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NOTES ON THE BASIDIUM—II*

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Some critical remarks are made on the treatment of the basidium in a recently published handbook on cryptogams by M. Chadefaud.

INTRODUCTION.—The following has been written as a comment on a recently published treatise on the basidium occurring in a handbook on non-vascular plants (Chadefaud, *1960*).

CHADEFAUD'S BASIDIAL TYPES.—Three basidial types are distinguished (pp. 690–695): (i) the basidium of the Archeobasidiae ("la basidie des Archéobasidiés"), (ii) the basidium of the Neobasidiae-Heterobasidiae ("la baside des Néobasidiés-Hétérobasidiés"), and (iii) the basidium of the Neobasidiae-Homobasidiae ("la baside des Néobasidiés-Homobasidiés"). To simplify these somewhat cumbersome indications they may be reduced as follows: (i) the archeobasidium, (ii) the divided neobasidium, and (iii) the undivided neobasidium. It must be understood that Chadefaud himself does not make use of these simplifications, except in the case of archeobasidium which term he defines in a somewhat restricted sense although he applies it in the circumscription here given.

In the archeobasidium the probasidial cell, generally short, sprouts a single basidial tube ("boyau basidial") which becomes transversally divided. (It is this divided tube which Chadefaud defines as archeobasidium.) In the divided neobasidium the probasidial cell itself becomes longitudinally divided and each resulting cell sprouts a basidial tube which itself remains undivided. The dividing walls in both these types are formed across mitotic division spindles of the diploid nucleus of the probasidial cell (probasidium). In the undivided neobasidium there is neither wall formation in the probasidium nor any striking sprouting of basidial tubes.

Setting aside the possibility of polytopic origin of the same basic ideas, I think it is clear that Chadefaud has taken up Neuhoff's conception of the basidium (*1924*) embellishing it with some new terms. The 'boyaux basidiaux' are Neuhoff's epibasidia. The omission of any direct mention of Neuhoff's publications devoted to the same subject attracts attention. The existence of other conceptions is not even hinted at. The reference "Rogers (A. H.), Mycologia, 28, 1936" (D. P. Rogers, "Basidial proliferation through clamp-formation in a new Sebacina"), does not lead even indirectly either to the work of Neuhoff (*1924*; *1935*: *Schwarzt. 1*) supported by Rogers (*1934*), or to that of Donk (*1931*); and no references are given to later

* The first paper was published *in* Blumea (Suppl.) **4**: 96–105. 1958.

publications in which different conceptions from Neuhoff's are defended: Talbot (*1954*), Donk (*1954, 1956, 1958*), Martin (*1957*).

It is not my intention to enter upon a critical examination of the basic principles of Neuhoff's—and Chadefaud's—conception: this was already done by myself and more recently *in extenso* by Talbot (*1954*) now several years ago. What I aimed at on this occasion was to find out if there was something new linked up with the introduction of still more new terms like Archeobasidiae and Neobasidiae. The answer is short: Very little.

CHADEFAUD'S CLASSIFICATION.—After having defined the main basidial types, Chadefaud proceeds to present a concise treatment of the classification of the basidiomycetes.

His Archeobasidiae comprize the Uredinales (inclusive of the Graphiolaceae), the Ustilaginales (inclusive of the Tilletiales), the Septobasidiales, and the Auriculariales. The association of these orders is one currently accepted. What is remarkable is that the Tremellales are not included but referred to the Neobasidiae, thus significantly divorced from the Auriculariales. Many authors, even those who adhere to Neuhoff's conception of the basidium, regard the Auriculariales and Tremellales as closely related and the two are sometimes even combined into one order.

Another peculiarity of Chadefaud's classification that leaps to the eye is that several groups are kept within the Archeobasidiae in accordance with current tradition although they do not answer to his definition: they lack the persistent probasidium which was made part of the definition of the group. For instance, among the Uredinales, the Coleosporiae 'form their archeobasidia inside the teleutospore'. The same situation (viz. that the probasidium itself is transformed into a transversally divided metabasidium) is also more or less completely realized in certain Auriculariales and Septobasidiales. Although Chadefaud acknowledges this situation for both the Uredinales and the Auriculariales, these facts seem not sufficiently to have disturbed his faith in his definition of 'the basidium of the Archeobasidiae': it would appear that although theoretically this basidial type ought to be characterized by a persistent probasidium, Chadefaud is disposed not to emphasize this point where convenient and to call by the same term any transversally divided metabasidium whether it replaces the probasidium or sprouts from it as a distinct outgrowth. A similar view has been accepted for some time by Donk, Talbot, and others. Chadefaud's archeobasidium is nothing else but one of the many aspects into which the metabasidium may develop: the transversely septate metabasidium.

The Neobasidiae-Heterobasidiae comprize only one order, the Tremellales. That this includes the Tremellales in the restricted current sense (longitudinally divided basidia only) is comprehensible in regard with the definition of the basidium characterizing the group. However, it will be difficult to digest that the Tremellales have also become the receptacle for the genus *Tulasnella*, the Dacrymycetales, and the genera *Vuilleminia* and *Brachybasidium*. The disaccord between definitions and

classification based on it will be confusing to the uninitiated reader; for it appears that the actual definition of the divided neobasidium in its adjusted form should read rather: any basidium (even undivided ones) that forms basidial tubes with the exclusion of those cases in which the metabasidium becomes transversally septate.

The Neobasidiae-Homobasidiae include all other basidiomycetes (inclusive of the Gastromycetes) as well as the Sporobolomycetaceae as a distinct order. A few words will be devoted below to this latter group.

ARCHEOBASIDIUM AND ASCUS.—According to Chadefaud (pp. 690–691 & *f.* 509) the archeobasidium (that is, the transversally divided metabasidium) 'is an ascus in which spore-formation has been transformed into a segregative division, and the ascospores, into ascosporal cells which are spore-producing segments.' This conclusion is presented as plain fact rather than pure speculation: Chadefaud knows precisely what happened to the ascus when it became the basidium, and the ascus that performed the feat was one sprouting from the equivalent of a probasidium.

To begin with, asci sprouting from a 'pro-ascus' are rare if they exist at all. What looks like one, for instance, the 'ascus' of *Taphrina* (where the 'pro-ascus' may be lacking), may even not really be an ascus (Lohwag, *1934:* 247). In any case it is chiastic (Juel, *1921:* 38–39) and the archeobasidium, stichic.

Further, I would contest that it is evident that 'the septation of the archeobasidium into sporiferous part-cells is equivalent to the delimitation of the ascospores in the ascus'. The cross-walls dividing the metabasidium into cells are formed in connection with nuclear divisions and perpendicular to and across spindles, while the formation of the ascospore walls depends on each of the individual nuclei irrespective of the spindles. The division of a metabasidium into four cells requires only three walls (1 + 2 division spindles), while the formation of four ascospores requires four. In my opinion, two quite different processes and types of wall formation are here equated without supplying any argument in support of the thesis. I would meet Chadefaud's derivation with greater accommodating spirit if he could have pointed to an ascus that first becomes divided into four cells and then forms a spore inside each of these part-cells. In such an ascus the spores would have become trapped (for they cannot be shot away from the ascus top) and they would perhaps have to germinate through the sides of the ascus producing secondary spores to be discharged violently from the germination tubes. Such an ascus or one coming near to it is not known to me, but in phylogenetic discussions it can easily be postulated.

Without the existence of such an ascus type, Chadefaud's derivation of the transversally septate metabasidium from the ascus is as speculative as any other one deriving the basidium from the ascus, for instance, the one now more currently favoured and which derives an undivided basidium from an undivided ascus.

Chadefaud's choice of the terms 'Archéobasidiés' and 'Néobasidiés' is evidently determined by his assumption that the transversally septate metabasidium is primitive, but he has not contributed any argument that would let this view prevail

over the one which considers the holobasidium as primitive. It is also arguable whether it is really necessary to derive the basidium from the ascus or the reverse.

CALOCERA.—Chadefaud (p. 691) stipulates as the one basic difference between the archeobasidium and the neobasidium that the former sprouts before the basidial diploid nucleus divides and that the neobasidium does so after this process has occurred.[1] Evidently, he homologizes these two types of sprouting, like Neuhoff did previously. This means homologizing certain sterigmata with metabasidia and in Chadefaud's case mixing the cytological processes occurring in the two organs. This homologizing of strongly developed sterigmata (cf. Donk, *1954*) with metabasidia has lead Chadefaud not only to postulate possible ancestral *Tremella* basidia with sterigmata behaving like archeobasidia by becoming one-septate and developing an extra lateral sterigma (*f. 510: 5, 6*) but also to present a truly remarkable version of the *Calocera* basidium.

Chadefaud's interpretation of the basidium of the Dacrymycetales (which order he sinks into the Tremellales) agrees with that of Neuhoff's, with one not too profound difference, viz. that he calls "boyaux basidiaux" what Neuhoff called epibasidia (and Donk, sterigmata). To illustrate these organs some remarkable figures of basidia of *Calocera* are offered, showing 'a non-septate probasidium and only two basidial tubes in which the second mitosis is staged and which are transversally divided by a cross-wall'; Chadefaud adds 'after R. Maire' (*f. 511: 4*). This is an erroneous representation of the actual situation, at least as far as published facts go. Maire (*1902:* 78) reported of *Calocera cornea* that the diploid nucleus of the basidium divides once or twice resulting into two or four daughter nuclei; each spore receives one nucleus which soon divides mitotically followed by the formation of a cross-wall. There is nothing in Maire's account that would suggest that the sterigmata are the seat of a nuclear division: if a second division occurs this is in the 'probasidium' (after it has become the metabasidium). Consequently division of the sterigmata by a true cross-wall across a division spindle was not reported by Maire, and as far as I know no one else has observed the true cross-wall Chadefaud depicts.

What is known is that, for instance, in the *Tulasnella* basidium a nuclear division may occur in the sterigmata (Juel, *1897*; Rogers, *1932*), but exactly from this example it can be deduced that no cross-wall formation need occur as a consequence of such a mitotic division. In fact formation of true cross-walls (cf. Donk, *1958:* 96–98) is rather a minority phenomenon: it is known only in the Uredinales and some comparative small groups, Septobasidiales, Auriculariales, and Tremellales, thus in the metabasidia of the Phragmobasidiae.

VUILLEMINIA AND BRACHYBASIDIUM.—Another unexpected representation of facts occurs in connection with these two genera (Chadefaud, p. 739 *f. 511: 3, 6*): the apical portion of the 'neobasidium' of *Vuilleminia* is interpreted as a single basidial

[1] 'As a consequence', he writes, the divided neobasidium becomes longitudinally divided (p. 691). I cannot follow this reasoning.

tube representing four fused ones, while the metabasidium of *Brachybasidium* is similarly derived from two fused basidial tubes, each of the fused tubes being indicated by a sterigma producing a spore. Chadefaud derives his knowledge of these basidial types from the work of Maire (*1902:* 81–82 *pl. 2 fs. 5–13, pl. 8 f. 3*) as to *Vuilleminia*, and from a publication by Gäumann (*1922*) as to *Brachybasidium*.

His interpretation implies that four (*Vuilleminia*) or two (*Brachybasidium*) daughter nuclei of the diploid nucleus migrate from a persistent probasidium through a single basidial tube into the spores, in the case of *Brachybasidium* apparently after having divided once more on their way judging from Chadefaud's figure 'after Gäumann' but which Gäumann never published. The published facts are quite different: in both genera it is the diploid fusion nucleus itself that migrates into the tubes (metabasidia) and there enters upon its first and second division(s). There is no reason to interpret the metabasidia of these genera as: basidial tubes homologous to the sterigmata of *Calocera* 'except that the basidial tubes have united into one'.

THE SPOROBOLOMYCETACEAE.—This group (of which Chadefaud mentions only *Sporobolomyces*) is considered to belong to the Neobasidiae (p. 737 *f. 516: 5*), the individual yeast cells becoming transformed into monosporous basidia. A considerable amount of literature has accumulated around *Sporobolomyces* and some other genera (*Tilletiopsis* Derx, *1930*; *Itersonilia* Derx, *1948*) from which it appears that no author has really definitely defended the above mentioned view although most authors seem to be inclined to consider all these genera basidiomycetous. Donk (*apud* Derx, *1948:* 468) found it necessary to propose the term ballistospore to replace the use of the term basidiospore in these instances and to avoid, *inter alia*, the short-circuiting to which Chadefaud has succumbed. It may appear in the future that Chadefaud is correct but some semblance of proof now would undoubtedly have been appreciated. In any case there is no sufficient cytological basis to support the view that the individual cells producing (sometimes more than one) spores may be homologized with basidia (Guillermond, *1928*). Or has Chadefaud taken Sainclivier's observations and theoretical suggestions (*1951a*; *1951b*; *1952*) as sufficient evidence and gospel?

HIRSUTELLA VARIANS.—This species (originally described as *Matruchotia varians*) is considered by Chadefaud (*f. 526: 1*) to represent a species of Cortiaceae producing not only conidia on conidiophores analogous in appearance to the phialides of imperfect Ascomycetes but also intermediate organs that show these conidiophores in reality to be homologous with basidia so that they should be regarded as basidia with single sterigmata. This view of Boulanger (*1893*) has been carried from handbook to handbook, but there is reason to believe that the species is non-basidiomycetous and nothing but an imperfect state, even though some of the conidiophores closely imitate two-spored basidia.

STICHIC CLAVARIACEAE.—Chadefaud (p. 694) contends that all Clavariaceae have stichic basidia. This is not the case. Although Juel (*1916*) and Bauch (*1927*) found that the species since referred to *Clavulina* and perhaps one other species had stichic basidia, it clearly appeared from Juel's publication that the basidia of other Clavariaceae in the wide sense he investigated were chiastic; the latter species are now referred to *Clavariadelphus* and *Ramaria*. I should not be surprised if the great majority of the clavarias proved to be chiastic or hemichiastic; the outstanding examples known of the stichic clavarias are nearly all species of *Clavulina*. *Clavaria falcata* of Juel which that author reported as being stichic does not belong to *Clavulina* but its identity is still an unsolved problem.

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