

ON THE TERMINOLOGY, ORIGINS AND FUNCTIONS OF CAVEATE POLLEN IN COMPOSITAE

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ABSTRACT

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The terminology applied to caveate pollen in the Compositae is reviewed. The term cavea (plural: caveae) is recommended in preference to cavus, the plural of which should be cavi although this has not been used in the literature. Caveae are interpreted as being potentially present in all Compositae since all the members of the family studied possess them during their early developmental stages. In some taxa the caveae are well developed in the mature pollen and function primarily as harmomegathia whilst in others the caveae are obscured by the later development of columellae which limit or prevent the harmomegathic function.

INTRODUCTION

In pollen grains of many members of the Compositae a cavity is present between the sexine and nexine. Such features were first given the name cavea (plural: caveae) by Iversen and Troels-Smith (1950) who proposed the term cavea with the definition "Hohlraum in der Exine, durch Ablösung der Ektexine von der Endexine entstanden". In fact, since a foot layer (or nexine 1) is present in Compositae pollen, such cavities actually occur within the ektexine, or in the alternative system, between the sexine and nexine. Later Wagenitz (1955) and Stix (1960) used "Hohlraum", the German word for cavity or hole, for the same feature, without providing a definition for the term.

Skvarla and Larson (1965, p.221) modified the terminology of Iversen and Troels-Smith giving the definition, "Openings within the exine where the columellae have separated from the foot layer are termed caveae; where the caveae are highly developed, the pollen grains are said to be vesiculate". These authors pointed out that vesiculate pollen in this sense was referred to as saccate by Erdtman (1947) and had earlier been described as bladdered by Wodehouse (1935). Skvarla and Turner (1966, p.227) expanded upon

the earlier definition using a different singular form, *cavus*, and discussed ways in which the development of such separations might occur. This maintained the essentially ontogenetic basis for the terms which Iversen and Troels-Smith had adopted. The singular form *cavus* was subsequently employed in many studies of *Compositae* pollen (e.g., Tomb, 1975; Nordenstam and El-Ghazaly, 1977; Blackmore, 1982). Skvarla et al. (1977, p.147) later employed the form *caveate* to describe exines possessing *caveae*. These authors restricted the use of the term *caveae* to cavities in which the sexine fuses with the nexine only at the colpus margins. Where there are some columellae traversing the cavities the term *cavus*-like space was used and this was adopted elsewhere where such a distinction was to be made (e.g., Blackmore, 1981).

A simple, unconfused morphological definition has not hitherto been available for the term *cavea*, neither have the origins of such features and their functions been fully explored. The present paper discusses and revises the terminology and presents a review of the origins and functions of *caveae*.

TERMINOLOGY

The terminology of *caveate* exines is confused by the existence of two singular forms of the noun and by the frequent misuse of plural or adjectival forms in the literature. The term *cavus* was originally used (Faegri and Iversen, 1950; Kremp, 1968) to refer, in gymnosperm pollen, to what would now usually be known as a *saccus*. It is a latin word, meaning a cavity, and as such the plural form should be *cavi* and the adjective *cavate*. Faegri and Iversen (1950) used the incorrect plural form with the correct adjectival form whereas Skvarla et al. (1977) used *cavea* incorrectly as a plural and *caveate* not *cavate* as an adjective. Horner and Pearson (1978) described a *cavus* 1 and a *cavus* 2 in the exine of *Helianthus annuus*. Of these *cavus* 1 refers to what may alternatively be known as the columellar interstices and *cavus* 2 to a *cavea* in the usual sense. It is clear that the term *cavus* (plural: *cavi*, adjective: *cavate*) may cause confusion and its use should be rejected.

The term *cavea*, with the plural *caveae* and adjective *caveate*, has more consistently been correctly applied, is linguistically preferable and should be adopted.

It is sometimes useful to use the term *acaveate*, signifying pollen without *caveae*, to facilitate comparisons between pollen grains.

ONTOGENY AND EVOLUTION

As mentioned in the introduction Iversen and Troels-Smith (1950) suggested that *caveae* originate by splitting of the *ektexine* from the *endexine*. This idea was enlarged upon by Skvarla and Turner (1966) who suggested three possible origins for the sexine layer bounding the *cavea*, the "stutzmembran" of Stix (1960). The *stutzmembran*, they argued, could be considered either as part of the foot layer which became detached during the

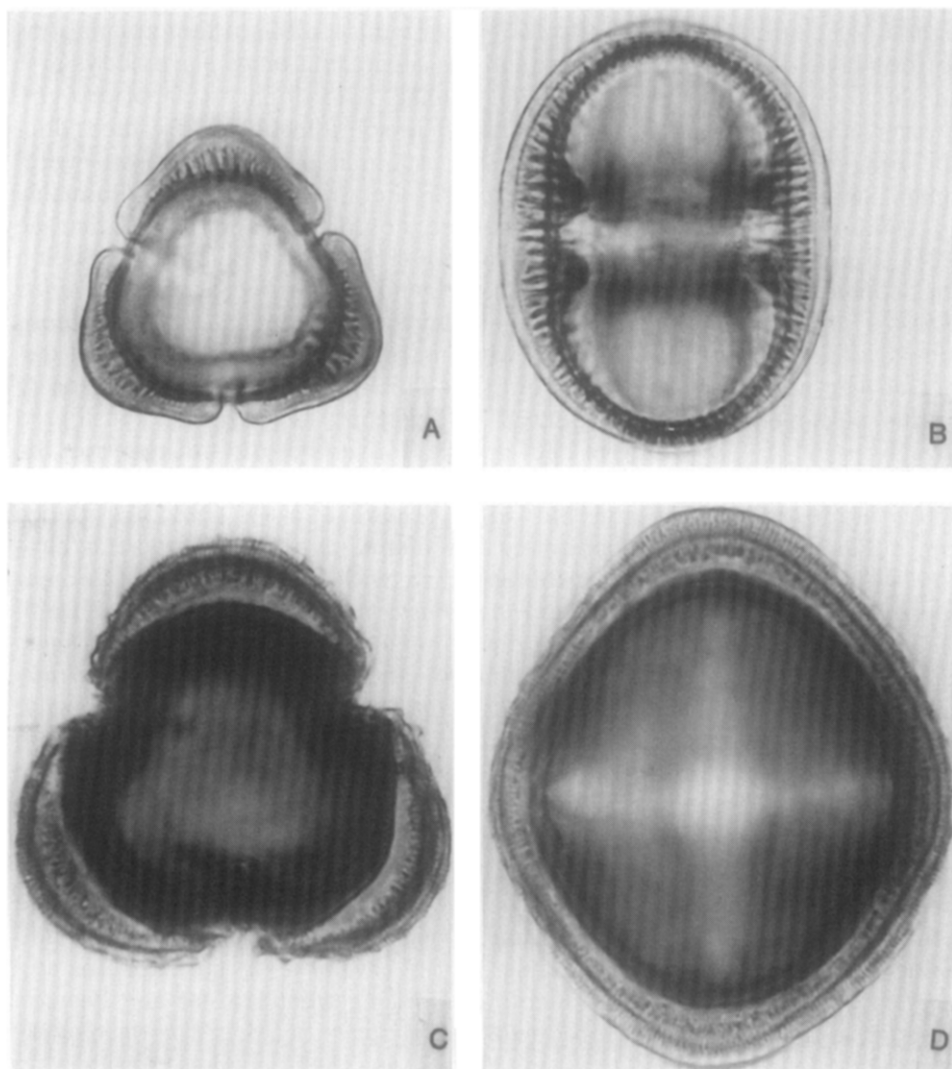
ontogeny of the cavea, as a second stratum of the foot layer or as an inherent part of the columellae. The first explanation suggests that caveae originate as a splitting within the foot layer whilst in the other explanations the foot layer would remain intact and the separation takes place between it and the free or fused bases of the columellae. Additional explanations are, however, also possible. Caveae might arise, in some instances, by the reduction and eventual loss of columellae. It is possible to envisage an evolutionary series of pollen grains starting with a complete layer of columellae and lacking caveae (acaveate) via reduced columellae and narrow caveae below to pollen grains with large caveae not traversed by columellae. Such a series appears to occur, for example, in the genus *Centaurea*, where *C. cyanus* possesses pollen grains with a complete layer of columellae, in *C. scabiosa* reduced columellae occur together with narrow caveae and in *C. jacea* distinct caveae are present (Plates I and II). This morphological series closely fits the phylogenetic series proposed by Wagenitz (1976) who considered acaveate pollen types primitive and caveate derived but did not mention the intermediate state.

It is interesting to consider the origin of caveae in the light of evidence from pollen ontogeny. Comparatively few members of the Compositae have been studied in this respect. Amongst taxa with acaveate pollen *Gerbera jamesonii* (Southworth, 1966) and *Artemisia vulgaris* (Rowley and Dahl, 1977) have been investigated. The development of caveate pollen has been studied in *Cosmos bipinnatus* (Dickinson and Potter, 1976), *Helianthus annuus* (Horner and Pearson, 1978), *Leontodon autumnalis* (El-Ghazaly, 1982), *Scorzonera hispanica* and *S. humilis* (Blackmore and Dickinson, in prep.). The latter three species, members of tribe Lactuceae, have very narrow caveae traversed in places by a few slender columellae.

In all cases the outer part of the sexine originates first in the form referred to by Rowley and Dahl (1977) and Rowley et al. (1981) as a prepectal mat. The nexine is subsequently deposited on white line centred lamellations and at this stage there is no direct continuity between the developing sexine and nexine except at the colpus margins. In the caveate exines of *Cosmos* and *Helianthus* microfibrillar components comprising what Horner and Pearson termed the spacer layer are produced in the space between the developing sexine and nexine at about this time. This space then becomes considerably enlarged, mainly as a consequence of the lateral growth of the prepectal mat. The ontogeny of acaveate pollen of *Artemisia* and *Gerbera* differs principally in that although the prepectal mat is at first isolated from the developing nexine by the microfibrillar spacer layer large columellae later develop within the separation and link the prepectal mat to the nexine. In pollen of *Leontodon* and *Scorzonera*, where the caveae are narrow, the ontogenetic processes are similar to those of acaveate pollen except that there are very few columellae formed which link the prepectal mat to the nexine. These columellae are often very fine strands of material and so are not always apparent in ultrathin sections.

Whilst these observations on pollen ontogeny in Compositae are based on

PLATE I



A. 1600 \times , *Centaurea cyanus*, polar view, acaveate.

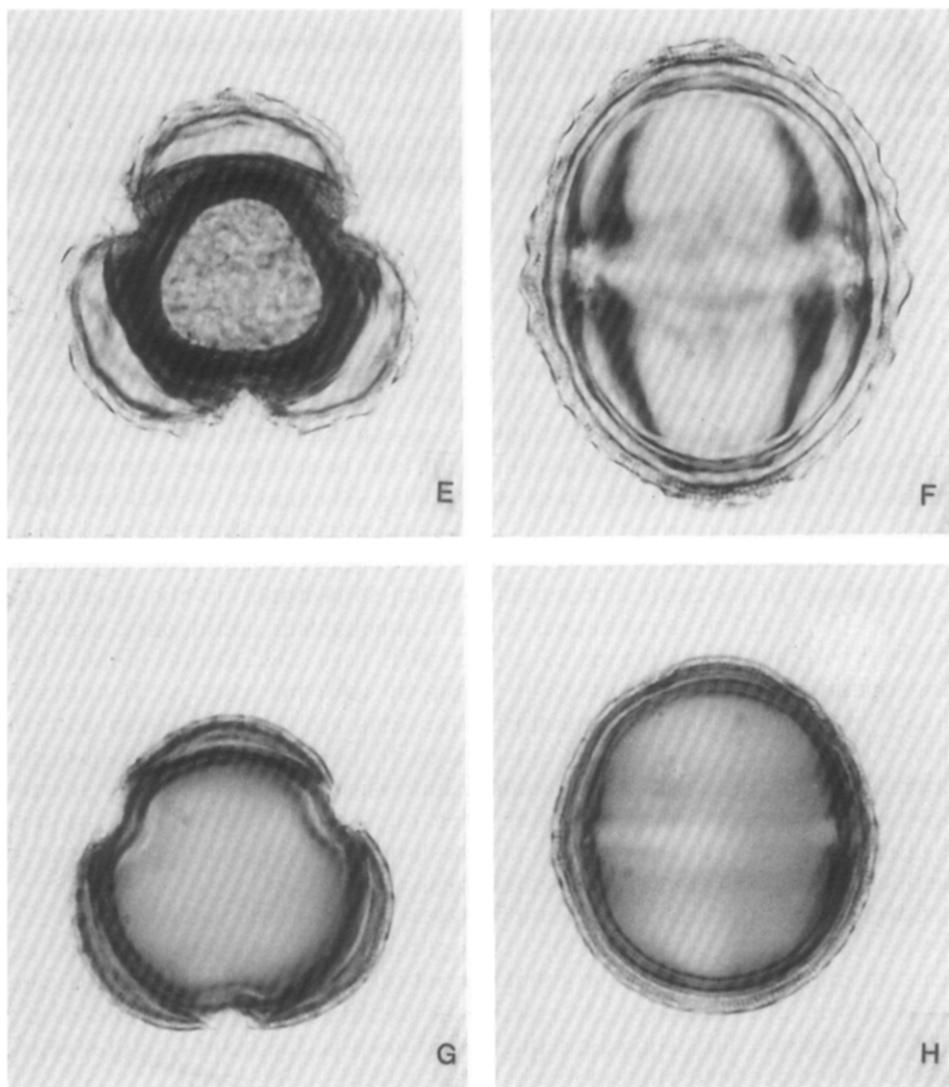
B. 1600 \times , *idem*, equatorial view.

C. 1600 \times , *Centaurea scabiosa*, polar view, caveate.

D. 1600 \times , *idem*, equatorial view.

only a small number of taxa one important generalisation may be made with reference to caveae. Namely that the spaces which may become caveae, and so could be called pre-caveae, are present in the early stages of all the taxa studied. These pre-caveae may subsequently be enlarged and become caveae or may be obscured by the development of columellae. In none of the taxa studied are the caveae formed by the physical separation of layers which were previously fused together or continuous.

PLATE II



- E. 1600 \times , *Centaurea nigra*, polar view, caveate.
 F. 1600 \times , idem, equatorial view.
 G. 1600 \times , *Centaurea pectinata*, polar view, slightly caveate.
 H. 1600 \times , idem, equatorial view.

Caveae could therefore be regarded as being potentially present in all Compositae exines. Selection in favour of the differing functional attributes of caveate and acaveate pollen has probably led, during the course of evolution, to the occurrence of both conditions and of intermediate forms. The functional attributes of caveate and acaveate pollen are discussed in the following section.

FUNCTION

In attempting to interpret the functions of caveae it must be borne in mind that the form of pollen reflects an interplay between a variety of functions, some of which may go unrecognised, and may also include non-functional elements. Here three main functions of caveae, as repositories for wall held substances, as dispersal mechanisms and as harmomegathia, are discussed.

Heslop-Harrison (1976) has pointed out the selective advantage offered by chambered exines in the storage of sporophytically derived substances which function both in recognition systems and as a waterproof layer (Heslop-Harrison, 1979). Observations of sectioned Compositae exines show that such substances are held not only on the pollen surface and in the columellar interstices but within the caveae, if present. One aspect of selection in favour of caveate pollen might simply be that it has a greater capacity for holding such substances. Caveae might also be interpreted as providing a means for actively releasing these substances. Blackmore (1982) in a functional interpretation of the pollen of tribe Lactuceae showed that demonstrable changes in volume of the caveae occur which might cause substances within them to be exuded when the pollen rehydrates on the stigma surface at the start of germination. Such a mechanism could only work effectively in caveate pollen or in pollen with very few, slender columellae. The operation of such a system is visible by light microscopy. If hydrated pollen grains from suitable undehiscent anthers are exposed to air and observed microscopically then air can be seen to be drawn into the columellar interstices and caveae as their volume increases. Conversely if dehydrated pollen is allowed to take up water on a microscope slide by placing it in a moisture-saturated atmosphere the wall-held substances can be seen to be released through the tectal perforations.

Several workers (Harrington and Metzger, 1963; Payne and Skvarla, 1970; Payne, 1972) have noted that in anemophilous *Ambrosia* species the caveae have an important function in the dispersal of the pollen by wind. Sufficient air is drawn into the caveae to reduce the density of the pollen and help it remain airborne. This shows a striking similarity to the main function attributed to the sacchi occurring on many gymnosperm pollen grains.

Anemophily is the exception rather than the rule in Compositae and the ability of the caveae to change volume has greater significance in harmomegathia than in pollen dispersal. Harmomegathia (Wodehouse, 1935) is the name given to the processes by which pollen grains respond to changes in the water availability of their environment. Usually it involves reversible changes in size or shape which cover or close the apertures and decrease the volume of the cytoplasm in a dry environment but enable the pollen grain to take up water again in a moist environment as, for example, at the onset of germination. The extent to which caveae are involved in harmomegathia depends upon their degree of development and the existence or otherwise of alternative methods of harmomegathia. Even the narrow caveae of lophate

pollen in tribe Lactuceae can contribute to harmomegathy (Blackmore, 1982).

In distinctly caveate exines the loss of liquid from the cytoplasm, which may begin before dehiscence of the anthers (Heslop-Harrison, 1979), causes a reduction in its volume. The relatively thin and flexible nexine adapts to the shape of the contracted cytoplasm but the more rigid sexine maintains its shape and the caveae increase in volume, taking in either substances from the anther locule before dehiscence or air after dehiscence. This has the effect of closing the colpi (Fig.1). Other modes of volume change involving caveae might occur, although these are less well documented. It is possible, for example, that the sporophytically derived liquids shown by Rowley et al. (1981) to be held in the caveae might themselves be capable of taking up or losing liquid depending upon the environment. This would bring about changes in volume of the caveae which would close or open the colpi (Fig.2). In such a mechanism the cytoplasm itself would change comparatively little in hydration or volume and the caveae would act as a buffer-zone between the external environment and the cytoplasm.

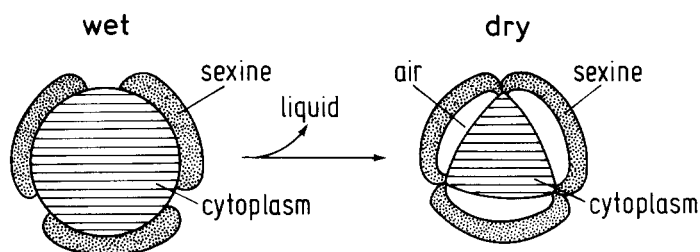
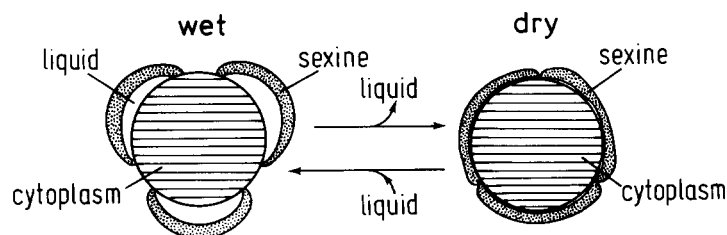


Fig.1. Mode of volume change by the loss of liquid from the cytoplasm.



In pollen grains with well developed caveae these features are interpreted as being of primary importance as harmomegathia although in some cases, for example in *Ambrosia* they have been further developed as aids in dispersal.

PROPOSED DEFINITION AND CONCLUSIONS

Cavea (plural: caveae): a cavity between the sexine and nexine which extends to the colpus margins where the sexine and nexine meet. Pollen grains with caveae are termed *caveate* whilst those lacking caveae may be described as *acaveate*.

This definition is based upon morphological features only in contrast to that of Iversen and Troels-Smith (1950) who included ontogenetic or phylogenetic concepts in their definition. Evidence from ontogenetic studies suggests that caveae are potentially present in the early stages of all pollen grains of Compositae. Caveae are highly developed in taxa where selection has favoured their role in harmomegathy, and sometimes in dispersal, rather than alternative harmomegathia. Pollen grains of such taxa are usually echinate, but not echinolophate, and their caveae are considered to have evolved by the suppression of the development of columellae in the spacer layer. Caveae are absent where selection has favoured more robust exine structures in which harmomegathy is accomplished by folding along colpi or by changes in thin walled regions, the lacunae of echinolophate pollen. In such pollen grains the development of columellae within the spacer layer has not been suppressed.

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