

On the Origin of Plant Species

By means of natural mechanisms of cooperation,
symbiosis and the establishment of a context of care

Or

How the Earth was won

A macroscopic history

Jet Wester ©

2021 / 2025

MMXXVI



This history is dedicated to our beautiful *Marchantia*. Mother of all further plants. And still
 alive today. You spawned rainforests. That cradled tigers. Cradled us.
 You should have continents named after you

Notions about evolution as hard and ruthless are ingrained, at least in popular thought. The same thinking also crops up in so-called real science, when evolution is blindly equated with natural selection. Our history will clean up this conceptual mess, that has bedeviled darwinian theory from the beginning. Evolution is a friend. To the fittest and the misfits alike. The granite wall of reality - the real watershed - is something else entirely. Evolution tries its best for all its offspring. As it must. It is mechanical, after all.

- This history, Part 1,
 from footnote 5

The footnotes with this history tend to be quite big, as they try to add serious depth and connective tissue to the tale. Arguably the most important work.
 And arguably the most fun parts to read, too

Impressum

The Late-Silurian herbaria behind this history reside with the national research institute for biodiversity of the Netherlands Naturalis. The material is available under the international Shenzhen Code. Every claim, photograph and fossil matrix of this history is thus open to peer review.

If peers can still be found. There has not been much to write home about from the Silurian fields for decades. Not until the rather overwhelming, game-changing material became available that is the subject matter of the present monograph. The earliest macroscopic life on land was more sophisticated than we knew. Suggesting that templates for plants above the waterline could have been available rather early. Indeed, many liverworts - the first plants on land - have to this day an aquatic form **next to** a land form. A botanical, amphibious phase? To test the land for living? Brace for terrestrial gravity? Learn to breathe air? Interfacing through their skin - like water plants - as the (non-vascular) liverworts still do, even on land, may well be an indication of their ancestry. As would their clonal reproduction. Down to an archaic but ruler-straight sh(r)edding of pieces of themselves.

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For a two-page observational summary of our history, see the first addendum at the back of this work. This book is a scientific manuscript, not a publication. There seems to be no academic context anymore for our Silurian botanical niche. Until you revive it. The material is here.

Arnhem, autumn, 2025

w h y t h i s b o o k

Biological analyses involving evolution most always show our hero in the middle of a task. Evolution is rarely seen taking a breath, holding still to reflect, hesitate, begin. Mass extinctions could help. To find out what evolution did next. But even that would still be in the *middle* of things.

A real treat would be a real beginning. Giving us time to actually meet the wizard. Learn about its character. Its playfulness. Its ethics and its visions, far and near.

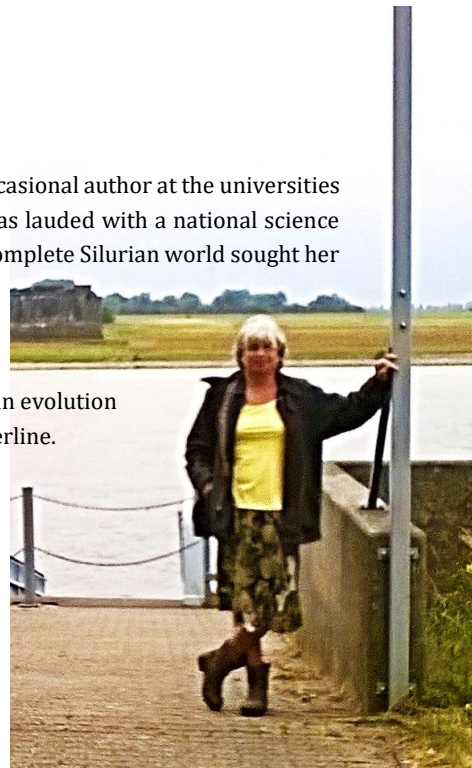
This history will bring just that. By closely following evolution as it made its first appearance on land. Making a home for its landlubber children in ways that will put evolution in a new but also a strangely familiar light. *Evolution as a friend*. That cares for and shelters its offspring. In ways we didn't know. Studying this history may well forge a bond. Between it and us. As with family.

About the author

Ms. Jet Wester is an emeritus research fellow and occasional author at the universities of Utrecht and Nijmegen in the Netherlands. She was lauded with a national science prize in 1989. During the covid lockdowns a fairly complete Silurian world sought her friendship, offering a treasure of fossil matrices, clear as photos. Begging equally clear analyses –

of the mechanisms, trials, choices and successes of an evolution at work in a brand new learning lab. Above the waterline. Where we may witness the actual formation of the first ever land plants; with evolution also helping these firstlings on their way. Organizing their first gatherings. And wanderings.

All this, it must be said, with evolution flaunting such convincing, elaborate genius, already in these earliest stages, that its work here may indeed be deemed a realistic cue for the whole party on land to unfold. Our Silurian material does have the serious markings of success. At least four of our fossil plants are here until this day. Which made the project worth the effort.



The author. Above the waterline

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Part one

Introduction

Section 1: The Late Silurian

0. Introduction

These pages aim to show how the Earth became a world - our world - some 470 million years ago. Based on newly found layers of a landscape, that were fossilized, giving us a time warp of the first and crucial steps of life on land. Large enough to be seen. Never observed before. The birth of literally the first upright, modern land plant. As it is happening. Inventions and strategies for building a world. A history built on, say, the Rosetta Stones of nature itself. Holding a wealth of information – of an actual creation day.

Our first land dwellers will indeed be plants. And fungi. Animal evolution would need a cradle of vegetation first. Four of our firstlings still live in our gardens today. With their fungi. Hiding from unwanted fame – for the last four hundred million years. If not five. And now only ten pages away. ↓ Sorry, guys.

So. The original fields. What they mean - and how they came to be. Touchable and *there*. Fossils are real things, after all. That literally let us sit next to what is happening 400 (!) million years ago. As it is happening. A full creation story. Preserved in stone. Our prime heritage.

And this. As these early worlds took shape, they also showed something of, let's say an evolutionary culture of beginnings. Evolution when it's at home. Still far removed from struggle and strife. Its own, free expression, showing what seems to be a mechanical slant towards the helpful and the benign. Evolution being a builder and shelter of life, after all. The expression itself also shaping that first, form-defining work. Where tasks - as befriending the wind, counteracting gravity, seeking moisture, leaf design - will instantly translate as the elegant integrity that is also & still our own context. ¹⁾

1. The reach of this history

This is a history of the Late-Silurian Period on Earth. It describes one of the farthest leaps of evolution ever. That will be but a small step for the actual players.

The Earth is still a barren place. The only life is water life. But things are changing. Freshwater

plants have been successfully negotiating the waterline and are establishing fledgling floras on the shores of streams and lakes. Which means land.

With all that would entail. Developing the equipment to breathe plain air. Finding the calibrations for these new gulps of gaseous exchange. Helping to build an atmosphere for the Earth, while at the same time preparing the ground, in more ways than one, for the young and vulnerable flora. To further establish and consolidate its foothold on land.

Which will of course mean building a safe and sturdy haven of terrestrial biodiversity. Plant species. Preparing for colonizations further afield. Things that will involve an acquaintance with many new parameters. Such as terrestrial gravity; good for many inevitable trials and sometimes dramatic errors.

The history will use Late-Silurian material, but in reality it also harks back considerably further in time. At least implicitly. Spores of the most important Silurian firstlings, the liverwort mosses, were already found a whole geological period earlier. Which means that our history will in fact cover a period from at least 470 million years ago - the Mid-Ordovician finds of liverwort spores - to the Late-Silurian Period, about 423 million years ago. Which is the time of the birth of the first 'modern', vascular-type land plants.

With the proviso that liverworts could in fact be (much) older than their first spores, if their simpler clonal propagation would have preceded their development of spores. See this footnote ²⁾ .

A full 500 million years for the first macroscopic liverworts on land wouldn't surprise us.

2. Thalli and fungi. Two friends that made our world

The work on this history began with a recent suite of uniquely rich, fossilized layers of land plants, harbouring a first terrestrial flora, large enough for the naked eye to see. The most important finds were unearthed in the summer of 2021. Details of their (now) mountain range location in Parts 2 - 4.

The new material provided a wealth of context for the plants, where the fossil record of the world until now could show little more than a few stray sporophytes, looking like rather beautiful if somewhat displaced hieroglyphs; each on their own, empty page.

The new finds let the Late Silurian come to life. With their very own beauty, their fledgling landscapes, and an often endearing closeness to our own world. Which would all be assets to our story, of course.

The greater importance of the material, however, stems from its unique level of completeness. Giving us a wholeness, at long last, for these firstlings, of which we were privileged to find their missing plant halves (in fact: more than halves) called gametophytes, or thalli. Which are the nourishing plant bases that sit on the ground. Never seen until now. In their equally observable and detailed habitat. Details that also predict how futures would fan out. How the Earth was in fact won. Pictures are waiting in the wings ↓ .

Next to these vascular-type plants we also found many equally new and equally stunning species of liverwort. Showing themselves - and their proverbial colours - equally by their thalli. By which we could establish that at least four of these heroes are exact images of liverworts still alive today. Truly jewel-like fossils that in comparisons (now possible) also show that the vascular vegetation on land unequivocally *evolved* from a highly recognizable liverwort. Possibly even still extant.

All this in contexts of fledgling ecosystems, with crucial roles for a fungal symbiosis, and for colony-like organizations. Two ways - two collaborations in fact - by which these earliest plants could get a foothold on land. At all. Some plants also working towards more individuation, in preparation of wanderings further afield. Which will show on, again, their thalli. This time as a very ingenious outgrowth, that will in fact be a horizontal taproot, above ground, that can be seen tapping into moisture- and nutrient-rich grooves and dells in the fledgling landscape. As the coveted hinterland will often be too forbidding, still, for vertical roots to penetrate (or find what they would seek).

Add to this an indeed amply observed fungal symbiosis. That will provide our fledgling flora with a rucksack of moisture-retaining nutrient medium, meant for its offspring. Which would be just as conducive to the colonization of a still barren & often hostile hinterland.

And this. These same fungi could, in passing, also enhance and even augment crucial CO₂ levels for our plants - as private 'hand-in-glove' exchange factories of carbon dioxide and oxygen, given a still less-than-robust atmosphere of the time. All the more so in the even earlier, Ordovician Period. Where our liverworts were born. So, structural, extra CO₂ as well. As a second royal fungal present. Possibly equally crucial. ³⁾

This on top of a general principle that local augmentations of carbon dioxide levels will *always* enhance the robustness of plant life subjected to it. Often greatly. Then as well as now. See Part 2 of our history, footnote 1. With thanks to Dr. Hope Jahren.

Which leaves us, for now, with an elephant. Still patiently standing in the living room of our history.

How come that we, here, now, would be able to present all these new & unheard of Silurian riches and insights... that really should have been the prerogative of heroes from 85 years ago? By names of Isabel Cookson (yes, she of the *Cooksonia* plant), her colleague William Henry Lang (who gave *his* plant *her* name), and the likes of the independent and independently famous Miss Mary Stopes (who got more than one part to play in her lifetime).

The answer is that the unprecedented, almost complete preservation, 423 million years ago, of the riches in our care would have been the result of a one-off calamity, momentarily freezing this whole fledgling Silurian universe in time. With all the information it contains. For nature to quickly seal and fossilize - think Pompei - and for us to unveil again and analyze, equally without delay. Almost as a sport - to mimic an equally swift safe-keeping of this cradle of land life, at our end of history. And take it from there.

The key here would again be the fabulous fungi; perhaps the real masters of the operation. To show them in full, these movers of the world, our history proper must first get going. So let's bring on some pictures. Long overdue.

3. Fossils and photographs. Comparing Then and Now

Both once-in-a-lifetime scientific windfalls as mentioned in previous pages - the gametophytes for the vascular types, and the six liverworts - suggest that for both types of plants the settling on land would have been a precarious undertaking. Both needing the help of a collaboration. The liverworts helped each other, where the vascular-type plants - such as the rather famous *Cooksonia* - were greatly, probably even crucially helped by a symbiosis with a fungus.

The reader may note that with an uncertain outcome for the vascular plants, our own implied existence would have hung in the balance as well, at that juncture in time, 425 million years ago. The order of things is inescapable. No upright plants, no rainforests, no tigers, no us. Here is what happened ↓ .

Gametophytes - thalli - will be known to many garden friends as the lobed, green, horizontal 'cushions' of an Umbrella moss, sometimes found as stowaways with a pot plant from the garden center. These are mosses, liverworts, not vascular plants, but still spore plants, same as ancient *Cooksonia*. And with helpful similarities.



Marchantia polymorpha liverwort - 'Umbrella moss'

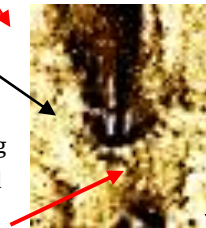
Compare the juvenile umbrellas on the right, sprouting from neatly tailored holes in the horizontal gametophyte half of the plant.

Notice the 'ring' of reinforcing tissue around this hole. *Cooksonia* will have similar sproutings, out of similar gametophyte rings...



...as does the equally early land plant *Salopella*. From our herbarium, some 423 **million** years old, standing a proud 9 mm tall - not half the size of a garden cress - in its very own gametophyte ring. With a similar 'hem' or 'seam' for the thallus.

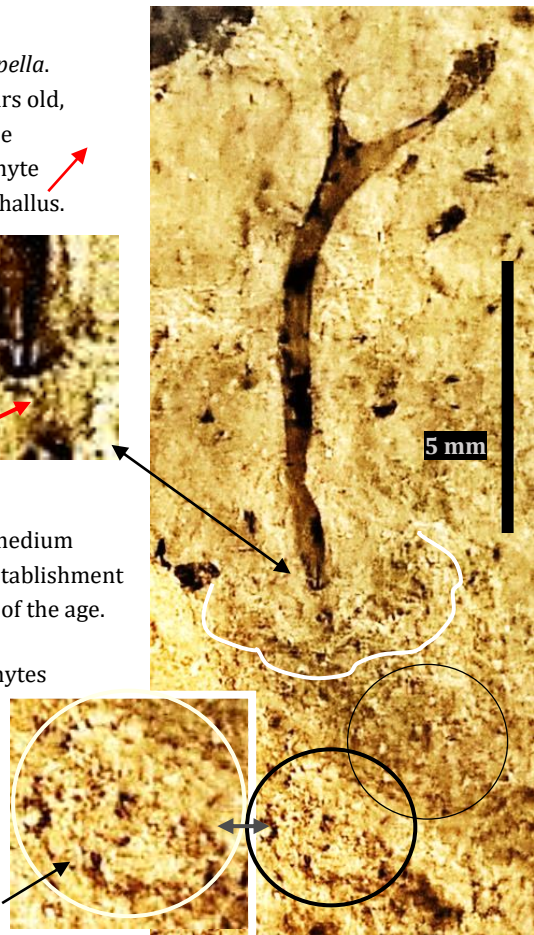
The gametophytes proper seem rather faded here, but still discernable. A friendly fungus gobbled them up, quickly recycling their precious nutrients in a world without soil or shelter, still.



In this the fungi were more than helpful. Their food- & moisture-retaining nutrient medium may easily have been crucial for the very establishment of a plant, at all, on the still barren grounds of the age.

Notice, with all this, that recycled gametophytes logically don't fossilize. Unless the fungi had something really lethal happening to them, freezing them in time, in the middle of their dinner. Which will be our analysis for this uniquely informative land layer.

Gobbled-up old rosette-like gametophyte of *Salopella*; used ring in the middle.



Salopella; Late Silurian (Ludlowian / Pridolian)

In some cases the recycling can be followed in its progress. The matrix on the right shows a *Cooksonia* gametophyte in the process of being eaten. Contours of the socket ring, and of the socket of the plant stem are still visible.

The plant stem is detached; its gametophyte half overgrown. Time stopped just in time, this time, to show what the fungi are about to erase further.



And one last & different sort of marvel, for now.

Cooksonia and the Umbrella moss shown earlier are not only evolutionary neighbours, convenient for explaining each other's workings: they were literal neighbours as well, a 423 million years ago. From this history, Part 3, and especially Part 5, footnote 1:

A nicely lobed *Marchantia* liverwort
Late Silurian; this herbarium. —————>
A living one next to it.



Detail of lobes, some cuticle missing; 3D fossil.
Possible gemma structures preserved
inside gemmae cups.

So. *Cooksonia*, and *Salopella*, may be the iconic first land plants - precious, famous and eons away; the tiny green, dragon-world cushions in our plant pot are in fact even (much) more ancient and as close to these heroes as anything ever was. Touching them is touching *Cooksonia*'s literal neighbour. Bridging more than four **hundred** million years.

And what's more: there were four of them. Liverworts. Or rather: there are. Still. On our doorstep. Their mutual friendship, forged worlds and worlds ago, not only let them survive: it let them survive together. And to this day. Which is why they - and their science - are such breathtakingly beautiful contraptions. And a superb blueprint for successful life on Earth.

4. On the nature of evolution (or skip to page 19)

This history was written as the work went along. The idea was to make the newfound Silurian wonders available as quickly as possible. As a result the history as it stands may not give all the *minutiae* of the textbook, yet. At least not in a systematic way. Which isn't a problem, as it also means not burdening our readers with more formality than would be needed for a sound & serious rendering of the tale.

An informal touch doesn't mean we will shy away from deeper layers of insight if we walk into them. A most welcome layer would be what our Silurian beginnings may tell us about evolution itself. A layer that already surfaced (e.g. in footnote 2, above). Also consider, even earlier, the title of our history. Which bears more than a chance resemblance to the title of the *magnum opus* of Charles Darwin, of 1859. His *On the Origin of Species*. The two titles next to each other will give this:

Charles Darwin	This monograph
On the Origin of Species	On the Origin of Plant Species
by Means of Natural Selection;	by means of natural mechanisms
Or the Preservation of Favoured Races	of cooperation, symbiosis and
in the Struggle for Life	the establishment of a context of care

The titles seem to describe rather incompatible vantage points. The difference, as we see it, would be that Darwin's book isn't about the origin of species at all. It is about a particular type of *development* of species - as brought about by natural selection, indeed. With some developments seen as firsts of a new line. Depending on the theory. Whereas proper origins, we say, would be about proper firstlings. That obviously don't depend on human theories to be. Or not to be. We'll try to clarify.

A species dies out. Another one lives. Evolution has nothing to do with that. It tried its best for everyone. For the deceased as much as for the this-time survivor. "Selection" comes not from evolution, but from the granite wall of reality. The same wall that determines if a trial will be an error or a success.

The only ripple in the pond of history, after an encounter with the granite wall, may come from man, who may draw a flag on his ledger. Or a new branch on his tree of descent. A good day's work of Attributed Significance. *Look, I did an **Origin!*** Nature itself, of course, will never know or care. ⁴⁾

So, what we have, then, are real origins, as a given (from nature), next to attributed firsts.

A most important practical difference between the two would be that real firstlings will still have the world to themselves. Without let or hindrance from scarcity or strife. Living, as they do, in recognizable, helpful, sheltering contexts. Made just for them. Their all-

important establishment on the planet. The peaceful stretch. Cradle of the limitless. Until scarcity kicks in.

The first macroscopic steps on land will show many such beginnings. Together with what could indeed be characterized as the establishment of a context of care (our title).

When scarcity is not a factor, evolution needn't give its attention to more than one, simultaneous, mechanical loyalty. In times of peace it may thus show itself more clearly as the best possible friend. That it indeed (always) is. Helping its children on their way. Trying to organize what they need – which in our case will be taproots, nutrient medium, augmentations of CO₂, angled branching, reproductive equipment fitted for the shelter of colonies. Our whole Silurian History, full of stuff. And always giving its best. Previous pages already spoke about this stuff, as it is the core of Silurian life & culture. ⁵⁾

But do not think that this peaceful stretch, this cradle of the limitless as we called it, would just be a preliminary phase, secretly waiting for evolution to get jazzed by scarcity, strife and worse, to roll out a healthy biodiversity. That is a fallacy. Our pristine, still frictionless Silurian world saw all aspects of diversification already laid out, tried out, and enjoyed for their first grand successes. Its incentive even *defining* all that is happening. Many plant species are seen fanning out in this way. Liverworts even giving birth to the vascular plants on Earth, *without need*, and without going under. (Still here and still crazy after all these years - that is: after they already **had** diversified into their many species; *right at the beginning*. Peacefully next to each other.)

Evolution really has no need for scarcity. Not even for its sharpest work. Whoever thought that helped protofascism become *salonfähig*. The Silurian history that you are in danger of reading would be proof that biodiversity may be disconnected from this fittest nonsense **as a necessity**. It isn't. Our meek, lovable, hurttable liverworts, all four still here, will be *All-Time Superior Winners*. But winning from whom? Pray tell. Superior to what? This great enchanted life is no stupid contest. Not intrinsically.

What we have, then, is the meek literally inheriting the Earth. Four species of them; over and over, as the very first of the first land plants; through the whole span of life on land – until today. Who among us evolutionists would have thought? Our right minds full of principles and game theory? While truth, of course, was only ever found in the ways of a child. The other Biblical proverb. Which gives us intelligence in motion. The way of a non-thinker. Like a bunch of bees. Or like evolution. *Not to be charted out*. Intelligence in motion is also how children - animal & human - learn. By play. Learning by play is intelligence in motion *par excellence*.

If you wish to regain this realm – go build something. Learn by doing. You had a surefire intuition once . . .

Section 2: The liverworts

In which six liverwort species are introduced. Four in detail. The very first of the first land plants, large enough to be spotted with the naked eye.

The plants were found a whole geologic period earlier than the earliest liverwort fragments that had sparsely dotted the fossil record until now. The rather primitive record holders were Mid Devonian.

This essay is not a summary of the essay in Part 3. The studies are supplementary. 6)

The essay

Six liverworts from the dawn of land life – *The Swiss Army Knives of evolution*

Liverwort equipment may often look quite ‘industrial’ - more like engineering than elegant fine art. Which seems an almost obligatory and vastly endearing trait of biological structures that are this mind-bogglingly ancient. Ordovician/extant marine animals would also be a case in point. Starfish and such. The somewhat later prawns. Elsewhere in our history this led to a honorary title for our beloved liverworts as the Swiss Army Knives of evolution. We now see that they are in fact the whole toolshed. But make no mistake. Industrial archaeology has its own & fully legitimate cult esthetic. We can see biker jackets.

- From this History, Part 5, page 149

Land plants on our planet had their beginnings at least 470 million years ago, when seaweeds and smaller algae had floated in from the oceans to freshwater reservoirs of streams and lakes - and gradually climbed ashore. With astounding creativity. One often thinks of evolution as an ever so gradual process of refinement. Yet nature also has its more sudden streaks. As with the appearance of the flowers. Or of the liverworts. With their more than 470 million years

of service (liverwort spores of that age were found), these were the first real land plants. Directly descended from complex freshwater flora - very probably an aquatic liverwort already - they needed little extra structural evolution. Some 25 million years later they appear to have a species richness of at least six readily recognisable plants; four of which cannot be seen as different from liverworts that still inhabit our parks and gardens today. In all their awkward splendour. Liverworts clearly were a superb idea.

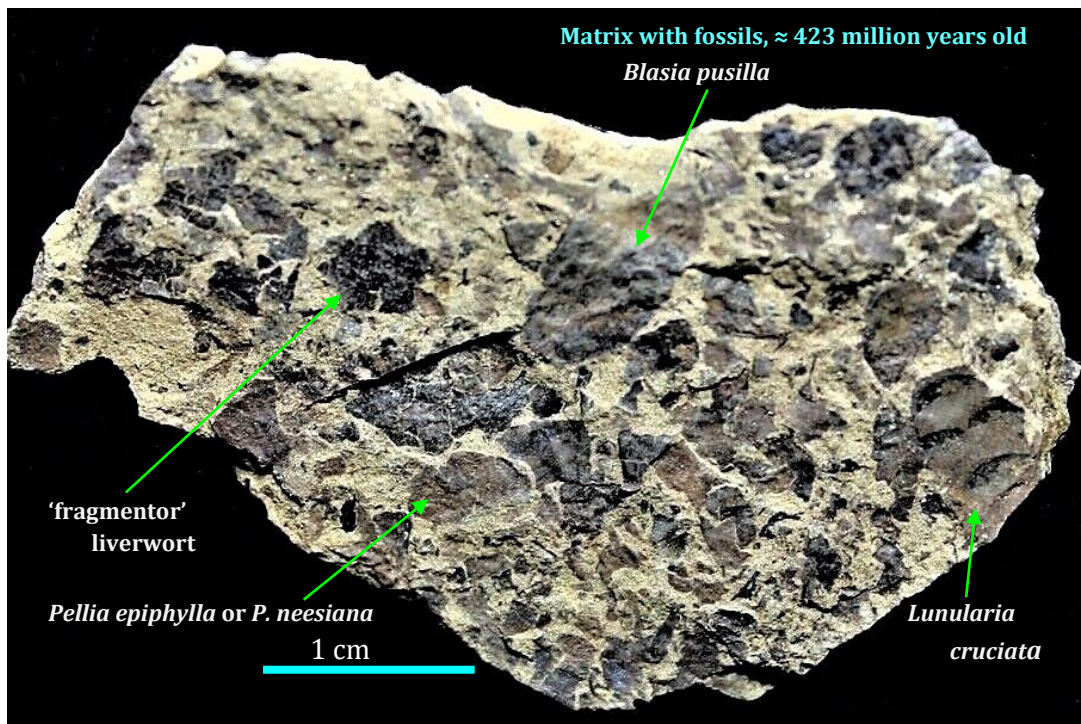
We had the privilege to find the first & only ever fossils of these six, intact down to the smallest detail. For four of them even their skin and pores will be indistinguishable from the defining skin and pores of the same or similar plants today. One extinct plant, a leafy *Naiadita*, briefly appeared again as a fossil in later Triassic layers. ⁷⁾

All our finds date from the Late Silurian; between 425 and 420 million years ago. Which is also the time when the vascular-type plants appeared - *Cooksonia* and friends. See Part 2 of this history. As a comparison: dinosaurs date back a 220 million years, the first flowers about 130 million years. Our jewels are hundreds of millions of years more ancient. Representing - being - the very dawn of life on land. And most of them still roaming the planet. As we speak. Gleaming & radiant as if they were minted yesterday.

Liverworts are mostly seen as an evolutionary branch of mosses. They are spore plants with no real vascular strands, that seek or make a moist context for themselves. Our four species will be similar to extant *Lunularia cruciata* (common name: 'Crescent cup moss'), *Pellia epiphylla* ('Common Pellia'), *Blasia pusilla* ('Common kettlewort') and *Marchantia polymorpha* ('Umbrella moss'). *Marchantia* has already been shown in the Introduction to our study, on page 16, above. See also Part 5, footnote 1. The others are equally common residents of the moderate climate zones of the world today. ⁸⁾

The fossils were found on many matrices (shards of slate). Often a whole tiny forest of them. Making their survival a communal effort. Giving each other all the breathing space they need, and creating for the community as a whole a sufficiently moist micro environment, with possibly even some level of temperature regulation. In an era where there was no shade from other plants yet, nor many of the other protectors from the elements we naturally take for granted. No topsoil to speak of, no shelter from wind, frost or heat by higher vegetation - and only a fledgling atmosphere with hardly a protective ozone layer. ⁹⁾

In this context beautiful micro worlds appeared. The forest on the next page shows three familiar species together. By far the first land plants ever. And precisely these, still here today. Survival by cooperation being their life-giving message?



Our proposed *Lunularia* fossil compares to the extant, still living ones in the following ways. Seemingly clear conceptacles, possibly with gemmae inside. Seeming slightly pushed-in aspect from a weight of sediment on top of the plant. Conceptacle rims still discernable despite this slight pressing.



An extant determination would be a thallus surface dotted with pores bound by pentagon-shaped

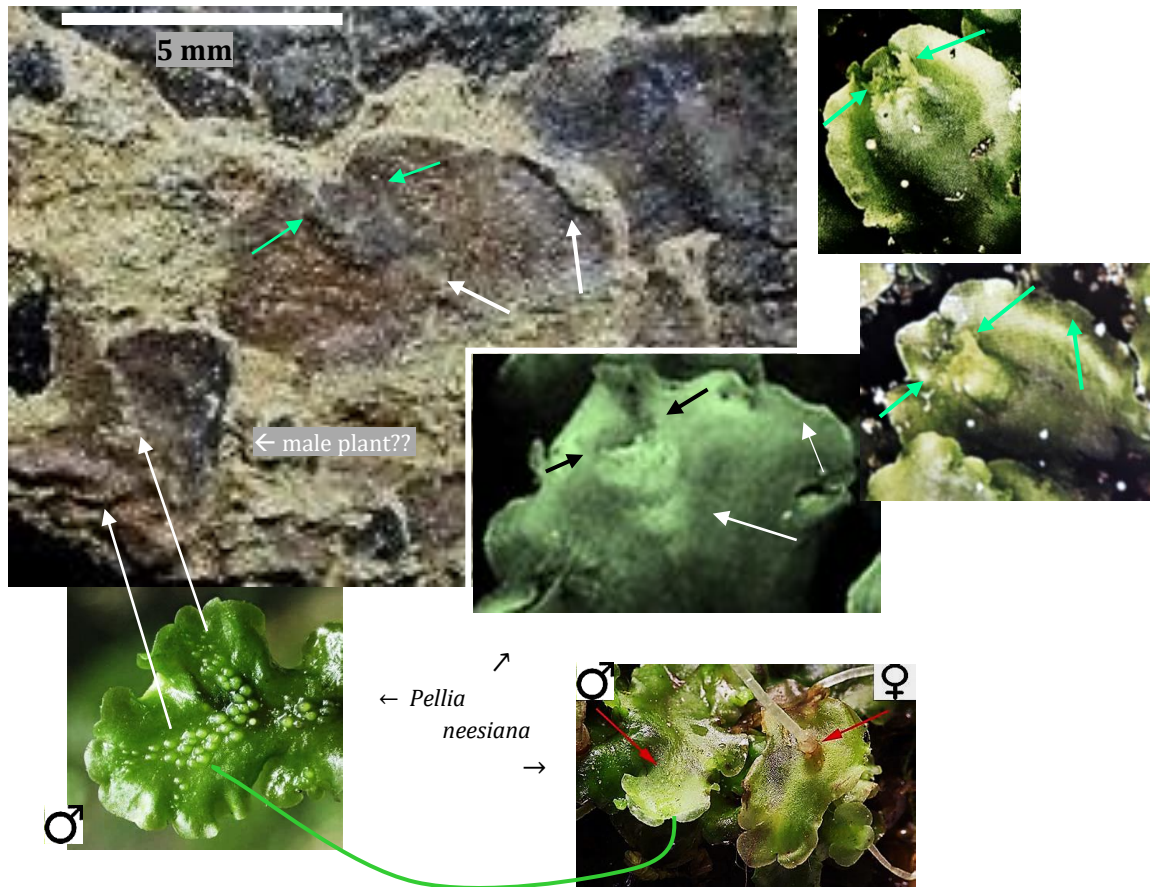
boundaries; see the example on the left.



Microscopic → analysis of our fossil seems to generously confirm this, where the thallus is still intact, on the right.



The next species, on the same matrix as the above *Lunularia* has many detailed similarities to an extant *Pellia neesiana*, a dioecious thallose liverwort, or its monoecious look-alike *P. epiphylla*:



With this species the thallus seems wholly different from the *Lunularia* above. No pores on top of cushion-like pentagons; these pores are seemingly sunken in indentations, reminiscent of more complex stomates, seemingly with guard cells.

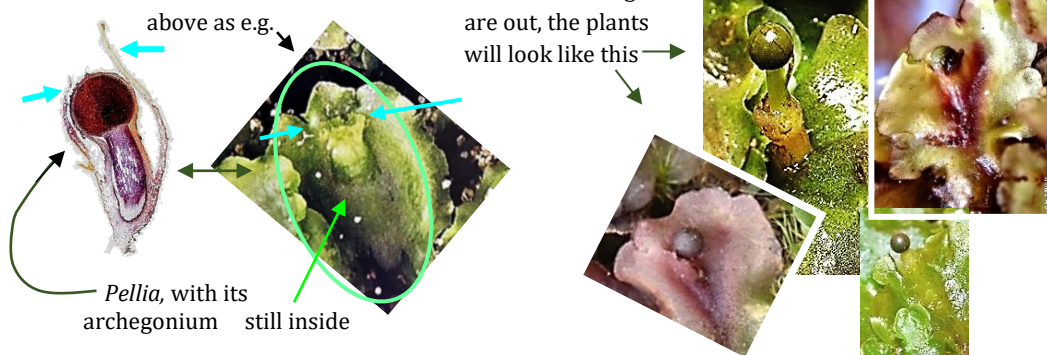
Compare these ↓ photos of similar stomate-like pores (structures resembling guard cells) of extant *Pellia neesiana* and its close relative *P. epiphylla*.



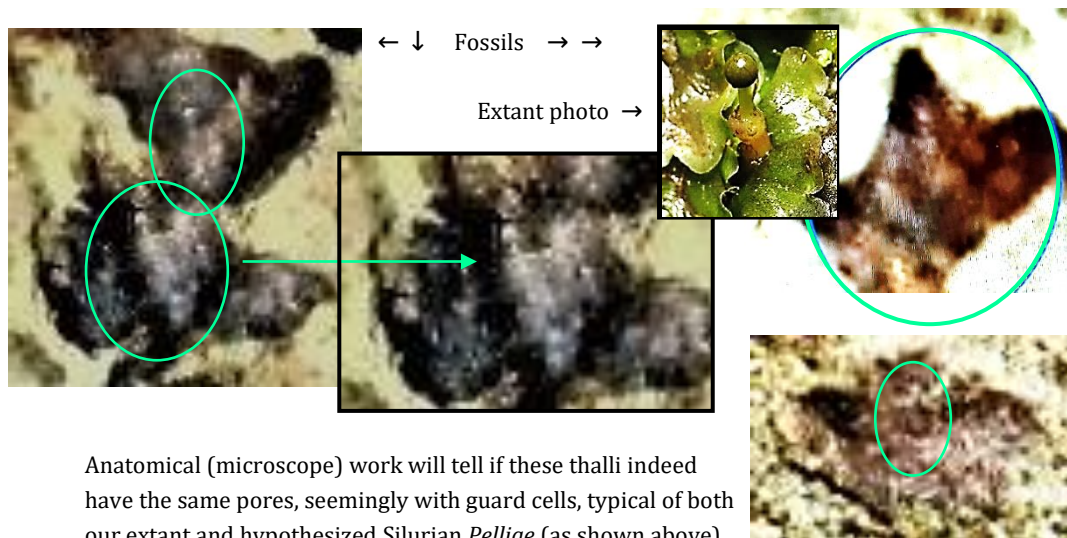
≈ 300x magnification of the above fossil ↑



Further work on the two *Pelliae* will also regard the sexuality of the plants. For example, the (female) archegonia - where fertilisation and spore production happen - will in due course come out of structures



The suite of matrices that holds the fossils of our *Pelliae* (as the one on page 21, above) indeed also flaunts probable archegonia, in the right dimensions, just coming out:



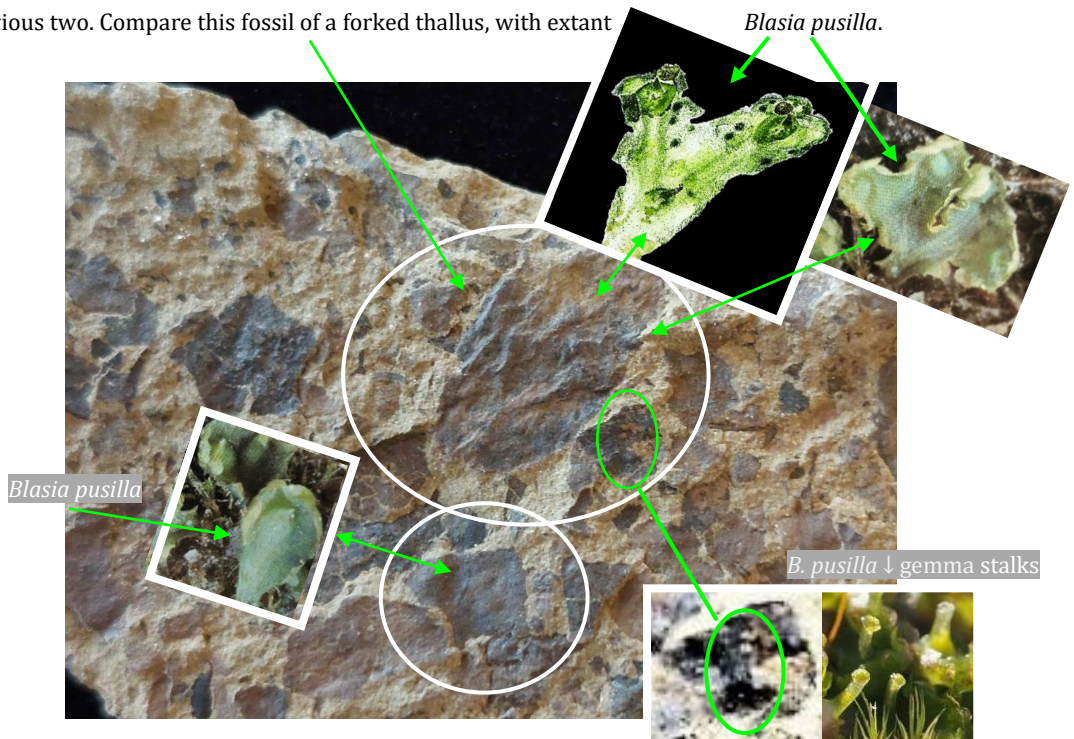
Anatomical (microscope) work will tell if these thalli indeed have the same pores, seemingly with guard cells, typical of both our extant and hypothesized Silurian *Pelliae* (as shown above).

The fossils could also qualify as archegonium structures of *Blasia pusilla* in our next analysis - if they happen to match the pore structures of that species instead of *Pellia*'s. See below. For now we do consider *Pellia* a more likely candidate, as none of these structures tends to fork, as many *Blasiae* do.

That these would be fossils of emerging archegonia of species of complex, 'modern', Late-Silurian - very possibly even Ordovician - liverwort seems uncontroversial, at this point.

The material is very rich.

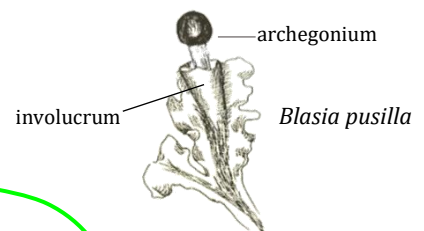
And a third species. This one resembling a *Blasia* liverwort, on the same matrix as the previous two. Compare this fossil of a forked thallus, with extant



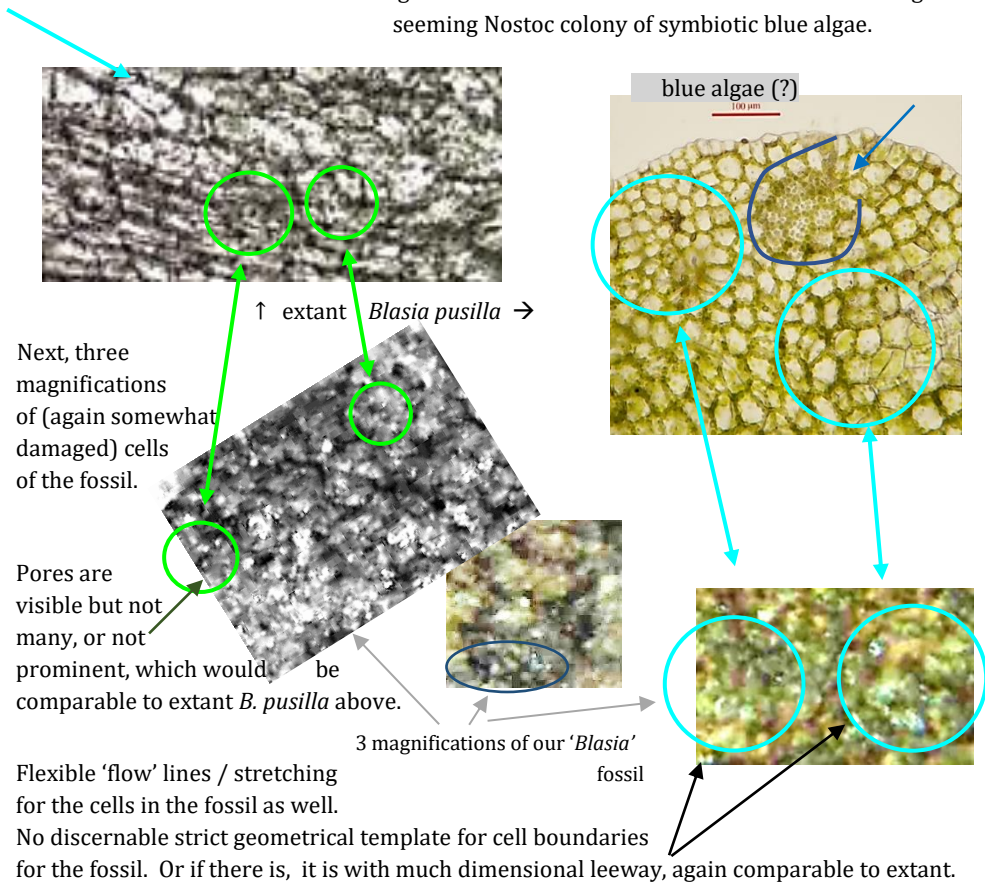
The sometimes flask-like aspect of extant *Blasia* will naturally give way to a slimmer shape - as seen in the fossil - when its archegonia come out.

See the schematic drawing on the right:

A magnification of the fossil indeed seems to show such a later stage in the life of the plant. The emerging archegonium would have just hatched, and seems to still be wearing a 'hat' of the broken involucre, where a rest has shriveled back.

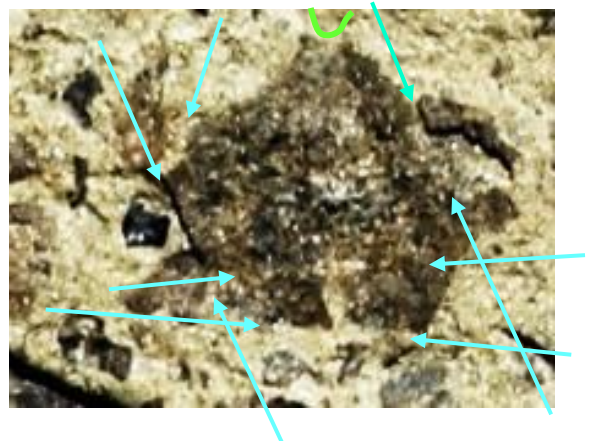


And two magnifications of the thallus surface of extant *Blasia pusilla*. Cells with chlorophyll that also allow a flexible stretching of the thallus. Cluster of smallest cells on the right as a seeming Nostoc colony of symbiotic blue algae.



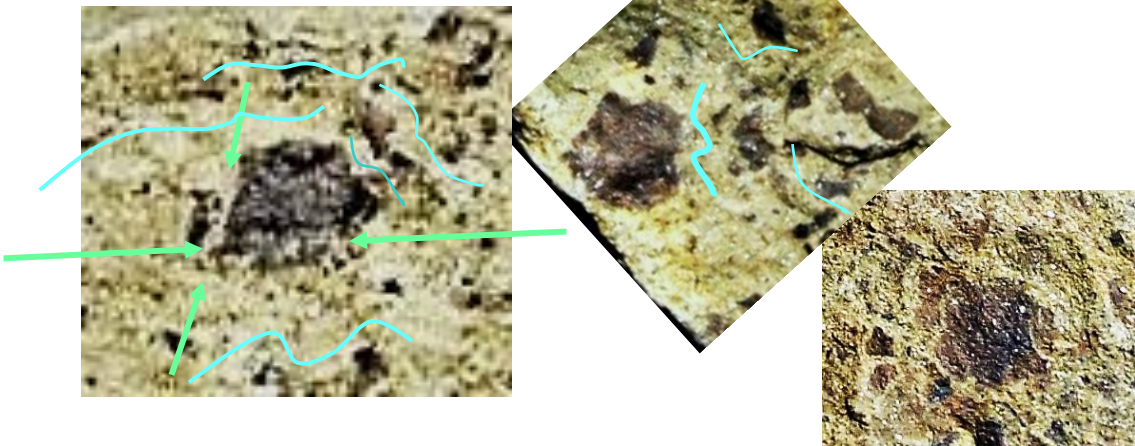
Our rich fossil material of Late-Silurian liverworts also seems to harbour other consistent but more enigmatic species; one of which we would like to present here together with the previous, more familiar ones. To be found on the same matrices. This liverwort is seen to have basically a pentagon shape (five sides), with a sort of 'cupid's bow' on top as a quick help with identification. The liverwort seems to shed rather big chunks of itself, very probably as a crude means of asexual reproduction.

Fragmentation of the thallus as cloning is known for liverworts (Armstrong (2014), p. 466). Also compare the more common and sophisticated home made 'cuttings' that are the 'gemmae' structures of some liverwort species. See Part 5 of this study. Further specimens seem to also show the dynamics of our more crude cloning.



Fragments seem to float concentrically away, like ripples
Walking on rhizoids? Nap in the sole of the rhizoid
the barbs on an ear of grain, walking up your

in a pond.
fabric? Like
sleeve?



A nap could grow concentrically outwards from the center of the sole of the mother plant.
(The 'nap' would be like the 'grain' that the fragment cannot go against. → Only outward.)

We have recently begun some comparative work with living specimens and communities of liverworts, to seek out parallels and behavioural patterns for the plants which might further illuminate our Late-Silurian data (to us). One very interesting result seems to be that extant liverworts can indeed also be seen to have these same (pseudo-)symbiotic relationships with fungi; to recycle remnants of their thalli as new nutritive medium for their next generations. In the Silurian era, such symbiotic friendships would have been instrumental for the establishment, at all, of the emerging vascular, *Cooksonia*-type plants, on the still barren grounds of the age. Liverworts seem to be showing, to this day, the same (sort of) processes and mechanisms in detail. Not as another tiny bryological side show, but as one of the very few pivotal moves of evolution that made you and me possible. 10) 11)

Notes

1) As a bit of a teaser, or even a spoiler, here some giveaways of where these marvels can be followed in the text.

Dealing with the pull of the wind is touched upon while discussing the neatly rounded, three-lobed floor plan of juvenile vascular plants, next to a more sprawling aspect of the bases of adults, that have to brace for the leverage of their full sporophyte 'pole', swaying in the breeze. Instances where animals would put their feet further apart. See Part 2, Section 4 and its footnote 4. Working with the wind on a much grander scale is the subject of footnote 2 with this Part 1 of our history; directly below ↓ .

A particularly beautiful case of dealing with **terrestrial gravity** is found in the difference between the curved branching of the first vascular plant *Salopella* (that branches as an U) next to the angled branching of the somewhat later *Cooksonia*; (as a Y). We have fossils of *Salopella*, busy making an angled branch Y , **above** its normal U. We won't spoil the point of the story, but we do somewhat proudly refer to footnote 7 with Part 5 of our history.

Leaf design had its place already underwater. In the Silurian, an aquatic template for leaf-like structures seems to have been transplanted **as is** to a land situation (probably via amphibious plants). Our history flaunts fossils of a leafy land plant (possibly a leafy liverwort; we have more of those) with what looks like a modern main vein running from the stem of the leaf to its tip. Which is actually an aquatic remnant. A reinforcing, *solid* rib, without sap vessels, to make the leaves sturdy in the flow, pull and turbulence underwater. Solid ribs thus imply an aquatic link. The same feature is known today. See Part 5, footnote 7, towards the end. Where we are very loudly not yet arguing for our extant amphibious leafy moss *Plagiomium affine* as being indeed this same, at least Silurian fellow.

The quest for **moisture** will be seen already in this Part 1 of the story, with the addition that the horizontal taproots of the first vasculars, tapping into moist to wet dells and furrows, above ground, may also readily explain the absurdly early emergence of sap vessels as such. Way before proper vertical roots would even be possible. Proper roots had to wait until a build-up of at least some semblance of a moist and nutritious soil. For the roots to crawl into, but also to find what the plants would seek. See e.g. Part 5, footnote 4.

And thus it goes on. A Silurian Period of miracles that lets us follow the beauty and integrity of our world as it unfolds. Which in a more attentive society could have gone a long way in helping man find his footing again in our almost equally strange and barren 21th century world. With the example and model of a caring and sheltering evolution; which today would probably be considered “woke” to the gills; not the favourite of our latterday public culture, with its every message in unrecognizable overdrive.

2.) Terrestrial liverworts – Silurians as well as extants – most often have two types of propagation on the same plant. One is a clonal propagation, yielding offspring close by, only the bounce of a raindrop away from the mother plant. Which will build and maintain a communal, colony-like way of life. Next to a production of spores, that may go with the wind; opening up new horizons with their much farther reach, through the air.

Still in habitats of streams and lakes, young clones would have the flow of water. For travel, near & far. Once on land, however, the far part would require a new type of transport. The air, indeed. Fixed in their new abode, having climbed ashore, the plants would be directly exposed to the pull of the wind. Echoing an experience. Of currents as travel. That may well have moved the liverworts to work on wind-sensitive solutions.

A deeper reason behind this order of things (land first, spores later) would be that evolution does not plan or foresee things millions of years ahead of a first necessity.

The matter of this planning - or even foreseeing - of evolution, eminently belongs to our Silurian Period, with its firsts, on land, for almost everything. A totally different world from the aquatic. Our history will obviously see this thing many times, with our conclusion that evolution seems to us evidently not a chess player, "thinking" many moves ahead. For one: evolution seems to intuit more than "think", at all. Secondly, planning ahead would be like building a house of cards - that would become more foolhardy with every added idea. If only for the unknown or evolving external parameters. And evolution's own trials.

The data seems to show evolution much more as 'intelligence in motion' (think beehive); often staying rather close to the business at hand. An example is the way evolution throws itself into the adventure of making the first vascular-type plant from a liverwort. *Without preliminaries*. The liverwort starting point is not just used in its details - literally "warts and all" - but also as a still rather moist and vulnerable riparian *type*. No toughening of its thallus first. See e.g. Part 5, footnote 5.

So, evolution as not anticipating many moves ahead. That evolution is also not god-like in its *insight* in what the future may hold, will be shown in Part 4 of our history, where evolution, like anyone, has to *learn*, in the field, and the hard way at that, about a crucial difference between the dynamics below and above the waterline. Under penalty of a lethal plant disease.

That this lack of, say, a direct, long-term vision of evolution may nevertheless lead to enormous long-term *effects* - built up, bit by consistent bit - will be touched upon in footnote 5, below, with the example of an increase of intelligence over time. Evolution does have its consistent, mechanical, benign characteristics, that may well accumulate to what can be seen as a benign, long-term answer. Without it having been anticipated beforehand. Nice people ***just happen*** to create nice contexts. Even when their not-so-nice children love to take advantage of precisely that.

In this same way the emergence of liverwort spores - which will also introduce sexuality to the plant world - could well be another gradual accumulation. This time building on templates of the (aquatic) animal kingdom, where sexuality is of course used to ensure genetically fresh blood, and to enhance biodiversity. For our earliest liverworts such genetic bonus would not yet be relevant (there are no 'others' to mingle with, for one), but when the time comes for an equally functional *floral* sexuality (with a nod to Father Gregor Mendel, sir) the mechanism to make it happen will already be in the building. **And until then, our first, still token liverwort 'sexuality' will already have smuggled in a brilliant mechanism to palpate, isolate & package your genes - small enough to be shippable by air.**

3) As a start, compare this quote from Part 2 of our History, page 53:

In extension of this it may also be noted that fungi, like animals and humans produce carbon dioxide, a thing that plants rather crucially need. Having symbiotic fungi at hand could thus well have an additional advantage for these earliest vegetations - that have to make do with a still rather poor, fledgling atmosphere. Having your own small CO₂ factory - your own little blanket of enhanced carbon dioxide levels (CO₂ is heavy) - could well be an equally life-enhancing, organic part of a much needed reliable micro-ecosystem.

Fungi may look somewhat plant-like - slow movers; smooth-skinned, sometimes rooted - but they use oxygen as animals do. To burn food for energy. And to build things. Breathing out CO₂ as waste. Think of the fizz of a bottle of champagne – carbon dioxide as the residue from a sugar-eating yeast. Same thing.

Now imagine a soft, rhizoid-friendly bed of fungal nutrient medium - also for our liverwort forests. Same as they often have today. But now as early as the Ordovician Period. The Ordovician cradle of liverworts had an even poorer atmosphere, still, than our later Silurian era. It seems legitimate to at least daydream about this fungal symbiosis as perhaps crucial, pivotal & essential for the entire operation of life, settling on land. At more than one level.

It is good to note that such crucial roles for fungi may well have begun rather early. The Earth may well have been covered, at least in some places, with land dwelling green algae - before our bigger land plants were flown in. Algae that could have had their nutrients recycled as well (possibly as a prerequisite for *their* being there). With thus a real chance that fungi were already friends with existing fledgling floras; well before the Silurian. Indeed, the fungi in our analysis must always have come from *somewhere*. Possibly having contributed still more CO₂ to the low reaches of our atmosphere, where the plants are. (CO₂ is heavy; it tends to hover low.) More magnificent CO₂ in footnote 1 with Part 2 of this history.

And yes, algae + fungi also forged another famous collaboration. Together they built the lichens of the world. A type of friendship that may have begun very early as well, and for which we are also keeping an eye open in our Silurian material (see Part 3, footnote 6).

4) We could go on a bit longer about the somewhat sorry title of Darwin's book. As with "the Preservation of Favoured Races". A string of misnomers that clearly suggests if not implies volition upon volition. Choice upon choice. Almost as bad as *selection*. Really -

Similar with notions like *survival*, *competition*, *struggle*, that echo thoughts, of the day, of a bleak human condition. Compare Karl Marx, Thomas Malthus and Charles Darwin; same era, same country. Perhaps the mind, in its more primitive recesses, could not help seeing things in a human, or even a hominid way. We had to start somewhere. Which doesn't mean we cannot shed this borrowed socio-economic drama a 150 years later. Do you *want* evolution to basically belong with the humanities - or shall we make it a science, after all? We should be overtly rigorous about a lack of (metaphorical) actors in nature. Anywhere.

5) We can well imagine our idealized reader to be a bit at a loss, at this point. If evolution shows itself here as a reliable and capable friend and carer for its offspring, how does that compare with its image of allowing or even encouraging carnage, cut-throat competition? Most dictators are nice to children. We could name a few. Is this the same sort of crazy abyss, or what?

Luckily, it is not. Let us first mention that not an idea, or some philosophy, but always a

concrete case, a concrete species will be the conduit through which evolution will occur. The equipment of that conduit - its anatomy, reproductive traits, etc. - will be the clay that evolution will work with.

So, evolution's direct, short term answer, when its offspring are in trouble, is to give all it can to let this species survive. Become extra fit. But evolution will do the same nice thing, indeed : mechanically, to the adversary in the conflict, which is equally its offspring. Honing its means to kill with finesse...

Until not evolution, but a real life test decides how the problem will be resolved. Same mechanism as the one behind trial and error. The granite wall of reality. Out of the hands of evolution - that is equally subject to it. Evolution not being God. So, evolution must first work with what is directly available. And with these short-term possibilities, it can only do so much. The problem not being evolution, but the hellish double-bind that scarcity brings to the table.

But unbelievably, even this problem is - in effect - slowly being met by evolution. Look at the longer-term increase of intelligence in nature - as always: bit by successful bit - as compared to, say, 220 million years ago; the time of the pea-brained fighting-machine dinosaurs. This added intelligence has traits beyond the usual, less complex assets. If it hadn't, it would be like everybody getting the same bigger teeth. That could be cancelled out against each other.

So, there must be something else. As in fact there is. An increase in intelligence will also increase the natural possibilities to a) work on the scarcity itself, and b) defuse the worst in potential conflicts (e.g. by negotiation). Two birds with one stone; if ever an image was flawed. Increase of intelligence thus logically allows for many more ways to spare life and effort - and even resources - as compared to the times of the Stupid Ones. The fact that evolution is actually doing this (an increase of intelligence for potential adversaries, such as humans) might just be, we say, evolution's benign disposition making its mark again. Letting the living world tumble, ever so slowly, towards a more life-preserving equilibrium. As proof that contradictions cannot exist.

Which will be our point. Again. Evolution having a mechanical slant - towards the helpful. As a bringer of life. And the point of life being life, after all. A benign head of state will sooner than not elevate their country's culture - just by protecting it. "Sooner than not" being the best that evolution - and logic - can do.

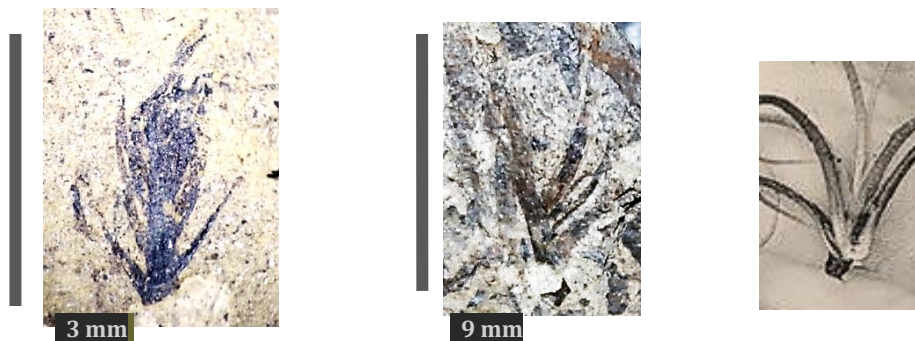
Notice that as intelligence can also backfire, evolution is thus also giving more responsibility to its offspring. This is no different from what any good parent would do, when its children are up to it. The modern weapons of mass destruction, say, are not evolution's fault. They're ours.

We wish to emphasize that evolution will indeed still display its original, free, creative and benign mechanical slant. Mentioning this may be relevant because of an all too easily entertained opposite idea, of evolution forcing situations to a head - *working towards* trials and errors - to obtain (in our view) nightmarish 'cutting-edge creations' (sic). Which, luckily, would be way beyond evolution's mandate. Evolution can only be a helper to its offspring. Indiscriminately. A trial of reality will do the rest.

Notions about evolution as hard and ruthless are ingrained, at least in popular thought. The same thinking also crops up in so-called real science, when evolution is blindly equated with natural selection. Our history will clean up this conceptual mess, that has bedeviled darwinian theory from the beginning. Evolution is a friend. To the fittest and the misfits alike. The granite wall of reality - the real watershed - is something else entirely. Evolution tries its best for all its offspring. As it must. It is mechanical, after all.

6) As a further example of treasures hidden in our fossil material we could also mention a possible fifth Late-Silurian and still extant plant. This one without a prominent thallus. Two of our Late-Silurian fossils rather resemble modern quillworts, or *Isoetes*. The plants flaunt quillwort-like sheathing onsets for their leaf-like appendages. The reason for showing these additional fossils, at this point, is not to make specific botanical claims, but to underscore the general richness of the data. And thus of the Late-Silurian Period itself. Time and again showing us what seem surprisingly familiar - highly *understandable* - plants already.

Anecdotally (this not being a textbook version) we may add that the same *Isoetes* family (genus of *Lycopod*) gave rise to tree-high vegetation in later eras. After which the plants, then, gradually would have shrunk again to our latterday quillwort proportions of about 10 cm high. As semi-aquatic plants. If our suggestion would hold, our modern quillworts could thus be seen harking back at least 423 million years. With rather conspicuous detours in all the worlds between then and now. Our tentative Silurian quillwort would look like this:



Two Late-Silurian plant fossils

next to an extant *Isoetes* ↑ or quillwort



Suggestions of sheathing onsets for both Silurian fossils. Borrowed from our Part 5, p. 169

7) Disclaimers such as ‘identical seeming’ or ‘same or similar’ are a nod to the evolutionary concept of “shape convergence” that warns us that similar features might always have evolved independently. Even where it regards the (extantly determining) “identical seeming, precisely dimensioned, somewhat elongated patterns of pentagon shaped cushions with such-and-such cells around the pores on top” for our *Lunularia*-type plants, below. Plants that in fact cannot be seen as different from extant in any respect. Other than that they are made of stone.

We will not be quarrelling with this principle here. One **can** logically (coincidentally) win five independent fifty million dollar jackpots in a row. Although the price for such a bland answer may be high. If dogma must win, no matter how nonsensical the cost, we will throw ourselves back into the 14th century. Ask William of Ockham. Ask any taliban victim.

8) One may further observe that regardless of their precise relationship to extants, the four Silurian liverworts would still bryologically belong with the moderns, not the primitives. Moderns at the dawn of life.

One also sees that they coexist on the same matrices, which tells us that their diversity, or variation, does not obviously indicate mutually exclusive habitats. As one might expect. As if evolution is *practising* with biodiversity more than anything - exercising rather than being driven by a necessity or strict causality (think beaks of finches). The plants are not out to kill, or shoulder each other away either. Just enjoying each other’s sheltering company, for various good reasons. Until today.

This lack of obvious or retrievable causality is a rather common Silurian trait. Apart from the mentioned modern liverworts, and their feast of variation within one habitat, one may equally observe remarkably early things like

- stomates with guard cells as dosing valves, way before the evolvement of the vascular plants that will crucially need them (see Part 3);
- a still token but already on-board sexuality, as a functional mechanism far before actually needed;
- a private hand-in-glove exchange of CO₂ and O₂ , (possibly far) before a reliably developed atmosphere;
- an unbelievably early evolvement of vascularity - sap vessels - far before the surface bed would be reliably penetrable by proper plant roots. Helped by totally ingenious horizontal taproots, above ground; ideal for wanderings further inland from the shores of freshwater streams and lakes.

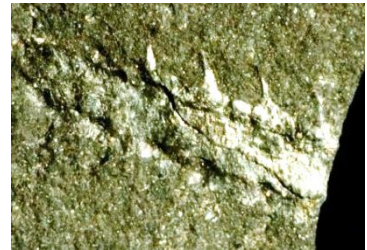
The list pretty much goes on. Practising with shapes and forms. As with thorns, of all things. Thorns, like those of roses, actually grow on a Silurian land plant. *Sawdonia ornata*. **Eons before terrestrial enemies**. Here it really becomes interesting.

A rather weak hypothesis could invent big animals with a reach on Silurian land. Such as

amphibious slugs - that didn't eat our fledgling *Cooksoniae* and *Salopellae* (as our world would have died with it); just these few tiny *Sawdonia*. But for their fierce little thorns. If evolution would be quick enough to invent those in time, too.

But if normal, functional analyses, like the one above, have little plausibility, what then? Thorns without any function at all would be ornaments. Props. Or worse: living prototypes, bred for a purpose. Like stem cells. Or lab rats. Freaks in a circus.

It could go like this. Thorns as animal deterrents had already been an aquatic device. Used for graptolites – small, underwater animal colonies that may indeed look remarkably like a *Sawdonia* plant. If we would allow an overshoot, a borrowing of the aquatic thorn template in a land situation, evolution would be able to compare materials. Chitin for exoskeletons (of the graptolites) next to new, botanical cambium skeletons, that would build future trees. One shape, fit to compare two types of material. Structure, pull, mechanical vectors.



graptolite fragment

To make things worse, such an engineering overshoot would also be highly economical. The predator problem is (aquatically) ongoing, and 2) will predictably pop up in any domain (as animals, after all, do *eat* things for a living). The problem for evolution could therefore indeed be both general & now. Figuring out thorn templates for land plant material today, may thus also prevent acute, highly time-sensitive causal needs tomorrow. For a still critically vulnerable flock. So, let's try the aquatic thing here too, as we are playing with land plant cambium anyway.



our Silurian *Sawdonia ornata*

Only: we still don't believe in evolution making species that have to tote around other people's crazy stuff. That violates the species' own functional sanctity, integrity and energy. They themselves still vulnerable and tentative fledglings; still barely an equilibrium. And all for having an - eons too early - thorn template. We don't agree. Either we're missing a real functionality for the thorns on *Sawdonia*, or we feel obliged to kill this darling. With no clue how to proceed, except not buying into a stem cell venture. We're romantics. We'll do the slugs. Sadly unfossilizable.

Which is not such a big deal, as the other miracles on the above list do have a proper shared functionality. They all are solutions for a smaller problem that later turns out to fit seamlessly (and miraculously) into a bigger scheme as well. Finished and half-finished products as future essentials – but also as full-fledged functional wonders in their original domain.

The interesting thing is the pattern: a limited treasure of a solution, fit for grander things,

indeed ***followed by*** those grander things. Could the whole thing be causal, after all? Not evolution *going back* to an already functional template, taking it from the shelf when needed – but the solution, made for a smaller problem, *actively triggering what comes next*? Determining evolution's further directions? Could it be that the contents of the toolbox (and what has been added to the toolbox) is *itself* the inspiration? It almost sounds too human to be true. Seeing what you have, which is what you know, and working from that. That simple? Did the invention of guard cells for pores on a liverwort as *Pellia epiphylla*, *itself lead the way* to eventually the vascular, upright plants? We hope to be able to get rid of some of the question marks here. It does sound like something a non-thinker could do. We could even ***look for*** the kernel, back in time, of a great evolutionary breakthrough.

Before leaving these considerations to stew, we have one more, somewhat relevant addition. In the case of beginnings, evolution is an initiator. The Silurian Period is full of this. So how would our Silurian unbridled freedom compare to evolution's mechanical character we are equally fond of in this history? This is an important question, as it touches on matters of intelligence as next to e.g. artificial intelligence; a rather tender nerve.

Elsewhere we have argued that the creative intelligence of evolution may indeed be compared to that of humans, not machines. Consider the fact that children learn by play - as a form of 'intelligence in motion' for non-thinkers. Which would also be evolution's hallmark. Consider the beehive. The essay we refer to and its online link can be found in the Bibliography, below. For now the following.

Our human, predictably limited, "mechanical" brain, yet with the ability to create, that is: to creatively transcend a system we are faced with, or live in, may well be a chip of the old block of evolution's own predictably limited traits, *yet with the same defining ability to creatively transcend its systems*. Which is very precisely what evolution - or being human - actually *means*. It is also where these two would differ from a benignly programmed Tamagotchi toy, that typically cannot outdo itself. No matter whom they may fool, the artificially intelligent will never be able to transcend *their* systems, leave their premises (sic), outdo themselves, step in the open, be alive. The thing has mathematical proof. With thanks to dr. Roger Penrose, mathematician-physicist & Nobel laureate - black holes - 2020.

9) If we allow our newfound, detailed liverworts to have non-trivial connections to their extant perfect images, this would leave a few rather important matters for further research.

Extant liverworts of the types at hand, to this day still demand moist-to-wet habitats, directly comparable to the riparian habitats close to shores of lakes and freshwater streams of the first Silurian (and earlier) land dwellers.

The extant liverworts, however, also share a second, equally strict demand on their environment. They not only love but insist on much more shade than the full bath of our latterday direct

sunlight. This trait might even show in their physiology, morphology, anatomy, cuticle. Which seem, up to microscopical likenesses, rather identical to those of the Silurians shown.

Which suggests a not implausible initial hypothesis - of (semi-)permanent shade as an equal must have for the Silurian liverworts as well. But where would this default shade come from, in their world still without the shelter of higher vegetation, let alone north walls of churches and garden sheds? Would the plants have had to make do with only shady crevices and the like, which would severely limit their presence to only a few difficult niches of their potential rich and lush, moist-to-wet environment? How would they jump from shady spot to rare shady spot, with their characteristic gemmae propagation, only the bounce of a raindrop away from the mother plant? Our fossil matrices of the fledgling Silurian landscapes seem to give no hint of any of such.

Could there, then, have been a permanent global dimming of direct sunlight - dimmed as compared to our modern world? We could, of course, do very well with the input of paleo-climatology here. Where we could have many things to offer in return as well, e.g. if there indeed are general physiological liverwort markers that show such serious demands for the proven firstlings on land. General liverwort traits as yardsticks for many phenomena; connecting then and now.

An excellent start might be this:

[Evidence suggesting that earth had a ring in the Ordovician - ScienceDirect .](#)

Also here: <https://plantevolution.net/wp-content/uploads/2024/09/ring-around-the-Earth.pdf>

In any case: our discovery of what exactly these Ordovician-born, Late-Silurian liverworts were like - who they in fact were - could very easily lead to a chain reaction into, or cross-pollination with other fields of enquiry. If only the material would become generally known.

10) Such research could perhaps also shed light on the following. One matter not touched upon as yet regards the fact that the fossils of our four liverworts are not just the first ones found: they are, to the best of our knowledge also their only known fossils. For the whole time span of 423 or even 450 million years. And for the whole world.

The reason for such a thundering absence in the larger fossil record might indeed be the same as the reason we were privileged to find for the first vascular-type plants. Liverwort thalli could well have been functionally recycled, just as the thalli of their one-time neighbour *Cooksonia*, to provide new nutrient medium for next generations.

The fact that our liverwort fossils were never found elsewhere, although they are still seen to be extant, could subsequently suggest that the calamity that froze our Silurian thalli in time - together with an equally fast, reductive sealing of that layer - would have been a one-off in the history of plant life on land. This suggestion could win in significance if it turns out that the organisms we simply overlooked during our inquiries until now, i.e. the fungi themselves, also never fossilized, apart from the once, in the context of our complex, one-off Late-Silurian *Holy Cross* calamity.

If fungi require a great calamity to be suddenly stopped in their tracks - and if the absence of thalli of both *Cooksonia* and liverwort in the larger fossil record suggests that such a calamity has only been found to occur once, it then could become likely that ours are not just the only fossils of *Cooksonia* and liverwort thalli - but also the only real fossils of our type(s) of fungi. We don't really know if the larger fossil record already has these fungi. But it is time to want to find out.



Emerging fungi on *Lunularia cruciata* and *Marchantia polymorpha* liverworts. Current experiment. Photos: the author. Preliminary findings show that the naturally moist habitat of the plants certainly seems conducive to a fast if not eager fungal overgrowth of remnants in our liverwort test plots.

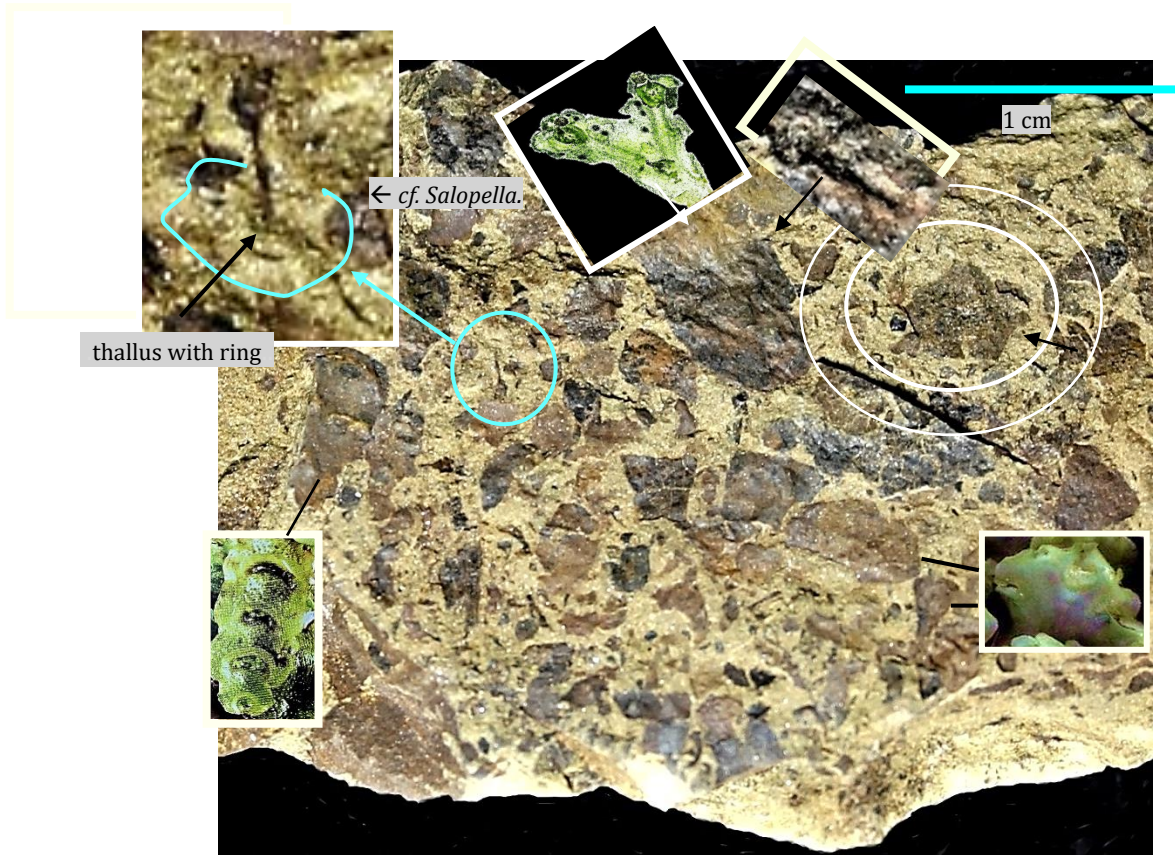
11) We have no direct evidence of liverwort thalli being eaten (overgrown with fungi) on our Late-Silurian matrices. There is only the circumstantial evidence of their absence in the larger fossil record (for the last 450 MY).

Which doesn't mean they weren't on the menu. Compare the photos above. That liverworts are intact in our finds may well be for the same reason as why juvenile *Cooksonia* thalli have been found whole on our matrices. While their elders literally next to them were being gobbled up by fungi.

Both the liverwort thalli and juvenile *Cooksoniae* lacked large, sporophyte 'antennae' with stomates open onto the universe. As the adult *Cooksoniae* had. So an environmental disaster that took adult *Cooksoniae* [see Part 2], might well have taken their juveniles - and the equally self-contained liverworts - later, closer to the time when the fungi expired as well. The environmentally more vulnerable adult *Cooksoniae* would then have been like canaries in a coal mine. They went, and were preyed upon by the fungi. The others, more clammed up, plausibly went later, nearer to the time when the fungi were done for as well. And therefore stayed intact. [These were no killer fungi. If they had been, spoiling the fragile first steps of plants on land - think garden cress; max. - we would not be here to observe them. They were allies, not parasites.]

Consider the following matrix. It is the twin or 'sister' matrix of the rich liverwort 'forest' of

page 21. The two matrices are each other's pos./neg. counterparts. That is: two halves of a split piece of slate, both showing the same fossil layer as horizontal halves. And often adding to each other's value (information) when found. Both matrices are residents of our Late-Silurian herbaria. See the Impressum; p. 4, above.



Unlike the first matrix on page 21 above, this one harbours additional (clearer) information about indeed a *Cooksonia*-type land plant, very probably a *Salopella*, with sporophyte, in the middle of many intact liverwort thalli. See this second matrix photo, top left. As always, the *Cooksonia*-type thallus - with sporophyte - is the only one overgrown with fungi. As a comparison see page 15, this Part 1, for a clear *Salopella* in its socket ring.

Finally note that our recycling fungi could also remind one of the mycorrhizae-producing ones that in our time are equally known for their symbioses with plant roots and rhizomes; underground. It is not unlikely that even with Late-Silurian *Cooksonia*-type plants, the still liverworty rhizoids - meant to attach the thalli to their surface bed - would evolve into more functional archaic rhizome structures, with a beginnings of an internal sap stream.

If we would be able to seriously look under the surface of the thalli, other quests could be envisioned as well. As for silica phytoliths and other helpful mineral deposits, transported (and doing good work) inside the plants. Minerals that are extracted from the surface bed. An extra bonus would be if we could find out if this process might even have helped a 'weathering' of rock layers - possibly still observable for extant plants growing on concrete, church walls etc. - while extracting minerals. In the process opening up a tiny bit of rock surface, making it slightly more brittle or 'spongy'. For the benefit of future plant roots as well as for a moisture and nutrient retention of the rock itself - the stony surface slowly becoming a richer nutrient medium.

This kind of daydreaming may not be without merit. We are looking, after all, at a rather crucial stage in the history of the planet, where the Earth is slowly becoming a world. So mechanisms conducive of this, hidden in our data will be actively looked for - and embraced when found. Perhaps the Late Silurian would still be a bit early for mechanisms such as these, but we see no reason not to expect them in, say, the Mid Devonian. Phytoliths were brought to our attention by researcher Marnel Scherrenberg.

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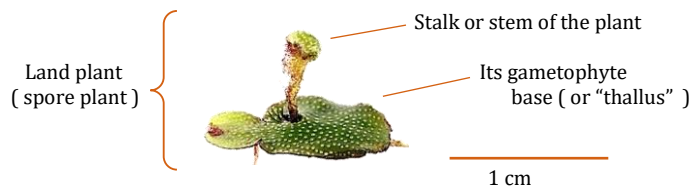
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Part two

Finding the missing half

P r e f a c e

On seeking a path . . . and finding a world



In this Part 2 of our history we heuristically seek a path through an abundance of information, which morphs into a whole and detailed Late-Silurian landscape. For the first time in the history of the world we are shown the other halves of the first upright land plants. In their cradle habitat of moisture- and nutrient-retaining furrows and small dells. The fossil matrices, clear as snapshots, allow us to determine for 90 - 100 % of the plant material why it is where it is in its environment.

The indeed snapshot-like character of many of the fossil matrices stems from the fact that they often show quite fleeting moments in a highly dynamic Silurian take on life - where the decay of a specimen (and with it, its irretrievable loss for posterity) would often be only days or even hours away.

All of which makes this fossil material a rich and highly 'readable' (understandable) treasure trove of information. Yielding insights into fledgling Late-Silurian ecosystems, but also into the anatomy of the plants, their vascularity, their juvenile and adult thalli - and *via* these into their relationship with their abundant liverwort neighbours as well. The fossils are mostly in a good to very good condition.

One of the greatest results was discovering how these plants would have been able to maintain themselves also further afield; further away from their still relatively rich and friendly cradle habitats along the shores of rivers and lakes - into a barren and stony hinterland. Friends gave them a fungal rucksack of moisture and nutrients, to help their next generations in their effort to colonize a still rather hostile Earth - a place without topsoil, shelter or shade, and with only a fledgling ozone layer for protection. This fungal symbiosis of the first vascular-type plants, vulnerable as garden cress, may well have been essential for the Earth becoming a lush and magnificent world. Essential in more ways than one, in fact. The fungi's other, equally crucial magnificence would be a perfect hand-in-glove exchange of oxygen and carbon dioxide - enhancing or even augmenting the plants' essential photosynthesis in these earliest of days. The story is only pages away.

Which leaves us with a third, equally brilliant form of help with wanderings further inland. Horizontal taproot appendices - outgrowths - above ground, that can be seen tapping into moist, often spongy furrows, small channels or dells. And which will be crucial for landscapes further away from the overall moist-to-wet cradle habitats. As vertical roots would not be feasible, yet, given a still rather harsh and barren surface of the Earth.

The essay

Context for *Cooksonia*

The other half of the first vascular-type land plants: gametophytes, with snapshots of their environment and of their survival strategy

0. Introduction

The summer of 2021 has seen a productive yield of material from the Late-Silurian (Ludlowian / Pridolian) plant deposits in the Holy Cross Mountains in Poland. For an introductory geographical and paleobotanical context, see Bodzioch, Kozłowski and Popławska (2003). [Also printed as an Addendum with this history at the back of the book.]

https://earthphysicsteaching.homestead.com/A_Cooksonia_type_flora_from_the_Upper_Silurian_of_the_Holy_Cross.pdf

In this essay we will explore the new finds.

As a first introduction to the fossils, consider the following matrix, which has a few of what we will call (for now) 'blobs' on it. The dorsal-ventral blobs are lobed, mostly three-lobed - perhaps even three-sphered - blackish organisms that are typical for the matrices of the summer of '21. The material is from a layer of land plants. The combination with sporophytes, mostly of a *Cooksonia* type is usual for this blob material. A typical matrix harbours some two blobs per sporophyte, or less.

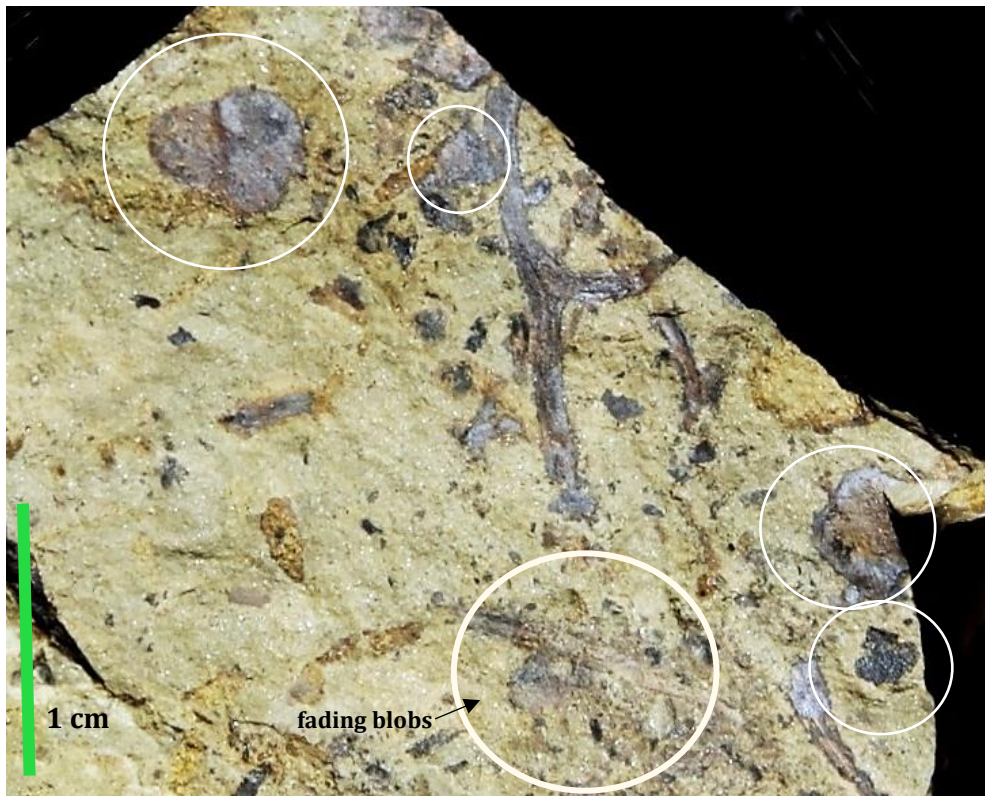


Fig. 1

In this essay blob material such as the above will be examined more closely; as follows.

- Section 1 asks the question how best to approach the material. A selection will be made employing a 'strategy of clear cases'.
- Section 2 argues for an interpretation, tentative at first, of the material as *Cooksonia* gametophytes; possibly juveniles.
- Section 3 offers a reason for the exceptional preservation of these gametophytes; juvenile as well as adult. The explanation at the same time accounts for the absence of gametophyte structures in the larger fossil record.
- Section 4 holds a collection of proposed gametophyte data. Young thalli, often with tiny sprouts of sporophytes and older plants associated with more adult sporophyte material.

Older gametophytes will often be overgrown with fungi. To aid the flow of the text these gametophyte data are shown together, in this separate section.

We will start with a few general remarks, possibly redundant, on land plant gametophytes, as they will become central to our investigation.

0.1. Land plant gametophytes

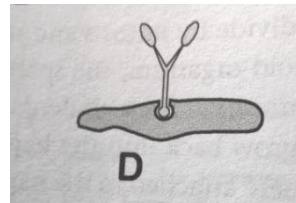
Gametophytes for *Cooksonia*-type land plants have always had their place in paleobotanic theory; even when they were never actually found. It is uncontroversial to presuppose a life cycle for *Cooksonia*-type spore plants that includes an important gametophyte phase.

No roots for *Cooksonia*-type plants were found; a *Cooksonia* sporophyte still dependent on a relatively large gametophyte base is most always assumed. As is the idea that the connection between the two was with a 'foot' that stood the sporophyte in the nutritive gametophyte - or 'thallus' - that gave birth to it.

See a recommended Armstrong (2014), p. 184, with image:

"Origin of the land plant cycle. [...] D. Cooksonia stage with partially (?) dependent, determinate, branched sporophyte. [...]

Image source: The Author)"

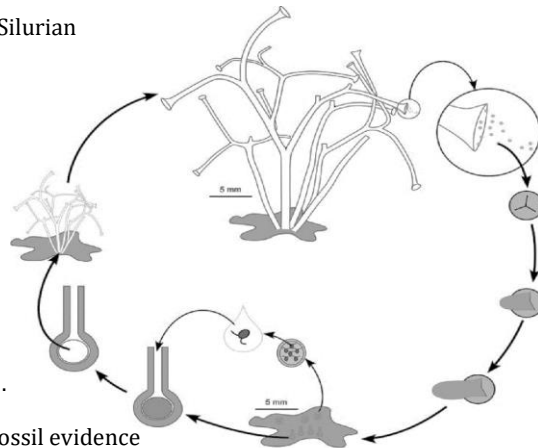


For a sketch of the assumed life cycle of late Silurian land plants, see the drawing on the right.

A self-fertilising gametophyte at 6 o'clock grows an embryo sporophyte that in its maturity produces spores that start the cycle anew.

The sperm of the gametophyte must swim, hence a likely preference of the plants for a moist environment (furrow, dell, taproot; see further in the text).

Our enquiry will indeed gradually meet the fossil evidence of such a complete Late-Silurian life cycle. But it will be evidence that botanical theory had already predicted for many decades, as shown above.



Cooksonia will be found to be whole. Which is well and good. Great news even. But expected. A real innovation would come from a general fungal symbiosis. And its multiple implications. And from a wealth of detail and context for the plants on - for the first time - abundantly rich matrices; snapshots of their real habitat and ecosystem. The thalli as found will also shed light on the relationship of the vascular-type firstlings with the liverworts next to them. The fact that the liverworts even and also gave rise to the vascular plants, shrubs and trees on Earth. As will be brought to the fore in Part 5 of this history.

1. The selection. Material that grew there

In our first exploration of the new, exceptionally rich summer of '21 finds, we will only consider vegetative material that gives clear indications of having grown where it fossilized.

Limiting the inquiry to material 'that grew there' is meant first to rule out loose, broken-off sporangia and other debris (possibly aquatic) that would have a more or less random distribution on the matrices.

Secondly: much of the new material that passes as 'no sporangium' still does not, in itself, give clear indications why it is where it is. This holds e.g. for the fossil blobs shown in Fig. 1 in the Introduction. Such material is also temporarily ignored, as we will commit ourselves to the adage that the intelligence of the clear cases will in itself go a long way to also attribute qualities, that is: bring order, to the less clear ones, if e.g. a morphological kinship with a clear case seems probable.

In short: we will limit our search to the most 'understandable' fossil blobs, as a means to aid the transparency of the survey and its presentation.

1.1. Clear cases. A river runs past it

There are indications that many of our complex 'blobs of vegetation' might indeed have grown where they are on their matrix. These are found in the direct vicinity of 'tappable' moisture and nutrients.

Observe the following 3-lobed fossils - next to small furrows, grooves & channels that would have held rich moisture. With an outgrowth - never seen or hypothesized before - that seems to work as a horizontal 'taproot', above ground, into them. Brilliant, of course, for tapping into the watering places of a more arid hinterland.



Fig. 2

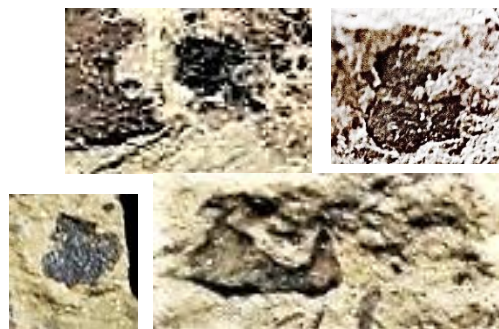
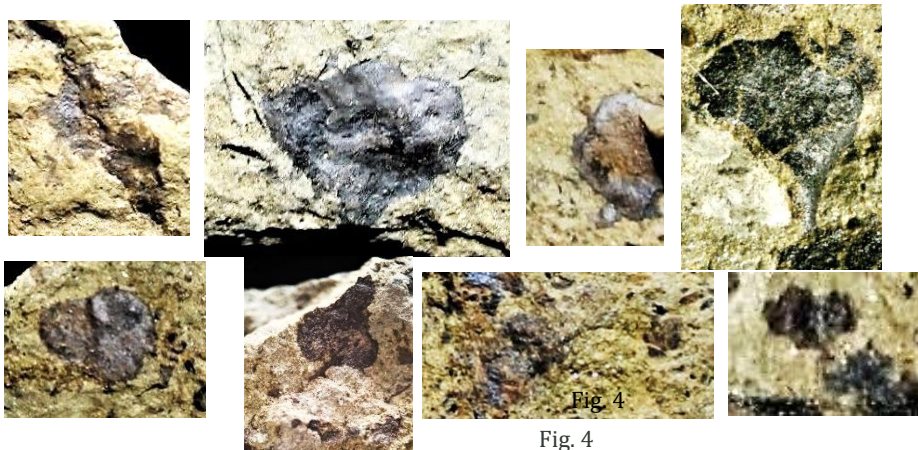


Fig. 3

A few more examples of these non-random, 'moisture-seeking' growths, and their taproot appendices:



Notice that the above blobs have a similar but flexible lobed, indeed often 3-lobed aspect, suggestive of an internal structure but with room for adaptations such as the growing of a flexible horizontal taproot, above ground, and a flexibility for folding around surface irregularities - or craning towards favourable conditions (such as light, warmth, shade). But never amorphous, always lobed, mostly 3-lobed. Brownish-black.

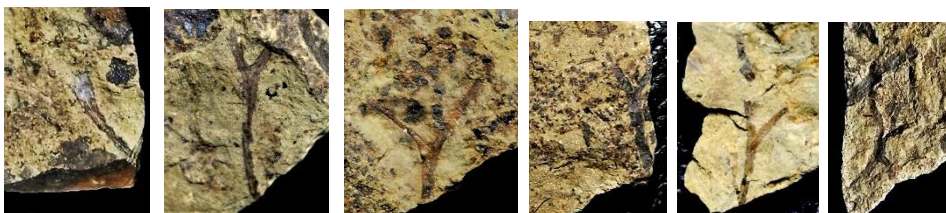
1.2. Enter *Cooksonia*

The same environment of moisture-supplying furrows or grooves might also be a preferred context for another type of fossil: land plants of the *Cooksonia*-type.

One of the enduring enigmas of Late-Silurian land plants is their seeming random and 'broken-off' appearance on the matrix. They seem to randomly lie where they fell, with no gametophyte in sight, nor evidence of their sporophyte 'foot' that would have stood them in such a nutritive, gametophyte blob.

However, our summer of '21 finds suggest that the whereabouts of *Cooksonia*-types on a matrix need not be that random, after all.

One preferred place for our *Cooksonia*-type plants (some 50% of the fossils) seems to be: with the foot end of their broken-off stem at the equally broken-off edge of a matrix. Observe these examples, of many more:



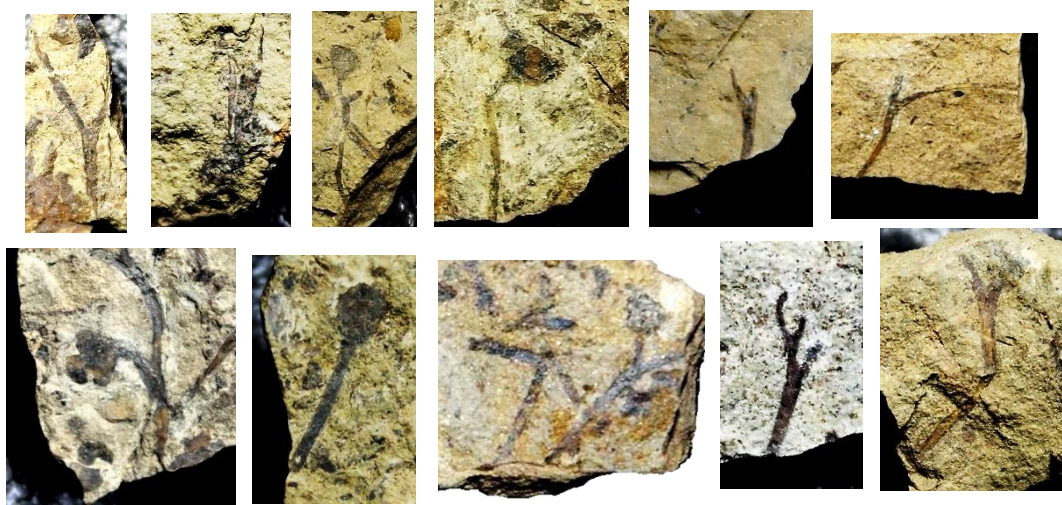


Fig. 5

An explanation can be that a matrix will typically break off where it is vulnerable, as on a 'fault line' made of a thinner or more brittle furrow or small channel in a layer of slate. If this is an acceptable suggestion, these plants are likely to have had their foot in what probably was a noticeably moist, sometimes even spongy, grooved environment. More examples are the following. This time of fossils at edges of grooves or rifts that have not (yet) broken off. These make up approximately the next 40% of all sporophyte fossils.

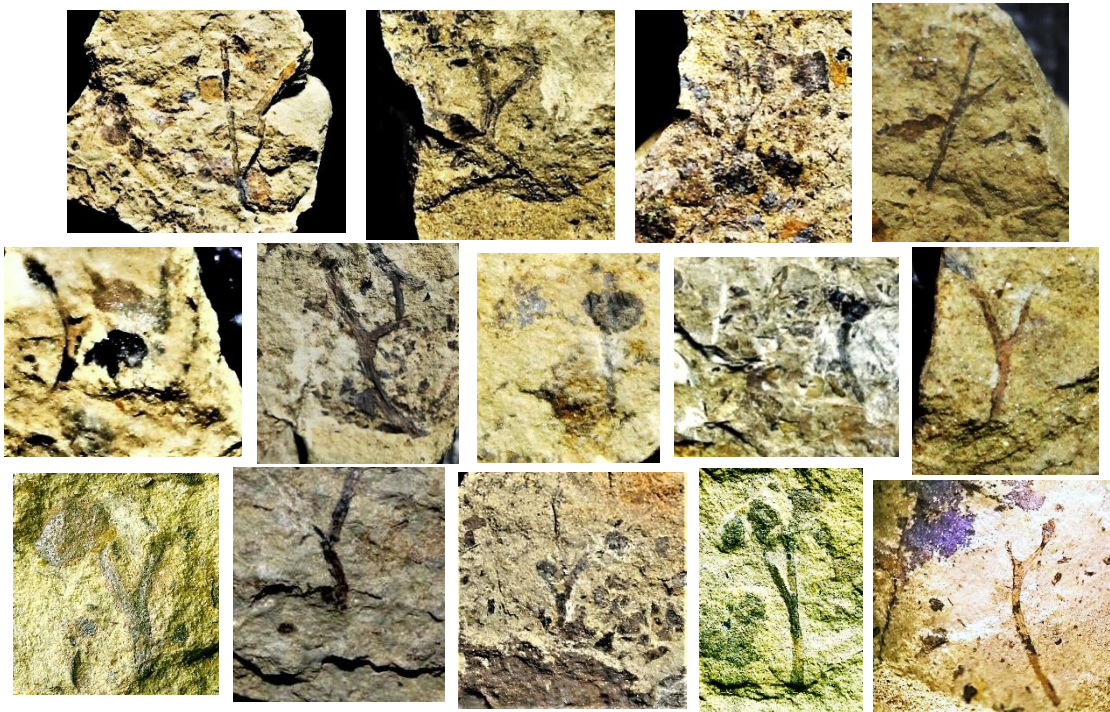


Fig 6

Notice that if the suggestions of Fig. 5 and 6 are sound ($50\% + 40\% = 90\%$ of all fossils non-random, at least), this will also mean that *Cooksonia* c.s. have not randomly fossilized after having *en masse* lost their moorings in equally massive coincidental storms or floodings, the world over (to explain an absence of gametophytes.)

2. Gametophytes

2.1. The choice. Towards a hypothesis

Section 1 showed that our lobed blobs and our *Cooksonia* sporophytes both seem to prefer the same environment: close to the edge of a furrow / groove that likely held a supply of rich moisture. This in itself does not seem to link the two types of fossils in a significant way. To be where the water is would be anybody's wish.

Not quite. The *Cooksonia* sporophyte is dependent on its other half. It has no will or choice of its own. Therefore, the statistically significant spots where the foot ends of *Cooksonia*-type stems appear to point to (they do), on a matrix, would *for that reason alone* also be the logical places where the gametophytes would be, if they ever fossilized. As the two would have been connected during their lifetimes. So the sporophyte layout, as a pointing arrow, predicts the sort of places where the gametophytes might be, without reference to moisture or anything else. Which is, indeed, where the blobs are. A suggestion of the blobs of Fig. 2-4 as thalli of *Cooksonia*-type land plants would thus be supported by their layout on the matrix, as marked by the sporophytes. Or *vice versa*: the blobs as thalli could account for the very precise layout of 90% of all sporophytes found, as in Fig 5-6, above.

The number of different Silurian land plants that have been seen to fossilize, until now, has been small. But evolution does allow for something like *Nematothallus*, an amorphous, dorsal-ventral land dweller.

One could argue that our fossils are an entirely new species of *Nematothallus*, shedding its defining amorphous property, due to an as yet unknown need for much more internal structure, giving rise to a three-lobed/sphered aspect. With

a newly evolved taproot as well. Moreover, the new *Nematothallus* would also be seen with a neatly tailored,

round dorsal recess - see Fig. 1a - but not to let something like a future sporophyte grow through it.



Fig. 1a

All this is possible. At a price. A *Nematothallus* - hypothesis would likely violate evolutionary and general scientific principles that demand that one be economical in one's theorizing..

The options seem to be

- a) the newly found blobs 'weigh' nothing at all: they are just gametophytes, possibly juveniles; theoretically amply accounted for. Only fossilized for a change, and thus giving away their location, shape and form on the matrix for a change. By which fact they also predict, for a change, the observed whereabouts of sporophytes;
- b) they are elaborate, new, 3-lobed or even 3-sphered structures, with a taproot and a round dorsal recess, of a *Nemathothallus*-like species. Such evolving was not expected, and has been seen only once: fully developed in the fossil yield under discussion;
- c) it is a mystery-type of vegetation, admittedly not random - no flotsam - but never seen before, just as gametophytes have never been seen before, and growing in the same places as gametophytes would, only not gametophytes
- d) but possibly feeding on the remnants of them. Which would give the same evidence of the location (and probably of the shape and size) of gametophytes on the matrix as option a) above. See there.

If we wish to continue our 'heuristic' search for some further, plausible order for the material, we will want to take one or two of these hypotheses as our lead. We choose a), with a special fondness for d).

A seeming flaw in the above reasoning could be the fact that whereas many of the places of the *Cooksonia*-type sporophytes on the matrices would be statistically significant, the places of the blobs might not be, because there are more of these blobs than there are observable furrows and other watering places seen on the matrices. A way out of this might first be the observation that the blobs also have their own 'pointing arrows', just as the sporophytes do: their taproots that indeed point to, or lie in watery furrows or indentations. Which suggests a non-random distribution for those as well. The somewhat freer distribution for the others might suggest that the surfaces of those matrices were not too dry for the gametophytes to begin with. In such more normal environments, possibly dells, they would perhaps choose their residence on the basis of other criteria such as light, shade, warmth, space, etc. The group of seeming randomly placed land plants (approximately the last 10% of all sporophyte fossils found) might have belonged to such freer gametophytes.

2.2. Clear cases revisited

There is one further matter with regard to the material that we should address: the relationship of blobs as in Fig. 2-4 (dwelling beside furrows), with the rather perfect blobs of Fig. 1, which we regarded as 'unclear cases', because they showed no good reason why they are where they are on the matrix. They do seem to live in a vague furrowy environment, but not clearly so. And their 'taproot' appendix has not become an elaborate outgrowth.

However, precisely this last fact could perhaps help to clarify their status.

Above, in Section 2.1, we observed that the blobs under analyses also have their ‘pointing arrows’: their taproots, that indeed point to, or lie in watery furrows or indentations, if there are any.

If it is true that the pseudo-randomly placed gametophytes live in a sufficiently moist, non-marginal environment anyway, one might also expect their taproot appendices to be not much more than ‘standard issue’. No need for extra, moisture seeking elaborations. This prediction would come true for blobs such as in Fig. 1.

And thus these blobs may also explain themselves into the set of ‘clear cases’ of gametophytes in our finds. Possibly even gaining pride of place as the clearest cases, that may then perhaps be informally regarded as optimally showing their basic, almost idealised template. Geometrically near-perfect 3-lobed, perhaps 3-sphered structures with token taproot and a still empty, round dorsal recess, as a probably still pristine, juvenile aspect.

3. The analysis

3.1. Fungi

As a first step towards an analysis, consider the fact that our ‘gametophyte blobs’ seem to fade very much faster than the sporophyte plant halves of the cycle. Observe the almost-no-fossils of Fig. 7 and 8, among many more: three-lobed structures in advancing stages of vagueness. The ones on the right have almost faded away.



Fig. 7



Fig. 8

These fading blobs are found on literally the same matrices as perfectly preserved specimens (see both in Fig. 1). Which suggests that the fading indeed takes place far before fossilization. And that the preservation of the good ones (the ones that did not fade) next to the fading ‘ghosts’, in this exceptional yield, might perhaps be due to some sudden and exceptional event. More of which later.

Notice, by the way, that the almost-no-fossil in Fig. 8 appears to be curiously 'radiating' plant material in all directions. Suggestive of things grown out of it?

It seems reasonable to regard these 'fadings' as decay, and the three-lobed structures as in Fig. 7 and 8 as being preyed upon by fungi. That seem to produce a layer of a white(ish), grainy appearance in the process.

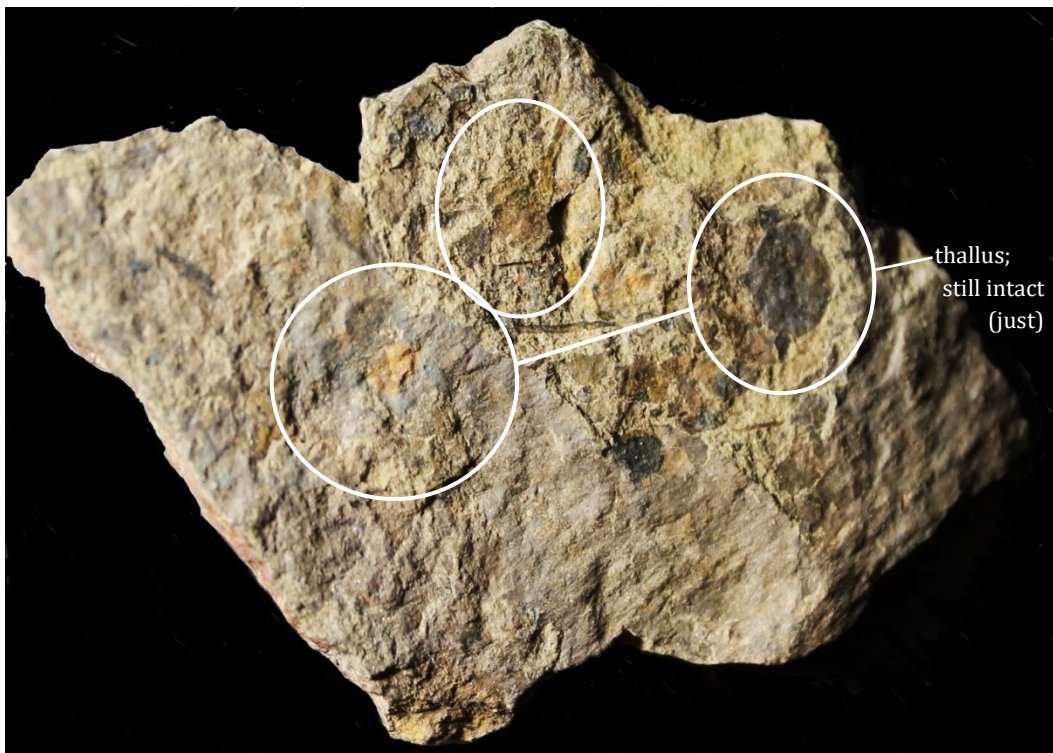
3.2. The explanation. Something happening here

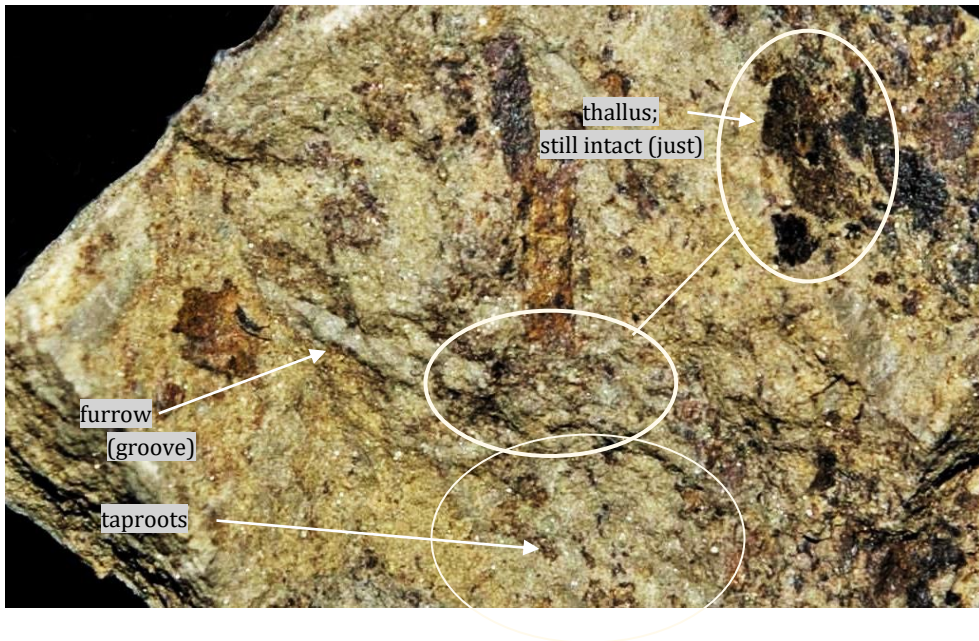
If our material indeed holds evidence of fungi, foraging on gametophytes of *Cooksonia* c.s., the material might logically also show evidence of the *dynamics* of this.

One could expect to see at least two things.

One. Gametophytes, or parts of them, in the process of being eaten. In which case gametophytes and their predators would probably both be seen.

And two: one might expect to see fungi that have gobbled up gametophytes, but that, at the same time, take up more place on a matrix than that precise form of their prey alone. The way that the shape of a rabbit may show in the bulge of a snake. The next fossils, also from our summer of '21 yield, can show precisely this. A 'ghost' of a gametophyte - a thing we are now actively looking for - in the belly of a fungus, mold or whatever it is. Next to a still intact thallus:





As we can see, gametophytes can easily become covered in foraging fungi. Section 4 shows this to be the normal situation. Which would, of course, also suggest why gametophytes don't fossilize. They would be eaten, first.

Which thought may give rise to another, rather important one: might not the uniqueness of these finds be that the fungi, not the gametophytes, were stopped in their tracks, for once, at all? In that case the 'why' becomes a different 'why' altogether.

Gametophytes could fossilize perfectly, but they were never there anymore to do it. As they would have been recycled. Then the question becomes why the fungi were stopped in the midst of their work, in this exceptional case.

Poison - sulphur, acidity, etc. - could explain things. Water or air, suddenly polluted (some $200 \mu\text{g}/\text{m}^3 \text{SO}_2$ would probably do), or freak heat, drought or frost, radiation, suffocation: one of these, killing the fungi - freezing them in time - would instantly account for this uniquely informative land layer, with all that is on it.

Note that this hypothesis does imply an order of things in which the calamity that took the fungi, affected the land plants first. As canaries in a coal mine. If not, the fungi would have been massively preying on healthy thalli. In which case the land plants would not have stood a chance of becoming land plants. Killer fungi would have stupidly ended all, themselves included, before all even began. They in fact did the opposite - helping others by helping themselves to their dead (and dying?). In the best of traditions - possibly hatched there and then.

Which also means that young thalli as in Fig 2-4, being unaffected, would now have to be seen as still unapproachable for the fungi. As if still (chemically?) taboo. Or they just lived longer.

Less vulnerable than their elders, more clammed-up - as still without sporophyte antennae with stomates open onto the universe - they may have gone a bit later, closer to the time when the fungi were done for as well. Which seems reasonable enough. That intact thalli as in Fig. 2-4 would indeed be the younger ones would be supported by their still empty sporophyte rings, or else by the tiny knobs of sproutings that are often peeping out of their sockets (see Section 4, further on).

And finally this. That sporophytes were left to fossilize - while their softer, more nutritious gametophytes were being functionally recycled - may also have something to do with a scarcity of specific, 'wood'-eating fungi in these early eras. The earliest land plants needed to strengthen their stems to support an upright position. At first, such strengthening might have been with sterome tissue (some mosses do the same), soon to be followed by the 'wood tissue' cambium as a more successful adaptation, especially when vascular strands in the stem appeared, as in our fossils (see e.g. footnote 3, below). As is well known, also in the much later Carboniferous era the woody structures of plants, shrubs and trees would indeed barely rot, for tens of millions of years, leaving behind the hugely thick coal deposits mankind has rejoiced in until today.

3.3. Conclusion

So, our rather 'heuristic' way of approaching the material may, all-in-all, have brought us a fine catch. Fungi, seen to be foraging on the remnants of possible gametophytes; helpfully recycling them on the still barren grounds of the age. A phenomenon that at the same time suggests a reason for the absence of Silurian land plant gametophytes in the fossil record. They would be quickly and functionally recycled, in a world that would (otherwise) largely be without suitable environments for the new pioneers.

The relationship with the fungi may well be symbiotic, to further explain the universality of the recycling; the total nature of the absence of the structures in the fossil record. While *botanically* a real symbiosis would of course be conducive to a more systematic securing of adequate moisture- and nutrient-retaining habitats for the plants; thus gradually but surely preparing the Earth for further and more elaborate land vegetation.

In extension of this it may also be noted that fungi, like animals and humans produce carbon dioxide, a thing that plants rather crucially need. Having symbiotic fungi at hand could thus well have an additional advantage for these earliest vegetations - that have to make do with a still rather poor, fledgling atmosphere. Having your own small CO₂ factory - your own little blanket of enhanced carbon dioxide levels (CO₂ is heavy) - could well be an equally life-enhancing, organic part of a much needed reliable micro ecosystem. ¹⁾

The equally brilliant innovation of horizontal taproots, above ground, standing in for vertical ones for the time being, will be elaborated on at several points in our history.

One general conclusion we may draw from all this, at least, is that heuristics can indeed be an interesting way to enter a jungle of data, yielding almost always creative catches and by-catches. By-catches that may just as easily become the main feature, in a next round.

4. The data. Fading as well as intact gametophytes, with socket rings

In Section 2 we argued for quickly fading gametophytes, showing on matrices as ‘ghost-like’ structures, if at all (anymore). See again our Fig. 7 and 8.

Further material seems to show more structure more clearly, even in advanced stages of fading: a ring, or at least an indentation, approximately in the middle of the blob structure, that might well have belonged to the ‘socket’ for a sporophyte foot.

And even in almost faded structures such a connective ring or indentation might still be seen – which suggests (not unexpectedly) perhaps sturdier material for the socket ring than for the rest of the gametophyte structure (we will come to that).

See Fig. 8a:



Fig. 8

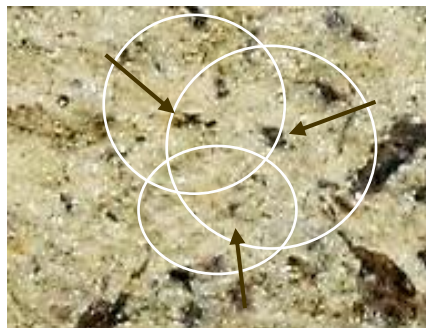
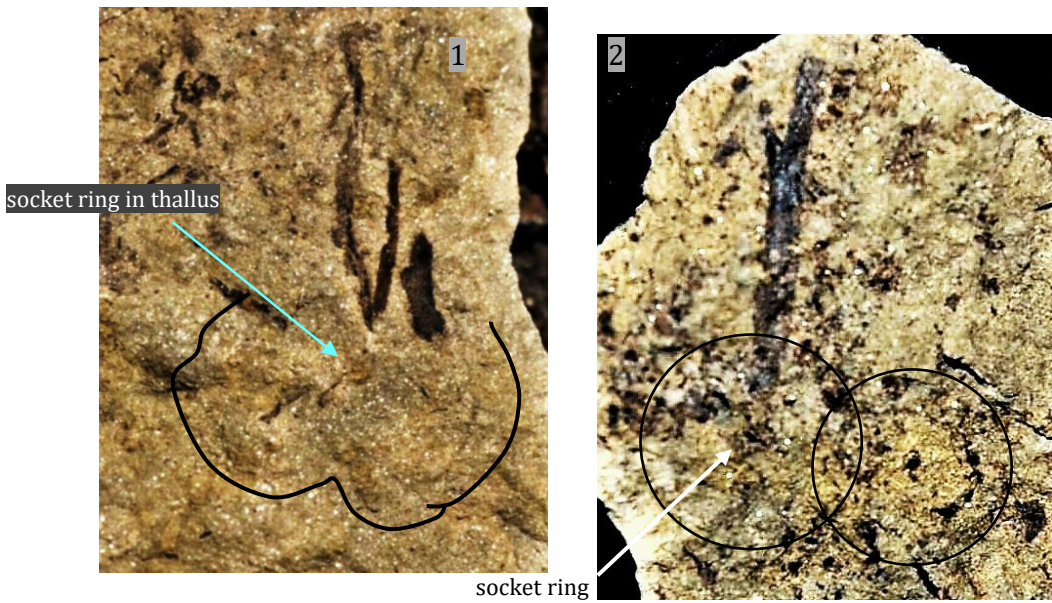


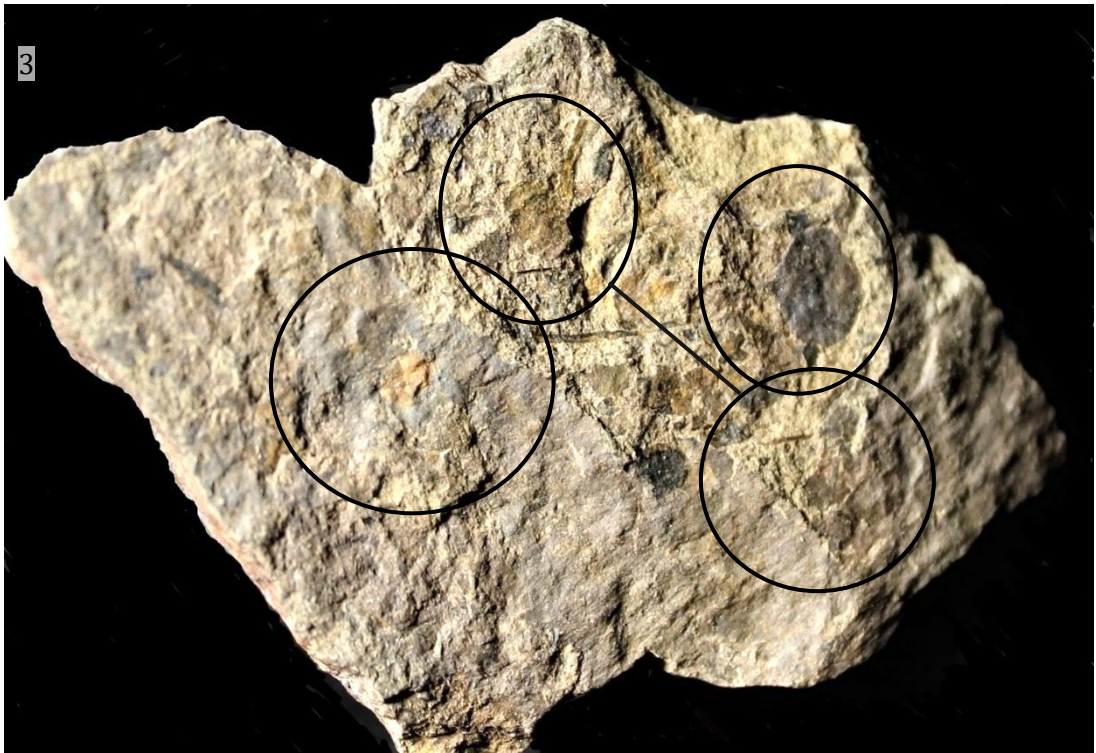
Fig. 8a

In Fig. 11, below, are more examples, taken from the material we collected, including those that were previously shown. Some blobs and rings might need an adaptation of the eyes first, in order to be seen properly.

Fig. 11:



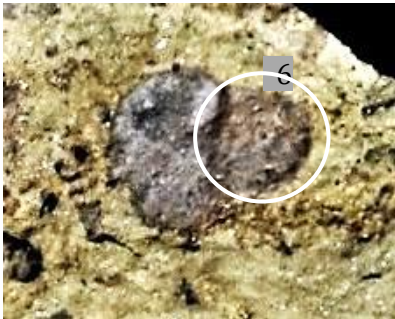
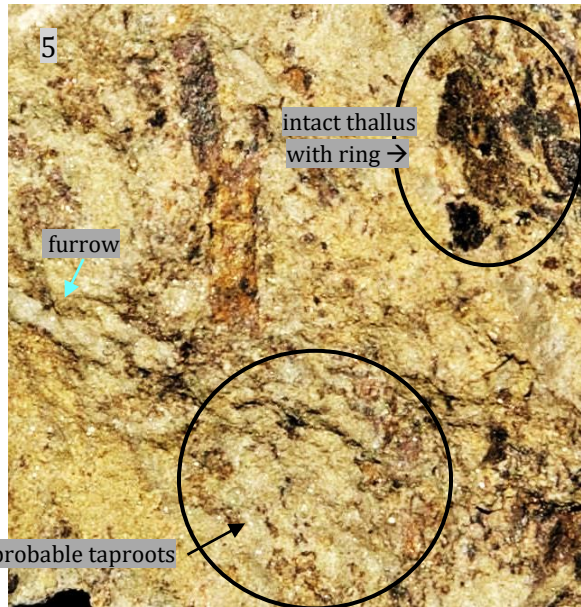
At least three stages of decay on one matrix; still lobed, still with 'socket ring' marker or indentation:



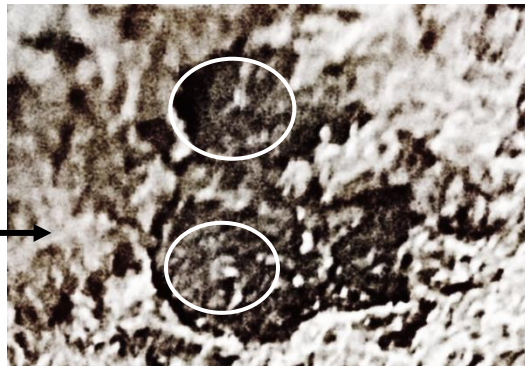
Proposed *C. bohémica* ↓ Compare Part Three of this history, Section 3.3.



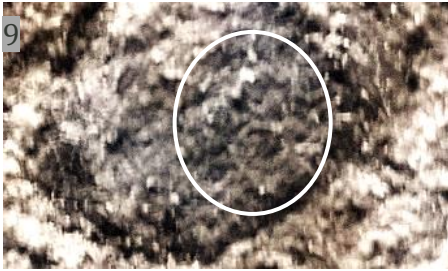
Three-lobed structure . . .



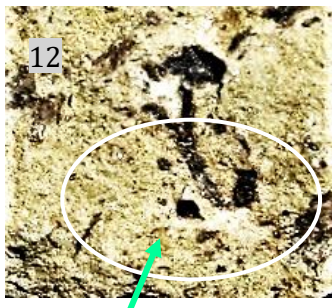
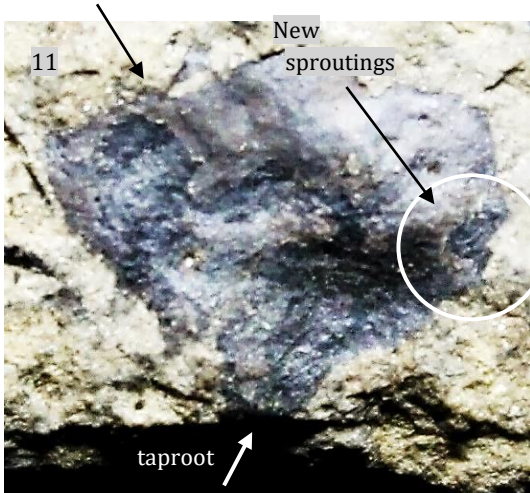
Similar three-lobed structure; taproot middle left, with sproutings



more examples of sproutings:



Used socket sheath. See footnotes 2 and 3

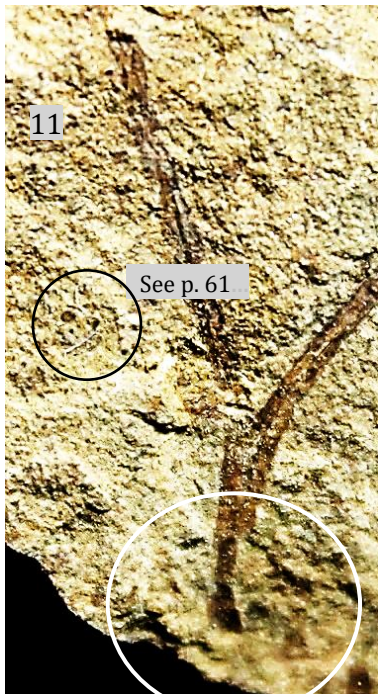
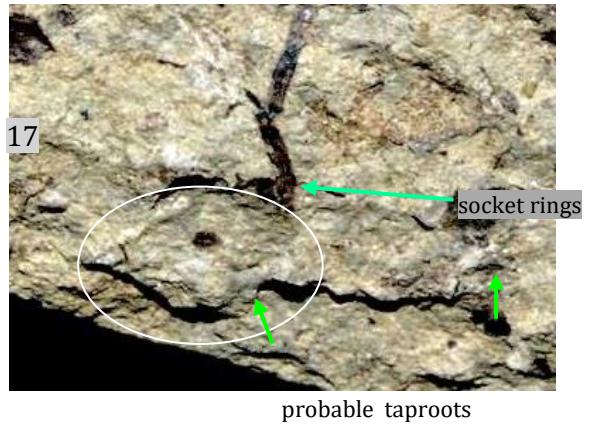


taproots ↔





↑ *Salopella* in its socket

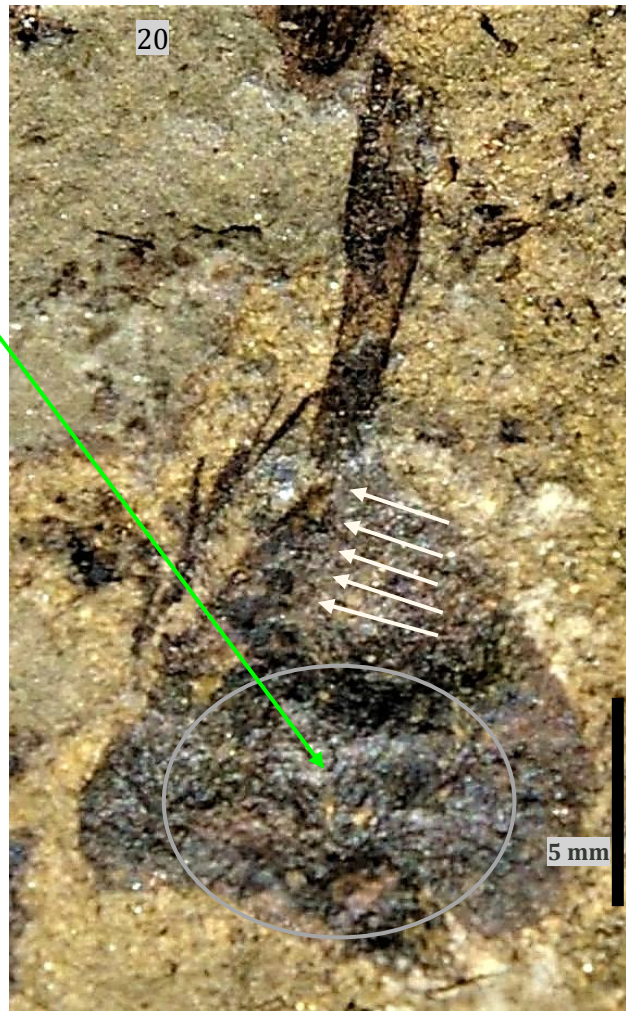


Gametophyte with an identical 3-lobed specimen as a ghost on the left of it. A mere imprint is left, but still unmistakable – even with a socket-like bump in the middle, with hole in it.

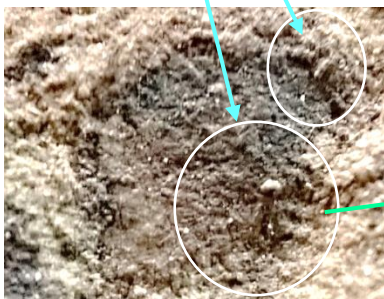
Gametophyte, decay just beginning; still looking like Fig. 1 - 4. Sporophyte seemingly still inside.

Large, slack-looking, probably old (used) socket ring with *striae* 'radiating' from it, suggesting a former flexible, more bulging volume, having accommodated a sporophyte foot's height inside.

Growing sporophyte feet will obviously alter the neat, 3-lobed shape of the pristine juvenile thallus, that at least has to adapt to a more outspoken third dimension and counteract the leverage of the upright sporophyte 'pole'. Possibly also with a more sprawling, rosette-like floor space to stabilise itself (animals put their legs further apart).



Again sproutings out of gametophyte socket rings

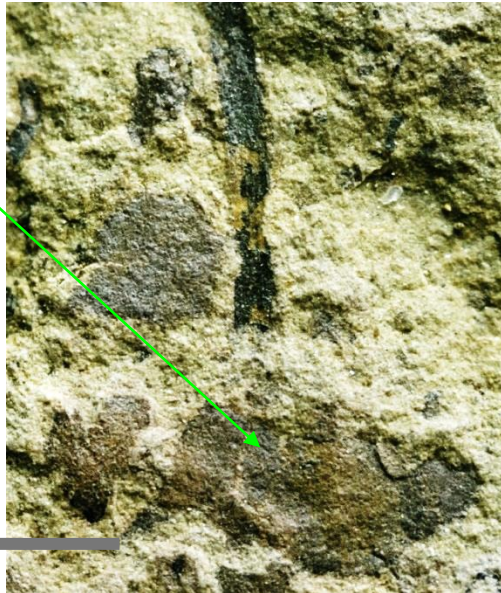


22

A thallus seemingly showing the complete socket (sheath?) as a discolouration around the sides and base where the sporophyte stood in it.

The sporophyte seemingly disconnected from the gametophyte; details being obscured by a growing horizontal band of white fungi, above and on the gametophyte and over the lowest part of the sporophyte. Time stopped just in time, this time, to reveal what the fungus is about to erase further.

1 cm



23



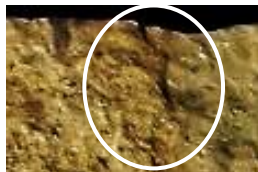
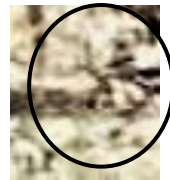
24



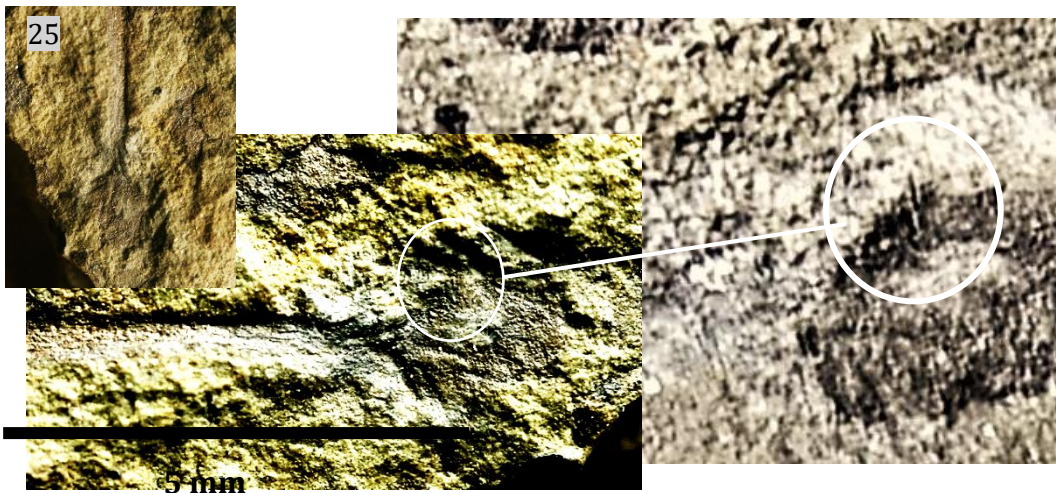
Juveniles growing out of a gametophyte socket. Fully branching:



Branching
juveniles,
up to 1 mm
in height



Seeming juvenile, sprouting from a gametophyte already in use, suggestive of possibly more than one generation of sporophytes *per* gametophyte:



Same situation for a previously shown elderly gametophyte. Seeming juveniles (trials?) among scars of older generations of sporophytes.

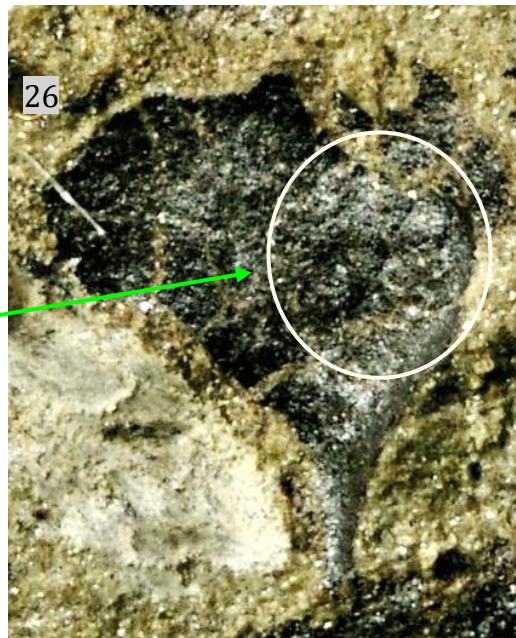
The thallus itself is more clear than an overview photo can show.



5 mm

Gametophyte with elaborate taproot (sperm must swim). Structure still intact, no fungi, little wear, several sproutings.

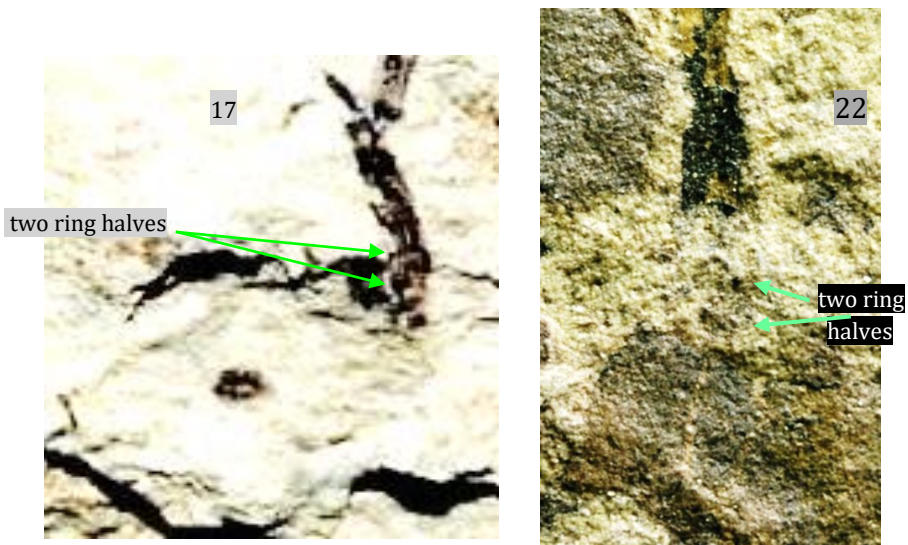
1 mm



Equally intact gametophyte, several possible sproutings; two seeming age groups.



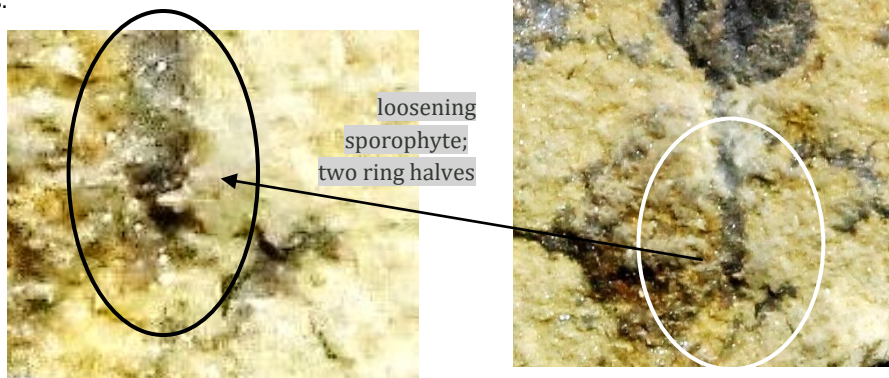
As to the precise connection of sporophyte and gametophyte: it might be that the gametophyte socket ring leaves a counterpart half behind on a broken-off sporophyte. Speculatively, the ring might grow a fault line at half height, possibly with a cambium membrane inside the ring, not unlike the way an autumn leaf is shed.



Or perhaps the whole socket lining / sheath might be or become cambium tissue. All this to prevent an open wound or tear for the gametophyte, while shedding an old, discarded sporophyte. The gametophyte would thus remain intact to support a next generation of sporophytes. A socket ring of cambium tissue generally, would also explain its fossilization, or at least its greater resistance to the fungi than the softer gametophyte tissue proper, as can be observed on virtually all our matrices. (Remember the coal deposits of Section 3.2. .)



There are rather more examples of these seeming double rings or half rings hidden in the material – awaiting a further anatomical analysis.



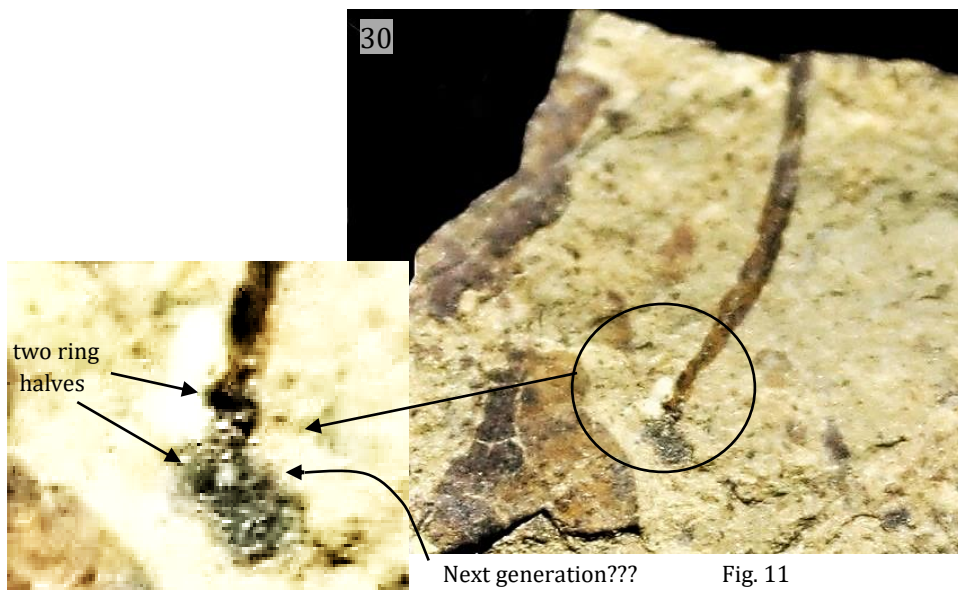


Fig. 11

This is probably about as far as our heuristic approach of the material will take us. A next natural step could indeed be an anatomical analysis of types of tissue, cuticle for the gametophytes, etc.. 2) 3) 4) 5)

And thus concludes a first presentation of our proposed gametophyte material at several stages of preservation and decay.

Notes

1) Fungi, and many bacteria, live the way animals do. Using oxygen to burn food for energy. And to build themselves up. With CO_2 as waste. Their breathing thus equally complementary to that of plants. The fizz in a bottle of champagne would be a case in point. Fame & fortune for simple carbon dioxide - as the residue of a yeast that liked to eat sugar. Same thing.

Calling the enhanced levels of CO_2 that stem from our early fungal symbiosis “blanket”-like is probably quite apt, as carbon dioxide is much more dense - and thus heavier - than a more regular air mix, with also O_2 . So CO_2 will tend to hover low, where the plants are, and not slip away. O_2 gas will mix well with the CO_2 of the fungi.

All of which will undoubtedly also mean something for, say, how *thin* our heavy little blanket

of an atmosphere might still have been. If, on land, it only needed to augment or facilitate the already pretty wondrous gaseous exchange between our pioneers - the fungi & earliest terrestrial plants. A hand-in-glove trade-off of oxygen and carbon dioxide, that will become more and more palpable as the heartbeat of the entire living planet. So. The mother of all *quid pro quos*: already, and quite explicitly present during the first steps on land. Much more explicit - and local - than any such exchange under the waterline could have been. For an idea how early these symbiotic gaseous friendships on land may have come up - even before our recorded history - and why so early: see footnote 3 with Part 1; this history.

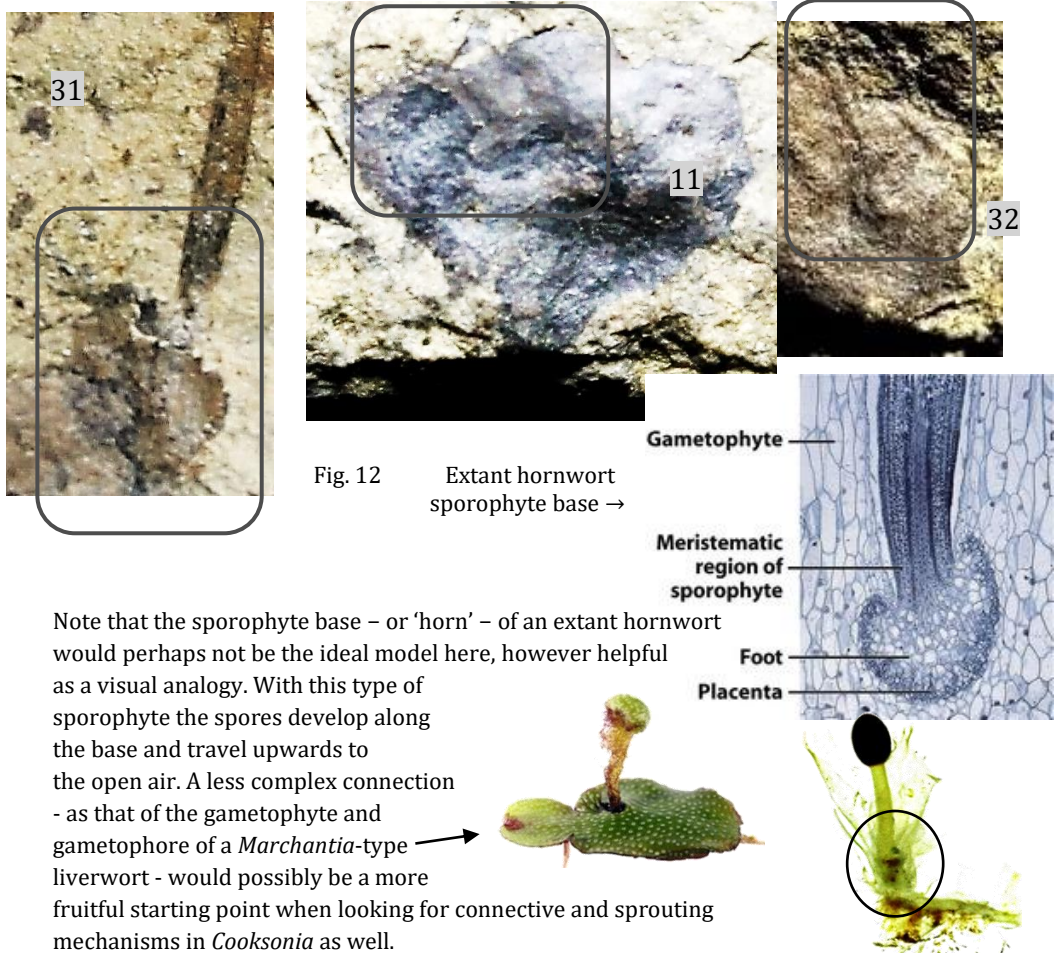
As an illustration of the benign power of CO₂ for the plant world, and not just at the dawn of life, we may quote the great botanist Dr. Hope Jahren. There is no good reason why what is good enough for botany now, should not also echo the evolvement of health, size, numbers and species at *that time when* as well:

“ [...] in 1994, some of the same researchers, plus a new generation of students, began building the most grand-scale and magnificent forest that had ever been attempted. They built huge ringed scaffolds 100 feet [30 meters] across, taller than the forest could ever grow, and they pumped carbon dioxide from massive tankers up through the pipes that lined the scaffolds, bleeding an extra dose of carbon into the air that the little trees used for growth. The deciduous understory decorated itself gaudily [...]. Across all this diversity, however, a general trend emerged: on average, most plants grew about 30 to 40 percent bigger at the higher levels of carbon dioxide than they did when grown at the normal ambient levels. It was perhaps the most important plant experiment of the 20th century, and it has since inspired thousands of spinoff experiments, such as the ones that I do in my lab [...] But there was another, more practical reason to end the experiment that was rarely mentioned: the trees had simply outgrown their scaffolding. [...] Fortified by health and maturity and untroubled by constraints of the past, they confidently reached out into something new. “

From: Jahren (2017); p. xvii .

Ring a bell? These same sorts of experiments can - in passing - also rather grandly illustrate the dimensional leap from our Silurian Period to the later Devonian age - with its much bigger and more diverse plant life, certainly partly due to the same principle. Increase of CO₂ in an atmosphere that is being built up. Perhaps even challenging evolution to be quick about its reactions (compare evolution's highly relevant initial errors-of-scale in Part 4 of this history).

2) Such anatomical research might also shed more light on the goings-on *inside* the gametophytes of *Cooksonia*, c.s., yielding more detail on e.g. the sporophyte-gametophyte connection of the plants. Consider the somewhat daring fossils of Fig. 12, promising a level of detail that would significantly deepen the knowledge of these earliest vascular plants. Knowledge just for the taking.



A nicely lobed *Marchantia*. Late Silurian, Holy Cross Mountains, Poland.
This herbarium.

A living one next to it.



↑ Detail of lobes, some cuticle missing; 3D fossil.

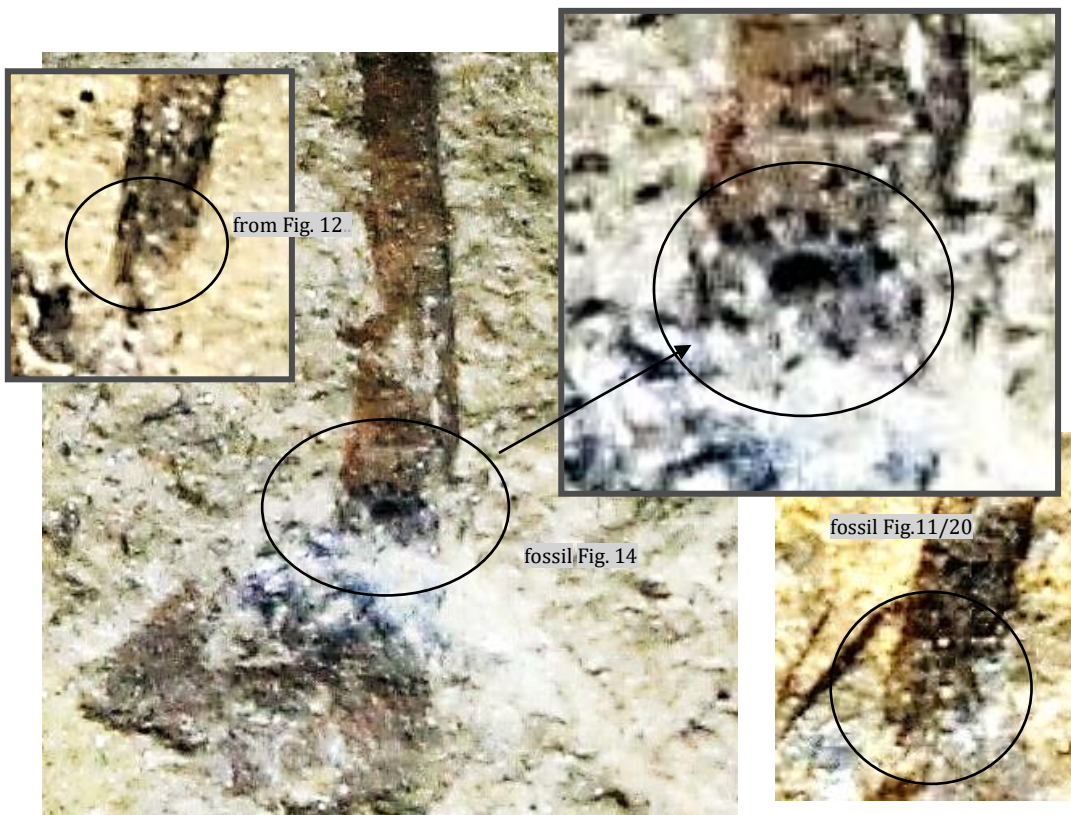
Probable gemma structures preserved inside gemma cups.

Significantly more detail for this plant in Part 5, footnote 1.

Extant liverwort with overlong socket sheaths. As a comparison for Silurian socket sheets, e.g. in Fig. 12, above.



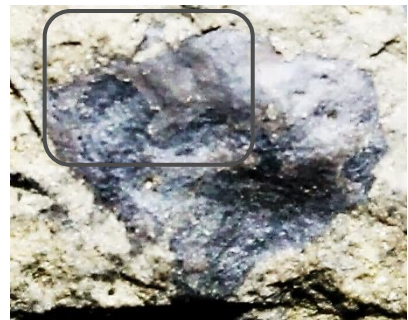
3) A sure and clean way for sporophytes to separate from their gametophyte would need a basis in the anatomy of their connection. The three fossils below show a glimpse of an architectural feature that might help in making a clean snap possible. Again just barely ahead of the fungi, one can still see a seemingly withered and brittle internal structure that may be part of the mechanism of a fault line (compare perforations for crackers or tissue paper):



A loose end here would be the broken-off sporophyte base still inside the thallus. Many fossils of Fig. 12 and 11 seem to suggest that this base will somehow vanish back into the gametophyte's soft tissue, reused. This may well be the case; perhaps in the following way.

The gametophyte socket, its rim being the conspicuous 'gametophyte ring' found on the matrices, seems to be of a sturdy kind, that could firmly harness a sporophyte base. If this is so, the growing point of the sporophyte - the 'meristem' for its vascular cambium - could be positioned high within this base, possibly anchored to the rim of the socket. As the observed second ring. From which the old stem may safely break off when its time has come. What is below this fault line, i.e. the content and volume of the sporophyte base seeking nutrition, would now indeed be of a softer non-cambium material that could indeed be reused by the thallus.

In this way no more than one half ring of harder material will be left on the thallus, possibly with some debris from the socket sheath. That might even get worked out of the —→ gametophyte if it hinders.



This suggestion of a high growing point is meant as an example to explain the vanishing sporophyte foot, in the context of phenomena previously observed, such as the two ring halves, that would thus also be accounted for.

A further speculation might regard different sorts of tissue for both rings. Top ring: more likely vascular cambium; lower, gametophyte ring possibly sterome tissue or bark cambium. The lowermost base of the foot could then be made of 'haustorial' cells that absorb the water and nutrients from the gametophyte (which is the known situation for *Anthoceros* hornworts). All this would be rather interesting (microscopic) anatomical work.

Finally we also like to mention, with so many words, the rather basic assumption throughout our history that we consider the *Cooksonia*-type plants under discussion as indeed already seriously vascular. We think there will not be much discussion needed on this, as the fossils themselves seem to show the already very intricate, even woody structures; incomparable to the small, watery, translucent 'stalks' that are the archegonia and antheridia of liverworts. Compare e.g. the tender extant liverwort archegonia on our page 68; above.

Two fairly offhand and possibly redundant photos indicative of this *Cooksonia*-type anatomically complex vascularity, in addition to e.g. Fig. 14 above, are given as →



4) This essay was written as the work went along. Which means that the text will reflect what may be called a heuristic process of discovery. In the words of the Conclusion in Section 3.3., above:

“One general conclusion we may draw from all this, at least, is that heuristics can indeed be an interesting way to enter a jungle of data, yielding almost always creative catches and by-catches. By-catches that may just as easily become the main feature, in a next round.”

Heuristics, as it goes along, would even allow one to discard a previously helpful stepping stone altogether, once a further goal has been successfully reached. The method does not deal in causality, just creative trials.

One stepping stone in our research, the first one in fact, was to regard the mysterious ‘blobs’ in Section 1 as juvenile thalli of *Cooksonia*-type plants. Later on, the adult thalli in our Fig. 11 would become such unequivocal ‘stand-alone’ evidence of indeed gametophytes of vascular-type land plants, that the initial hunch about the blobs as juveniles - the hunch that spawned the search - could now in principle even be abandoned without damaging the greater discovery.

We do think it is wise, however, to hold on to the idea of the blobs as juvenile vascular thalli as well, because the idea seems to have accumulated enough value in its own right.

* On the one hand. Fig. 11 does seem to show many 3-lobed echos, also in adult vascular thalli. See e.g. Fig. 11 (photos 11, 20, 22); Fig. 12, Fig. 14. Moreover, the small sproutings out of gametophyte rings of the 3-lobed structures in Fig. 11 look identical to those out of the equally identical seeming gametophyte rings of established, older vascular thalli. So, rings and sproutings seemingly identical, even on the same matrix. And this: the 3-lobed thalli also - and somewhat conspicuously - seem to live in the precise places (Section 1; this essay) where *Cooksonia*-type gametophytes are expected to be (Section 2). Liverworts, for example, never show individual preferences, and certainly not on edges of furrows. They never have taproots either. Liverworts will just be filling a reliably moist surface with a forest of one or several species. For this definingly different and communal behaviour of liverworts, see Part 5 of this history.

* On the other hand. It would be naïve to expect the shape and form of the juvenile template, only bigger, in the adult phase of the plants. As mentioned earlier: the growing of a sporophyte foot will obviously alter the neat, 3-lobed shape of the pristine juvenile thallus, that at least has to adapt to a more outspoken third dimension (meaning: up) and counteract the leverage of the vertical sporophyte 'pole' swaying in the breeze. Possibly requiring and filling a more sprawling, rosette-like floor space to stabilise itself (situations where animals put their legs further apart). Juvenile structures needn't look like miniature adults. They rarely (if ever) do.

Moreover, keeping the hypothesis of 3-lobed juveniles morphing into more sprawling forms toward adulthood also seems to give us a good first handle on a future approach to the properties of the vascular plants. Juvenile thalli might become helpful stepping stones once more, possibly harbouring further information on the anatomy (three separate, sphered compartments?) and workings (taproot internalised - overgrown - after fertilisation?) of adult vascular thalli.

With regard to the visibility of taproots during adulthood it should be noted that taproots overgrown with fungi can often still be discerned as appendages of the thalli. See e.g. Fig. 11, fossils 10, 13, 15 and 17; some matrices show two. Of course, the more floor space the thallus is going to use, the more chance of the taproot eventually getting incorporated in the whole.

But certainly not always.

A significant heuristic 'by-catch' of the blobs-as-thalli - and a real advertisement for the method at that - was of course finding out why at least 90%, and perhaps even 100% of our *Cooksonia*-type sporophytes are where they are on their matrices (Fig. 5 and 6 in Section 1, plus Section 2.1.; last paragraph). It led us to notice the context of the fossils on the matrix - i.e. the matrices themselves - as indeed jewels of botanically significant information, revealing more insight than ever before about the habitat of the plants, and their needs and choices.

5) With regard to the fungal symbiosis as portrayed in these pages we wish to be clear that, of course, crucial roles for fungi may well have begun earlier than in the (Late) Silurian. The Earth may well already have been covered, at least in some places, with e.g. land dwelling green algae, that could have had their nutrients recycled as well (possibly as a prerequisite for *their* being there). But this merely pushes back the timeline of things.

It does not alter the story when the fungi were already friends with existing fledgling floras at the time when our bigger, stomatic land plants were flown in. Indeed, the fungi must always have come from *somewhere*. More on this possibly of an even earlier symbiosis in footnote 3 with Part 1 of our history.

And yes, algae + fungi also give us another famous collaboration. Together they build the lichens of the world. A type of friendship that may have been forged very early as well, and for which we are also keeping an eye open in our Silurian material (see Part 3, footnote 6).

Acknowledgement

Many thanks go to professor Joseph E. Armstrong for writing a most comprehensive textbook on the emergence of the earliest - especially the microscopic - flora. Armstrong's treatment of his subject as intellectual high adventure remains a prime example of how a textbook can also look and sound. It made the book a meal skipper. Twice.

A quote and a drawing from the book feature in the Introduction to this essay. With kind permission.

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Part three

A cradle of land life

*Take me outside, sit in the green garden
Nobody out there, but it's okay now*

– Laura Mvula, *Green Garden*

Preface to A Cradle of Land Life

Late-Silurian floras, as cradles of life, are by their nature highly dynamic. This Part 3 opens with what would be an intermediate plant, tentatively searching for a more complex and larger form as known from the later, Devonian age. A second case will be about a rather thorny fellow that will also figure as an example of how a clear demarcation of plant life and (aquatic) fauna is of the essence, in these early phases of history. With the additional theoretical bonus that the thorns of the plant will, in passing, also touch, if not pierce the very core of our early evolution; as shown in Part 1 of this history, footnote 7.

After this the investigation finds itself on a very different road - flanked & adorned by six totally unique liverworts. Found a whole geologic period earlier than any previous liverwort fragment. And these not just some tentative fragments but impeccably beautiful miniatures. And bryologically modern ones at that. Four of them would still be living in our parks and gardens today. After their Silurian counterparts, without much ado, first gave birth to the vascular plants, shrubs and trees on Earth. See Part 5.

We've started a comparative survey with three of these living liverwort jewels, which is a rather fun and highly recommended way to literally get in touch with these mind-bogglingly ancient, probably Ordovician heroes. Feel how they feel. See how they work. Their gleaming, intricate little machines. Perfectly engineered for kids as well - harking back at least 470 million years. Dinosaurs, eat your heart out.

The essay

A Cradle of Land Plants

World Heritage from the Late Silurian – including six liverworts

0. Introduction

Recent publications have documented part of the Late-Silurian (Ludlowian/Pridolian) plant deposits in the Holy Cross Mountains in Poland. For an introductory geographical and paleobotanical context, see Bodzioch, Kozłowski and Popławska (2003). [Also available as an addendum to this history; found at the back of this book.]

https://earthphysicsteaching.homestead.com/A_Cooksonia_type_flora_from_the_Upper_Silurian_of_the_Holy_Cross.pdf

The above article describes *Cooksonia* in this cradle of land plants. A further article (Popławska-Raszewska and Bodzioch (2007)) also alludes to material resembling the Silurian Argentinian and Australian floras.

The present essay will discuss some specimens of this same sort of plant material, from the same site, followed by utterly unexpected Late-Silurian liverworts as their literal neighbours. A next logical step would be a search for their (microscopic spores, on the same matrices.

The essay is structured as follows.

Section 1 starts out with a brief mention of some more or less random *Cooksoniae* from this site, as a prelude to some very recent (summer of '21) finds of larger and stronger *Cooksonia*-type fossils, that may well have reason to be an intermediate stage to early Devonian *Renalia*.

Section 2 first addresses the danger of 'overcrowding' the Late Silurian. Not everything that resembles a land plant in this era will necessarily be one. Better explanations can sometimes be found in an equally existing reservoir of aquatic species – plant or animal. Cautioned by these warnings, a Late-Silurian *Sawdonia ornata* will, however, still be argued for.

Section 3, as an intermezzo touches upon some material that seems either unproblematic or too enigmatic, at this point, to warrant elaborate affinity research. A Late-Silurian *Salopella* will be mentioned, as will a possible *Cooksonia bohémica*.

Section 4 presents what will indeed be Late-Silurian botany of the highest order. Six Late-Silurian liverworts, four of which (the thallose ones) seemingly still alive today - as most probably the very first of the first land plants on Earth. And still here.

First a leafy liverwort is shown, that bears close resemblances to a Triassic *Naiadita* as thus a plausible candidate for the Late Silurian as well. Next, four thallose liverworts will be presented, one of which, a *Marchantia*, was already described in Parts 1 and 2. The plant will get closer analysis in Part 5 of this history, footnote 1. The three 'new' species would be a Late-Silurian *Pellia neesiana* (or *P. epiphylla*); a *Blasia pusilla* and a *Lunularia cruciata*. One more friend, number six, (that fragments its thallus as 'cuttings') will be visiting in a footnote. The liverwort essay in Part 1 of our history is a highly relevant additional source of information; we therefore try to avoid too much redundancy in the essay in this Part 3.

1. A glimpse of a possible *Renalia* intermediate

An important find in the Late Silurian in the Holy Cross site is, not unexpectedly, *Cooksonia*. Certainly in quantity. A few token fossils of a common - we are tempted to say garden variety - in our herbaria would be the following. Many more and more interesting specimens are shown in Parts Two and Four of our history. The relevant information for what follows is that a typical *Cooksonia* sporophyte (also of other species, like *C. cambrensis*) is about 1 cm tall.



Fig. 1

While these kinds of fossils await further analysis, one of our general *Cooksoniae* may already be showing something beautiful to the world. A sporangium that seems to be emptied, and rather looks like a lobed, deflated skin of a tiny balloon. Notice the smooth, almost silky, indeed skin-like aspect of what could well be the *operculum* in the macro photo on the right.

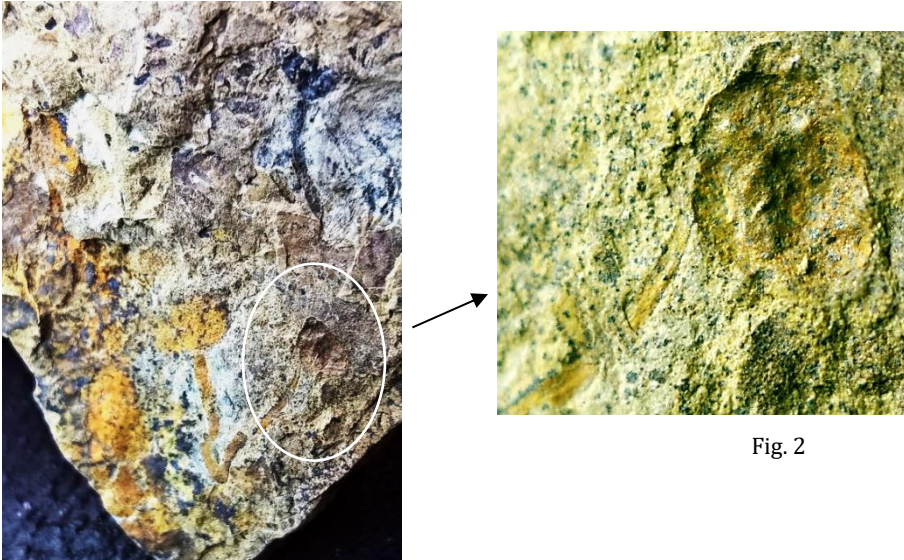


Fig. 2

In this same spirit we would like to present some exceptional, significantly bigger and stronger *Cooksonia*-type fossils, found in the summer of '21. Such as these:



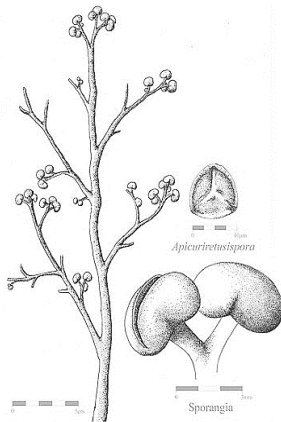
Fig. 3



Fig. 4

Next to these finds was another matrix of similar, exceptionally large, strong specimens, with their own strangely beautiful complexity; see Fig. 5 on the right.

The question is: are these finds still *Cooksonia*? How do the two seeming kidney shapes on the matrix on the right



Renalia reconstruction

compare? A number of early land plants are known for their *reniform*, kidney-(bean-)shaped sporangia. Among these is *Cooksonia caledonica*. But also early Devonian *Renalia*; a plant directly evolved from *Cooksonia*, that carries its sporangia in bunches.

Another characteristic of *Renalia*, but not of *Cooksonia* is its pseudomonopodial branching: one of the branches of a pair can/will be shorter than the other, thus allowing the creation of main axes



Fig. 5

and side shoots. See the reconstruction on the left, and again the tentative form of the fossil of Fig. 5.

As to the kidney-shaped sporangia: compare the further find of Fig. 6, below right, as recent as the previous. Hesitating shapes (kidney beans to Crusader cross?), making up a complex sporangium, suggestive of a tentative 'experiment'. The photo of Fig. 6a of the same fossil seems to show at least three recognisable kidney shapes.



Fig. 6



Fig. 6a

Big, strong fossils as described above are not very scarce in the finds of the summer of '21. Below, two more examples. On the right a slender *Cooksonia* next to much larger branching plants.

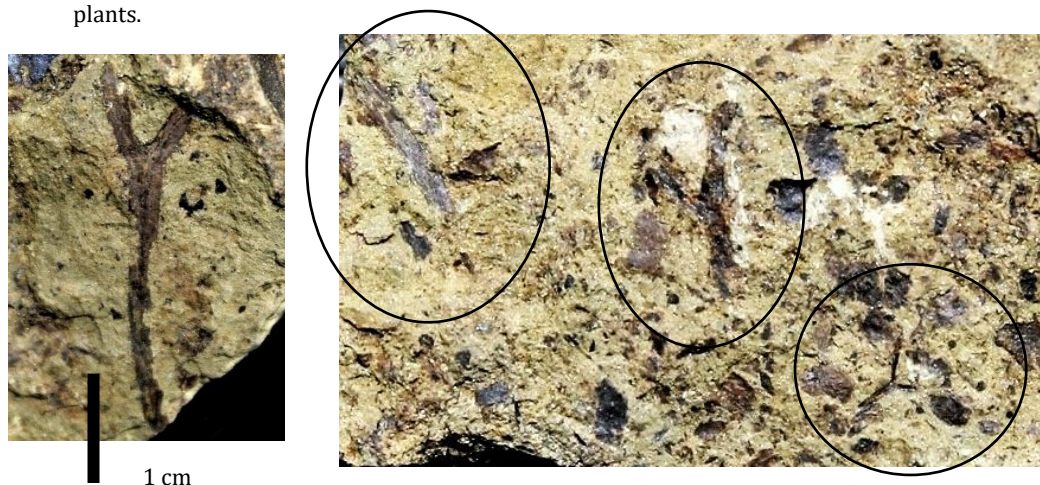


Fig. 7

However, even the 'slender *Cooksonia*' in Fig. 7 may be sporting an experimental extra, higher branch, with complex sporangia (Fig. 7a) that seem to hold tentative kidney-bean echos as well: Fig. 7b – compare Fig. 5a.

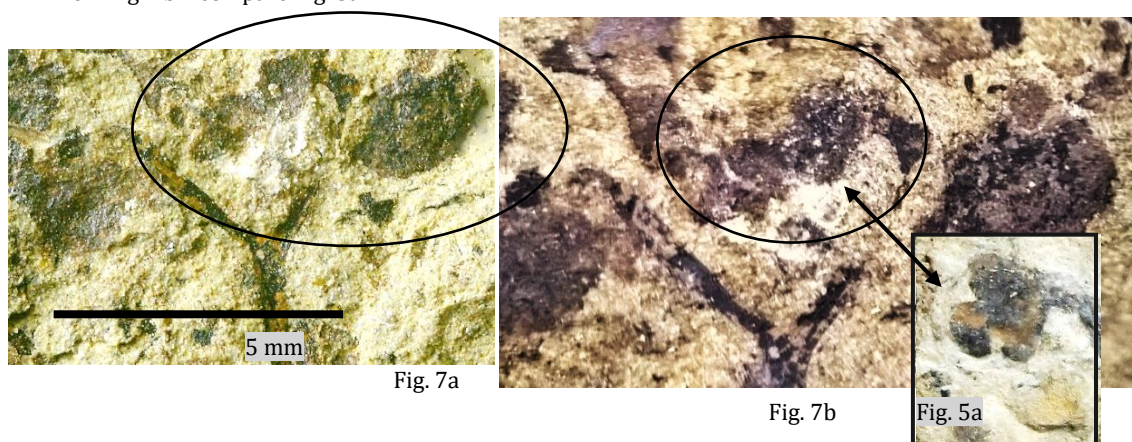


Fig. 7a

Fig. 7b

Fig. 5a

So, what we have seen are *Cooksonia*-like plants, some seemingly experimenting with pseudo-monopodial branching and also with complex sporangia - seemingly kidney-shaped and clustering; possibly working towards a separation into a bunch. All-in-all, a situation suggestive of what might be an intermediate stage towards a *Renalia*-type plant of the coming Devonian age. Complexes of sporangia, evolved halfway from *Cooksonia* but not yet separated into the real bunches of *Renalia*.

For the sake of completeness it should be noted that hints of pseudomonopodial branching and kidney bean-like structures need not always go together in the material under consideration. There also seems to be evidence of stems with side shoots in combination with seemingly normal, or at least non-complex *Cooksonia*-type sporangia.

2. *Sawdonia ornata*

The Late-Silurian era just doesn't allow for all the diversity that one might dream up while inspecting material that is morphologically a bit further away from *Cooksonia*. Instead of new hypotheses, or even of more conventional comparisons with established land plants, better answers can sometimes be gotten from the record of aquatic species of the same era – algae, or even animals, such as the animal colonies known as graptolites.

In this case, our strategy will be that when the fossil displays what resembles 'usual' remnants of cuticle (instead of a chitinous outer shell of an animal colony) and if it also displays what looks like 'just' vascular tissue we would be inclined to give the fossil the benefit of the doubt as a land plant. Pending further anatomical analysis. For this fossil, in Section 2.2., below.

2.1. *Sawdonia ornata*

The Late-Silurian *Hostinella* ('unknown but branching land plant') from the Holy Cross Mountains that we wish to present is at this point in time a much rarer find than *Cooksonia* and even than our hypothesized intermediate *Renalia* of Section 1. The fossil on the right is one we have available at this moment.

The large photograph of the plant is meant to show its full splendour as indeed a normal-seeming land plant among land plants, wide at the base and tapering upwards like a plant. As far as we can see, the fossil also shows inconspicuous remnants of cuticle (to be checked) as well as a rather fine display of what should be vascular tissue, almost laid bare.

Possible sporangium →



Fig. 8

5 mm

Add to this the context in which the fossil was found (land layer with *Cooksonia*) and we feel free, for the moment, to continue to think of the fossil as a land plant - not e.g. an acanthograptid, such as *Thallograptus*, below:



Thallograptus, a colony of animals

Notice that even on the basis of this one, small, tentative picture of *Thallograptus* one can already well imagine that these kinds of likenesses (in this case: of dendrite graptolites) can be so compelling that they make an almost-more-basic-than-basic determination check a necessity.

But, to move on, for now: here are some details of our mystery plant -



Fig. 8a



Fig. 8b

There are several plant species with the surname '*spinaeformis*' in the Devonian, such as this one. A seemingly reasonable match while it indeed has spines - but on inspection not as pronounced, long or 'claw-like' as our much earlier (but no less developed) Silurian fossil.



Devonian *Drepanophycus spinaeformis*

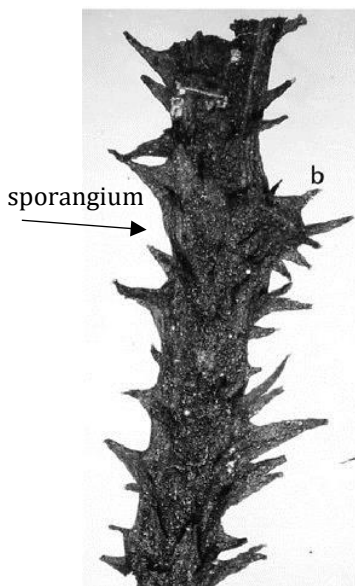
A closer match
seems to be
this species:



Psilophyton crenulatum

However, the spines of these plants seem (in these and similar photos) still less regular and more tentative than those of our best candidate, *Sawdonia ornata*.

Sawdonia ornata looks much more fierce than the above *Psilophyton*, with much more regular, and for the first time also unmistakably thorn-like spines, as does our fossil.



Three Devonian *Sawdonia ornata*



our candidate

See also: [Nonfertile axes of *Sawdonia ornata*, Gaspé, A. B. Closer views of... | Download Scientific Diagram \(researchgate.net\)](#)

Moreover, *Sawdonia ornata*, on the basis of the two fossils in the middle above - conserved in resin - has been described as quite possibly Silurian. Gaspé, Quebec:
https://grad.biology.ualberta.ca/paleobotany/?page_id=28

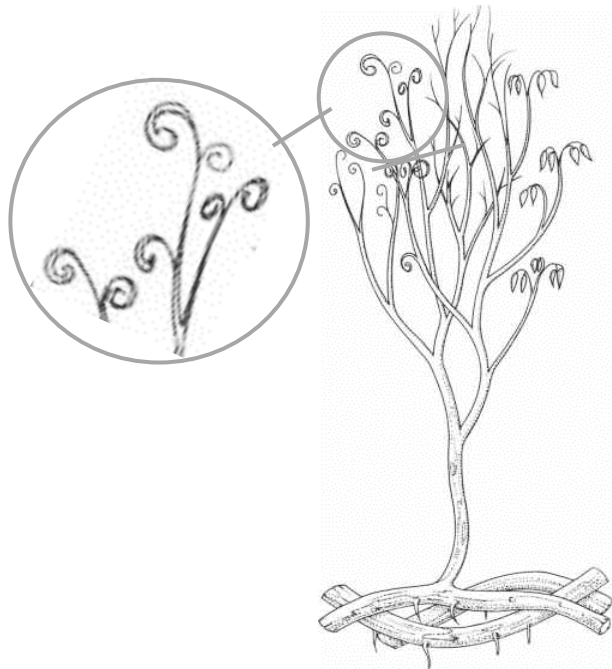
2.1.1. And a second fossil

And a further argument. A new fossil has been found this summer in the same stratum, that seems to have a natural resemblance to a plant called *Psilophyton princeps*. See fossil and *P.* reconstruction:



Recent second fossil

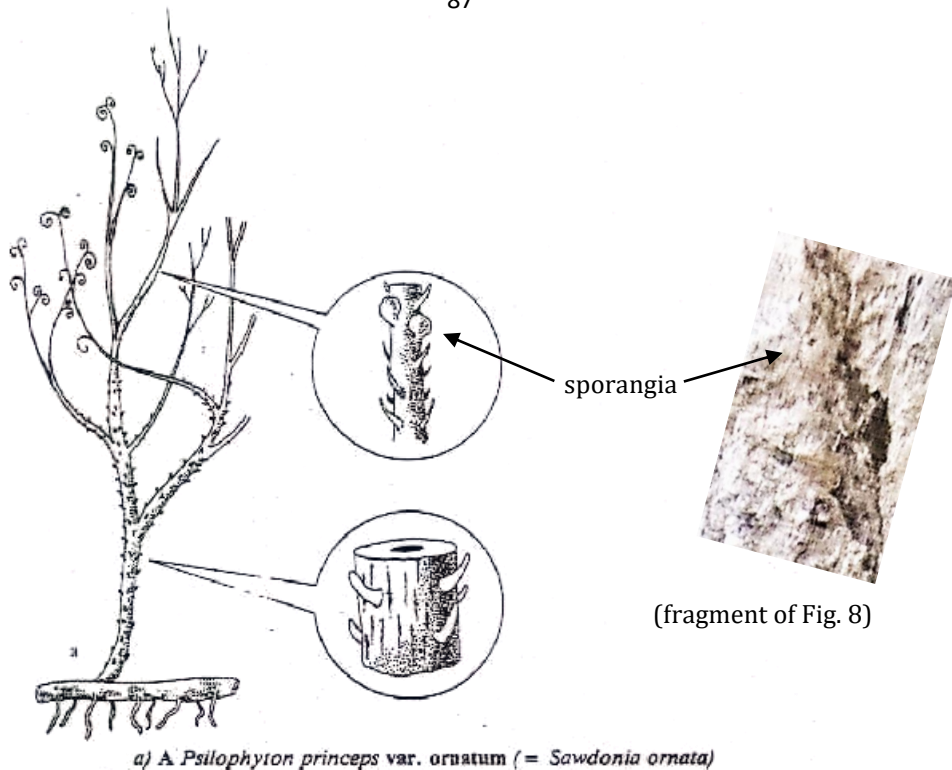
Fig. 9



Psilophyton princeps reconstruction

Now, it turns out that *Sawdonia ornata* was first described in 1859, by Sir J. William Dawson, and was originally named *Psilophyton princeps* var. *ornatum*. See this reconstruction, and its small print





Thus, our newer fossil seems to fit perfectly as the topmost part of our earlier thorny find, if that earlier find would indeed be a plant now called *Sawdonia ornata*, as in the reconstruction above. Notice that the onset of the largest curly shoot in our fossil of Fig. 9, as well as its right branch, could well be echoing a thorny architecture.

At this point it seems very natural to adhere to the simple scientific adage that the better hypothesis is the one that has to lean the least on colossal coincidences. The more so in a Silurian world that does not allow for more than a handful of land plants anyway. With this consideration in mind we rest our case for a Late-Silurian *Sawdonia ornata*, for now.

With regard to a theoretically still possible affinity of our first fossil with graptolites: only an anatomical analysis, checking the cuticle, will bring clarity.

2.2. Anatomical analysis – cuticle and stomates

The features that tell if a fossil is of a land plant (and not of an algae/animal (colony)) are - theoretically - rather straightforward. Only land plants have a waxy 'skin' of cuticle, to keep the plant from drying out, with complex pores ('stomates') for their photosynthesis. Cuticle and stomates can be seen with a micro-scope. Magnifications of the best preserved cuticle-like layer fragment of Fig. 8 indeed gives stomate-like figures.

Compare these magnifications of our fossil of Fig. 8; some showing seemingly even the guard cell 'lips':

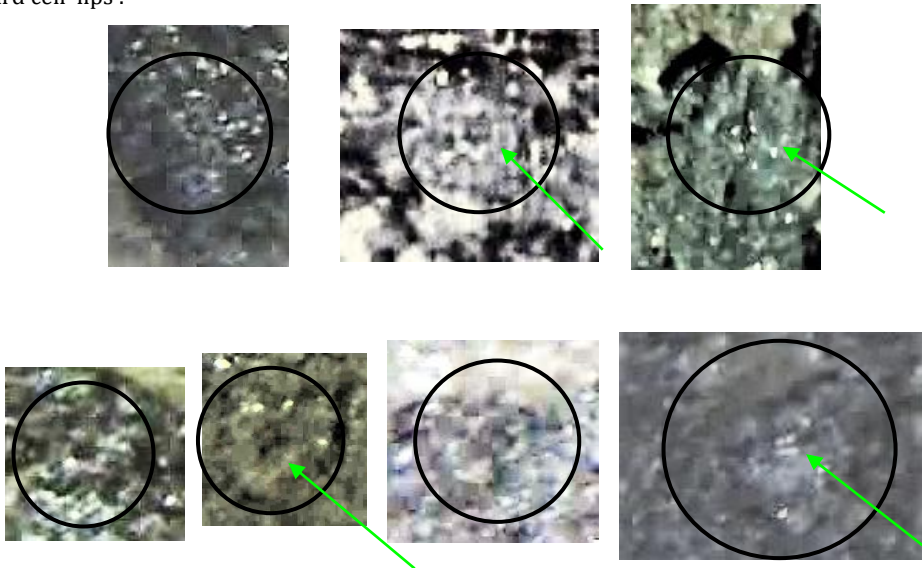


Fig. 13

As a comparison, observe a *Lithograptus flaccidus*, a saw-tooth graptolite with much less magnification.

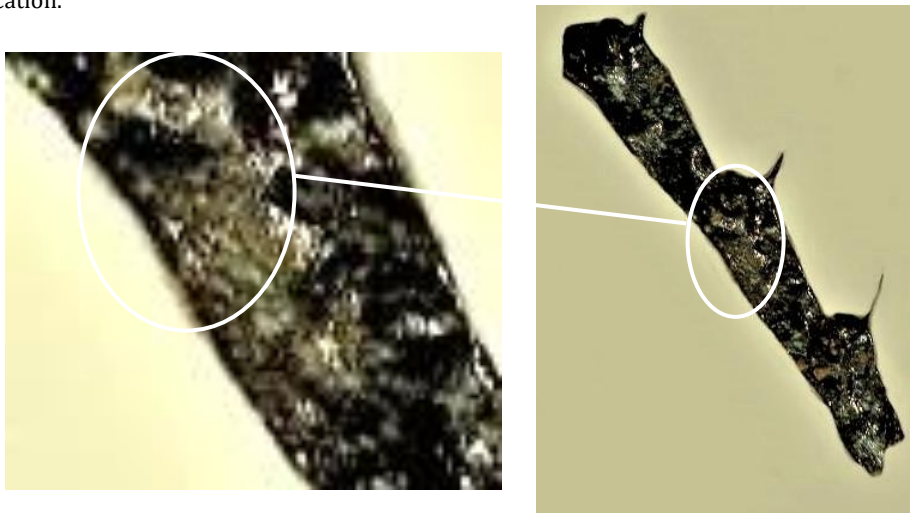
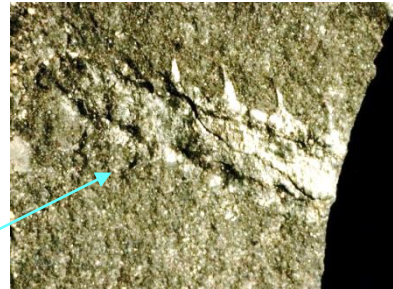


Fig. 14 Source [Mic-UK: Grappling With Graptolites \(microscopy-uk.org.uk\)](http://microscopy-uk.org.uk)

Here also 'stomate-like' structures might be construed, but in an unusual mix of dimensions, as well as much too large for plant stomates. Moreover, the high-gloss chitinous shell of the graptolite is much less structured than our layer of proposed cuticle, with its already vaguely discernable epidermal patterns (certainly around the stomate guard cells) and its clearly visible flexibility to fold over proposed vascular tissue underneath.

The fact that graptolites equally naturally need connections with the outside world - which necessarily must be through their armour - could readily account for their equally pore-like portals; not unlike plant pores.

So, the spikes and thorns of graptolites as possible deterrents for animal predators indeed rhyme with the spikes and thorns we just saw in Silurian and Devonian terrestrial botany. Which, in line with footnote 7 of our Part 1 may tell us something about these spikey botanical outgrowths as very possibly made with a same sort of early template as already known for graptolites.



graptolite fragment

We could now even suggest that next to the thorns, also the interfacing 'pores' (with something like guard cells?) of graptolites could likewise imply a template that could also have been available for adoption by the earliest liverworts - such as *Pellia*. See p. 34 of this history, first paragraph.

For our (im)possible explanation of the analogy of the graptolite and *Sawdonia ornata* thorns we do refer to footnote 7 with Part 1 of our history.

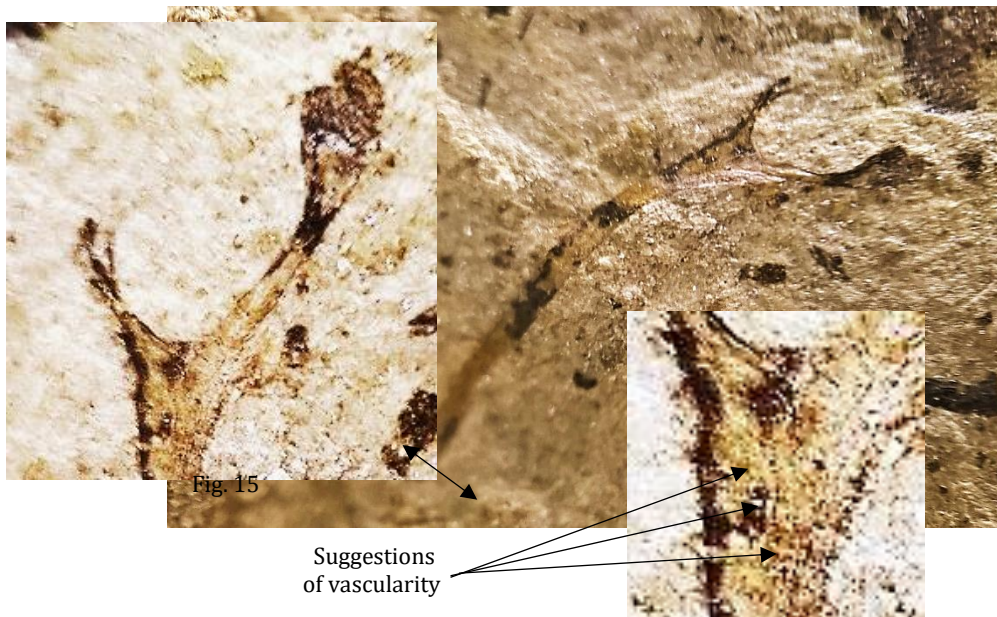
This is stuff that harbours rather invaluable information about evolution itself. Two other, even more basic things this casus seems to teach us is that a) the divide of the waterline would, most likely, not have meant anything for a practical evolution at all - as opposed to for us, incorrigible *attributors*. Same even with b) the division between flora and fauna, as such. Both of which could well be an evolutionary (theoretical) big deal for the Silurian, as well as for even earlier worlds.

3. Two more, equally recent finds

If the Silurian layers of the Holy Cross site have shown anything, it is a richness of plant deposits, in quantity and quality. The two likely to go together. The more there is, the more chance of significant material among it. This section will briefly present two of these riches that are not yet actively embedded in an explicit theoretical framework, because their affinities seems relatively straightforward, or because they are too enigmatic for useful hypotheses, as yet. In short, interesting enough to briefly mention.

3.1. *Salopella*

First a seemingly straightforward find from august 2021. Many *Salopella* were found, tiny and slender. One photo shows its sporangium. A second photo, under grazing light, means to capture some relief to help establish the likelihood of vascularity.



Calling the plant a *Salopella* is our working hypothesis, based partly on a mention in Popławska-Raszewska and Bodzioch (2007). At this moment we cannot be sure yet of the demarcation between *Salopella* and e.g. equally early *Steganotheca striata*. For now, and with this proviso, this plant - that will become rather pivotal in Part 5 - will be called *Salopella* in our history.

3.2. *Cooksonia bohémica*?

The second fossil is interesting as it is enigmatic. Consider the 'bunch' of stems, some with sporangia, on the left, that seem to be connected at the base, suggestive of one plant stem.



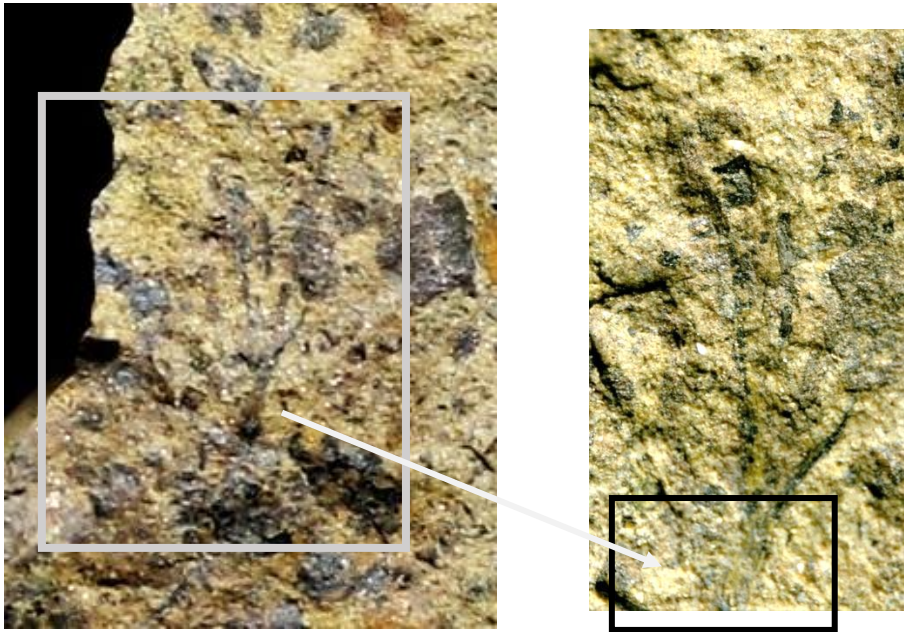


Fig. 16/a

The degree of complexity in branching as in this fossil is not found very often. As a first opening, compare the following fossil (in the Swedish Museum of Natural History) of a *Cooksonia bohémica*:

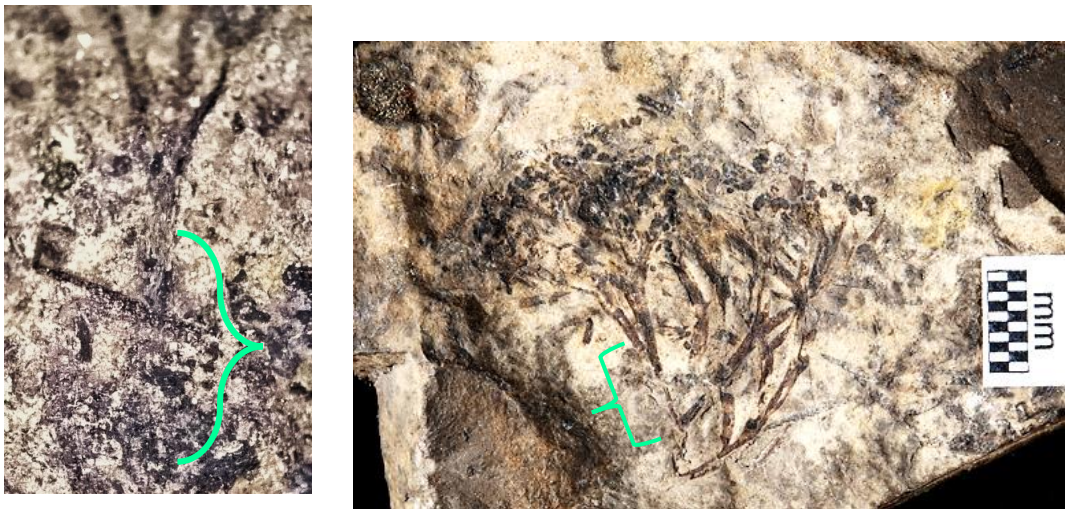


Fig. 17

As in the case of *C. bohémica*, our fossil allows its 'bunch' of sporophytes to come out of a remarkably long stem. As better seen in the macro photo of Fig. 17 above, of our fossil of Fig. 16, revealing more detail under more direct light.

4. Six Late-Silurian liverworts

In this section five proposed Late-Silurian liverworts will be presented. With a sixth in a footnote. First a leafy liverwort, that looks much like a known Triassic *Naiadita*. Followed by four thallose ones that may well still be with us today. More about these plants in a supplementary essay in Part 1 of this history.

4.1. Towards a Late-Silurian *Naiadita lanceolata*

The first fossil seems enigmatic. We could be looking at leaf-like appendages of a moss or an algae, or at sporangia. The easiest starting point would perhaps be an 'ear' of sporangia at the top of a stalk of independently possible, Late-Silurian *Zosterophyllum*.

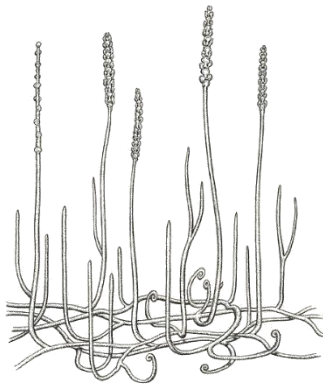
First the fossil, in Fig. 18:



Our Late-Silurian fossil

Fig. 18





Zosterophyllum myretonianum
reconstruction

Zosterophyllum may well be independently present in these layers. Consider the following photo of a matrix (one of a few not in our possession) from the same Late-Silurian site:

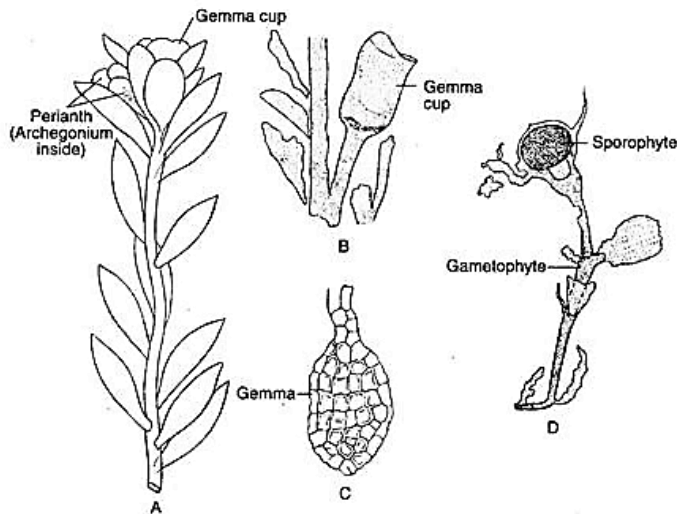


Two seeming ears of sporangia of possibly *Zosterophyllum*

This is all still rather tentative, at least for our fossil of Fig. 18, and the chance that the above association is the final say on the matter is slim. Aquatic or bryophytic affinities could be at least as interesting.

To this end: for a possible, even rather probable bryophytic affinity, first see the following drawing, taken from

<https://www.biologydiscussion.com/botany/bryophytes/list-of-4-important-fossil-bryophytes/46208>



Naiadita lanceolata (after Harris) : A. Gametophyte plant, B. Gemma cup, C. A gemma, D. Plant with mature sporophyte

Another reconstruction of this same plant, from Stewart and Rothwell (1993), p 80:

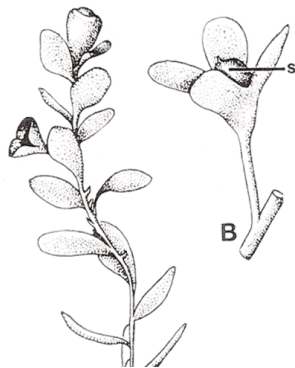
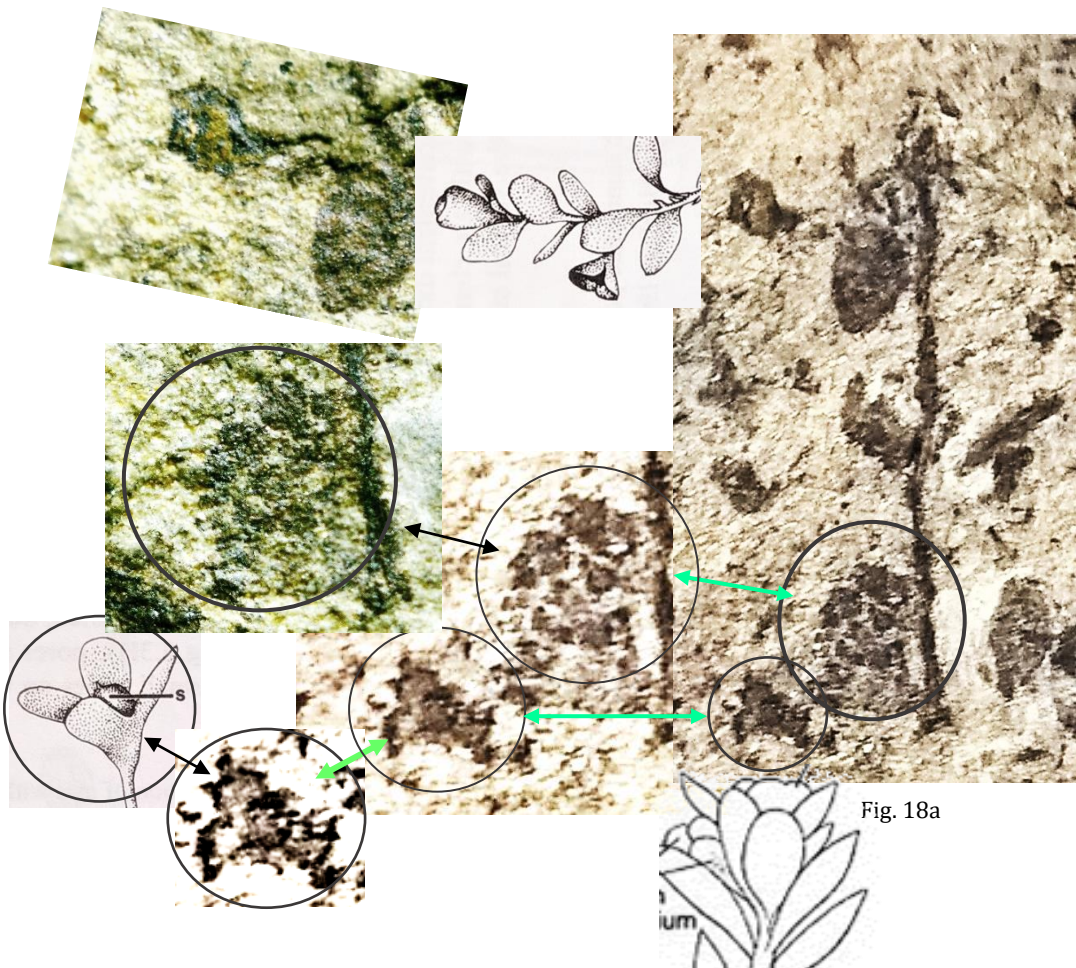


Figure 8.3. A. Habit drawing of *Naiadita lanceolata*. Triassic.

B. *N. lanceolata*, sporophyte(s) at tip of branch. (A,B redrawn from Harris, 1938.)

Going back to our Late-Silurian fossil of Fig. 18: a *Naiadita* sporophyte bending over above its gametophyte seems - at first and second glance - entirely to overwhelmingly possible:



What is suggested is a perhaps withering gemma cup/perianths of the plant, flower-like seen faceup. Sporophyte of possibly an adjacent plant, faceup between petal-like appendages. For an extant rather striking likeness, with at least more insight into the fossil apparatus of Triassic *N. lanceolata*, and our Silurian leafy liverwort here, see the leafy moss *Plagiomnium affine* in footnote 7 with Part 5 of this history.

4.2. Four thallose liverworts as precise images of extant *Marchantia*, *Lunularia*, *Pellia* and *Blasia*

The *Naiadita* of the previous section was a leafy liverwort. Our Late-Silurian material also features at least four probable thallose ones: a *Marchantia* [in this History: Part 2, Fig. 13, and Part 5, footnote 1], plus newly found probable *Lunularia*, *Pellia* and *Blasia*, below.

For the sake of completeness, and of love, first a brief reappearance of *Marchantia*, taken from our Part s 1 and 2:

A nicely lobed specimen; a living one next to it.



Possible gemma structures preserved inside gemma cups.

↑ Detail of lobes, some cuticle missing; 3D fossil.

For an analysis see Part 5, footnote 1.

The next fossil rather resembles a Late-Silurian / extant *Lunularia cruciata*; same Late-Silurian site. Part 1 of this history already showed most of the plant.



Fig. 19



1 cm

Such as the determination of extant *Lunularia* on the basis of its thallus surface dotted with pores bound by pentagon shaped boundaries, which seems also the wording one could choose for the Silurian liverwort of also the same macroscopic form. Photo's were shared in the essay in Part 1; here as an *encore* repeated somewhat smaller: on the left the extant thallus surface; right the Silurian fossil.



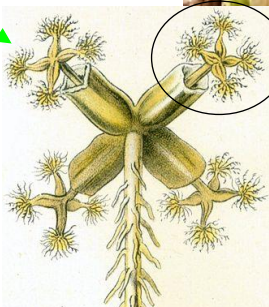
One possible extra windfall on the same fossil, admittedly still a bit speculative - pending a microscopic closer reading - may be the find of an archegonium of the plant; the female sexual organ used for sexual propagation (which is still only a token sexuality, see footnote 2 with Part 1 of this history). Many liverworts, extant and Silurian have this propagation next to the asexual way (cloning) of begetting offspring.

The archegonium equipment would be a tiny structure on a tiny fossil, but as spores of these liverworts were already found in the Mid Ordovician, it is likely that a numerous and advanced plant as *Lunularia* would indeed already have the dispensers for these spores.

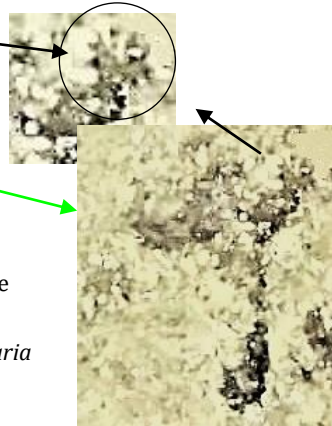
Which may be compared to extant as follows:

Extant *Lunularia cruciata*
Archegonium,

and its archegonial head
with sporophytes.



Microscope photo of the small fossil on the above matrix; $\approx 300\times$ magnification. If it is indeed also an archegonium, it would show that Late-Silurian *Lunularia* would be dioecious as the extant.



0,05 mm

A fossil found directly next to the above *Lunularia* on the same matrix has many detailed similarities to an extant *Pellia neesiana*; a dioecious thallose liverwort, or its monoecious look-alike *P. epiphylla*:

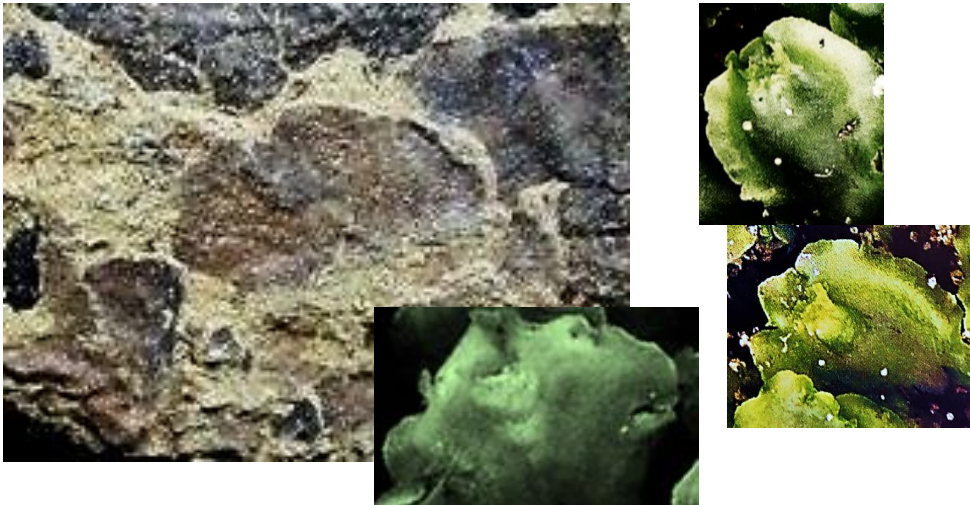


Fig. 20

A co-occurrence of two independent plants, visually in the image of the male and female of extant *P. neesiana*, side by side, as we seem to have here, would not be unexpected. With the proviso that the sexes as such are not always clearly visible in exants; let alone in fossils. We refer to this footnote ¹⁾. For the manner in which the archegonia seem to have fossilized, coming out of their thalli, we refer to Part 1 of our history.

One further thing that certainly merits mentioning is the fact that extant as well as fossilized cf. *Pelliae* can both be seen with what seem to be guard cells as dosing valves for their pores, making them in fact complex, 'modern' stomates - such as can be seen in all vascular-type land plants that came *after* the liverworts (our Part 1, page 22 above). It is quite possible that Late-Silurian *Pelliae*(-style) liverworts already had them. Not to prevent a loss of moisture (a mechanism against drying out, as with the vasculars), **but to invite water in**. Elsewhere (Part 1 footnote 7; Part 5, footnote 4) we have made quite a big deal of this - liverworts suggestive of why the template for modern stomates was already available at the moment the first vasculars did indeed need them. To keep from drying out, especially during their first colonizations of a harsh planet.

What we see for the fossil of Fig. 20, are what seem to be guard cell lips, resembling the equal novelty of similar **extant** *Pellia* liverwort pores, also with seeming



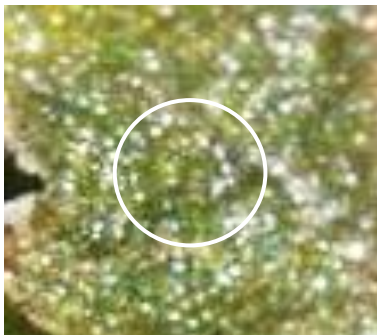
magnification of the cuticle of Fig. 20

guard cells; indeed in the process of absorbing water. See Fig. 20a, below.

These extant pores are easy to spot if the thallus is wet with water, as they seem to visibly *absorb* the water. *Viz* the moist reflections around the pores on the right. Some functions for stomates with guard cells in bryophytes have been described. This water regulation here can then be added to the list. Not just retention **but equally regulated absorption**. Which would be very significant news, indeed. As stomates as dosing valves belong to the pivotal equipment for life on the planet. We also refer to p. 34 of this history.

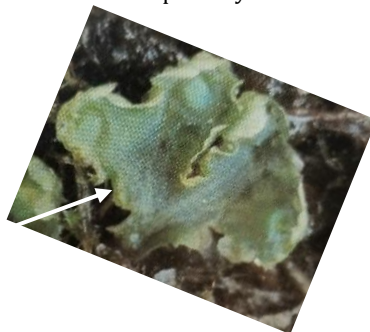


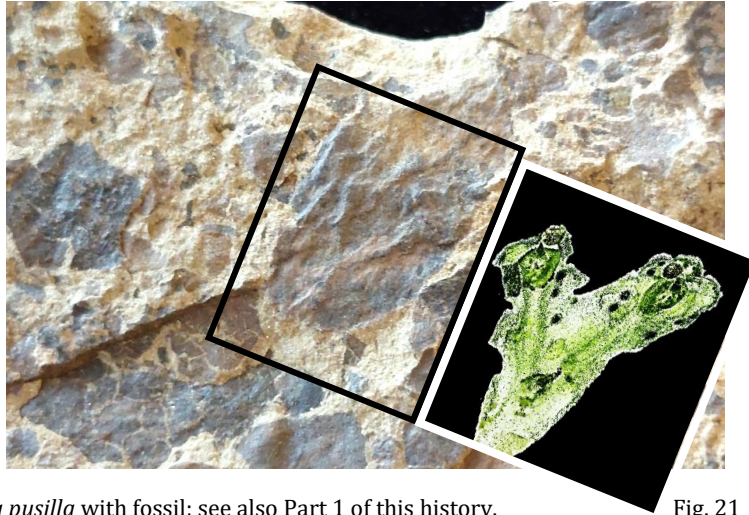
Fig. 20a



Extant pores of *Pellia*. Two as enlargements of the above wet photo.

And a third find. An exact image, equally down to microscopic level, of what extantly would be a *Blasia Pusilla* on the same matrix as previous *Lunularia* and *Pellia*. *Blasia* has been described in the essay in Part 1; with the addition here of one extra possible affinity check. Extant whitish stripes indicative of calcium carbonate - possibly still on the fossil as well.





Blasia pusilla with fossil; see also Part 1 of this history.

Fig. 21

And as in Part 1 also the full matrix that harbours three of the thallose liverworts together. Their survival seems a collective venture, with obvious room for each plant to cooperate in building a tiny forest, as a sufficiently moist and nutrient rich microworld; probably a colony-like habitat for the plants, with advantages elaborated on in Part 1 of this history. For the 'fragmentor' liverwort, see footnote 2, below. Notice that every plant's breathing space seems well-respected. 2) 3) 4) 5)

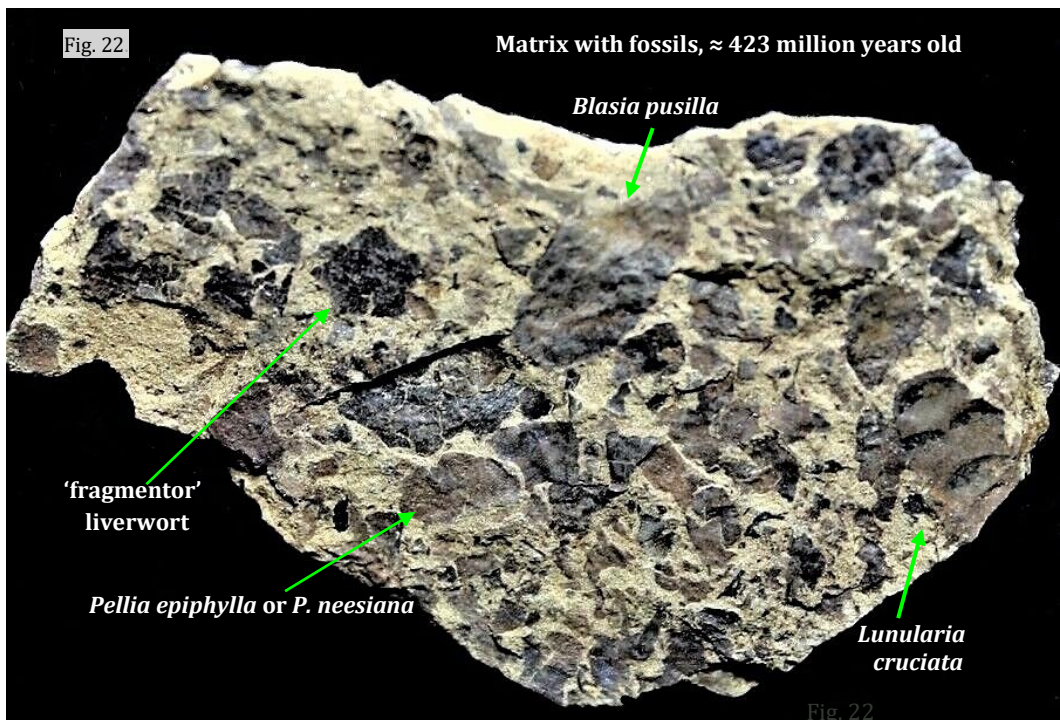


Fig. 22

Matrix with fossils, \approx 423 million years old

Blasia pusilla

'fragmentor'
liverwort

Pellia epiphylla or *P. neesiana*

*Lunularia
cruciata*

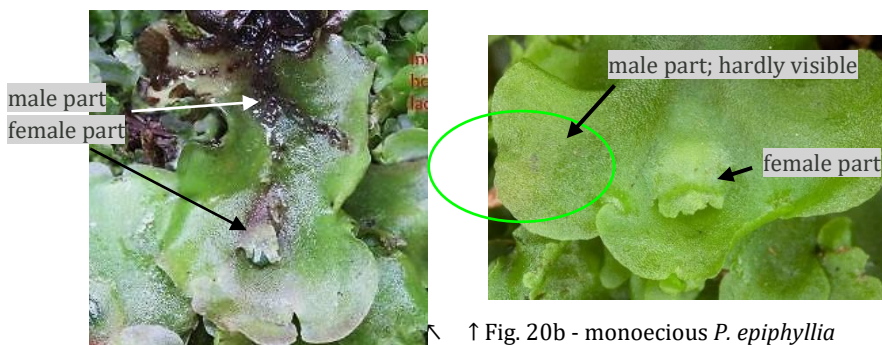
Fig. 22

Notes

1) Two autonomous plants, a male and a female of a dioecious species, found close together would in this context be entirely possible. But what we see need not be this. What we fondly regard as the male plant, on grounds of its possible antheridia, might also be a glimpse of a monoecious one. Apparatus of the other sex could be there as well, even if we don't see it. Compare Fig. 20b, below, for the sometimes elusive character of precisely this; even extant. There is indeed also some - about equal - ground to assume that we could be dealing with the (extantly more common) monoecious look-alike *Pellia epiphylla*, such as in the photo on the left, below. If we can reasonably presume male antheridia to be present on the thallus of our fossil on the right as well.

In reality we are not too worried about which of the two *Pellia* we have here as fossils, as we remain quite confident of it being one of these two; or a near identical third relative..

To underscore the similarity of the two plants, below some more photos of *Pellia epiphylla* next to the *neesiana* photos shown above (the smallest photo in Fig. 20 was in fact already a photogenic *P. epiphylla*).



↑ Fig. 20b - monoecious *P. epiphylla*

For further microscopic work and also more fossils see Part 1 of this history.

2) One of the further mysteries that we would like to share already at this stage would be a thallus, possibly juvenile, that looks as if it is in a process of unfolding, or uncoiling; somewhat origami-like:

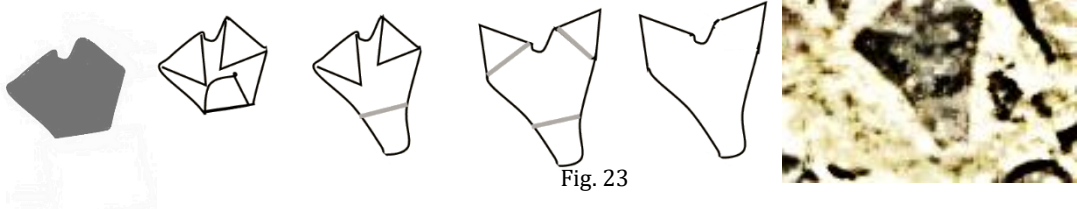


Fig. 23

A closer reading of matrices does yield further likenesses (pentagons to sharpish triangles), but the results do not seem unequivocal.



However, a larger photo of a typical pentagon fossil found on these matrices (also with a 'cupid's bow', same as Fig. 23) does seem to typically show debris, where on the origami fossil the triangles and other folds are.

Might the folded material of a pentagon be meant to ultimately be shed? Perhaps as a crude means of asexual reproduction?

Fragmentation of the thallus as cloning is known for liverworts (Armstrong (2014), p. 466). Also compare the somewhat more sophisticated home made 'cuttings' that are the 'gemmae' structures in some liverwort species. And how would these cuttings here get away from the mother plant? As a sail on the wind while unfolding (thus upright as well as still loose of rhizoids); breaking on a fault line?

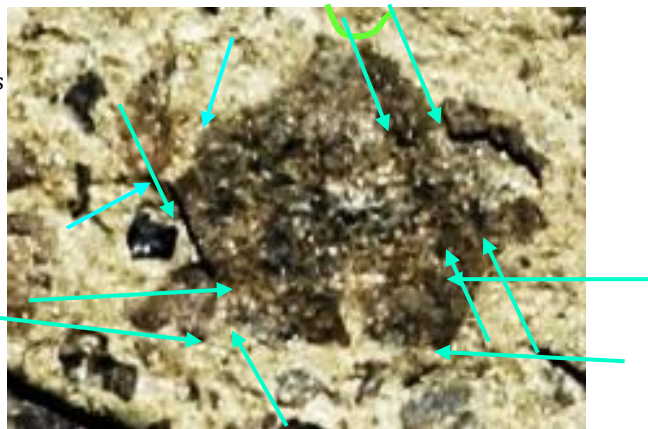


Fig. 24 (from matrix Fig. 26)

We believe this material to be rich enough to allow ourselves some bold questions. Things may get confirmed here.

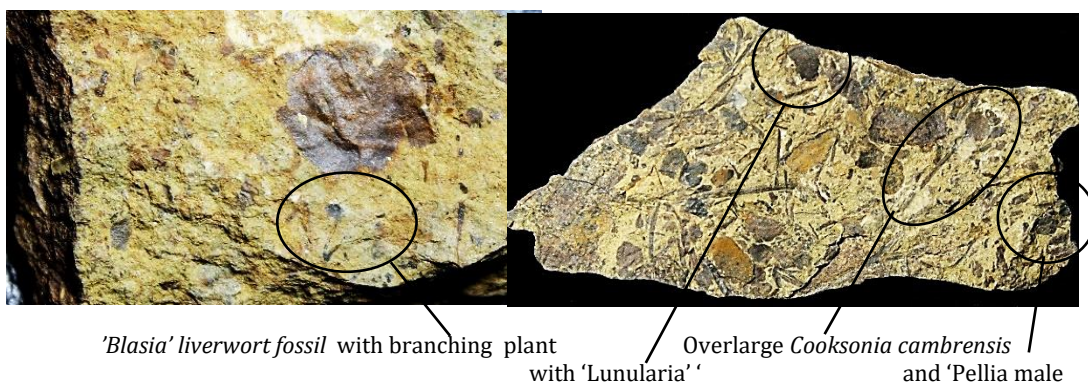
One further observation might be that the direct vicinity of this pentagon on the matrix seems relatively empty of other liverwort species (see also Fig. 26). Which could mean room for short distance cloning without hindering others. More on this fragmenting liverwort in the essay in Part 1,

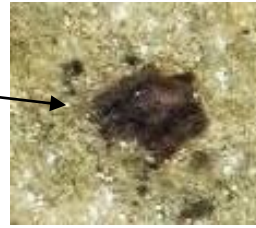
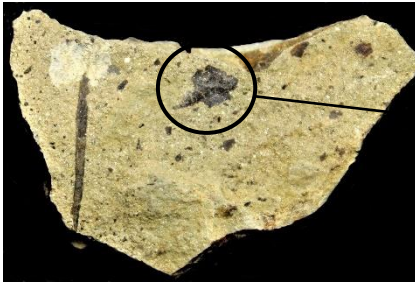


3) The matrix of Fig. 26 is the twin of the one in Fig. 22, above. The matrices are each other's 'pos. / neg.' -counterparts. That is: two halves of a split piece of slate, both showing the same fossil layer as horizontal halves. Often adding to each other's value (information) when found. For this aspect, see Part 1 of this History.



4) There are more 'tiny forests' of liverworts found in the summer of '21 in this same land layer. Matrices with one or two liverworts - sometimes recognisable as proposed ones - next to *Cooksonia* and friends are not un-common either. Below a few examples. Small photos; only meant to give an indication. Our herbaria hold many matrices such as in Fig. 27, below. See also <https://silurianflora.net/wp-content/uploads/2023/05/Fragmentor.pdf>





Further pentagons, cupid's bow, shedding fragments

Liverworts with proposed *Renalia* intermediate and intact vascular thallus; see Fig. 7, this essay. The material is abundant and available.

Fig. 27



And finally, we also wish to mention some subjects that have been left for future analyses in the material at our disposal. Until now, we have found only one leafy liverwort: the 'Triassic' *Naiadita* of Fig. 18a. What if we would actively look for more? See the photo on the left below. Compare Part 5 of this History, footnote 7.

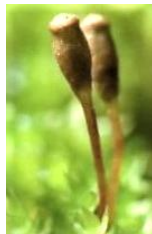
And what if we would focus on what comes out of the liverwort thalli?

We have seen the by-catch of proposed *Blasia* archegonia, and a wishful one for *Lunularia*.

But how about this rather unbelievably graceful watercolour

on the right? A long stalk of sorts, ending in an elegant, elongated lyre - and twining with one that does an overlong, equally classy, hollow cigar?

Just things gleaned amongst other things. See again Part 5, footnote 7. All this the same Late Silurian.



5) Our new finds of many intact and familiar-looking liverworts - with their archegonia and microscopically quite familiar pore structures - are quite unprecedented as macrofossils for the Late Silurian. The first macro fragment that we know of (a thallose 'ribbon' liverwort) has been dated as later; Late Devonian. From Stewart and Rothwell (1993), p. 79. →

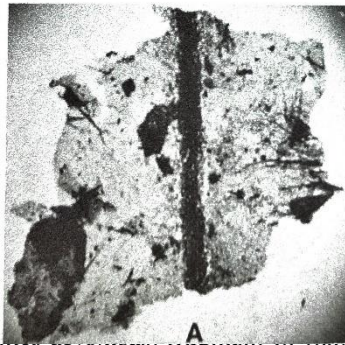


Figure 8.2. A. *Pallaviciniites*, a fossilized liverwort fragment.

Our Late-Silurian herbarium harbours a few specimens of a mystery plant, e.g. Fig. 29, for which we will also need to look into these ancient 'ribbons'. *Pallaviciniites* are still extant, which might give photographs for a first query of likenesses.

P. devonicus helpfully bifurcated at its tips.

As an example of our work this one is far from anywhere yet.

Macroalgae? Twining? Braiding even?

Pores? Cuticle? Microscope work. See also Part 5 of this History; footnote 7.



Fig. 29

... next to mid Ordovician liverwort spores from Argentina: [Marchantiophyta - Wikipedia](#) and <https://sciencestruck.com/an-overview-of-flora-fauna-during-ordovician-period>

For the not mid but Late Ordovician: Late-Ordovician (Caradoc, ≈ 450 million years old) spores are said to have "distinctive layered walls that among modern plants are found only among liverworts (occurring within fragments of enclosing material interpreted as sporangial epidermis)". And are thus interpreted as liverwort microfossils:

<https://www.pnas.org/doi/10.1073/pnas.0400484101>

See also Crandall-Stotler and Stotler (2000):

<https://www.cambridge.org/core/books/abs/bryophyte-biology/morphology-and-classification-of-the-marchantiophyta/7396D0B0F7DE76DBD03BB5249BAB5028>

6) Note that this essay has not addressed the question if our fossil matrices might also harbour 'modern'-type lichens, next to liverworts and early vascular-type land plants. An answer would call for a clear demarcation with still unidentified species of liverworts. Such a demarcation might be hinted at by the way some fossilized organisms have grown on the surface of the terrain. An example is Fig. 30, a matrix with a small *Cooksonia*-type plant next to almost dendritic- seeming 'growths', perhaps reminiscent of *Frullania*-like (a species of liverwort) colonizations, but then perhaps also reminiscent of lichens.

If what can be seen is true. A microscope should first rule out possible deceptive fossil damage for these cases; patterns of remnants of cuticle-like skin where a rest has chipped off.

Ruling out a likelihood of lichen-like expansive growths in such cases would then also be useful information, of course. We do not have a decisive picture yet, at this point. But the fossils do ask the question.

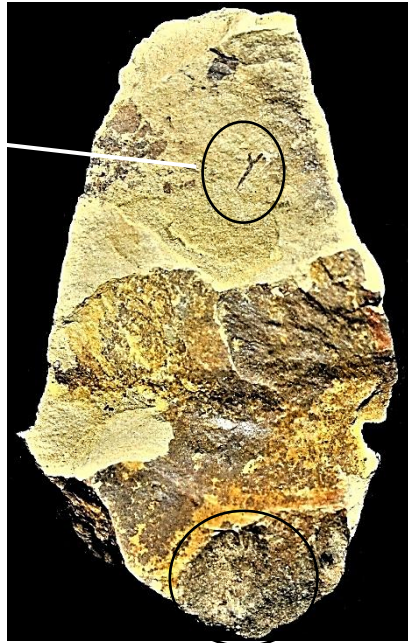


Fig. 30

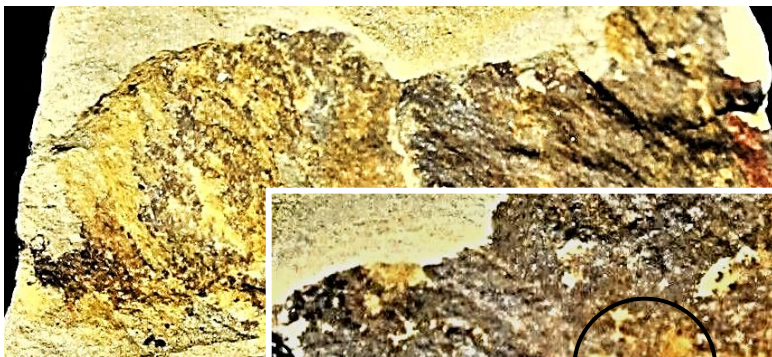


Fig. 30a

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Part four Of Earth and Water

P r e f a c e

Of Earth and Water. Two land plants. One badly hurt

Organizing a first fledgling flora on land will be a momentous feat for evolution; in extension of already existing aquatic habitats. This crucial step, that will mark the macroscopic beginnings of all life on land, will necessarily entail - and also lavishly show - rather abrupt changes in many botanical and more general parameters. As compared to those below the waterline. Changes that will involve most interesting trials, errors and successes. To eventually establish our known, familiar world on land.

The first plant in this essay shows a typical, early ambiguity. It could be one of the new land dwellers, or a more established (aquatic) macroalgae. Defining anatomical traits of the plant will bring clarity.

The second plant is one of the grand heroes of our history. A plant that shows - or lives - many of the challenges for evolution in this first learning lab above the waterline. The plants already flaunt many pivotal evolvments and adaptations of their own. Their most conspicuous feature, however, would be that they - suddenly - ALL suffer the same, lethal hurt. That may be seen as stemming from an essential trial or teaching for evolution as it is stepping on land.

The essay

Of Earth and Water

Two plants from the Late Silurian - and a beautiful plant disease

I am the daughter of Earth and Water,
And the nursling of the Sky;
I pass through the pores of the ocean and shores;
I change, but I cannot die.

— Percy Bysshe Shelley, (1820).
From "*The Cloud*"
According to Shelly, inspired
by Erasmus Darwin

Organic Life beneath the shoreless waves
Was born and nurs'd in Ocean's pearly caves;
First forms minute, unseen by spheric glass,
Move on the mud, or pierce the watery mass;
These, as successive generations bloom,
New powers acquire, and larger limbs assume;
Whence countless groups of vegetation spring,
And breathing realms of fin, and feet, and wing

– Erasmus Darwin,
The Temple of Nature; 1803

0. Introduction

The Late-Silurian era, some 423 million years ago, saw the birth of the first vascular-type land plants, evolved from freshwater algae, *via* liverworts. Liverworts, of the non-vascular moss lineage, would have been the earliest of the real land plants on Earth. ¹⁾

In these early times both the liverworts and the first vascular-type plants still lived in their cradle habitats on the rather moist shores of rivers and lakes. Vascular *Cooksonia* can also be seen preparing for adventures further afield. Where no fossils will be found of them. No suitable sealing sediments for fossilization yet, in a more barren hinterland.

But where we *can* see them, through their fossils, the plants would still very much be daughters of both earth and water. Their riparian, or shoreline environment could possibly still get flooded from time to time. Aquatic debris on the matrices of these land plant fossils is not common, but not impossible either.

This essay will first present a seemingly normal land plant - that may nonetheless still have to be evaluated as an aquatic species. Its anatomy will be decisive.

The second plant may in other ways still be close to a watery ancestry. It is a prime example of evolution's probes, trials, errors and likely learning processes in its early days on land.

The essay is structured as follows.

Section 1 starts out with a hopeful jolt of possible recognition, as a newly found plant seems to have a fine resemblance to members of the famous (and thoroughbred Australian) *Baragwanathia* clan. But with provisos attached. It might be an algae. Anatomical detail in Section 1.1. is meant to bring clarity.

Section 2 presents quite a different plant. Probably a *Cooksonia cambrensis*. With problems. Problems that may well stem from the still reasonably new habitat - above water - for these plants. A habitat that will hold very real surprises for a land evolution in its earlier learning stages.

An Appendix with a fledgling analysis of the indentations of the sporophytes of *C. cambrensis* will be part of the presentation.

1. Land plant (*Baragwanathia*?) or algae

The plant fossils in this essay again come from the Late-Silurian plant deposits in the Holy Cross Mountains in Poland, that were studied before; viz. Parts 2 and 3 of this History.

For an introductory geographical and paleobotanical context, see Bodzioch, Kozłowski and Popławska (2003); the article has been added as an Addendum to this history.

A further article (Popławska-Raszewska and Bodzioch (2007)) also - and significantly - alludes to material resembling the Silurian Argentinian and Australian floras. The Australian

reference will be relevant for our analysis as well. See this conclusion of the article (translated from Polish):

“Morphological research carried out so far showed that all discussed plant fossils belong to the subgroup of *Rhyniophytina* and represent the taxonomically quite diverse group of Fig. 2, in which "European" types of *Cooksonia* and *Hostinella* dominate. Moreover, also specimens of the genus *Salopella* were found, as well as problematic forms, resembling the Silurian Flora from Argentina (EDWARDS et al. 2001) and Australia (TIMS and CHAMBERS 1984).

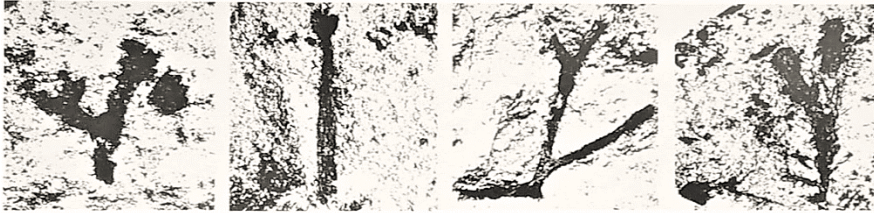
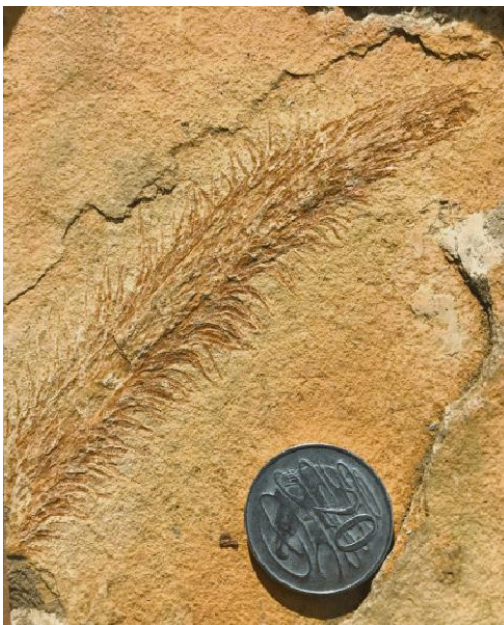


Fig. 2 "

[End of quote]

Note that the above research suggests a possible association of Late-Silurian Polish plant material with e.g. the Australian flora of Tims and Chambers (1984). Which might readily invite dreams of a Polish *Baragwanathia longifolia*. And indeed, the Late-Silurian strata of the Holy Cross Mountains do show what might be thought of as a somewhat smaller (precursor of ?) classical *Baragwanathia*. Compare the fossil of Fig. 1b, below. The plants to be presented were found from July 2020.



Baragwanathia longifolia, Lang and Cookson (1935)

Fig. 1a



Plant fossil, Late Silurian, Poland,

Fig. 1b

That *Baragwanathia* was at home in the northern hemisphere has been argued independently - for the early Devonian - by e.g. Hueber 1983.

A similar fossil from the same Polish layer with equally long *foliae*:



Fig. 2

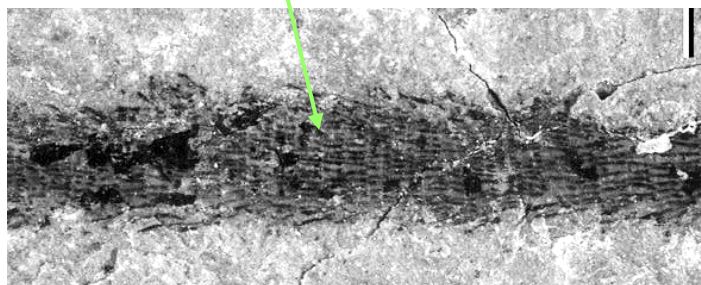
For some further fossils from the same layer the initial likeness to *Baragwanathia* seems less compelling. Smaller leaf-like appendages and a more obvious 'banding' of sorts. Which compared to a method of enquiry followed in Kenrick and Vinther (2006) could well lead to a determination of the fossils as macroalgae.

The give-away in the case of Kenrick and Vinther were half-hidden patterns of whorling - spirals, concentric circles - in the 'branching' of the seeming leaflike material. Compare our Polish *Baragwanathia* aspirant number 3 -



Fig. 3

- with this non-calcified dasycladalean algae in the genus *Chaetocladus* from Kenrick and Vinther (2006):



his kind of likeness could well lead to an evaluation of our third *Baragwanathia* candidate as an algae. The two others, Fig. 1 and 2, might possibly also have a bit of whorling in places, if not obvious to our eye. They both have longer 'leaves' as well, which might even suggest two species of algae.

So the first & crucial question is all the more relevant: are these fossils of Fig. 1-3 land plants, found in the midst of land plants, or indeed algae? The way forward would be an analysis of anatomical detail.

1.1. Anatomical detail

Land plants have a waxy skin of cuticle to keep them from drying out. Algae do not. And more obvious, or more conspicuous: land plants have stomates, which are structured pores with guard cells, regulating the gaseous exchange (i.e. their photosynthesis) and limiting a loss of water in that process. Only land plants have these guard cells. Algae again do not.

Cuticle and stomates can be seen with a microscope.

Fig. 5 gives a magnification of the richest part of the fossil of Fig. 2, above, subjected to a microscope, with seeming cuticle and guard cells of stomates.

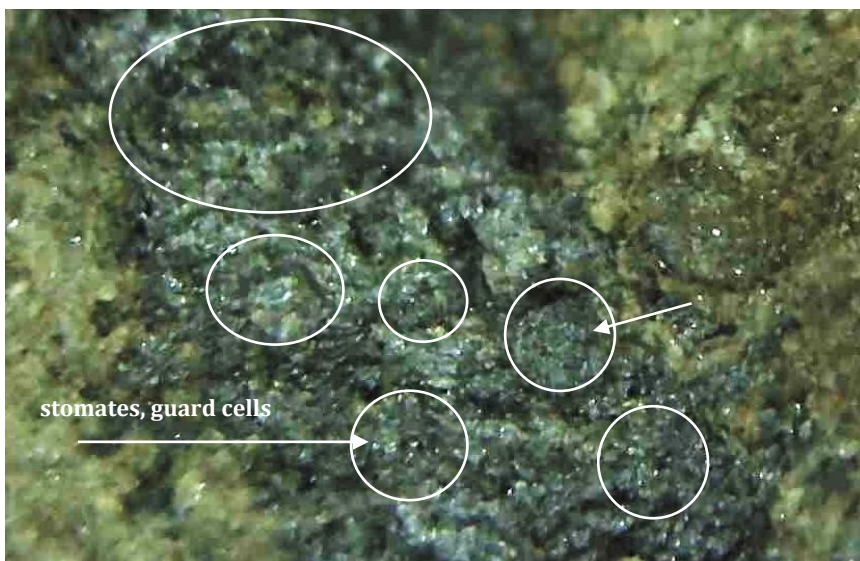
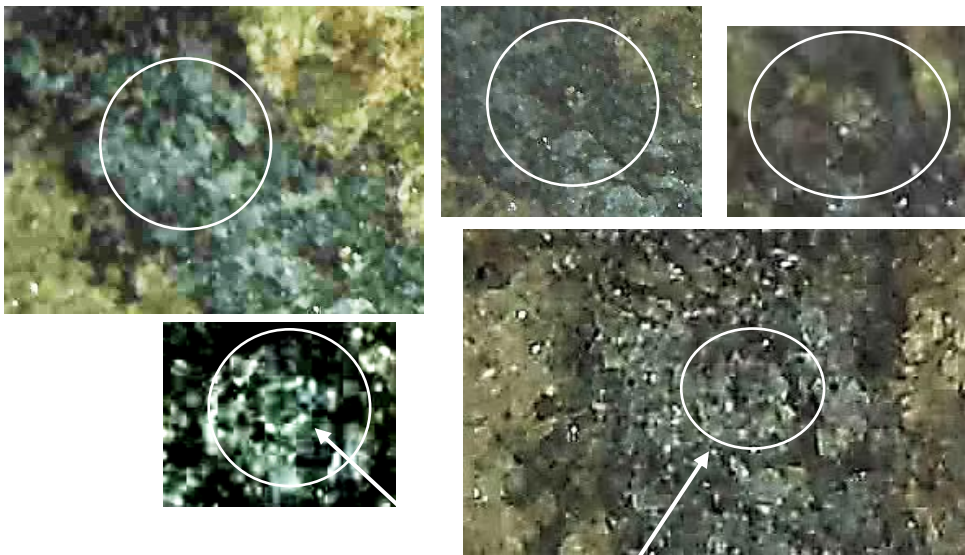


Fig. 5

Some more seeming guard cells of stomates of the same fossil of Fig. 2, in Fig. 6:



seemingly the two guard cell 'lips'

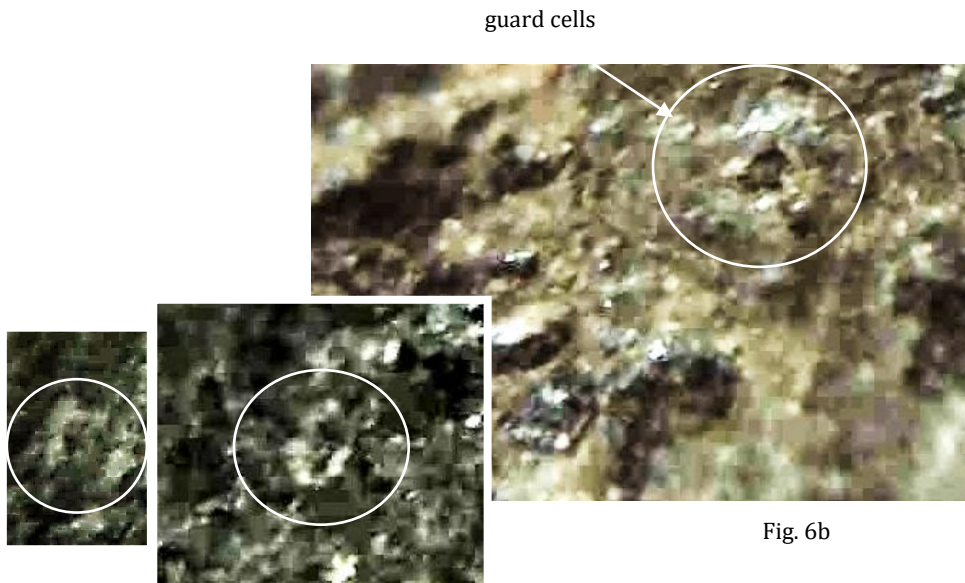
Fig. 6

Our fossil of Fig. 3, gives what seem rather beautiful stomates as well, with seeming guard cells in Fig. 6b. And possible sporangia higher up the fossil in Fig. 6a:



Fig. 6a





Without making a statement about other fossils than the ones in our Fig. 2 and Fig. 3, the above microscope photos do seem to suggest land plants. Which leaves the possibility of a *Baragwanathia* for these Late-Silurian fossils still or again quite open. Both fossils are available for further scrutiny.

2. Twisting by the pool - *Cooksonia cambrensis*?

In January of 2022, as a present from a conveniently mild winter, a fine suite of plant fossils could be unearthed in a Late-Silurian land layer at the site in the Holy Cross Mountains.

What follows is a first presentation.

First a suite of most of the specimens that were found. Overlong stems, hardly any branching, or at most pseudo-monopodial (main stem with side shoots). Overlarge and mostly overheavy sporangia, seemingly ripe and close to bursting or dispersing; more than a few seemingly in the process of falling off, as if being shed. *Cooksonia* types from this site are normally no more than 1 to 1,3 cm high; sporophyte plus sporangium. These new finds are at least twice as large.

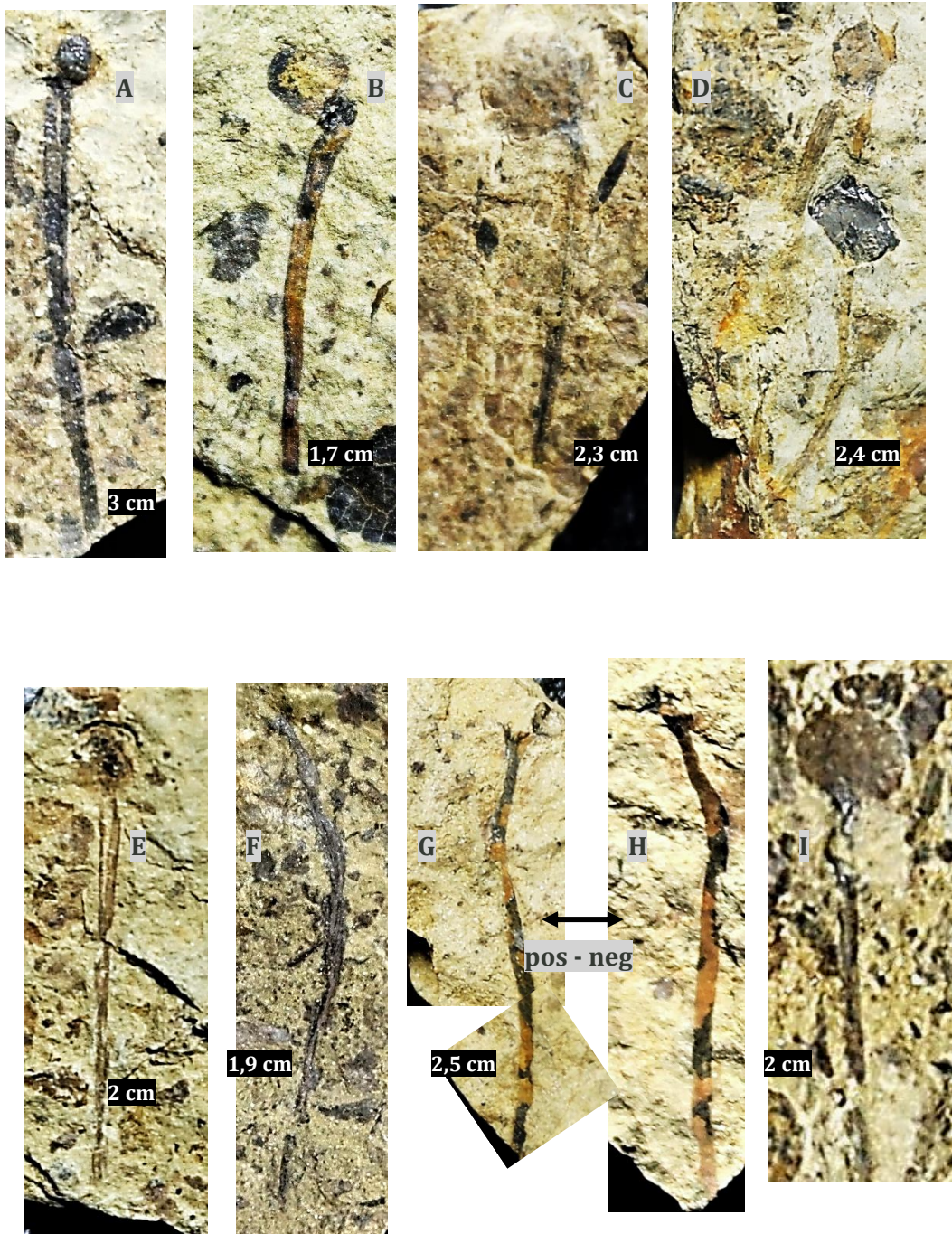
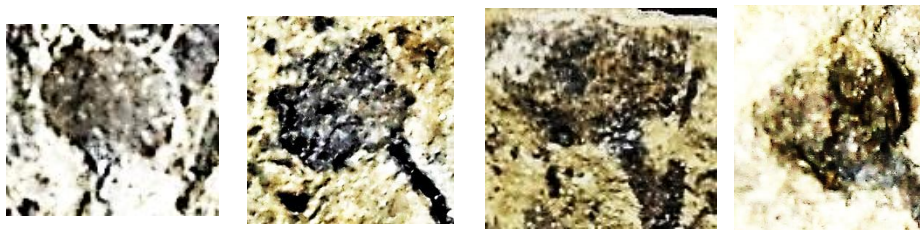
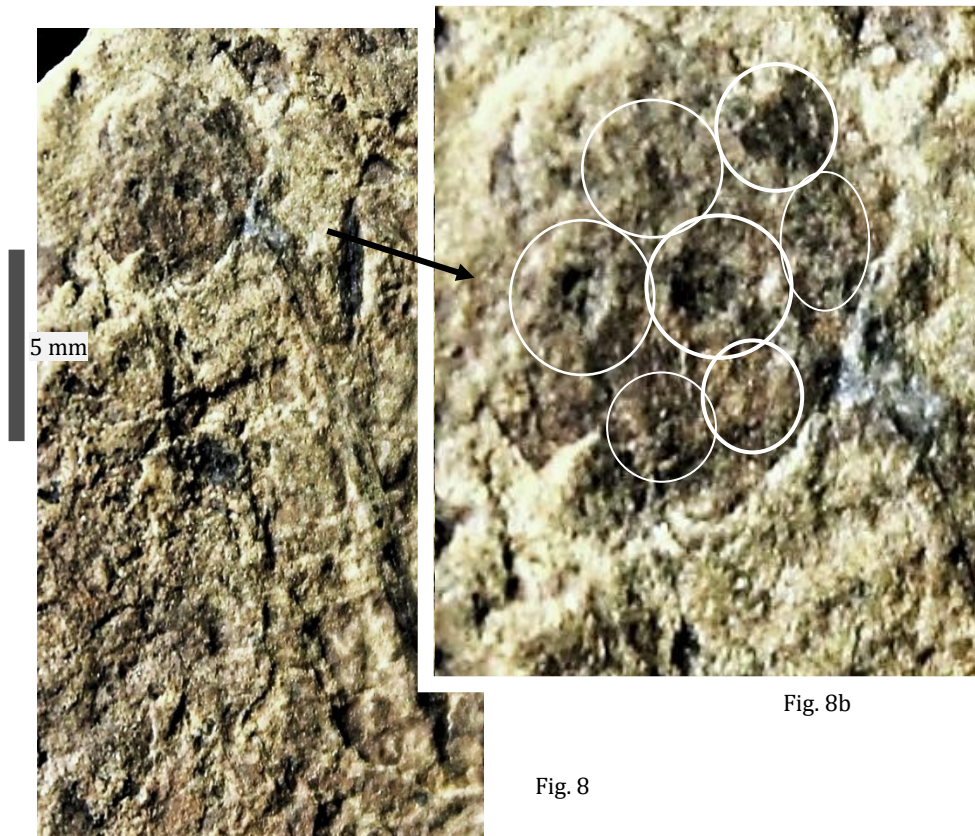


Fig. 7

The plants appear to have very characteristic, detailed sporangia, with indentations harbouring stomates with guard cells (Fig. 8) that would be exceptionally large for these still smallest of plants (Fig. 8b). We will come to this.



other detailed sporangia ↖ ↑ ↗

Overheavy sporangia on the verge of / coming off, showing some details of the connection of stem and sporangium suggestive of the 'wiring' of vascular strands.

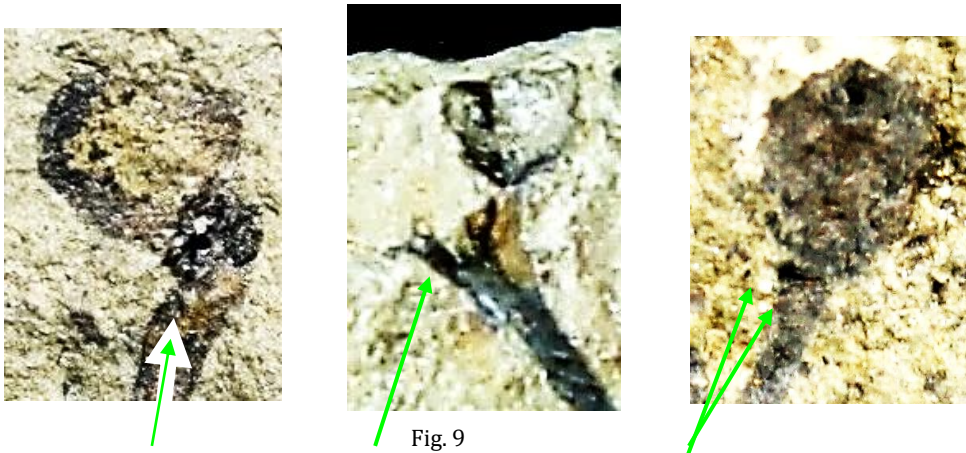
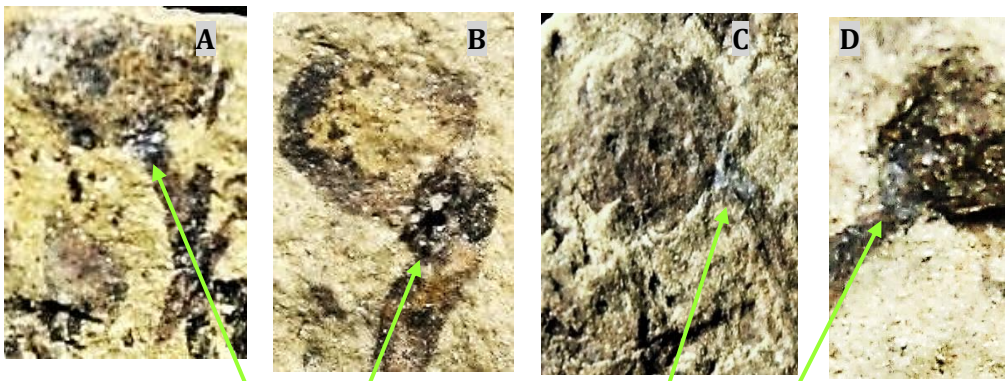


Fig. 9

Internal structure; possibly vascular strands

Seemingly breaking sporangium



Discolourations. Blackish to (pewter-like) metallic on the fossils



Fig. 10

Unusually elongated stems, seemingly twisting (C) or more clearly composed of parallel strands (A, B). Split stems? (D).

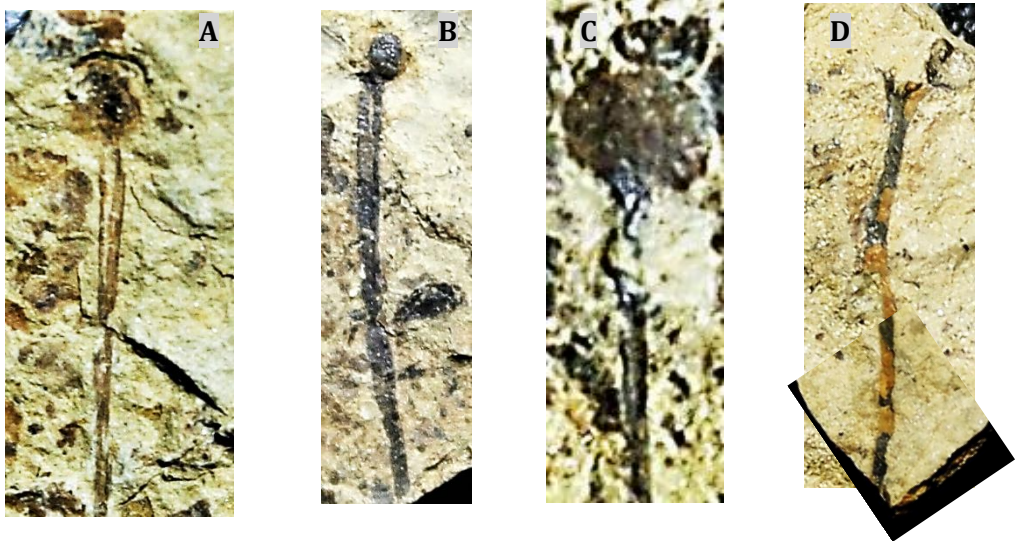


Fig. 11

If we add up these characteristics of the plant (it seems uncontroversial to think of what we are seeing as mostly the same plant throughout this presentation, its specimens found together in the same layer, in two adjacent sessions) – if we add up the impressions, one is left with a few serious questions.

Even if we ignore some seeming leaf-like appendages, which, close-up, very much resemble sporangia depleted of spores –

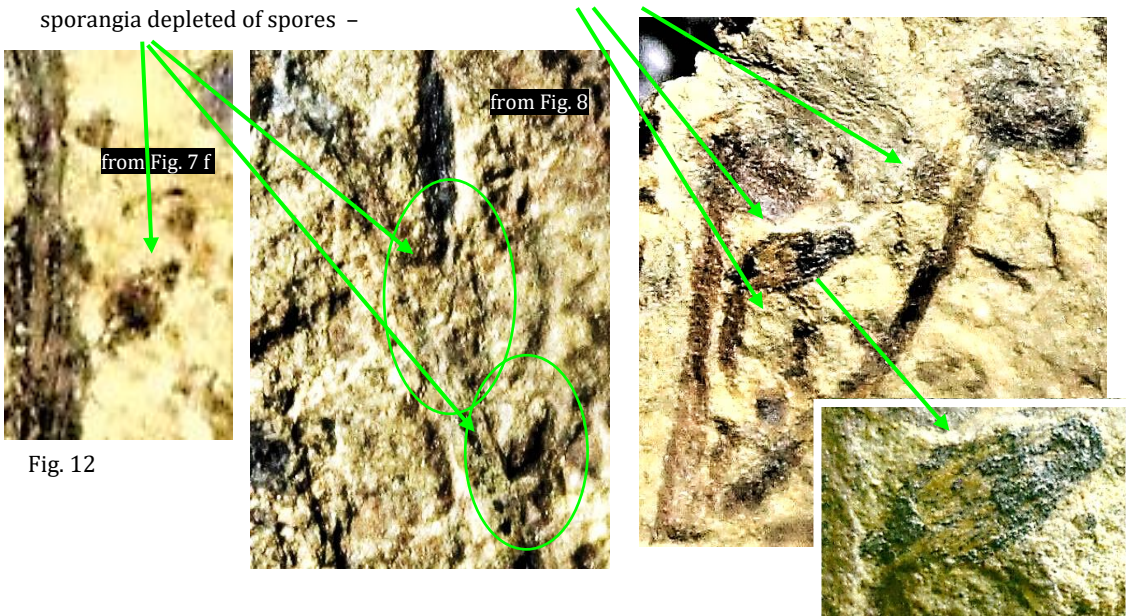


Fig. 12

– and even if we ignore the tumour-like anomalies of Fig. 10, we would still be somewhat at a loss comparing what we see to the types of *Cooksonia* we know.

Some pseudomonopodial branching next to strangely vertical, parallel branches or shoots – possibly even split stems (Fig. 11a, b). Roundish sporangia with a markedly lobed silhouette from the many indentations all around the sphere that give the sporangium a somewhat colander-like appearance. Indentations with internal structures as in Fig. 8b. Depleted sporangia still on the branch next to functioning ones, as in Fig. 8 and 12 (see also the Appendix, below).

We know of no *Cooksonia* that would readily fit such an enigmatic description, other than that the sporangia of the plants do show a basic resemblance to a usually quite a bit smaller *Cooksonia cambrensis*. An iconic, somewhat famous fossil of the sporophyte of this plant is 5 mm tall. ²⁾

2.1. A plant disease

There is, in extension of this, a rather persistent feeling that keeps coming up. The feeling while handling our fossils is: *fast grower*. Overlarge sporangia, burdened by their own weight, overlong stems of a strange but also somehow familiar shape. *Reed-like*. The plants are at least twice the size of all other vascular types in our Late-Silurian herbaria. They look a lot less healthy as well.

Is this kind of feeling to be taken seriously - a basically abnormal growth? Could we then also be witnessing the dynamics of a plant disease, in growth and in tumour-like growths? We think so.

An overkill from an unknown fertilizing agent, forcing the outlandish growth of the plants, could perhaps also have been responsible for the chemical tumours that are visible, even obvious in Fig. 10. Even if we don't see how a plant could become so totally 'encased' in that way - as one continuous tumorous growth from the ground up, reaching all the way to the sporangium (Fig. 11b). Evidently without destroying or clogging the vascular system along the way (the disease reached as high as the sporangium). A chemical poison - but at least with a delay, then. Shall we say, a heavy metal?

2.1.1. Oxygen poisoning

There is another possibility. The exceptional growth and the tumours in Fig. 10 may also be two separate phenomena. The growth accidentally leading to stomates with functional guard cells, and thus apertures of almost a millimeter wide (Fig. 8b). Which seems impossibly large, crude even, for these still smallest of plants. The height of a normal *Cooksonia* in our herbaria

- sporophyte with sporangia - being at most about ten millimeters in all. Often less. The iconic *C. cambrensis* of footnote 2 is only 5 mm high, which is the size of about five of these apertures in all. 3)

Would a Late-Silurian firstling be able to cope with the gulps of photosynthesis taken by such Gulliver-style pores – given the overwrought scale, the internal mechanisms, chemical constraints and natural calibrations of gaseous exchange of these already near-collapsing plants?

It may well be that the plants indeed couldn't cope. Which could give a different reading to what we are seeing, when looking at the exploding, lethal cell growths of Fig. 10. A problem, sadly, of the plant's own making. Overdose of its own photosynthesis as poison.

As is well known, oxygen poisoning leads to grave cellular problems, such as necroses of regions steeped in the overdose. Next to general explosions of free radicals, damaging the DNA, giving way to structurally incorrect information during cell division, i.e. general tumourous growths. Such as can be seen.

The necrotic vascular bottlenecks between stem and sporangium in Fig. 10, and also a stem such as Fig. 11b indicate that the problem could damage more of a plant than just the sporangium. It is not hard to imagine the gaseous overdose indeed spilling over, or pushing itself a bit into the vascular system; perhaps along with migrating photosynthetic sugar / starch.

The concentration of the tumours on sporangia - where most of the stomates are - could indeed favour a respiratory (oxygen) poisoning. Over a vascular intrusion ('heavy metal' for short). Oxygen poisoning causing tumourous growths is rather basic biology (and medicine).

2.2. Of Earth and Water

If the observed disease would indeed be due to side effects of a gross over-fertilisation, it would be interesting to know how evolution at a later, more informed date would have deflected the resulting errors of scale, perhaps also regarding cellular strength & growth issues. With more apt, fixed calibrations, leading to perhaps more exuberant but less forced, less self-damaging growths. Possibly even with backstops for size, cell growth and / or shut-downs for function.

We thus may have chanced upon a rather significant learning phase of a young land plant evolution. Fact is that evolution could never have encountered these problems of scale in directly preceding phases; i.e. during the evolution of algae up to complex macroalgae, that were often still unicellular; however complex-seeming. And definitely still without stomates as well (the point of the previous Section of this essay).

Whatever further analyses may bring, our case of the too big vascular-type land plants must have been one of the earliest opportunities for evolution to learn, in the field, about bigness – even scale itself – as a crucially relevant new factor for multicellular, stomatic plant design. On land.

In extension of this there would also be simple gravity as an equally new and equally important parameter, above the waterline. The plants seemed burdened if not damaged by their own weight as well; already in Fig. 7.

So. If we may assume that evolution employs (or is employed by) the rather basic mechanism of trial and error - even at a more basic architectural level than natural selection - this could well be an instance. Of a rather timely trial, and a hugely valuable error. Our case could help a young land branch of evolution to make the calibrations with regard to its photosynthesis as agile as possible. Together with many other corrections. Weight, under a quite new terrestrial gravity (what *is* that thing??). A much graver impact of local influences - all of a sudden not diluted anymore, as under the waterline. And not just flowing away either. Much is anchored here; and so are we. Lots of work for a fledgling land evolution; needing increasingly sophisticated templates for an increasingly complex '*plein air*' sort of life.

All this because we cannot very well imagine a mature evolution allowing its offspring to be force-fed and then explode by every stray chemical willing to bond. Without having some smart answer at the ready. For the benefit of (at least) plant life, on land, a system, an equipoise, a buffering and normalizing balance did obviously evolve. Which is what we're after – and also rather need.

2.2.1. A slightly broader picture

In this light, compare also our very first vascular-type land plant (named *Salopella*; subject of Part 5 of this history). Having just evolved from a liverwort, these vascular-type firstlings were still very much bound to a typical moist-to-wet liverwort habitat. A next step (sic) would be an adaptation as e.g. a *Cooksonia*-type plant, that is able to find what it needs in moisture- and nutrient-rich grooves and small channels in the landscape. Making wanderings into a much more barren hinterland feasible. And for which major adaptations had to be made.

We would very much expect that, for the purpose of such adaptations, all vascular-type plants would have needed the sort of buffering as just asked for by *C. cambrensis*, above. Not as nice to have, but acutely needed for a further colonization of the planet. **On-board reserves, taproots, defence moats, dosing valves (stomates); vascular drawbridges; insulation (thickness of skin),** ideally doubling as a basic **thermal and uv-regulation; smart self-monitoring,** etc. would all be crucial adaptations – away from the initial, 'naked', watery vulnerability of the liverwort firstlings on the freshwater shores.

Adaptations our material could well be able to account for in even more detail.

Notes

1) Liverworts were found to be Mid Ordovician. For an analysis of the evolutionary relationship between liverworts and vascular-type plants we refer to Part 5 of this History.

2) *Cooksonia cambrensis* is the only plant that does come to mind. Compare this iconic photograph, with indeed a long, non-branching stem and a sporangium that seems to have very much the same sort of indentations.

Specimen from the Lower Red Marl Group of Freshwater East Bay, Dyfed, Wales, Late Silurian (Pridolium), 420 million years old. Hight of the plant 5 mm.

We do not know, however, how this plant would branch if it would branch, or how defining our highly structured indentations of Fig. 8 would be for the species. But tentatively, this could well be the one. More in the Appendix below.

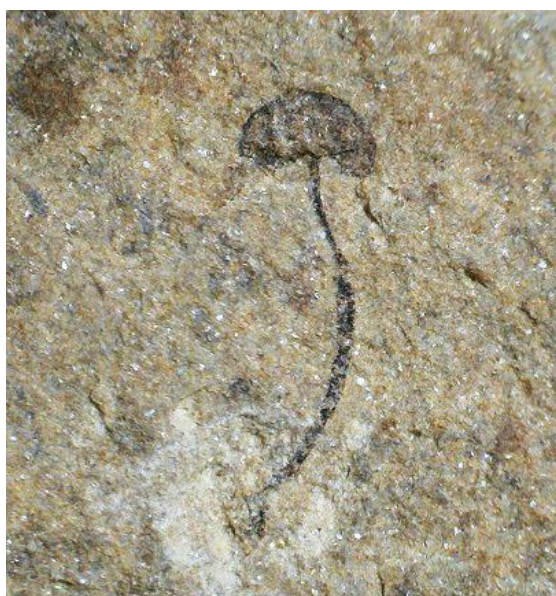


Photo from Edwards (1979)

3) A smart calibration can and will often call for more stomates instead of for just bigger ones; thus honouring a proper scale of things - chemically and otherwise - including the gasses, cells and sap vessels of the plant, that equally won't be crude blow-ups of the smaller precursor, even as a plant may become larger. The anatomical, chemical and functional constituents and constraints of the biology of the plant world just have their own parameters, setting the scale for, indeed, stomatic design as well.

Practically speaking this will also mean that the amount of stomates and their size will become largely indicative of e.g. quality and composition of the atmosphere a plant lives in. Simply counting and measuring fossil stomates may thus tell a great deal about the world of the living plant.

On a large scale, a rising proportion of CO₂ in the atmosphere, e.g. in the Devonian Period, led to an availability of more photosynthesis, resulting in bigger plants, with a stomate

configuration to reflect the new situation. On a more local scale, perhaps due to a natural phenomenon, the size and amount of stomates may equally reveal the way the need for photosynthetic CO₂ has been met by a plant.

All this would translate as subtle re-calibrations within the plants, showing as equally subtle adaptations, over time. The mature opposite of the dramatic, sudden events under analysis here.

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Appendix

Cooksonia cambrensis; stomates and spore dispensers. Sketch of anatomical detail

A loose end in our *exposé* would be what is behind the indentations of the sporangia of our fossils. Our limited means to disclose such data (microscope photos pending) do not allow for a remotely rigorous analysis here. Even though the data themselves could well promise gold. But we can try.

Let us begin our sketch with a somewhat vague observation about the sporangium of Fig 8:

Stomate-like shapes, of stomates



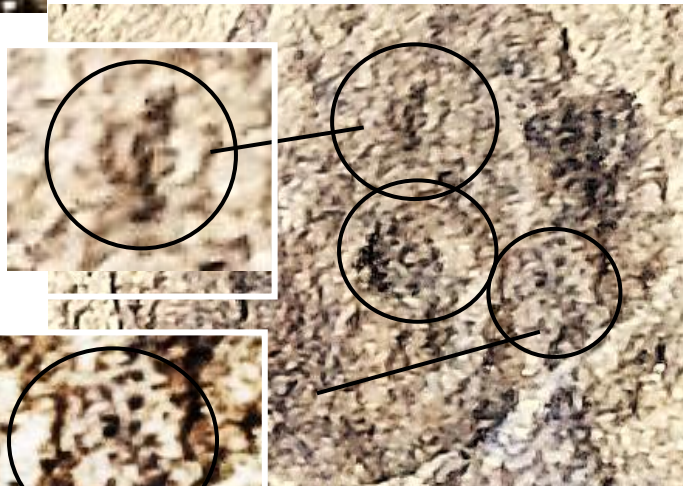
A different shape colour and structure. Flat, disk-like, possibly with holes.



Fig. 8a

The same sporangium of Fig. 8 under harsh light will give the same result, if somewhat more clear. Again the two kinds of structures: ↓

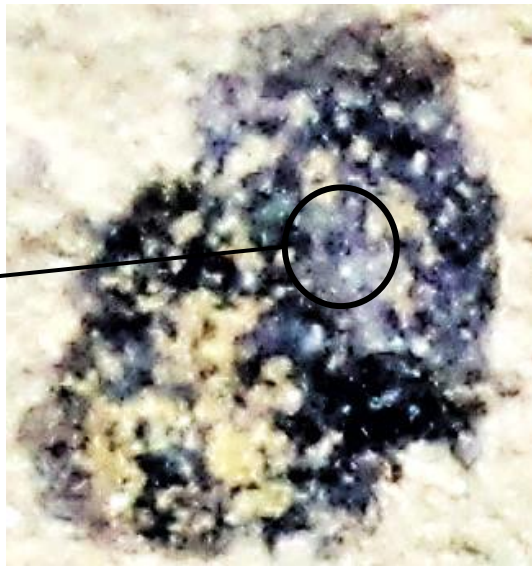
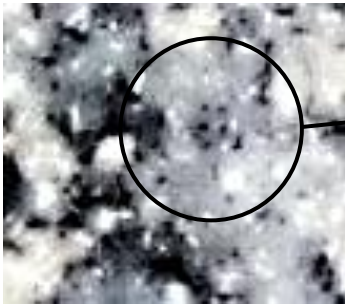
Stomate, two guard cells inside
→



Wheel- or rosette-like flat structure, probably laced with holes →



Other, comparable sporangia might show the same kind of structures, defined by patterns of holes and embedded in the cuticle ↓



For some further clarity - by looking behind the cuticle where it chipped off - consider again a seeming sporangium that was shown in Fig. 12, depleted of spores but perhaps still available for service (the cuticle chipped off of the fossil, not of the living plant).

More magnification of the fossil gives Fig. 14: ↓

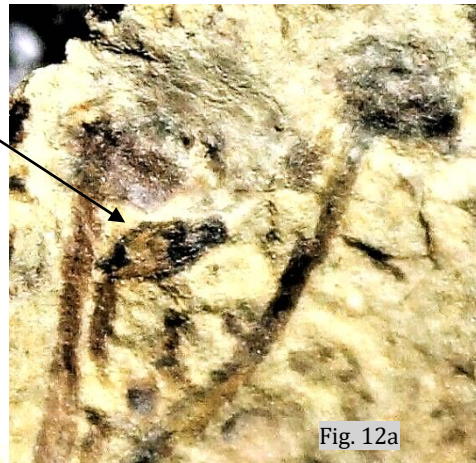
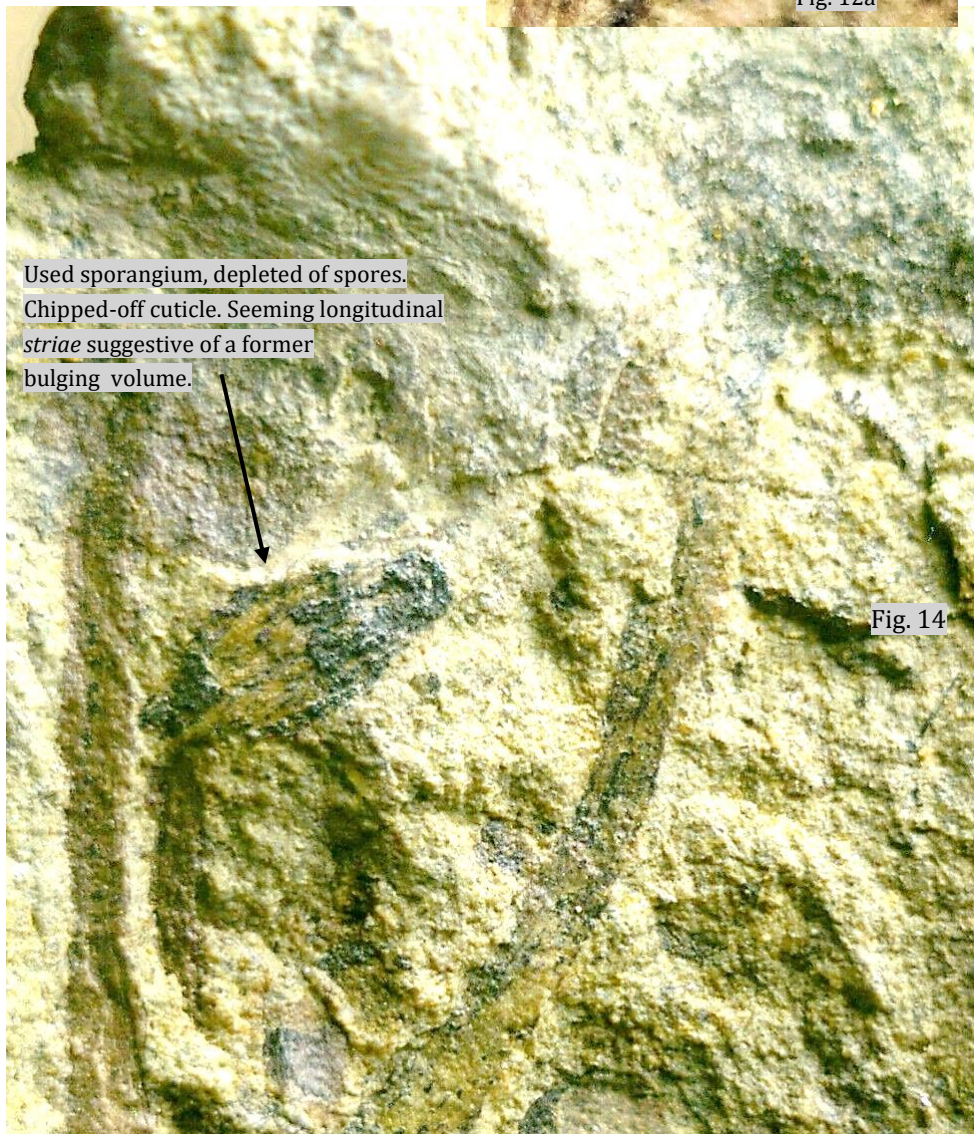


Fig. 12a



Used sporangium, depleted of spores.
Chipped-off cuticle. Seeming longitudinal *striae* suggestive of a former bulging volume.

Fig. 14

A further enlargement of this depleted sporangium, in Fig. 15, seems to show regular groups of holes that are revealed where the cuticle is missing. White arrows point at guard structures such as they are, bare of cuticle. Green ones point to groups of holes, some patterns of which seem wheel-like. These could possibly be 'saltshakers' for spores in the skin/wall of the sporangium. (Compare the round, what are indeed called 'sporeshakers' in *porcini* mushrooms.)

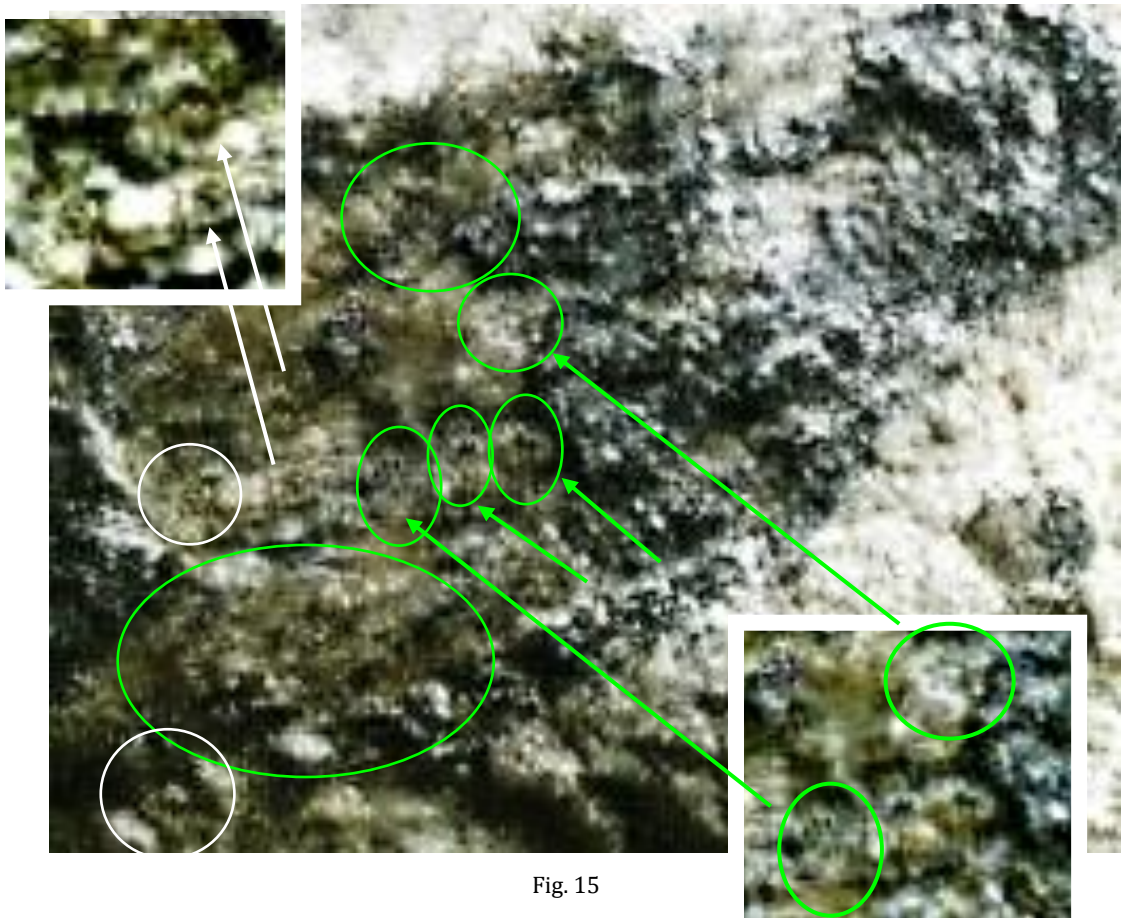
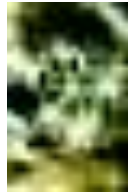
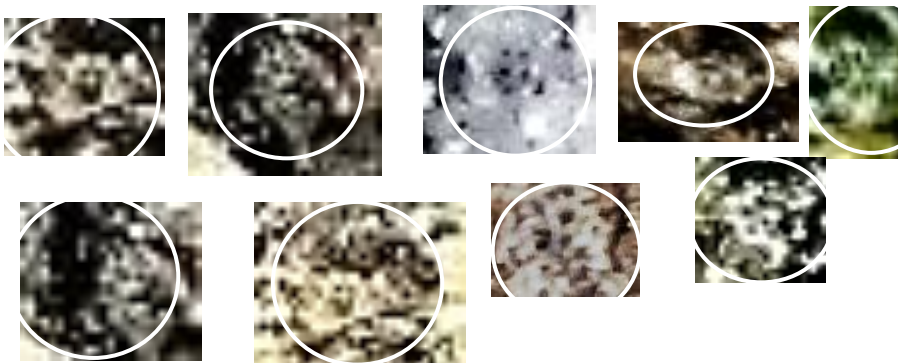


Fig. 15

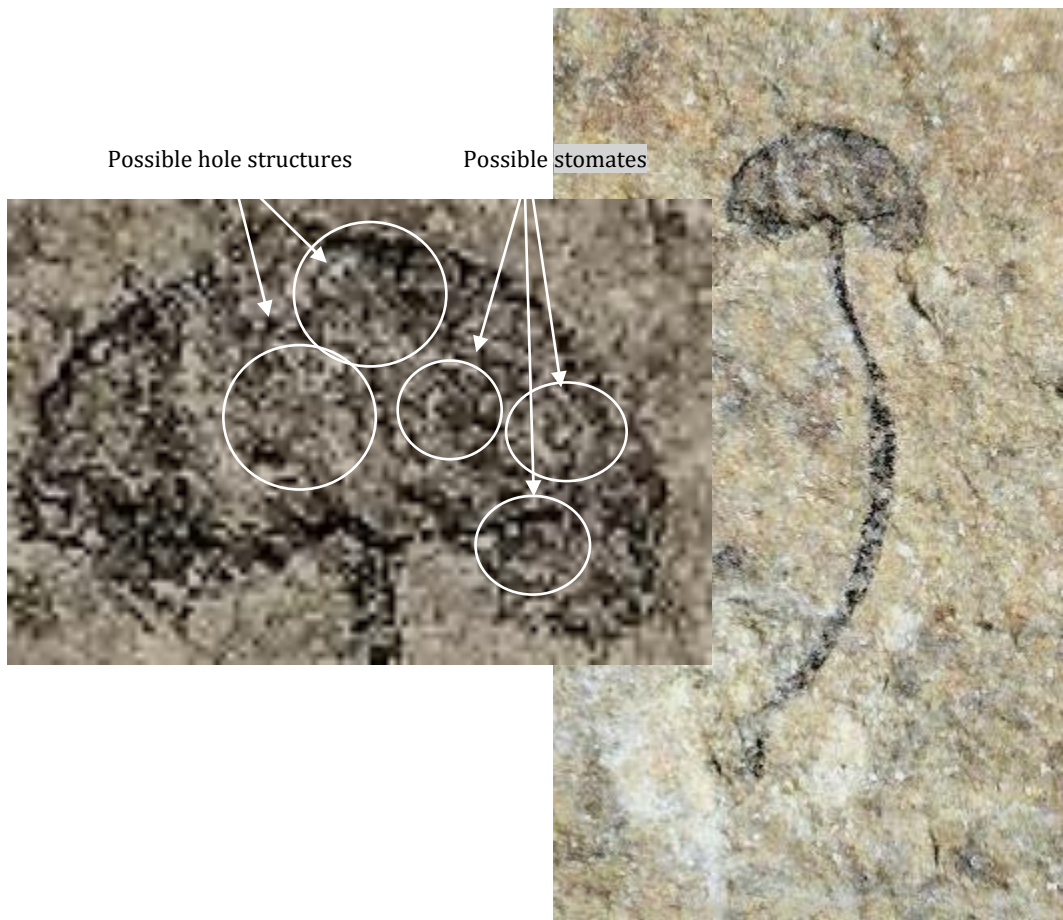
Comparing Fig. 15 with the photos above gives not dissimilar, rosette-like images:



On this basis we suggest, still rather tentatively, that our proposed *Cooksonia cambrensis* might indeed have had a system for the dispensing of spores, without obvious guard cells. Next to the stomates.

How the rosettes of holes connect to what kind of - possibly reusable - spore factory in the sporangium is a good question. If the phenomenon of these hole patterns and or stomates has been observed earlier, for example on the basis of earlier photographs of *C. cambrensis*, as the iconic 'colander photo' from Edwards (1979), we do not know it. This would be completely our ignorance.

But for the sake of completeness, and possibly redundant, here an enlargement of that photo as well. See also footnote 2) to the main text, above.



Part five

Evolution

Preface

This Part 5 of our history aims to literally show how in the Silurian Period the very first upright plant came into being, next to its liverwort neighbours. That the liverworts were here first had already been established. Their much earlier, Mid-Ordovician spores had been found. So now the next question would be: if this is so, that liverworts came first, did they *give rise* to the upright, vascular-type plants, or are they a parallel evolution?

Lack of macro evidence (fossils larger than spores) always let this question linger a bit. Until our new, information-rich, Late-Silurian fossil herbaria came along –

The essay

On the Origin of Plant Species

The descendance of vascular land plants from a liverwort

A comparison of the Late-Silurian land plant Salopella with Cooksonia as well as with Silurian and extant liverworts. Salopella is seen descending from a liverwort in grand and unexpected ways. With Cooksonia in its wake.

There is grandeur in this view of life [...] having been originally breathed into a few forms or into one; and [...] from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

- Charles Darwin, *On the Origin of Species*
Last paragraph, first printing (1859)
CONCLUSION. CHAP. XIV, page 490

The named is the mother of the Ten Thousand Things.

- *Tao Te Ching*, Chapter 1

0. Introduction

The exceptional scientific windfall of complete and detailed Late-Silurian liverworts on the one hand, and their equally complete vascular-type neighbours (sporophytes *with their gametophytes*) on the other also allows for actual and detailed comparisons of the two types of plants.

Such an avenue of research never had serious macrodata to work with. Which meant that reasonable assumptions about evolutionary relationships between these plants could never be more than that. The most important question here is: are vascular-type plants, such as *Cooksonia* and *Salopella*, descended from the earlier, Mid-Ordovician liverworts, or did they evolve independently?

It would be of importance, not only to botany but to evolutionary theory (and to world history), to find out if liverworts would indeed be the direct ancestors of the vascular plants, shrubs and trees on the planet. A definitive yes should bring with it otherwise unobtainable insights into the mechanisms, choices and strategies (or a notable absence of strategies) of a young evolution, at a most pivotal moment in history. With worlds upon worlds of plant and animal evolution fanning out right after it.

Liverworts appear to have been the only macrobotanical flora on land for quite a long time. Which is not too surprising, as they to this day often have an aquatic form next to a land form. Amphibious liverworts thus rather naturally suggest that the first macroscopic plants to venture on land could easily have been liverworty already. And if liverworts also were the basis for the evolution of vascular-type plants, it could double their importance as the nexus of what would be a most crucial phase of plant and, arguably, general evolution. The whole adventure from aquatic to terrestrial to vascular; solely by the grace of the humblest little liverworts. With their early (Mid-Ordovician) evolution of sexual spore propagation as just another brilliant calling card.

But regardless of what new analyses may bring, liverworts would already be heroes. The first of the first, and also the last and only Silurian land plants still standing today; exactly as they always were. And now also the mothers of all, as unassuming as they are regal?

This essay hopes to demonstrate that this is indeed so. The vascular-type land plant *Salopella* of our Silurian herbaria will be seen to have kept a number of liverwort traits. Bold but vital choices that in the situation of the plant would be nothing less than indeed grand - to borrow Darwin's wording. Choices that actually will have prevented the plant's extinction during its evolution, while also giving this newfangled vascular type what it most acutely needs in the still wet-riparian living conditions of its unavoidable first base camp. Before adapting to more general habitats. Our *Salopella* would thus really be a very first vascular-type plant. **Still in diapers, if you will.** But *there*. Embodying evolution's highly articulate earliest choices and triumphs in its new, vascular learning lab.

We will start with an inventory of bryological characteristics for the plant.

1. Seams and thallus flaps

The Introduction to our history in Part 1 shows a Late-Silurian fossil of a *Salopella*; a vascular-type land plant, standing in its gametophyte base. To be compared to the gametophyte of an extant *Marchantia* liverwort; a liverwort that would also have been a Late-Silurian neighbour of *Salopella*. [Based on our fossils. See e.g. footnote 1, below.] The information is repeated here as follows.

In the photo on the right, juvenile archegonia of an extant Umbrella moss, *Marchantia polymorpha*, are seen sprouting from neatly tailored holes in the horizontal gametophyte half of the same plant. Notice the ring of reinforcing tissue around this hole. Our Late-Silurian land plant *Salopella* appears to flaunt the same equipment. From our herbarium, some 423 million years old, standing a proud 9 mm tall - not half the size of a garden cress - in its very own gametophyte ring. With a similar 'hem' or 'seam' for the thallus .



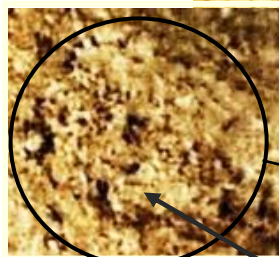
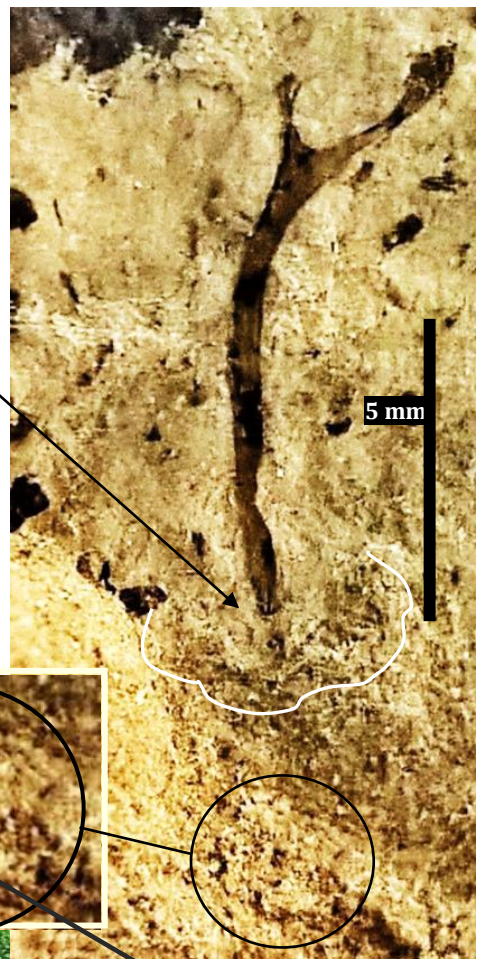
The gametophytes proper seem rather faded here, but still discernable. A friendly fungus gobbled them up, quickly recycling their precious nutrients in a world without soil or shade, yet.



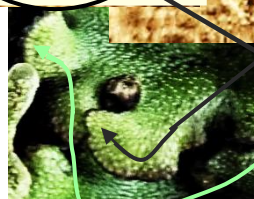
This concludes the information from the introduction in Part 1.

Many matrices show that even such half-faded thalli may still hold a lot of quite precise detail. Macro photography, often under grazing light, sometimes aided by a bit of botanical sketching (tracing) may indeed palpate further information about the morphology and the anatomy of the plants.

The interesting thing in the above case is a precise tailoring of the thallus of *Salopella* with a seam that cannot seriously be seen as different from the seam closing two thallus flaps in extant liverworts. The architecture, organization and functionality of this type of thallus, and flaps, would be standard fare of bryological textbooks.



Flaps can also overlap to close. A seam is a double hem – the border of a flap.



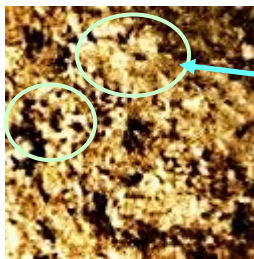
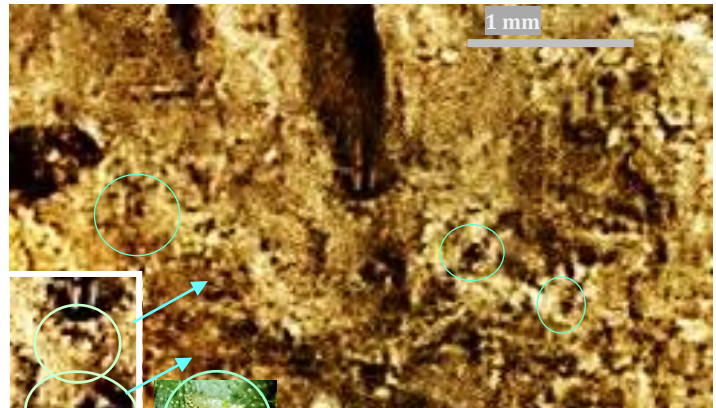
2. Lobes and gemmae structures

A closer scrutiny of the same *Salopella* matrix may yield further information.

A starting point can be an even more enlarged photo of the fossil.

This close, the thallus of the plant no longer has a simple rosette shape. What unfolds begins to look markedly like lobes for the thallus, of the liverwort type.

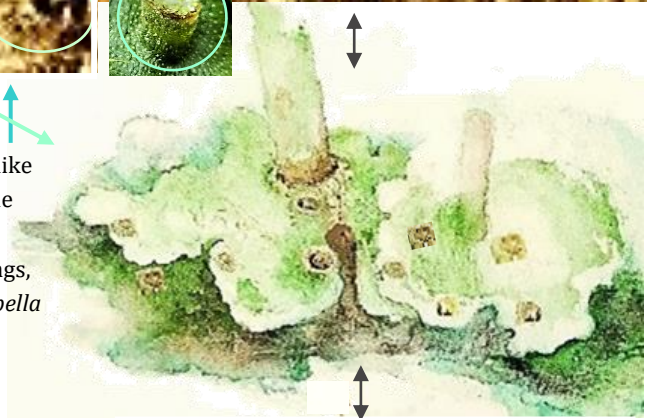
A tracing of some basic contours of the fossils may elucidate an affinity with the timeless shapes and functions of indeed liverwort lobes, such as those below the sketch.



Note the rather significant cup-like structures on the surface of the thalli. Socket rings, where our *Salopella*

stalks come out of, never have these high rims. Nor have stomates.

Liverwort gemmae cups, harbouring home-made 'cuttings' of a plant, could not function without these rims.



Lunularia cruciata



All Marchantia polymorpha



close-up of a gemmae cup with gemmae ('cuttings') inside. The rims make raindrops bounce back, dispersing the gemma clones.



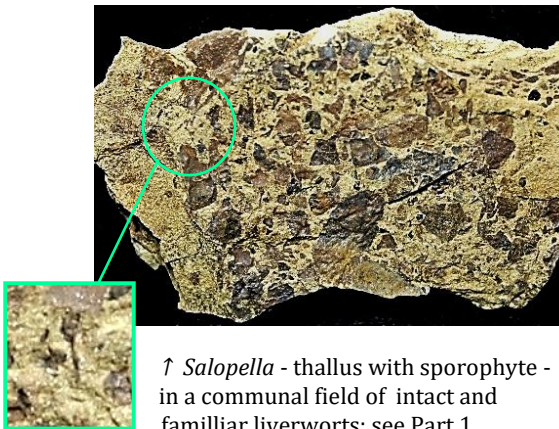
The high-rimmed, cup-like structures on the *Salopella* fossils can be interpreted as either anomalies - strange growths - or as, again, regular liverwort-like equipment. Gemmae cups; bryologically fully in line with the liverwort lobes, flaps and seams that were already seen. And standing in proper gemmae cup places on the lobes as well. Moreover, gemmae cup structures generally would be no strangers to these herbaria. Late-Silurian liverworts are seen with what may well be growing points (meristem 'fingers') and/or gemmae tissue inside such cups; see Parts 1 and 3 of this study. But especially this footnote ¹⁾, below.

3. Communal living

Liverworts are characterized by their elastic & gymnastic ways to maximize every inch of potential surface space for the benefit of the whole of their circle of friends. This holds for both extant and Silurian community members. ²⁾

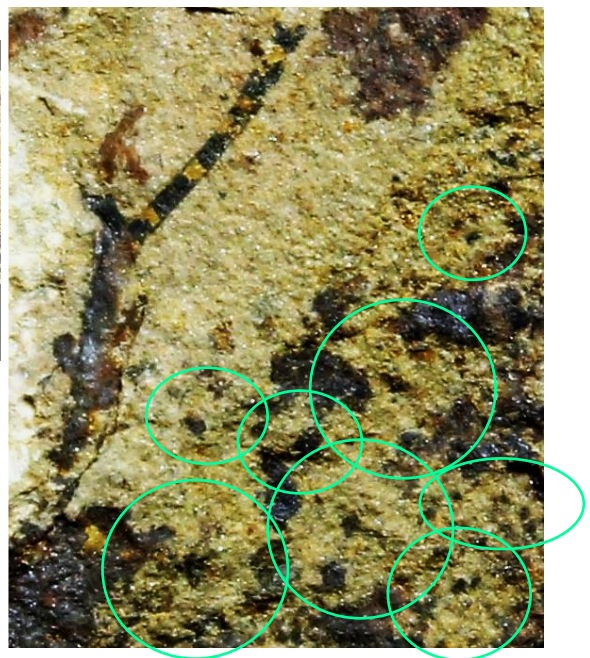
Our Late-Silurian *Salopellae* matrices show the same. Thalli systematically covering a surface, pretty much like pieces of a jigsaw puzzle; each with their old sporophyte socket hole still in the middle. *Cooksoniae* do not seem to show any relationships with fellow specimens.

Salopella would in fact be at home in more than one type of community. The plant either stands in the middle of a proper liverwort field (photo left, below), or it makes its own little forest with fellow *Salopellae* (photo on the right). More examples to be found here ³⁾.

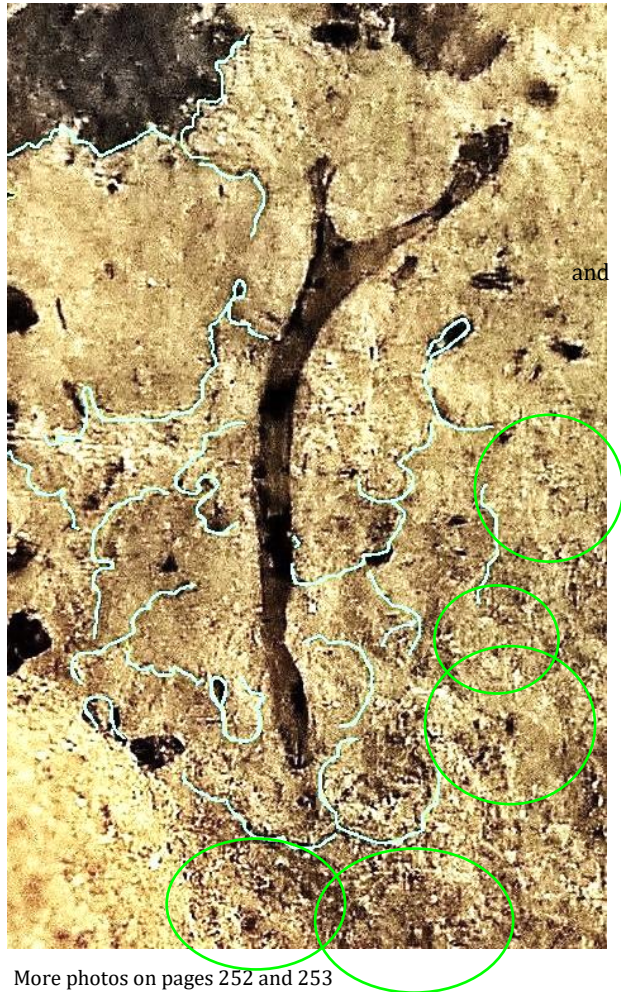


↑ *Salopella* - thallus with sporophyte - in a communal field of intact and familiar liverworts; see Part 1, this history, p. 37.

Sporophyte and fading thalli of *Salopella*; the thalli are overgrown with fungi →

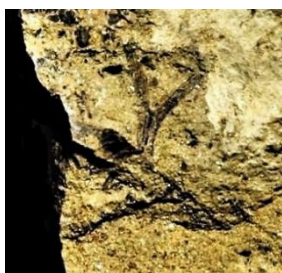


And again the same part of the *Salopella* matrix of Sections 1 and 2. Now with some schematic tracing of the contours of its still largely intact, decaying thalli. Compare a typical extant liverwort habitat with layers of half-compost and fungal nutrient medium.



More photos on pages 252 and 253

Cooksonia has quite a different habitat, where individual (!) plants seek out moisture- and nutrient-rich grooves and channels in a landscape. Which may well be further away from shoreline environments.



Cooksoniae, standing in or next to often spongy moisture- and nutrient-rich grooves (Part 2; this history).

4. *Salopella* next to *Cooksonia*: different morphologies and behaviour

Both *Cooksonia* and *Salopella* are seen with fungal fading for their thalli. Which need not tell us much about the thalli themselves. A plant could have a liverwort-like thallus or a somewhat more evolved one: either way it is not the thallus that would be responsible for the plants' demise and subsequent fungal overgrowth, but the relatively enormous stomatic sporophyte of the adult vascular types. Enormous relative to their own thalli and to those of liverworts.

The bigger & larger these sporophyte 'antennae' onto the universe, the more environmentally vulnerable the plant, due to a more precarious gaseous and thermal exchange (bad and poisonous air, heat, frost), a much greater dependence on windows of proper humidity; mechanical risks - wind and storms; temporary flooding; much more exposed stomate surfaces and cuticle to be damaged; more susceptible to fire, UV-radiation, etc. .

Cooksonia and *Salopella* do not differ in this high sporophyte vulnerability. Thalli **without** sporophytes would be the opposite - as much more clammed-up and less exposed; less in direct contact with the environment. Which is why precisely the plants naturally without large sporophytes - that is: proper liverworts and juvenile vascular thalli - gave us such beautifully intact and detailed fossils. Without fungal fading. They lived long enough not to be taken by their friends, the fungi. The fungi perished around the same time they did. And thus didn't have time, anymore, to eat them. See particularly Part 2 of this history. [The fungi eventually perished in the same disaster that gave us all this great information. Fossilized fading - i.e. half-eaten debris, *fossilized instead of just gone* - implies fungi frozen in time while dining. Ours may be the only such evidence in the fossil record. If we disregard meals caught in amber.]

Having thus established that *Salopella* and *Cooksonia* can have the same fungal fading for their thalli even if the thalli themselves could differ, we may, tentatively, also try to catch some hints from the fossil material of possible morphological and functional differences between both plants.

[**NB** - The textbook demarcation for the plants up to now has been: an angled branching - as a Y - for *Cooksonia*, next to a curved branching - as a U - for *Salopella*. See footnote 7, below.]

Firstly: Part 2 of our history shows what we propose to be juvenile thalli for *Cooksonia*. *Cooksonia* sporophytes are often found next to these juveniles on our matrices. The *Cooksonia* thalli would have had, in their youth, a three-lobed or even a three-sphered shape, with a more 'prefab' socket hole for the future sporophyte; without a visible seam such as *Salopella*'s. Where it was indicative of a coming together of two thallus flaps (liverwort growth habit and morphology). *Cooksonia* juvenile thalli would also be thick-skinned. Good for thermal

isolation, against evaporation, etc. For *Salopella* we do not know this, as we have seen no juveniles. The adult thalli, next to each other still look rather similar. As follows:



Cooksonia's three-lobed/sphered pristine juvenile thallus with socket hole and still token taproot, above ground. Part 2, Fig 1a

Two older thalli of *Cooksonia*, with a more sprawling form; having had to counteract the leverage of a standing sporophyte. Adult *Cooksonia* thalli resemble *Salopella*'s. Same mechanics do apply. Part 2, Fig. 11

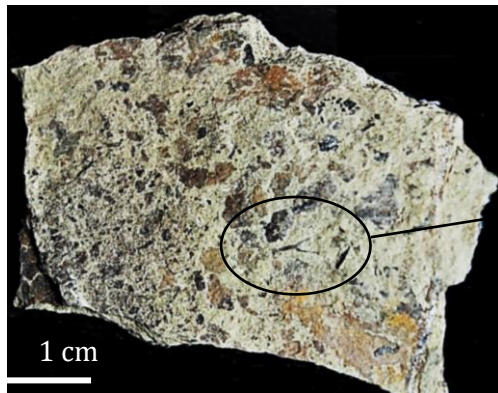
Used lobed *Salopella* thallus as described in the present essay

Differences for the plants - in addition to their different socket holes - and tallying with differences in their preferred habitats are as follows.

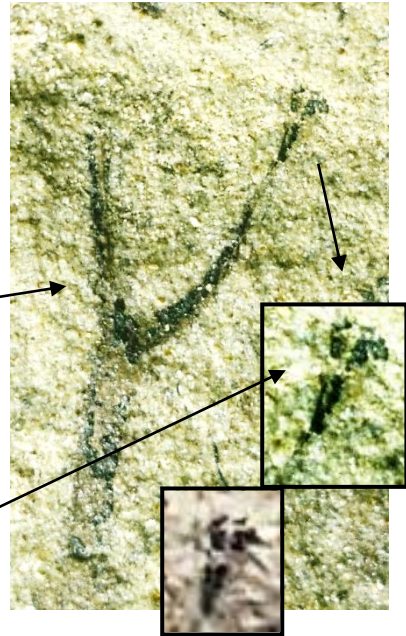
Cooksonia thalli show in their youth a horizontal taproot, above ground, tapping into the nutritive moisture of a furrow or groove directly next to them. Fig. 5 and 6 of the essay in Part 2 suggest that a total of 90% of adult *Cooksoniae* indeed stand in or near such narrow grooves, rifts or furrows. Their much more sprawling thalli in adulthood have by then often (but not always) grown over or incorporated these taproots, which would then no longer be visible as a conspicuous feature.

The adaptation would be wise, of course, for a more focused attention to moisture in a less watery environment than that of a liverwort. As would a thick skin. *Salopella* typically does not seek out these furrowed or grooved environments. The *Salopellae* in the present essay stand in what seem pretty large and shallow water catchment areas, in whole forests of their kind (see e.g. pp. 139 & 140, above). This we have not seen for the more individualistic *Cooksonia*. Other complete *Salopellae* fossils in our herbaria literally stand in the middle of a field of liverworts (*Cooksonia*, again, does not), which thus will be a moist liverwort habitat also, with no need or regard for further pockets of moisture, as in less humid terrain. ³⁾

Below, we will give one more *Salopella* fossil, as part of an, again, identifiable liverwort matrix, that will become important later on in our analysis:



sporangium of *cf. Salopella*, with perhaps crossed fault lines to quarter the operculum for release of spores



So, what we are observing seems to confirm a not too subtle difference in behaviour between *Salopella* and *Cooksonia*, reflecting a real difference in function and morphology as well. *Salopella* with its rather liverwort-like thallus - the seam, hem, two gametophyte flaps; structures like gemmae cups and lobes - still seems at home in an overall moist and communal liverwort cradle habitat. 4)

Cooksonia would be far less liverworty (we also found no gemma cups on them), seemingly ready for individual travel, at least somewhat further afield, with a horizontal taproot, above ground, to tap into nutritive moisture of small furrows and grooves along the way; a thick cuticle skin against drying out and generally scorching climates, and of course the masterly stroke of a symbiosis with a fungus (which they both have), giving them an essential rucksack of moisture and nutrients for their offspring, in the still barren hinterland. That would be entirely up to them to cultivate. No backstops for these grandest of heroes.

The world should have a *World Plant Day* every year, to honour these fellows for their invaluable gift to the world. They made us happen.

And what's more: we may have a lead on who they were, exactly. We might just be owing our life, wealth and culture to the grandest little society of liverworts. Still silently here, as for the last 450 million years. Out of harm's way behind the garden shed.

The human narrative could benefit enormously from this sort of humbling input. If only to counterbalance a blind and all-to-eager acceptance of aggression as evolutionary inevitable. Or even natural.

5 Both *Salopella* and *Cooksonia* have vascular-type sporophytes

The *Salopella* matrix of the previous Sections seemed to be harbouring a number of clear liverwort echos and similarities. Without forcing the matter in any way, the resemblances until now seemed almost literally for the taking - not least for & by the plants themselves.

Of course, additional anatomical and morphological research should clarify matters even further. The material certainly warrants the most thorough investigation. What we have here may well be the only macroscopic evidence man will ever find regarding the mechanisms, the first and crucial macroscopic makings of what will become all life on land.

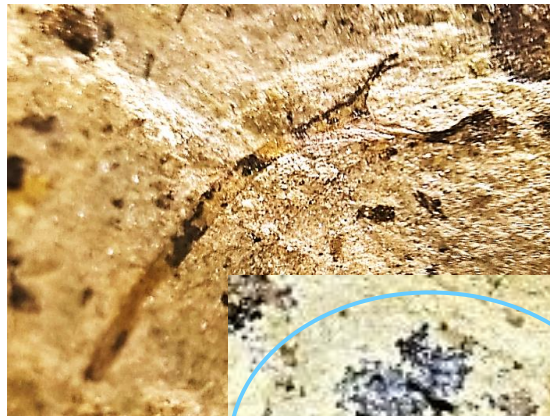
A further avenue of enquiry that we can envision - as a thought experiment - would be one where our '*Salopella*' **as is** would be taken as a liverwort, whereas e.g. the *Cooksonia* next to it would still show no reason to be one. However, immediate hurdles for such a distinction between both species would be at least two.

The first is that under grazing light → *Salopella* tends to look equally vascular; not at all different from *Cooksonia* or e.g. *Sawdonia ornata* in this respect (see Parts 3 and 2 of our history). Preliminary anatomical / microscopic tests also clearly suggest similar developments. See also p. 152, below, left.

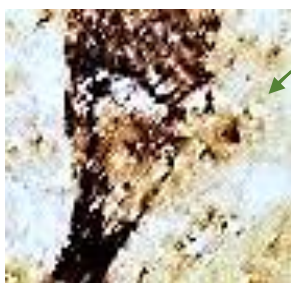


The second hurdle would be ← that the defining size of *Salopella* seems utterly normal for a Late-Silurian, vascular-type sporophyte. All well-established in paleobotanical theory. The flurry on top of the double (???) sporangium of the specimen on the left could be

seen as something of an atypical growth.



Or it could just be what it looks like: a flight of spores, just breaking free from a bursting and splitting **single** sporangium, that is . . .



partly curling back. Having been ripe - and thus burst - just before a fast and dense, reductive sealing sediment landed on top of the plant layer. Which must have arrived within hours, or less. Also, *Salopella* is known for its single, not double sporangia. Compare again the specimen of p.143 above; same location. That, moreover, showed what may well be crossing fault lines over the sporangium. One fault line seems to have opened up for the spores in the photo on the left. Where the other fault line - front to back in the photo - would remain unused; and still be intact. Larger photos on pages 152 and 153, below.



But to return to our subject: both *Salopella* and *Cooksonia* seem to flaunt the same sort of normal vascular-type sporophytes. That already are relatively enormous as compared to their own thalli, and certainly as compared to the petite - and tender, watery, translucent, young - liverwort 'stems'; the archegonia or antheridia. Apart from their markedly different relative size, liverwort stalks would thus also differ in their watery, 'mossy' aspect from the more complex sporophytes of both *Salopella* or *Cooksonia*.

Additional photographic (fossil) confirmations of the different leagues of dimensions for vascular-type stems next to those of liverworts may be found in the middle of footnote 3, below.

A hypothesis that could come to mind at this point would be an *intermediate* status for at least the *Salopellae* in our herbaria. A plant halfway between liverwort and a full-fledged vascular-type plant, with vascular-type sporangia, still standing in a somewhat archaic, even ana-chronistic, still very liverwort-like thallus. Which will limit the habitat of the plant to 'moist-to-wet'; its initial environment when it came ashore. All of which won't do for all plant species for always, as there is a whole Earth to be won.

6. Recapitulation. Still work to do

Until now, this essay has essentially been an inventory of things liverwort and things vascular for the Late-Silurian land plant *Salopella*. With *Cooksonia* as a more or less implicit but unequivocal model or comparison for vascular.

We saw that *Salopella*, next to its quite normal-seeming, adult, vascular-type sporophyte also sports quite a few significant, liverwort-like features, especially for its thallus.

However, the fact of these features does, in itself, not allow for any unequivocal conclusions, yet. Let alone wider evaluations.

Which, in short, indicates that the work our essay set out to do - obtaining definite answers - is not yet finished.

So, in our continued search for a grand and inescapable answer, let us go in once more. Into an already intricate but still understandable and overseeable Silurian world of beginnings and supportive evolutionary contexts. If our liverwort botany, with its still modest complexities, is not yet, as they say, full-blown rocket science, it can certainly qualify as *early* rocket science. We'll ask the analysis to lead the way. Inspect the Sputnik.

7. Some deeper probing. And the answer is Yes

There are more crucial differences between the stalks of vasculars and of liverworts than the dimensions relative to their thalli alone. Vascular-type sporophytes grow out of their thalli **after** fertilization, which happens inside the thallus, not in the open air. The vascular-type plants are quite self-sufficient in this respect. They self-fertilize inside their gametophyte, with sperm they themselves produced. The only extra thing the vascular types need is some water inside, as their sperm must be able to swim.

For liverworts the situation is diametrically different. The stalks that come out of liverwort thalli are either archegonia, which are female sperm receivers and later spore bearers, or antheridia: male sperm dispensers. Liverworts thus have separate male and female equipment *outside* their thali; monoecious (both on one plant) or dioecious (male and female plants). Fertilization occurs in the open, during rain or generally moist phases, which are rather common in the liverwort habitat. Both sexes may also sport gemmae cups for non-sexual cloning; often the most important and/or the most frequent form of propagation for the most common extant liverworts.

Hornworts, by the way, also have their male and female organs outside, on top of the plants.

→ These facts will also mean something else. A fatal problem, perhaps. Because all this also means that a plant like *Salopella*, with a vascular-type sporophyte, could not possibly stand in a proper liverwort gametophyte. As the thallus must sooner or later become enabled to produce and receive its own sperm, internally, for a sporophyte to make sense. As we just saw, none of this equipment would originally be available inside a liverwort thallus.

Moreover, the former liverwort thallus must also be fitted with a sturdy enough sporophyte socket, plus matching internal nutrient- and moisture-transporting machinery and tissue for the newfangled sporophyte base inside the thallus, where the sporophyte is fed.

In other words, what we would be seeing when we see *Salopella* as an intermediate – a suggestion alluded to in the previous Section – is a plant with many old liverwort paraphernalia still visible, skin deep on its thallus, but in reality probably giving all it has to become a vascular-type plant underneath.

The intermediate phase would thus be a much longer process and a much more complex affair than just putting a different type of mast on the ship, with some tweaking and fine-tuning of the rest of the equipment at your convenience.

This would take generations upon generations. **But where are these generations?** How will the plant survive until its new thallus - as a vascular plant's - is functional? How can it ensure its own continuity, prevent its dying out? One cannot be *somewhat* pregnant. Or *just a bit* extinct.

Or can one? What if there is a real answer to this question, this time?

What if *Salopella*, in its intermediate stages, would ensure its reproductive capabilities by just Doing Nothing. Zen style. Which only needs to mean: not shutting down its archaic but extremely reliable, simple and superficial gemmae cups - the meristem fingers inside them - during the transition. Not until the new equipment is ready. (Clones reflect your genetics-of-the-moment. More intermediates might even speed up the evolution, on top of mere survival.)

Gemmae cups here would thus be perfectly feasible. They moreover require not much energy, and the growing points inside the cups - that make the little clones - are just meristems. Not too specialized at all. They would in fact be a brilliant (and brilliantly simple) solution to an otherwise well-nigh unmanageable, terminal problem. And indeed also only about skin deep, so as to not needing to bother the evolutionary processes inside the thallus, or their results.

Asexual reproduction can thus be a very convenient back-up system for many intermediate botanical cases we could think of. But never more so than with this almost casual liverwort cloning apparatus, already in place, that will virtually exclude time-related pressures for evolution during its first vascular-type trials & triumphs. It all seems to fit perfectly. It will also readily account for the veritable forests of its own kind where *Salopella* habitually & literally stands in. Gemmae clones germinate nearby (just the bounce of a raindrop away), whereas spores may well go with the wind.

Does this make a difference for our *Salopella* story? Indirectly yes, with a very strange twist in the tail, yet to come.

Thinking about this gemmae cup cloning, this “trick-of-no-trick” that instantly organizes all the time in the world for evolution to do its work, made us wonder again what exactly it was that we have seen for *Salopella*, in the preparation for this essay. Which brought us a totally weird answer.

What we had seen all along but only noticed anecdotally (which means: not), was in actual fact no intermediate *Salopella* at all but a full-fledged vascular-type spore plant, giving a full performance of its own proof of same by releasing its spores almost in our face, at the bottom of page 144 of this very essay. And which no microscope could deny.

So, what the analysis in fact seems to be offering is something very unexpected, and also very natural. And perfectly logical.

Salopella is not an intermediate, but a *former* intermediate organism (aren't we all), that is keeping some of the best stuff of its previous world as well. And indeed, why not hold on to this asexual reproduction, even after it has ensured your survival into your new self? You still have it, it obviously still works, it costs you nothing & does not hinder.

Moreover, for as long as the new plant needs or wishes to stay in this habitat, its home would also remain eminently suited for the happy landings of gemmae; the clones. No falling on dry earth. Extant gemmae in their own moist world strike root - rhizoids - within hours. And because the gemmae clones will always propagate nearby, characteristic fields of *Salopella* will indeed be the expected - predicted - and wished-for context.

So: many reasons why precisely these gemmae cup structures would still be so conspicuously present on our vascular *Salopellas* - even if they may look somewhat clumsy or unsexy, indeed.

And while we're at it: why not keep the elastic and agile old-style thalloid lobes as well, if they keep you nimble, let you shift a bit in your surroundings, help to better tweak your thermal well-being?

And finally also: why not keep profiting from a whole era of experience with a proven - and often proven essential - solid social network, with all advantages that come with even a sort of colony? That is, as long as you're happy with your rather static, or at least not very dynamic moist habitat, that has always been perfectly suited to your type of communal living?

Aren't there dinosaurs with chicken feathers, and chickens with dinosaur feet? And why on earth wouldn't there be? For lack of snob appeal?

So, here goes.

We put it to the universe that our Late-Silurian fossil material offers, with a plant we call *Salopella*, a land plant that has crossed the demarcation line from liverwort to a vascular-type plant. As evidenced by a characteristically large, unequivocally vascular-type sporophyte, that is seen to release a flurry of spores, which also implies - for such a sporophyte to work - a sufficiently evolved vascular-type thallus, that can service such sporophytes, and self-fertilise as well.

We further contend that the plant, in its evolution, used all sensible assets at its disposal. Even some of its old but proven liverwort assets, if they suit it and its moist habitat like no other. And of which the physical equipment, about skin deep, remains visually prominent on the thallus. We contend that the morphology of the plant (up to a jigsaw-like communal aptitude, showing on the matrices) thus also implies an unequivocal yes, as the answer to our original question, whether vascular plants evolved from liverworts.

The beautiful thing is that *Salopella* as the first proven vascular-type plant would indeed be able - by a marvelous stacking of evolutionary mechanisms - to literally **show**, on itself, its ancestry, its evolution from a liverwort. Teaching by its own sheer presence. The little zen devil. While almost brazenly ignoring the hundreds of millions of years between us. Botany may feel honoured. Touched, even.

So, as far as we're concerned you did it, you liverworts, you lofty beings you. You spawned rainforests. That cradled tigers. Cradled us.

The final word here must be in the liverworts' esthetic defence. Liverwort equipment may often look quite 'industrial' - more like engineering than elegant fine art. Which seems an almost obligatory and vastly endearing trait of biological structures that are this mind-bogglingly ancient. Ordovician / extant marine animals would also be a case in point. Starfish and such. The somewhat later prawns.

Elsewhere in our history this led to a honorary title for our beloved liverworts as the Swiss Army Knives of evolution. We now see that they are in fact the whole toolshed. But make no mistake. Industrial archaeology has its own & fully legitimate cult esthetic.

We can see biker jackets.

Liverwort Piece

1978. Approx. 35 x 21 cm.

Industrial readymade
(*objet trouvé*).

Dada after M. Duchamp.

Private collection,
the author.



8. Further research. *Salopella's* as the primal form for all vascular types

That the first vascular-type plant would be found in a moist liverwort environment as a riparian plant (shore plant) can come as no surprise. It would be reasonable to expect the evolution to have occurred in a context where the liverwort starting points would have been happy & healthy, with even some energy to spare. Which at this early time in history would still be the liverworts' cradle habitat on the shores of rivers and lakes.

Moreover, such a riparian context, close to the shore, also seems perfect for the evolution in practical ways. No worries, distractions or delays for lack of moisture or nutrients. The habitat is the parental home of the liverwort mothers, where these same mother plants can also make the most of the amply proven toolbox for their moist environment; possibly even as something of a first-aid kit. Gemmae; colony-like shelter; moist microclimate; possible thermal tweaking; etc. .

And with an environment this well-suited to the evolvment it would seem equally natural for the liverwort subjects to enter the evolutionary process just as they are. Instead of with strategies where they would harden, steel themselves first. Seeking survival in more marginal environments, building a more allround thallus as an evolutionary first step. In the riparian context *as is*, evolution may remain more local, more spontaneous if you will; its work less cumbersome - less elaborately *planned*, in time and space. With no extra preliminary demands for the liverwort starting points. Just aim for a safely placed vascular-type shore plant - and take it from there. 5)

It seems that such a reasonable enough strategy (or lack of it) has indeed been the one.

Liverworts have proven themselves still eminently suited for (only) moist habitats even after 423 million years. As we humans can testify. And way down, on the other side of history the evidence is no less compelling. The evidence here being the gentle liverwort traits, indeed, on these first vascular-type *Salopellae*.

Which, moreover, may also give us a lead for further research. If *Salopella* as a real vascular type is still this close to its liverwort ancestry, will this not suggest an order for the evolution as *liverwort* → *Salopella* → *Cooksonia*? That is: *Salopella* as also the basis for later adaptations, that would become more allround thalli? *Cooksonia* as an adaptation of *Salopella*?

The material - and the analysis - may certainly point in this direction of our *Salopella* as **evolved** into a vascular-type shore plant, and after the deed is done also appearing with **adaptations** for more neutral habitats as well. Our *Cooksonia* gametophytes - with their adult passing resemblance to *Salopella*, but also with juveniles showing functional adaptations such as horizontal taproots for pockets of moisture, prefab socket holes and thick skins - would certainly merit such a hypothesis.

So, *Cooksonia* might be next on our list to try to determine their evolutionary pedigree. If such research is still needed. In a way, the crucial answers seem already here, or at least close. There already is a much higher probability that *Cooksonia* would indeed be an adaptation of a pre-existing vascular type than that it would be its own development, parallel to e.g. our *Salopella*.

Cooksonia never shows any morphological nearness to shore-type plants. Which would be a prerequisite, as we saw, for an original, direct evolvement from liverworts. On the contrary, these plants seem to be ready or readying themselves for colonizations further afield, with matching morphological, functional and behavioural characteristics, that will be very much their own. As amply described in this essay and elsewhere in this history.

It seems safe to say that the *Cooksoniae* we know show at least **some** adaptations, crucially away from the morphology, functionality and life style of (all and any) liverworts. And of *Salopella*'s.

The plausible solution - if we insist on *Cooksonia*'s own, parallel evolvement and subsequent adaptations, on the basis of a very own primal *Cooksonia* - would be to posit as a primal *Cooksonia* a plant that can hardly be very different from our *Salopella*. As its liverwort-inherited features can hardly be seen as just nice to have. There would sooner be, again, a recognisable liverwort heritage from a straight evolution from liverworts on their own wetland turf. With *Salopella*, evolution did not do embellishments for fun. (Or riparian entertainments, for that matter.)

Moreover, no known liverwort living in a moderate climate zone, not even after 450 million years has shown any appreciation for any other environment than a moist to wet world. They

are not classified with the (non-vascular) mosses for nothing. So, the *Cooksonia* in our Late Silurian cannot very well have been the product, the descendant of a sturdier liverwort either. As, by their non-vascular, mossy/watery nature there would not have been any. Not in this moderate climate zone.

All of which begs the question: is a theoretical proposition of what amounts to a second, necessarily more or less comparable *Salopella* still serious evolutionary theory - just in case this **might** do justice to the more famous *Cooksonia* as a parallel (if modified) evolution? Would we learn anything we have not learned already from the real *Salopella*, literally at hand, smack in the middle of its real narrative?

Is two *Salopellas* really more interesting than viewing the Silurian age in 3D stereoscopic vision? Or than a bottle of Islay, with the same result? Footnotes ⁶⁾ and ⁷⁾ below will further elucidate this matter.

Summing up, we do think our *Salopella* has already done all the work needed to determine how the vascular plants on planet Earth came into being. Which indeed **include** the more famous *Cooksoniae*.

To show *Salopella* our appreciation we will proudly share our Nobel with it, to boost its celebrity status.

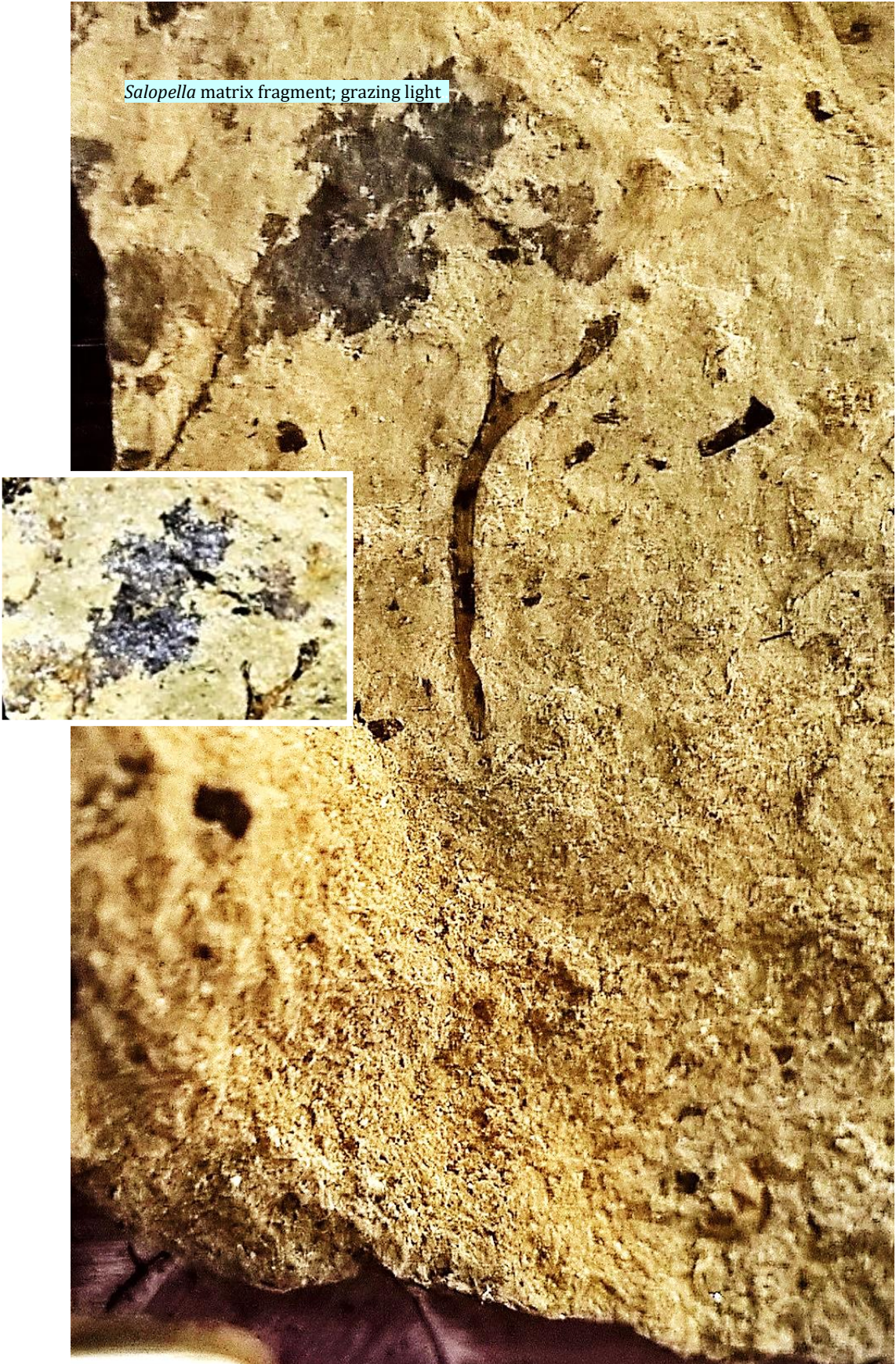
As the little engine that could.



Portrait of the *Salopella* matrix; the Late-Silurian landscape that is the subject of this essay

Relief stripes, also turning left in the fork of the sporangium, as a further indication of vascular complexity.

Salopella matrix fragment; grazing light



Notes

1) In the context of this essay a few extra remarks on the gemmae cups of our Late-Silurian liverwort fossils may be in order. The mechanics involved - raindrops bounce back, taking gemmae clones with them - should be straightforward enough.

In the extant world especially *Marchantia* and *Lunularia* are characterised by gemmae cups. A plant like *Blasia pusilla* has gemmae stalks. For these three liverworts, their Late-Silurian fossils have been found; *Lunularia cruciata* being the most frequent guest on our matrices until now. Theoretically, a bit of a problem might be that gemmae cups of any era are by their nature rather vulnerable. Silurian ones would be less than millimeters wide, with their rims much thinner than paper. So the very placement of a good and firm sediment on top of them (required for an intact reductive fossilization) could well damage the structures before fossilization. Compared to an extant Crescent cup moss, a slight pushed-in aspect can indeed be seen for a fossil as the one on the right, below. But even here, the most vulnerable ridges of the crescent rims of the gemmae cups are still discernable.



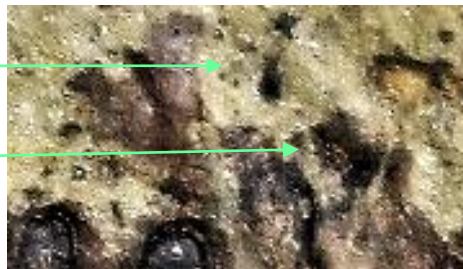
Extant *L. cruciata*
next to a Late-
Silurian
counterpart



Silurian Crescent cup moss, with gemmae or at least with their meristems (growing points) still inside are not too scarce on our matrices.

The rounded gemmae cups of the Late-Silurian *Marchantia* liverwort look quite similar to those of extant *M. polymorpha*. First a fragment of a fossil (with some cuticle missing):

Late-Silurian 3D fossil of the *Marchantia* liverwort. Notice the familiar liverwort lobes, above right, and the inner rings inside the gemmae cups. Gemmae and/or their growing points - meristem 'fingers' - may be discernable in several gemmae cups.



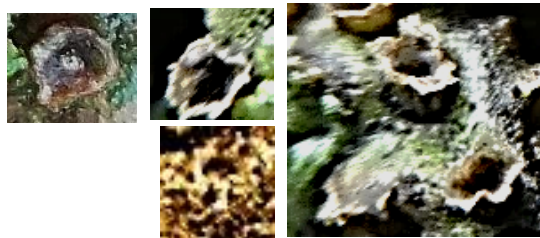
This close up, we can also begin to glean what would be remnants of proper but battered, thinner-than-paper gemmae cup rims for the fossil.

Seen as skirt-like drapings around the inner rings of the cups. Extant as well.

Follow the inner and outer arrows on the right. The Silurian cups would thus not be significantly different from extant.



The rims of this fossil could even be very precise preservations - notably of elderly cups. Compare elderly extants from p. 141, above.



And also the full fossil of the Late-Silurian *Marchantia*, next to extant.



Patches of cuticle missing for the fossil may somewhat obscure a resemblance in characteristic lobes, 3D wrinkles and folds that is still quite prominently there, after 423 million years.

For an introduction to the Late-Silurian liverwort fossils in our care see our essay *Six liverworts at the dawn of land life* in Part 1 of this history. For an analysis that also includes a leafy liverwort *Naiadita* and possible archegonia for *L. cruciata* see Part 3. Archegonia for *Pellia* or *Blasia* in Part 1.

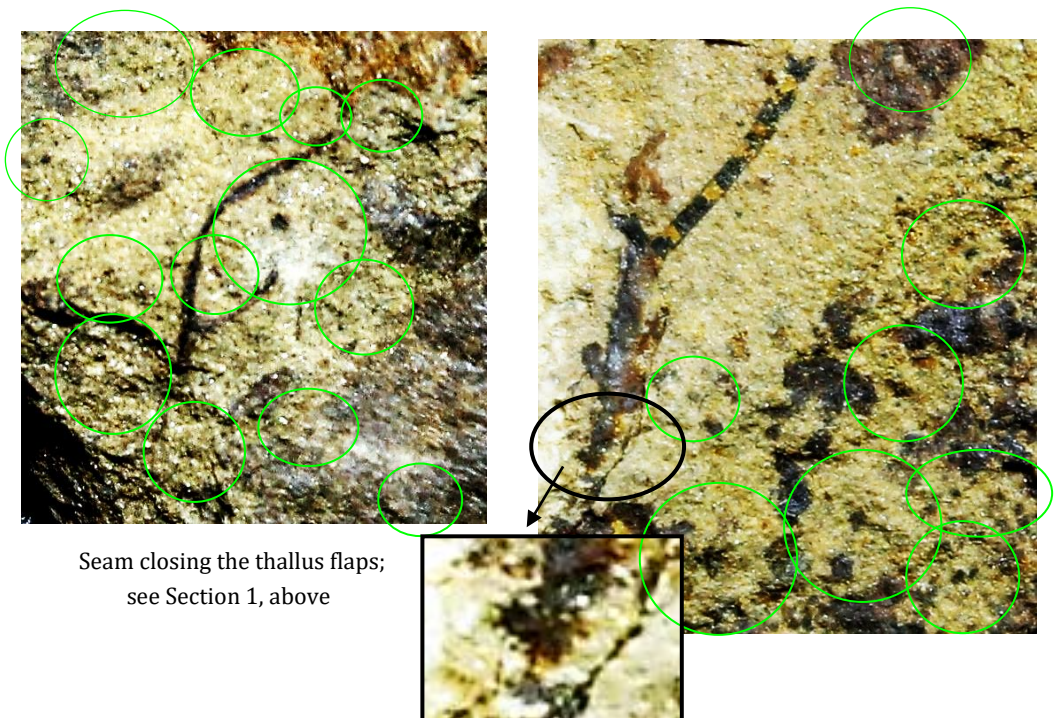
For the record we also like to state here that the *Marchantia* liverwort (marchantioid group; liverworts with complex thalli) we looked at in this footnote will also be our candidate liverwort to have given rise to the first (*Salopella*) vascular-type plant on Earth. More specifically: comparing the morphology and anatomy of extant *Marchantia polymorpha* next to the equally detailed, identical-seeming shapes and forms of the fossilized lobes, seams and gemmae cups on pages 137 and 138, above, makes this an obvious analysis, as far as we are concerned.

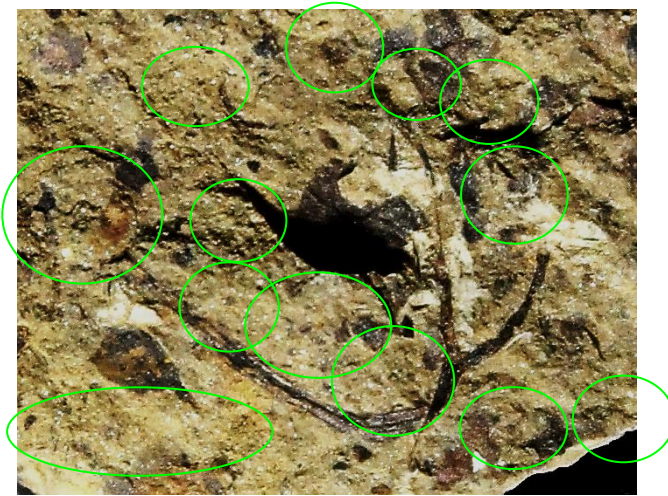
2) Further communal characteristics of extant specimens of our liverworts to be found in the Appendices to this history at the back of the book.

3) Our herbaria harbour at least eight abundant *cf. Salopella* matrices from the same Late-Silurian quarry; some of which show their communal inclination by literally standing in a forest of familiar, determinable liverworts (see also Parts 1 and 3 of this study):



Others show an inclination to build a jigsaw-like community with their own kind, paving the surface in the same way as our fossils did on p. 141, above. Here three, somewhat grainy photos of examples; *Salopella* sporophytes included. The rings indicate fading thalli:





And this. These same photographs can, in passing, also help to shed more light on the size of vascular-type sporophytes next to the 'stalks' that are the archegonia / antheridia of our Silurian liverworts.

In Section 4 above, attention is drawn to a defining difference in size for these 'stems'. It is not difficult to give a further

idea of this dimensional

difference. To illustrate further that our *Salopella* indeed belongs in the vascular-type category.

So: above, again, some *Salopella* sporophytes, plus thalli. *Cooksonia* is of a very similar size - sporophytes as well as thalli. Compared to, below, some Silurian liverwort 'stalks' and their thalli. Where liverwort thalli are about the same size as vascular ones, a 'stalk' (or archegonium) of a liverwort ✓ ↓ ✎ is never larger than its thallus. *Cooksonia* and



Salopella sporophytes are both about ten times as large as these thalli.

Archegonia of Silurian cf. *Pellia*, *Blasia* and *Lunilaria*. This history, Parts 1 and 3.

There is one more thing about *Salopella* clones as the above that calls for further analysis. In Part 2 it was shown that fossils of juvenile *Cooksonia* thalli are often intact; untouched by their fungal friends. As still clammed-up structures, still without vulnerable, stomatic, sporophyte 'antennae' open to the universe their demise would have come well after that of the adults. Which would then be about the same time the fungi were done for as well.

But we now see that *Salopella* clones, often also somewhat smaller than a mother plant (the

one with an intact, large adult sporophyte stalk) *would* be overgrown with fungi. Suggesting that these gemmae clones were different from the *Cooksonia* offspring coming from spores. And indeed, none of these *Salopellae* show the clammed-up, pristine aspect that would have kept them alive long enough. They have rather noticeable used sporophyte rings, suggestive of at least fertile adolescence. Some still with sporophyte stalks; some with empty thalli.

These facts could suggest that not all *Salopella* gemmae clones were meant for full adulthood *per sé*. Due to their natural redundancy. Compare the way a sprouting tapistry of acorns or beechnuts will more often than not seem in vain. In the case of our early *Salopellae* the extra photosynthesis of a surplus clonal offspring would at least add significantly to a rich nutrient medium - if not to a 'herding' of CO₂-supplying fungi (!). Both mechanisms would be most useful in preparing the ground for more, and more firm terrestrial vegetation. Which wouldn't yet explain a possible scarcity of fossilized sporophytes associated with these *Salopella* thalli. Does their woodiness come with age, i.e. with advancing adulthood?

4) It is worthwhile to look at more comparisons of our *Salopella* and further adapted *Cooksoniae*. As their analyses may show a rather marvelous, fully interlocking evolution.

First example. *Cooksonia* has prepared itself for a life further inland in more ways than one. One way is the evolvement of guard cells for its pores - as dosing valves, designed to prevent evaporation of moisture. The plant can close or open its stomate apertures with a tightening or slackening of the new guard cells. *Salopella* in its traditional liverwort environment could theoretically still make do, certainly during its fledgling beginnings, with somewhat simpler pores - with e.g. more tentative guard cells, still in the process of evolving. As drying out is less of a risk for the plant, there.

But we found the opposite. Even a Silurian **liverwort** already possessing what clearly looks like guard cells; see Part 3, pages 97 and 98 of this history. And what's more: extantly, the same plant also suggests that apart from a standard retaining of moisture, **absorption** of moisture by its stomates also seems to occur, quite likely equally regulated. Which could indeed be functional for this liverwort - catching scarce rainwater during dry spells. So, guard cells, crucial to vascular photosynthesis (the basis for the whole of evolution) could have been already, independently developed. Open to allow moisture into a liverwort thallus - then closing to keep it in. A perfect winner. Template already at the ready.

A second example of a beautifully efficient evolution shows itself when we look at how *Cooksoniae* already have full vascularity. See e.g. footnote 9 with Part 1 of this history. We are seeing the same for *Salopella*, on the basis of the analyses so far.

Vascularity, in a normal situation would suggest that a species would be getting at least some of its moisture and minerals from the surface bed, below ground. This seems plausible for the moist-to-wet, liverworty habitat of *Salopella*. Where rhizoids could indeed be reliably sufficient.

However, ample evidence also shows that for *Cooksonia*, preparing for wanderings into a possibly much more arid and stony hinterland, a *horizontal taproot*, above ground, tapping

into nearby moist furrows and dells will have assumed an extra, full root function, for now. To at least ensure swimming capabilities for the sperm inside the thalli, during fertilization in drier habitats. It would be silly to assume that the plants would waive further, more general services these taproots can freely offer. Especially as these same taproots - above ground - would also be the perfect life insurance for any adventures further afield, given the harsh and rocky grounds the plants will surely encounter. Where vertical roots cannot go. Or wouldn't find what they would seek.

These rather brilliant taproots thus also allow, in passing, for a head start for the use of sap vessels, also with colonizations inland - away from the moist-to-wet cradle habitat - at an otherwise still absurdly early stage in history. With the real probability of a still largely impenetrable Earth. Which apart from being, again, a beautifully interlocking evolution, also implies that Silurian rhizoids indeed did not need to pull their full weight as real roots, yet. Not more than in the known riparian environment of liverworts, and of *Salopella*. See also footnote 9 with Part 1, for a suggestion that extracting silica phytoliths and other minerals from the surface bed - in fact: nibbling at rocky habitats - would be at least as apt at these early stages. To prepare the ground (sic) for proper plant roots, and a further retention of nutrients and moisture. Rhizoids could of course also provide much of a starting point for a speedy further development of proper rhizomes and roots.

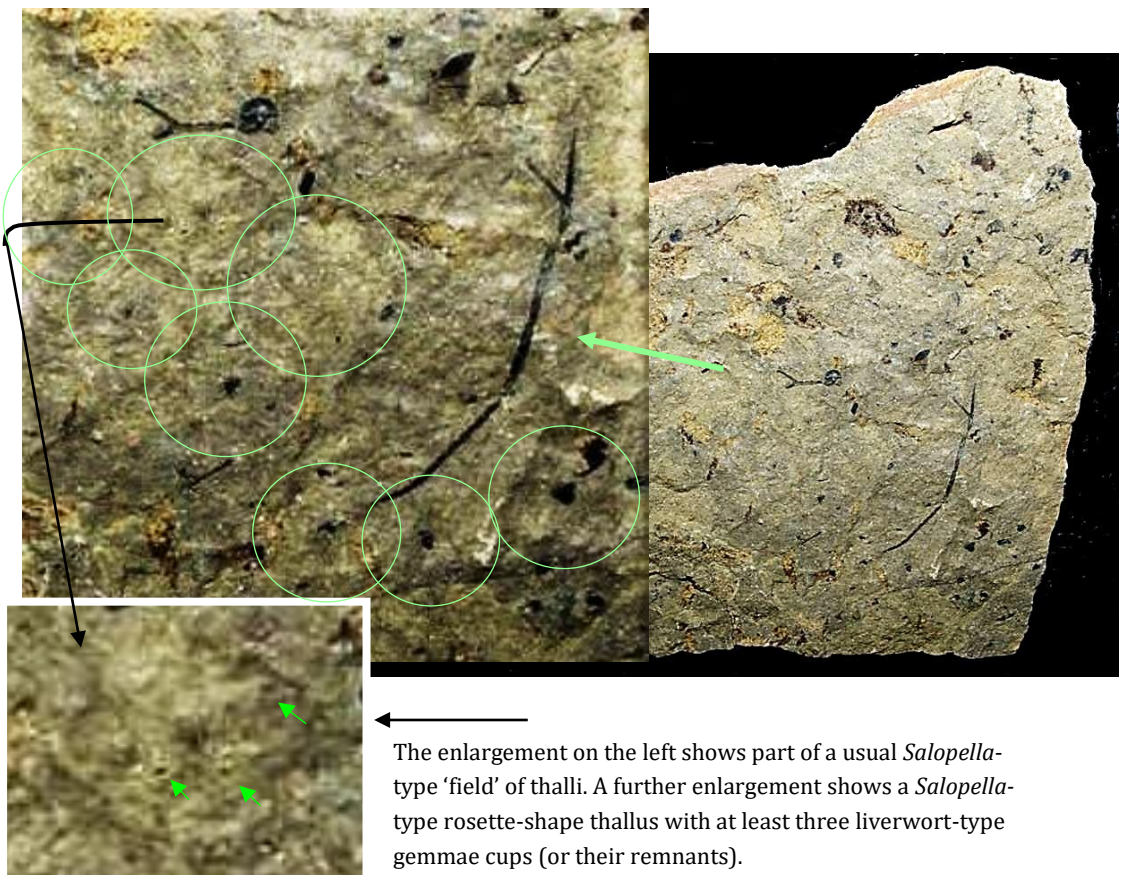
5) Evolution obviously took this road, and it will be interesting to ask why. Can we say that evolution *has considered* that mosses only really thrive, with some energy to spare, in these moist environments? And that this would thus be the best, lush starting point for the evolution? Or would it be that evolution, by its nature, generally cannot or will not (or could not or would not) think or plan ahead in this (rather 'human') sort of fashion - as would certainly be required for the planning of a sturdier thallus for an intermediate plant, first? Could it be that to plan many moves ahead, say, like a chess player, in time and/or space, would just mean adding to an ever more shaky and risky house of cards with every new, hypothetical move? Would that be a reason for evolution to adopt a more local, or more modular stance? Or should the question be even deeper: evolution as unwilling to '*think*' at all? Just taking one real step at a time - and then take that result as genuinely new input for a next, fresh decision, in extension of the previous? Would it be justified *at all* to say that evolution ever *considers* anything? We think not. ***To think and to intuit are already very different things.*** Think beehive.

It would be great to further follow evolution's behaviour, and perhaps rationale in these matters. The rather unique emptiness, still, of our Silurian canvas, together with what would largely be a lack, yet, of routines and templates to fall back on, could possibly reveal character traits of an evolution caught in the act of choosing, hesitating, blundering, trying - for once seen in a quite rarified but also stark and vulnerable [Lucian Freud kind of] light. See our Part 4 for an analysis leading to such Silurian, evolutionary nakedness. A world, moreover, also without competitive, game-theoretical mechanisms, yet. Which just adds to the uniqueness of this encounter with evolution as still undistracted by many of its later levels of work. That are often taken as defining. Here is the stuff that defines the defining.

6) For some suggestions of what an adaptation of a *Salopella* as a typical *Cooksonia* would actually mean for an early and still quite inexperienced land plant evolution, compare page 126 of Part 4 of our history, in the context of its main text. In leaving their moist to wet riparian cradle habitat for a more 'regular' environment (from an overall perspective), the plants would need a number of fundamental adaptations or augmentations for their general templates. The plants should be able to suffer, but ideally also partly **buffer** a rather sudden loss of their lush, moist, safe and nutrient-rich surroundings in all kinds of ways. Which would be evolution's task.

As for the **process** of the adaptation of *Salopella* into a not yet typical but still already identifiable *Cooksonia* (or a still liverworty *Cooksonia*, as a parallel descendant next to *Salopella*) we have found a matrix with an exceptionally long *Cooksonia*-type sporophyte, forking like an angled 'Y' as a real *Cooksonia*, not curving like an 'U' as would be defining for a *Salopella*. However, the plants are *Salopella*-like in making a 'surface-paving' colony (a direct liverwort inheritance) while the thalli also flaunt a more than passing resemblance to those of *Salopellae* - or those of liverworts.

Some photographic images are the following. The matrix on the right measures 90 x 75 mm; the large *Cooksonia* type is a full 26 mm.



The enlargement on the left shows part of a usual *Salopella*-type 'field' of thalli. A further enlargement shows a *Salopella*-type rosette-shape thallus with at least three liverwort-type gemmae cups (or their remnants).

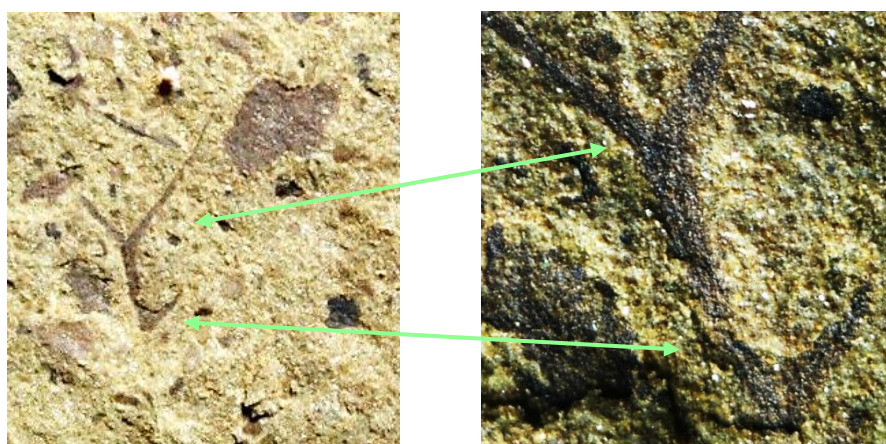
These plants would come rather close to what we meant by a 'double' *Salopella* - a fledgling *Cooksonia* that in tandem with *Salopella* could almost make a '*Salopella* in 3D'.

We would like to stress that the above, seeming baby *Cooksonia* (equally 'still in diapers', just as the still liverworty *Salopella*) would not at all be like other *Cooksonia* we found. All other *Cooksoniae* we have seen are typically of the much further adapted kind; away from their liverwort ancestry. But in this curious single instance it looks as if the whole visible demarcation of *Cooksonia* and *Salopella* in this early phase is not much more than an angled versus a curved forking of sporophytes. Same product - two brand logos. More in footnote 7, directly below.

7) The richness of our fossil material has by no means been exhausted by the present analyses. It is entirely possible that we would find within our finds (herbaria) further cues, leads or evidence of more specific ways in which the presented evolvments and adaptations were brought about.

We can give two fairly offhand examples of mysteries the material might still possess.

First a weird *Salopella*-like plant, that is: one with a typically **curved** 'U' branching, standing



next to liverworts, in the midst of its own, fading kind. Seemingly spawning a *Cooksonia*-type, **angled** Y branch above it, where any branching branch would already be highly inappropriate. *Salopella* with something up its sleeve?!

To add to this curious little stack: compare footnote 6, above, which is very much in extension of this find. Here also, it seems that the only initial thing *Salopella* would have to do, for now, to become a fledgling *Cooksonia*, would be changing the fork in its sporophyte from a curved 'U' to an angled 'Y' shape. Further demarcations could be taken from there. What we mean is that the material seems to show that the plants could indeed still be this alike (with *Salopella* still first).

Fungal 'bridge'. Or the base of the impromptu extra growth in the above stem; improvising a prototype. Evolution caught sculpting. If we could call this intermediate a chimera, it could perhaps even speed up the *Cooksonia* brand's viability. History shows that the happenings here are more than a one-off event, to be sure.



We could even think of a reason **why** our *Salopella* above, with its initial curved branching, would be starting to make angled branches of the future *Cooksonia* brand - the same style our modern plants, shrubs and trees still have. Consider the following.

The larger and the more upright a plant becomes, the more it needs to channel its forces, especially its weight, downwards. Vectors to its center of gravity should go more or less as a straight line down into the stem, the 'trunk' of the plant or tree, to prevent heavier branches from breaking off. A curving *Salopella*, inventing an angled *Cooksonia* fork would, with that mechanical move, do precisely this. Preparing itself & the plant world on land for more branching, more sheer weight, and a greater 'uprightness' – think wind & storms, dangerously toying with gravity centers. And a timely invention at that, in a soon fairly rapidly accelerating evolution (after just such sensible adaptations).

We could further informedly speculate - not least for the fun of it - that starting out, on land, with a wrong but existing *curved* botanic template for *Salopella* would not be wholly unexpected, either. As curves and rounded-ness were (and are) of course & indeed the obvious ways for an earlier, aquatic plant to live with currents and other water dynamics. To stay undamaged. And energetically intact. In motion and in repose. You can't resist the flow of water. But you can deflect it.

Be this as it may, if our analysis holds, the new, angled, oh, so natural archetypal form and shape of every tree, shrub and plant on land, in any child's drawing, is at least partly determined by a gravity thing that seems not too difficult to deduce - especially when a fossil literally seems to show how, and when, and *that* it was actively (!!!) done. Pretty soon after the first, sometimes messy confrontations with the very much heavier new reality above the waterline. See our Part 4. Indeed, don't we all know about the burden of weight that is sadly added, with every higher swimming pool step? While rising out of the water? Each step a quantum leap of gravity?

So, lessons received. Again. Over a span of four hundred and fifty million years. Fresh as yesterday.

If we wish to be very precise, the previous sketch could benefit from one more step. A close scrutiny of the lighter, smaller photo of our curved/angled fossil could suggest an ambiguity that the close-ups do not seem to have. The smaller photo could leave room for the lower branching as perhaps so overgrown with fungi that a curvedness cannot be 500% established.

However, the fossil itself does seem in line with the close-ups. With 3D strands of tissue that make and follow a curved, not an angled path. The problem seems to be a shadow on the smaller photo, of a relief that should turn out to be insignificant with flatter lighting (as in the close-ups).



Higher, experimental branch of the fossil



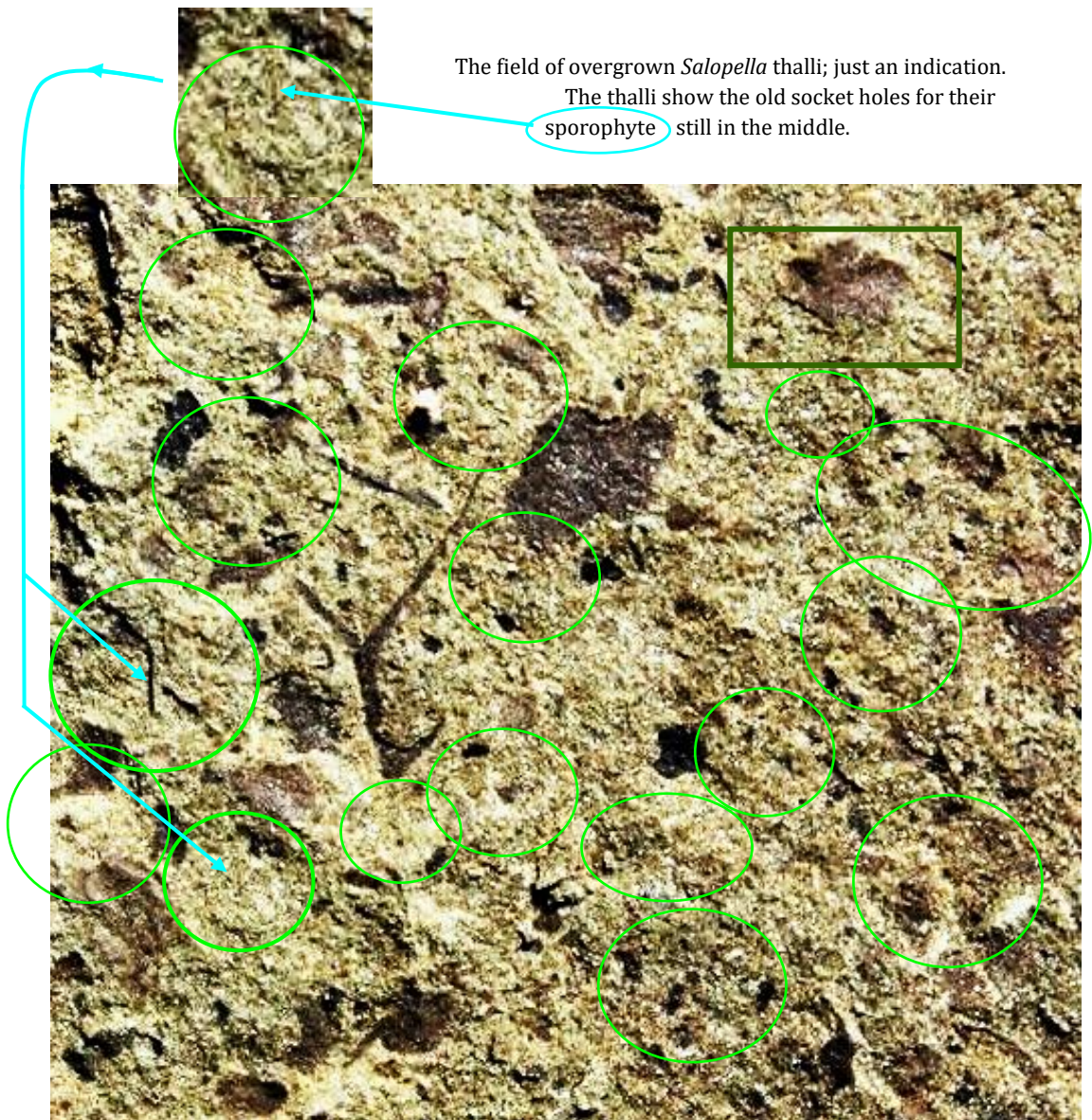
Lower, normal *Salopella* branch

The more informed answer, however, would be: but never mind. As the real problem is not the lower branch but the higher, definitely angled Y.

A second tell-tale sign that the fossil at hand is definitely a *Salopella* (with definitely at least one highly anomalous angled Y branch; trademark of future *Cooksonia*) is that the plant indeed typically stands in a field of (overgrown) *Salopella* thalli on its matrix (compare the photo below ↓). Which is only possible because *Salopella*, next to its spores still also has a liverworty gemmae propagation, allowing for many offspring [sic] to land right next to it, only the bounce of a raindrop away. *Cooksonia*, as a plant without such gemmae 'cuttings', will - for that reason - not have this sort of defining habitat; snug in the middle of its own kind. Liverwort-like. Even if it wanted to. Which it doesn't, by the way. On the contrary: *Cooksonia* is emancipating from colony-like habitats; individuating and preparing for wanderings further inland.

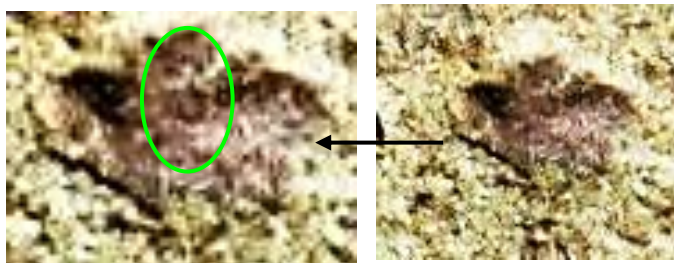
So, the additional, equally serious argument here is that *Cooksonia* does not make gemmae; only spores. With offspring that thus fly much farther away. Which equally makes our matrix a determining *Salopella* habitat. ***With thus at least one member going rogue, trying out a prototype Cooksonia emblem.***

We do, however, also firmly stay with the evidence for our elegantly dynamic gem of a curved/angled intermediate plant as well. And will make a better photo. For more on the *Cooksonia* adaptations from *Salopella* see footnote 6 with Part 5 of our History. For *Cooksonia*'s individuation see Part 5.



The dark structures are thalli of liverwort. The center, spread-wing shape may be a *Pellia epiphylla* (precursor). A *Pellia* at one o'clock in the above matrix seems to have its archegonium out.

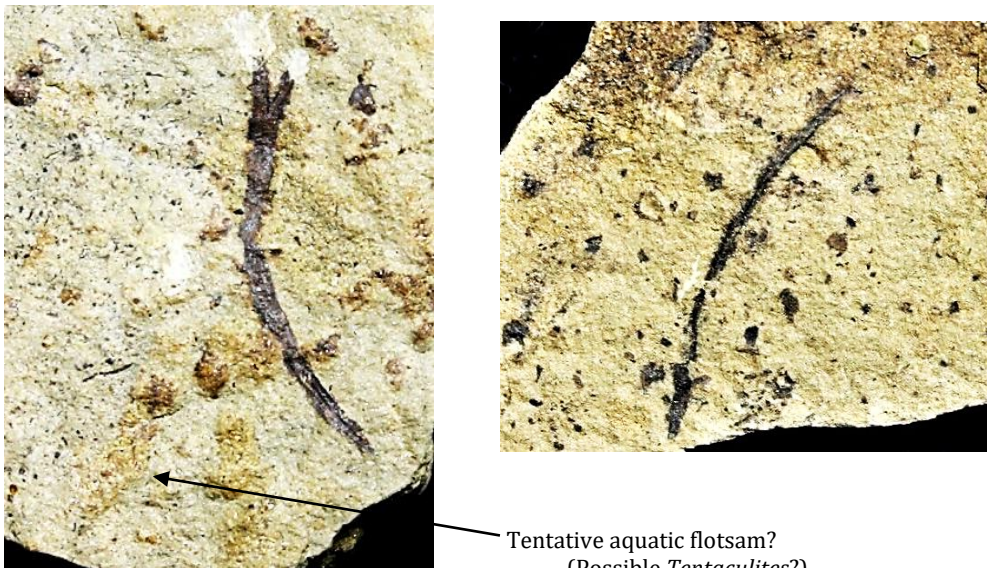
Seeming *Pellia* liverwort on the above matrix, with archegonium; compare Part 1, Section 2. The herbaria are still full of small and large discoveries awaiting their 423 million year turn.



As a second example of the richness of our material: a *cf. Salopella*, already shown some pages ago (now lying down), with what look a bit like leaf-like pockets - see the photo below, left. That would be somewhat reminiscent of a suite of mystery fossils in our care - right photo - possibly earlier, and more wet-to-aquatic even. Notice the beautifully twined or even braided ribbon(s) for the 'pocketed' fossil on the right.



The pockets here could be thallus-like appendices. Or spore containers. Or they could mean something more interesting. As the matrix on the right above, and the three matrices of the same plant below seem to show, the pockets would perhaps be able to sort of 'detonate' - smearing themselves all over the matrices. Which may well be a type of fragmentation of thalli, as another, known, Late-Silurian means of asexual propagation or cloning.



Tentative aquatic flotsam?
(Possible *Tentaculites*?)

Part 1 of our study, from page 25, already showed a quite convincing fragmenting liverwort. We could speculate that this new, possibly crudest form of cloning (*Explode into cuttings and strike root!*) would also work well underwater.

Throwing yourself into a water current, instead of to the wind would probably give your ambitions to propagate even more pizzazz.



We have not yet finished our reveries about aquatic precursors for our terrestrial liverworts (*...climbing ashore in full liverwort garb*). We are thus always on the lookout for shapes, forms and behaviour - and functions - that might work even better in even wetter shallow shoreline environments. One can buy several species of underwater liverworts by mail, by the way. Aquarium webshops.

Moreover, a simple internet search for images of “underwater liverwort” will equally spawn pages of aquatic pictures, that will at least include ‘our’ Silurian land species *Pellia (endiviifolia)* and *Marchantia polymorpha* (Parts 1 and 3 of this history). That require little imagination as to where our very first liverwort land plants may very well have come from. As an almost trivially simple proposal.



← *Marchantia polymorpha*

Plants that can spawn rainforests and in passing literally survive a timeless 423 million years are the greatest of geniuses in our book. Capable, time and again of much more than what could have spontaneously entered the heart of this starry-eyed human.

Taught by these plants, we are keeping our eyes & our options wide open. We’d like to find a fellow Silurian, somehow visibly crossing the demarcation line of the water surface. On its fossil matrix.

The extant liverwort *Ricciocarpus natans* - aquatic and terrestrial forms



"Floating form in stagnant water "



Terrestrial form

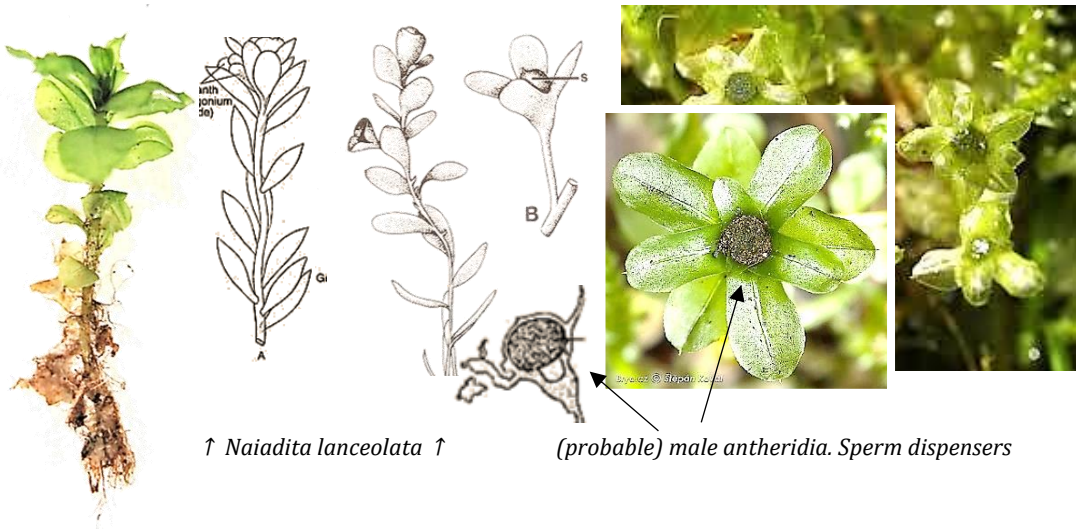
One of the modes of increase in this species, is by the thallus splitting along the median line, the halves separating and forming new plants.

Goebel mentions that the ventral scales of the water form may be considered as leaves. They possess chlorophyll and thus co-operate in assimilation. They increase the surface by which water may be absorbed and also give the plant more stability. In the land form these scales are much reduced and only serve to protect the vegetative point.

In: S.M Macvicar (1926),

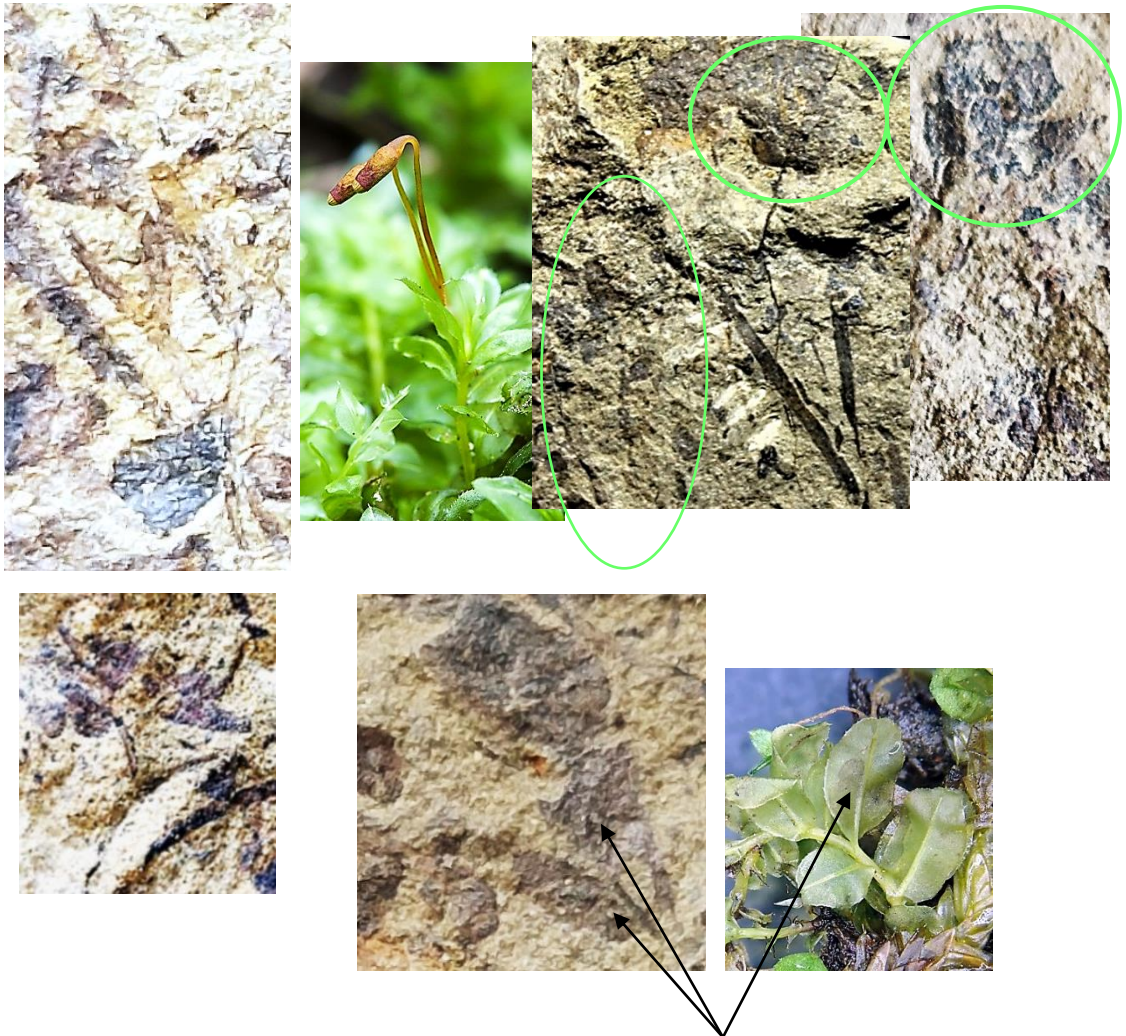
The Student's Handbook of British Hepatics,
Second Edition Revised and Enlarged, page 31.
Invermoidart, Archdale.

We would like to conclude with an extant, this time leafy moss, *Plagiomnium affine*, with also an aquatic as well as a terrestrial form. The plant has a fine resemblance to our Late-Silurian leafy liverwort *Naiadita lanceolata* (Part 3 of our History, from p. 92) and also seems to 'rhyme' rather well with some of our fossil matrices waiting to be researched further. The green photos below are all of the extant terrestrial form of the leafy moss, *Plagiomnium affine*. The matrices are from our Late-silurian herbaria. The reconstructive sketches are all of *Naiadita lanceolata*.



↑ *Naiadita lanceolata* ↑

(probable) male antheridia. Sperm dispensers



Late-Silurian fossil next to extant *Plagiomnium affine*. These are not midribs with sap vessels. They're solid ribs, as reinforcements for the moss leaves, indicative of an aquatic connection. They make the blades sturdier & safer in an underwater current.

We think it is quite possible that this Late-Silurian fossil material also harbours more information about e.g. first terrestrial steps of a readymade aquatic / amphibian liverwort, which would then lead the quest for ancestors into the lakes and streams in a very concrete, even extantly comparable way. With aquatic plants that would quite probably be anatomically rather more highly evolved than expected. Just as our 'modern' terrestrial liverwort fossils turned out to be at least Silurian and very possibly Ordovician.

But what our *Plagiomnium* shows would be equally inspiring: asking about the evolution of leafy, **non-liverwort** mosses, and about evolutionary relationships between these and indeed the liverworts; leafy and otherwise.



Aquatic form of the same *Plagiomnium*; seemingly popular as an aquarium plant for freshwater prawns to seek refuge in. Lucky things.

Our most recent focus is on the following, equally Late-Silurian friends in our herbaria; 3 - 9 mm tall. Are they the earliest quillworts, still living today; now as semi-aquatic plants again, after an evolutionary episode as a giant tree form (really) in the Late-Carboniferous era? Or could they indeed belong to the earliest leafy mosses? They do stand in liverwort vegetation.



For a comparison of the seeming sheathing onsets of 'leaves' of the fossils with extant *Isoetes* or quillwort, that further indeed suggests *Isoetes*, see Part 1 of this history, footnote 6.

Addenda - three family members

About these addenda

Below we have added three pieces that are easily accessible on the website version of our history. Here also printed on paper as they indeed closely belong with our story. The first two texts are taken from the website itself; the third is a photographic reprint of a pivotal piece of background: a Polish paper on the *Fundstelle* and pedigree of also our fossil material.

Through the looking glass. How worlds are made

A preview of On the Origin of Plant Species

In the lazy water meadow
I lay me down

– Roger Waters (Pink Floyd) 1969,
Grandchester Meadows

If we could visit the first botanical fields, the landscapes of our history, what would we see?

Plant species large enough to be seen would still be lingering by the shores of freshwater lakes and streams where the earliest flora came on land. Shores that would first harbour the moist-to-wet habitats of many species of liverwort; organized in colony-like little forests. In which at least six species can be readily recognised. Our herbaria have their near pristine Late-Silurian fossils. Four of these first Silurian friends - botanically known as moderns, not primitives - will still be living in our parks and gardens today. Equally communally. Having been here for at least 450 million years. None of which was remotely known. Until the essay in Part 1 of our history reveals them in their glory. From the Silurian to today. Down to the pores on their skin. Very possibly on your doorstep.

Next to and within these liverwort forests we would also see another type of spore plant. Still equally liverwort-like in its floor plan, but now with a stem or stalk at least ten times as large as any liverwort equipment. This newer plant, named *Salopella* in these pages, fertilizes internally, is of a vascular type, and can actually be seen releasing a flight of spores to the wind. This large non-liverwort would be the first working, upright, vascular-type plant in our Silurian fields. Having just evolved from a liverwort. Still “in diapers” if you will – still showing its liverwort ancestry at its base. But *there*. As a most plausible candidate mother for all further plants, shrubs, trees and rainforests to come. As confirmed by her offspring in the next paragraph ↓. And by the anchor of her rather robust context – of the four ultra stable, still extant liverworts.

Not just a trial balloon then. Part 5 of our history will tell all. Something to do with brand logos.

As we would stroll on, these firstling *Salopellas* would in turn also be seen giving rise - to yet another plant. An adaptation, that will fan out as several iconically Silurian *Cooksonia* species. Unlike *Salopella*, these *Cooksoniae* are busy emancipating from their communal and moist cradle habitats. Individuating and preparing for harsher environments that colonizations further inland will bring. With a thickness of skin, and a very ingenious horizontal taproot, above ground, that taps into moisture- and nutrient-rich grooves and dells in the fledgling landscape. As the coveted hinterland will often be too forbidding, still, for vertical roots to penetrate (or find what they would seek).

An equally magnificent preparation for the harsh unknown will be a fungal rucksack of moisture-retaining nutrient medium given to these plants; meant for their offspring. One of two crucial - and wonderful - gifts from their symbiotic friends, the fungi.

The second symbiotic marvel would be a private extra hand-in-glove exchange of oxygen and carbon dioxide between our plants and the fungal companions that make their bed. An exchange that may further enrich their micro environments, given a still fledgling atmosphere for the planet. Even more so in the still earlier Ordovician Period, where our liverworts were born. This on top of a general principle that local augmentations of carbon dioxide levels will *always* enhance the robustness of plant life subjected to it. Often greatly. Then as well as now. See Part 2 of our history, footnote 1. With thanks to dr. Hope Jahren.

A colonization of the larger Earth may thus proceed. Our Part 2 will capture these grandest of feats.

And this. None of the above would have to be deduced, as all these facts and mechanisms can indeed simply be *seen*. Which makes our Late-Silurian landscape a sanctuary as well as a time warp; preserving a historical first detailed and tangible creation story - until this day. The actual cradle (fossils are real things) of all that will ever be.

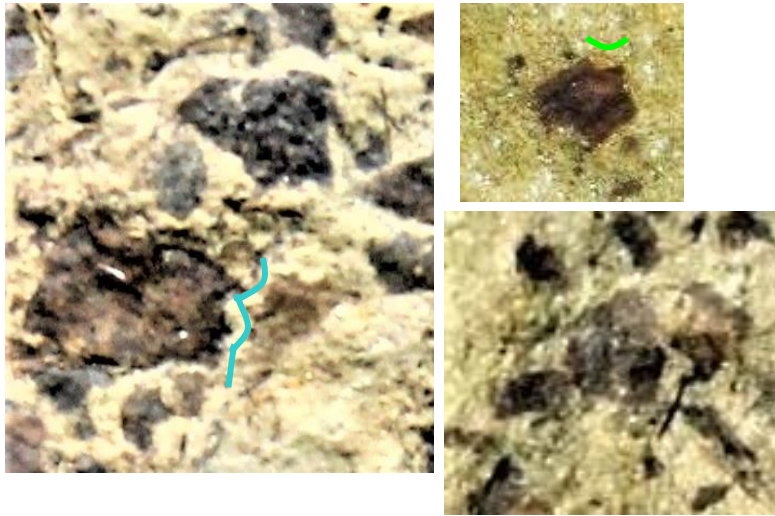
And there is much more. An intricate but not unexpected first plant disease (Part 4; this history), that tells us rather a lot about a young and probing evolution above the waterline. More new plants. An intermediate fellow, already tentatively striving for the greater complexity and *largesse* of the coming Devonian age. And what to think of a Silurian land plant with thorns? Like a rose? Eons before animal predators would even be possible? Not only do we have the plant, we have a fearsome explanation . . .

In short, a unique jewel of a world, at the dawn of life on land, that is an absolute delight to visit. And a most precious garden of gardens for a scientist to fall in love with. Not least because of what our Silurian beginnings may have to say about evolution itself. For a slight lifting of veils shrouding these things, see Part 1, and the footnotes with our history.

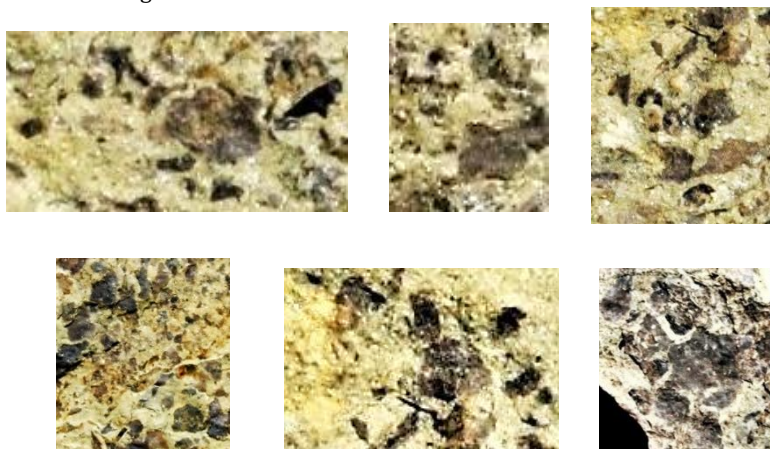
Some liverwort-related Late-Silurian finds,

relevant but yet to be properly processed. With Some not yet formalised Silurian / extant liverwort suggestions; loosely belonging to our macrobotanical history.

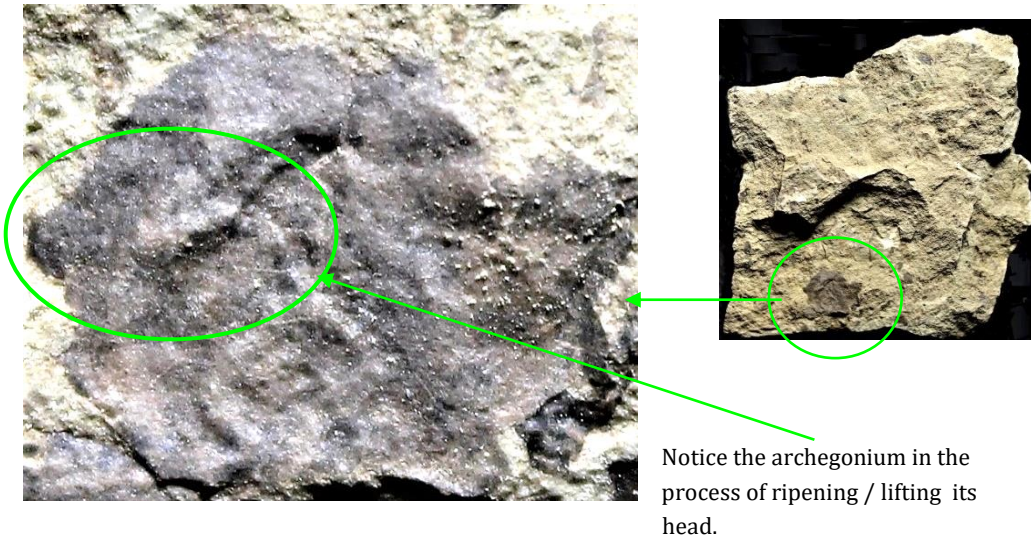
Some more configurations suggestive of cloning-by-fragmentation in the proposed manner of our pentagon fossil dubbed '*fragmentor*'. See Part 1, Section 2 of our history. There are no frayed edges that would be indicative of remnants, or decay.



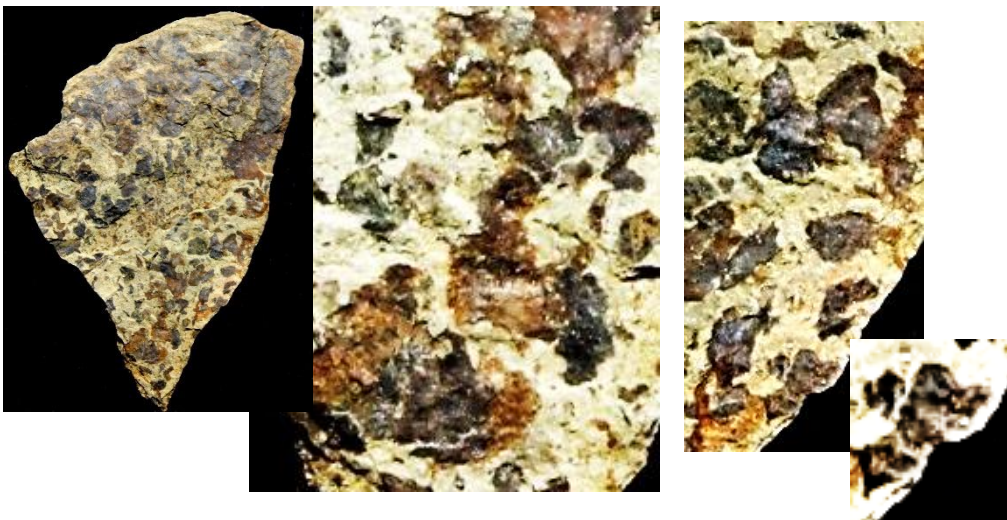
Some of more configurations seemingly shedding complementary 'puzzle pieces' - that are awaiting a closer reading:



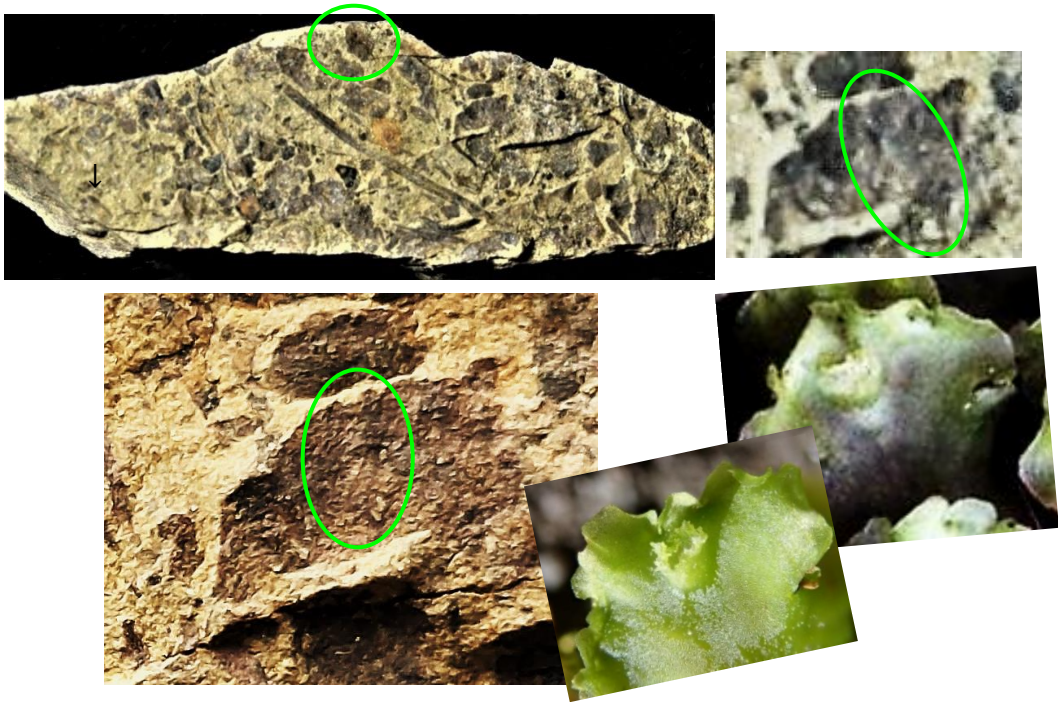
As an example of some further preliminary work on the liverwort matrices in our care, first another of a few more '*Blasia*'-like fossils found independently, on a different matrix:



Nests of seeming *Lunulariae* are seen on several matrices. Such as these somewhat messy ones:



'*Pellia*' are not difficult to find if they take on their typical 'spread wings' silhouette. Here one on another matrix:

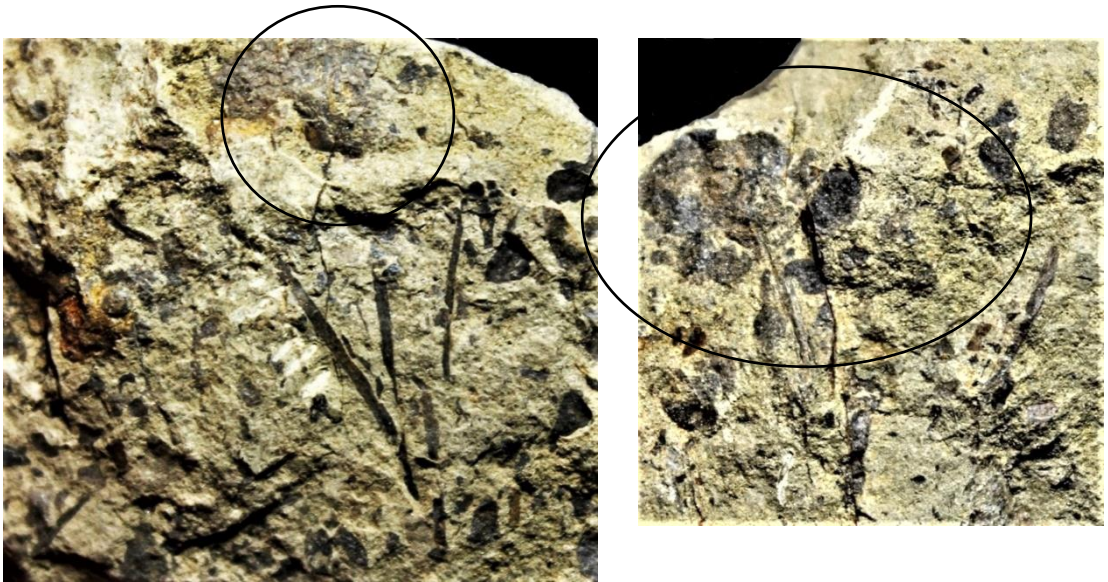


And some rather ambiguous but intriguing patterns, suggestive of gemmae cups and/or sporangia of a leafy liverwort.



The flower-like aspect of some of these fossils is hard to interpret as anything other than indeed leafy liverwort structures, leaf-like appendages and all.

A closer, more serious scrutiny should bring more clarity. The eye can be a bit fast - and thus biased - to interpret; especially with well-known and well-loved patterns. Most of these photos can thus still be interesting anythings. They are shown here as examples of the sometimes thin line between what is there, and the mind slipping into patterns. It is however a line that can be identified. Hence these borderline photos. As before, a microscopic anatomical analysis of cuticle, pores etc. should bring the clarity needed.



As there are more of these 'flower-like' structures found, a possible coincidence may go over in a feeling of something more systematic; such as e.g. a hitherto unseen species of liverwort with clustering thalli. ***Mother with satellites?*** Here another somewhat similar enigma (again, if you want to see it):

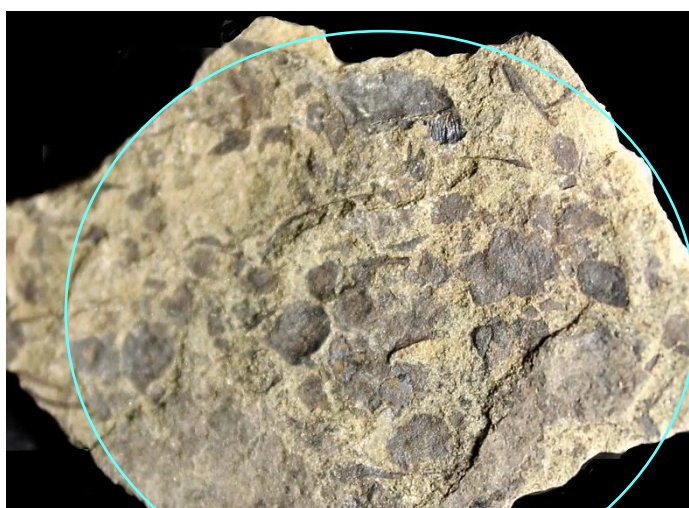
These late-Silurian matrices harbour a wealth of information, the decoding of which we think we might as yet have merely touched upon.



We would, in the future, also like to present more and annotated examples of the ‘tiny forests’ of different species of liverworts that show their indeed cooperative nature.

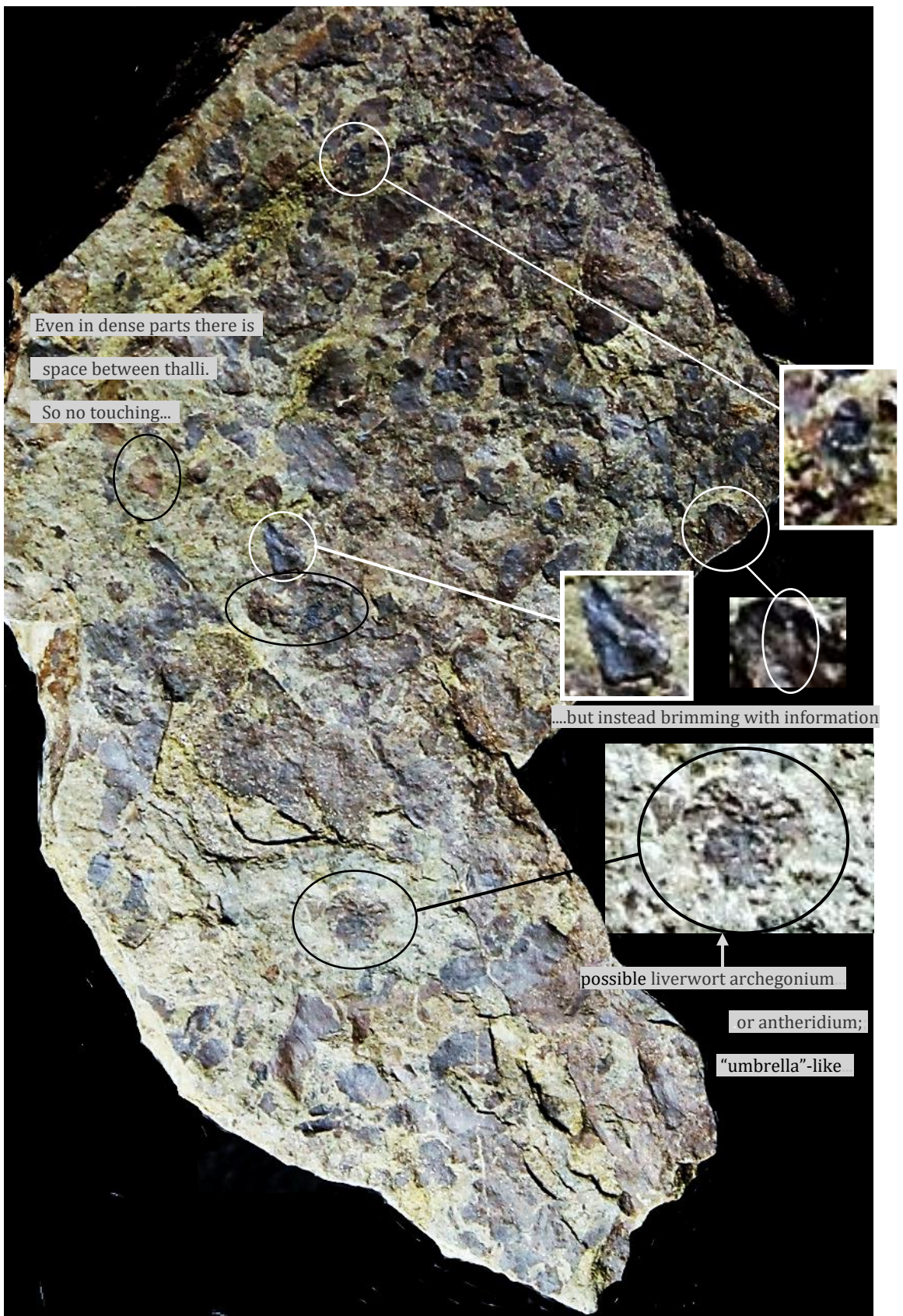
There are many such matrices. The plants are in no way competing but on the contrary give each other all the breathing space they need. We have found among our abundant material not one chaotic tableau of plants climbing on top of each other, pushing each other away - or upside-down specimens or fragments (as would also be the case in a random distribution of flotsam).

There are also not many fragments (incomplete specimens) in the material. We assume that the liverwort thalli that we see on the matrices - almost always in good order - rest on an even bed of fungal nutrient matter. Recycling of liverworts, due to their moist to wet context could well have been very quick. Compare our preliminary extant results in Part 5 of our history, or here: <https://silurianflora.net/wp-content/uploads/2023/04/Liverwort-remnants.pdf>



‘Mother’ with satellites?

Below some of the fuller liverwort matrices, next to those shown in the main text and above; often with some recognizable debris of *Cooksonia*-type sporophytes / sporangia. Nothing aquatic was found. These few matrices are only to suggest the (order on this) type of material. The matrices themselves are available for further research.





It is tempting to think of this kind of 'good order' as perhaps more than just a reasonable coexistence. The formal neatness here could be more reminiscent of a colony than of a mere forest of species and specimens. Which could mean that our overly familiar, 'modern' individuations of species could (speculatively) still be something for the future. Liverwort species might then be closer to each other than the later, more individuated vascular plants.

However, functional divisions of labour within such a colony do seem a little far-fetched. The organic 'machine' to be serviced by the 'cells' in this case, could require e.g. a build-up or regulation of pH, moisture and temperature levels; coherence for the colony, some sheltering shade for youngsters and perhaps also a herding of fungi - to name a few of the most obvious aspects that directly spring to mind. Division of these labours on the basis of e.g. morphological differences in the plants would be hard to imagine.

But it would also be unnecessary. Another, less complex possibility could be to more simply regard a field of diverse species of liverwort as evidence of a non-differentiated organism, such as, say, the leaves on a single tree, that will not compete with each other as the tree strives for a most economical growth (lay-out) for all its leaves. Which for the liverworts would give the same benefits - such as moisture retention etc. - as any group would muster, but without a more strict division of tasks.

It would be interesting to see if specimens of a species of liverwort together indeed behave as one organism (leaves on a tree). Or even - the even more interesting case - several species together behaving this way. (With thus also no competing *among* species). At this moment we have not seen extant (or Silurian) behaviour for liverworts that would contradict such fine and polite relations.

We do have many extant examples, next to many fossil matrices - in total more than a square meter (these plants are small) of dense to very dense communities of small extant liverworts, transplanted as whole sods, just as they grew in the wild; their stages extensively photographed.



Consider this small, in fact random community of at least three species. A very healthy *Lunularia* - even with archegonia about to come out, with *Marchantia* and *Conocephalum* or *Pellia*. A part, in close-up shows the considerate behaviour among these three, precisely as it seemed 423 million years ago.



The plants - just like those on the fossil matrices - seem to seek out the best conditions for all 'leaves' - thalli - on the same 'tree' (which would be the same colony of species).

What we see on our Silurian matrices, as well as in our extant plots, seems to be nothing short of uniquely successful **communal** effort. The plants, all four species of them, survived for the whole span of macrobotanical land life, after all.

Finally, also notice the rather obvious fact - that is: obvious after this, our Silurian history - that these and similar habitats, of these particular extant liverworts will then also & actually be the first highly realistic **reconstructions** of the Mid- and Late-Silurian world. Just before, or next door to *Salopella* and later *Cooksonia*. That will only be coincidentally missing in these photos; and still not at all dominant, 425 million years BC.. Their sporophytes just better fossilizers. (See Part 5 of this history). One for the road:



A *Cooksonia*-type flora from the Upper Silurian of the Holy Cross Mountains, Poland

ADAM BODZIOCH, WOJCIECH KOZŁOWSKI, and ANNA POPŁAWSKA

Silurian land plants from the Holy Cross Mts. are described for the first time. The fossil assemblage occurs in a near-shore, marine, terrigenous deposit of Ludlowian/Pridolian age. It contains *Cooksonia* sp., *Cooksonia*-related species, and some problematical forms. The flora, which needs further study, is of importance to our understanding of early vascular plants and Late Silurian palaeogeography.

Our knowledge of Silurian floras is based on a very sparse collection of fossil sites spanning Asia, Australia, Europe, Northern Africa, and the Americas (Edwards et al. 2001; Edwards and Wellman 2001). There is an extensive microfossil record of spores and other plant fragments (Wellman and Gray 2000) that is augmented at a handful of sites (some 15–20) by the fossilised remains of the plants themselves (Edwards and Wellman 2001). The latter are of exceptional interest because they provide the only direct evidence on the morphology of the earliest land plants. In Europe, Silurian land plants have been described from Wales, England, Ireland, the Czech Republic, and the Ukraine. Some plant remains have been recorded from the Silurian formations of Poland (e.g., Tomczyk 1958; Kozłowski 2000), but these have not been described or illustrated. Here, we report a new mass occurrence of fossil land plants from the Upper Silurian of the Holy Cross Mountains.

All specimens described here are housed in the Institute of Geology of the A. Mickiewicz University in Poznań, Poland, abbreviated IGUAM.

Geological setting

The site of the Silurian land flora is located at the western margin of the Winnica village, about 1.5 km NE of the centre of Nowa Słupia, within the Słupianka river valley, directly below a small waterfall (Fig. 1, GPS 50°52'36"N, 21°06'27"E). A monotonous series of olive-green clay shales, mudstones, and siltstones is exposed at both banks of the valley. The strata dip at about 50° NNE and are intercalated with marly-calcareous horizons, occurring occasionally in lenses.

Formerly, the strata were included within the Upper Rzepin Beds (Filonowicz 1968). In this paper, the authors use a new informal term "the Winnica Mudstone Complex", which will possibly be the basis of a formal lithostratigraphic unit in the near future. The Winnica Mudstone Complex is equivalent to the upper part of the

Lower Rzepin Beds (*sensu* Czarnocki 1950; Tomczyk 1970), series A of the Rzepin beds (*sensu* Malec 2000), series "2" of the Rzepin beds (*sensu* Kozłowski 2000) and, most probably, also the Lipniczek mudstones (*sensu* Tomczyk 1970). The strata in question reach a thickness of about 100 m, and the succession exposed in the analysed section represents their middle part (Kozłowski, unpublished data). According to Kozłowski (2000), oolitic limestones and calcareous sandstones representing the lowermost member of the Rzepin beds (*sensu* Czarnocki 1936) occur below the Winnica Mudstone Complex. The deposits crop out about 70 meters SSE of the analysed section on arable land and in the north-eastern bank of the Słupianka valley. Grey-red mudstone shales representing the Upper Rzepin Beds, well exposed along the river, overlie the Winnica Mudstone Complex.

Stratigraphical position and paleoenvironment

Index trilobites, occurring rather sparsely within the section, and much more frequently in the overlying and underlying strata, provide evidence on the stratigraphical position of these deposits. The underlying strata contain *Homalonotus knighti*, *Acastella spinosa*, *Proetus signatus*, *Calymene beyerrii*, and *Richterarges convexus* (Kozłowski 2000). This assemblage is characteristic of the Upper Siedlce on the East European Platform (see Tomczykowa 1991) and indicates the latest Ludlow (Tomczyk 1990). In the Winnica section, representing the middle part of the Winnica Mudstone Complex, the trilobites *Acastella spinosa*, *Calymene beyerrii*, and, in the uppermost part, also *Acastella* cf. *prima* have been found. The presence of the latter species is characteristic of the lowermost Podlasie (Lower Pridoli) of the East European Platform (Tomczykowa 1991; Tomczykowa and Witwicka 1974). Unfortunately, the poor preservation of the specimen does not allow an univocal diagnosis. On the other hand, the Early Podlasie (Early Pridoli) age of the upper part of the Winnica Mudstone Complex is confirmed by the ostracode assemblage (*Amygdalena subclusa*, *Cavellina angulata*, *Clavofabella pomeranica*, *Healdianella magna*?, *Hemisiella sphaericuminata*, *H. loensis*, *Kuresaaria circulata*, *Neodibeyrichia* cf. *bifida*, *Primitopsis minima*, *P. suaris*?, *Retisacculus semicolonatus*, *Scaldianella simplex*), which was found in the lithological equivalent of the Winnica Mudstone

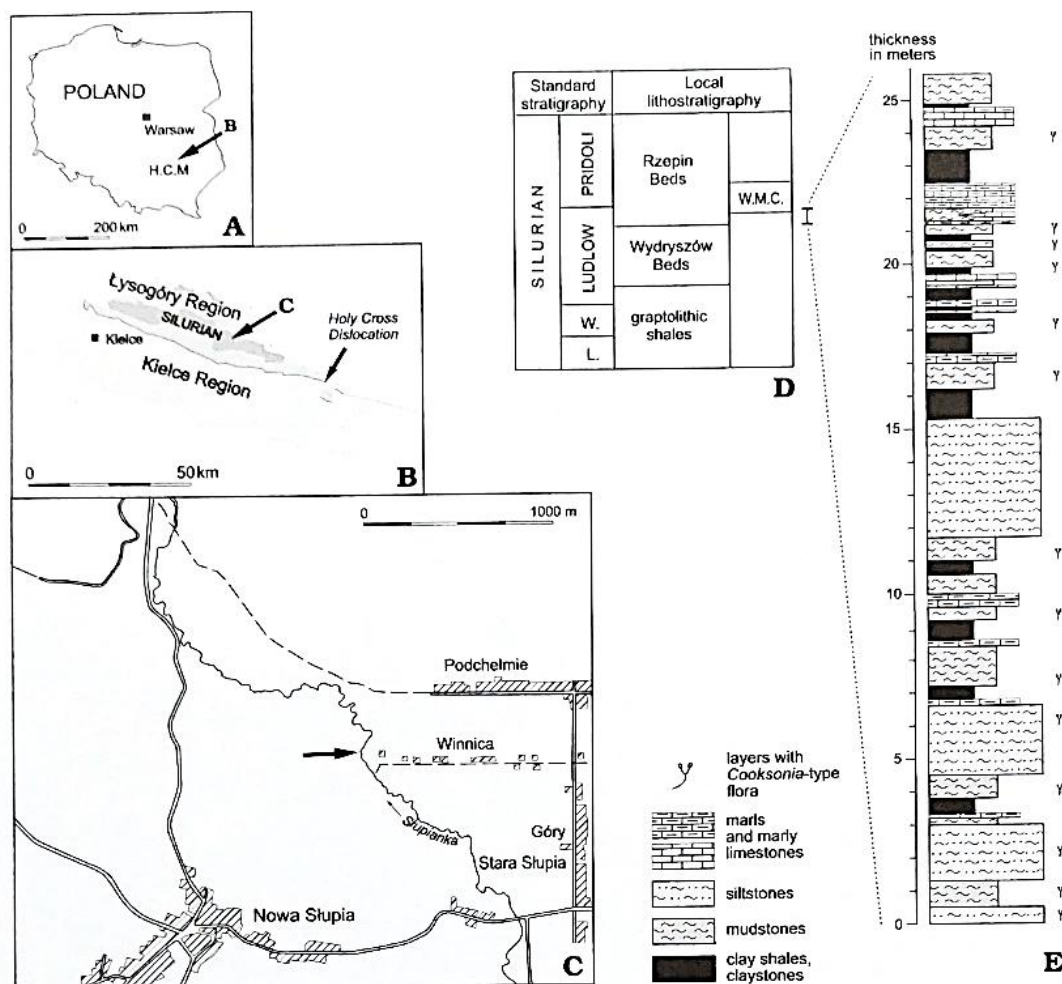


Fig. 1. Geological setting of the described Silurian flora. A. Geographical position of the Holy Cross Mountains. B. Geological sketch map of the Paleozoic rocks of the Holy Cross Mts. C. Geographical position of the described outcrop (arrowed). D. Stratigraphical position of the flora-bearing complex. E. Geological column of the Winnica Mudstone Complex in the type locality shown in C (after Kozłowski 2000). Abbreviations: H.C.M., Holy Cross Mts., L., Llandovery; W., Wenlock; W.M.C., Winnica Mudstone Complex.

Complex near Rzepin (about 15 km north of Winnica, in the Wydryszów Anticline) (Malec 2000). The deposits occurring above the Winnica Mudstone Complex contain fauna indicative for the Early Podlasie (Early Pridoli), such as *Acaste dayana* or *Leonaspid bidentata* (Tomczykowa 1991; Kozłowski unpublished data). Therefore, the biostratigraphical data indicate a lowermost Pridoli age for the flora.

The clastic deposits forming the Winnica Mudstone Complex contain a very characteristic fossil assemblage, consisting of lingulids, leperditiid ostracods, gastropods, eurypterids, bivalves, fragments of agnathids and rich plant debris (Kozłowski

2000). Together with lithology, there are strong similarities to the British Downtonian, which was deposited in a shallow-water environment (see Antia 1980; Allen 1974; Calef and Hancock 1979). The carbonate layers reveal fauna characteristic for more distal parts of the shelf (i.e., brachiopods, crinoids, trilobites, rugose corals, tabulates, numerous stromatoporoids). Excluding stromatoporoids and tabulates, the fauna is strongly crushed, which might suggest the allochthonous character of most of the bioclasts. According to Kozłowski (2000), both the clastic and carbonate deposits represent back-barrier, periodically brackish environments.

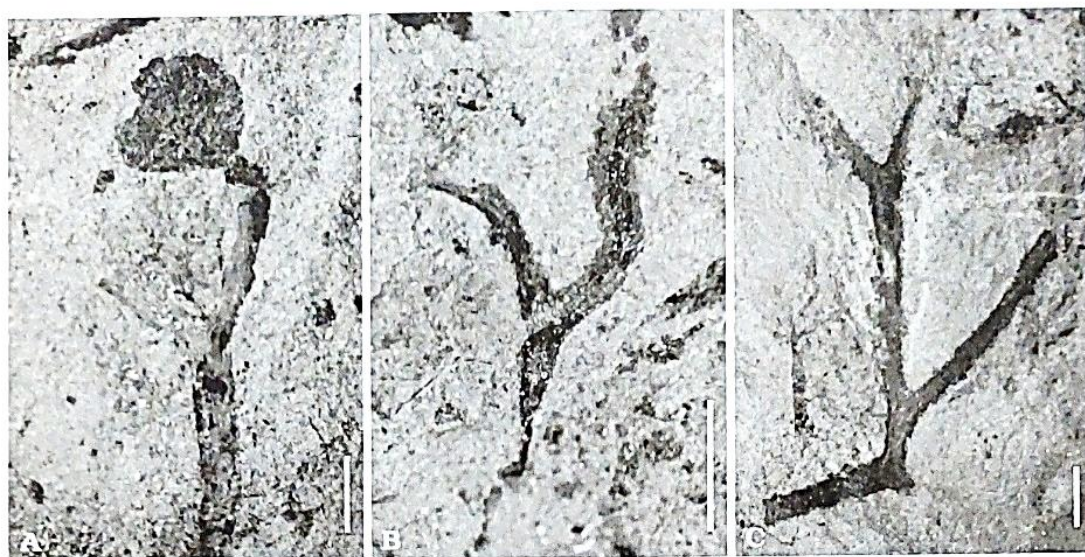


Fig. 2. Examples of land plant fossils from the Winnica section. A. *Cooksonia* sp. (IGUAM-0460-01) with preserved sporangium. B. Problematical form (IGUAM-0460-02) showing atypical shape of axes. C. Problematical form (IGUAM-0460-03) showing considerably different types of branching in its lower part. Scale bars 1 mm.

Description of fossil flora

Fossil plants occur in greatest number in fine-laminated mudstones and siltstones, whereas they are almost absent from shales and limestones. Usually, they are preserved as coalified compressions of highly fragmented axes and isolated sporangia, forming accumulations of plant debris at the top of laminae. Impressions also occur, and these are commonly covered by a thin film of iron or manganese oxides. Secondary mineralization by those oxides also caused the apparent irregularity of axes of some specimens (Fig. 2B, C). Collected material contains about 180 samples. Among these samples, there are only 20 larger specimens that are complete enough to enable an evaluation of the morphology and systematics. One of these is a specimen of the genus *Cooksonia*, which has been found together with some *Cooksonia*-like and problematical forms.

The specimen of *Cooksonia* sp. is shown in Fig. 2A. This is a branched, leafless axis terminated with sporangium. The total length of the specimen is 6.6 mm. The width of its main axis is 0.55 mm, and this increases slightly at the point of branching. Above the bifurcation, the width of axes is about 0.4 mm, and the angle between them is about 70°. The sporangium is oval, its height is somewhat less than its width (1.65 mm and 1.98 mm respectively). The axis terminating in the sporangium is broken, therefore, its orientation is probably not natural. Consequently, both the shape and dimensions of the sporangium could have been altered somewhat during fossilization. Nevertheless, all the features described above conform with the original definition of the genus *Cooksonia* given by Lang (1937) and with

other more recent descriptions (e.g., Edwards 1979; Edwards and Rogerson 1979).

Most of the other relatively well preserved specimens show morphological features, which may correspond to the genus *Cooksonia* but none of these bears sporangia. Such sterile axes are conventionally named *Hostinella* (e.g., Edwards et al. 2001). These specimens have slender, naked and bifurcated axes, sometimes with two orders of branching. Their height varies from 3.6 to 8 mm, width of the main axis varies from 0.22 to 1.55 mm, and width of secondary axes is around 0.1 mm. The considerable differences in size range could reflect the ontogenetic stage of a given specimen as well as depend on the order of branching, however, at present, collected material does not permit to solve this problem.

Problematical forms differ from the specimens described above in considerably lower angle of branching (about 40°), unusual shape of axes which is unknown in *Cooksonia* (Fig. 2B), or in considerably different types of branching (Fig. 2C), which can be referred to some problematical *Hostinella* forms described from the Silurian of Bolivia (Edwards et al. 2001). At present, it is not possible to say whether these represent original morphological features of the plants or come from post-mortem alteration of plant remains.

Conclusions

- Upper Silurian sediments from the Holy Cross Mts (Poland) contain *Cooksonia*-like fossils. The range of morphological variation, as well as their mass occurrence, augurs well for

further studies which may bring new data about the oldest vascular plants.

- The Winnica Mudstone Complex was deposited at the Ludlow/Pridoli boundary, the evidence of which is based on a trilobite and ostracode fauna. The age of the plant remains falls within the well-known stratigraphic range of the genus *Cooksonia*.
- The flora-bearing beds represent a marine, near-shore environment, and this is typical for other *Cooksonia* assemblages of Late Silurian age.
- Most probably, the plant remains come from islands which surrounded the sedimentary basin of the Holy Cross Mts. from its south-western margin in the Late Silurian times. Further studies should give a better understanding of the Silurian palaeogeography of Europe, and provide a better explanation of the relationships between Silurian land plants coming from isolated localities.

Acknowledgments.—We are indebted to Prof. Dianne Edwards (Cardiff University), Dr. Paul Kenrick (Natural History Museum, London) for critical reviewing the manuscript and comments, and to Dr. Danuta Zdebska (Jagiellonian University, Kraków) for helpful discussions.

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