DISPERSED CUTICLES

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MANY people have some line of work they make specially their own as I have done with cuticle fragments.

I remember how I started. During the first weeks of my first palaeobotanical work — on the Rhaeto-Liassic of Greenland — I had a poorly preserved leaf which I could not remove from the rock to prepare the cuticle. Instead of removing it properly with hydrofluoric acid, I lazily put the whole lump of rock in the macerating mixture of nitric acid and chlorate. After the usual time I put it in alkali, I forget whether I obtained the cuticle I wanted but I certainly got a whole lot of unexpected ones from the interior of the rock including some entrancing little seeds (*Amphorispermum*) of entirely novel aspect. And so after this I macerated every fragment of unwanted shale and as a result added materially to my flora. Since I usually macerated my rock in glazed earthenware jars holding about a kilogram I called the procedure ' bulk maceration'.

Later I went to Greenland and collected much larger samples of the same rocks and also sacks full of coal and micaceous shales with plant fragments which I thought might yield useful cuticles, as well as surplus rock from the better plant beds. I certainly increased the length of my papers and I may have doubled the time I took to write them (for work with dispersed cuticles is slow) but I thought it worth while. Later still in my work on the Yorkshire Jurassic I have collected systematically for preparations of dispersed cuticles from bulk macerations.

Although the Yorkshire Jurassic flora is famous, there are but few localities good enough to take a visitor to. Their number is about 14. We may add to these about fifty localities where some sort of determinable leaf is to be found but there is also a far larger number of shales which contain dispersed cuticles. I have macerated well over a thousand that seemed to me hopeful and of these 575 have until now yielded specifically determinable fragments. The number of localities yielding dispersed spores would indeed be even greater but I do not deal with spores here. After I had realized I had a useful method I found that others before me had obtained cuticles or megaspores by rather similar methods, so I claim no invention but merely that I did it independently. In fact no one before me had made much use of the cuticles obtained and I dare say I have macerated more rock than anyone else, for the dispersed-spore workers though they macerate numerous rock samples mostly use samples of only a few grams.

I will first describe the methods and then the useful results.

As a rule I collect a kilogram sample for a bulk-maceration, but occasionally much more. At first I used methods which gave cleanly macerated cuticles and indeed I described how I did it (HARRIS, 1926) but later I realized that my aim should be to release plant fragments from the rock as little altered as possible, that is in large pieces and chemically unchanged. However useful a slide of a clean cuticle, may be the plant organ previously had more to show than the cuticle, and of course a cuticle can be prepared from it later. Thus with rocks that respond to mild methods I always now use such methods.

Three mild methods of maceration are: 1. To soak the dried rock in cold water. Surprisingly many rocks will swell up and disintergrate, like aspirin tablets. 2. Often a shale which is unaffected by water will slowly swell when soaked for a few weeks in hydrochloric acid and the acid does not affect the plant fossils. Of course if the rock is calcareous the effects of the acid are rapid. 3. Sometimes I have used hydrofluoric acid, which has no effect on the plants but dissolves nearly all rocks; however I seldom use it because it is expensive, corrosive and poisonous. Where I have used hydrochloric acid to cause the shale to swell, I wash away the acid with running water (a large flower pot under a tap serves well) and then soak it for a day in dilute sodium hydroxide when the swollen shale breaks into mud. Once distintegrated the plant fossils are gently washed onto coarse

or fine wire gauze strainers and allowed to dry.

These macerations are quicker when hot solutions are used but the plant fragments seem more broken and it is best to have a good many slow macerations proceeding together. I start with fairly large pieces of rock, each a hundred grams or more because breaking the rock breaks the plants and of course the rock should be collected from as deep as possible; even so macerations will often yield Recent roots, small insects that lurked in the crevices and what is worse, rotted fragments from the local vegetation. One gets to know these, but the less there are of these contaminants the better.

Many rocks are not attacked by hydrochloric acid within a reasonable period, perhaps because they are largely organic like coals and oxidative maceration is needded. Again I find slow maceration is best. I add a little commercial nitric acid to the rock (but no chlorate) and leave it a few hours, this is because the reaction may be immediate and violent. If it is violent I eventually add diluted nitric acid, but if the reaction is slow I just fill the jar up with the strong acid and leave it until the rock has swollen noticeably. This usually happens in one or two weeks. Then I wash away the acid and extract with alkali and strain off the plant fragments as before, but this time they are cuticles and must be kept and examined wet.

Nitric acid does damage and eventually destroy cuticles and more especially the walls of Lycopod megaspores but by the time the acid has penetrated into lumps of coaly rock much of its strength is spent. I use an excess of rock so that the middles of some of the lumps are unaffected, and thus cuticles of different specimens are in various states, some badly damaged, some perfectly macerated and some under macerated. This sounds inefficient but rock is plentiful as a rule and the acid is cheap, only time is precious and it seems better to select the best from a lot of crudely macerated rock than to work meticulously and precisely with a little. Sometimes material is precious and then one must continually test the material as maceration proceeds.

Since the interior substance of leaf fragments will have dissolved nothing remain to hold the upper and lower cuticles together unless the margin is present. In the same way the various cuticles of a seed are apt to come apart. This is regrettable but where oxidative maceration is necessary, the specimens though imperfect are the best one can have.

Whether the maceration is by mild methods or by oxidation with strong acids one does not in fact obtain every plant organ, but only ones sufficiently robust to cohere when unsupported. In general this means organs with well developed cuticles for the cuticle is what gives most fossils their strength. Fern leaves are scarcely cutinized and break up into fragments no bigger than pollen grains and so do Selaginella-like leaves and so do Bryophytes. (Such generalizations are not safe, for Walton obtained coherent liverworts by macerating a shale with hydrofluoric acid). Equisetum stems have often cuticles strong enough to hold pieces a few square mm. together. Even Gymnosperms with delicate cuticles, like the conifer *Elatides williamsoni* break up into pieces too small to be much use. I should also mention Lycopod megaspores which are retained on the finer strainers, and I may add that though these have robust cuticles, they may be rather quickly altered by nitric acid followed by alkali, so much so that they change their 'genus'. The milder methods of maceration are preferable, if possible.

Another class of material that survives on the strainers is fusainized wood, and this is specially abundant when nitric acid and alkali have been used because all the wood preserved as a bituminous coal then disappears. I am sure it represents true charcoal, produced in forest fire, it is in small angular pieces and has the properties of charcoal. Very few have paid attention to it and ordinarily it is a nuisance for it has the same density as spores and cuticles and conceals them when the concentrate is searched. It can however be made to reveal fine structure by sufficiently long maceration with nitric acid and chlorate — up to two months if necessary — and I once made much use of it in investigating the conifer *Cheirolepis*. Where there is fusain formed from wood there may be other plant organs preserved in exactly the same way though I do not know whether the word "fusain" is correctly applied to charred Equisetum stems, conifer male cones and the like. However, once charred by fire any plant organ may survive the maceration of the rock, even fern leaves, and suitable

oxidative maceration afterwards will reveal every cell of which they are composed in the minutest detail.

Now I will consider the useful results of maceration of rock in bulk. It yields all the cuticles the rock contains, not merely what happens to be exposed on broken surfaces and it yields small fossils, little seeds and the like which are ordinarily overlooked. Of course such specimens are only of value where they can be determined and I will admit that very many plant fragments defy determination — though occasionally I may learn to recognize them after all.

With a rich bed containing excellent fossils, maceration in bulk of spare shale will add a surprising number of species to its flora. And of course with rocks that show no determinable leaf, cutile fragments may give all the information about its macroscopic flora.

Such determinable fragments may have either Geological or Botanical values: I will take Geological first. Plant beds often have an enormous number of specimens of one or two species and this individual peculiarity makes their zonation difficult. At one time, such beds were indeed themselves called ' zones ' but I am sure they are purely local. When their rock is macerated in bulk, in addition to the cuticles of the main species one does find fragments of a dozen or more others, and these may be good zone fossils (as for example *Lepidopteris ottonis*). I find it hard to imagine that I could have reduced the thirty rich plant beds of the Greenland Rhaeto-Liassic with their very individual floras to just two plant zones without the information given by macerations of rock in bulk. This information assisted me also very greatly when I tried to correlate the Greenland beds with those of Sweden.

In my recent work on the Yorkshire Middle Jurassic flora bulk macerations have certainly demonstrated the essential unity of the whole flora. There are indeed four stages separated and dated by marine layers but the main changes in flora seem to be mainly fluctuations in relative abundance; a species is at first found in a large fraction of the available localities; then in a small fraction and then in a large fraction again. Seward's statement that the flora is very uniform from top to bottom has been remarkably confirmed, though there are a few species with limited ranges.

Macerations in bulk from numerous localities sometimes gives information about the environment in which plants grew, a subject on the border of Botany and Geology.

The Yorkshire Middle Jurassic plant-bearing rocks were deposited by fresh water in a large delta which rests on marine Liassic rock. The transition is abrupt and usually marked by a certain amount of erosion and the flora of the basal fresh water beds is usually just like what occurs rather higher up. But in twenty five localities the basal beds have a peculiar flora dominated by the leaf described by Thomas & Bose as *Pachydermophyllum papillosum* (I have placed it in the old genus *Pachypteris*). Along with *P. papillosa* there may be any of the numerous species found in the lower part of the Deltaic series, but always with this peculiarity that *P. papillosa* is the commonest species. The remaining 213 plant bearing localities of the Lower Deltaic have no *P. papillosa* at all, and this statement is unusually reliable as a fragment of its cuticle is exceptionally easy to recognize in a bulk maceration. A peculiarity of its distribution is thus that it is dominant or it is absent.

Along with *P. papillosa* there are usually some specimens of the conifer *Brachyphyllum expansum*; *B. expansum* is not found separately. Also in most of these twenty five localities are marine microfossils, hystrichospheres and *Tasmanites* and these have not been found in the ordinary plant bearing rocks. (The localities in which they were not found were unsuitable for the study of microfossils). If this relation were merely for a few localities it would still be suggestive but for a considerable number it cannot be dismissed as a coincidence. It must have a cause. I suggest that *P. papillosa* grew, like a mangrove, on the tidal reaches of a delta and here it was dominant and accompanied by *Brachyphyllum expansum*. The marine microfossils were washed in from the sea and the ordinary plant fossils were carried down by the flowing river where they lived above the range of sea water.

There is another peculiar flora in the Yorkshire delta where bulk macerations have contributed evidence. After one of the major marine incursions over the delta the rivers at first deposited a great thickness of sand which is in general barren. But at a few places there are micaceous shales full of cuticle fragments, many of them naturally macerated and even with the upper and

lower sides separated. Instead of the usual preponderance of Equisetales and Bennettitales there are very numerous Conifers, Araucarians, Taxaceae and others described by Florin in his recent memoir on the Jurassic Conifers. At later stages such floras are not seen, but the normal mixture of the period. A suggestion made to me by Dr Chaloner is that the transgressive sea drowned the whole delta and destroyed its flora, so that when plants are seen they are mainly ones from the higher reaches of the rivers. Ordinarily this element of the flora is concealed by the overwhelming abundance of the species which grew in the delta itself, on the mud flats or on river banks.

I suppose it would have been possible, with nearly 600 localities to work out correlations between the occurrences of species and so to get information about plant associations. Unfortunately perhaps I kept no complete records, and the work would be very laborious, more suitable for a computor than for ordinary inspection.

Botanical progress consists chiefly in building up something approaching a complete plant from the scattered organs that are what are ordinary fossil species. In the main this must be done by the study of good specimens. For example Thomas established his Caytonia (known from the leaf, microsporophyll and megasporophyll) on good specimens (the stem came later) and he could scarcely have done his work without good specimens. But once you know the organization of, say, the megasporophyll you can use fragments for further study, and the maceration in bulk of a kilo of a suitable part of the Gristhorpe Bed (the original source of Caytonia) may provide a hundred detached Caytonia fruits and a thousand or more isolated seeds; so number of specimens ceases to limit study and you need not hesitate to sacrifice dozens in trying different methods.

I will end by describing some recent work on *Pachypteris papillosa*, a species I mentioned earlier. Along with the leaves one finds peculiar succulent stems, and Thomas had known about them for a long time though he had not described them. Reproductive organs were unknown. However, Thomas did collect some strange microsporophylls (*Pteroma*) from one of the localities and these I studied after his death. I was able to show that their cuticles were rather like the leaves but the evidence was not impressive, and as I said there was merely association in the one locality. However, the microsporophyll contains very characteristic pollen (like that of the Gondwana-Land *Pteruchus*). I searched the 25 localities where *P. papillosa* occurs as good specimens or as bulk maceration fragments. In all that yielded microfossils I found this pollen; sometimes there was so little pollen of any kind I had to concentrate from several hundred grams of rock but I found it. What is significant is that such pollen is scarcely ever found in the absence of *P. papillosa*, thus Couper who did not study any *P. papillosa* localities saw none in Yorkshire.

Again this association in numerous localities is too striking to dismiss, particularly when it reinforces agreement in structure.

I have selected *Pachypteris papillosa* as a rather elaborate case where evidence from bulk macerations has helped. As a rule the evidence is altogether simpler and no doubt more convincing but at the same time less interesting.

REFERENCE

HARRIS, T. M. (1926). Note on a new method for the investigation of fossil plants. *New Phytol.* **25** (1): 58.