Basidiome polymorphism in *Volvariella bombycina*

SIU WAI CHIU AND DAVID MOORE

Microbiology Research Group, Department of Cell and Structural Biology, Stopford Building, The University, Manchester M13 9PT, U.K.

SHU TING CHANG

Department of Biology, The Chinese University of Hong Kong, Shatin, N.T., Hong Kong

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Developmental plasticity of fruiting morphogenesis in *Volvariella bombycina* is reported. In addition to the normal hemi-angiocarpous mode, fruit bodies developed either angiocarpously, with enclosed hymenium, or gymnocarpously, with exposed hymenium. In gymnocarpous fruit bodies the generic basal volva might be absent or abruptly bulbous in contrast to the normal membranous form. Fruit bodies, either solitary or in aggregates, could be sterile carpophoroids, gasteromycetoid forms, normal agaricoid forms, agaricoid forms with upturned/inverted pilei or supernumerary hymenia, or morchelloid forms. Heterogeneity in the hymenophore ranged from the sinuous, labyrinthiform hymenium resembling that of a *Morchella* or *Tremella* fruit body to the normal radial lamellae of a typical lamellate agaric. Some fruit body variants showed irregularities in the hymenium: spore tetrads enveloped in mucilage, occasional asynchrony of spore maturation, variation in number of spores borne by a basidium from 2 to 4, and variation in spore form from ovoid to cordate. This spontaneous basidiome polymorphism, observed in two independent strains in various media tested, is suggested to imply that an ontogenetic programme is a sequence of subroutines which can be modulated independently. Co-ordinated activation of the subroutines specifies the ontogeny and the architecture of a fruiting structure. Development plasticity may be a response to environmental stress and an expression of the invocation of these morphogenetic subroutines in the wrong sequence and/or in the wrong place.

Key words: *Volvariella bombycina*, Morphogenesis, Basidiome polymorphism, Environmental stress.

Volvariella bombycina (Schaeff.: Fr.) Sing., the silver-silk straw mushroom, in contrast to *V. volvacea* (Bull.: Fr.) Sing., fruits readily in culture (Flegler, 1981). It is an edible fungus (Zoberi, 1972; Dickinson & Lucas, 1979) with potential for commercial cultivation (Huang & Wu, 1982; Elliott & Challen, 1985). During fruiting trials of this fungus, an unexpectedly wide variation in forms of fruit bodies has been encountered. Similar flexibility in fruiting morphogenesis has been reported in other species, and may be a strategy for adaptation to environmental stress caused by a range of extrinsic factors.

Buller (1922) showed that infection of *Lactarius piperatus* (L.: Fr.) S. F. Gray by *Hypomyces lactifluorum* (Schwein.) Tul. caused the former to produce alamellate fruit bodies as a result of parasitism. In the case of the 'rose-comb' disease of the cultivated mushroom, *Agaricus bisporus* (J. Lange) Imbach, which is characterized by hypertrophied growths of hymenial surface all over the pileus, the cause seems to be mineral oil fumes in mushroom farms (Lambert, 1930; Flegg, 1983; Flegg & Wood, 1985). Additionally, many morphological mutants or variants have been induced or isolated from nature, especially in *Coprinus cinereus* (Schaeff.: Fr.) S. F. Gray and

Schizophyllum commune Fr. (Raper & Krongelb, 1958; Takemaru & Kamada, 1972; Kanda & Ishikawa, 1986).

In *V. bombycina*, we have found that two strains from different sources under various aseptic conditions produced different forms of fruit bodies simultaneously and spontaneously, suggesting that the cause was neither parasitism nor mutation. This sort of fruit body polymorphism, perhaps better described as developmental plasticity, has been reported in various fungal species (Buller, 1922, 1924; Keyworth, 1942; Singer, 1975), but thorough studies have only been done with *Psilocybe merdaria* (Fr.) Ricken (Watling, 1971; Reijnders, 1977) and *Agaricus bisporus* (Worsdell, 1915; Atkins, 1950; Reijnders, 1977; Flegg & Wood, 1985). In the latter, the following developmental variants have been reported: carpophoroids (sterile fruit bodies; Singer, 1975), forking (a single stipe bears two or more pilei; Atkins, 1950), called bichotomy by Worsdell (1915), proliferation (additional secondary pilei arise from pileal tissues; Worsdell, 1915), fasciation (a bundle of conjoined fruit bodies; Worsdell, 1915), and supernumerary hymenia (the fruit body has additional hymenia on the upper surface of the pileus; Langeron & Vanbreuseghem, 1965). All of these forms were observed in *V. bombycina* in the present

Fig. 1. Fruit bodies of *Volvariella bombycina* grown on a cotton-waste compost. The fruit bodies are of normal morphology, but show the phenomenon of fasciation (= aggregation); scale bar = 2 cm. **Fig. 2.** A collection of bisected fruit bodies illustrating the normal pathway of development.
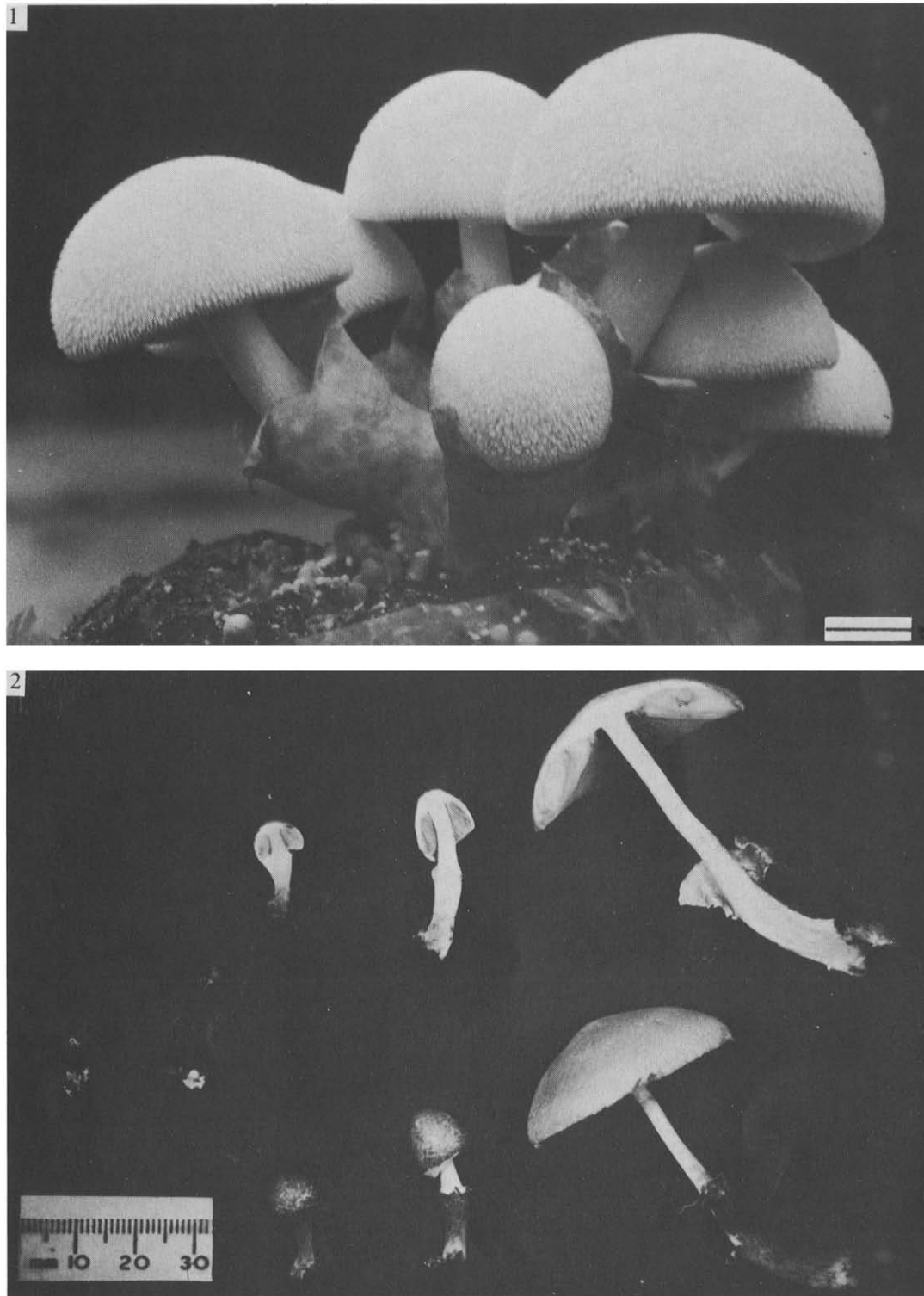

study. In *P. merdaria*, various teratological forms ranging from morchelloid, cyphelloid, pleurotoid and gasteromycetoid fruit bodies arose spontaneously with the normal agaricoid fruit bodies (Watling, 1971).

The range of 'abnormal' basidiome architecture observed may indicate lines of relationships between very disparate groups of fungi, and it certainly prompts theorizing about developmental mechanisms. Regardless of these interpretations, though, the function of the plasticity in fruiting morphogenesis can be seen to be to maximize spore production and favour the dispersal of spores even under environmental stress in *Volvariella bombycina*.

Fig. 3. An exposed fruit-body primordium of *Volvariella bombycina* initiating the abnormal gymnocarpous mode of development; scale bar = 1 mm. **Fig. 4.** Gymnocarpous fruit body with a thick crenate volva; scale bar = 2 mm. **Fig. 5.** Gymnocarpous fruit body with a grossly enlarged volva; scale bar = 2 mm. **Fig. 6.** Gymnocarpous fruit body without a volva; scale bar = 5 mm. **Fig. 7.** Two primordia, normal on the right but that on the left showing an exposed pileus through a hole in the volva; scale bar = 5 mm. **Fig. 8.** Fruit body with a smooth-lipped basal volva resulting from penetration of the pileus through a hole such as that shown in Fig. 7. Compare with the torn appearance of the normal volva in Fig. 1. Scale bar = 5 mm.
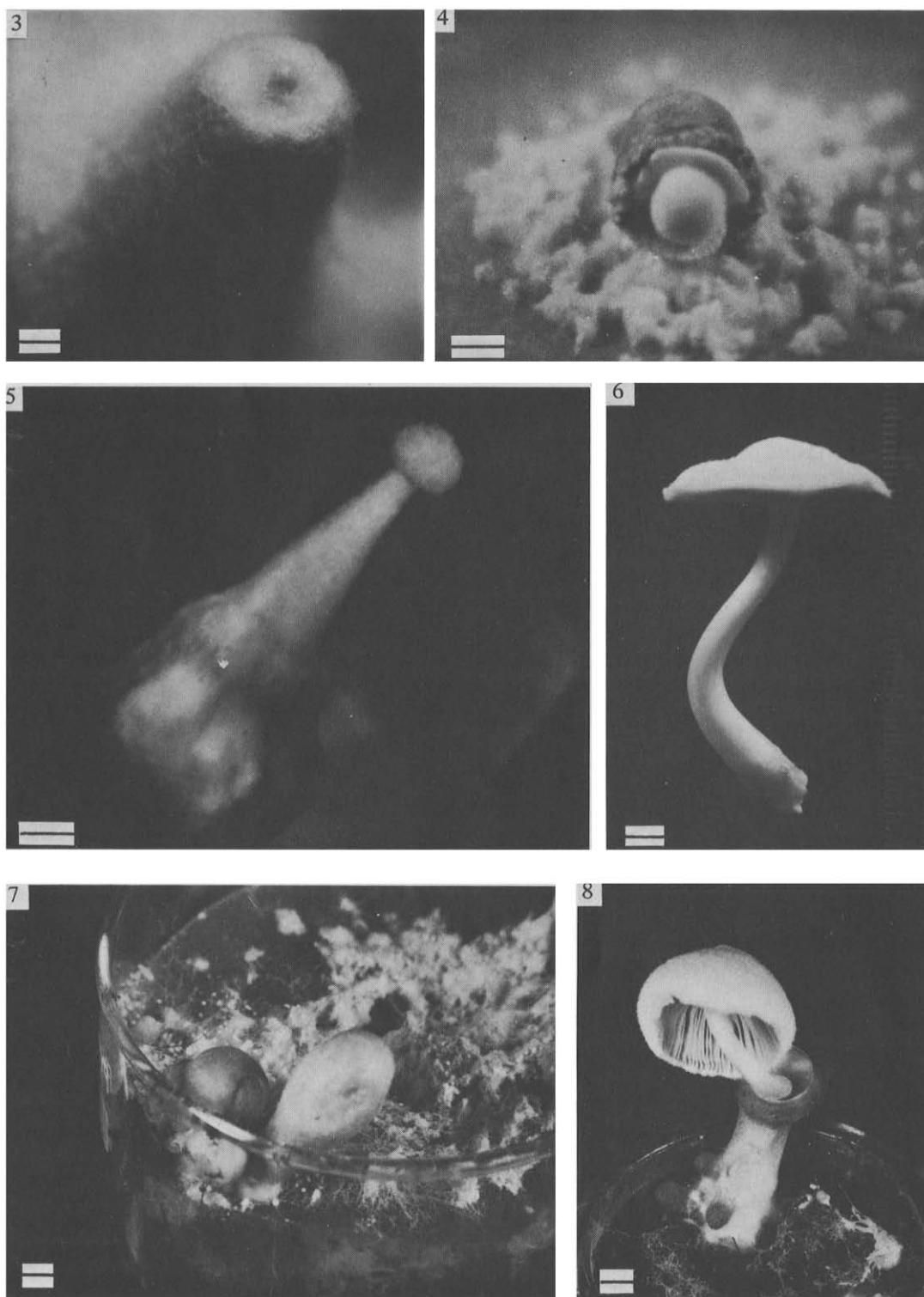
Fig. 9. Hemiangiocarpous primordium of *Volvariella bombycina* with two pileus initials; scale bar = 5 mm. **Fig. 10.** Gymnocarpous primordium with two pileus/stipe initials; scale bar = 2 mm.
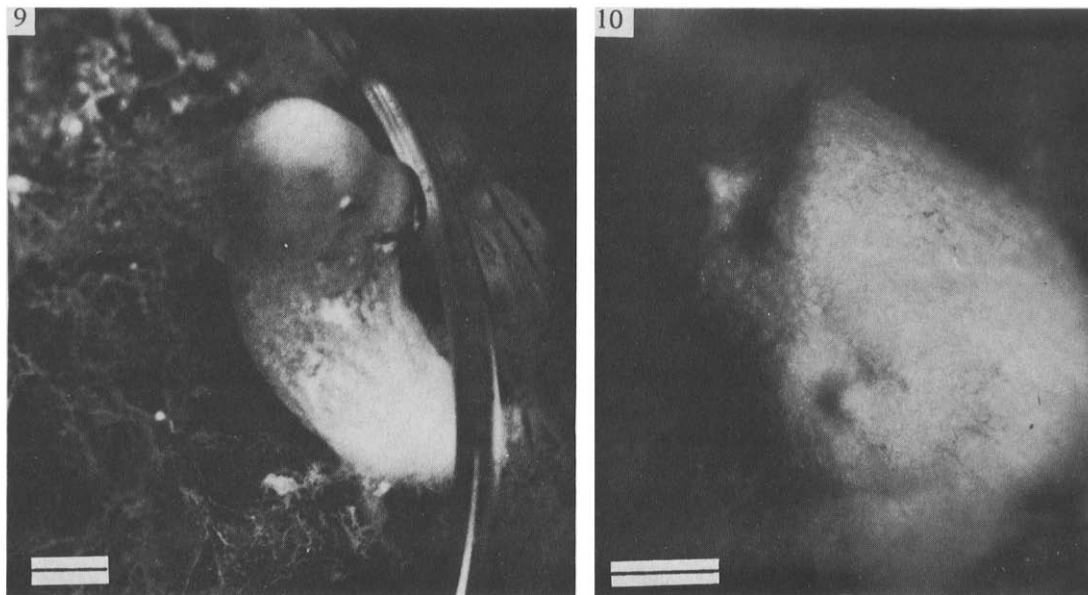
MATERIALS AND METHODS

Volvariella bombycina strains Vo-1 and Vo-7 were used. Strain Vo-1 originates from strain AS 5.164 kept in the Institute of Microbiology, Academia Sinica, China, and strain Vo-7 was obtained from the Sanming diqu Mycological Institute, Fujian, China (Huang & Wu, 1982).

Cultures were maintained on the complete medium (CM) of Raper & Miles (1958), consisting of (g l⁻¹): glucose (20); yeast extract (2); Difco Bacto-peptone (2); KH_2PO_4 (0·46); K_2 HPO_4 (1); $MgSO_4.7H_2O$ (0·5) and Difco Bacto-agar (15). Besides CM, other substrates used to fruit *V. bombycina* were: cotton waste compost, straw-and-dung mixture and Integrated Potato Dextrose Agar (IPDA), consisting of (g l⁻¹); Sigma PDA (39), thiamin-HCl (0·5) and $MgSO_4.7H_2O$ (3).

Test-tubes, Petri dishes and bottles with foam plastic plugs (Chiu & Chang, 1987) were used for growing cultures on semi-synthetic medium (CM or IPDA) and bottles or plastic bags for cultures growing on cotton waste compost or straw-and-dung mixture. Cultures were illuminated on a 12 h light/ 12 h dark cycle at 28 °C (Chiu & Chang, 1987). Mature fruit bodies were usually obtained within 2–3 weeks.

For examination by scanning electron microscopy (SEM), samples of hymenia were doubly fixed with glutaraldehyde–osmium tetroxide, dehydrated with alcohol, and critical-point dried (Chiu & Chang, 1987).

RESULTS

Normal development

The normal development of *V. bombycina* (hemi-angiocarpous – opening before full maturity) with the universal veil characteristic of the genus *Volvariella* is shown in Figs 1, 2. The progress of this normal development started after 1–3 wk incubation, when aerial hyphae aggregated into knots on mycelial cultures, switching from the mode of divergent growth into that of coherent growth (Gregory, 1984). Under favourable conditions, these primordia (= bulbs), would grow into the button stage. Differentiation of the universal veil and hymenophore of the genus *Volvariella* is described as bulbangiocarpous and schizohymenogenous (Reijnders, 1963), i.e. the universal veil originates exclusively from the tissues of the basal bulb, while the hymenophore forms in the apical schizogenous cavity enclosed by the universal veil. Succession of the development of the various tissues is described as pileocarpous (Singer, 1975), differentiation of the pileus being visible before differentiation of the stipe. From this stage onwards, the central stipe elongated while the pileus continued differentiation, giving an elongated egg shape. At the brief elongation stage, the universal veil was ruptured by the stress of stipe expansion, leaving the conspicuous basal membranous volva, enclosing half of the length of the stipe. The fibrillose-silky pileus continued to expand, while the stipe went on elongating. The free lamellae, radial, linear and non-anastomosing, changed from white to brownish pink, ready for spore discharge at the final mature stage.

Size variation in fruit bodies was obvious with different substrates, with different flushes and with different cultures. In general, solitary fruit bodies were larger; first-flush fruit bodies were larger, and so were fruit bodies grown on cotton waste compost or straw-and-dung mixture.

Lamellae samples examined by SEM showed that in normal fruit bodies all the basidia examined were four-spored or bore four sterigmata, and maturation of spores on the same basidium was synchronous (Chiu & Chang, 1987).

Variant development

Teratological forms arose spontaneously, and were found in cultures bearing normal fruit bodies in both strains tested,

Fig. 11. Fruit body of *Volvariella bombycina* with an inverted pileus; scale bar = 5 mm. **Fig. 12.** Hymenophore on the upper surface of the inverted pileus shown in Fig. 11; scale bar = 5 mm. **Fig. 13.** Fruit body with sinuous, labyrinthiform supernumerary hymenia formed by curling of the proliferating margin of the hymenophore to the upper surface; scale bar = 10 mm. **Fig. 14.** SEM view of a sinuous, labyrinthiform supernumerary hymenium formed by proliferation from the upper pileal surface; scale bar = 1 mm. **Fig. 15.** Fruit body with a morchelloid hymenophore; scale bar = 5 mm. **Fig. 16.** SEM view of a bisected morchelloid fruit body showing that the hymenophore covers the whole pileal surface; scale bar = 0·5 mm.
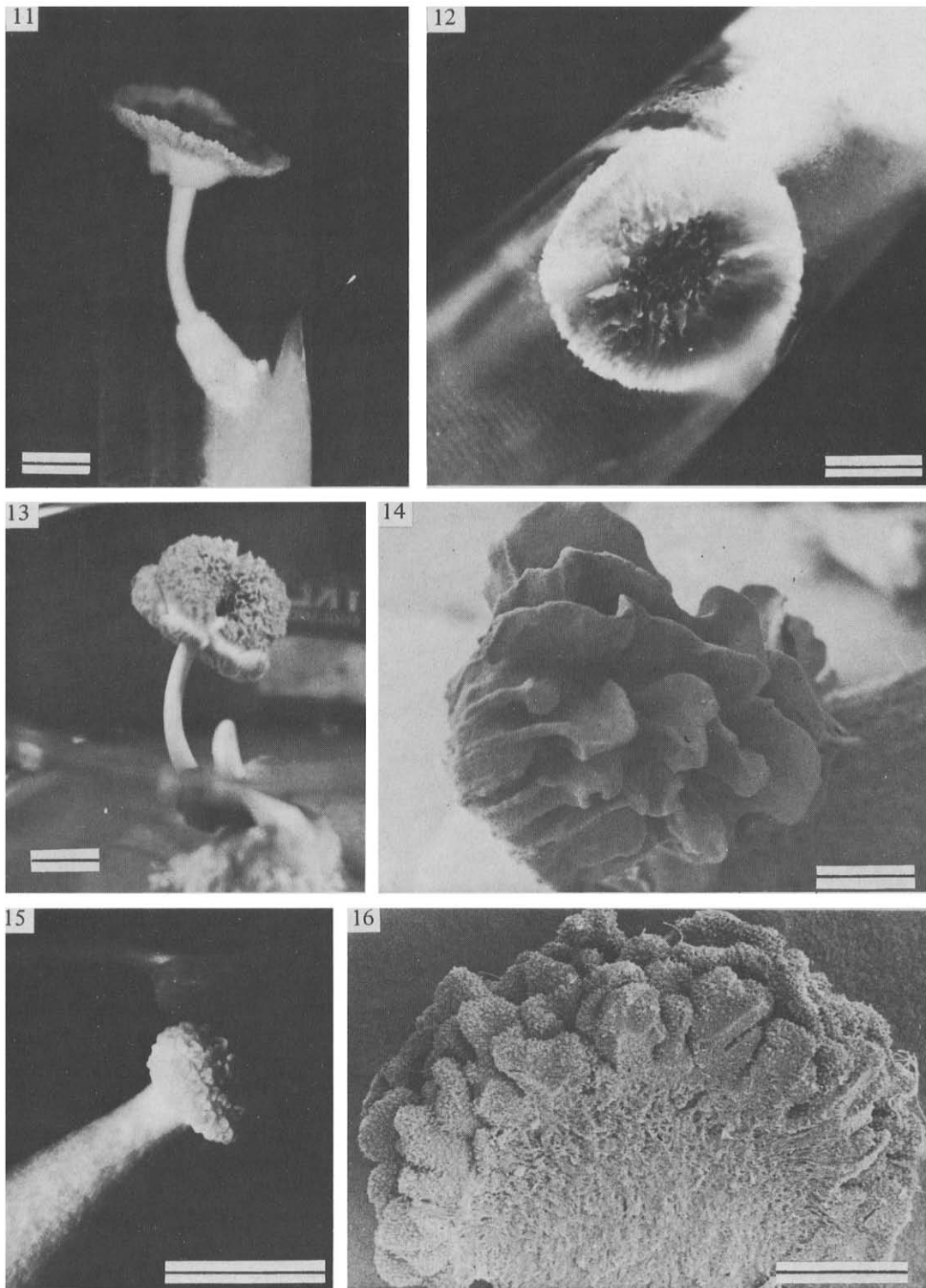
Fig. 17. Left: SEM view of a normal agaricoid hymenium (i.e. radially lamellate) from a gymnocarpous fruit body of *Volvariella bombycina*; scale bar = 100 μm. Right: × 5 magnification of the highlighted area. Fig. 18. Left: SEM view of a supernumerary (labyrinthiform) hymenium from a gymnocarpous fruit body; scale bar = 200 μm. Right: × 8 magnification of the highlighted area.
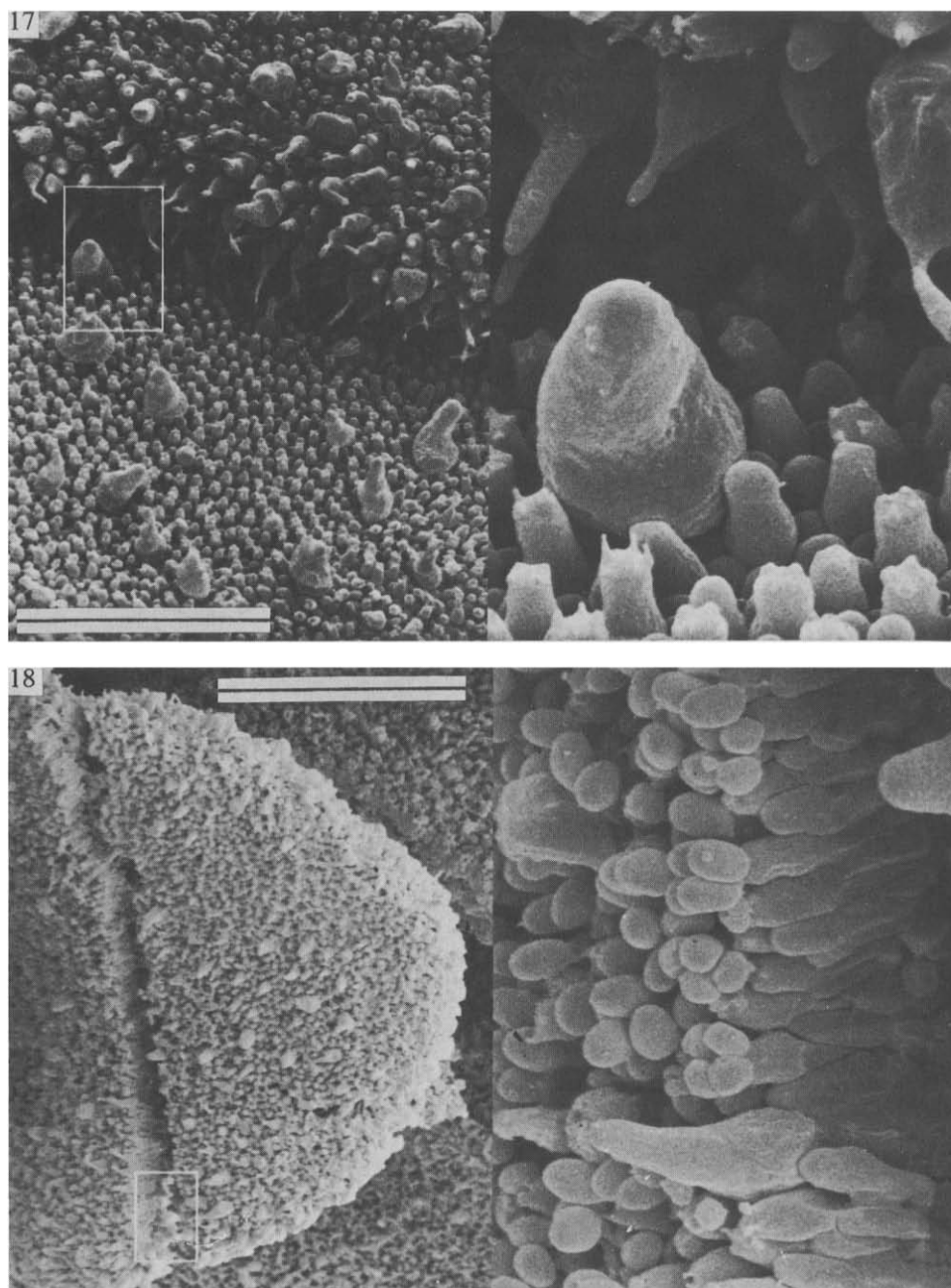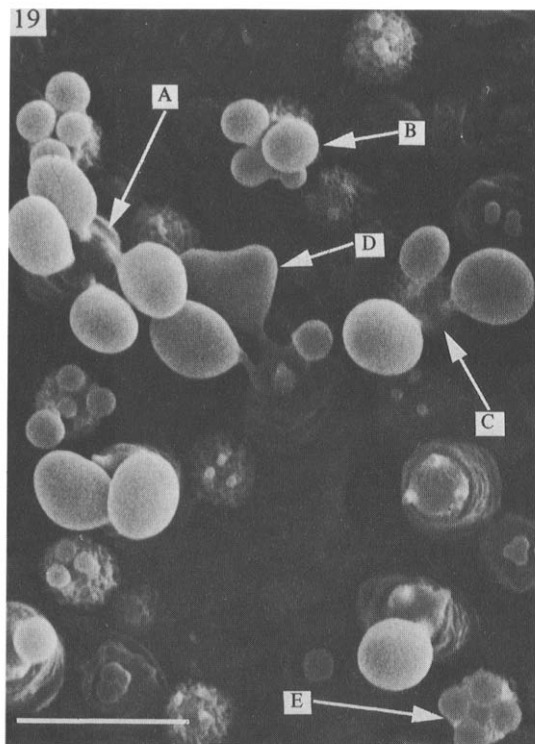

regardless of the composition of the substrate. In contrast with the hemi-angiocarpous mode of development, some primordia developed gymnocarpously (exposed hymenium; Fig. 3), the stipe/pileus initial being exposed at the very earliest stage. Differentiation of the pileus and stipe was visible. Depending on whether the tissue differentiation into basal volva and stipe/pileus initial was completed, such a fruit body might mature to have a thick crenate volva (Fig. 4), a giant volva (Fig. 5) or a smooth stipe base (Fig. 6). Sometimes a crevice appeared in the apex of a bulb, and enlarged into a hole in the universal veil visible at the egg-stage of the primordium (Fig.

7). The elongating stipe erected the differentiating pileus out of the universal veil, so that a mature fruit body had a normal appearance except for the smooth-lipped basal volva (Fig. 8).

Under the laboratory conditions employed, both solitary fruits and aggregates of fruit bodies (fasciation) (Fig. 1) were observed. Yet not all primordia found in a culture reached maturity; the arrested primordia remained sterile, and hence are termed carpophoroids (Singer, 1975) or bulbs if they have not initiated pileus differentiation (Reijnders, 1977). Primordia in some cultures were so crowded that a developing fruit

Fig. 19. SEM view of the hymenium of an enclosed fruit body of *Volvariella bombycina*; scale bar = 10 μm. A, synchronous maturation of all spores of a tetrad; B, asynchronous spore maturation; C, three-spored basidium; D, cordate spore; E, developing tetrad enveloped in mucilage.

body revealed sporulation irregularities including two- or three-spored basidia, asynchronous spore maturation, basidiospores enveloped in mucilage and spore morphologies deviating from the normal ovoid to cordate basidiospores (Fig. 19).

DISCUSSION

Fruiting in haploid, primary homothallic species, such as *V. bombycina* and *V. volvacea* (Chang & Yau, 1971; Chiu & Chang, 1987; Royse *et al.*, 1987), and in homokaryons in heterothallic species (Uno & Ishikawa, 1971; Stahl & Esser, 1976; Dickhardt, 1985; Elliott, 1985; Graham, 1985) shows that fruiting is independent of the sexual cycle regulated by the incompatibility system in heterothallic species (Raper & Krongelb, 1958). Fruiting itself is a complex polygenic process (Leslie, 1983; Meinhardt & Esser, 1983; Prillinger & Six, 1983; Leslie & Leonard, 1984) further modulated by environmental factors (Manachère *et al.*, 1983; Raudaskoski & Salonen, 1984; Manachère, 1985; Leatham & Stahmann, 1987). There is some genetic evidence that different structures (specifically sclerotia and fruit bodies) share a joint initiation pathway (Moore, 1981), and the common growth of fruits directly from sclerotia may also suggest morphogenetic similarities. It is against this sort of background that the variants of fruit bodies of *V. bombycina* must be interpreted.

Parasitism or disease as the cause of variation is rejected, as fruiting trials were under aseptic conditions, and cytological examination of cultures did not reveal any micro-organisms other than *V. bombycina*. With the demonstration of polymorphism in all the media tested and its occurrence in two strains from separate sources, it is believed that the variation in forms of fruit bodies reflects the natural developmental plasticity of *V. bombycina*, similar to the spontaneous abnormal or teratological fruit bodies reported in other fungi (Worsdell, 1915; Buller, 1922, 1924; Keyworth, 1942; Atkins, 1950; Watling, 1971; Singer, 1975; Reijnders, 1977).

In nature, *V. bombycina* fruit bodies are usually solitary (Zoberi, 1972; Dickinson & Lucas, 1979). The rich nutrients and/or luxurious environmental conditions employed in the present study supported the initiation of numerous primordia resulting in fusion and fasciation. Although fusions of initially independent primordia and subsequent raising of a smaller primordium on to the pileus of a developing fruit body (Worsdell, 1915; Buller, 1922; Atkins, 1950) can generate supernumerary hymenia, the supernumerary hymenia in *V. bombycina* are not similar, as in most cases the hymenophore lost the radially lamellate pattern and was sessile. Further, fusion of two pilei seems unlikely in *V. bombycina* as the mushroom normally develops bulbangiocarpously. Rather, proliferation of the upper part of the pileus into sporogenous tissues and the raising of the lower hymenial surface to the upper position seem to be the causes of the supernumerary hymenia in *V. bombycina* (Figs 13, 14).

body carrying 1–3 primordia at its basal volva was often observed (Fig. 8). Two primordia sharing the same basal part were encountered (Figs 9, 10). Whether this represented forking of one primordium or fusion of two intimate initials is uncertain.

Regardless of the mode of development, the whole pileus, in some cases, was upturned to the extent that it became totally inverted (Fig. 11). The hymenium was labyrinthiform in the centre but retained the straight, non-anastomosing lamellae at the periphery (Fig. 12). Some gymnocarpous fruit bodies also had similar hymenophores, but most were radially lamellate in the typical agaricoid manner. Fruit bodies with supernumerary hymenia which might be labyrinthiform were also encountered (Figs 13, 14). Sometimes the growth of the hymenophore was so extravagant that a morchelloid form (Fig. 15) was produced, with the hymenium covering the whole of the pileal surface (Fig. 16). All hymenia in these forms were functional in the sense that they produced normally pigmented spores. SEM examination of both sinuous, labyrinthiform and radially lamellate hymenia revealed in most cases basidia bearing four similar-sized spores (Figs 17, 18.)

In fruit bodies with endocarpous/angiocarpous development, sporulation was completed without rupture of the universal veil. These enclosed fruit bodies (gasteromycetoid forms) usually possessed thickened universal veils and/or had fused pileus and universal veil. A lamella of an enclosed fruit

As the variants appeared spontaneously, it is difficult to trace the exact cause. Gymnocarpous fruit bodies were more frequently encountered in test-tube cultures with paper plugs and on old cultures in dried media. So aeration and moisture

level seem to be important at the bulb stage. Watling (1985) suggested that the xerocomoid boletes are strictly gymno-carpous, and fertile basidia may occur very early in primordial development. Thus it is speculated that the abnormal gymnocarpous development is an adaptation to aridity, and the same may be true when similar forms arise in agarics as abnormal expression of morphogenesis. Forms with exposed supernumerary hymenia did not show any sporulation abnormality beyond their having a much-expanded surface for spore production. Within an enclosed structure, however, the conditions seem to lead to excess production of mucilage, asynchrony of spore maturation, variation in number of spores borne by a basidium, and plasticity in the shape of the basidiospores, resulting in heterogeneity of the hymenium. Cordate spores, such as those observed in enclosed fruit bodies, have never been reported in agarics (Pegler & Young, 1971).

The *V. bombycina* fruit bodies with supernumerary hymenia or inverted pilei demonstrate the interesting phenomenon of two different patterns of hymenia present in the same fruit body. The straight non-anastomosing lamellae are typical of a lamellate agaric, while the labyrinthiform (supernumerary) hymenium resembles that of a *Morchella* or *Tremella* fruit body. Morchelloid/tremelloid forms are not uncommon in agarics (Worsdell, 1915; Buller, 1924; Keyworth, 1942; Atkins, 1950; Watling, 1971; Flegg, 1983). There is no evidence that the morchelloid forms of different species are induced similarly. In the case of *Agaricus bisporus*, the production of numerous intumescences and patches of lamellae over the surface of the pileus is induced by the spraying of mineral oils on primordia 2–10 mm in diameter (Lambert, 1930; Flegg, 1983). In the case of *Flammulina velutipes* (Curt.: Fr.) Kummer and *Psilocybe merdaria* (Buller, 1924; Watling, 1971), however, morchelloid forms arose spontaneously as they did in *V. bombycina*. In *C. cinereus* there is a stable mutant bearing labyrinthiform hymenia (unpubl. obs.). Transition of the hymenial pattern to the morchelloid one, and the position of the hymenium on the upper surface, have been suggested to be phenomena of reversion or atavism to a carpophore organization seen in ascomycetes (Worsdell, 1915). Also, the abnormal hymenium fits with the description of the pseudo-hymenium of the gasteroid genus *Brauniella* Rick ex Sing., which Singer (1955, 1963, 1975) suggested to be ancestral to the large-spored species of *Volvariella*. Although *V. bombycina* belongs to the small-spored group, the appearance of such an abnormal hymenial pattern might, by the same logic, be taken to indicate relationship with the gasteroid genus *Brauniella*. However, making phylogenetic points on the basis of morphological variants is inherently dangerous. Plasticity in form may only imply response to environmental stress. But these developmental variants can be used legitimately to comment on the ontogenetic programme. Since they are actually or potentially functional as meiospore production/dispersal structures, they seem to us to imply that normal carpophore development comprises a sequence of independent but co-ordinated morphogenetic subprogrammes, each of which can be activated or repressed as a complete subroutine. For example, we would say there is a 'hymenium subroutine' which, in an agaric, is normally invoked to form the 'epidermal'

layer of the hymenophore (lamellae); but if it is invoked aberrantly and additionally to form the upper epidermis of the pileus it forms, not a chaotic travesty of a hymenium, but a functional supernumerary hymenium. Similarly, the 'hymeno-phore subroutine' produces the classic agaric form when invoked on the lower surface of the pileus, but if wrongly invoked on the upper surface it produces, not a tumorous growth, but a recognizable inverted cap. Thus we hypothesize that the development of fungal structures in general depends upon organized execution of such subroutines, the sequence and location in which they are invoked determining the ontogeny and form of the fruiting structure. Invocation of these developmental subroutines may be logically equivalent to the 'mode switches' between different mycelial states discussed by Gregory (1984) and Rayner & Coates (1987). Some of the subroutines can be identified with specific structures, such as basal bulb, stipe, pileus, hymenophore and hymenium, but others are rather subtle, affecting morpho-genetic features – such as the subroutine (seemingly inactive in morchelloid forms) which ensures that the lamellae are strictly radially arranged.

Identifying the subroutines is a task for developmental biologists; establishing how (and why) the subroutines have been assembled into the different developmental programmes that give rise to the characteristic structure of the major fungal groups is a phylogenetic pursuit requiring a wider range of detailed comparative studies.

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