AMANITACEAE

Irregular newsletter of the Herbarium Rooseveltensis Amanitarum

Rodham E. Tulloss, PhD, Curator, P. O. Box 57, Roosevelt, NJ 08555-0057, U.S.A.
telephone: +1 609 448 5096 – email: ret@eticomm.net

Vol. 1, No. 1, December 9, 2009

Editor's welcome and cautions

By means of this irregular publication, I hope to share knowledge among those with a serious interest in the family *Amanitaceae*. While one of my motivations is to provide broader access to information about the family, another is to expand the number of persons capable of reliably collecting, describing, determining, and publishing morphological taxonomic information concerning the curious taxa within the *Amanitaceae*. I have no idea how long this newsletter will last, but I thought I would give it a try.

There are few obligations placed upon the readers of *Amanitaceae*. However, they are obligations to humanity and the human knowledge and appreciation of the wonders, the factual workings, and the social value of knowledge of the organisms of the natural world. We are constantly reminded of the waning of education of traditional taxonomists. Over and over it is stated that we may have a multigeneration gap between today's active morphological taxonomists and those that hoped-for resurgent morphological taxonomic education may be able to generate in the future. One hopes for such a resurgence in order to educate the many taxonomists that the world needs in order to understand our planet sufficiently so that we do not destroy it and its inhabiting organisms.

Over and over it has been stated that morphological taxonomy may fall (or is falling) into the hands of persons that lack relevant scientific training. In the area of mycology in particular, the number of university trained professionals with an opportunity to research and report on a wide range of organisms is limited by such things as (1) the understandable demand for commercial work in plant and animal mycopathology, (2) the absence of jobs in academia, (3) the necessity of directing funding to inventorying, (4) the excitement over the novelty of molecular phylogeny, etc. At the same time that a few morphological taxonomists can be paid to support inventorying important landscapes, there are fewer and fewer positions (hence, less and less pay) that support major revisions of large taxonomic groups—one of the most important tasks of morphological taxonomy and one very likely to reduce the number of undescribed taxa in a thoroughly restudied group. It is more than a little distressing to have developed the ability to do necessary taxonomical work, and realize that the world appears to expect that a taxonomist will do her/his work for free in her/his retirement. But that's the way it is; and that's the way it may be for awhile. Hence, taxonomic knowledge needs to be distributed to the people who will do the work because they care to do it at least as much as they care to eat. I hope some of you are reading this newsletter.

There is a knowledge base and a skill base that takes decades for a taxonomist to develop. As many of you know, I did it the hard way. Because of my circumstances, I had to work alone a great deal of the time. I have made my share of embarrassing mistakes (sometimes clearly due to my lacking formal training) and probably will continue to do so. Nevertheless, I have come to a point at which a certain fraction of the world's knowledge about *Amanita* is embedded in my wetware. I want to get as much as possible out to those persons who may make a commitment of their wetware to carrying that knowledge forward through a possible Dark Age of morphological taxonomy.

As to those obligations, if you read this first issue of *Amanitaceae*, please pass it on. If you're reading this, you must have an interest in the curious species of the eponymous family of agarics. If you can do so, I hope you will follow where this interest leads you for as long as you can. I hope that your interest to know more will eventually exceed the availability of information, and that you will have to devise a means of getting the information for yourself. When you get that information, I hope you will not be satisfied, but that you will want to share that information as broadly as possible. Remember that there is an extra responsibily placed on persons that are largely self-educated. You have to create for yourself the discipline of doing science. You have to really commit yourself to the process of peer review. What if there is a "Dark Age" of morphological taxonomy in mycology? It is the under paid and under educated who will be utterly responsible for the quality of the science that is done. In the past, lack of such responsibility have led to individual and journals that have trashed regional taxonomy to the extent that an outsider has had to come along and reassess everythin. Vast numbers of varieties and forms of fungi are named based on things like small variations in cap color. If there is a "Dark Age" of morphologically-based taxonomy in mycology, then those who attempt to carry the work forward will be responsible for setting high scientific standards and maintaining the highest possible quality of research and publication. I regard this obligation as a fundamentally moral one.

A reputation can be made easily; but a good reputation that is deserved takes hard work.

—

Those lucky enough to have had a great teacher, realize in a heartfelt manner how many doors were opened for them and value greatly the enabling of understanding that such a gifted person is capable of giving away day after day, student after student. In this year, which is the fortieth anniversary year of his seminal publication on *Amanita* section *Lepidella*, I wish again to express my deep affection for, and sincere gratitude to, my dear mentor, Dr. Cornelis Bas. – RET

Determining an *Amanita* to section without a microscope—a synopsis

R. E. TULLOSS

< ret@eticomm.net >
P. O. Box 57, Roosevelt, New Jersey 08555-0057, U.S.A.

This document is a work in progress.
This draft was produced December 9, 2009 2:04 pm.

Introduction

For many years I've given a lecture on this topic, but I've never written down a text that would supplement the slides (of long ago) or the Powerpoint presentation of today. I hope this will serve to fill the gap.

The basic concept is that with a few directions and a set of "typical" images of key species, it is feasible to determine a fresh specimen to section using the naked eye. Without the ability to test for amyloidity of spores (by placing a drop of an iodine-containing solution on a small pile of spores gathered from a spore print), the greatest difficulty is in separating taxa of sections *Amanita* and *Validae*. The availability of tincture of iodine and aqueous KOH solution (about 5% to 10% concentration) in a collector's field gear should raise the accuracy of the following method to over 85%.

Within the *Amanitaceae*, *Amanita* is by far the largest genus with an estimated 900 (C. Bas) to 1,000 (RET) species worldwide. *Amanita* has an apparent "older sister" in the genus *Limacella*, a genus of only about 30 species worldwide and a likely evolutionary relict group with much to teach us about the origins of *Amanita*. I hope to discuss *Limacella* and some interesting hypotheses about the origin of *Amanita* in a future issue of *Amanitaceae*. Over the last century, two genera (*Torrendia* and *Amarrendia*) have been described that are now believed by several authorities to be synonyms of *Amanita*—they comprise sequestrate amanitas that seem assignable to *Amanita* sect. *Caesareae* (about which, more to follow).

Of course, you need to know when you have an *Amanita* in the first place.

Developmental definition of *Amanita*

Sufficient information exists about this unusual group of taxa so that we have several way to approach this definition. Of all known agarics, only *Amanita* manufactures its fruiting bodies in the "*Amanita* Way." The primordium of an *Amanita* is a solid mass that doesn't have any obvious morphological similarity to a mature fruiting body of the genus. As many field guides warn, a developing *Amanita* primordium may look (for example) like a puff ball. Guides often go on to urge the collector to make a vertical section through the supposed puffball, predicting that *if the "puffball" is an Amanita*, the collector will then be saved from possible poisoning because the shadowy form of a compressed *Amanita* fruiting body will be found inside the "puffball." The specific concern over mistaking amanitas for puffballs is not due to a guide's author saving keystrokes or ink by not listing examples from other genera. There are not other examples from other genera.

Amanita unique in having what is called a "gill-splitting" (schizohymenial) for of growth. Not only do the gills originate maximally tightly packed with hyphae intergrowing between their future spore-bearing surfaces; but the universal veil is thoroughly attached to the skin and/or flesh of the cap; the partial veil is connected to the gill edges and to a bit of volva that lies between it and the stipe; and the universal veil is originally interconnected to every part of the fruiting body that becomes exposed to the world as the primordium parts begin to separate during fruiting body expansion. Another way of saying this is that there are no gaps, no air spaces, in the primordium. Probably guided by a sequence of hormonal triggers, the parts of an

Amanita form and displace the less organized primordial tissues. Similarly, pigment production often is well underway prior to the break up of the primordium.

The webbing between the fingers of a human embryo disappears before birth. Somewhat similarly, all tissues connecting major agaric components (e.g., gill edges and the stem) within a primordial *Amanita* must break, gelatinize, decay, or be transformed into an easily broken intermediate surface (remember this is happening in three dimensions) so that the fruiting body can open. The powder material seen on the edges of almost all amanitas is an example of a friable surface—it allows the stem and gills to separate. Gelatinization of the cap's upper surface and/or the volva's lower surface allows the cap to slide out of a saccate volva in some species. In others a powdery layer allows separation of the cap from an otherwise membranous volva. There is a considerable diversity of mechanisms for the separation of cap and volva or for the break up of the volva.

At any rate, I think the point is made that the mode of development of the *Amanita* fruiting body (its ontogeny) is unique in the agarics and could served to define the genus.

Micromorphological definition of *Amanita*

Of course, most specimens of amanitas do not preserved cross-sections of primordia; so we need to know when we are looking at a specimen of a mature *Amanita*. If we were operating with a microscope, there would be two tissues to check. In fact these tissues can often serve to define an *Amanita* after it has been cooked. (I once used these two tissues to identify a curry that had killed its preparer.) The two slide preparations that are needed are a vertical cross-section of a gill and a bit of stipe context (again removed from the stipe's interor tissue by a vertical razor cut). In the stipe, the typical *Amanita* tissue is longitudinally organized and includes plentiful club-shaped inflated cells that Dr. Bas named "acrophysalides." These cells often dominate the stipe tissue. The cross-section of an *Amanita* gill could be described as follows: The outline of the cross-section has the shape of an elongated "V" with the sides somewhat curved so that while nearly parallel for much of the "V's" height they do finally come together at the bottom of the cross-section. Down the center of the "V" one observes a cable-like structure (actually the cross-section of a layer) of intertwined hyphae with some hyphal segments inflated like elongate balloons (these inflated cells are intercalary—not terminal on the hyphae). To both the right and left of the "cable" (the central stratum), hyphae and some inflated cells spread outward and downward in tree-like structures that give rise the basidia on the gill's two faces—as though the basidia were the leaves of the trees. This orientation of downward and outward divergence is described by saying that the tissue (trama) of the gills is "bilateral" or "divergent" trama. Hence, an agaric is an *Amanita* if its stipe tissue is longitudinally acrophysalidic *and* its gill trama is bilateral/divergent.

Now that we can see that there is no guess work about defining the genus *Amanita* if given time for observation and the appropriate resources (including a good microscope), we turn to the core of this note. How do we identify an *Amanita* to section in the field with limited resources and, in particular, without a microscope.

Macrocharacter-based definitions of *Amanita*

Traditional macroscopice descriptions often *Amanita* sometimes attempt to list the range of variation of character states for characters shared with other mushrooms. For example, cap color (character) can range through shades or white, gray, brown, red, orange, yellow, etc. (character states). This has always struck me as quite frustrating. *Amanita* is a rather large genus with a great diversity of characters, each often having more than two states. As we have seen above, it is unique among the agarics, in several, very easily defined ways. Can we capitalize on this in some way to simplify a definition of the genus from the point of view of field recognition?

PRESENCE OF A VOLVA (UNIVERSAL VEIL) AND ITS INTERNAL LIMB: "Volva present" doesn't cut it. A well-known mycologist recently described in the genus *Amanita* a lepiotoid species with a volva at the stipe base. It has also occurred on multiple occasions that amanitas with grassland habitats have originally been described in the genus *Lepiota*. One characteristic shared by most amanitas is, as noted above, a portion of the volva is actually "inside" the mushroom during development—between the underside of the partial veil and the stem (if there is a partial veil) or between the gill edges and the stem (if there is no partial veil). In many taxa this so-called internal limb (*limbus internus*) is often preserved in some form in expanding or mature mushrooms. In sect. *Vaginatae* it can leave a darkened circle around the lower stem in species with friable volvas or be found as a "volva inside the volva"—an extra limb attached at its base somewhere on the inside surface of the primary (external) part of a saccate volva. The same is true in sect. *Caesareae* with the additional wrinkle that the internal limb often has a felted extension that is often left in shreds on a mushroom's stem. In section *Amanita*, the internal limb is seen as a layer of powder on top of the bulb in some species, one or more persistent rings around the stipe base and top of the stipe's bulb in another, as an ocreate ("rolled sock") volva in others, or as an irregular limb attached near the stipe base in still another. The forms of volvas and their internal limbs will be treated below, section by section. The presence of a volva with a distinctive internal limb is a result of schizohymenial development; hence, it is a good marker for the genus *Amanita*.

GILL EDGE CELLS: Other genera may have a fertile gill edge (a gill edge populated by spore-bearing basidia) or a gill edge dominated by cystidia; however, neither of these possibilities are available in the case of an *Amanita* because the gill edge serves the purpose of bearing inflated cells that are to be sacrificed to the separation of the gills from the annulus or the stem. So it is of great value for the purpose of defining an *Amanita* in the field to use a 10× lens to examine the gill edges to see if they are marginate with white or pigmented powdery material. Because this latter material exists in or to be disrupted and lost, the gills may be imperfectly, irregularly, or incompletely marginate. Hence, irregularity in the form of, or the occasional absence of part of, gill edge decoration is actually supportive of the diagnosis of *Amanita*. Beware that in older material the gill edge cells will be dessicated and less obvious or may, in some cases, actually be lost. Again, because of the linkage between the *Amanita* type of sterile gill edge and schizohymenial development, the gill margin decorated with deciduous cells is a good marker for *Amanita*.

SPORE COLOR: The spores of *Amanita* are predominantly white or very pallid. There's nothing wrong with using this character as part of our arsenal. However, there is a pitfall that you will want to avoid. If at all possible do not let the gill edges of the mushroom you are spore printing touch the paper. If they do the cells on the gill edges may stick to the paper among the spores. If the gill edge cells are pigmented (e.g., they are yellow in *Amanita flavoconia* and many other taxa with yellow stems or yellow annuli and red in *A. rubromarginata*) and they are present on your spore print, they will distinctly alter the color of the spore print. Beware.

Unfortunately, of necessity, field guide rules for recognizing an *Amanita* are generalizations (like the ones just presented above) and some are not as reliable as others. For example, there are quite a number of amanitas with non-white gills; there are many amanitas with gills attached to the stem apex; there are several amanitas with forked gills. However, combining a mental or printed set of pictures of typical amanitas of various sections, sizes, and shapes (especially "rule-breakers") with the generalities of most field guides should be quite adequate to prepare a collector for identification at the level of genus.

Readers should obtain good illustrations of the taxa that may occur in their collecting region. Obviously, readers with broad travel plans will have to collect pictures for more regions. I have endeavored to make a list of "typical pictures," both relatively short and relatively adjustable to a wide variety of regions. I will introduce these lists throughout this note to back up and strengthen the reader's understanding of each section of the genus. One source of pictures covering a wide range of regions is the *Amanita* Studies web site that I edit with Dr. Zhu L. Yang (Kunming Inst. Bot., Yunnan Prov., China):
< http://eticomm.net/~ret/amanita/mainaman.html >.

The subgenera—*Amanita* and *Lepidella*

Here we are starting with concepts that may be unfamiliar to some readers, but they ought to make sense to all.

It is estimated that there are 900–1000 species in the genus *Amanita*. Possibly there are more than 1000. Of these, something less than 600 have been named according the research of Dr. Cornelis Bas (Leiden), Dr. Zhu L. Yang (Kunming Institute of Botany, Yunnan Province, China), and myself. Both from morphological studies of about the last 90 years and molecular studies of about the last 10 years, the genus is a natural group of species very likely to have descended from a single ancestor.

Within the genus, there appear to be two groups that are called "subgenera." A genus could have any number of subgenera; however, there seems to be a very natural division into two in the case of *Amanita*.

One subgenus includes all the known species with spores that do not become dark in iodine solution (called "inamyloid" spores); and this subgenus includes the defining species (or type) of the genus—*Amanita muscaria*. According to nomenclatural rules, this subgenus must have the same name as does the genus; so the subgenus including taxa with inamyloid spores is called "*Amanita* subgenus *Amanita*." Notice that the naming system has two parts (just as in the name of a species).

The second genus, in which are placed all the taxa with spores that do darken when placed in an iodine solution, is called *Amanita* subgenus *Lepidella*. To date, this method for segregating the genus into two subgenera has been shown to be very likely to represent the actual genealogy of *Amanita*, through molecular studies.

The two subgenera do not evenly divide the known taxa of *Amanita*, but both subgenera are still large enough and diverse enough to be unwieldy. At present, morphological taxonomists generally agree on dividing the two subgenera into seven sections. There are very few of us. We do not always use the same names for these divisions. I am in favor of a stable framework that is offered by the work of doctors E. J. H Corner and C. Bas as published in 1962. This framework included six sections. It became evident toward the end of the Twentieth Century that we needed to add a seventh; but this involved dividing one of the Corner-Bas sections in two, with no impact on any other sections. In this sense we have preserved a workable, stable structure...at least so far.

The sections of *Amanita* subgenus *Amanita*

The basic technical division here is based on ontogeny (the process of development of the "fruiting body" or mushroom). It's our good luck that the relevant results of the development process can usually be seen in an unopened button (a good reasons to look for specimens showing varying stages of fruiting body expansion) or (slightly less so) in maturing mushrooms.

Amanita section *Amanita*

The first key separating character can be seen by cutting an incompletely expanded button of an amanita longitudinally (top to bottom) through its center. If you cut a button of *A. muscaria* in this manner, the ghostly outlines of the mushroom cap, gills, and stem will be crowded into the upper part of the cross-section you've made. The position of the developing fruiting body is "eccentric upward." Most of the button is not participating in making the above ground parts of the eventual mushroom. That "uninvolved" part of the button is going to be a bulb. The bulb may shrink in width with water loss during further development; but much of the time, the bulb is going to be easily detectable at the base of the stem in the mature mushroom. Species of *Amanita* belonging to subgenus *Amanita* that develop so as to produce such a bulb include the defining species of the genus (just used as an example). Nomenclature rules required that we name the section including *Amanita muscaria*, *Amanita* section *Amanita*. Again, note that the name has two parts (is "binomial"), just like a species name. We have now defined our first section. Six to go.

Amanita section *Caesareae*

If the reader were to find a button of a species similar to *A. vaginata* and another similar to *A. jacksonii*, similarly sectioning the button would show the outlines of the maturing fruiting body approximately centered in the button; and there would be no "uninvolved" region. In the two cited species, the whole stem elongated without any bulb present at all. Oddly enough, the stems in such taxa are called "totally elongating stems." I chose to use two examples for this form of fruiting body development, because there are two sections that have this character. EXCEPT WHEN A SPECIMEN WITH AN ANNULUS HAS LOST THAT ANNULUS (also called "skirt," "ring," or "partial veil"), the two sections appear at present to be separable very simply. If there is never any partial veil (heavy flocculence at the top of a specimen's stem doesn't count as an annulus), then the specimen in question belongs in *Amanita* section *Vaginatae*. On the other hand, if there is an annulus on a specimen's stem and the mushroom meets the other conditions we have just discussed, the specimen can be assigned to *Amanita* section *Caesareae*.

Amanita section *Vaginatae*

You will notice that I've said nothing about the sort of volva that may appear on a specimen of any of the three sections of subgenus *Amanita*. This is because, the more we learn, the more we find that the form of a volva (or "universal veil") on a given specimen is NOT a good indicator of the sectional placement of that specimen. Studies in South America and Australia have produced several examples of species with a bulb at the base of the stem (species of sect. *Amanita*) that have that bulb enclosed in a membranous to submembranous saccate volva. Many of the readers of this article will be experienced with a species similar to *A. ceciliae* which has a totally elongating stem, but lacks a saccate volva enclosing that stem's base. Note that what may look like a bulb at the base of the stem in some species of the "*ceciliae*-type" is actually the cup-like base of the volva.

We have finished with the job of cutting three sections out of subgenus *Amanita*. This subdivision was developed from entirely morphological information. At present, it appears to be supported by results of molecular studies.

In order to fix a broad set of species images in the reader's mind ain association with the sectional names, I will make some suggestions of species images for each of the three sections. The purpose of the suggestions is to provide as broad a perspective of species color and habit as is necessary with a relatively small number of examples.

> Authorial citations are omitted for readability. Authors' citations are available on the pages dedicated to the cited species on *Amanita* Studies website: http://eticomm.net/~ret/amanita/mainaman.html

Amanita section *Amanita*—gestalt

This list of taxa will cover section *Amanita* rather well no matter where in the world the reader happens to collect. The individual taxa are usually restricted to a specific continent unless they have been moved by human means (usually as symbionts with a transplanted tree): (1) *A. muscaria*, (2) *A. xylinivolva*, (3) *A. pantherina*, (4) *A. farinosa*, (5) *A. roseitincta*, (6) *A. mira*, (7) *A. parcivolvata*, (8) *A. concentrica*, (9) *A. sinensis* [these latter two east Asian species are quite unusual in that they could be mistaken for taxa in sect. *Lepidella* (see below)], (10) *A. umbrinella* [as a representative of taxa with a bulb and a weak, sack-like volva—known from Australia and from Southern Beech (*Nothofagus*) forest in southern South America], and (11) *A. lanivolva* [as a representative of taxa with a bulb and a membranous, sack-like volva—known from South America].

Amanita section *Caesareae*—gestalt

With the same caveats as in the case of section *Amanita*: (1) *A. spreta*, (2) *A. caesarea*, (3) *A. jacksonii*, (4) *A. princeps*, (5) *A. egregia*, (6) *A. virginiana* [representing a group restricted to eastern North America], (7) *A. tanzanica*, and (8) *A. calyptroderma* [representing a group restricted to western N. America]. The *Amanita* entrants in the "puff-ball on a stick" parade are presently classified in the genus *Torrendia*. The *Amanita* entrants in the "let's be a truffle" reality program are classified in the genus *Amarrendia.* Tulloss and Yang argue that both of these genera comprise taxa that are assignable to section *Caesareae*.

Amanita section *Vaginatae*—gestalt

With the same caveats as in the case of section *Amanita*: (1) *A. fulva*, (2) *A. pachyvolvata*, (3) *A. ceciliae*, (4) *A. colombiana*, (5) *A. flammeola*, (6) *A. crocea*, (7) *A. sinicoflava*, (8) *A. liquii*, (9) *A. umbrinolutea*, and (10) *A. punctata*. This section appears to be very large, and a great majority of the taxa have not been formally described.

The sections of *Amanita* subgenus *Lepidella*

The existing technical division of this subgenus begins by segregation of two pairs of sections. The first pair (*Amanita* sect. *Lepidella* and *Amanita* section *Amidella*) is segregated by the presence of material of the universal veil on the margin of the cap ("appendiculate material"). However, this is a bit difficult to use because of the minimal and/or varying amount of appendiculate material that can appear on the cap margin in individual specimens. For example, it is very challenging to find appendiculate material on older specimens or on small, fragile specimens. To add to the difficulty, there has been some concern expressed about the dividing lines between the two sections traditionally said to have appendiculate margins. I propose to confront the situation as it stands and leave the necessary rethinking of section boundaries for another day.

Amanita section *Amidella*

This section is typified by the North American species Amanita volvata. Four major characters that are common to the bulk of taxa in the present section are the following:

(1) The stem is totally elongating, or would be if not for a brief flaring at the very base of the stem suggesting the open end of a bell. The known exceptions apparently have firm basal bulbs on the stipe: *A. neoovoidea* (eastern Asia), *A. ovoidea* (Europe, western Asia, and northern Africa), and *A. proxima* (Mediterranean region in a broad sense).

(2) The base of the stem is enclosed in a sack-like volva that is usually complexly layered and is often thick enough to suggest the presence of a basal bulb even though there may not be one.

(3) While the upper part of the stipe may be densely floccose, the majority of the taxa in sect. Amidella have an annulus on the stipe. The following are the exceptions: *Amanita neoovoidea* (eastern Asia - a floccose-subfelted and friable annulus may persist at maturity and is usually eventually lost), *Amanita peckiana* (North America - a transient membranous annulus is present in immature material only), *Amanita proxima* (Mediterranean region in a broad sense - a membranous and persistent annulus is present).

(4) The volva often separates from the cap by the breakage of a powdery (friable) layer that is usually the innermost layer of the volva or the next to innermost layer (in which latter case, the innermost layer is thin and fibrous). The species least likely to preserve remnants of volva on the cap (in my experience) are the North American *A. peckiana* and *A. whetstoneae* nom. prov.

(5) The internal limb is more or less floccose and often persists for some time on the surface of the stem.

In many species, flocculent material on the stem bruises/oxidizes brick-red or brownish red. In very fresh material (especially in rainy weather) pink staining of cut flesh may be noticed, although the color often fades rapidly. While a large piece of the entire volva may remain on the cap in some species, it is often the case that powdery or fibrillose volval remnants on the cap (above) will oxidize to red-brown and form patches or delicate decorations on the cap surface (sometimes even suggesting cuneiform writing).

This section contains three taxa that are not very similar to the section's type. Of those three taxa, one (*A. ovoidea*) could fit rather well in sect. *Lepidella*; and proper placement of the other two (similar) taxa—*A. neoovoidea* and *A. proxima* has not been sufficiently addressed to date. I will simply state that regardless of the above approach to recognizing section *Amidella*, the above three taxa are widely held at present to be included in the section.

Amanita section *Lepidella*

This section is a diverse collection of groups within *Amanita*. Many of the groups include only one or a small number of species. None are very large. Some of the larger ones appear to be restricted in occurrence to a single continent. The most primitive seem to represent a relatively successful group that are the surviving descendants of saprobic species with many

morphological similarities to the sister genus of *Amanita* in the family *Amanitaceae—Limacella*. The latter group includes taxa that are now thought of as pasture or lawn mushrooms because they are very well adapted to living on cellulose—grass clippings.

Exclude those species of section *Amidella* in which an appendiculate is visible. The remaining *Amanita* species having caps with appendiculate margins belong in section *Lepidella*. There are a few small species in which the appendiculate margin may be hard to see, and I'll address that in a moment. The appendiculate matter about which I'm speaking normally does not include parts of a broken partial veil that may hang from the cap margin, although such pieces may be present in addition to the appendiculate parts of the volva. The parts of the volva may those that are connected directly to the flesh of the cap, connected directly to the skin of the cap, or belonged originally to that portion of the volva that was originally included between the gill edges (or annulus) and the stipe when the mushroom was in the button stage. Sometimes the volval material appears as small crumbs; sometimes (as in *A. cinereoconia*) the appendiculate matter hangs like flocculent icicles from the cap margin.

Because the species of sect. *Lepidella* represent the present day relict descendants of what was probably an ancient period of great diversity of *Lepidella*-like ancestors, they are like the few groups of leaves on the many still living branches of a great evolutionary bush that, with the utter lack of fossil history for the *Amanitaceae*, we will never know. There are lepidellas with bulbs and lepidellas without bulbs. There are lepidellas with skirt-like rings on the stipe. There are lepidellas that are exannulate. The are odorless lepidellas, but a lot of them have very, um, "distinctive" odors. Most have white, cream or yellowish cream gills, but some have café-au-lait, brown, grass green, brilliant pink, various shades of ochraceous, or bright yellow gills. Many have a skin on the cap; however, a significant number have the volva directly connected to the cap flesh without an intermediate skin. Several well known taxa will leave flocculent volval material on your hands when you touch them. The variation in the microscopic structure of the volva is also great resulting in a wide range of the sizes and shapes of warts that are left on caps and/or basal bulbs. At least two have volvas that bruise blue-green. One species bruises raspberry red (and, to top it off, smells of anise). In a way, studying section *Lepidella* is like taking a world tour of the ruins of all known ancient, human cultures

Let's return to the species that may be the hardest to place in sect. *Lepidella*. In my personal experience, these taxa all fall into one group called *Amanita* subsection *Limbatulae* by Dr. Bas. These taxa have, at least, a marginate bulb or, at most, a thin membrane of hyphae standing up from the top of their stipes' basal bulbs. In both cases, the volva left on the cap is, at least, a thin layer of powder or, at most, that thin layer topped by a bit (or bits) of the hyphal layer that originally covered the powder and the rest of the fruiting body. It is the thin powdery layer and whatever remains there may be of the volval portion that once segregated the stipe from underside of the annulus (which is usually present in the species of subsection *Limbatulae*) that is responsible for what appendiculate matter may be found on the edges of their caps. To be utterly frank, sometimes the powdery layer is not very easily seen on the cap. For example, rain can wash it off. If you want to be sure that the powder is present on the inside of the membranous limb standing from a stipe's bulb, you will have to use a microscope. Indeed, without a microscope, it will often be difficult to tell a very depauperate specimens of *A. bisporigera* from these strange little beauties. Indeed, the extremely long and thin spores, which several of them produce, simply cannot be appreciated fully until viewed under an oil immersion lens at magnification of 1000× or more. It may help the non-microscopist, that these taxa are often found in deep sandy or gravelly soil of coastal plains. In addition, they are often deeply inserted (or even completely buried—with caps largely expanded) in the soil. My wife, Mary, once found a cluster of *A. cylindrispora* accidentally by kicking sand...and, coincidentally, exposing the tops of the caps of the expanding, long-stemmed mushrooms.

Amanita* section *Phalloideae

Amanita* section *Validae

***Amanita* section *Amidella*—gestalt**

The species for which images would be especially helpful to the reader are as follows: *A. ovoidea, A. neoovoidea*, *A. proxima*, *A. volvata*, *A. peckiana*,

***Amanita* section *Lepidella*—gestalt**

The species for which images would be especially helpful to the reader are as follows:

***Amanita* section *Phalloideae*—gestalt**

The species for which images would be especially helpful to the reader are as follows: *A. bisporigera*, *A. verna*, *A. ellipto-sperma*, *A. phalloides*, *A. fuliginea*, *A. longitibiale*, and *A. pseudoporphyria*.

Amanita section *Validae*—gestalt

The species for which images would be especially helpful to the reader are as follows: *A. citrina*, *A. brunnescens*, *A. rubescens*, *A. rubescens* var. *congolensis*, *A. excelsa*, *A. morrisii*, *A. perphaea*, *A. submaculata*, *A. cyanopus*, *A. squamosa*, ??

Acknowledgments

I wish to express my gratitude to Dr. Else Vellinga (Univ. California, Berkeley), Paul Derbyshire (Ontario, Canada), and Daniel Garton (Roosevelt, NJ) who provided thoughtful and thorough reviews of this article during its writing.