

Problems in application of the terms 'blastic' and 'thallic' to modes of conidiogenesis in some onygenalean fungi

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Abstract

In 1969, specialists at the Kananaskis hyphomycete workshop coined the terms 'blastic' and 'thallic' to describe two distinct modes of conidiogenesis. Since then, the original concepts have been slightly modified and redefined, and the terms have been widely adopted in taxonomic descriptions of conidial fungi. Problems arise in the application of these terms to conidial development in fungi which demonstrate morphological plasticity ranging from fragmentation of a hypha to extrusion of a portion of a hypha or cell. A number of fungi, such as anamorphs of Onygenales which includes many of the fungi pathogenic to man, demonstrate intergradations between blastic and thallic development. Because development in this group of fungi is difficult to categorize, it has led to an inconsistent treatment of taxa which share many other developmental features in common. In using these terms, it should be remembered that they represent extremes in a developmental spectrum.

Historical background

The processes by which fungi form conidia have been subjected to a great deal of scrutiny during the past 35 years. The development of a conidium depends on some modification of a hypha or part of a hypha (cell) to form a propagule which can be dispersed. The degree of elaboration of the hyphal modification formed the basis of the eight types of development recognized by Hughes [11] and modifications of his scheme adopted by other workers.

In 1969, specialists at the first Kananaskis conference attempted to provide a nomenclatural basis for developmental processes then re-

cognized [14]. Since then, the terminology has been widely adopted in descriptions of conidial fungi, and there has been a proliferation of a new taxa of Hyphomycetes, often distinguished on a single ontogenic character.

Despite optimism that conidiogenesis might provide the basis on which new classifications could be made, recent work has called for a reevaluation of the degree of distinction among the different types of development heretofore recognized [18, 19, 20]. Further it has been questioned whether some of the terms are adequate to describe the processes of development in morphologically plastic fungi.

Cole and Samson's [6] elegant study of

conidial fungi using both scanning and transmission electron microscopy provided much information on the mechanisms by which conidia are formed. As more taxa have been critically examined, however, our concepts of development no longer appear as rigid as they once did, and we begin to question the basis on which generic circumscriptions can be made. Indeed, this reassessment is now leading to the combination of some genera formerly separated on the basis of apparent ontogenic differences. As stated by Kendrick [16], '...we have come to realize that ontogeny is often much less conservative, and much more plastic, than we had hoped.... and it is being relegated to the status of just another character, rather than *the* character.'

To some degree this reassessment has arisen because of the movement toward a natural, i.e. phylogenetic, classification of anamorph taxa according to their teleomorph connections. Genera of conidial fungi are now often treated as true genera comprised of anamorphs of related teleomorphs rather than form taxa based on morphological similarity of anatomic stages of the life cycle. It has been argued that anamorph relationships may provide criteria to achieve a better classification of ascomycetes [1], and that relationships to teleomorphs provide characters on which anamorph taxa can be circumscribed [21]. Others [Carmichael, in 17] have argued that a strictly morphological classification of anamorphs serves a more useful function for identification. These topics were the subject of the second Kananaskis conference [15] and symposia following the International Mycological Congress in 1983 [24] and during the 1988 Congress of the International Society for Human and Animal Mycoses [25].

The present work was a contribution to the latter symposium, and represents an attempt to show the difficulties that I have encountered in applying the terms blastic and thallic, which supposedly represent fundamentally different forms of ontogeny, to a group of fungi which demonstrate all manner of gradation, from the development of solitary, terminal or lateral conidia to intercalary arthroconidia.

Origin of the terms blastic and thallic

The 1969 Kananaskis conference established the terms blastic and thallic to distinguish two distinct modes of development. Since then, the original concepts have been slightly modified and redefined, notably by Cole and Samson [6] who provided these definitions: 'Blastic - ...the conidium differentiates from a fertile hypha (i.e. conidiogenous cell) by the blowing-out and *de novo* growth of part of the hyphal element and is delimited by a septum.' 'Thallic - ... the conidium differentiates by conversion of a segment of a fertile hypha which may involve some enlargement and secondary wall growth; the conidium is delimited by a septum or septa.'

At the Kananaskis meeting, Carmichael [5] noted the difficulty in evaluating developmental processes and concluded that 'the various methods of spore production described.... are not separate and distinct kinds, but outstanding parts of a continuously intergrading and overlapping spectrum of methods for releasing propagative elements.' He [5] recognized only three basic processes by which fungi form conidia: 'fragmentation' in which the cytoplasm becomes concentrated in some cells of the hypha while remaining ones are exhausted; 'fission' in which the filament breaks apart at double septa, or 'extrusion' from the ends or sides of the hypha (cell). The process of extrusion describes development now generally accepted as blastic. The processes of fragmentation and fission describes development now generally accepted as thallic, but Carmichael recognized that even such broad categories foundered on the evidence of intermediate types of development.

In 1981, Ingold [13] provided examples of some aquatic Hyphomycetes with solitary tetra-radiate conidia in which development of a single conidium could have both blastic and thallic aspects. While he recognized several different types of development, he voiced concern about the 'wisdom of trying to impose a blastic-thallic dichotomy on the whole system.' The problem in interpreting conidial development in morphologically plastic fungi has been recognized by other workers [2, 6, 18, 19].

Application of the terms to fungi with solitary conidia

Inconsistencies are evident in the treatment of a group of fungi which produce solitary conidia. The conidiogenous cell consists of a portion of a hypha which is usually not well differentiated from other adjacent cells. Conidia are single celled or multicellular, solitary, arising terminally or laterally, and may intergrade with alternate arthroconidia. A number of these fungi are anamorphs of Onygenales, an order of the ascomycetes which includes the teleomorphs of agents of dermatophytosis (in the Arthrodermataceae) and systemic infection [in the Onygenaceae, see 7]. Fungi with single celled conidia are placed in the genera *Chrysosporium* Cda., *Myceliophthora* Cost., *Histoplasma* Darling, *Emmonsia* Cif. & Mont., *Malbranchea* Sacc. and others. Fungi with multi-celled conidia are placed in *Epidermophyton* Sab., *Microsporum* Gruby and *Trichophyton* Malmsten, but the latter two genera are linked to the others by development of unicellular conidia.

Cole and Samson [6] noted the problems in assessing development in onygenalean fungi as either blastic or thallic since 'The anamorphs of several genera of Gymnoascaceae, e.g. *Arthroderma* Currey, *Gymnoascus* Baran.) often referred to *Chrysosporium* Corda, demonstrate both fragmentation of fertile hyphae and blastic development of microconidia.' Microconidia produced by *Chrysosporium*, some anamorphs of *Arthroderma* Berk., and *Myceliophthora* were treated as blastic, whereas thallic-arthric conidia of *Chrysosporium*, macro- and microconidia of *Trichophyton* and *Microsporum* and some other anamorphs of *Arthroderma* were treated as thallic.

In a study of *Chrysosporium* and allied genera, van Oorschot [26] used modes of conidium development as key characters in separating *Chrysosporium* from other similar genera. In contrast to Cole and Samson, she considered the conidia of *Chrysosporium* to be thallic rather than blastic, and differentiated the genera *Myceliophthora*, *Zymonema* de Beurmann & Gougerot, *Emmonsia* and *Trichosporiella* Kamyschko ex Gams & Domsch by development of blastic conidia.

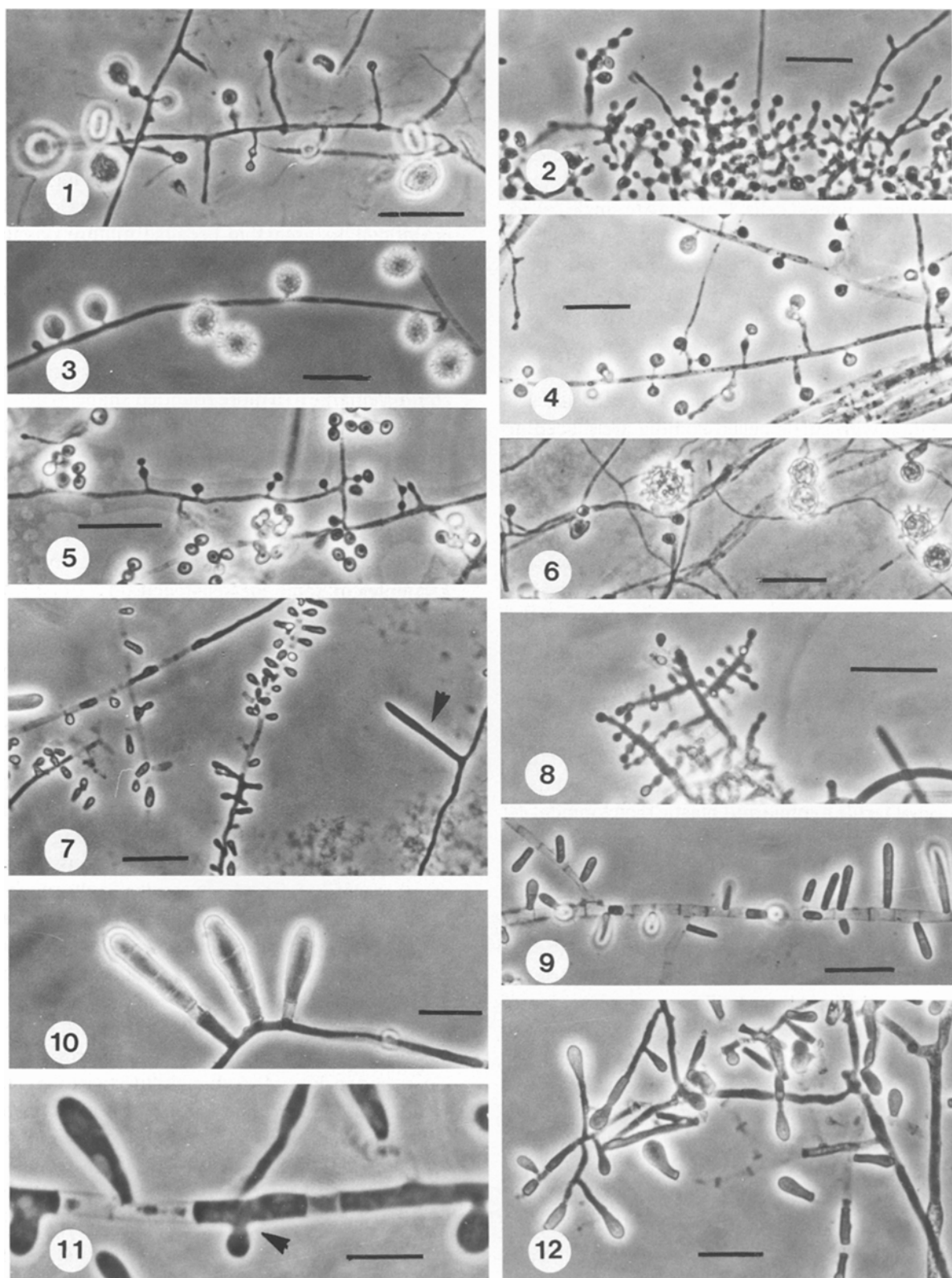
Conidia attached to the supporting hypha by a narrow base were interpreted as blastic in origin whereas thallic conidia had a broad attachment base. Likewise, the process of development of macroconidia of *Trichophyton*, *Microsporum* and *Epidermophyton* has been variously described as holothallic [6] or holoblastic [9, 10].

Part of the reason that conidium development is difficult to assess is because mature conidia frequently assume a cylindrical shape only slightly broader in dimension than the conidiogenous cell (hypha) and their development is then considered to occur by modification of an existing hyphal element. Blastic ontogeny is assumed where the conidia enlarge to a more rounded shape. Whether such distinctions represent the most accurate interpretation of conidium development in this group of fungi will be assessed by means of some examples.

Examples of some inconsistencies

In the first three species, conidia are borne singly from swollen conidiogenous cells or are sessile on the side of the hypha. All three are currently accommodated in *Myceliophthora*. Fig. 1 shows the anamorph of *Ctenomyces serratus* Eidam, moved from *Chrysosporium* to *Myceliophthora* by van Oorschot on the basis of blastic development of conidia from a swollen conidiogenous cell. The type species, *M. lutea* Cost. (Fig. 2), also produces conidia from short swollen cells, but in another species moved from *Chrysosporium*, the anamorph of *Arthroderma tuberculatum* Kuehn, the conidia are sessile on the hypha or borne on short non-swollen stalks (Fig. 3).

Three species placed in monotypic genera, maintained on the basis of dimorphism, are illustrated in Figs. 4–6. Fig. 4 illustrates the anamorph of *Ajellomyces dermatitidis* McDonough & Lewis, named *Blastomyces dermatitidis* Gilchrist & Stokes in most medical literature, but accommodated in *Chrysosporium* by Carmichael and *Zymonema* by van Oorschot. The conidia borne laterally on the sides of the hypha or on short pedicels have been called blastic. The develop-



ment is similar in *Emmonsia parva* (Emmons & Ashburn) Cif. & Mont. (Fig. 5) and *Histoplasma capsulatum* Darl. (Fig. 6).

Cole and Samson called the microconidia of *Trichophyton mentagrophytes* (Fig. 8) thallic, but van Oorschot considered their development more similar to that of *Myceliophthora*. The conidia arise from slightly swollen cells or are sessile.

In the next two examples, development of lateral conidia has been called thallic since there is little expansion (swelling) of the developing conidium and the width of the attachment is broad. Fig. 7 demonstrates the sessile microconidia and a developing macroconidium (arrow) of *Trichophyton raubitschekii* Kane *et al.* In *Trichophyton terrestre* Durie & Frey (Fig. 9) both multiseptate macroconidia and microconidia are formed directly from the sides of the hypha. Similarly, the lateral macroconidia of *Epidermophyton floccosum* (Harz) Langer. & Milochevitch may be sessile or on short stalks (Fig. 10).

When the examples are compared, it is apparent that there is substantial wall building involved in the development of all the lateral conidia which involves extrusion from the sides of the hypha or from a swollen conidiogenous cell. By definition blastic development involves the blowing-out and growth of part of the hyphal element.

Even if agreed that the previous examples show developmental similarity, intergrading forms are more difficult to evaluate. At the other end of the spectrum are fungi in which terminal conidia intergrade with alternate arthroconidia, such as the *Chrysosporium* anamorph of *Aphanoascus fulvescens* (Cke.) Apinis (Fig. 12). This type of development, which has been called fragmentation, is difficult to categorize as strictly thallic since solitary lateral conidia are formed by new growth from the side of a hypha (Fig. 11). A similar situation occurs in *Sporotrichum* Lk. (now recognized as including anamorphs of lignicolous basidiomycetes). Solitary conidia have been de-

scribed as blastic yet in species such as *S. pruinosum* Gil. & Abbott (formerly treated in *Chrysosporium*), the terminal conidia intergrade with intercalary arthroconidia, appearing similar to the type of development seen in *A. fulvescens*.

Although the timing of septum formation has been considered important in distinguishing between thallic and blastic development, careful scrutiny has shown that septum formation is often variable, sometimes occurring following significant swelling of the developing conidium (Fig. 11). The same variability in the timing of septum delimitation has been observed in the formation of macroconidia in *Epidermophyton* and *Microsporium* [9, 10].

In 1976, I [22] described *Arcuadendron* for fungi which resembled *Malbranchea*, but the fertile hypha continues to grow after initiation of a conidium. In *A. ovatum* Sigler & Carm., the conidia develop by swelling of an intercalary cell. Often the swelling occurs following delimitation by a basal septum, but septum formation is not always discernible prior to enlargement. The intercalary position of the developing conidia suggested a thallic type of development, but it was evident that the ontogeny of development in this fungus did not readily fit either of the blastic-thallic concepts.

The concept of aleuriospores

One feature common to all these fungi is the mechanism of conidium dehiscence involving lytic degradation of the supporting hyphal cell. Carmichael [4], following his assessment of Vuillemin's concept of aleuriospores based on the 'reference species' *Sporotrichum merdarium* Lk, used dehiscence as a key character on which he based the generic circumscription of *Chrysosporium*. His concept of aleuriospores based on dehiscence was not accepted at the Kananaskis conference and the term was rejected as confused. More

◀ Figs. 1–12. 1. *Ctenomyces serratus* (UAMH 4583). 2. *Myceliophthora lutea* (UAMH 4306). 3. *Arthroderma tuberculatum* (UAMH 3182 ex type). 4. *Ajellomyces dermatitidis* (UAMH 5584). 5. *Emmonsia parva* (UAMH 4770). 6. *Histoplasma capsulatum* (UAMH 3536). 7. *Trichophyton raubitschekii* (UAMH 4314 ex type). 8. *Trichophyton mentagrophytes*. (UAMH 6256). 9. *Trichophyton terrestre* (UAMH 3420). 10. *Epidermophyton floccosum* (UAMH 6208). 11–12. *Aphanoascus fulvescens* (UAMH 4114). (bar = 20 µm, Figs. 1–10, 12; bar = 10 µm, Fig. 11).

recently the term rhexolytic involving a 'fracture of the subtending cell' [see 12] has been taken up to describe conidium dehiscence in onygenalean fungi [7, 26]; however, in many instances the supporting cell or hypha is entirely dissolved (e.g. Fig. 9). In discussing ontogenic development of chlamydospores, Hughes [12] distinguished lytic secession involving decay of 'intervening cells or segments of the emptied mother-cell' as distinct from rhexolytic secession, involving a mechanical fracture of a subtending cell. In a study of some dermatophytes, Galgoczy [9, 10] clearly illustrated the autolysis of subtending cell(s). Some fungi, such as *Trichosporiella* which shares a developmental similarity in the formation of sessile lateral conidia, are not closely allied to onygenalean anamorphs since the conidia do not undergo lytic dehiscence [8].

It has been suggested that the term aleurioconidium applies to the whole sequence of development [20], but Carmichael clearly applied the term to a conidium which undergoes a type of dehiscence in which the subtending cell lyses. This character has been used to correlate teleomorph relationships. Currah [7], in a major revision of the families of Onygenales, emphasized anamorphs with lytic conidium dehiscence, the capacity to degrade keratin and the nature of the ascospore wall as key characters used to distinguish the families Arthrodermataceae and Onygenaceae.

Summary

The conidia of onygenalean anamorphs may form terminally, laterally on short stalks or sessile, or in an intercalary position. In interpreting the development of solitary conidia as blastic or thallic, the main distinction is that the former involves significant new wall growth whereas the latter involves the conversion of an existing hyphal filament. In many of the fungi treated here, examples have been found in which the formation of solitary lateral conidia occurs by extrusion or a blowing out of a portion of a hypha. This process requires new wall growth. In my view, to differen-

tiate between these fungi on the basis of supposed ontogenic differences is arbitrary, and may result in the separation of fungi which are similar in many respects. The group as a whole represents a spectrum of developmental types which share a similar type of dehiscence.

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