

Pezizaceae taxonomy and classification: Boudier, Cooke and Korf

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Summary: Richard Korf is an important figure in the study of discomycetes. His contribution as teacher and scholar in relationship to Boudier's masterwork, the *Icones Mycologicae*, is commented upon particularly in regard to the classifications used for the *Pezizaceae*. Although it has been common practice to recognize a single genus *Peziza* for most of the species in the *Pezizaceae*, molecular phylogenetic studies have shown that the genus *Peziza* is diverse and is not monophyletic. Boudier's classification shows a more accurate picture of the diversity within the family than later classifications. Comments on the *Icones* and Cooke's *Mycographia* are included as they relate to graduate training and opportunities offered by Richard Korf in his long career as a teacher.

Keywords: classification, discomycetes, *Galactinia*, generic concepts, *Pezizaceae*.

The celebration of Richard Korf's career in his 91st year provides an occasion to reflect on things I learned from this master teacher and reflect, as well, on the part he played in fomenting change and in accepting the change that comes with the application of new and varied techniques. There is much that could be written about Dick — his presence in class, his acting career, his strong political views, his purple-inked editorial scribbles and his enduring interest in cup-fungi. The operculate discomycetes, *Pezizomycetes*, held a special place in his studies. From the start, he intensely collected and worked on these fungi. He published a brief outline of the order *Pezizales* early in his career (KORF, 1953) and had plans for a major overview that was realized, in part, in his chapter in *The Fungi: An Advanced Treatise* (KORF, 1973a) and in his Mycological Society of America Presidential address (KORF, 1972). Well documented and innovative, these works direct us in our studies. He was particularly keen on using Boudier's *Icones Mycologicae* as a way to ground the user of his keys; in *The Fungi 4A*, he listed Boudier's illustration as a guide. He also provided the updated nomenclature for most of the *Pezizales* for the reprinted version of the *Icones* (KORF in BRUMMELEN *et al.*, 1985). In this short paper, I make some general comments on Boudier's work both from the standpoint of its importance in thinking about classification and as a resource for students and professionals. The classifications employed by Boudier and Le Gal and as reformulated by Korf ultimately have informed the phylogenetic classification we undertake today. My primary focus in this paper is on the *Pezizaceae*, that is, those larger taxa with asci that generally become blue in iodine solutions, complex often fragile excipular tissues frequently composed of globose cells and hyaline or light brown ascospores. Boudier's work across the *Pezizomycetes* presents a classification scheme that has been one of the most successful and enduring. In many cases, the classification points to relationships that have now been confirmed in phylogenetic studies. It presents a unified view of these fungi as known from temperate regions.

Although quite different in character, the illustrated work of M. C. Cooke, the *Mycographia*, also relates to classification of the order,

particularly in term of making names for groups that have been taken up at various times. As an illustrated work, the *Mycographia* leads us to further investigations but rarely does one have the confidence in Cooke that one can place in Boudier. But, Cooke too had a major influence on the classification of the operculate discomycetes.

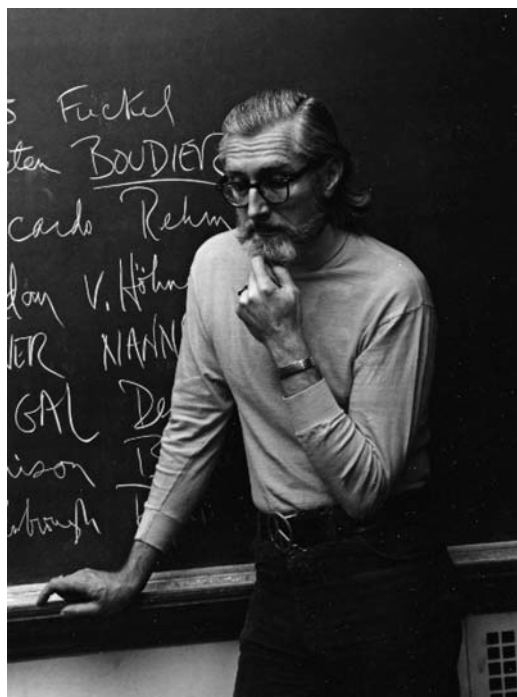
Within the first few months of my settling down to study mycology at Cornell University, Dick introduced me to Émile Boudier's *Icones Mycologicae*. This was not the reprint of 1986, but rather one of the original copies. These volumes, borrowed from the library, were under lock and key in his office/lab and had belonged to Elias J. Durand, another discomycetes researcher. Boudier's *Icones* is per-

haps unique in the mycological literature in the quality of the lithographed illustrations, the broad scope of the work in its coverage of temperate fungi and the detail of the illustrations. The dazzling renderings of cup-fungi in these volumes guided me in my investigations. KRIEGER (1922) said of the *Icones* that, "it is a positive delight to use them; indeed, were all published plates like these, there would be little question as to the identity of species."

In retrospect, I think it is fair to say that having the *Icones* encouraged me to study these fungi; Korf himself writes in much the same vein regarding his own experience (KORF in BRUMMELEN *et al.*, 1985). It was not just that the apothecia were so well rendered but with these illustrations one could see the fungus *in situ*, look at a magnified view and see the microscopic details of asci, spores, paraphyses and tissue structure. The descriptive text filled in where the illustrations left off. These were measured drawings done from living specimens; but, as BRUMMELEN (1969) pointed out, the measurements were not accurate because of a

miscalibration of the magnification of Boudier's microscope. They are 10% larger than in fact because of this mistake. Still, one learned from the plates which characters were important for making identifications. The plates took one from the field to the microscope and then to a name. Boudier's fungus names have been catalogued and commented on by VAN VOOREN (2011, 2012).

My experience in graduate school would have been much different today. Boudier's *Icones* is now readily accessible to the beginner



R.P. Korf, photograph by Howard Lyon, March 1972
Courtesy Cornell University Plant Pathology
Herbarium, CUP-052456

because of the bibliographic publications by Korf and Van Vooren, access through the reprinted volumes, and on-line through the Biodiversity Heritage Library (<http://dx.doi.org/10.5962/bhl.title.49695>) and the Hathi Trust (<http://catalog.hathitrust.org/Record/100699252?type=all&lookfor=boudier&ft=ft.>). Whether my experience would have been as exciting or as special using these internet resources I do not know, but access to these along with supplementary guides to the names surely informs and enlightens. Still, to be sequestered with the books themselves was inspiring and to have the master teacher, Dick Korf, to interpret the work was an exceptional experience for a young mycologist.

For the beginner in those days, the classification scheme and particularly the nomenclature of the *Pezizales* as presented by Boudier was not completely transparent. For starters, one needed to know that rules for naming were not solidified in Boudier's time and that the French perhaps had a special view of nomenclature. As a neophyte, I needed an explanation of why it was that the species of *Aleuria* in Boudier had asci that were blue in iodine solutions and had little to do with the species that I was taught belonged to *Aleuria*, that is, the orange peel fungus, *Aleuria aurantia* (Pers.) Fuckel. That fungus was *Peziza aurantia* Pers. in Boudier's classification. To further complicate this picture, *Peziza* species, that I was then just learning, were also to be found in the genus *Galactinia* in Boudier's system. Korf made it simple. In one of his many nomenclatural works (KORF, 1960) he explained, in a discussion of the name *Plicaria*, that essentially all larger species with iodine positive asci, whether with spherical or ellipsoid spores and whether guttulate or not, were to him *Peziza*. *Aleuria* was the genus for the orange fungus because of the technicalities of typification. In Korf's judgment, the form of the ascospores, their guttulation, or their ornamentation were not alone sufficient characters to recognize multiple genera. I examined Boudier's *Icones*, I tussled with the nomenclature, and I learned from both Korf and Boudier. As will be seen later in this article, the tangle of nomenclature plays out in quite a different way in the present era where phylogenies often give us a refined way to look at the classification.

I have made the case that Boudier's *Icones* was and still is important for identification and classification. To the researcher, it holds a wealth of information; but, to the bibliophile, it is also an object of interest. The illustrations were published along with preliminary text in fascicles, 30 in all, from 1904 to 1910. All fungi were included but the discomycetes took center stage, particularly the *Pezizales* that took up all of volume two. STAFLEU & COWAN (1976), BRUMMELEN *et al.* (1986) and VAN VOOREN (2012) laid out the publication history with dates of issuance of the plates and the exact dates of publication for nomenclatural purposes. The plates were numbered in two ways, a preliminary number and a final number. The purchaser held the plates until all were issued and then they were bound, generally as three volumes. The final descriptions constituted a fourth volume. In some libraries and in the reprint, the preliminary text descriptions, important in some cases for establishing priority, are also preserved. The final version of the text includes a subscription list where one can find an enumeration of the sets purchased by a particular institution or individual. There were 125 complete sets. The Durand copy that I used at Cornell University was number 35.

Boudier's *Icones* was a project of great ambition. At the beginning, 250 fascicles were published but subsequent fascicles were printed in editions of only of 125 copies as mentioned above. A partial set of the plates is found at The Ohio State University accompanied by a letter dated April 6th, 1907, from C. G. Lloyd stating that the publisher gave him several sets of 72 of the excess plates which he, Lloyd, distributed (<http://hdl.handle.net/2027/osu.32435031374077?urlappend=%3Bseq=1t>).

Lloyd writes that, "the plates are the ideal of perfection in mycological illustration." Thus, this is a rare and special book and was of quite limited distribution. I realize now that being able to use this book and learn by examination of the plates was one of the special privileges of my mycological training with Dick Korf, and even today a trip to Boudier's *Icones* can provide a simple and elegant solution to a vexing problem.

On coming to Harvard, I was fortunate to have access to the *Icones* in the Farlow Library. This time it was William G. Farlow's copy¹, number 40 on the subscribers list. I noted that there was also a Harvard College copy, number 46. This copy was outside the domain of the Harvard Botany Libraries. A search began for set 46 and lasted for perhaps 15 years. It seems it was transferred within Harvard, but where could not be determined. My hopes of locating it were dashed when the Botany Libraries received several loose plates from the *Icones* with the Harvard College stamp prominently displayed on them. Surely somewhere living rooms are graced with these precious lithographs that were somehow either deaccessioned or stolen from a Harvard Library and obviously disassembled. Very shortly after I wrote the sentence above, I was in an antiques market and saw— to my dismay— several framed plates from the *Icones*. In the upper part of one, peaking out from under the mat was the embossed shield of the Harvard College Library. Authorities in the library were not inclined to follow-up. My fear of the desecration was well founded it seems.

That Farlow used his copy of the *Icones* in his preparation of plates for his illustrated work is clear. As was his habit, he showed the preliminary renderings to mycologists around the world and annotated the originals accordingly. He used Boudier's *Icones* often. In Fig. 1 we have reproduced one of L.C.C. Krieger's original illustrations with Farlow's notation.

Some years ago I was in Paris at the Laboratoire de Cryptogamie, Denis Lamy, then the archivist for the unit, kindly allowed me to see some of Boudier's drawings and paintings housed there. To see these gives a full impression of the artistic ability of this man.

Boudier's hand on discomycete classification first was shown when he (BOUDIER, 1879) published a paper on the importance of the mode of ascus dehiscence in classification of the discomycetes. With this paper two groups of discomycetes were characterized: those with operculate asci, *Operculatae*, and those with a pore or irregular opening, the *Inoperculatae*. This classification was presented in his *Nouvelle classification naturelle des Discomycètes charnus* (BOUDIER, 1885) and elaborated in *Histoire et classification des Discomycètes d'Europe* (BOUDIER, 1907). The *Histoire* laid out a classification that was followed by subsequent French workers and has been the framework for much of the modern systematic work on these fungi. Not all of Boudier's contemporaries followed him and several systems came into use — most notably those of Saccardo, Rehm, Fuckel and later Seaver. Boudier considered his system to be a "natural" one; those of his contemporaries were perhaps more utilitarian. He used ascomal shape and color as primary characters, but importantly he used ascus reaction in iodine as a critical character. Features of spores such as guttulation, ornamentation and anatomical details of tissue construction were used to support his groupings. Because he knew these fungi well from field studies of fresh samples, he was influenced as well by ecological factors — where they grew and when they occurred.

By 1907 and the publication of the *Histoire* he recognized several groups among the operculate series. In the subsection Cupulés in family Pezizacées he recognized the tribe Aleuriées. The Aleuriées represent the core taxa of the *Pezizaceae* as currently recognized. The following genera were included: *Lepidotia* Boud., *Aleuria* (Fr.)

¹ The Farlow – Boudier connection is a strong one. They corresponded from 24 April 1892 until 24 December 1918. Farlow visited Boudier in Montmorency and they forayed there together. Farlow sent Boudier specimens for identification and Boudier sent Farlow specimens from France; these are in the Farlow Herbarium. Boudier also helped with the identification of the illustrations that Farlow had made for his illustrated *icones*, *Icones Farlowianae*. Boudier wrote with distress and sadness about his move to Blois during the war. According to University records Boudier's portrait hung in Farlow's office.



Compare specimen in alcohol
and dried specimens.

The drawing is not very characteristic

Helvella lacunosa vel aff.

See Plate in Weberbauer, Bulliard 466.

Sharon Moss. Not like the plate in Boudier Icones.

Piquet. 1911

Ar. 340

Fig. 1 — *Helvella lacunosa*

Illustration prepared for W. G. Farlow by L. C. C. Krieger. The text reads, "Compare specimen in alcohol and dried specimens. The drawing is not very characteristic. *Helvella lacunosa* vel aff. See Plate in Weberbauer, Bulliard 466. Not like the plate in Boudier Icones. Sharon, Mass. Piquet [Farlow's assistant and the collector of this fungus], 1911." Weberbauer refers to Otto Weberbauer, Die Pilze Nord-Deutschland mit besonderer Berücksichtigung Silesiens.



Aleuria *Reziya "repanda"*
June. 1904

Krieger 140

Fig. 2 — *Aleuria* sp. illustrated by L. C. C. Krieger from a specimen collected June, 1904

Gillet, *Galactinia* (Cooke) Boud., *Sarcosphaera* Auersw., *Plicaria* Fuckel and *Pachyella* Boud. Following Korf (1960, 1973a) and many modern treatments *Lepidotia*, *Aleuria* in his sense, *Galactinia* and *Plicaria* are referred to *Peziza*. In phylogenetic treatments, each of these genera represents a distinct clade. Hansen *et al.* (2001) recognized eight primary groups within the *Pezizaceae* and of these all six of Boudier's genera can be recognized and all but *Galactinia* represent monophyletic clades. *Aleuria sensu* Boudier is considered to be *Peziza sensu stricto*. Fig. 2 is one of Farlow's plates by Krieger showing a *Peziza* of the *sensu stricto* group. Farlow dutifully followed Boudier and labeled it *Aleuria* but without a species epithet.

Boudier (1885) first recognized *Galactinia* at the generic level. Cooke (1879) had proposed this name for a subgenus of *Peziza*. Boudier distinguished *Aleuria* and *Galactinia* by the presences or absence of spore guttules. In *Aleuria*, in his sense, the spores are generally without prominent oil droplets and, if ornamented at all, the ornamentation is generally composed of low warts. These are fragile fungi, their flesh being composed of mostly globose cells. In iodine solutions the asci generally show an intensely staining ring at the apex. Hansen *et al.* (2002) discuss this group as the core group of *Peziza*. It includes the type species of *Peziza*, *P. vesiculosa* Pers. Thus, these phylogenetic studies provide some good evidence that one could restrict the use of the name *Peziza* to members of this group. So far as is known, no member of the genus *Peziza* in the restricted sense are ectomycorrhizal; they are considered to be saprobic. The broad species concepts within the *Peziza sensu stricto* group, as presented by Hansen *et al.* (2002), needs critical review.

The *Galactinia* species of Boudier have been treated almost universally as *Peziza* species following Korf (1960, 1973a). These have asci that are blue in iodine but do not have the characteristic ring of the *Peziza sensu stricto* species, rather the reaction is intense at the tip and extends over the upper half of the ascus wall. Differences in the blueing reaction among members of the *Pezizaceae* were highlighted in Hansen *et al.* (2001). In *Galactinia* the spores are ellipsoid and generally biguttulate and are often ornamented with warts and ridges. At least some of the species included by Boudier produce a colored juice when the flesh is damaged. The flesh is composed of globose cells and interwoven hyphal elements. The accepted type species of *Galactinia* is *Peziza succosa* Berk. Phylogenetic studies show variation within *P. succosa* complex (Smith, 2014). The species that no doubt belong in this lineage are: *Galactinia succosa* (Berk.) Sacc., *G. succosella* Le Gal & Romagn., and *G. michelii* Boud. There are at least two hypogaeous members of the genus that should be moved to *Galactinia*: *P. erini* M. E. Smith and *P. infossa* Fogel & States. Members of the genus are ectomycorrhizal (Jabeen *et al.*, 2015; Lang *et al.*, 2011; Smith, 2014; Tedersoo *et al.*, 2007, 2009). Other species treated as *Galactinia* by Boudier fall primarily into another group, group VI of Hansen *et al.* (2001), for which there are several competing names.

A cautionary note is in order regarding the names combined in *Galactinia*. Like *Peziza* and *Aleuria* concepts have been broad, thus not all species named *Galactinia* belong in this genus in this restricted sense. The sorting of the species at this time is fragmentary, at best.

As mentioned above, the name *Galactinia* had its origins with M.C. Cooke, whose illustrated work introduced to me to another resource in pezizalean studies. This is COOKE's (1879) *Mycographia, seu icones fungorum* with its illustrations of discomycetes from around the world. In regard to classification, Cooke's contribution is a series of subgenera proposed in *Peziza*. Some of these, like *Galactinia*, came into use at the generic level. As compared to Boudier's *Icones*, Cooke's illustrations in the *Mycographia* are not beautiful. Sold also by subscription, it appeared in six parts over a four-year span. This, the only volume published in what was to have been a series containing other fungi, includes the so-called "fleshy" discomycetes. The illustrations were produced by lithography, but they are primitive in comparison to Boudier's *Icones*. The registration is not always accurate and the color ranges are limited. But, here one finds page

after page of illustrations, generally four to a page with descriptions on facing pages. The illustrations are simple and colors are, in most cases, best estimates from a dried specimens and descriptions. Microscopic features of asci, ascospores, and paraphyses are shown. Unlike sitting down with Boudier to feast on the nuisances of a well-served plate, Cooke always seemed half-baked. Where with Boudier one can say that you know something more for having studied the plate, with Cooke one leaves with an appetite for more information, for the need to return to type specimens. Thus, it was not uncommon that a researcher would borrow a specimen from Kew for study only to find that the image in the *Mycographia* was highly imperfect. Still, one can get a taste for the exotic that Boudier, with his illustrations of fungi mostly from France, could not offer. In Cooke's book, one finds fungi from Ceylon, Australia, Cuba or the Himalayas in this post card-sized format. It is appropriately subtitled "Figures of fungi from all parts of the world."

Boudier, Cooke and Korf intersect over considerations of Boudier's genus *Lepidotia*. Boudier described the genus, Cooke illustrated and described the type species and Korf sorted out the nomenclature, the morphology, and added information on an anamorph (Korf, 1973b). Following his consistent view that *Peziza* is a large genus in which, because of intergradations and ambiguous characters, segregates could not be recognized, he stated that its only indisputable species, *Lachnea hispida* Quél., should be included in *Peziza* as *P. quelepidotia* Korf & O'Donnell, a substitute epithet for one, *hispida*, that had already been used in *Peziza*. In this paper, Korf published plates taken from Boudier's *Icones* and Cooke's *Mycographia*. Phylogenetic studies now show that this species is distantly related to *Peziza sensu stricto* and *Galactinia* and should be recognized as an independent genus in the *Pezizaceae* with at least one other species. The name to be applied is *Lepidotia hispida* Quél.

When we look at the *Pezizaceae* as recognized today, the taxon is basically as circumscribed by Boudier with the exception of the several hypogaeous species that are now included. The number of genera has increased with additions such as *Scabropezia*, *Iodowynnea* and others, particularly from among the hypogaeous representatives, and we do understand more about the relationships within the genera and families. That still more genera will be needed to accommodate the many species referred to *Peziza* is unquestionable. All genera of Boudier's (1907) tribe Aleuriées, *Lepidotia*, *Aleuria* (= *Peziza sensu stricto*), *Galactinia*, *Sarcosphaera*, *Plicaria* and *Pachyella* can be recognized based on phylogenetic studies (Hansen *et al.*, 2001, 2002, 2005).

In conclusion, I suggest that several names that trace to Boudier and Cooke can be reinstated in the *Pezizaceae*. Although phylogenetic studies are still incomplete, it is evident that the broad definition of *Peziza* that has been applied for many years is untenable. As ecological, morphological and molecular data accumulate, we will surely see more lineages defined and we should name them. To name things clearly and unambiguously, according to the rules and with a feel for the organism, should be the goal. It is to Dick Korf who so clearly demonstrated the need for precision and the feel for the organism that I dedicate this paper. Thanks to Dick Korf and our illustrious mycological forebears, we are equipped to look deeply into questions of morphology, taxonomy, classification and history and in those investigations to find new insights.

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