the cortex and superficial characters.

Cosmochlaina TYPE 1 (Fig. 3A-I; NMW2013.39G.7)

This well preserved specimen is unique in that an intact cortex is present with traces of a further thinner inner layer of cortical cells (Fig. 3D). Paradermal section shows typical ‘*Nematothallus*’ type construction. Below the cortex, an up to 400µm thick palisade zone is preserved containing some discrete elements 3D, E). Least well preserved is the basal tissue of fragmentary, very thin-walled and occasionally branched narrow tubes, and some wider, also fragmented hyphae (Fig. 3I).

The fragment has one possible intact edge with triangular shaped projections (Fig. 3A, B). The upper surface presents a wrinkled appearance, sometimes smooth, but usually with circular to oval indentations (Fig. 3C). The resulting structures very occasionally possess a further indentation forming a rim. Sections through the cortex indicate variation in cell shape (Fig. 3D, F-H) and

thickness (26µm - 30µm), the most notable being inverted flask-shaped cells with basal tapering (Fig. 3F, G). It is tempting to relate these to the discoidal structures on the surface, but we failed to find a section that included both. However the pin-shaped structure (head c. 5.2µm diameter), may reflect either a detached inner cell wall or cytoplasmic remains (Fig. 3H).

Comments. Surface features are closest to Edwards' *Cosmochlaina maculata* (1986) originally based on a single specimen recovered from slightly older strata. The 'cuticle' is described as possessing protruding disc-like structures, 3.5-11µm diameter, x = 7.5µm delimited by elliptical to circular indentations. The air -dried specimen viewed in SEM (Edwards 1986, figs 18, 19) shows shrinkage of the surface very similar to that illustrated here (Fig. 3C).

Cosmochlaina TYPE 2 (Fig. 3J-O; NMW2013.39G.8-10)

These specimens are united in the possession of papillate outgrowths (here interpreted as emerging cortical cells), ranging from almost spherical (Fig. 3L) to compressed and present on smooth to wrinkled surfaces. Gross morphologies are irregular but edges, where recurved, may represent the original margins of the organism (Fig. 3M). The outgrowths may be isolated by incisions (Fig. 3L), but more commonly the surface is continuous. Such variation is considered developmental and shows different stages of the emergence of cortical cells.

The fractured cortex comprises outer periclinal walls c. 4µm thick with relatively short anticlinal walls (Fig. 3J), sometimes with remnants of inner periclinal walls (Fig. 3M). Palisade hyphae are similar in specimens NMW2013.39G.9 and NMW2013.39G.10 in that they have a robust appearance, as if thick-walled (Fig. 3N, O). They are unbranched and parallel sided. Differences in diameter may result from the deep longitudinal furrows in Figure 3N, where there is an intact rounded cell. The one specimen with preserved innermost zone provides little relevant information. Narrow, irregularly sided small tubes (Fig. 3K) are intermingled with occasional broader ones and also with banded tubes that are thought indicative of decay.

Comments. Although difficult to compare with the species of *Cosmochlaina* based on isolated cuticles, the surface features in Type 2 are closest to those placed in *C. versiformis* (Edwards, 1986) where hollow projections of variable length are each associated with a single unit of the reticulum.

Cosmochlaina TYPE 3 (Fig. 4A-K; NMW2013.39G.11-13)

The distinguishing feature in this group is the bilayered external wall of the cortex (Fig. 4D) accompanied by some variation, even within a single specimen, of the degree of fusion and persistence of the outer wall of the cortex and in surface appearance. Most show regularly spaced perforations some of which are occupied by disc-like structures: others are imperforate or with occasional perforations.

Specimen NMW2013.39G.11 is unique in showing relatively well preserved tripartite organization (Fig. 4A). The outer periclinal wall of the cortex comprises two sometimes separating layers, the outer thin and slightly granular (Fig. 4D) and the inner much thicker, homogeneous in section and with very smooth outer surface (Fig. 4D, E). Complete fusion may occur. The outer layer may be perforated or show shallow depressions sometimes surrounding a disc-shaped structure. Similar perforations are illustrated from a second specimen (NMW 2013.39G.12) with identical superficial layering (Fig. 4F-H). In both there is evidence for a *Nematothallus* type cortical construction from surface indentations where the outer cuticle is absent (Fig. 4D) or from periclinal fracture at the recurved margin (Fig. 4F). The surface sometimes displays mounds ('volcanoes') ridges or folds (Fig. 4D, H) but their relationship with underlying features, where separation has occurred, cannot be determined. The cortex may be almost intact but the region immediately below is completely disorganized, thus providing no detailed information on the junction with the underlying palisade zone (Fig. 4B) in which individual hyphae cannot be resolved. Narrow interwoven hypha-like fragments with occasional short lengths of wider forms are seen in the innermost basal layer (Fig. 4C).

A third specimen (NMW2013.39G.13) shows traces of sloughing off of the outer layer but mostly comprises only unusually the thick outer periclinal walls of the cortex with short anticlinal walls marking out relatively small cells (Fig. 4K). The surface of the specimen is either flat with perforations or very irregular,

sometimes with hemispherical mounds (Fig. 4J) or volcano-like structures each with a central apical depression sometimes with a papillate structure isolated by incisions (Fig. 4I). Figure 4K shows a fracture through the unusually thick outer periclinal wall of the cortex and an empty inverted funnel-shaped cavity.

Comments. When perforated, specimens (e.g. Fig. 4G;NMW2013.39G.12) may be superficially very similar to type 4, but differ in the bilayered nature of the outer periclinal wall of the cortex, a feature not observed in dispersed examples of *Cosmochlaina*. The possibility that the isolated example comes from an arthropod cannot be completely discounted, the perforations representing the sites of hair attachments. However, it is quite different from the rare unequivocal arthropod fragments, some with hairs, recovered from the same macerates.

Cosmochlaina TYPE 4 (Figs 4L-P, 5; NMW2013.39G.14-20)

Superficial features in this group of seven specimens are circular to elliptical perforations at variable densities with *Nematothallus*-type reticulum on the inner surface (Fig. 5D, F, N). The majority of the fragments, although small, show some aspects of gross morphology (Fig. 4L-P) but lack internal anatomy except for some traces of palisade hyphae. The outer cortical walls are sometimes much thicker than in other types. Margins believed to be intact show slight inrolling (Fig. 5G, H, O). We use the term ‘perforation’ because we have evidence from a number of fractured cuticles, that periclinal walls are pierced by

narrow channels (Fig. 5E) although examination of internal surfaces rarely shows their positions (Fig. 5D, M, N). Channels are very occasionally occupied by parallel-sided structures tentatively named hyphae (e.g. Fig. 5L), which can also be seen on the surfaces but rarely beyond (Fig. 5C). Specimen NMW2013.39G.14 (Fig. 4L, M) with lowest frequency of perforations has a cylindrical gross morphology with an intact end showing typical inrolling. Similar superficial features with margins recurved to form a possible border are seen in a spoon-shaped fragment (NMW2013.39G.15: Fig. 4N, O). One strap-shaped fragment (not illustrated) also shows recurved margins, well preserved anticlinal walls, a central longitudinal ridge and vestiges of palisade hyphae. Intact margins are also seen in NMW2013.39G.16, the most conspicuous being triangular outgrowths (Figs 4P, 5A, D). Here perforations are evenly spaced and quite widely separated (Fig. 5B). Those in NMW2013.39G.14 are somewhat closer and occasionally occupied by a circular structure in surface view, sometimes with central depression (Fig. 5K). In contrast to this example and others where hyphae occur throughout the channel and may terminate level with the surface (Fig. 5C, 5L), some channels appear empty or show traces of membraneous material (Fig. 5I, J). The latter is clearer on specimens with more sporadic perforations (e.g. Fig. 5B). Variation in types or absence of perforations may well reflect staggering of hyphal development on the same organism. It should be noted that the diameters of the cortical cells exceed those of the hyphae themselves.

Specimen NMW2013.39G.20 (Fig. 5P-R) is rare in this group in that all three layers are preserved if somewhat badly. The perforations (Fig. 5P) mostly lack hyphae and dominate the outer cortex wall when seen in fractured section (Fig. 5Q). This perhaps represents a late stage in the maturation of the thallus.

By contrast, NMW2013.39.17 (Fig. 5S-W) presents opportunities for measurement of palisade and basal zones although interpretation of their configuration is conjectural. Palisade hyphae, at least 430µm long, show sudden changes in diameter after branching (Fig. 5S) and give the impression that they are covered by mucilage. This raises the possibility that they represent fused clusters of hyphae (Fig. 5T, U). Intact rounded tips are sometimes preserved below the remains of the cortex (Fig. 5V). The basal zone appears dominated by short lengths of branching hyphae (Fig. 5W), not much narrower (c. 11µm) than the palisade forms, but between them are much smaller collapsed and irregular hyphae, that are of similar dimensions (c. 4.4µm) to those recorded in similar position in both *Cosmochlaina* and *Nematothallus*. This specimen is also unusual in that surface features are very variable, ranging from smooth with faint 'ghosts' of underlying cortical cells, discoidal protrusions near margins and very rare finger-like outgrowths of varying lengths (Fig. 5C).

Comments. Where well-preserved underlying zones are absent and specimens possess occasional hair-like protuberances or truncated structures within channels, there is the possibility that, as described for Type 3, some 'cuticles'

derive from arthropods rather than belonging to the *Nematothallus/Cosmochlaina* complex, although the *consistent* presence of an internal reticulum reinforces affinity with the latter. Again direct comparisons with dispersed cuticles, predominantly known from light microscopy studies, are difficult, but the variation in the degree of development of the protruding hyphae and the associated thinning of the cuticle indicate similarities with *C. versiforme*. The thickness of the cuticle and examples of occasional empty perforations also prompted comparisons with *Spongiophyton* as originally interpreted by Kräusel (1954) although we have no evidence for the gross, bifurcating cylindrical organization in our material.

Cosmochlaina TYPE 5 (Fig. 6A-G; NMW2013.39G.21)

This is a three dimensionally preserved triangular fragment, with no intact edge and included in *Cosmochlaina* because it has very occasional perforations or depressions (Fig. 6A, B). Its surface is generally smooth except for a small area of interdigitating furrows and ridges. All three zones are present. The basal one comprises wefts of occasionally branching hyphae of varying diameter, although this may be consequent on their thin walls (Fig. 6F, G). The palisade zone shows gross orientation perpendicular to the surface, but no individual hyphae could be resolved and amorphous sheets containing small holes are sometimes associated with irregular cavities (Fig. 6C, D). The junction between palisade

and cortex is again poorly preserved (Fig. 6E). The most striking differences between this thallus fragment and almost all others described here is the three layered cortex, comprising cells with irregularly shaped lumina, and the amorphous sheets interpreted as sheaths presumably of cyanobacterial colonies associated with poorly preserved hyphae where other samples have a dense palisade layer. These are reminiscent of many thalloid lichens, but in this case no photobionts are preserved (Honegger, Edwards & Axe, 2013a).

Comments. Anatomically this fragment resembles the Lower Devonian, lichen-forming ascomycete *Cyanolichenomycites devonicus* with internally stratified thallus and a cyanobacterial photobiont, as found in the same facies (Honegger *et al*., 2013), but in this case only the gelatinous sheaths of the cyanobacterial colonies are preserved, and no photobiont cells proper. By contrast, the gelatinous sheaths, but with only very few cyanobacterial cells, were retained in *C. devonicus*. The presumed cyanobacterial photobiont of specimen NMW2013.39G.21 most likely belongs to a non-filamentous, unicellular representative of the Chroococcales or Pleurocapsales which comprise common and widespread lichen photobionts (Friedl & Büdel, 2008). By contrast, the *Nostoc* photobiont of *C. devonicus*, has cells that are arranged in linear filaments and whose gelatinous sheaths reveal constrictions between adjacent cells (Fig. 2c-e in Honegger *et al*., 2013a). The gelatinous sheaths of the presumed photobiont of this specimen do not show the characteristic features as seen in

Nostoc colonies, although pores, presumably between former sister cells, are visible (Fig. 6D, arrows).

Thalli with incised surfaces and emergent hyphal protrusions (Figs 6H-L, 7-10; NMW2013.39G.22-43; Table 2)

The current study has revealed a completely novel group of fragments showing the same overall stratified construction as in *Nematothallus* and *Cosmochlaina*, with three zones: cortex, palisade and wefts of hyphae. They differ in details of the cortex, whose outer surface possesses circular to elliptical areas of varying density that are delineated by furrows or incisions to varying depths, and produce structures that are here interpreted as hyphal protrusions. This variation is considered developmental with a number of stages sometimes present on the same fragment. Isolated 'cuticles' with similar markings have not been recorded in coeval strata. This fact, together with the unique cortical characteristics, initially encouraged us to erect a new genus for the fragments, but instead we postulate a developmental relationship with *Nematothallus*.

Gross morphology. The most complete specimen (NMW2013.39G.23: Fig. 6I) is pear-shaped, 2.2mm long and 1.3mm at maximum width. In this highly compressed example, the palisade zone extends around the entire periphery and the central area comprises wefts of thick walled hyphae. Similar organization is present in more fragmentary examples including one where the

margin is scalloped (Fig. 6H). A few show a border formed from recurvature of the upper surface (NMW2013.39G.24; Fig. 6J). The latter may be gently (Fig. 6K) or more deeply folded (Fig. 6L), the most irregular occurring in the largest fragment (NMW2013.39G.36: 7.4 x 5.0mm) and forming crater-like structures Fig. 9D-F). The edge of specimen NMW2013.39G.27 (Fig. 7A) shows interlocking folds, in a curved marginal fragment, with typical deeply incised superficial appearance.

Surface features. In *Nematothallus,* the surface of the thallus is usually smooth and unornamented although it can be wrinkled and folded. By contrast, the surface in this group possesses numerous circular to oval imprints, variously differentiated hyphae or a lattice of voids (Fig. 7A-Q). Imprints may be limited by shallow depressions (Fig. 7C), 'ghosts' marking their future positions (Fig. 7B), or shallow incisions (Fig. 7D). Deeper incisions are accompanied by separation/isolation of circular or elliptical structures which may be flush with the surface of the cortex (Fig. 7D, E), slightly elevated (Fig. 7G, H) or protruding (Fig. 7Q). There is slight variation in the shape of imprints but greater differences in their distance apart, although this is more or less consistent within a single specimen. However there are some examples where small areas that are smooth or faint with well delimited imprints integrate with apparent perforations in the surface (e.g. Fig. 7F). In some specimens the latter predominate over wide areas (Fig.7L, O, P). Considering some of the examples with variation plus comparisons with those with reticulate systems, it is clear that the voids form on

disintegration or separation of the central isolated hyphal protrusions (Fig. 7K), sometimes resulting in a very disorganized superficial appearance (Fig. 7M, N).

Fortuitous anticlinal fracture of almost all fragments reveals a single cell layer thick cortex which provides a three-dimensional explanation for the various appearances of the surface ornamentation just described. Some present a uniform appearance, others possess variation in both surface and internal cortical features (Figs 7R-Y). Deep incisions produce separation of the outermost regions of the anticlinal walls although they may remain fused basally to the now distally isolated 'column' (i.e. the original homogenized basal anticlinal walls) (Fig.7R, T). These 'columns' vary in width proportional to the original distance apart of the incisions. The separated cortical entities now resemble the hollow fingers of a glove (Fig. 7R, U) and are seen in transverse section in Figure 7W. Most are rounded apically, a few are truncated and may be collapsed centrally forming a rim. Most of the tips are at the same level (Fig. 7T, U) or very slightly above the thallus surface (Fig. 7R). Bases are broken off and incomplete (Fig. 7T, U), showing an abrupt transition with disintegrated or possibly collapsed hyphae of the palisade zone (Fig. 7V, X). Rare examples are tapered and possibly intact proximally (Fig. 7S, Y, arrows).

Treatment with Schultze's solution (Fig. 10A-G) for several hours produced some colour differentiation, possibly indicating chemical differences between a continuous more or less transparent covering layer and the amber coloured hyphal elements (Fig. 10G). It emphasized the marked apical thickening of the ovoid to globular cortical hyphae with only traces of the transparent conglutinate

layer on the apices or between the cortical cells. Isolated elements usually comprised these apical cells with very rare examples of collapsed attached hyphae. (Fig. 10C, D)

The role of these cortical hyphae with walls that initially appear to have been much more resilient than the remaining thallus areas, remains enigmatic. It seems likely that they were shed, leading to a further problem. What happened on the surface of the thallus? In some cases it appears disorganized, but there can also be a continuous wall below dislodged cells (Fig. 7M, N). In others there is a reticulum (Fig. 7P). Some specimens with smooth or typically incised surfaces also possess areas where cortical hyphae appear as flattened ring-shaped structures (Fig. 7P) or granular residues (Fig. 7K) and occur alongside similar shaped voids. Figure 7L, illustrating another part of the specimen, has a reticulate appearance and lacks any evidence of hyphae.

.Further variation may reflect differences in the development of a thallus in a distinct taxon, although gross morphology where preserved is similar to other incised examples (Fig. 8L). Figure 8A shows a section through cells with completely homogenized walls, whose essentially smooth continuous exposed surfaces are marked by shallow depressions with occasional shallow incisions. This and a few other sections are unusual in that the lumina of some of the cells are occupied by fusiform processes (Fig. 8C, arrow). Here the superficial incisions are discontinuous and more sporadically arranged (Fig. 8B, J). Other

areas lack any incisions or appear perforated as in *Cosmochlaina*. There are occasional protruding hyphal cells (Fig. 8D) or a reticulum containing vestiges of hyphae beneath (Fig. 8E). Similar surfaces in Figures 8F and G cover wefts of poorly preserved narrow tubes. Specimen NMW2013.39G.41 is representative of a small number of fragments where dimpling (Fig. 8N) is seen in the otherwise smooth surface. It shows a three layered construction with recurved scalloped edges (Fig. 8L). Fractured examples show a typical cortex except that there is some evidence of internal separation of cortical cells even when no superficial incisions (Fig. 8O). The fractured thallus shows poorly preserved palisade hyphae (Fig. 8R) some with intact tips (arrowed in Fig. 8Q). This provides evidence that the palisade hyphae do not extend into the cortical zone. The cortex with hyphae in Figure 8P covers almost completely homogenized internal zones. The latter are lacking in specimen NMW2013.39G.43, but hyphal cells are apparent below a surface with some dimpling (Fig. 9A). This specimen is unique in that it has a surface with a series of indentations forming a polygonal pattern (Fig. 9B, C).

Specimens in this group may provide an anatomical, possibly a developmental, continuum between *Nematothallus* and perforated forms as will be further discussed below.

Palisade zones. In most specimens this is represented by traces of hyphae orientated perpendicular to the surface (Fig. 8G, H), and where more material is preserved, measurable hyphae are very few. These were parallel-sided with thin

walls and show little evidence of branching. They ranged between 5 and 18µm in diameter. Continuity between cortex and palisade hyphae could not be demonstrated.

Wefts. Preservation ranges from complete homogenization to flattening and fusion (Fig. 8F), with the impression of immersion in mucilage (Fig. 8K), to three-dimensionally preserved aggregations of hyphae. Figure 8I shows some alignment of hyphae, but the majority are interwoven. They range between 1.6 and 6.7µm in diameter, but the majority are between 3 and 4µm (Table 2). Collapse of hyphae on twisting is suggestive of thin walls. Branching is rare as is evidence of septa. In rare examples, the lowermost surface comprises aggregations of hyphae forming a kind of honeycomb (Fig. 8K, M). The sizes of the depressions are larger than sediment grains making it unlikely the shapes result from adpression to the stratum.

Comments. There is no direct counterpart of the incised superficial layer of these specimens with surface incisions in the record of dispersed cuticles, but re-examination of our original material mounted on SEM stubs has revealed a small number of specimens attributed to *Nematothallus* in which a faint circular to oval outline may occur within a unit of the reticulum. We suspect that during the development of the thallus the chemical composition of the outer part of the cortex changed making it less resistant to decay, while the perforations in the

cortex in the putative most mature forms would have increased its fragility. However, well preserved fragments of this type of cuticle with superficial incisions, together with fragments of *Nematothallus* and *Cosmochlaina* cortices, are contained in coprolites (fossil faecal pellets; figs. 5G, H in Edwards, Selden & Axe, 2012c) and thus were robust enough to survive the passage through the digestive tract of a presumed Lower Devonian millipede.

A dense cortex may be a hindrance to gas exchange; thus smaller or larger pores might facilitate the biological functioning of the thallus irrespective of it being built up by a heterotroph, photoautotroph or a symbiotic system comprising both types of organism. Relatively simple to anatomically complex aeration pores such as cyphellae or pseudocyphellae are found in the dense cortices of extant lichens (examples in Büdel & Scheidegger 2008; Honegger 2012). Of the specimens described in this paper, circular zones with less conglutinate material overlying the cortex are seen in *Nematothallus* specimen NMW2013.39G.2 (Fig.1F, G), and in pore-like structures in the specimen NMW2013.39G.36 with incised surface (Fig. 9D-F).

Lang (1937) described a number of discrete circular to oval thalloid compressions in which he identified a fragmentary cuticle with pseudocellular pattern overlying systems of tubes, irregularly arranged centrally and with the impression of radiating wider tubes particularly at the margins (plate 10, fig 54). He also noticed a difference in colour (brown) in these areas. In gross

morphology, his specimens assigned to *Nematothallus* (?) *radiata* resemble some examples in this group (e.g. Fig. 6H, I), but they could also belong to *Nematothallus* as described here. Palisade tissues may be represented by occasional stray hyphae or in relatively well preserved examples either apparently continuous with the cortex, (Fig. 8R) or with intact rounded tips beneath it (Fig. 8Q, arrow).

DISCUSSION

RELATIONSHIPS BETWEEN THE THREE GROUPS

In the three major groups of cuticles described here, united in their possession of three types of similarly organized, tissue-like zones, distinction has been based, initially for convenience, using an informal classification for *Nematothallus* and *Cosmochlaina*, on superficial characters of the cortex. The vast majority of cuticles and to a lesser extent the intact thalli have been assigned to *Nematothallus*, but some of these show very small areas of indentations and incisions reminiscent of the other two types, which may also show smooth areas between perforations and indentations. This, while reinforcing the artificial nature of the classification, allows the inference that *Nematothallus* thalli may represent developmental stages of the vegetative state of the organisms and the others, some type of reproduction, as yet exceedingly conjectural. Particularly relevant

to this scenario are the specimens with incised surfaces. Although most show a very uniform appearance of superficial imprints, uniform depth of incision and equal protrusion of hyphae, occasional examples possess small smooth areas surrounded by imprints displaying differing degrees of incision and protrusion of presumed cortical cells (Fig. 7F, O, P). Thus it is possible to construct a developmental series ending in deep superficial depressions and the disappearance of the protruding cells. Such a sequence would necessarily involve changes in the chemistry and construction of the outer cortical wall layers. This was initially manifested by a thinning of the outer periclinal wall in the position of the subsequent incision, followed by further thinning of the wall centripetally and subsequent separation of the cortical cells (Fig. 7H, I, Q). Relationships with the original cortical cells remain conjectural. The 'pillars' remaining between the separated cells are sometimes broader than the 'flanges'/anticlinal wall of those that typify *Nematothallus* and the resultant tips are smaller than the 'lumina'. The sequence in the inner periclinal walls of the cortex is similarly unclear, as is the proximal development of the hyphae, and their relationship to the underlying palisade zone (Fig. 7R-Y). Oxidized examples emphasise the thickness of the tips, which are far more resilient to acid treatment than the original outer cortical surface (Fig. 10A-F) and indicate the loss of the outermost**,** once continuous**,** layer (cf**.** Fig. 10G). The latter might partially account for the lack of dispersed reticulate sheets. The fate of the cortical cells remains ambiguous. Did they round off and form some kind of vegetative reproductive propagule (Fig. 7S, Y) or remain attached to the thallus via very

thin-walled extensions? Could such structures be analogous/homologous to either thalloconidia (Thallosporen) of lichenized ascomycetes, i.e. cortical or other peripheral cells, respectively, which detach and serve as vegetative fungal propagules (Hestmark, 1990, 1992; Poelt & Obermayr, 1990) or to hyphal outgrowths as a water-absorbing tomentum? Some rare examples show an intact wall at the base of the depression**,** presumably vacated by the hypha (Figs 7N, 8E).

A different developmental sequence is postulated to have occurred in the case of perforated *Cosmochlaina,* because here hyphae appear within the cortical cells below a dimpled surface implying that subsequently there was localized dissolution of the overlying outer periclinal walls to form the perforations. Such hyphae are not connected to the underlying palisade zone such that their origins remain unknown. In this group, perforated 'cuticles' are recovered from dispersed assemblages.

ANATOMICAL SYNTHESIS AND COMPARISONS WITH ENIGMATIC DEVONIAN FOSSILS

The three-dimensionally preserved fragments described here confirm that Lang's concept of *Nematothallus* as possessing a single layer of cells covering tubes of two distinct sizes was correct (Lang, 1937, 1945), although we have found no evidence of spores. Lang's unevenly thickened tubes being present throughout

his fragments are considered as epi- and endobionts as seen on coeval fossils (e.g. Edwards *et al*., 1996). A similar organization has been observed beneath cuticles assigned to *Cosmochlaina* (Edwards, 1986) and the new material with incised surfaces.

The 'cuticles' named *Nematothallus* when recovered from macerates represent the outer periclinal and anticlinal walls of the upper cortical zone, the inner periclinal wall usually not preserved as is the contact between this layer and the underlying system of the palisade zone of wide tubes which is orientated at right angles to the surface. The contact between this system and the usually randomly orientated wefts of smaller tubes is also obscure. Comparisons (see below) suggest that the anatomy of these thalloid organisms is closer to that in fungi than algae, and hence the tubes are better described as hyphae, although we have limited evidence of septa only in the most completely preserved material of *Nematothallus* (Fig. 1C). Such a conclusion would strengthen links between *Nematothallus* and *Prototaxites*, more recently described as a fungus (Hueber, 2001) as originally hypothesized by Lang (1937). He had noted the co-occurrence of the two genera in Silurian and Lower Devonian strata and overall similarities in 'tubular' construction. He also speculated that *Nematothallus* could have been 'expansions' attached to *Prototaxites*, a relationship also postulated by Jonker (1979), although the latter concluded that the parent organism was a red alga in the Rhodomelaceae. Had Lang been aware of our new evidence of the *Nematothallus* thallus, he would undoubtedly have made comparison with a specimen he described with Kidston (Kidston & Lang, 1921, plate 10, figs 113,

114) as the outer surface of a new species of *Prototaxites*, then named *Nematophyton* Penhallow. Although lacking a well-defined cortical layer (and hence no *Nematothallus* 'cuticles'), they described an outer zone of "tubular filaments" at right angles to the surface and inner zone of irregularly orientated "tubes or filaments", the wider tubes continuous with those in the outer zone and some with internal spiral thickenings. Spherical darker areas were compared with medullary spots. Between the aligned tubes were zones of granular material, so badly preserved that Kidston and Lang (1921) did not think it profitable to comment on their significance! However they did speculate on affinities of the organism with both the Laminariaceae (Phaeophyta) and the Udoteaceae (Bryopsida, Chlorophyta). New finds of this material possess a surface covering resembling isolated *Nematothallus* cuticles, thus reinforcing Lang's decision to include *Nematothallus* with *Prototaxites* in the Nematophytales.

There are a number of Devonian non-vascular thalloid or cylindrical fossils that are predominantly preserved as cuticles. Among the most intensively studied is *Spongiophyton* Kräusel (1954) diagnosed from the Middle Devonian of Brazil although it was already described, but not named, from the Emsian of the Gaspé (Penhallow, 1889). It comprises dichotomously branching thalloid organisms often occurring in great abundance (Gensel, Chaloner & Forbes, 1991). The fossils consist of flattened cylinders of cuticles of considerable thickness (<250µm) on the dorsal surfaces that may be completely perforated by narrow channels but unlike in some of the thicker 'cuticles' recorded as *Cosmochlaina*

here, these lack hyphae. Further species have been defined on pore morphology and size, thallus size and cuticle thickness (Chaloner *et al*., 1974). A reticulum of ridges similar to that in *Nematothallus* has been recorded on the inner surface of the cuticles (Gensel *et al*., 1991), the outer surface being smooth, although a depressed reticulum has sometimes been recorded on that of the upper cuticle (Taylor *et al*., 2004). Filaments occurring inside of the tubular structure have been interpreted as medullary hyphae of lichens (Stein, Harmon & Hueber, 1993), while chains of cells within the 'cuticle' have been interpreted as a cortex embedded in the gelatinous covering of a lichen (Taylor *et al*., 2004). Lichen affinity was also inferred from stable carbon isotope data that aligned with those from extant lichens rather than bryophytes (Jahren, Porter & Kuglitsch, 2003). However, Fletcher, Beerling & Chaloner, (2004) queried this conclusion having found no statistical differences between $^{13}\delta C$ values in *Spongiophyton* and those derived from bryophytes and lichens grown in a variety of habitats with compensation for diagenesis and the atmospheric composition in the mid Palaeozoic. Early geochemical analysis had indicated a small percentage of nitrogen (<2.7%) (Gensel *et al*., 1991). Niklas & Chaloner (1976) found no evidence of lignin-like polymers and deduced that a vascular plant affinity was unlikely. Thus the status of *Spongiophyton* remains conjectural. As for *Nematothallus*, lichen affinities may be a strong possibility although a photobiont is either missing or not preserved.

Beyond possessing a resilient cuticle with occasional perforations, some superficial similarities based on depressions on a curved surface (Fletcher *et al.,* 2004, fig. 1) and a few specimens with an internal raised reticulum, *Spongiophyton* remains distinct from both *Nematothallus* and *Cosmochlaina*. For the most part, the perforations in *Cosmochlaina* are more frequent and the cuticles much thinner. However in view of the global abundance of *Spongiophyton* at Devonian localities in Canada, South America, Africa and possibly Russia, it is surprising that it is not present in the Anglo-Welsh Basin.

Gensel *et al.* (1991) provided a short review of other Devonian genera, possibly closely allied to *Spongiophyton*. These include, *inter alia, Orestovia* Ergolskaya and *Aculeophyton* Kräusel and Venkatachala, which possessed a ribbon-like organization with cuticles, of uncertain composition, showing various types of reticulate patterning, some with perforations. Suggested affinities ranged from vascular plants to algae. None show the anatomy described here. Gensel *et al.* (1991) postulated that they represented extinct algae-derived clades showing adaptation to the terrestrial environment, but not yet having attained embryophyte complexity.

COMPARISONS WITH BRYOPHYTES

Fossils. The patterning of superficial cells in the best preserved Devonian hepatics (Hueber, 1961: *Pallaviciniites devonicus*; VanAller *et al*., 2008: *Metzgeriothallus sharonae)* resembles that in *Nematothallus,* and the darker

cells, the outgrowths of *Cosmochlaina*, but the underlying parenchymatous tissues, when present, are quite different.

Extant forms. Although there is a general resemblance to the three-dimensional construction of thalloid gametophytes in the Marchantiales (eg. the dorsal chlorenchymatus filaments in *Riccia,* and a ventral rhizoidal system), liverwort rhizoids with or without their associated fungi and the rhizoidal filaments found in mosses are anatomically quite distinct from the sparingly branched hyphae in the nematophytes (J.G. Duckett, pers comm., 2012; Duckett, Schmid & Ligrone, 1998), while Strother (1988) had earlier emphasised the lack of a (heavily) cutinized superficial layer in bryophyte thalli. The residues of modern bryophyte tissues recovered following acetolysis or prolonged rotting, summarized above on page four, superficially resemble some of the banded tubes and 'cuticles' described here. In particular those produced by Graham *et al*. (2004) from the rhizoid–bearing, lower epidermis from marchantioid gametophytes were compared favourably with perforated cuticles (not unistratose cell sheets) of *Cosmochlaina.* We note differences in cell arrangements, orientation and attachment of rhizoid bases and, from their illustrations (Fig. 1G, H), an almost three-fold difference in cell dimensions. On the basis of the above, we discount bryophyte affinity for the *Nematothallus* complex.

COMPARISONS WITH ALGAE

Fossils. Jonker (1979) thought that *Nematothallus* represented the phylloids attached to *Prototaxites* axes, the latter being interpreted as cauloids, and concluded affinities with the red algal family, Rhodomelaceae. Although both taxa are frequently recorded in the same assemblages, we have found no evidence of connection (see also Lang 1937).

Extant forms. Examples of palisade-type thallus organization occur in a wide range of brown algae (Phaeophyta), whose thalli are built up of systems of coordinately growing filaments (e.g. in the encrusting thalli of Ralfsiaceae). In the red algae (Rhodophyta), such thalli may show a multiaxial 'Springbrunnen' (waterspout fountain) type of growth or parallel filaments deriving from a system of basal filaments and bound together with mucilage (e.g. *Peyssonelia* spp (Peyssoneliaceae), *Hildenbrandia* (Hildenbrandiaceae), or may be present in calcified and non-calcified representatives of the Corallinaceae). Well preserved non-calcified, pseudoparenchymatous red algal thalli of this growth type are known from the phosphatic rocks of the Neoproterozoic (approx. 600 Myr old) Doushantuo Formation (Xiao *et al*., 2004). However, being mostly marine, rarely freshwater inhabitants, neither brown nor red algal thalli differentiate a peripheral, degradation-resistant cuticle. Smith and Butterfield (2013) described isolated cuticles with complex perforations, as illustrated by Edwards and Rose (1984) in *Nematothallus* cuticles, as members of a new red algal genus *Nematothallopsis*. They considered the perforations, fringed with filaments, as the openings to conceptacles whose surface developments share similarities with those found in the extant calcified coralline red algal genus, *Bossiella*. We

are absolutely convinced that this Ludlow (Upper Silurian) material, recovered from marginal marine rocks derives from *Nematothallus*, especially as the authors found some cuticles with numerous filaments attached that are comparable with the palisade zone described here, although we have no evidence to support their interpretation of the attachment of the filaments to the cuticles. There is no evidence of underlying conceptacles or other types of sexual reproductive structures in any material, although the circular holes with fringing filaments are very conspicuous. We would interpret the latter as either hyphae similar to those of the palisade zone, but of more resilient composition or, should the circular holes indeed represent ostioles of perithecia, as periphyses as typically found in Verrucariales (examples in Henssen & Jahns, 1974; figs. 4.16, 13.49). Similar structures termed spiracles are found in arthropod cuticles of extant centipedes (Klok, Mercer & Chown, 2002), spiders (de Bivort & Giribet, 2004, plates 36, 37) and other arthropods (Grimaldi & Engel, 2005). However, Smith and Butterfield (2013), in their fig. 7D, refer to filaments with interspersed spherical elements attached to the inner side of the cuticle of *Nematothallopsis gotlandii*. This rare feature very strongly reminds us of the algal layer adjacent to the peripheral cortex of a lichen thallus as found among the Verrucariales (e.g. in the genera *Dermatocarpon*, *Endocarpon;* examples in Jahns, 1973; Henssen & Jahns, 1974), while also reminiscent of the hyphae of the palisade zone in *Nematothallus.*

We must emphasise that, although older material of *Nematothallus* has been recovered from marine rocks, in the Lower Devonian of southern Britain, it occurs

in great abundance in sediments deposited by rivers and is associated with terrestrial plants. While this does not eliminate a fresh water origin, it is difficult to envisage how charcoalification could have occurred in this setting or indeed in a marine one. Thus we do not support the hypothesis that *Nematothallopsis* was a non-calcified coralline seaweed but agree with Lang (1937) that *Nematothallus* colonised land surfaces.

COMPARISONS WITH ARTHROPODS

Mineralised parts of the exoskeleton of arthropods, usually termed cuticles, are commonly found in sedimentary rocks throughout the Phanerozoic (see numerous examples in Grimaldi & Engel (2005)). In the mid Palaeozoic they mark the first direct occurrences of elements of the terrestrial fauna (e.g. Jeram, Selden & Edwards, 1990; Shear *et al*., 1984**).** Records comprise fragments, often with hairs (e.g. Gensel, Johnson & Strother**,** 1990) or more complete limbs, carapaces or thoracic segments (e.g. Shear & Bonamo, 1988). Examples of the former type were recovered from the macerates studied here. The majority are highly folded amorphous, diaphanous fragments, while a few show perforations with thickened margins or, even more rarely, with attached hairs. Eurypterid cuticles with characteristic scales are also seen. The vast majority are easily distinguished from the *Nematothallus-Cosmochlaina* complex, but some are more equivocal and nicely illustrate the difficulties articulated by Gensel *et al.* (1990) of distinguishing between animals and plants s.l. An example is

illustrated here (NHM2013.39G.13, Fig.4I) where volcano-like structures resemble the bases of hairs, although in other areas the layering of the cuticle is identical to specimens assigned to *Cosmochlaina* Type 3. Arthropod affinity might more confidently be concluded for those specimens comprising isolated perforated cuticles assigned to *Cosmochlaina* Type 4 and which are extremely thick (Fig. 5E, F), although again such cuticles may cover a stratified thallus. Nevertheless, we are convinced that the majority of specimens assigned to the *Nematothallus –Cosmochlaina* complex did not derive from animals.

COMPARISONS WITH LICHENS

Fossil forms. The absence of a photobiont prevents direct comparison with either extant or extinct lichens, but lack of anatomy did not deter Retallack's assignation of the Cambrian-Ordovician terrestrial compressions, named *Farghera robusta,* or certain ediacaran taxa to lichens (Retallack, 1994; 2000; 2009; 2012), although no extant lichenized or non-lichenized fungal taxa reveal the growth patterns observed in these enigmatic fossils. By contrast, Taylor *et al*., 1995 and Taylor, Hass & Kerp (1997); described *Winfrenatia reticulata* as a consortium of cyanobacterium and zygomycete in exquisite detail and although such a combination is unknown in lichens today, it has been generally accepted as the earliest terrestrial lichen (Karatygin, Snigirevskaya & Vikulin, 2009). The fungal component is quite unlike that described here. There are greater resemblances with the mycobiont in the two lichens recently described by

Honegger *et al*. (2013a) as the earliest stratified cyanobacterial and algal lichens from the same locality, in that the thallus is tripartite comprising a conglutinate cortex, single layered in *Chlorolichenomycites*, a photobiont layer and a medullary layer composed of interwoven narrow hyphae. They differ in the lack of a palisade layer; instead their photobiont layer is present. Indeed in the thallus of *Chlorolichenomycetes* even bacterial epibionts and actinobacterial and fungal endobionts are preserved (Honegger Axe & Edwards 2013b, In only one specimen in the present investigation is the palisade less well-defined and might equate to the photobiont layer present in the two lichens above (Fig. 6A-G). A partial view of the inner surface of the outer walls of the single layered cortex in *Chlorolichenomycites* resembles a 'cuticle' of *Nematothallus* (Honegger *et al.,* 2013a, fig.4b).

The absence of photobionts in our new material could be taphonomic. The unicellular, presumed green algal cells in the thallus of *Chlorolichenomycites salopensis* are retained as pyrite framboids; only rarely was a cell wall found around the framboids. Without this permineralisation process, nothing would have been left from these algal cells. In an attempt to simulate charcoalification, desiccated examples of the extant lichen-forming ascomycete *Leptogium lichenoides* (L.), with *Nostoc* as photobiont, were wrapped in aluminium foil and placed in a furnace preheated to 400ºC for five minutes. Subsequent scanning electron microscopy showed well preserved fungal hyphae and the gelatinous sheaths of the *Nostoc* colonies, but no cyanobacterial cells (Honegger *et al.,*

2013, fig. 3c, d). Incidentally the section through the cortex of this *Leptogium* species, reinforces the opinions of the Munster team (Kerp & Krings) cited in Steur and van der Brugghen (1998) of similarities between that genus and *Nematothallus*, and hence the lichen affinities of the latter.

Honegger *et al*. (2013) tentatively concluded that the mycobiont in their two taxa were lichenized members of the *Pezizomycotina*, a group we consider in the discussion below.

Extant lichens. All our fossils comprise only the fungal component, and none are an exact match in terms of anatomy, although there are broad similarities (Jahns, 1973; Henssen & Jahns, 1974; Büdel & Scheidegger, 2008; Honegger, 2009, 2012). Some lichens possess a unicellular cortex (e.g. *Leptogium*) that may be covered by a polysaccharide layer. The globose to ovoid, apolar cortical cells may grow out into filamentous hair-like polar hyphae, either as a water-absorbing tomentum (examples in the genera *Sticta*, *Teloschistes*; Honegger, 2009) or for capturing cyanobacterial partners (examples in the genus *Peltigera*; Honegger, 2012). In crustose forms, wefts of branching hyphae showing variation in degrees of fusion are in contact with the substrate, some even incorporating sand grains (cf. Fig. 8K, M). The major difference from most lichens is the parallel arrangement of septate hyphae below the cortex, the usual site of the photobiont, throughout the thallus. There are some extant examples with such

arrangement (e.g. in the genera *Roccella* and *Dermatocarpon*; examples in Henssen & Jahns, 1974). However such organization is far commoner in the reproductive parts of ascomyetes, i.e. apothecia of lichenized and non-lichenized taxa, where paraphyses may terminate in club-shaped cells (see numerous examples in Henssen & Jahns, 1974), but we have no evidence of asci in these coalified fossils (but see granular material in the Kidston & Lang fossils of *Prototaxites taitii* in a similar position; Kidston & Lang, 1921, figs 113, 114).

Among the extant fungi, morphologically and anatomically complex structures comprising diverse tissue-like pseudoparenchymata and plectenchymata are formed not only in fruiting bodies of non-lichenized and lichenized asco- and basidiomycetes, but also in the vegetative thalli of lichenized taxa as an adaptation to the symbiotic lifestyle; these are considered as the morphologically most advanced fungal taxa (Honegger, 2009, 2012). Considering the fact that lichen-forming ascomycetes with anatomically complex thalli with internal stratification and green algal or cyanobacterial photobiont, respectively, existed in the Lower Devonian (Honegger *et al*., 2013) we favour the interpretation of Nematothallales being lichenized ascomycetes.

WEATHERING

Putative affinities and environmental consequences.

Much has been written on the consequences of the diversification on land of embryophytes and particularly deep rooted vascular plants for the evolution of ecosystems, lithosphere and atmosphere within a time frame based on records of spores and megafossils although with little quantitative data on extent of these vegetation types (Lepage & Pfefferkorn, 2000). The identification of thalloid organisms in the Lower Devonian as fungi and probably lichens introduces further diversity into these terrestrial ecosystems, while the presence of *Nematothallus* 'cuticles' extends these components some fifty million years into the Middle Ordovician and focuses attention on the need to identify the affinities of coalified thalloid fossils in Middle Ordovician to Lower Devonian rocks. Some undoubtedly were produced by microbial mats/biofilms in which cyanobacteria and bacteria have been demonstrated in early Silurian examples (Tomescu & Rothwell, 2006; Tomescu *et al*., 2006, 2008, 2010; Tomescu, Rothwell & Honegger, 2009a), while Strother (1988) has found tubular/hyphal nematophyte remains, that he attributed to *Nematothallus* in Ludlow (Upper Silurian) strata. He later re-examined Lang's Downtonian (Prídolí) and Dittonian (basal Devonian) collections and showed that thalloid compressions accounted for 10-50% coverage of a bedding plane compared with c. 1% from axial fossils. While estimates of this nature undoubtedly are affected by a number of taphonomic biases, they at least emphasise the dominance of organisms with thalloid organisation in vegetation colonising the catchment area of the fluvial systems. An alternative approach to identifying its composition has involved extraction of stable carbon isotopes from coalified material scraped from numerous

compressions including *Prototaxites* and *Nematothallus* at seven localities in the Ordovician and Silurian of the Appalachian basin including the Upper Silurian Bloomsburg Formation (Tomescu *et al*., 2009b). In comparisons of these values with those predicted for Ordovician and Silurian liverworts, six of the localities yielded compressions with values indicative of land plants, including those at a bryophyte grade of organization as well as lichens. However the complexity of land vegetation was ignored by Lenton *et al*. (2012) who concentrated on the roles that embryophytic land plants, as recorded by their spores, played in enhancing chemical weathering (from Mid-Ordovician onwards) and hence the draw down of carbon dioxide in the atmosphere, which they postulated produced the Hirnantian (Upper Ordovician) glaciations. Their weathering experiments, involving the growth of the moss *Physcomitrella patens* on granite and andesite, showed enhanced silicate weathering and also increased release of phosphorous and iron via organic acids into the media. Similar and perhaps even greater weathering would have been produced by lichens (Banfield *et al*., 1999; Chen, Blume & Beyer, 2000; Favero-Longo *et al*., 2007; Gadd & Raven, 2010; McIlroy de la Rosa, Warke & Smith, 2012) with further contributions from biological crusts (Belnap & Lange, 2001; Chen *et al*., 2000).

It is pleasing that, as we discover more of the heterogeneity in land vegetation through time, the importance of extant communities variously composed of lichens, algae, cyanobacteria and bryophytes, and collectively called cryptogamic covers, to the global cycling of carbon and nitrogen has recently received some

attention (Belnap, 2012; Elbert *et al*., 2012). Such vegetation today contains c. 1% of the carbon content of terrestrial vegetation and contributes to almost half the nitrogen fixation and c. 7% of net primary production on land. We are now beginning to trace the early evolution of such communities in the Palaeozoic and, in the case of cyanobacteria and algae, much earlier (e.g. Westall *et al.,* 2006). Given the numerous studies surveyed by Elbert *et al*. (2012), we can perhaps begin to quantify their roles in global geochemical cycles in the distant past in the absence of vascular plants.

There remains, however, an outstanding enigma concerning *Nematothallus* and its allies. Our studies have shown they were important components of terrestrial ground cover particularly in the Upper Silurian and Lower Devonian, their well-preserved debris being present even in coprolites, presumably produced by Devonian millipedes (Edwards *et al*., 2012c), yet their 'cuticles' subsequently disappear from the rock record. This is paralleled by the record of cryptospores and spores of pioneering tracheophytes (Edwards *et al*., 2012a, b; Morris *et al.,* 2011, 2012a, b; Edwards *et al.* in preparation). For the latter we postulated somewhat simply that taller plants might have outshaded the 'turf' vegetation. However in the case of presumed lichens, while competition for space and light might have restricted their distribution, their poikilohydrous water relations would have allowed them to thrive in climatically extreme environments; thus they should perhaps be recorded in palynological preparations even if not as meso- or megafossils. We have no answer, except to point to a further parallel. While

cryptospores are now known to derive from basal embryophytes, and molecular studies indicate an earlier divergence of bryophytes than vascular plants (e.g. Qiu *et al*., 2006), there are no records of bryophyte spores or indeed unequivocal cryptospores, entities that might be anticipated in palynological preparations, from later Devonian rocks (Taylor *et al*., 2009; Kenrick *et al*., 2012).

ACKNOWLEDGEMENTS

This study has been funded by grants from the Leverhulme Trust and the Gatsby Charitable Foundation which are very gratefully acknowledged. We thank Alun Rogers and Louis Emery for help in preparing the figures.

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Table 1. Summary comparisons of hyphal dimensions in *Nematothallus*, *Cosmochlaina* and specimens with incised surfaces. n = number of specimens measured.

	Nematothallus (µm)			*Cosmochlaina* (µm)			Incised cuticles(µm)			Intermediate (µm)		
Cortex: max. unit width	6-16	x=12	n=4	5-12	x=9.5	n=1				5-12	x=9.5	n=1
Cortex: min. unit width	5-15	x=11.9	n=4	4-11	x=7.3	n=2				4-11	x=6.9	n=1
Palisade hyphae width	7-28	x=14.8	n=2	5-13	x=7.3	n=2	10-22	x=15.2	n=15			
Diameter of small hyphae	2-8	x=4.1	n=40	2-7	x=3.8	n=3	2-7	x=4.4	n=8	1-7	x=5.0	n=9

Table 2. Dimensions of surface features in incised specimens. Extent of incision/hyphal protrusions increases from top to bottom. (v) = incision depth variable on same specimen.

	Diameter incisions/hyphal protrusions (µm)						
	Maximum			Minimum			Cortex thickness (µm)
NMW2013.39G.22	5.3-9.8	x=7.5	n=19	4.9-7.6	x=6.3	n=19	22-24
NMW2013.39G.23	6.3-14.8	x=9.5	n=30	4.4-10	x=6.6	n=30	25-30
NMW2013.39G.24	4.2-13.3	x=9.5	n=26	4.2-10.9	x=6.8	n=26	
NMW2013.39G.26	3.3-11.7	x=8.3	n=90	2.9-9.6	x=6.4	n=90	
NMW2013.39G.27	4.3-10.0	x=6.9	n=36	3.9-8.0	x=5.3	n=36	c.30
NMW2013.39G.28	2.6-11.1	x=6.7	n=100	2.6-8.5	x=5.7	n=100	c.30
NMW2013.39G.29	1.5-9.1	x=5.3	n=47	1.5-7.1	x=4	n=47	20
NMW2013.39G.30	6.2-9.4	x=7.7	n=20	3.6-7.8	x=6.0	n=20	12
NMW2013.39G.31	3.9-13.6	x=7.8	n=50	4.9-12.5	x=8.4	n=50	c.25
NMW2013.39G.32 (v)	4.9-12.1	x=8.6	n=25	3.6-9.7	x=6.8	n=25	
NMW2013.39G.36	5.6-16	x=10.5	n=50	4.9-12.5	x=8.4	n=50	<30
NMW2013.39G.37 (v)	6.2-11.1	x=8.3	n=34	4.4-8.8	x=6.7	n=34	14-15
NMW2013.39G.38	3.5-10.6	x=8.1	n=30	3.1-8.9	x=5.6	n=30	
NMW2013.39G.42 (v)	3.5-12	x=5.6	n=22	2.8-6.5	x=4.3	n=22	

Legends to figures

Figure 1. SEM images of *Nematothallus* sp. A-E, NMW2013.39G.1. A, intact fragment with three zones. Scale bar: 200µm. B, close up showing hummocky cortex and palisade zone. Arrows indicate crater-shaped outgrowths. Scale bar: 100µm. C, septate hypha in palisade zone. Scale bar: 50µm. D, fractured fused small hyphae in wefts. Scale bar: 10µm. E, magnified walls of small hyphae; cf ultrastructure in *Nematasketum*, Scale bar, 2µm. F,G, NMW2013.39G.2. F, imprinted surface reminiscent of aeration pore (pseudocyphella) formation in cortical layers of extant lichens. Scale bar: 500µm. G, magnification of part of F. Scale bar: 100µm.

Fig. 1

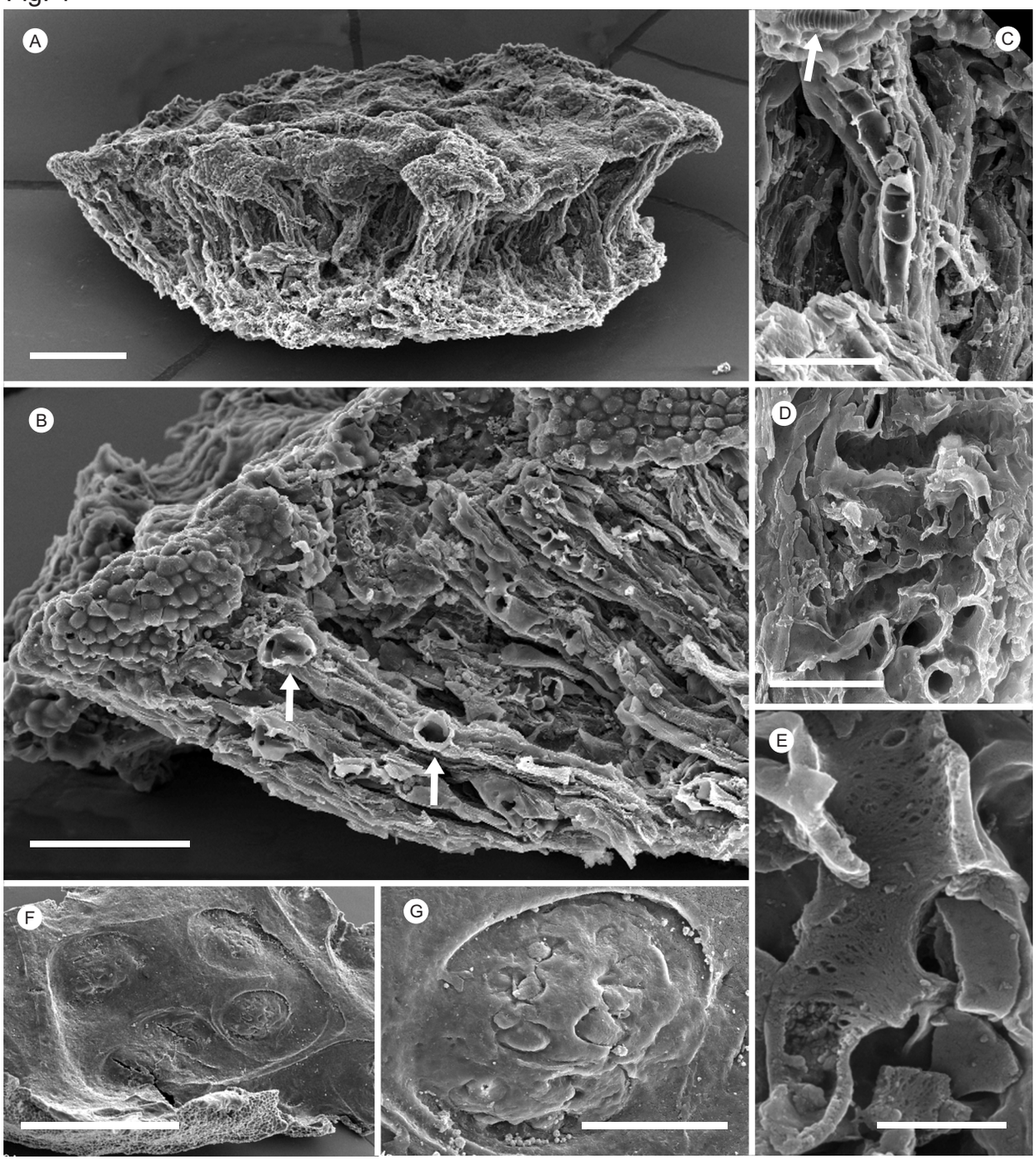


Figure 2. SEM images of *Nematothallus* sp. A-G, appearances of inner surfaces of outer periclinal walls of cortex (cf. dispersed 'cuticles'). A,C, NMW2013.39G.3; Arrows in C indicate traces of fused hyphae. B, NHM2013.39G.2. Scale bars in A and B, 50µm: C, 20µm. D, curved fragment with outer periclinal walls absent at margin. NMW2013.39G.4. Scale bar: 50µm. E, continuous outer layer ('cuticle') missing revealing cortical cells beneath. NMW2013.39G.4. Scale bar: 50µm. F, curved margin showing cortex in section. Note contaminant hypha below outer covering. NMW2013.39G.5. Scale bar: 50µm. G, contaminant hyphae, some with unevenly thickened walls resembling a variety of banded tubes on surface of thallus. NMW2013,39G.5. Scale bar: 20µm. H, typical example of poorly preserved palisade zone. NM2013.39G.6. Scale bar: 20µm. I, outer surface showing cratering typical of charring on outermost 'cuticular' layer. NMW2013.39G.6. Scale bar: 50µm. J, poorly preserved basal zone hyphae of different sizes, NMW2013.39G.5. Scale bar: 20µm.

Fig. 2

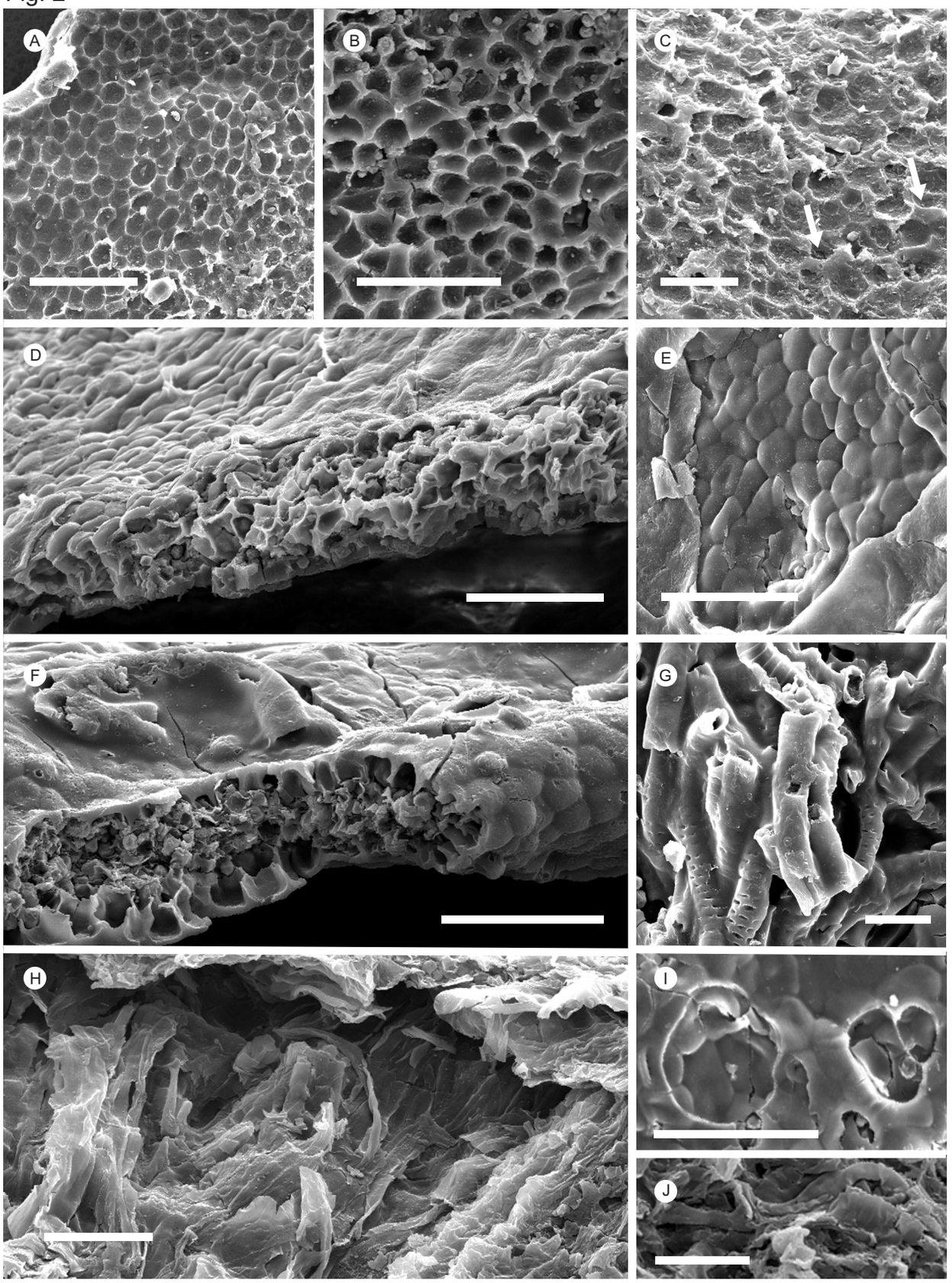


Figure 3. SEM images of *Cosmochlaina* sp. A-I, TYPE 1. specimen with intact cortex. NMW2013.39G.7. Scale bars: 20µm except in A: 1mm and D, E: 100µm. A, complete fragment, lower edge probably intact. B, reticulum on inner surface of outer periclinal wall. C, discoidal structures on surface. D, fractured section of entire thallus. Note remains of a second cortical layer (arrows) and obliquely orientated palisade zone. Hyphae of basal zone not preserved. E, palisade zone and partial cortex in LS. F-H, fractured cortex magnified with two types of cells. Note hyphal remains occupying a cortical cell in H (arrow). I, basal zone with two sizes of hyphae. J-O. TYPE 2. J, fractured detached surface of cortex, NMW2013.39G.8. Scale bar: 20µm. K, fragments of hyphae in basal zone, NMW2013.39G.9. Scale bar: 50µm. L, surface with papillate structures. NMW2013.39G.8. Scale bar: 20µm. M, recurved edge of thallus with intact surface of cortex. NMW2013.39G.10. Scale bar: 50µm. N, remnants of palisade zone of previous specimen. NMW2013.39G.10. Scale bar: 100µm. O, longitudinal view of palisade hyphae with rounded tip and possible septum (arrow). NMW2013.39G.9. Scale bar: 20µm.

Fig. 3

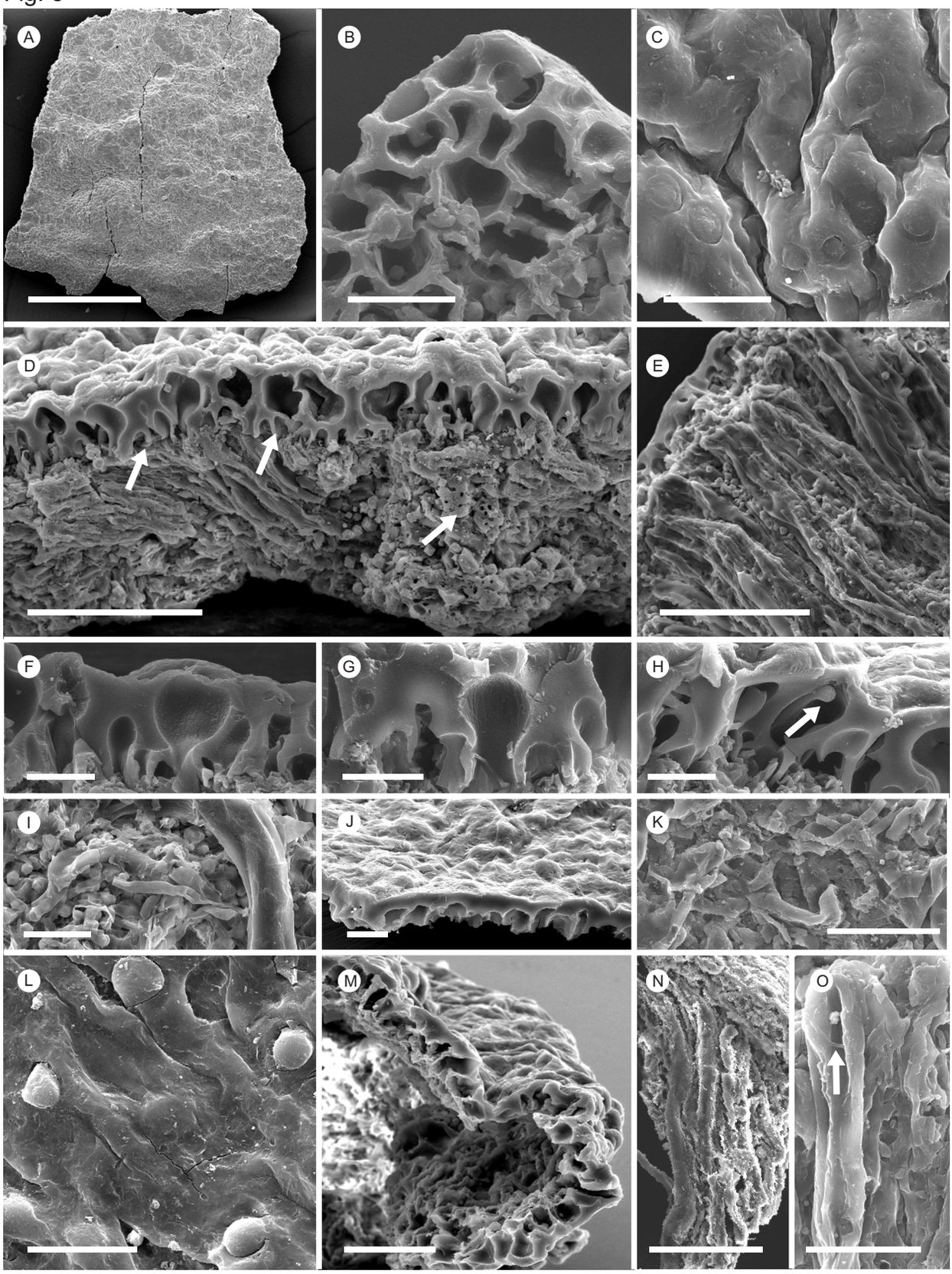


Figure 4. SEM images of *Cosmochlaina* sp. A-K. TYPE 3. A-E, NMW2013.39G.11. A, specimen with tripartite organization (inverted). Scale bar: 500µm. B, anticlinally fractured cortex and palisade zone. Scale bar: 50µm. **C,** wefts of basal hyphae, arrow indicates banded tube. Scale bar, 20µm. D, surface with outer covering layer partially removed revealing outer walls of cortex beneath. Scale bar: 100µm. E, detached outer layer of part of cortex. Scale bar: 20µm. F-H, NMW2013.39G.12. F, outer periclinal wall of cortex absent at margin. Scale bar: 100µm. G, intact outer surface of F with perforations. Scale bar: 100µm. H, outer covering layer absent with raised areas marking sites of perforations (arrows). Scale bar: 50µm. I-K, NMW.2013.39G.13. I, intact outer surface with perforations and structures within mounds. Scale bar: 20µm. J, wrinkled surface with imperforate protrusions. Scale bar: 50µm. K, fractured outer periclinal walls with internal reticulum and a single perforation (arrows). Scale bar: 20µm. L-P. TYPE 4. L, M, NMW2013.39G.14. Two surfaces of intact specimen. Scale bars: 500µm. N, O, NMW2013.39G.15, two surfaces of intact specimen. Scale bars: 1mm. P, fragment with wrinkled surface and intact margin at top with two triangular projections (arrows). NMW2013.39G.16. Scale bar: 500µm.

Fig. 4

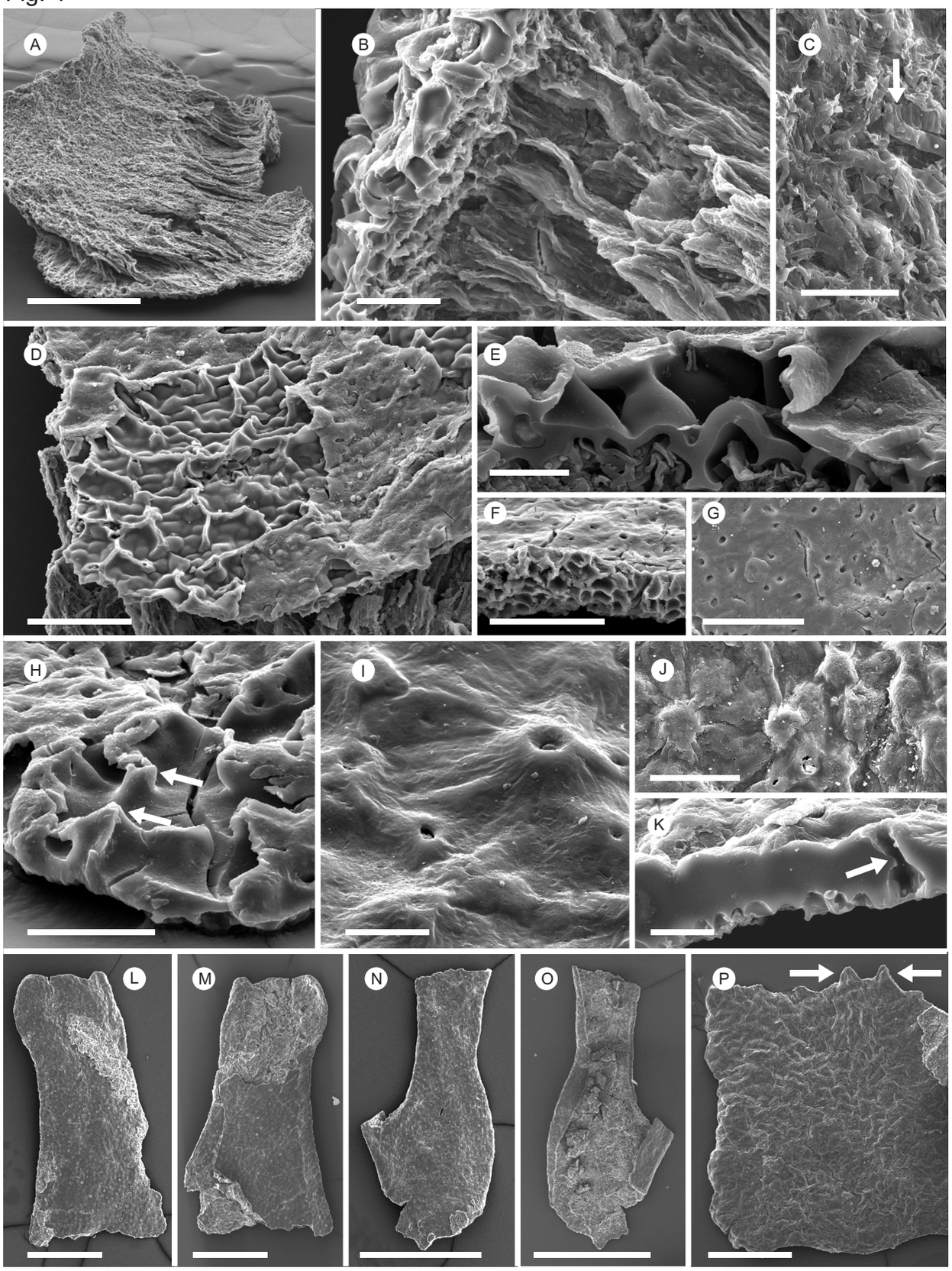


Figure 5. SEM images of *Cosmochlaina sp.* TYPE 4. A, marginal projections in Fig. 4P magnified. Scale bar: I00µm. B, regularly spaced surface perforations lacking hyphae. NMW2013.39G.16. Scale bar: 50µm. C, surface of different specimen with occasional protruding hyphae. NMW2013.39G.17. Scale bar: 50µm. D, part of lower surface of specimen in Fig. 4P. Scale bar: 100µm. E, section through outer periclinal wall with perforations. NMW2013.39G.18. Scale bar, 50µm. F, section through outer periclinal wall. NMW.2013.39G.16. Scale bar: 100µm. G, H, recurved margin. G, NMW2013.39G.16. Scale bar: 50µm; H, NMW.2013.39G.14. Scale bar: 100µm. I, J, NMW2013.39G.14, remains of cuticular covering of perforations. I, Scale bar: 10µm. J, Scale bar: 20µm. K, hyphal tip in perforation. NMW2013.39G.14. Scale bar: 20µm. L, longitudinal fracture through hyphae in perforations. NMW2013.39G.16. Scale bar: 20µm. M, remains of cortical cells. NMW2013.39G.16. Scale bar: 50µm. N, remains of anticlinal walls of cortical cells. NMW2013.39G.19. Scale bar, 20µm. O, inner surface of cortex with traces of palisade hyphae. NMW2013.39G.14. Scale bar: 50µm. P-R. NMW2013.39G.20. Scale bars: 50µm. P, outer perforated surface. Q, section through cortex. R, inner surface of cortex. S-W, NMW2013.39G.17. S, general view of palisade zone. Scale bar: 100µm. T, U, magnified hyphae. Scale bars: 100 µm (T), 50 µm (U). V, fractured outer wall of cortex with rounded ends of hyphae below (arrow).Scale bar: 20µm. W, fragmented narrow hyphae in basaltissue. Scale bar: 20µm.

Fig. 5

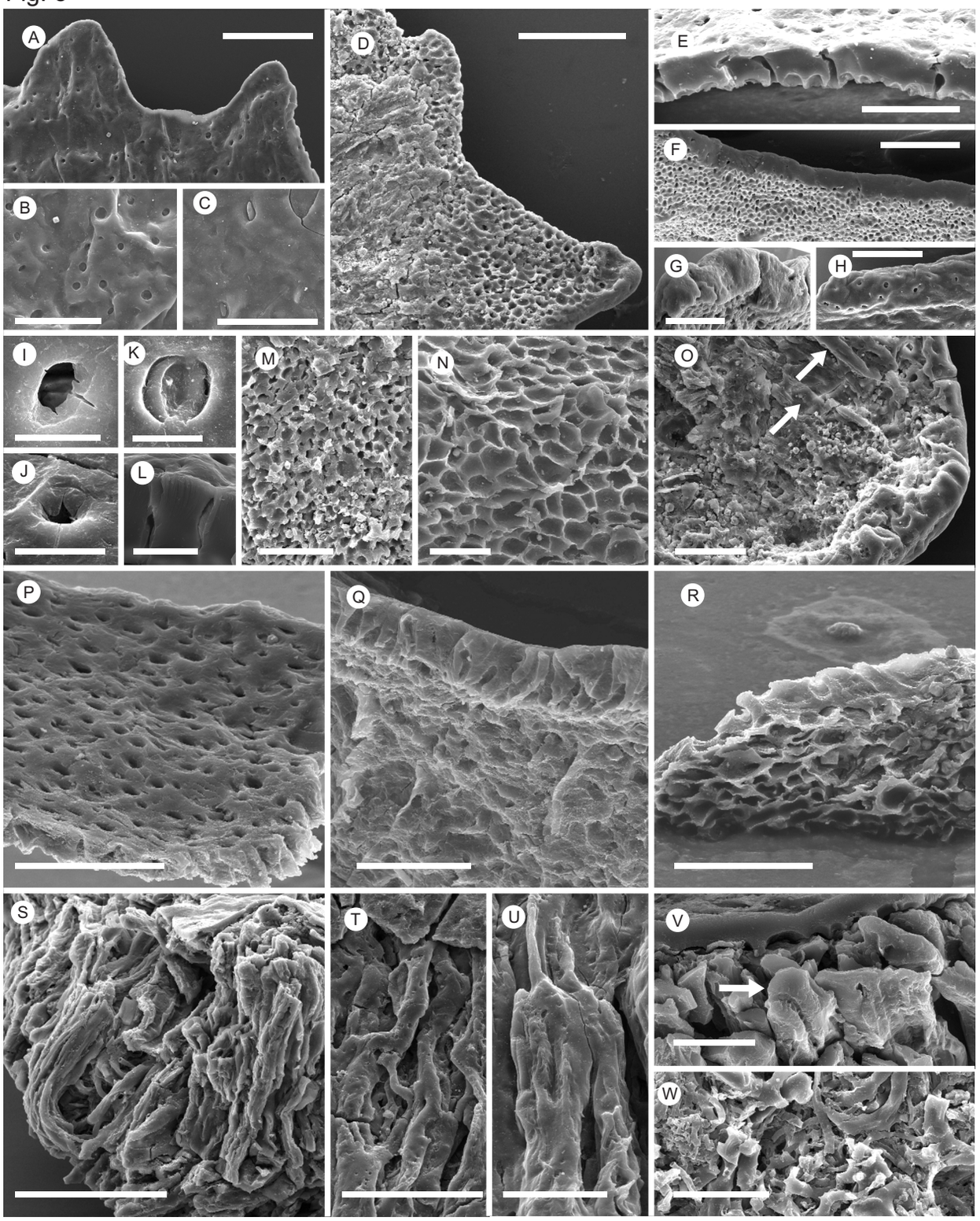


Figure 6. SEM images. A-G, *Cosmochlaina* sp TYPE 5. NMW2013.39G.21. A, fragment before dissection. Scale bar: 1mm. B, upper surface. Scale bar: 20µm. C, anticlinally fractured thallus. Note multilayered cortex overlying a presumed photobiont layer with remains of putative cyanobacterial sheaths. Scale bar: 100µm. D, minute perforations (arrows) in presumed cyanobacterial sheath. Scale bar: 50µm. E, obliquely fractured thallus with three zones. Scale bar: 100µm. F, G, narrow hyphae in basal zone. Scale bars: 20µm. H-L. Thalli with incised surfaces. H, three layered fragment with lower surface uppermost. Note scalloped margin with recurved border. NMW2013.39G.22. Scale bar: 500µm. I, almost intact specimen. Lower surface uppermost. NMW2013.39G.23. Scale bar: 500µm. J, fragment with partially intact recurved border. NMW2013.39G.24. Scale bar: 500µm. K, presumably intact specimen. NMW2013.39G.25. Scale bar: 1mm. L, folds on upper surface of thallus.NMW2013.39G.26. Scale bar: 200µm.

Fig. 6

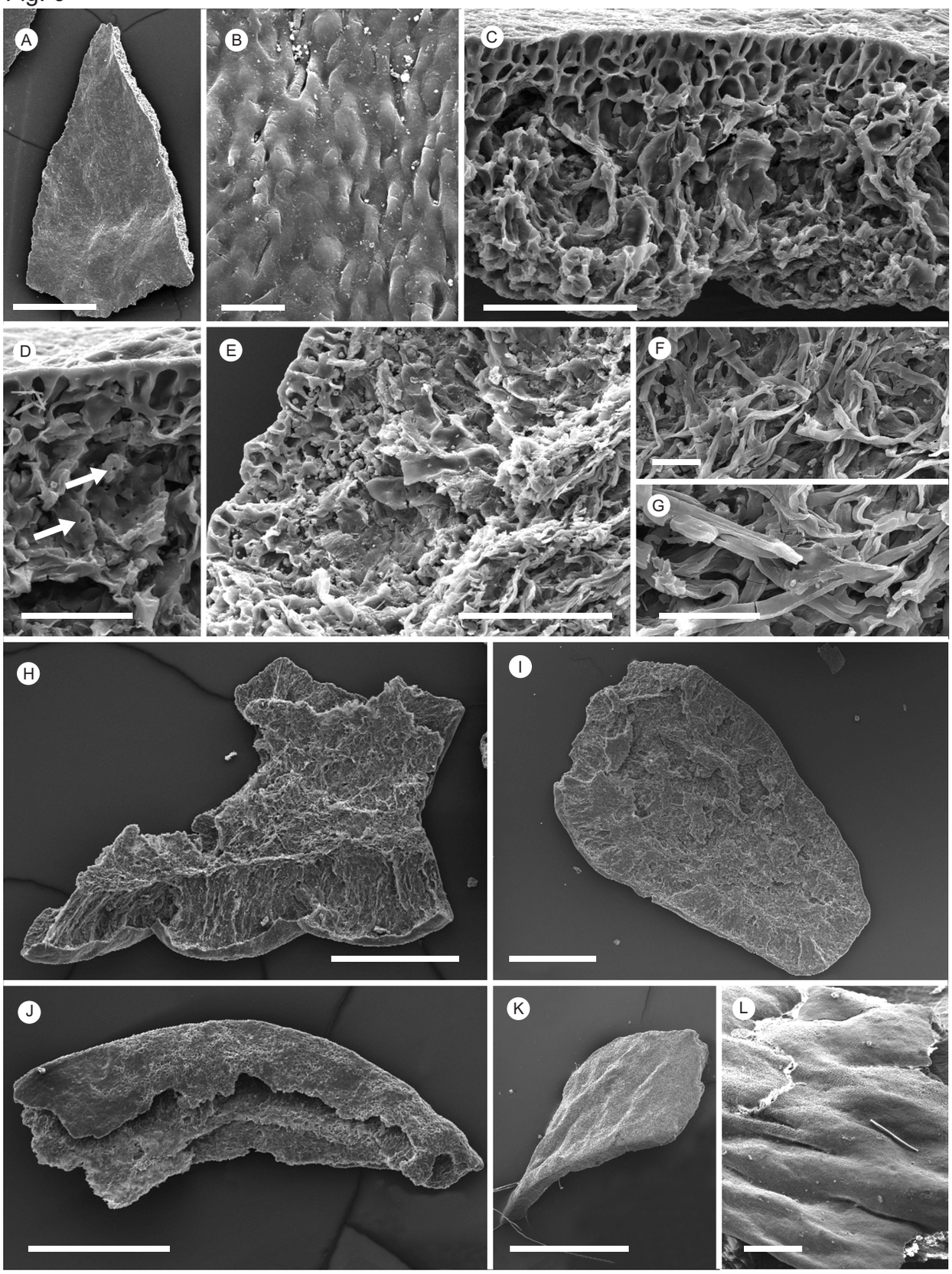


Figure 7. SEM images of thalli with incised surfaces. A, margin of specimen with protruding cortical cells. NMW2013.39G.27. Scale bar: 200µm. B, C, oval areas before incision. B, NMW2013.39G.22. Scale bar: 50µm. C, NMW2013.39G.28. Scale bar: 20µm. D, E, presumed early stages in delimitation of cortical cells. D, NMW2013.39G.28. Scale bar: 50µm. E, NMW2013.39G.23. Scale bar: 20µm. F, variation in extent of cortical cell development including voids. NMW2013.39G.24 Scale bar: 20µm. G, H, fully differentiated cortical cells. Scale bars: 10µm. G, NMW2013.39G.26; H, NMW2013.39G.29. I, J, slightly protruding cortical cells. I, NMW2013.39G.30. Scale bar: 20µm. J, NMW2013.39G.31. Scale bar: 10µm. K, protruding cortical cells and area where cell disintegrated or removed (arrow). NMW2013.39G.32. Scale bar: 10µm. L, voids forming reticulum. NMW2013.39G.25. Scale bar: 20µm. M, N, disorganized surfaces following loss of cortical cells. NMW2013.39G.33. M, Scale bar: 20µm. N, Scale bar: 50µm. O, P, variation in surface development. NMW2013.39G.25. O, Scale bar: 50µm. P, Scale bar, 20µm. Q, emerging cortical cells. NMW2013.39G.31. Scale bar: 20µm. R-Y, fractured cortex with hyphal tips. Arrows indicate possible intact proximal ends. Scale bars: 20µm, except V: 50µm, Y: 10um. R, NMW2013.39G.29; S, NMW2013.39G.26; T, NMW2013.39G.31; U, NMW2013.39G.27; V, NMW2013.39G.28; W, NMW2013.39G.34. X, Y transversely fractured cortical cells. X, NMW2013.39G.22; Y, NMW2013.39G.35.

Fig. 7

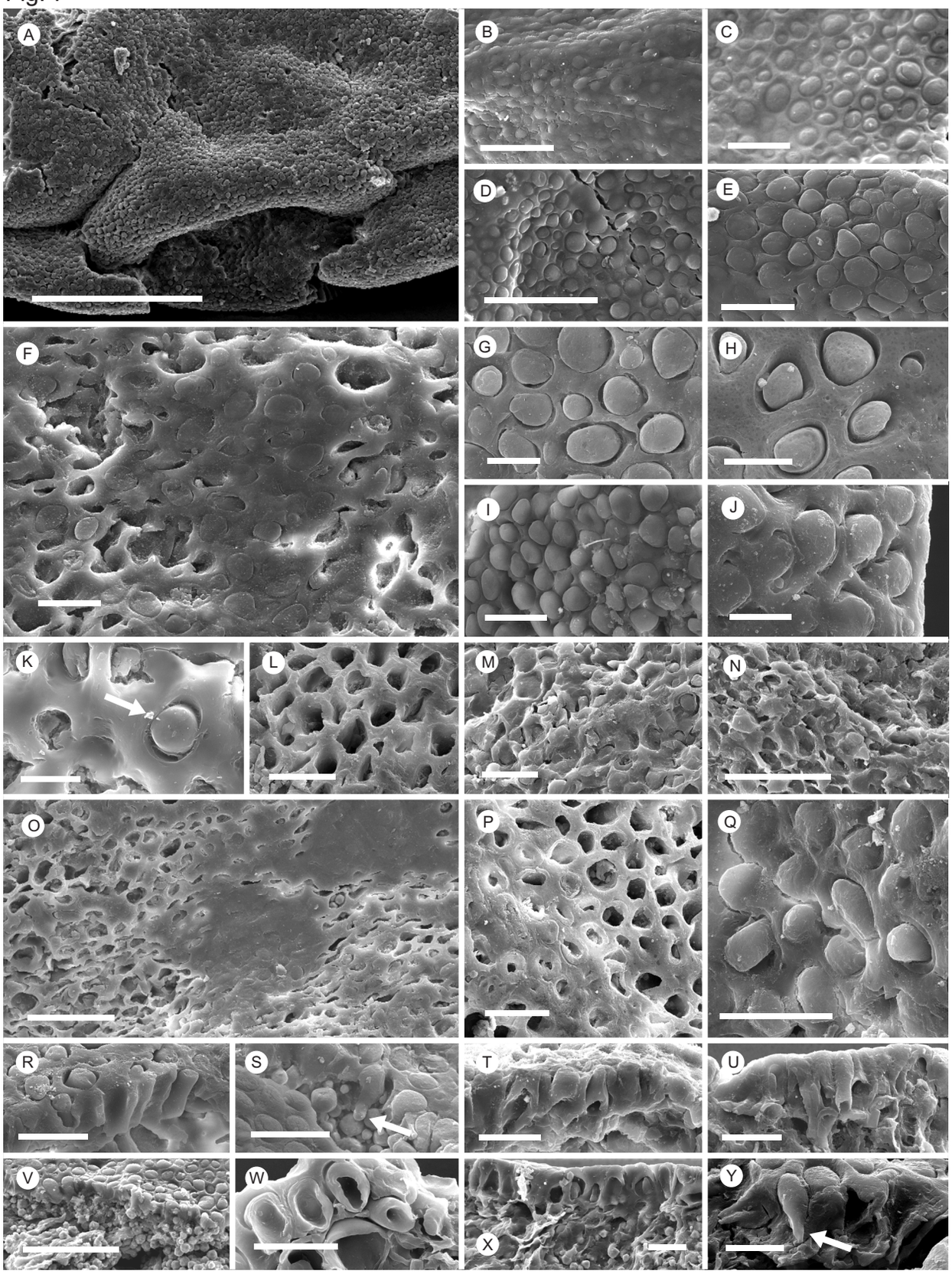


Figure 8. SEM images of specimens (possible intermediates) with variation in cortical incisions. A, C, anticlinally fractured cortex. Scale bars: 20µm. A, NMW2013.39G.36; C, NMW2013.39G.23. B, D, NMW2013.39G.37. B, surface of thallus with incomplete incisions. Scale bar: 20µm. D, protruding cortical cells. Scale bar: 5µm. E, surface with cortical cells missing. NMW2013.39G.32. Scale bar: 20µm. F, fragment of cortex overlying layer of narrow hyphae. NMW2013.39G.38. Scale bar: 100µm. G, poorly preserved palisade hyphae below perforated cortex. NMW2013.39G.39. Scale bar: 100µm. H, remains of palisade zone hyphae below cortex. NMW2013.39G.27. Scale bar: 20µm. I, aligned narrow hyphae of basal layer. NMW2013.39G.35. Scale bar: 50µm. J, surface with sporadic perforations intermediate with *Cosmochlaina* sp. NMW. 2013.39G.40. Scale bar: 50µm. K, M, lower surface of thallus with remains of hyphae. K, NMW2013.39G.29. Scale bar: 20µm. M, NMW2013.39G.39. Scale bar: 50µm. L, fragment with recurved surface viewed from below. NMW2013.39G.41. Scale bar: 500µm. N, dimpled surface of L. Scale bar: 20µm. O, P, fractured cortex with cortical cells below surface. O, NMW2013.39G.41. Scale bar: 20µm. P, NMW2013.39G42. Scale bar: 50µm Q, R, Fractured thalli with cortex and palisade hyphae. NMW2013.39G.41. Scale bars: 50µm. Q, arrow indicates rounded tip of palisade hypha.

Fig. 8

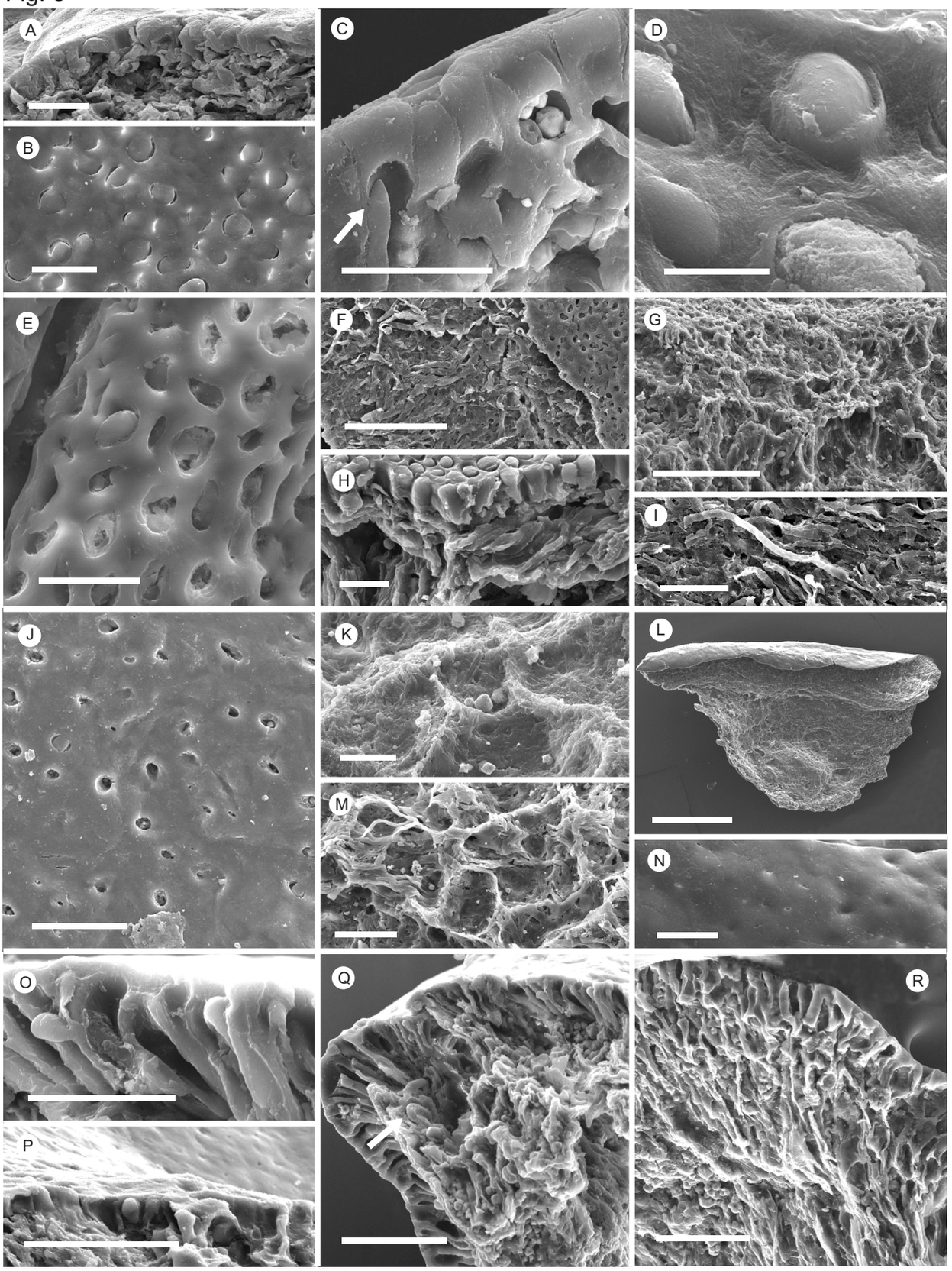


Figure 9. SEM images of thalli. A-C, fragment of cuticle with marginal folds (B) and unusual markings (C) on predominantly smooth cuticle. NMW2013.39G.43. A, fractured edge with presumed hyphae below the surface (*cf* Fig. 8O-R). Scale bar: 20µm. B, Scale bar: 200µm. C, Scale bar: 50µm. D-F, incised specimen with raised areas and central depressions. cf. lichen pseudocyphellae. NMW2013.39G.36. D, Scale bar: 200µm. E, F, Scale bars: 50µm.

Fig. 9

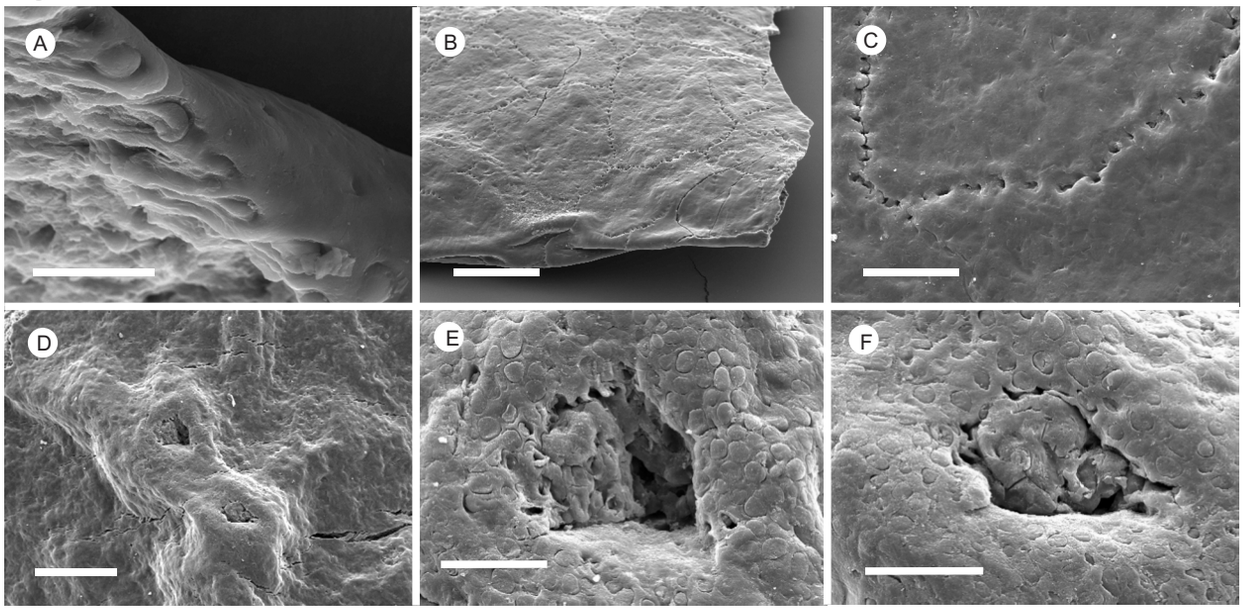


Figure 10. Light micrographs of thalli with incised surfaces following treatment with Schultze's solution. Scale bars: 20µm. A-B, NM W2013.39G.28. C-G, NMW2013.39G.27. Outer cuticular covering remains in G.

Fig. 10

