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Giant ubisch bodies and other 'throwaway sporopollenin' as sources of information

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Passiflora incarnata L. produces relatively large 'opercula' that readily drop off the pollen exine in the course of preparation for microscopic study, leaving 'windows'. Presumably opercula also do this during germination and sedimentation under natural conditions. *Ipomoea alba* L. produces very large (200 μm) pollen grains. During the synthesis of the exines, giant (ca. 10 μm) ubisch bodies are generated, as well as equally large sculptural gemmae that are readily detachable and which simulate ubisch bodies in pollen preparations. They could be designated 'pseudo-ubisch bodies'. Both the opercula and the ubisch bodies are interesting in terms of 'throwaway' structures in nature, and the ubisch and pseudo-ubisch bodies offer potential for future study of the chemical and physical properties of relatively pure samples of sporopollenin. Similarly, excised elaters and sculptural elements of fossil pollen and spores offer a good source of pure fossilized sporopollenin for study by modern techniques requiring only very small samples.

SPOROPOLLENIN is a large molecule C-H-O compound of still uncertain exact structural composition. The empirical formula is approximately $\text{C}_{90}\text{H}_{142}\text{O}_{27}$, and the chemical robustness and general behaviour of the substance bespeak a similarity to rubber and to various terpenoid/carotenoid compounds (see discussion with references in ref. 1). The chemical sturdiness of this compound, plus the somewhat similar properties of chitin, account for the preservation since about 1×10^9 years of various categories of palynomorphs. It is probable that unrelated or remotely related organisms have adopted walls of sporopollenin as coatings for their cysts and spores for different reasons. Algal acritarchs of the Precambrian may have used sporopolleninous envelopes primarily for UV-shielding, whereas it is clear that for modern pollen grain exines

the structural strength, elasticity and to some extent, the waterproof nature of the compound, are primary reasons for its retention as part of the inventory of modern plants' manufacture—in other words, the employment of sporopollenin now has a primarily architectural 'rationale', as described by Payne².

Because of the near indestructibility of sporopollenin under non-oxidizing conditions, pollen exines comprise a larger fraction than might be expected of the organic contribution to the muds of the continental shelf, from which shales and sandstones of the geologic record are derived (see ref. 3). This sort of 'non-recyclable waste' is a blessing for science, as it has permitted the development of palynostratigraphy, as well as various sorts of pollen/spore-based palaeoecology. The present paper is a preliminary look at a peripheral aspect of the utilization of sporopollenin by plants—the 'deliberate' throwaway production of superfluous sporopollenin parts. This is an analogue to the fast-food styrofoam cups and dishes of modern human culture. On the whole, nature is a good recycler, but sporopollenin and chitin are big exceptions, and even *within* the production of spores and pollen, plants are somewhat profligate in the 'careless' disposal of sporopollenin.

Methods

This paper looks generally at 'throwaway' sporopollenin, with special reference to (i) 'opercula' of *Passiflora incarnata* L. (Passifloraceae) pollen, taken from a specimen in the herbarium of the Palynological Laboratories of the Pennsylvania State University (A. Traverse collection number 110; Harris County, Texas, USA, 24 May 1956; determined by L. H. Shinnars), and (ii) giant ubisch bodies and separated gemmae (= 'pseu-

do ubisch bodies' removed from a specimen of *Ipomoea alba* L. (Convolvulaceae), same herbarium (A. Traverse collection number 637; Monroe Co., Florida, USA, 25 April 1958; determined by L. H. Shinnars as *Calonyction aculeatum* (L.) House, a synonym of *I. alba*).

Flowering material was processed by acetolysis and mounted in glycerine jelly, according to the methods described in ref. 1. Photomicrographs are by bright field, using polaroid 665 professional film.

Elaters and opercula

Elaters are strap-shaped exine attachments of certain spores and pollen, for example, of *Equisetum*. They are thought to function in spore dispersal but are rather narrowly attached, are found loose in reference preparations of horsetail spores, and presumably could occur in sediments containing *Equisetum*. Elaters are common in various taxa of pollen of the Lower Cretaceous ASA (Africa–South America) Province: *Sofrepites*, *Elateroplicites*, etc. I have not studied preparations of samples of this provenance, but I am confident that loose elaters occur in them (cf. Plate X in ref. 4).

Opercula of dinoflagellate cysts consist of the plates that are dropped from the cyst, leaving a hole or archeopyle, when the organism excysts. In some marine samples I have studied, the characteristic plate arrangement of these separated opercula provided the initial clue that the rather 'bag-like' and often very much folded-up cysts from which they came are dinocysts and not inaperturate pollen.

In a few angiosperms, 'windows' or fenestrae are formed. These very large holes may involve, or be in addition to, the normal germinal apparatus consisting of colpi and/or pores. Presumably the windows become relatively enormous germinal apertures, in some instances leaving the ordinary colpi and/or pores that were also present as vestigial structures. In *Passiflora incarnata*, the opercula that fall out of the windows (Figure 1, *e,f*) look themselves at first glance like inaperturate pollen grains, and one thinks when casually examining reference slides that one is seeing dimorphic pollen, with pollen in two size ranges. Then one notes that some of the windows have opercula in the process of falling out (Figure 1, *a,c*). In my preparation the grains have 6–7 windows. In each grain two of the windows seem to be in polar positions (see Figure 1, *a,c,d*), and there are either 4 or 5 windows on the sides of the grain. *Passiflora pinnatistipula* Cav. is described and illustrated by Heusser⁵ as having a similar structure, but with only three windows and three opercula. (Heusser also calls them 'lids' and 'plates'.) Heusser interprets each operculum as resulting from a single syncolpate colpus. Ikuse⁶ illustrates *Passiflora racemosa* by line drawings. It resembles *P. pinnatistipula* very

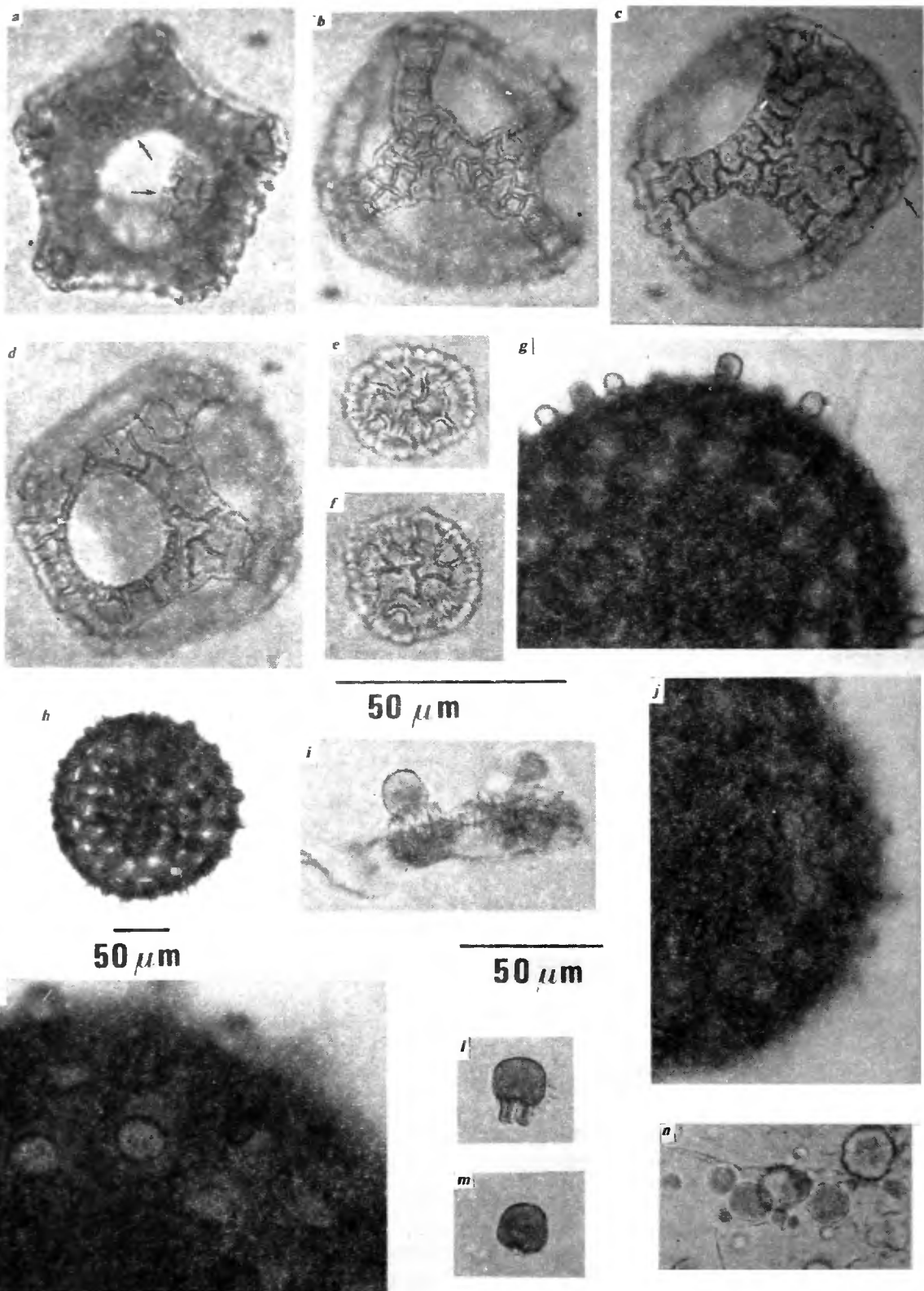
closely. But Ikuse shows no excised opercula or windows, although circular sutures are shown, and the grain presumably would behave in the same manner as *P. pinnatistipula* and *P. incarnata*. Larson⁷ describes *Passiflora caerulea* pollen as 3-colpate and states that it has furrow-enclosed areas that break free. Some species of *Passiflora* have quite 'normal' periporate, stephanocolpate or stephanocolporoidate morphology without opercula, as seen in the illustrations of *P. caerulea* L., *P. holosericea* L. and *P. suberosa* L. in Huang⁸, and of *P. maculiflora* in Erdtman⁹. In Erdtman's illustration there are islands of exine that one can easily imagine as 'excisable' opercula. *P. lutea* in my own collection is stephanocolporoidate, with features similar to those of *P. maculiflora* as illustrated by Erdtman. It seems to me that, at least in *P. incarnata*, the 'opercula' have nothing to do with normal colpi, particularly in view of the 'polar' windows!

Regardless of how the 'plates', 'lids', or 'opercula' of *Passiflora* are interpreted morphologically, there is no question that they represent disposable chunks of sporopollenin produced at energy-cost to the plant and seemingly not conferring a commensurate benefit on the manufacturer, unless it turns out that, for example, a pollinating animal seeks to collect them. It is also interesting to contemplate how opercula such as those of *Passiflora* would be interpreted if they occurred as fossil palynomorphs. Unlike, for example, excised sacci of saccate pollen, opercula do not necessarily display any signs of being part of something else.

Ubisch bodies (= orbicules), giant ubisch bodies, and disposable sculptural elements (= 'pseudo-ubisch bodies')

The sporopolleninous exine of embryophyte spores and pollen is manufactured from the tapetum and is applied externally as a final act in the production of the outside of mature grains. In the process, sporopollenin is sometimes left over and can often be seen in preparations of some pollen, for example, of *Ipomoea* (Figure 1, *g–n*). These globules are called ubisch bodies or orbicules (see discussion with references in ref. 1: p. 92 and glossary). Ubisch bodies occur commonly as palynological fossils, even from rocks as old as Palaeozoic.

Ipomoea produces extremely large pollen grains, easily visible to the naked eye. *I. alba*, studied here, has grains around 200 µm in diameter. They are periporate with scabrate pore membranes and general sculpture consisting of relatively small scabrae and verrucae, and enormous gemmae. Giant ubisch bodies of *I. alba* are up to 10 µm in diameter, as large as some whole angiosperm pollen! In addition, the gemmae which comprise the larger positive sculptural elements are rather loosely



rooted' by columellae in the ectexine (Figure 1, *i*) and are easily 'uprooted' during processing. This is evident in gemmae with multiple 'roots' such as the one illustrated in Figure 1, *l*, but can be observed even in gemmae such as illustrated in Figure 1, *m*, in which the columellae-'roots' have been torn from the gemmae (or vice versa). Surely such gemmae could occur as fossils and would be interpreted as orbicules.

Research possibilities with giant ubisch bodies, excised giant sculptural elements, and elaters

Passiflora-type opercula are probably just an interesting palynological curiosity, but the structures derived from *Ipomoea*, and similar sorts of particles, offer some exciting possibilities for research.

For several decades various researchers have attempted to characterize sporopollenin chemically. As yet, the problem is still not completely solved. The very toughness of sporopollenin contributes to the difficulty. Because of its recalcitrance, investigators have been compelled to study the synthetic pathways of sporopollenin in anthers, or to investigate the chemical structure by selective destruction of sporopollenin. Even the latter approach has been further handicapped by the fact that exines employ sporopollenin as a structural compound thrown up into struts, laminations, cellularizations², the interstices of which are filled and plastered with many other compounds. Preparation of pure samples of sporopollenin is therefore very difficult. Giant ubisch bodies and detached very large sculptural elements, such as the gemmae of *Ipomoea*, or the huge echinae of *Hibiscus* (which are also known to shed freely), offer an excellent opportunity for preparation of practically pure samples of sporopollenin which can be investigated by modern chemical techniques that employ very tiny samples. Elaters and large sculptural elements removed from fossil spores will also make it possible to compare data from modern sporopollenin with those of fossilized sporopollenin. Such studies are underway in our laboratory.

Summary and discussion

Sporopollenin and chitin, which provide the structural basis for the walls of most palynomorphs, are significant exceptions to the efficiency of the organic cycle. Because of the almost indestructible nature of sporopollenin, pollen and spore exines are recoverable from most non-oxidized, non-metamorphosed, non-calcareous sedimentary rock deposited since mid-Palaeozoic. Sporopollenin is a 'throwaway', non-recyclable compound, but its energy cost is repaid by reproductive advantage. Spores and pollen also produce, however, apparently unnecessary sporopollenin in the form of unneeded, detachable opercula and ubisch bodies, which are manufactured at energy-cost and yet serve no evident function in spore architecture or even, for example, as an animal pollination-reward. Ubisch bodies, which are chunks of pure sporopollenin, offer a marvellous opportunity to investigate the chemical and physical properties of the substance, a still vexing and unresolved problem of palynology. Pieces of elaters and detached sculptural elements from both living and fossil plants will prove an important control on ubisch body sporopollenin chemistry.

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Figure 1. *a-f*. Pollen of *Passiflora incarnata* L. *a*, Polar view of grain with seven windows, two at poles and five around the sides. Two excised opercula are shown sticking to the grain (arrows). *b, d*, Different views of grains with six windows, two at poles and four around the sides. *c*, Side view of '7-holer' (as in *a*), with a window at each pole and five windows around the sides. An excised operculum (arrow) is still clinging to the grain. *e, f*, Excised opercula showing their reticulate sculpture and columellae within the muri. *g-n*. Pollen of *Ipomoea alba* L. *g, h, j, k*, Views of pollen grain at increasing levels of magnification, showing the periporate morphological type, gemmate (close to baculate) and scabrate/verrucate sculpture, and scabrate pore membranes. *l*, Pieces of broken exine provide accidental 'sections' such as this one demonstrating the 'rooting' of gemmae in the ectexine. *l*, Gemma with two columellate 'roots'. *m*, Gemma with 'roots' broken off near their top. *n*, Ubisch bodies on a piece of cellulosic floral tissue. Scattered ubisch bodies and broken-off gemmae are present throughout the preparation and are the same density and colour as attached gemmae. The scale for *h* is indicated by the bar directly under it. The scale for *g* and *j* is indicated by the bar under *l*. The scale for all other photomicrographs (*a-f*; *i*; *k-n*) is shown under *l*.