form dense cloud lines as over the Agulhas Current itself and that this would happen only under exceptional circumstances. A proper climatological study is required to establish the occurrence frequency of these clouds and how important their role is in the weather and climate of the southwestern part of southern Africa.

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Analysis of conidiogenesis: helical conidiotaxis in percurrently extending conidiogenous cells

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Analysis of scanning electron micrographs of conidiogenous cells in several conidial fungi exhibiting sympodial and pseudosympodial conidiogenesis provided evidence that their conidia develop in an organized helical sequence. This is a phenomenon parallel in many ways to phyllotaxic patterns in plants and its occurrence in fungi was previously recognized in sympodulae of *Hortaea*. The phenomenon is analysed in *Leptographium*, and proposed as an addition to the lexicon of taxonomic characters.

Hughes[1] delineated several apparently distinct ways in which asexual spores (conidia) could be formed on or from conidiogenous cells by anamorphic fungi, most of them involving the production of several conidia from a single conidiogenous cell.

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Ostensibly, one of the easiest of these to recognize was what he called 'sympodial conidiogenesis'. Here, following the 'blowing out' of a first apical conidium, the conidiogenous cell briefly resumes extension growth from a new growing point just behind and to one side of the first conidium, forming a new apex. This second apex is, in turn, converted into a conidium, and a third new, subterminal apex continues the extension-conidiation process.

This process of conidium formation and renewed apical growth is repeated many times in some taxa, and because the new apices are completely separate from the old conidiogenous locus, the conidia are not displaced by the renewed growth, and remain loosely attached along the sides of the cell. In such taxa, after repeated conidiation, the cell has become longer, and often bears a large number of lateral conidia in a single layer surrounding a significant portion of its length. This is what gives the characteristic appearance to the conidium-bearing rachis of *Tritirachium oryzae* (Vincens) De Hoog (Fig. 1a), and to the conidiogenous cells in *Acrodontium hydnicola* (Peck) De Hoog after the conidia have seceded (Fig. 1b). The same is true of many other genera of conidial anamorphs (see ref. 2, plates 21–30).

Following the appearance of Hughes'[1] classification, several genera were described to accommodate anamorphs of *Ceratocystis sensu lato*. When viewed under the light microscope, conidial arrangement alongside the tip of the conidiogenous cell produces the illusion that the conidiogenous cell is extending sympodially (Fig. 2a). However, the scanning electron microscope reveals that these conidia are in fact attached to a percurrently proliferating conidiogenous cell (Fig. 2b). Van Wyk,[3] accordingly suggested that incomplete secession of conidia in the percurrently extending conidiogenous cells of some anamorphs such as *Leptographium truncatum* (M.J. Wingf. &
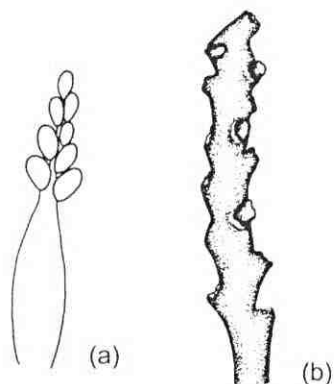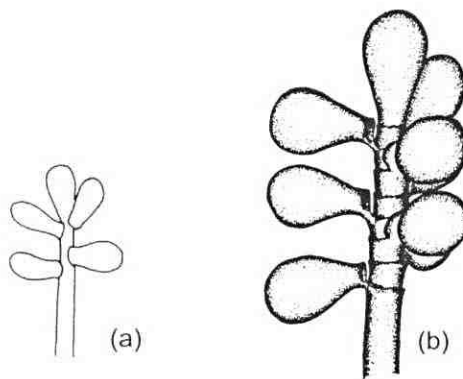
Fig. 1. Sympodial production of conidia by conidiogenous cells of *Tritirachium oryzae* and *Acrodontium hydnicola*: **a**, low magnification image illustrating arrangement of conidia in *T. oryzae* along the axis of the conidiogenous cell; **b**, SEM view of a conidiogenous cell in *A. hydnicola* after dehiscence of the conidia, showing the secession scars left after true sympodial extension growth (redrawn from Cole and Samson,[7] p. 37).

Fig. 2. Pseudosympodial production of conidia by a conidiogenous cell of *Leptographium truncatum*: **a**, redrawn from light micrograph; **b**, redraw from SE micrograph.

Marasas) M.J. Wingf. had been misinterpreted as sympodial development. During the course of this and subsequent studies, representatives of some other supposedly sympodial anamorph genera, such as *Hyalorhinocladiella* Upadhyay & Kendrick,[4] *Pesotum* Crane & Schoknecht[5] and *Verticicladiella* Hughes,[6] have been re-examined in the scanning electron microscope, and have been found to develop in this way. We introduce the term pseudosympodial to describe this kind of development. We are not suggesting that this is a general phenomenon, and we are not attempting to repudiate the concept of sympodial extension of conidiogenous cells: in many genera of conidial fungi the conidiogenous cells do indeed extend sympodially, and this also has been confirmed by scanning electron micrographs.[7]

This paper is concerned with the elucidation of this pattern, as part of our ongoing analysis of the processes involved in the development of conidia. Our aim in this work is to recognize new and useful taxonomic characters.

## Comparison of arrangement of leaf traces and pseudosympodial conidia

Our observations indicate that the conidia in both sympodial and pseudosympodial anamorphs are often attached to the conidiogenous cell in a more or less helical sequence. This leads us to consider the possible parallels with phyllotaxis, the regular sequence and pattern of leaf primordium development observed in plants.[8] The following discussion is included because this phenomenon has previously been recorded only once in the mycological literature.[9] Many mycologists will accordingly be unfamiliar with the terminology involved. Several types of phyllotaxis have been observed, but by far the most common is spiral (or more correctly, helical) phyllotaxis. In plants, this pattern has presumably evolved at least partly to ensure that each new leaf does not shade those produced previously. It is also a logical way for a temporal sequence of radially produced organs to be distributed over the limited surface available on a narrow cylindrical vertical axis, and it shares the load placed by the leaves on that axis equally around the perimeter of the axis.

Where a phyllotaxic 'spiral' exists, and the points of origin of successive leaves are linked by a line, a helix will be outlined, moving up the outside of the axis. The implication appears to be that there is an inherent and precise progression and rotation of whatever organizing principle initiates the meristems that give rise to leaves. This rotation means that successive leaves

will arise at regular vertical intervals along the axis, and will be separated around the axis by a fairly constant horizontal angle (known as the angle of divergence). Sometimes, if the internodes are short, two helices may be recognized, passing around and up the stem in opposite directions. These helices are known as parastichies.

In most plants the leaf primordia are crowded around the apical meristem, and the bases of the members of each parastichy will grow upward parallel to, and in contact with each other. A transverse section of the shoot apex of a plant will often show that the members of these 'contact parastichies' are arranged in centrifugal spirals (real spirals) (Fig. 3). If the primordia are numbered in reverse order of their development, starting closest to the apex with zero, it will be seen that the members of the contact parastichies form an arithmetic series in which the numbers of successive primordia increase by a constant integer. Figure 3 shows two such parastichies in the shoot apex of *Pinus pinea* L.[8] Here, successive members of the spirals that move out to the left increase by 5, while those that move out to the right increase by 8, as the numbers in Fig. 3 clearly show.

It has been observed that the two numerical increments of the contact parastichies in any particular apex are always successive terms in a Fibonacci series (a mathematical series in which each term is the sum of the two preceding terms: the simplest example is 0, 1, 1, 2, 3, 5, 8, 13, 21...). Church[10] described systems of 'spiral' phyllotaxis in the most economical way possible by simply citing the numerical increments of the two intersecting sets of contact parastichies in the format $(x + y)$. Those shown in Fig. 3 can thus be designated as $(5 + 8)$. If the nodes are very close together and the numbers of the contact parastichies are situated
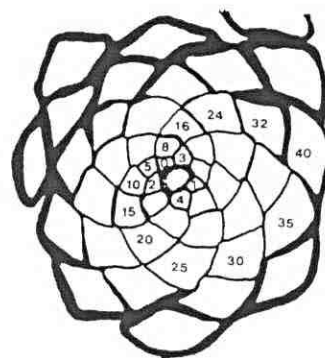
Fig. 3. Transverse section of growing shoot apex of *Pinus pinea* showing two contact parastichies (after Cutter[8]).
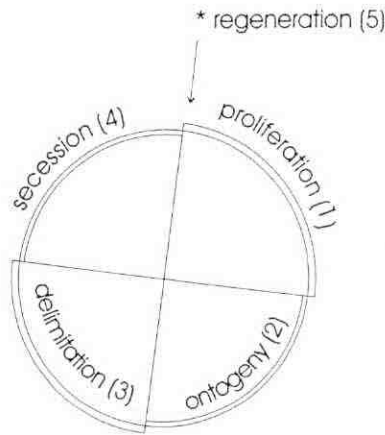
Fig. 4. Schematic representation of steps involved in conidium development (after Van Wyk *et al.*[3]).

much further along the Fibonacci series, as, for example (55 + 89), the angle of divergence of the primordia will approach the Fibonacci angle of approximately 137.5 degrees. How much of this can be applied to the arrangement of conidia on the axis of a conidiogenous cell?

Conidiotaxis

We here introduce the term conidiotaxis to describe in conidial anamorphic fungi a process that appears, at least in some ways, to be equivalent to phyllotaxis in plants. Comparable analysis of conidiogenesis is complicated by the fact that conidia do not usually extend upwards as leaf bases do, and thus do not establish contact parastichies. We cannot, therefore, expect to derive any useful information from transverse sections. In many taxa, conidiogenous cells are so small that only if scanning electron micrographs are made of mature cells it is possible to extract much useful information. We have made line-drawings and models from a number of scanning electron micrographs, and an analysis of our data is presented below.

In percurrently extending conidiogenous cells, each conidium (other than the first) arises following a percurrent extension of the cell (distally, directly outward through the circular scar left by the secession of the previous conidium, and in the direction of the longitudinal axis of the conidiogenous cell). This conidium is forcibly detached as development of the new apex begins below its base. Since extension is essentially linear, it might not be expected to impose any organized pattern on the secession of
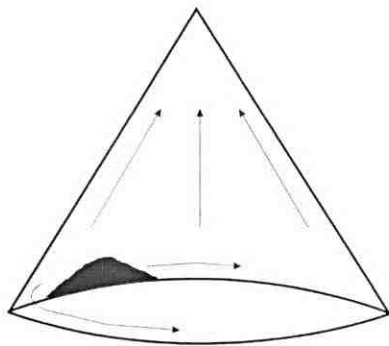
the conidia, and there seems to be little reason to expect that any particular organization would be discernible in the process of secession. In many anamorphs with percurrently extending conidiogenous cells, however, each conidium secedes completely as the next one begins to develop. Even if some organizational principle was involved, all evidence of this would automatically be destroyed as the conidia secede and accumulate around the conidiogenous cell in a slimy mass, their orientation determined by surface tension rather than by order of production. The incomplete dehiscence observed in *Leptographium truncatum* (Fig. 2) and some other anamorphs of *Ophiostoma* presents us with an unusual opportunity to examine the process of percurrent conidiation in a retrospective manner.

The original premise concerning percurrent conidiogenesis is that it is a pulsed process in two major phases, conidium development alternating with somatic extension in a simple linear relationship, each phase occurring directly distal to the previous one. Yet it is clear from a consideration of Fig. 2, which is derived directly from a scanning electron micrograph of a conidiogenous cell of *L. truncatum,* that the conidia are attached to the mother cell in a rather regular pattern. Indeed, they are arranged in such a manner that their points of attachment can be linked by at least one ascending helix (Fig. 6). There is what may be termed a 'conidiotaxic helix'. It would appear that, since the arcs of wall material connecting the conidia to the parent cell are arranged in a helical succession, the processes involved in the original laying down of the wall around the base of each new conidium must have been influenced by some rotational principle, and that this principle must also advance with the growing cell axis.

We are therefore suggesting that there is, at least in some percurrently extending conidiogenous cells, a phenomenon
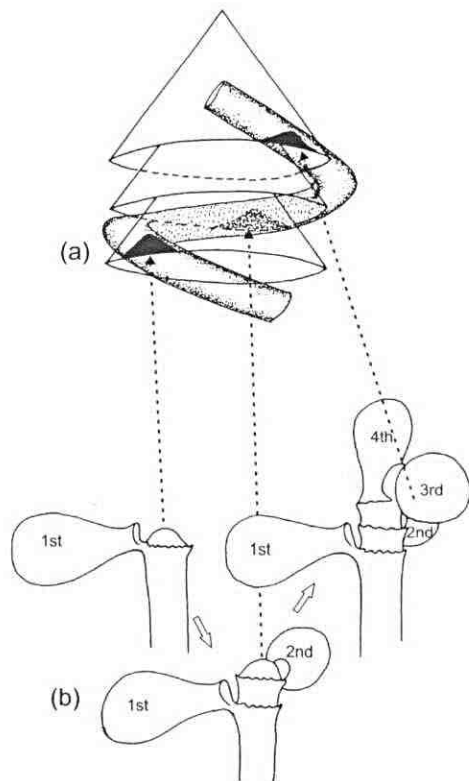

Fig. 5. Schematic representation of the early developmental stages (regeneration and centripetal onset of proliferation) involved in the production of a new conidium. The dark triangular segment represents the zone of regeneration (introducing proliferation), which moves around the periphery of the cell and upward. The later stages of proliferation and then ontogeny continue by means of apical wall-building.

Fig. 6. Analysis of pseudosympodial configuration of conidia on percurrently extending conidiogenous cells. **a**, Zone of proliferation initiating the development of new conidia, moves up and around the cell in a helical manner (dark triangles show three sequential positions of this zone); **b**, three diagrams showing the appearance of the conidiogenous cell at the three times represented in (a).
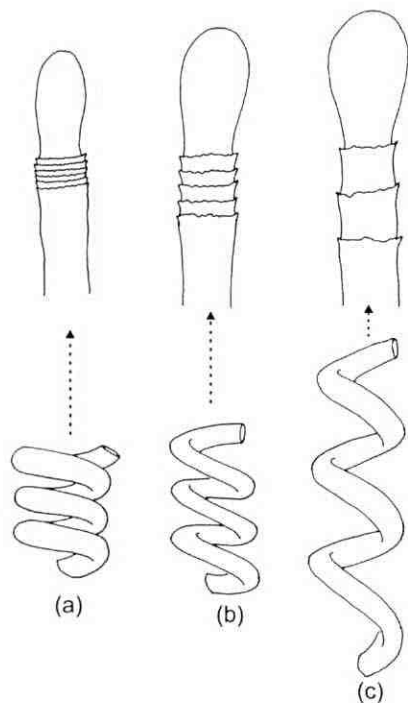
Fig. 7 a–c. Diagrams showing the relationship between the spacing of annellations and the helical movement of the conidiogenous locus. **a,** *Leptographium procerum*; **b,** *Leptographium terebrantis;* **c,** *Leptographium truncatum.*

directly comparable to that found in many plants: successive conidia will be initiated at regular intervals, with the points of initiation being separated by a fairly constant vertical distance and by an equally constant angle of divergence. Nishimura and Miyaji[9] observed a similar phenomenon in the sympodially extending conidiogenous cells of *Hortaea werneckii* (Horta) Nishimura & Miyaji.

Before we can postulate on the detailed nature and behaviour of the organizing principle, we must first analyse the overall process of conidium development into its different stages. The most recent analysis is that by Minter *et al.,*[11,12] in which the following stages were recognized (Fig. 4): 1) 'Proliferation' — reorientation of the conidiogenous cell apex to commence production of a new conidium or conidiogenous cell (meaning extension or swelling). 2) 'Conidium ontogeny' — restricted to the building of the conidial walls. 3) 'Conidium delimitation' — production of the demarcation layer. 4) 'Conidium secession' — detachment of the newly produced unit from the conidiogenous cell. 5) 'Regeneration' — the stimulus to initiate proliferation

We suggest that, in order to explain the observed helical arrangement, the process of regeneration is localized to a small zone at the periphery of the conidiogenous cell (Fig. 5). This moves, first circumferentially, clockwise or anticlockwise, around the cell. It then moves upward (distally) on a circular front, as shown diagrammatically in Fig. 5). This phase represents the onset of proliferation and can more specifically be described as centripetal. Apical wall-building can then inaugurate the 'ontogeny' phase. The observed arrangement strongly suggests that the initiating principle moves upward in a helical manner, as shown in Fig. 6a,b. This inaugurates the 'proliferation' process at a predetermined distance distal from that of the previous conidium, and at a predetermined angle of divergence from it.

How do the conidia remain attached to the mother cell? It is possible that the first or last part of the circumferential wall to be laid down at the base of each conidium may be slightly thicker or stronger than the rest. Alternatively, the enzymic processes involved in the 'secession' process may also sweep around the periphery of the cell along a helical track. Once the conidium has tilted sideways far enough to allow the new percurrent apex to grow past it, there is no need for the secession process to be completed and the 'centre of secession' moves on without finishing the job. This can happen in both sympodial and annellidic conidiogenous cells.

We note that in different species of *Leptographium*, the intervals between annellations vary (Fig. 7a–c). In *L. procerum* (Kendrick) Wingfield these intervals are very short, and we assume this to mean that the helix is very tightly wound or compressed (Fig. 7a). We note that only a few of the broadly based conidia typical of this genus can be fitted into a single gyre around the narrow conidiogenous cell. In *L. terebrantis* Barras *et* Perry the interval between annellations is larger, and we assume this means that the helix is more loosely wound, or less compressed (Fig. 7b). In *L. truncatum* the annellations are widely spaced, and the helix is assumed to be yet more lax (Fig. 7c). We hope that in future it may be possible to add a new character to the description of these species by specifying the nature of the helix, as expressed in the vertical distance between successive annellations and the angle of divergence between successive conidia.

Although we have not yet been able to determine whether any equivalent of contact parastichies exists in fungi, we intend to carry out computer modelling in which the axis and equatorial outline of each conidium will be extrapolated upward and fitted among those of the other conidia to determine whether contact parastichies result.

Conclusion

The arrangement of conidia on or around conidiogenous cells is a potential source of information concerning the intricate and invisible developmental processes involved in producing many mitospores from a single mother cell, but the possible taxonomic significance of this feature has previously been explored in only one other paper[9] We believe that this phenomenon must be examined in a wide range of fungi, and this will be the subject of a future communication.

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