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**MORPHOLOGY AND SUBDIVISION OF AMANITA AND
A MONOGRAPH OF ITS SECTION LEPIDELLA**

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(With 382 Text-figures)

A historical survey of the delineation of the genus *Amanita* and its infra-generic classification is given. Morphological and other characters of *Amanita* are discussed, with emphasis on the characters and the behaviour of the volva. The term 'pileipellis' is proposed to replace Fayod's term 'cuticula'. In the taxonomic part synonymy and descriptions are given of the genus *Amanita* and its subgenus *Lepidella*, together with a key to the subgenera and the sections. Section *Lepidella* is provisionally monographed on the base of exhaustive examinations of type material, as far as available, and a usually limited number of additional collections. Of the 93 species recognized, sixteen are described as new, and seven provisionally as new species; three new names and four new combinations are introduced.

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PREFACE

The genus *Amanita* belongs to the oldest segregates of the Linnaean genus *Agaricus*. One of its most pronounced features is the wide variety of characters of the universal veil or volva. This makes it easy to understand why right from the earliest time that *Amanita* was recognized as a genus down to the present day the distribution and nature of the volval remnants on the mature fruit-body have played a leading part in nearly all infrageneric classifications that have been proposed for it.

Use of the characters of the volva in combination with a few other characters has resulted in an admittedly still rough—though on the other hand fairly satisfactory—sectioning of *Amanita*. If, however, an effort is made to determine the relationship between the large subdivisions and to arrange the constantly growing number of species in smaller units within these subdivisions it soon becomes evident that scarcely anything is known about the structures determining the diversity

of volval characters in *Amanita*. It is only fairly recently that a number of authors publishing on species of *Amanita* have begun including the microscopic structure of the volva in their descriptions.

When I began with the observations that resulted in the present study it was my intention to select a fair number of species of *Amanita* that represented all the different types of macroscopic volval structures that could be distinguished so that in these species I could study the connection between the microscopic and macroscopic volval structures.

Section *Lepidella*, because of its relatively wide variation in volval structures, appeared to be the most promising subdivision of *Amanita* to commence with. Moreover I supposed this section to be the most primitive in *Amanita*.

At that time I had assumed that Gilbert's (1940-41) monograph covering the entire world was a reliable source of information on specific delimitation in *Amanita*. But in 1963, during a trip of four months to the U.S.A., I became aware of the great wealth of the North American mycoflora. Soon I was forced to admit that the keys I had made for the species of *Amanita* as set forth in Gilbert's monograph, especially my key to his only five North American species in section *Lepidella*, was of no use at all!¹ The material in the few American herbaria I visited also presented puzzles. In general a large number of sometimes very different forms were filed under only a few frequently used names.

Thus it became clear to me that a monographic study of *Amanita* would have to precede my morphological study of its volva, as originally planned. I decided to combine the two but to restrict the detailed descriptions to section *Lepidella*.

This of course had the disadvantage of starting from a preconceived sectioning of the genus. I had the general impression, however, that the sections as circumscribed by Corner & Bas (1962: 243) were reasonably natural and that they provided a suitable starting-point for further observations.

I have studied the type collection of most of the species and varieties treated here and when possible also some additional collections. In all the collections cited I have examined the microscopic and macroscopic structure of the volva and the covering layer of the cap, the trama of the gills and stem, and the more usual microscopic and macroscopic characters. However I did not even attempt to bring together all the material of *Amanita* section *Lepidella* preserved in herbaria throughout the world. For a monograph the average number of collections studied is therefore very low. Not only would an exhaustive study of many more collections have taken far too much time but I was also faced with the difficulty that the tissues of many of the herbarium specimens were in such poor condition that examination of them would have contributed nothing to our knowledge of the morphology of the species involved. Furthermore descriptive notes on the fresh fungus were all too often lacking.

¹ Subsequently this was no longer surprising. Here more than 35 North American species of section *Lepidella* are treated.

For these reasons I restricted my studies to types, critical collections and a small number of illustrative collections selected from the material in a number of herbaria or sent to me by fellow mycologists.

The condition of the material examined often made the complicated microscopic structures difficult to analyze so that I am well aware that many of my findings will prove to need correction or completion once they have been tested on fresh or recently well-dried collections. Nevertheless I have good hope that in the main the arrangement of the species in section *Lepidella* proposed here will turn out to be satisfactory.

It is my intention to carry out a similar series of observations on the other sections of *Amanita*. Section *Amidella* will be the next.

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First of all I wish to express my deep gratitude to my senior colleagues Dr. R. A. Maas Geesteranus and Dr. M. A. Donk; to the former for making a mycologist of me, to the latter for trying to instil in me the principal problems of the present-day taxonomy of fungi, and to both of them for constant guidance, criticism, and inspiration. To Prof. Dr. C. G. G. J. van Steenis and Prof. Dr. H. J. Lam, present and former Directors of the Rijksherbarium at Leiden, I am greatly indebted for giving me the opportunity to carry out free mycological research.

My warmest thanks are extended to Prof. E. J. H. Corner, Cambridge, for putting at my disposal the extensively annotated collections, with excellent illustrations, of Asiatic species of *Amanita* that awakened my interest in the genus *Amanita* outside Europe, and to Dr. A. H. Smith, Ann Arbor, for inviting me to the U.S.A., thus giving the decisive impulse to my study of *Amanita* section *Lepidella*. The financial support for my trip in 1963 to the U.S.A. received from the Netherlands Organisation for the Advancement of Pure Research (Z.W.O.) and from American funds through Dr. A. H. Smith, Dr. L. S. Hesler, Knoxville, and the late Dr. A. H. Stockard, Ann Arbor, is gratefully acknowledged.

In a taxonomic study covering a cosmopolitan group of fleshy fungi an author must largely depend on the observations of other mycologists and collectors for the description of the characters of the fresh fruit-body. This is particularly so because in older descriptions these characters are often mentioned too briefly and because in many older collections descriptive notes are either lacking or else insufficient. To both Dr. A. H. Smith and Dr. L. R. Hesler I am therefore very much indebted for the generosity with which they put their herbaria, private notes, and photographs at my disposal. I am also greatly indebted to the following people for supplying me with valuable collections, notes, and illustrations of the species treated in this work: Dr. J. C. Aberdeen, Brisbane; Dr. S. Ahmad, Lahore; Mr. R. Bertault, Tanager; Dr. V. Demoulin, Liège; Dr. Ding Hou, Leiden; Mr. R. L. Homola, Orono (Maine, U.S.A.); Dr. T. Hongo, Ōtsu (Japan); Dr. E. Horak, Birmensdorf (Switzerland); Dr. G. Malençon, Rabat; Mr. A. Marchand, Perpignan; Mrs. M. B. Mills,

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MATERIAL, METHODS, AND PRESENTATION

Of the ninety-three taxa recognized here I studied only ten in fresh condition (three from Europe, seven from North America). Most of the collections examined were dried, some were preserved in liquid and a few of them both.

In general the tissues of well-dried material can be studied under the microscope without too much trouble. Unfortunately many old and even several recent collections have not been well dried. In these cases material preserved in liquid² is a great help, especially when it is the large, thin-walled elements of the trama of the gills and the stem that are to be studied. It would be advisable if future collectors of species of *Amanita* were to dry the largest part of their collections but at the same time preserve in liquid fragments of the essential parts of one fruit-body from each collection, especially when the drying conditions are not ideal.

With the fleshy fungi in dried material great reliance must be placed on collector's data for many characters of the fresh fruit-body. The collections cited here frequently proved to be incomplete, particularly as to data on colour, smell, and taste. Spore prints were often lacking and where this was not the case it was only rarely that the colour of the fresh print had been noted. Ecological data were extremely scarce.

The descriptions in this work are composed of (i) data derived from observations on the collections cited, (ii) data taken from labels, collector's notes and accompanying drawings, photographs, and colour-slides, and (iii) data borrowed from

² The material preserved in 25 % alcohol—4 % formalin by Prof. E. J. H. Corner, Cambridge, gave the best results.

published descriptions and illustrations relevant to the collections I myself studied. By way of exception data from other sources have been added between square brackets.

The terms referring to the size of the fruit-body have been standardized. Species of *Amanita* with caps up to 30 mm wide are called 'very small', 30–50 mm wide 'small', 50–90 mm wide 'medium-sized', 90–150 mm wide 'large' and 150 mm and wider 'very large'. For terms denoting the properties of the volva, partial veil, spores, covering layers and trama, see the relevant chapters.

Terms describing smells are so subtle in meaning that I have simply taken them over from the collectors' notes and original descriptions.

The structures of the tissues in the descriptions were studied in free-hand sections or minute, severed fragments soaked in drops of a 10 % NH_4OH solution or, if necessary, a mixture of equal parts of 10 % NH_4OH and 5 % KOH (referred to in the descriptions as 'alkaline solution') heated on a glass slide (without cover glass!). If the first results were poor the same process was repeated several times.

After the colours of the tissue in the alkaline solution had been noted the fragments were coloured by heating in an ammoniac 1 % Congo Red solution, then rinsed in 10 % NH_4OH and subsequently examined in 5 % KOH . The walls of the cells had usually turned bright red in colour and the tissues were easy to dissociate by gentle tapping on the cover glass.

Because of the large size of the cells (in the stems sometimes up to $400 \times 80 \mu$) and their thin walls it was usually necessary to first examine rather thick fragments in order to ascertain the disposition of the elements of the tissues. Following this the tissues were crushed under a cover glass or torn with needles for further analyses.

The amyloid reaction of the spores was studied in Melzer's reagent (see recipe in Singer, 1962: 82). It turned out that it was not affected by preservation in an alcohol or alcohol-formalin solution.

Within the subsections of *Lepidella* I have arranged supposedly related species in groups called 'stirpes'. As many species are still imperfectly known various minor shifts in the present system can be expected. In order to avoid a kind of fixation of it in detail I have therefore refrained from validly publishing a large number of 'series'. The naming of each stirpe after one of its species indicates which species I consider to be its 'type'.

My keys to the species of section *Lepidella* proceed step by step through subsections and stirpes. I considered adding a direct key to all the species of the section, but found that, after keying out a few species and groups of species with salient characters, I would have been left with a large group of species for subdivision for which I would have had to use the same characters that had already been used to distinguish the subsections and stirpes. This would only have made large parts of the supplementary key practically the same as those presented.

A disadvantage of the present key is that the stirpes are delimited rather vaguely so that there is a fair risk of looking for a species in the key of the wrong stirpe. I have

tried to meet this objection by including in the keys to the species many references to similar species in other stirpes.

Because of the fairly large variation in habit of the fruit-body in section *Lepidella* drawings of the fruit-bodies of nearly all the taxa treated have been made. In the many cases where there was no picture of the fresh fungus available I added drawings of a preserved fruit-body.

The illustrations of the fruit-bodies were drawn in natural size and reduced to $\times \frac{1}{2}$ (except that of *A. nauseosa*, which was reduced to $\times \frac{1}{4}$). The microscopic details of the volva were drawn with a magnification of $\times 650$ and reduced to $\times 325$, the spores drawn with $\times 2500$ and reduced to $\times 1250$. The scale of other illustrations is indicated in the legends.

Institutes from which material or documents were received on loan are indicated in the text by the following abbreviations, borrowed from Lanjouw & Stafleu (1964).

| | |
|------|--|
| ADW | Waite Agricultural Research Institute, Adelaide, South Australia, Australia. |
| BAFC | Department of Botany, University of Buenos Aires, Buenos Aires, Argentina. |
| BO | Herbarium Bogoriense, Bogor, Indonesia. |
| BR | Jardin Botanique de l'Etat, Bruxelles, Belgium. |
| CUP | Department of Plant Pathology, Cornell University, Ithaca, New York, U.S.A. |
| FLAS | Herbarium, Agricultural Experiment Station, Gainesville, Florida, U.S.A. |
| IA | Department of Botany, State University of Iowa, Iowa City, Iowa, U.S.A. |
| K | The Herbarium, Royal Botanic Gardens, Kew, Great Britain. |
| L | Rijksherbarium, Leiden, The Netherlands. |
| LE | Herbarium of the Komarov Botanical Institute, Leningrad, U.S.S.R. |
| LG | Institut et Jardin de Botanique de l'Université de Liège, Liège, Belgium. |
| LPS | Instituto de Botánica C. Spegazzini, La Plata, Argentina. |
| MICH | University Herbarium, University of Michigan, Ann Arbor, Michigan, U.S.A. |
| MPU | Institut de Botanique, Université de Montpellier, Montpellier, France. |
| NCU | Herbarium of University of North Carolina, Chapel Hill, North Carolina, U.S.A. |
| NY | The New York Botanical Garden, New York, New York, U.S.A. |
| NYS | Herbarium of New York State Museum, Albany, New York, U.S.A. |
| PC | Muséum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris, France. |
| PR | Botanical Department of the National Museum, Praha, Czechoslovakia. |
| S | Botanical Department, Naturhistoriska Riksmuseum, Stockholm, Sweden. |

Other abbreviations used:

| | |
|----------------|---|
| l/b | length-breadth ratio. |
| misappl. | misapplied. |
| not val. publ. | not validly published. |
| Spores [40/5] | Spores, forty from five specimens measured, |

For the use of 'per' in author's citations one is referred to Donk (1957: 255).

Most of the notes of my observations on the individual collections cited in this work, together with copies of collector's notes, drawings, labels etc. are kept in files at L and are available for consultation.

For names of species mentioned in the general part of this work and not treated in the taxonomic part, full authority is given below:

- Amanita ampla* Pers. per Larber
A. argentea Huijsman
A. aurea (Beeli) E. J. Gilb.
A. bisporigera Atk. apud Lewis
A. caesarea (Scop. per Fr.) Grev.
A. calyptroderma Atk.
A. citrina (Schaeff.) per Roques
 var. *alba* (Gill.) E. J. Gilb.
A. cocolla (Scop.) per Bertillon
A. cylindrispora Beardslee
A. excelsa (Fr.) Bertillon
A. farinosa Schw.
A. frostiana (Peck) Sacc.
A. fulva (Schaeff.) per . . . ?
A. goossensiae Beeli
A. hemibapha (Berk. & Br.) Sacc.
 'A. inaurata Secr.'
A. junquillea Quéf.
A. lepiotoides Barla

A. muscaria (L. per Fr.) Hook.
A. ovoidea (Bull. per Fr.) Link
A. pantherina (DC. per Fr.) Krombh.
A. phalloides (Fr.) Link
A. princeps Corner & Bas
A. rhodophylla Beeli
A. rubescens (Pers. per Fr.) S. F. Gray
A. rubrovolvata Imai
A. strobilaceovolvata Beeli
A. subjunquillea Imai
A. vaginata (Bull. per Fr.) Vitt.
A. valida (Fr.) Bertillon
A. verna (Bull. per Fr.) Roques
A. virosa (Fr.) Bertillon
A. volvata (Peck) Lloyd
A. xanthella Corner & Bas
Limacella guttata (Pers. per Fr.) Konr. & Maubl.

HISTORY

THE DELINEATION OF THE GENUS AMANITA

In 1797 Persoon separated from the Linnaean genus *Agaricus* the species with a distinct, membranous to friable volva. He re-introduced for this new genus the classic name *Amanita*, although that name had formerly been applied by Dillenius (1719: 177) to the main body of the genus *Agaricus* L. By the time the name *Agaricus* had become generally accepted, however, *Amanita* had lost its original meaning. This is probably the reason why Persoon thought himself free to use it again for another genus.³ As the presence of a distinct volva was the main character of Persoon's *Amanita*, it also included some pink-spored species at present placed in the genus *Volvariella* Speg.

At first Fries (1815: 1; 1818: 1) accepted *Amanita* Pers. in its original sense and status. But rather soon (1821: 12) he reduced it to the rank of 'tribus' of *Agaricus* and removed the pink-spored species to his 'tribus' *Volvaria*. Several other authors, however, continued to regard Persoon's *Amanita* as a distinct genus; Hooker (1821: 19) was the first to publish it as such after 1 January 1821, the nomenclatural starting-point established later.

Since Fries removed its pink-spored elements the concept of *Amanita*, treated either as a genus or as an infrageneric taxon of *Agaricus*, has been disputed remarkably seldom.

S. F. Gray's (1821: 601) attempt to remove the ringless species (still including the pink-spored ones) from *Amanita* to a new genus *Vaginata* at first met with little

³ Persoon (1797: 65) introduced *Amanita* as though it were a completely new name, that is to say without reference to earlier authors.

approval. But in the second half of the 19th century, when great taxonomic value was attached to the presence or absence of a velar ring on the stem, Roze's (1876: 50) introduction of the genus *Amanitopsis* for the ringless species of *Amanita* was more successful. Although a fair number of authors never accepted *Amanitopsis* as generically distinct from *Amanita*, nearly all the ringless species of *Amanita* were transferred to it at one time or another. Ringless species are now admitted to all sections of *Amanita*, but the original species of *Amanitopsis* ("*Amanitae vaginatae*") represent the core of what may prove to become a subsection of section *Vaginatae*. Much later *Amanitopsis* was one of the nine genera into which Gilbert (1940: 63-79) divided *Amanita*.

In 1891 (: 867) O. Kuntze introduced *Pseudofarinaceus*⁴ as generic name to replace *Amanitopsis*. A few years later (1898: 539) he rejected this name in favour of *Vaginata* S. F. Gray.

Earle (1909: 449-51) likewise replaced the name *Amanitopsis* by *Vaginata* S. F. Gray. He also created the new genus *Amanitella* for the ringless Amanitas with friable volva (type: *A. farinosa*). At the same time he introduced the new name *Venenarius* to replace *Amanita* Pers.⁵ and the new genus *Leucomyces* for the annulate Amanitas with saccate volva (type: *A. cocolla* = *A. ovoidea*).

Neither Earle's genus *Amanitella* nor his *Leucomyces* has been generally accepted, even by Murrill, though he followed Earle consistently in substituting the names *Vaginata* for *Amanitopsis* and *Venenarius* for *Amanita*.⁵ On one occasion Murrill (1911: 80) described a new species in *Leucomyces*,⁶ viz. *L. mexicanus*, that later (Singer, 1944: 366) became the type of *Smithiomyces*, a genus not closely related to *Amanita*. *Amanitella* Earle was later taken up again by Gilbert (1940: 63, 71, 77).

Earle (1909: 447) was also the author of *Limacella*. Formerly the species of that genus, now considered to be very closely related to *Amanita*, were placed only occasionally in the latter genus, but for the most part in *Lepiota*, probably because the viscid layer on the cap and sometimes on the stem was not recognized as a volva.

Formerly a few species of the present genus *Amanita* were also placed in *Lepiota*, mainly on account of the non-gelatinizing covering layer of the cap and, consequently, adnate volval remnants on the cap. This was particularly the case with *A. vittadinii*, which owing to its cylindrical, non-bulbous stem has a very strongly lepiotoid habit. To solve this problem Gilbert (1925: 303) described the new genus

⁴ This name was borrowed from Battara (1755: 29), who, however, did not use binary nomenclature. Battara's *Pseudofarinaceus* was therefore not a generic name. Later on it was also taken up by Earle (1909: 449), but then for the present genus *Volvariella*.

⁵ Earle and Murrill regarded *Amanita* Pers. as a later homonym of *Amanita* [Dill.] Hall. (type: *Agaricus campestris*). The latter generic name, however, became devaluated when the later starting-points were introduced for names of fungi.

⁶ From the accompanying text it appears that at that time Murrill had intended to replace the name *Amanita* Pers. by *Leucomyces* Earle. Later he changed his mind in favour of *Venenarius* Earle.

Lepidella with *A. vittadini* as type and included *A. echinocephala* and *A. solitaria* sensu Coker in it. As characters he mentioned the usually adnate volva, the solid, squamose stem, the inflected, appendiculate margin of the cap, the coloured gills, the not truncate short gills, the bilateral trama of the gills,⁷ and the subvirescent spore print. Its intermediate position between *Amanita* and *Lepiota* was stressed. By contrast *Amanita solitaria* (sensu auct. europ. = *A. strobiliformis*) was mentioned as a typical species of *Amanita*.

Gilbert & Kühner (1928: 151) also transferred the European *A. boudieri* (= *A. baccata*) and a number of American species from *Amanita* to *Lepidella* but without giving a new description of *Lepidella*. In his monograph Gilbert (1940: 63-79) proposed a division of *Amanita* into not less than nine smaller genera (viz. *Amanitopsis* Roze, *Amanita* sensu stricto, *Ariella* E. J. Gilb., *Amanitaria* E. J. Gilb., *Amanitella* Earle, *Amidella* E. J. Gilb., *Amanitina* E. J. Gilb., *Amplariella* E. J. Gilb., and *Aspidella* E. J. Gilb.).

Aspidella was the genus that Gilbert had previously named *Lepidella*, but that he had to rename because of the earlier homonym *Lepidella* Tiegh. (Loranthaceae; 1911). Without admitting it in so many words Gilbert then strongly emended this genus. This appears not only from his own words (1940: 74): "Il groupe toutes les Amanites blanches à volva non membraneuse et à spores amyloïdes," but also and even more clearly from the list of species he (1940: 79) admitted to *Aspidella*. Only a few authors (e.g. Maire, 1933: 85; Konr. & Maubl., 1948: 68) accepted *Lepidella* or *Aspidella* respectively, at generic level, but in 1933 (: 214) Veselý already reduced it to subgeneric rank.

Gilbert's excessive splitting up of *Amanita* has not or scarcely been followed. Probably it was Gilbert himself who was responsible for the swift degradation of his generic derivatives of *Amanita*. In the descriptive part of his monograph (1941) he continued to use the generic epithet *Amanita* in the specific names. Moreover in a paper printed privately in May 1941 he reduced nearly all the genera⁸ proposed in the general part of the monograph (1940) to subgenera of *Amanita*.

Summarizing, it may be said that since the early removal of a few foreign elements the genus *Amanita* Pers. per Hook. has successfully resisted every attempt to subdivide it into smaller genera and has proved to be a very natural and easily recognizable taxon. Microscopic and ontogenetic characters that have been gradually recognized have even emphasized its oneness. Such characters are, e.g. the bilateral trama of the gills (see p. 324), the 'Amanita-structure' of the trama of the stem (see p. 328) and the schizohymenial type of development of the fruit-body (see p. 300).

⁷ A character discovered by Fayod (1889: 314) in his tribus 'Amanitacés' and several other groups, that proved to be a great help in distinguishing *Amanita* and its closely related genera (his 'Amanitacés') from *Lepiota* and its close allies (his 'Lepiotés').

⁸ Not all of them, since in this paper he was treating only European taxa.

THE INFRAGENERIC CLASSIFICATION OF *AMANITA*

The genus *Amanita* is found throughout the world and is generally easy to recognize. In large areas it is a conspicuous and attractive component of the mycoflora. It is therefore not astonishing that *Amanita* has been treated more or less extensively in a large number of floras, textbooks, monographs, etc. As, moreover, the genus is rich in striking macroscopic characters, many authors have proposed new infrageneric classifications, but unfortunately usually without taking into account earlier published subdivisions and names in *Amanita*.⁹ A limited number of these infrageneric systems will be mentioned here in historical sequence in order to give a picture of the main characters on which they were based.

Persoon (1797: 66; 1801: 247) distinguished three unnamed groups of species in *Amanita*: one with a membranous volva and without a ring, a second with a membranous volva but with a ring, and a third with a friable volva and with a ring.

Fries (1821: 13) divided his *Agaricus* 'tribus' *Amanita* into four unnamed groups viz. (i) one with a saccate volva and a smooth margin of the cap, (ii) a second with a saccate volva and a striate margin of the cap; (iii) a third with a friable volva and a striate margin of the cap; and (iv) a fourth with a friable volva and a smooth margin of the cap. Later Fries (1854: 2) introduced the following names for these groups: (i) *Phalloideae*, (ii) *Vaginatae*, (iii) *Muscariae*, and (iv) *Validae*.¹⁰ By attaching great taxonomic value to the striation of the margin of the cap Fries was remarkably 'modern'!

Rather curious was the division of *Amanita* (still including *Volvariella*) by Mladý (1838: 11), who distinguished the following sections: *Xanthispori* (only species, *A. caesarea*), *Rhodospori* (= *Volvariella*) and *Leucospori* ("*Amanitae verae*").¹¹ His first section was apparently based on the erroneous assumption that *A. caesarea*, with its yellow gills, produces yellow instead of white spores.

At first Quélet (1872: 65) followed Fries' division of *Amanita*. But later (1888: 302) he switched to a new classification, recognizing two subgenera, viz. *Vaginaria* Forq. ex Quélet without a ring and *Peplophora* Quélet with a ring. The latter was subdivided into the following three sections: (i) *Oblitteratae*, with a friable volva and a bulb without rim or edge, (ii) *Circumscissae*, with a friable volva and a bulb with volval rim or edge, and (iii) *Limbatae*, with a saccate volva.

⁹ More than fifty sectional names have been introduced in *Amanita*. Corner & Bas (1962) chose lectotypes for many of them in such a way that they have become typonymous synonyms of older sectional names.

¹⁰ In 1854 Fries added a fifth section, named *Denudatae*, for species with an entirely disappearing volva and a non-bulbous stem. Formerly (1849: 272) he had called this group "stirps *A. persoonii*"; therefore I propose *Agaricus persoonii* Fr. ex Fr. as lectotype for it. The identity of *A. persoonii* is uncertain. Some authors assume that it is a species of *Limacella* (e.g. Konr. & Maubl., 1948: 70), others (e.g. Gilbert, 1941: 350) that it is *Amanita excelsa*.

¹¹ Unfortunately these are the oldest sectional names in *Amanita* that I have been able to find. I propose *Amanita muscaria* (L. per Fr.) Hook. as lectotype for *Amanita* section *Leucospori* Mladý (1838: 15); thus it becomes a typonymous synonym of *Amanita* section *Amanita*.

Schroeter (1889: 677) treated *Amanitopsis* as a distinct genus. He divided *Amanita* into about the same three sections as Quélet had divided his subgenus *Peplophora* but gave them a new set of names, viz. (i) *Incompletae*, (ii) *Marginatae*, and (iii) *Volvati*.

Ricken's (1913: 306) sections of *Amanita* (inclusive of *Amanitopsis*) has as sole characteristic the structure of the volva; this appears clearly from the names: *Volvatae*, *Limbatae*, *Circumscissae*, *Oblitteratae*.

The only author who considered the shape of the spores to be of greater importance than the structure of the volva was Lange (1915: 5). He divided *Amanita* into the subgenera *Eu-Amanita*, *Amanitopsis*, and *Lepiotopsis* (= *Limacella*), and his subgenus *Eu-Amanita* into two sections based on the shape of the spores, viz. *Sphaerosporae* and *Ovisporae*. Both of these sections consisted of the same pair of subsections, viz. *Volvatae* and *Circumscissae*.

Noteworthy was Coker's (1917) arrangement of the species of *Amanita*. On the one hand his genus *Amanitopsis* was a heterogeneous gathering of ringless species from at least three of the present sections of *Amanita*. On the other, the arrangement of the species in his genus *Amanita* in six unnamed groups was fairly natural according to present-day standards, partly because Coker reintroduced the sulcation ('striation') of the margin of the cap as a character for some of his groups.

In 1918 Gilbert was still dividing *Amanita* into three subgenera (*Amanita*, *Amanitopsis*, *Limacella*) and his subgenus *Amanita* into three sections based on the characters of the volva (*Limbatae*, *Semi-Limbatae*, and *Floccosae*). But in 1928 Gilbert & Kühner published the results of their observations on the spores of *Amanita* in Melzer's reagent and this brought the first fundamental change in the infrageneric classification of *Amanita* since Fries. Gilbert & Kühner found that the species of *Lepidella*¹² and many species of *Amanita* combined amyloid spores with a smooth margin of the cap and that the species of *Amanitopsis* and the rest of the species of *Amanita* combined non-amyloid spores with a sulcate margin of the cap. This striking correlation between two independent characters¹³ established the taxonomic value of the absence or presence of a sulcation at the margin of the cap already observed by Fries (1821, 1854), Coker (1917), and Gilbert (1925: 212).

Veselý (1933, 1934) reduced *Lepidella* E. J. Gilb. to a subgenus of *Amanita* and placed it beside *Amanitopsis* and *Amanita*. He divided his subgenus *Amanita* into three sections that were still based on volval characters only (*Volvatae*, *Limbatae*, and *Floccosae*).

In his monograph on *Amanita* Gilbert (1940) worked out the consequences of Gilbert & Kühner's discovery by splitting *Amanita* into two groups of taxa, one group with amyloid and the other with non-amyloid spores. At first (1940: 63) these were groups of genera, but in 1941 Gilbert reduced the genera to subgenera

¹² A genus segregated from *Amanita* by Gilbert in 1925 and later renamed *Aspidella* see p. 294.

¹³ Meanwhile it has emerged that this correlation is not 100 %, though it is still very high.

of *Amanita*, arranging them as follows:¹⁴

1. Spores non-amyloid. Margin of cap sulcate.
 2. Volva membranous to submembranous.
 3. Spores rounded. Subgen. *Amanitopsis* (type: *A. vaginata*).
 3. Spores ellipsoid. Subgen. *Amanita* sensu E. J. Gilb. (type: *A. caesarea*).
 2. Volva floccose. Subgen. *Amanitaria* (type: *A. muscaria*).
1. Spores amyloid. Margin of cap smooth.
 4. Volva membranous or floccose-membranous.
 5. Spores ellipsoid to subcylindrical. Fruit-body white. Ring often disappearing. Subgen. *Amidella* (type: *A. volvata*).
 5. Spores globose to broadly ellipsoid. Cap usually coloured. Ring persistent. Subgen. *Amanitina* (type: *A. phalloides*).
 4. Volva floccose.
 6. Spores ellipsoid, medium-sized. Cap coloured. Subgen. *Amplariella* (type: *A. ampla*).
 6. Spores ellipsoid to elongate, large. Cap white. Subgen. *Aspidella* (type: *A. vittadinii*).

The delimitation of Gilbert's taxa was still rather cursory¹⁵ and most of his names have had to be replaced by older ones. Furthermore, his subgenera were soon reduced to sections. Nevertheless his internal classification of *Amanita* sensu lato provided the pattern underlying the systems of most later authors.

Konrad & Maublanc (1948: 57) recognized two subgenera, viz. *Eu-Amanita* with non-amyloid and *Amidella* with amyloid spores, both divided into a number of sections that in the main corresponded with Gilbert's subgenera of 1941. Gilbert's *Aspidella*, however, was maintained as a distinct genus (exclusive of *A. strobiliformis*) on account of its adnate volval remnants on the cap and the virescent gills.

In 1951 Singer divided *Amanita* into three subgenera, two with non-amyloid spores, viz. *Pseudoamanita* and *Vaginarina* (the first usually with, the second usually without a ring), and one, *Euamanita*, with amyloid spores. But in 1962 he combined the first two subgenera into one. Singer's system also deviates from that of Gilbert in that *Amanitopsis* is split up into sections *Vaginatae* (with globose spores) and *Ovigerae* (with ellipsoid spores), while *Aspidella* is split up into sections *Strobiliformes*

¹⁴ Two of Gilbert's genera of 1940, viz. *Amanitella* Earle and *Ariella* E. J. Gilb., escaped degradation because in Gilbert's paper of 1941 only European taxa were treated. *Amanitella* is monotypic and based on *A. farinacea*; in my opinion this species, with its bulbous stem and friable volva, must be placed in *Amanitaria* E. J. Gilb. (= *Amanita* section *Amanita* in my classification). *Ariella* (type: *Amanita rhodophylla*) may turn out to be a distinct taxon but it is still insufficiently known. Horak (1968: 93) described the tramal hyphae of the gills in the type of *A. rhodophylla* as regular.

¹⁵ With the help of Gilbert's generic descriptions I made a key to his genera of 1940. Thereby several of the species in Gilbert's monograph appeared to key out in genera other than those in which Gilbert placed them!

(with wart-like volval remnants) and *Roanokenses* (with powdery volval remnants).

Corner & Bas (1962: 242) recognized the same two subgenera as Konrad & Maublanc (l.c.) and Singer. However, they rejected Singer's section *Ovigeræ* as not sufficiently distinct from section *Vaginatæ* and maintained *Aspidella* undivided as section *Lepidella*. Moreover they united Gilbert's *Amanita* sensu stricto (= sect. *Caesareæ* Sing.) with section *Vaginatæ* because they did not consider the presence or absence of a ring to be a sectional character.

Moser (1967: 125) sectioned *Amanita* in almost the same way as Corner & Bas (l.c.) except that he maintained the *Caesareæ* as an independent section.

It seems that recent authors have arrived at a rather natural arrangement of the species of *Amanita*. But working with this system shows that it is still very cursory, with the delineation of the sections still vague. At the same time the number of species to be accommodated is rapidly growing.

As is apparent from the foregoing, the structure of the volva has always been a leading character within *Amanita*. Its taxonomic importance is surpassed only by that of the iodine-reaction of the spores and the sulcation of the margin of the cap. In contrast to these last two characters, those of the volva are very complex. There are good reasons for believing that a study of the microscopic structures underlying the outer appearance of the volva will provide us with a key to a better understanding of the relationship and phylogeny in *Amanita*.

TREATISES

The genus *Amanita* has frequently been monographed. As early as 1826 Vittadini published his 'Tentamen mycologicum seu *Amanitarum* Illustratio'. In 1838 this was followed by Mladý's little known publication 'Synopsis *Amanitarum* in Agro pragensi sponte nascentium'.

Later many monographs followed, that of Gilbert even covering the whole world. Naturally *Amanita* was also treated in many floras, floristic notes, etc. The most important of these publications are for:

Europe and N. Africa: Fries (1854), Quélet & Bataille (1902), Gilbert (1918), Vesely (1933, 1934), Singer (1950), Kühner & Romagnesi (1953), Parrot (1960), Bertault (1964, 1965).

North America: Peck (1883), Lloyd (1898), Murrill (1913, 1917), Coker (1917), Hesler (1930), Hotson (1936), Murrill (1948), Pomerleau (1966).

Asia: Boedijn (1951), Hongo (1959), Corner & Bas (1962).

Africa (except the northern part): Beeli (1927, 1931, 1935).

Australia and New Zealand: Cleland (1934), Gentilli (1953), Stevenson (1962).

The whole world: Gilbert (1940-41).

MORPHOLOGICAL CHARACTERS IN AMANITA

THE DEVELOPMENT OF THE FRUIT-BODY

The development of the fruit-body in *Amanita* is relatively well known; it has been studied in several species, viz. *Amanita excelsa*—Reijnders, 1963: 131; *A. muscaria*—de Bary, 1866: 70, Brefeld, 1877: 123; *A. rubescens*—de Bary, 1866: 70, Reijnders, 1963: 127; *A. strobiliformis*—Reijnders, 1963: 125; *A. vaginata*—Atkinson, 1914: 369; *A. vittadini*—Reijnders, 1963: 121. Some of the results of these studies are of great taxonomic interest.

The development of the fruit-body in *Amanita* is hemiangiocarpous,¹⁶ as the hymenium is endogenous and becomes exposed just before the start of sporulation. This is in the first place caused by a well-developed volva. As, moreover, primordial tissue (the "lipsanenchyme" of Reijnders, 1963: 23) is present between the primordial gills and the primordial stem, the type of development is further specified by Reijnders (1963: 235) as bivelangiocarpous.

In *Amanita* the fruit-body is initiated in a primordial bulb whose tissue gradually differentiates into the special tissues of the different parts of the fruit-body. As early as 1889 (: 290) Fayod drew attention to the fact that in *Amanita* the position of the primordial fruit-body within the bulb is not the same in all species.

In most species (e.g. *A. muscaria*, *A. rubescens*, *A. vittadini*) the primordial fruit-body develops excentrically near the upper surface of the bulb (Reijnders, 1963: pls. 53–55), but in *A. vaginata* it develops in or near the centre of the bulb (Atkinson, 1914: pl. 17).¹⁷ This explains why in section *Vaginatae* a basal bulb is lacking in the mature fruit-body; nearly the whole inner part of the primordial bulb is replaced by the tissues of the fruit-body.

The first tissue to differentiate from the primordial tissue of the bulb is the outer layer of its upper part; this becomes later the universal veil or volva. Usually the boundary line between the volva and the cap becomes visible at a very early stage; this is true in those species in which at later stages a distinctly gelatinized surface-layer of the cap facilitates the separation of cap and volva. In *A. vittadini*, however, with its adnate volval remnants on the mature cap, such a boundary line is lacking during the whole development. Thus the difference between an adnate and a discrete volva is, at least sometimes, determined in early ontogeny.

In *Amanita* the first part of the fruit-body itself to differentiate is the cap; the stem and the gills soon follow.

The ontogeny of the gills is very unusual. In most Agaricales a pre-hymenial

¹⁶ Since I find it necessary to distinguish the 'pseudangiocarpous' and 'hemiangiocarpous' development in Agaricales from the truly 'angiocarpous' or 'endocarpous' development in Gastromycetes, I use the terminology accepted by Singer (1962: 28). In view of the confusion about the meaning of some of these terms, perhaps the time has come to introduce a new terminology, as van Brummelen (1967: 25) did for Discomycetes.

¹⁷ Fayod (1889: 290) stated erroneously that *A. phalloides* also has a central primordial fruit-body. In this connection Vittadini's plates (1832–5: pls. 1, 2, 11, 16, 17, 39, 44) are very instructive.

palisade layer develops on the underside of the primordial cap. From this layer the lamellae originate in the shape of ridges or folds projecting downward; increase in number of the elements of the palisade layer and growth of tramal hyphae from the cap downward cause them to increase in width. These primordial gills protrude into a pre-existent, annular gill cavity between stem and cap, which means that originally, at least, they have free edges.

During the development of the fruit-body in *Amanita* no gill cavity between cap and stem ever occurs. The gills differentiate from the primordial tissue like closely packed plates of parallel hyphae separated by hymenial palisades covering their sides. On one side the trama of these plates is connected with the trama of the cap, on the other with the primordial tissue around the stem that later forms the partial veil or ring. Thus the edges of the gills in *Amanita* do not become free until the expanding cap tears them loose from the ring. This type of development of the hymenophore, named schizohymenial by Reijnders (1963: 247), seems to be the sole type in *Amanita*; it is not known in other genera. In the only species of *Limacella*, a genus considered to be closely related to *Amanita*, that has been investigated for this, the gills develop as folds with free edges. The same applies to *Termitomyces* (Heim, 1940: 46).

After comparison of the habits of fruit-bodies in many species I have come to the conclusion that in *Amanita* the stem does not always elongate in the same way.

In *A. vittadinii* (Fig. 1a) it is especially the part of the stem below the level of the margin of the primordial cap, including the primordial bulb, that elongates. The result is that in the mature fruit-body the primordial bulb cannot be distinguished from the stem and that the adnate volval remnants covering the lower part of the primordial stem and bulb become scattered over the whole part of the stem below the ring. In *Amanita* this 'base-elongating' stem is restricted to several species in subsection *Vittadiniae* and one or a few in subsection *Solitariae* (*A. timida*; see Fig. 96).

In most species of *Amanita* it is the part of the primordial stem above the level

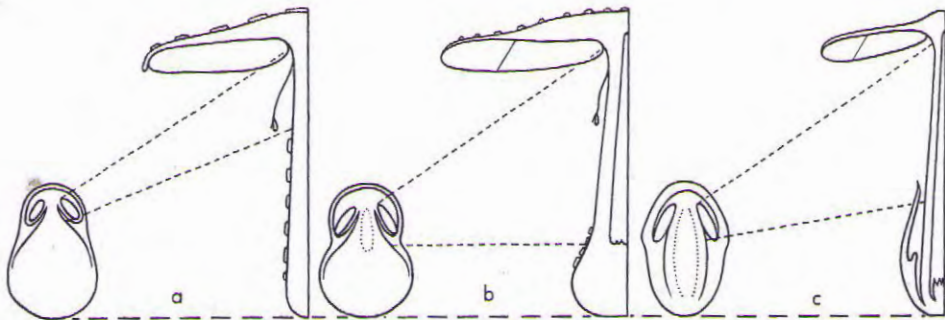


Fig. 1. Diagrammatic sections of primordia and mature fruit-bodies, illustrating zones of elongation of stems. — a. *Amanita vittadinii*. — b. *A. muscaria*. — c. *A. vaginata*.

of the margin of the primordial cap that elongates (Fig. 1b). In the 'apex-elongating' stem the lower part of the stem and the primordial bulb do not or scarcely become longer. Consequently in the mature fruit-body there is a usually distinct basal bulb (= the former primordial bulb) and the volval remnants on stem and bulb are concentrated at a narrow basal zone of the stem and/or the upper half of the bulb.

In section *Vaginatae* (Fig. 1c) the 'totally elongating' stem is found. A result of the above mentioned more or less central position of the primordial fruit-body in the primordial bulb is that the tissue of the lower part of this bulb is almost completely replaced by that of the primordial stem. Later the entire stem participates in the elongation. Consequently in the mature fruit-body the lacking basal bulb has so far appeared to be a good character for the delineation of section *Vaginatae* as opposed to section *Amanita*. The volval remnants usually have the shape of a saccate volva, rarely of floccose girdles around the base of the stem.

There are indications that the 'totally elongating' stem also occurs in another section with a usually saccate volva, viz. section *Amidella* (see Gilbert, 1941: pl. 32, 34, 35, 36). Thus far I have found no indications of this in the saccate-volvate species of section *Phalloideae*.

It should be mentioned that the three cases described here are the most extreme. Several intermediate types exist. Nevertheless knowledge of these characters will help further understanding of the pattern of relationship in *Amanita*.

In my opinion the excentric primordium combined with the 'base-elongating' stem is probably the most primitive structure; from this the excentric primordium with the 'apex-elongating' stem may have developed and later the central primordium with the 'totally elongating' stem.

CHARACTERS OF THE MARGIN OF THE CAP

The marginal sulcation.

In many species of *Amanita* the margin of the cap is radially striate with shallow grooves corresponding with the places of attachment of the gills at the underside of the cap. Although the taxonomic value of this character had been recognized by Fries, it was not fully appreciated until Gilbert & Kühner (1928: 52) demonstrated its high degree of correlation with the reaction of the walls of the spores in Melzer's reagent (see p. 320).

The biological value of the sulcate margin of the cap in agarics is evident; it facilitates a rapid expansion of the cap. It can be expected in those groups of agarics where during development a period of differentiation is distinguishable from a succeeding period of elongation and expansion (Fayod's "période primordiale" and "période d'élongation"; 1889: 279, 292). It is possible for agarics with this type of development, which Reijnders (1963: 221) called "développement concentré," to construct a complete fruit-body under the protection of possible primordial covering layers and in or near the relative safety of the substrate, under favourable conditions allowing the fruit-body to grow out in a short time. Thus the vulnerable

fruit-body is completely exposed to the hazards of the environment for a period only slightly longer than necessary for the successful liberation of the spores.

By the time the cap of an agaric has fully spread, the edge of the cap will have become about four to eight times longer than it was just before the cap started to expand. This means that in species with a smooth margin of the cap a strong intercalary growth and/or a large-scale inflation of the cells and/or a rearrangement of the hyphae is necessary; these processes take time and energy. In species with marginal sulcation a certain (in extreme cases probably very high) percentage of the increase in the length of the marginal zone of the cap is obtained by a passive opening out of the preformed grooves. This 'parasol-mechanism' occurs in several unrelated groups of agarics (e.g. *Coprinus*, *Leucocoprinus*, *Bolbitius*, *Amanita*). Its most extreme form has been described by Buller (1931: 26, 34, figs. 16, 19) for *Coprinus curtus* Kalchbr. and *C. plicatilis* (Curt. per Fr.) Fr., where upon expansion of the cap the trama of the cap splits radially from above downward, the splitting continuing downward into the trama of the gills along their median plane. To a much lesser extent this also happens in some of the most strongly sulcate species of *Amanita* section *Vaginatae*, as was previously pointed out by Huijsman (1959: 22).

Generally speaking the sulcate margin of the cap is characteristic of subgenus *Amanita*.¹⁸ It is, however, important to mention that in all sections of subgenus *Lepidella* one or a few species occur with the same character, though usually to only a slight degree; e.g. in sect. *Lepidella*, *A. limbatula* (see p. 530); in sect. *Amidella*, *A. goossensiae* and others; in sect. *Validae*, *A. xanthella*; in sect. *Phalloideae*, *A. subinquinillea*. Perhaps these species indicate the places at which connections between subgenus *Lepidella* and subgenus *Amanita* must be sought.

There is scarcely any doubt that the sulcate margin is a character derived from the smooth margin of the cap.

It should be emphasized here that in order to facilitate comparison between specimens and species a more exact method for recording the length of the marginal sulcation of the cap than is usual is needed. I found it satisfactory to measure the length of the grooves in tenths of the distance (R) from the centre of the cap to its edge.¹⁹

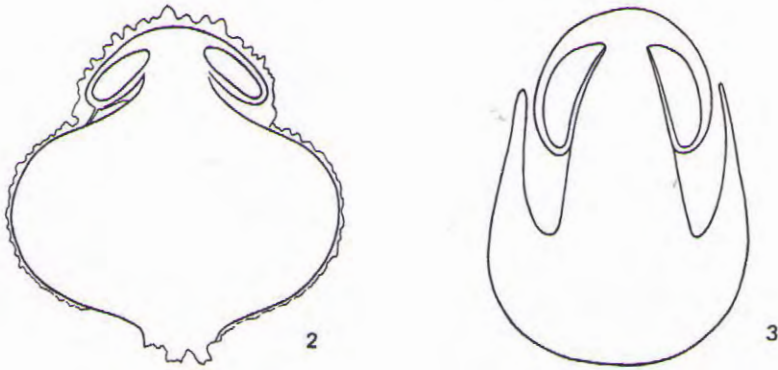
The appendiculate margin of the cap.

In many, if not all species of sections *Lepidella* and *Amidella* the edge of the freshly expanded cap is more or less conspicuously appendiculate with remnants of the partial veil. In the key to the sections of *Amanita* (p. 341) I have used this character, among others, to delimit section *Lepidella* against sections *Validae* and *Phalloideae*.

In advanced primordia cut lengthwise (Figs. 2, 3) it is easy to see that at the edge of the cap the trama of the cap corresponds with the tissue of the partial veil.

¹⁸ The species placed by Gilbert in *Ariella* E. J. Gilb. are left out of consideration for reasons mentioned on p. 297.

¹⁹ According to this method the length of the marginal sulcation in *A. argentea* proved to be 0.1–0.2 R and in *A. vaginata* 0.3–0.4 R (Bas, 1967: 125).



Figs. 2, 3. — Median sections of primordia. — 2. *A. virginea* ($\times 3/2$; after drawing in Corner's field-notes, 13 Dec. 1933, Singapore). — 3. *A. virosa* ($\times 3/2$; from de Cock Buning, 19 Aug. 1967, Doorn; L).

When the margin of the cap is appendiculate, the line of separation between the margin of the cap and the partial veil is apparently not predetermined exactly. I can think of five reasons for this:

(i) The trama of the cap is relatively thick at the edge of the cap, so that the strip along which there is contact with the partial veil is broader than in a thin-fleshed cap.

(ii) In the primordium the early-developing hyphae of the margin of the cap penetrate into the lipsanenchyma (primordial tissue between stem and gills which later, to some extent at least, forms the partial veil). This was observed by Reijnders (1963: 126) in "*A. solitaria*" (sensu auct. europ. = *A. strobiliformis*). But in *A. vittadinii*, where I should have expected the same thing, Reijnders (1963: 124) found that the hyphae of the cap terminated abruptly at its edge.

(iii) The pileipellis is poorly developed. In species with a distinctly gelatinized pileipellis this layer terminates at the edge of the cap, causing a sudden change of structure whose importance increases in accordance with the thinness of the trama.

(iv) In species with a non-appendiculate margin of the cap a loose tissue with many inflated cells is formed at the junction of the trama of the cap and the partial veil; this tissue is lacking in species with an appendiculate margin. My observations on free-hand sections of young caps of *A. timida* and *A. virosa* indicate this.

(v) The partial veil is incoherent. It should be pointed out, however, that in some species with a substantial ring the cap is strongly appendiculate, while several species with a friable partial veil (e.g. in section *Validae*) have a non-appendiculate edge of the cap. The degree of coherence of the partial veil therefore seems to be of little importance for the appendiculate edge of the cap.

In my opinion the appendiculate margin of the cap is more primitive than the non-appendiculate margin, since the latter results from the greater differentiation

and independence of the parts of the fruit-body involved in its formation (partial veil, trama of cap, and pileipellis).

THE VOLVA

Terminology.

In many agarics the primordial fruit-body is surrounded by an outer veil; this may be formed by either (i) the mycelium ('primordial veil', 'problemm'), (ii) the early differentiating outer layer of the primordium ('universal veil', 'blematogen', and 'teleoblem', 'voile inné') or, (iii) hyphae growing out from parts of the young fruit-body ('voile émané', 'universal pseudoveil').

As already mentioned in the chapter on ontogeny (p. 299), the outer veil of *Amanita* belongs to the second category, although sometimes at least, it is reinforced by elements growing out from the primordial cap (*A. vittadini*; see Reijnders, 1963: 124, 207).

It is a long-standing tradition to name the outer veil or universal veil in *Amanita* a 'volva', irrespective of its structure. Micheli, Bulliard, Persoon, Fries, Vittadini, and others called the friable universal veil in species like *A. muscaria* and *A. rubescens* a 'volva', as they also did in the case of the saccate universal veil in *A. vaginata*.

Several recent authors (Ainsworth, Jossierand) prefer to restrict the application of the term 'volva' to the saccate universal veil, others (Gilbert, Snell & Dick) to Atkinson's teleoblem (a universal veil that becomes separated from the cap by a cleavage layer); Lohwag and Singer, however, regard the term 'volva' as a synonym of 'universal veil'.

I agree with Lohwag and Singer.²⁰ Judging by my own experience, especially in *Amanita* section *Lepidella*, there are many intermediate forms between the saccate and the friable volva (see subsection *Limbatulae* on p. 528), just as there are all degrees of separation between the volva and the surface of the cap. Moreover, compared with 'volva', 'universal veil' is a rather clumsy term.

For the most salient modifications of the volva, even though nearly all of them are connected by intermediate forms, descriptive terms are needed.

The 'adnate volva' does not become separated from the cap by a cleavage layer. This in contrast with the 'discrete volva', which becomes more or less separated by the development of a gelatinous layer, a friable layer or both between volva and cap.

The 'saccate volva' remains behind at the base of the stem as a sac, cup, or sheath and usually leaves the cap naked, whereas the 'friable volva' breaks up into

²⁰ Without studying the development of the fruit-bodies of a species it is difficult to tell the origin of its outer veil. Therefore it would perhaps be useful to call any outer layer a volva. Once the origin is known it could be further specified as a 'mycelial volva' (if formed by the mycelium), a 'true volva' (if differentiated from primordial tissue) or a 'spurious volva' (if grown out from parts of the young fruit-body).

fragments, usually embossing both the stem and the cap after expansion of the fruit-body.

The 'layered volva' consists of two or more layers differing in structure.

The 'obliterate volva' leaves scarcely any remnants on the mature fruit-body.

Many different types of friable volvae can be distinguished according to the shape and structure of the volval remnants on the cap.

The 'pulverulent volva', the 'floccose volva', and the 'lanose volva' form respectively powdery, floccose or woolly layers on the whole cap, or parts of it.

The 'crust-forming volva' covers one area or more with a thin, incoherent and to the naked eye amorphous layer of volval tissue.

The 'patch-forming volva' breaks up into thin to thick, usually more or less felted patches.

The 'scale-forming volva' forms adnate, often imbricate, scale-like patches that are thin and vaguely delimited towards the centre of the cap but thick and terminating abruptly towards the margin of the cap.²¹

The 'wart-forming volva' forms remnants which are relatively narrow and high, such as pustules, warts, and spines.

The volval remnants at the base of the stem often differ in size and/or shape from those on the cap. Terms are available for a few special cases in which the upper, but not the lower part of the volva is friable.

The 'circumscissile volva' has the lower part adnate to the basal bulb. The upper part detaches itself along the relatively sharp edge of the bulb.

The 'ocreate volva' is adnate to the base of the stem, sheathing it like a stocking; often it has a rather sharp edge somewhere against the base of the stem, but no free marginal limb.

The 'limbate volva' is adnate to the base of the stem but has a narrow, free, membranous margin.

Structure and behaviour of the volva.

The unique variation in volva patterns in mature fruit-bodies of species of *Amanita* is determined by a large number of factors. First there are the properties of the volva itself, then those of other parts of the fruit-body and finally environmental influences.

Properties of the volva itself.

THE TEXTURE OF THE VOLVA.—As is the case with the tissues in nearly all the parts of the fruit-body of *Amanita*, the volva is usually composed of branching, not or slightly inflated hyphae, inflated cells single or in rows terminal on the hyphae, and fairly often also 'oleiferous hyphae'. The last mentioned elements are left out of consideration here because they rarely seem to affect the behaviour of the volva (but see *A. xanthogala* on p. 490).

²¹ The term 'scale' is often used rather indiscriminately in descriptions of *Amanita*. Therefore it seemed advisable to define its meaning here.

The inflated elements in the volval tissue are either single and terminally attached to hyphae, or arranged in short to long terminal rows. Only rarely have I seen inflated intercalary cells. Sometimes, however, it is as though the inflating habit of the terminal cells also invades the hyphal system bearing these cells; in that case there are inflated branching elements and/or subcylindrical elements at the base of terminal inflated cells.

In general long rows of inflated cells will make the volval tissue looser and more friable than when the inflated cells are single and terminal, especially when the rows tend to fall apart easily. On the other hand a volva with abundant or very large, terminal inflated cells can be strongly friable, as is the case in some species of the *A. rubescens*-group, whereas in subsection *Vittadiniae* the volva consists of long rows of mainly fusiform to subcylindrical inflated cells, even though in some species it is fairly coherent.

THE RATIO OF HYPHAE AND INFLATED CELLS IN THE VOLVA.—In rare cases the volval tissue consists almost solely of one type of element. The outer limb of the saccate volva in *A. phalloides* and *A. virosa*, for instance, is composed merely of interwoven hyphae; on the contrary the wart-forming volva of *A. virginea* (p. 487) and the pulverulent volva of *A. tephrea* (p. 452) are almost completely made up of inflated cells. But most types of volval tissue are a mixture of hyphae and inflated cells.

No comment is needed to show that the ratio of hyphae and inflated cells is one of the main factors determining the degree of consistency of the volval tissue. Unfortunately it is very difficult to put this ratio into words, mainly because of the wide variability in the size and shape of the elements, especially the inflated ones. In the descriptions I have restricted myself to the application of a scale of frequency (scarce, scattered, rather or fairly abundant, abundant, very abundant) to both types of element.

THE DISPOSITION OF THE VOLVAL ELEMENTS.—The second most important structural character of the volva is the disposition of the elements which may be (i) disposed in a position perpendicular to the surface of the fruit-body (anticlinal position), (ii) interwoven in all directions, or (iii) disposed in a position parallel to the surface of the fruit-body (periclinal position). In the last case the elements are usually interwoven in periclinal directions.

(i) The volva that has its elements in anticlinal position has a tendency to split perpendicular to the surface of the expanding fruit-body; the more perfect the anticlinal position of the elements, the easier the splitting of the volva and the smaller the resulting warts (see *A. daucipes* on p. 447, *A. solitaria* on p. 394, and *A. salmonea* on p. 360). If, however, the cells in the rows easily become disconnected, the volva becomes completely pulverulent (see *A. chlorinosma* on p. 450). In subsection *Solitariae* it is not rare to find a type of volva in which the rows of inflated cells and single, elongate inflated cells have an anticlinal position even though to a certain degree the hyphae are interwoven (see *A. cokeri* on p. 390).

(ii) More common is the type of volva of which the elements are interwoven in all directions. What happens when the fruit-body expands depends entirely on the coherence of the volval tissue, its thickness, the degree of its adhesion to the surface of the fruit-body, and environmental factors. The resulting volval remnants may have any form from a pulverulent layer to large warts, or patches, or even a (sub)-membranous basal sac, though generally this type of volva will tend to break up into patches.

(iii) The type of volva with all its elements disposed in a periclinal position is probably rare. In some species (e.g. *A. vittadinii*, *A. codinae*) of subsection *Vittadiniae* I found the chains of long inflated cells in the volva in a periclinal position, at least on the limb of the cap. The margin of the volval limb of *A. phalloides* and related species consists almost solely of periclinal hyphae. Perhaps this type of volval structure is also to be found in other species with a membranous volva.

Less rare are periclinally disposed elements in layered volvas. The outer layer especially may then consist of periclinal hyphae, as is the case in most species of subsection *Limbatulae* (see p. 528). The friable layer between the cap and the solid part of the volva sometimes found in section *Amidella* consists of periclinal, large, elongate cells.

THE LAYERED VOLVA.—It is only rarely that the parts of the volva close to the surface of the cap have exactly the same structure as the parts close to its outer surface. Very often in the inner parts of the volva the hyphae are more abundant, the inflated cells larger, etc.

In a number of cases these differences in structure are so great that two or three layers are discernible in the volva.

Probably the most common type of layered volva is that in which the main part of the volva consists of intermixed hyphae and fairly to very abundant inflated cells, but the outer, or both the outer and inner surface layer of the volva mainly of periclinal hyphae.

The type of volva with only the outer layer made up chiefly of hyphae is common in subsection *Limbatulae* (Figs. 358, 359, 362, 363, 371, 372). This is intermediate between the friable, more or less homogeneous volva, composed of interwoven hyphae and inflated cells, found in many species of subsection *Solitariae*, and the saccate volva in section *Amidella*.

Preliminary observations revealed that in section *Amidella* the type of volva that mainly occurs has periclinal elements in the outer and inner layers. In some of the species of this section (e.g. *A. volvata*, *A. lepiotoides*, etc.) the inner layer of periclinal elements is friable, as it consists of few hyphae and abundant large, elongate cells (Figs. 4-6). In these species the greater part of the volva forms a sac at the base of the stem of the mature fruit-body, but the inner layer of the volva breaks up into small fragments which become scattered over the surface of the cap. Later these fragments sometimes turn rusty or red-brown after which they contrast strongly with the usually pale surface of the cap.

Quite another type of layered volva is found in stirps *Ravenelii* and, less conspicuously, also in stirps *Solitaria*, both in subsection *Solitariae*. There the volva consists of mainly anticlinal elements; the inner part of the volva contains for the most part only hyphae and the outer part chiefly inflated cells. Especially in the type specimen of *A. crassa* (Fig. 118) the contrast between the fibrillose lower part and the more or less felted upper part of the warts on the cap is very clear.

A peculiar type of layered volva has been found in an as yet undescribed species of *Amanita* from northern India (*Bas* 4378; L) in which the inner part of the volva consists of densely interwoven hyphae and scattered small inflated cells, and the outer part of very abundant globose cells and hyphae. This volva forms a sac at the base of the stem, the outside of which is covered with rather prominent brownish conical warts. The species is probably closely related to *A. strobilaceovolvata* (Beeli, 1935: pl. 1 fig. 4; Gilbert, 1941: pl. 8) from the Congo, which judging by the illustrations has a similar volva.

In species where the pileipellis gelatinizes early the volval layer close to the pileipellis as a rule also participates in this process; in that case the volva has a thin but distinct gelatinous inner layer.

THE COHERENCE OF THE VOLVAL ELEMENTS.—The elements of the volva sometimes become very easily disconnected. Naturally this affects the behaviour of the volva which in these cases tends to become pulverulent.

In *A. solitariiformis* (p. 495) it is practically impossible to examine the structure of the volva because in all mounts, no matter how carefully they are prepared, nearly all the elements are found disconnected. On the other hand even in species with very large inflated cells in the volva the connections between these and the much narrower hyphae are often fairly easy to study.

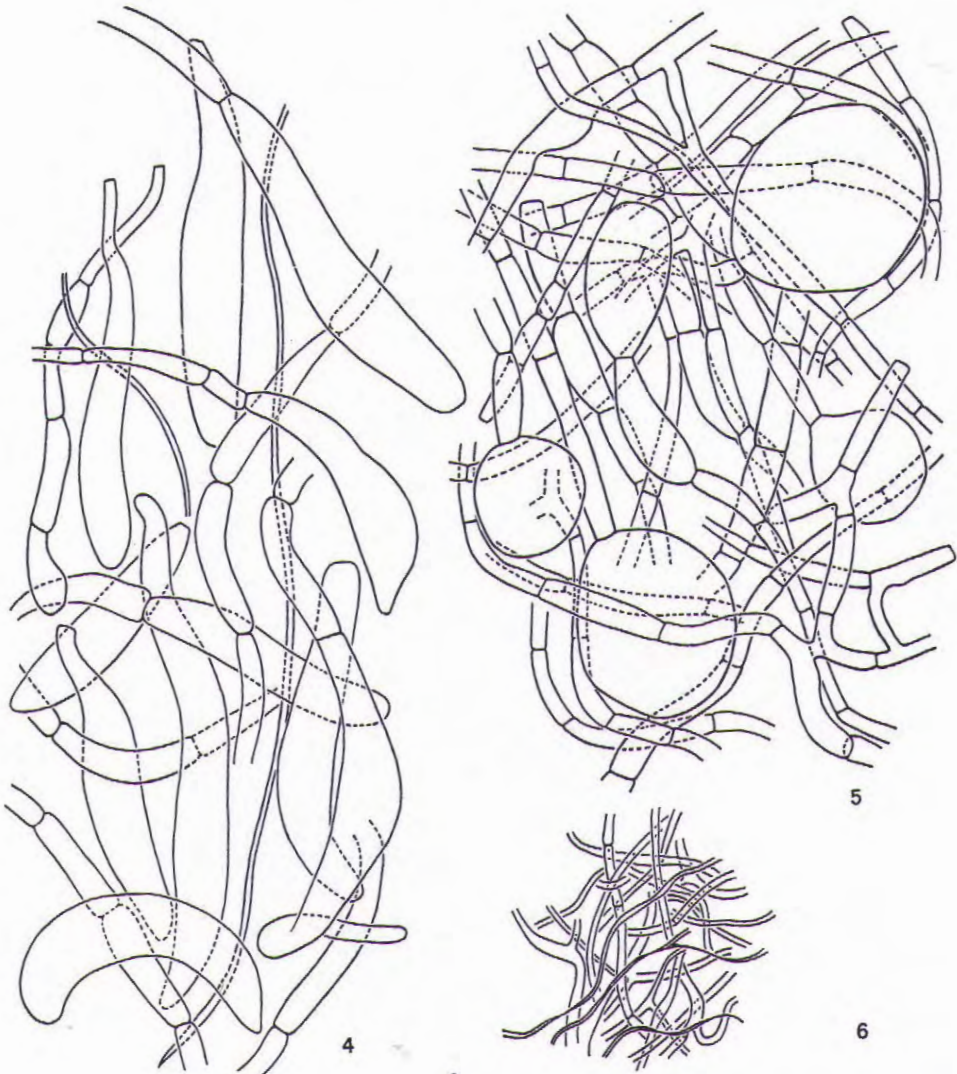
THE THICKNESS OF THE VOLVA.—In general a thin volva will be more easily disrupted than a thick volva of the same structure. Actually *Amanita* varies rather widely in the thickness of the volva; compare for instance *A. sculpta* (Fig. 242) with *A. borneensis* (Fig. 234), or *A. abrupta* (Fig. 154) with *A. onusta* (Figs. 158, 160).

Effects of other parts of the fruit-body on the volva.

THE STRUCTURE OF THE PILEIPELLIS AND THE BEHAVIOUR OF THE VOLVA.—The pileipellis may be strongly differentiated, gelatinizing very early, or well differentiated but not gelatinizing, or poorly or not differentiated and not gelatinizing. These types of pileipellis are, however, connected by intermediate forms.

The gelatinizing pileipellis tends to be slippery during the expansion of the fruit-body and unless the fruit-body has been growing under very dry conditions this will only affect the behaviour of a volva which is more or less friable. (Even in *A. phalloides*, with its membranous volva and gelatinizing pileipellis, the upper part of the volva may under certain conditions form patches on the cap.) Under normal conditions, however, the adhesion between the volva and the gelatinous pileipellis seems to be strong enough to disperse the fragments of a friable volva

over the whole surface of the cap as, for instance, is usually the case in *A. muscaria*. But under other conditions the gelatinous pileipellis may be so slippery that even a friable volva remains at the base of the stem as a sheath. Such an incidental form of *A. muscaria* has been given the name *A. aureola* Kalchbr.



Figs. 4-6. Structures of volval limb of *A. volvata*. — 4. Inner surface layer. — 5. Inner tissue. — 6. Outer surface layer ($\times 325$; from *Bas 3799*; L).

When the pileipellis is well differentiated but does not gelatinize or else only late, the adhesion between volva and pileipellis is much stronger than in the foregoing. The parts of the remnants of the volva that are close to the pileipellis are stretched in periclinal directions when the cap expands, the closer the remnants are to the margin of the cap the more so. Thus warts tend to become low warts or scales, patches tend to become crusts, etc.

When a pileipellis is absent or indistinct the tissue of the volva passes more or less gradually into that of the cap. It is then very difficult to determine which part of the structures on the cap belongs to the volva and which part to the cap itself. The whole surface of the cap tends to become warty, patchy, floccose, lanose or fibrillose, depending on the structure of the outer layers. But even then, under special conditions (heavy rains?) the outer parts of the volva may become detached in the shape of patches from the surface of the cap; this I observed in *A. vittadinii*.

In some species with a pileipellis which is poorly developed but which can still be located, and with conical volval warts on the cap, it can be demonstrated that the clefts between the warts sometimes continue downward into the trama of the cap (see *A. strobilacea*, p. 406, and *A. ravenelii*, p. 400); in this way the volval warts appear on tubercles of tramal tissue. In some of the specimens studied this structure seems to have become more prominent by the drying process (see *A. strobilacea*, p. 406). In various other species where the pileipellis cannot be located the same structure probably exists (see *A. crassiconus*, p. 500 and *A. perpasta*, p. 412).

THE SHAPE OF THE CAP AND THE BEHAVIOUR OF THE VOLVA.—Young caps do not have the same shape in all species. Some are decidedly more acute, others more obtuse than the average. The acute cap tends to perforate the volva, the obtuse cap to carry the upper part of the volva aloft. Both cases are well demonstrated by the photographs of *A. fulva* and *A. calyptroderma* simultaneously published by Smith (1963: 172–174) and some plates published by Gilbert (1941: pls. 2, 4, 8, 11, 14, 15, and 23).

Environmental effects on the volva.

METEOROLOGICAL CONDITIONS.—The influence of the weather during the development of the fruit-body is considerable. Desiccation by insolation and dry winds causes collapse of cells and consequently felting of the outer layers of the volva, which thus becomes more coherent. At the same time the gelatinous pileipellis, if present, acts more like a layer of drying gum than a cleavage layer so that there is more adhesion between the volva and the surface of the cap. Moist weather on the contrary maintains or even increases the readiness of the friable volva to break up into fragments; it makes a gelatinous pileipellis slipperier, thus reducing the adhesion between the volva and the cap. Heavy rains may completely wash away the volval remnants from the cap, even when the pileipellis is only poorly developed.

Desiccation and humidification (together with other factors) also determine

the degree of expansion reached by the fruit-body; the expansion in turn affects the volval remnants on the cap.

During the expansion of the cap the degree of humidity may provoke two more or less contrasting processes: desiccation → greater adhesion of the volva to the cap but less friability of the volva; humidification → less adhesion to the cap but greater friability of the volva, both with somewhat unpredictable results. This is probably the chief reason why in various groups the infrageneric classification of *Amanita*, which to some extent has always been based on the macroscopical structure of the volva, has produced such poor results.

SOIL AND THE BEHAVIOUR OF THE VOLVA.—The influence of the soil on the fruit-body increases according to the depth of initiation of the primordium. First of all the action of soil on the volva is mechanical. For instance solid clay rubs off the remnants of the volva passively while the fruit-body is breaking out of it, but a loose, thick layer of humus has hardly any influence on the volva at all. In the second place soil can protect the young volva and pileipellis against the effects of desiccation as described above. Finally the degree of humidity of the soil in the wider surroundings of the primordium will affect the degree of expansion of the fruit-body.

SURROUNDING VEGETATION.—Vegetation, if it is not too low, will to a certain degree protect the young fruit-body against desiccation. Deep moss and dense grass usually have an elongating effect on the stem; it is not rare that the volval remnants are then left behind near the base of the stem in species where normally they emboss the cap.

The shape of volval scales and warts.

In some species of *Amanita*, e.g. in *A. ravenelii* (Fig. 111), the volval remnants on the cap have the shape of more or less imbricate scales. These structures develop in species in which a poor or lacking pileipellis renders the volva closely adherent to the cap and in which the volval elements are anticlinal at the centre of the cap but increasingly slanting outward towards the margin. The schematic drawings in Fig. 7 illustrate these cases.

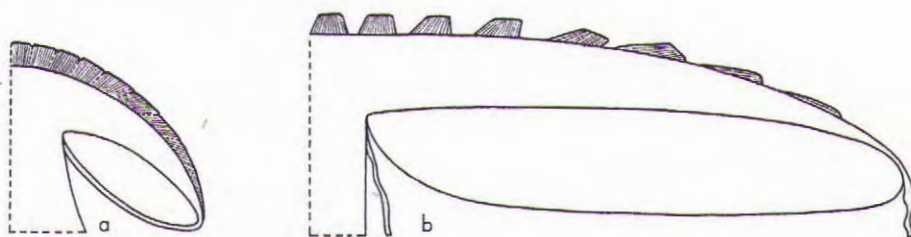


Fig. 7. Diagrammatic sections of young and mature cap, illustrating formation of volval scales; lines in volval remnants indicate main direction of elements.

Volval warts are often cone-shaped. This is probably due to one or more of the following conditions:

(i) From the beginning the volva consists of more or less periclinal elements growing out in tufts from the primordial surface, with the tips of the rows of cells and/or hyphae inclining towards each other. This would explain the conical warts on the caps of very young primordia, for instance in *A. virginea*, long before there is any sign of expansion of the cap.

(ii) If the young volva is a fairly continuous layer over the primordial cap, at a given moment the growth of probably first the outer and subsequently the inner layer stops, the continuing growth of the cap underneath causing it to break up into fragments. Especially where the volva is thick, broad-based warts would be formed like this. It would explain the large conical warts consisting of irregularly disposed elements, like in *A. crassiconus* (Fig. 269).

(iii) The tissue in the tip of a volval wart is more subject to desiccation than that in the base. Desiccation checks the inflation of cells and provokes the collapse of inflated cells.

(iv) When the adhesion of the volva to the surface of the cap is sufficiently strong the base of the warts will be stretched in periclinal directions, the closer they are to the margin of the cap the more so.

The processes described under (i), (iii), and (iv) undoubtedly take place in *Amanita*; that under (ii) very probably, but this remains to be proved.

The inner limb of the volva.

In the primordial fruit-bodies of *Amanita* a ring-like band of tissue fills up the space between the partial veil and the stem (Fig. 8a); downward it passes gradually into the tissue of the volva. Sometimes it is very strongly developed (see Fig. 2 of *A. virginea*), sometimes scarcely discernible (see Fig. 8f of *A. citrina*). It forms the rest of the primordial tissue (Reijnders' lipsanenchyma) between gills and stem after this has been partially transformed into or replaced by the partial veil.

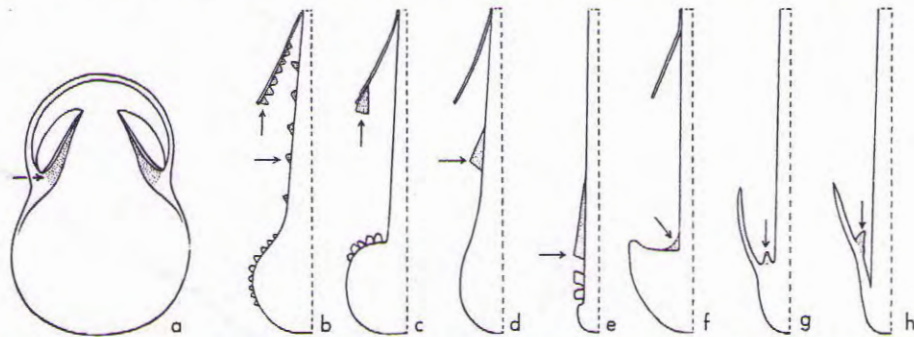


Fig. 8. Diagrams showing original and final positions of inner volval limb (dotted areas). — a. Section of primordium. — b-h. Sections of stems. — b. *Amanita virginea*. — c. *A. muscaria*. — d. *A. ochrophylla*. — e. *A. inaurata*. — f. *A. citrina*. — g. *A. argentea*. — h. *A. vaginata*.

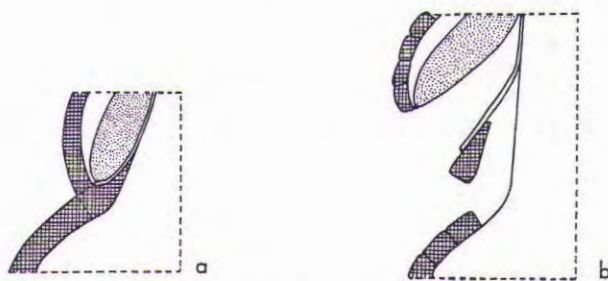


Fig. 9. Diagrammatic sections of young fruit-bodies of *Amanita muscaria*, illustrating position of inner volval limb just before and after expansion of cap ($\times 2$).

In longitudinal sections of advanced primordia this band of tissue presents itself as an inward limb of the volva penetrating between partial veil and stem (shaded area in Fig. 8a). Since Atkinson's publication on the ontogeny of *Amanita vaginata* (1914: 383) it is usually called the inner limb of the volva (*limbus internus volvae*).

According to Atkinson (1914: 390) in *A. vaginata* the inner limb in the mature fruit-body has the same microscopic structure as the volva. I observed the same in some species of *Amanita* section *Lepidella*. (e.g. *A. virginea*, *A. ochrophylla*, and *A. perpasta*).

In mature fruit-bodies the remnants of the inner volval limb may end up at many different places according to the type of development of the various species. In *A. virginea* they form warts on the underside of the ring, and warts or rags on the stem (Fig. 8b). In *A. muscaria* we find them in the shape of a ring of warts on the underside of the margin of the ring (Fig. 8c). In *A. ochrophylla* they usually form a ring-like belt (spurious ring) on the stem somewhere below the (true) ring (Fig. 8d). In *A. inaurata* they are found as a belt near the base of the stem just above the remnants of the volva (Fig. 8e). In *A. citrina* they form a scarcely discernible strip of tissue at the transitional zone between stem and bulb (Fig. 8f). In *A. argentea* they are found as a circular rim situated in the angle between the base of the stem and the limb of the volva (Fig. 8g). In *A. vaginata* they form a similar rim but situated at the inside of the volval limb (Fig. 8h).

When in mature fruit-bodies both the volva and the partial veil are friable the remnants of the inner volval limb are difficult to locate.

In the schematic drawing of Fig. 9 it is demonstrated in detail, what happens to the inner volval limb in *A. muscaria*.

Volval structures on the stem.

In view of the wide differences between the volval structures on the stem caused by a friable, a circumsessile, a limbate, or a saccate volva, these four cases are taken up separately.

With a friable volva the remnants on the stem usually have practically the same microscopic structure as those on the cap, although the elements tend to be disposed more irregularly, the hyphae to be more abundant, and the inflated cells to be scarcer or less voluminous. Sometimes, on the contrary, the inflated cells are larger than those on the cap or are shaped differently. Downward, usually at the base of the stem, the volva becomes thinner and thinner, its tissue passing gradually into that of the stem.

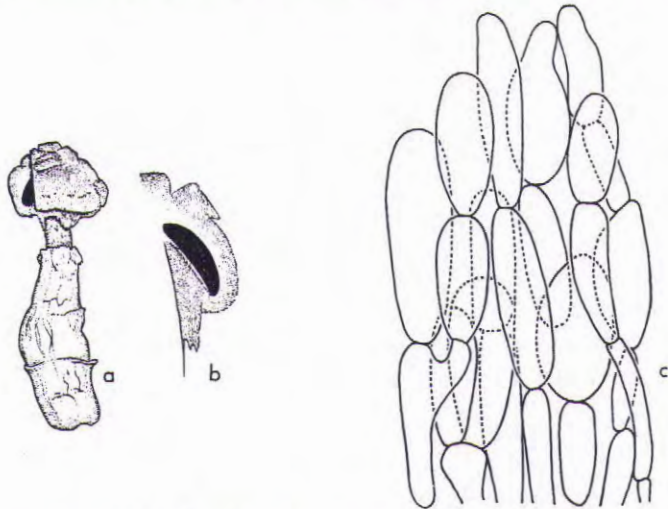


Fig. 10. Young fruit-body of unidentified species of subsection *Vittadiniae*; dotted lines in sectioned cap indicate direction of volval elements. — a. Habit ($\times 1/2$). — b. Median section of cap ($\times 5/4$). — c. Elements of volval remnants on cap ($325 \times$; all figs. from *F 38904*; FLAS).

In some species of subsection *Vittadiniae* the volval elements are disposed perpendicular to the surface at the centre of the cap of a button but towards the margin slanting outwards more and more until they are roughly parallel with the axis of the stem. Downward, in the volval tissue covering the stem, the elements continue in the same direction. This is demonstrated in Fig. 10 which represents an unidentified button of a species (*F 38904*, FLAS) of that group. This type of volva seems to be restricted to species in which it is especially the basal part of the stem that elongates (see p. 300).

The final shape of the volval remnants on the stem depends not only on the microscopic structure of the volva, but also in no small measure on the behaviour of the part of the stem to which they are attached. If, after the volva stops growing, the tissue of the stem underneath continues to elongate, the volva is stretched longitudinally, often breaking up into circular belts. If at the same time that part of the stem continues to become thicker, the volva is also stretched transversally, often breaking up into warts.

Apparently in *A. pantherina* the upper part of the volval sock around the base of the stem usually covers the lowest part of the stem, which continues to elongate after the volva has stopped growing. Therefore the upper part of the volval sock is often separated from the lower part in the shape of the circular volval rim so characteristic of this species.

In general the higher the volval remnants on the stem the more they are subject to stretching.

As a cleavage layer is lacking, the remnants of a friable volva on the stem are usually adnate. This means that when the stem continues to grow, its parts directly underneath the volval remnants become more or less fixed. Thus these parts are then separated by longitudinal clefts from the tissue of the stem, which is growing unhampered, and the volval remnants end up on the tips of scales. In this way for instance the flat membranous scales on the stem of *A. vittadinii* (Fig. 27) and the recurving scales on the base of the stem of *A. solitaria* (Fig. 104) are formed.

When the volva is circumscissile the upper part is usually friable, but the lower part is adnate to the bulb of the stem and difficult to distinguish from the covering layers of the bulb. In this case the bulb does not or scarcely participate in the elongation of the stem and it has a sharp edge along which the upper part of the volva is torn loose when the fruit-body starts to expand. This line of separation usually lies somewhat higher than the level of the margin of the cap in its original position.

Probably this type is due not so much to a specially structured volva as to a position of the young fruit-body in the primordial bulb deeper than in species with an immarginate bulb.

In section *Lepidella* a usually circumscissile volva is found in *A. silvicola* (Fig. 315) and *A. inodora* (Fig. 355).

The limbate volva is intermediate between the friable volva on the one side and the saccate volva on the other. The lower part is adnate to the base of the stem; its upper part, which originally surrounded the cap, is partly (sub)membranous (usually in the outer layer) and partly friable. Normally the mature fruit-body has volval remnants on the cap and a narrow volval limb at the base of the stem.

In the mature fruit-body the volval limb is found more or less appressed against the base of the stem (Figs. 328, 330, 361), or separated from the base of the stem by a circular groove which originally contained the margin of the cap (Figs. 336, 350). The presence of this groove seems again to depend on how deep in the primordial bulb the fruit-body is formed. Sometimes the bulb itself is apparently marginate from the beginning and the limb of the volva is inserted half-way between the base of the stem and the margin of the bulb (Fig. 321).

Within section *Lepidella* the limbate volva is here considered to be the main character of subsection *Limbatulae* (p. 528). It is very well possible, however, that this type of volva will also appear in other sections where intermediate forms between

a friable and a saccate volva may be expected, viz. in sections *Phalloideae*, *Amanita*, and *Vaginatae*.

The saccate volva is normally left behind at the base of the stem as a membranous to fleshy sac, sometimes with the exception of fragments of a friable inner layer (see p. 307) left behind on the cap. This does not necessarily mean that this type of volva is made up mainly of hyphae. My preliminary observations have shown that a saccate volva usually consists of a membranous inner and outer layer consisting mainly of hyphae, closing in an inner tissue made up of hyphae and rather abundant inflated cells; downward this inner tissue passes gradually into that of the base of the stem. The limb of the volva in mature fruit-bodies of *A. phalloides* and *A. virosa*, however, consists almost completely of hyphae.

All grades of separation between volva and base of stem occur. The lower part of the saccate volva may be completely adnate to the base of the stem, as in *A. fulvopulverulenta* (see Gilbert, 1941: pl. 38 or Beeli, 1935: pl. 3 fig. 1) and *A. ovoidea* (see Vittadini, 1832-35: pl. 2), or attached only to the outermost base of the stem, as in *A. princeps* and *A. hemibapha* (see Corner & Bas, 1962: pl. 10, 11).

These differences will certainly be important in a classification of the species in the sections of *Amanita* with a saccate volva. Huijsman (1959: 18) has pointed out that in the *Vaginatae* the position of the inner volval limb is a great help in classification. He introduced the adjectives 'unitangent' for the type of saccate volva in which the inner limb is in the angle between the volva and the stem (Fig. 8g) and 'bitangent' for that in which it is on the inside of the volva (Fig. 8h).

THE PARTIAL VEIL

In *Amanita* the primordial tissue between the primordial gills and stem usually differentiates for the greater part²² into a veil covering the edges of the young gills from the top of the stem to the margin of the cap. This type of veil is often called 'partial veil', sometimes 'annulus superus'. In the present work it is mostly referred to as 'ring', another common term for it, convenient but just as little precise as the others.

When the partial veil in *Amanita* is well developed and sufficiently coherent it loosens from the margin of the cap²³ and the edges of the gill on expansion of the cap. Finally it generally hangs down from the top of the stem like a skirt-like ring.

When in mature, normal fruit-bodies of *Amanita* a distinct ring is lacking, this may be because it is aborted (cf. Atkinson, 1914: 386), as is the case in many species of section *Vaginatae* and probably also elsewhere in the genus, or because the tissue is so incoherent that the ring falls to pieces on expansion of the cap, as happens

²² Usually a small, but in section *Lepidella* sometimes a fairly large part of this primordial tissue forms the inner limb of the volva; see p. 312.

²³ For some notes on the connection between the margin of the cap and the ring, see p. 302.

in several species of sections *Lepidella* and *Amidella*. Quite often the ring is both poorly developed and incoherent.

The place of a well-shaped ring on the stem depends mainly on the extent to which the upper part of the stem to which the ring is attached participates in the elongation of the stem. In section *Lepidella* this is very slight, so that the ring, if present, is usually strictly apical. Among the *Validae*, however, there are several species in which this part elongates considerably. In the mature fruit-body the ring is then subapical or even median, very rarely basal. The upper adnate part of the ring is then broken up into the small, usually transverse-elongate, irregularly shaped patches so characteristic of the upper part of the stem of species like *A. rubescens* and *A. excelsa*.

Although in the ring microscopic characters of taxonomic value are to be expected, I have not studied this part of the fruit-body systematically. Its cells often turned out to be difficult to reinflate. Moreover the ring is frequently such a delicate structure that in dried fruit-bodies it tends to fall to pieces when a section is removed for examination. Nevertheless a few remarks are called for.

In several species of *Amanita* the upper surface of the ring is marked with radial grooves and ridges corresponding with the gills. To be more precise, in the species I studied (*A. rubescens*, *A. phalloides*, *A. strobiliformis*) the edges of the gills correspond with the grooves on the ring. Before expansion of the cap the whole upper surface of the ring is covered with a loose tissue with many small inflated cells, strips of which are taken away by the edges of the gills when the cap starts to expand. The marginal tissue of the young gills (see p. 324) is in fact very similar to the tissue of the ridges on the ring.

De Bary (1866: 71) suggested that the ridges on the ring were formed by the remnants of plates of primordial tissue enclosed by the primordial gills. In view of the above this seems improbable.

In some species (e.g. in *A. muscaria*, *A. pantherina*, *A. crassa*) the smooth upper surface of the ring consists almost exclusively of hyphae, but this certainly does not hold for all species with a smooth ring.

In species where the ring is (sub)membranous in the mature fruit-body, its inner part very often, if not always, consists mainly of abundant, strongly branching and anastomosing, interwoven to radial hyphae.²⁴ This contradicts the statement of Singer (1962: 11) that the ring of *Amanita* consists mainly of isodiametric and inflated cells, and Gilbert (1925: 294) that the ring of *A. vittadinii* consists of only large fusiform to elongate cells similar to those in the volva. As mentioned above, it is only the upper surface layer that may often mainly consist of small inflated cells.

The tissue inside the thick but rather incoherent ring of *A. strobiliformis* appears

²⁴ Observations made in *A. muscaria*, *A. rubescens*, *A. solitaria*, *A. cokeri*, *A. timida*, and *A. vittadinii*.

to be composed of very irregularly shaped, branching, elongate, somewhat coral-
loid cells.

The structure of the lower surface layer of the ring is fairly variable. Sometimes it is made up exclusively of interwoven hyphae (e.g. in *A. phalloides*), sometimes of longitudinal hyphae and scattered elongate cells resembling those in the trama of the stem (e.g. in *A. cokeri*; there the underside of the ring is strongly fibrillose), sometimes (especially in section *Lepidella* ?) it is covered with fragments of a tissue resembling that of the volva and belonging to the inner volval limb, as discussed on p. 313, where the warts along the underside of the margin of the ring of many species are also considered.

CLAMP CONNECTIONS

Thus far the presence or absence of clamps has played scarcely any part in the taxonomy of *Amanita*, probably because in most of the common species of this genus in Europe and North America clamps are absent or difficult to find.

In section *Lepidella*, however, clamps occur rather frequently and have turned out to be a great help in disentangling the species, especially those from North America.

Looking for clamps in the tissues of dried fruit-bodies of *Amanita* is a dispiriting business. In each case it is necessary to examine many different types of tissue and their frequently largely inflated cells are often hard to reinflate. This makes it difficult to decide whether, simply because they have not been found, clamps are really lacking.

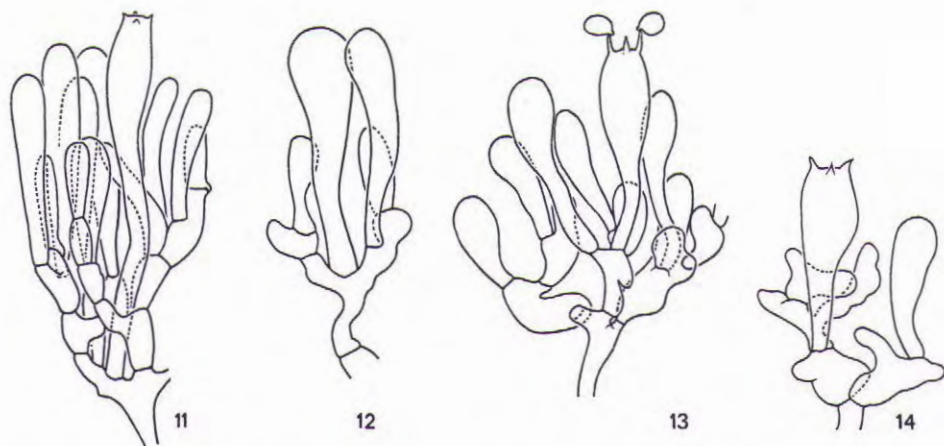
After examination of a fair number of collections, it appeared to me that in all the cases in section *Lepidella* where I had found clamps somewhere in the fruit-body,²⁵ they were also present on the basidia. Moreover in a number of collections I found clamps only on the basidia. It looks as though the genus *Amanita* is in the process of losing its clamps, the basidia being the slowest elements to do so.

This led me to examine especially the basal septa of the basidia²⁶ for the presence of clamps and to note the occurrence of clamps in other tissues only when I came across them. An additional advantage of this method is that even in poorly dried fruit-bodies it is often still possible to reinflate the basidia.

For the examination of basidia for the presence of clamps it is recommended that only very small parts of the gills be coloured in Congo Red (see p. 290), these pieces be put into a drop of 5 % KOH, and that they be torn into the smallest possible fragments with needles before they are dissociated by gentle tapping on the cover glass.

²⁵ Sometimes in the volva, the pileipellis, the trama of the stem or the trama of the gills, sometimes practically everywhere.

²⁶ Kühner & Romagnesi (1953: 179) quite successfully used the presence or absence of clamps on the basidia as a key-character in *Rhodophyllus*.



Figs. 11-14. Elements of subhymenium and hymenium. — 11. *A. subsolitaria* ($\times 500$; from Murrill, 28 June, Tung-oil Mill). — 12. *A. solitariiformis* ($\times 850$; from type). — 13. *A. polyphyramis* ($\times 500$; from Sharp 25000). — 14. *A. sublutea* ($\times 500$; from type).

Sometimes the clamps at the base of older basidia have grown out to form new basidia (proliferation of clamps; see Bas, 1965: 355). Then true clamps are only to be found on the youngest basidia (Fig. 11). Usually, however, the typical shape of the base of the older basidia betrays the original presence of clamps. Their basal septa then often consist of two planes meeting at an obtuse angle (Fig. 12).

In section *Lepidella* I have met with real difficulties as to the presence or absence of clamps in only two cases.

In the type of *A. subalbida* (p. 510) most basidia were clampless but a small number showed distinct clamps; no clamps were found in other tissues. Perhaps clamps are formed here only on the first-born basidia. The species is placed here among the clamped species.

In *A. crassifolia* (p. 516) the shape of the base of the basidia intimated the presence of clamps but not a single distinct clamp was found; consequently it is placed among the clampless species. For safety's sake both *A. subalbida* and *A. crassifolia* are keyed out here among the clamped as well as the clampless species.

Aside from section *Lepidella* clamps seem to be relatively rare in *Amanita*. Thus far I have found them only in some species of section *Vaginatae* (e.g. *A. caesarea*, *A. hemibapha*, and *A. princeps*) and in the basal tomentum of *A. muscaria* of section *Amanita*.

In several genera of Basidiomycetes clamps are present in the secondary mycelium but lacking in the fruit-body. For *Amanita* Kühner (1947: 142) mentioned the presence of small clamps in the mycelium of *A. caesarea*, and clampless septa in the mycelia of *A. citrina*, *A. junquillea*, and *A. valida*, whereas Semerdžieva (1965) found some clamps in the mycelium of *A. muscaria* and only clampless septa in the mycelia

of *A. citrina*, *A. phalloides*, *A. rubescens*, and *A. strobiliformis*. These results agree with my observations on the fruit-bodies.

SPORES

Like in most other genera of the agarics, in *Amanita* the characters of the spores are of great taxonomic importance.

The genus can be divided into two subgenera based mainly (but not only!) on the reaction of the walls of the spores to iodine (see p. 296). In subgenus *Lepidella* the walls of the spores are amyloid (except in one species, see p. 342), in subgenus *Amanita* inamyloid. Thus far no dextrinoid reaction of the walls of the spores has been recorded. There are a few species, however, in which the contents of the spores turn reddish brown in Melzer's reagent (*A. westii*, see p. 486; *A. mutabilis*, see p. 542), sometimes even so strongly that the amyloid reaction of the walls is only perceptible in empty spores. It is uncertain whether or not a true dextrinoid reaction is involved here, as the contents of the spores are yellow brown in alkaline solution.

In one species of section *Lepidella*, viz. *A. roanokensis*, the apical parts of a small to fairly large percentage of the spores appeared to be decorated with minute amyloid warts (Figs. 366, 368). In alkaline solution these warts were scarcely perceptible, even after colouring in Congo Red. The amyloid warts are probably not the result of a break-up of an amyloid layer.

The size of the spores plays an important part in distinguishing species, sometimes stirpes. The smallest and largest are found in section *Vaginatae* (from about $4.5\text{--}5.5 \times 4\text{--}5 \mu$ in *A. aurea*, up to $16 \times 15 \mu$ in some forms of the *A. vaginata*-complex); in section *Amidella* the longest bacilliform spores (up to $21 \times 5.5 \mu$ in *A. cylindrispora*) occur.

As the value of the measures recorded depends on the number of measurements, I have indicated this number in the descriptions, together with the number of fruit-bodies from which the measured spores were taken.²⁷ In my experience it is usually sufficient to measure ten spores per sample; in special instances (few specimens available, or great variability of spores) I measured twenty per sample; in additional collections only five when the measures found fell within the range already established. Extreme values have been placed between brackets where they represented no more than 10 % of the spores.

As the spores in 1- to 3-spored basidia tend to be larger than normal it is advisable always to examine the number of sterigmata per basidium, which is fairly variable in *Amanita* (see discussion on basidia below).

The shape of the spores in *Amanita* ranges from globose to bacilliform. As this variation is mainly due to the variation of the length-breadth ratio (l/b), I have

²⁷ "Spores [40/5] . . ." means: Spores, forty from five specimens measured, . . .

determined the ratio for each spore measured, as well as its extreme values and average in each collection studied. This considerably facilitated comparisons between collections and species. I have defined the terms denoting the shape of spores in *Amanita* as follows:

| | | |
|-------------------|-----|-----------|
| Shape: globose | l/b | 1.0 -1.05 |
| subglobose | | 1.05-1.15 |
| broadly ellipsoid | | 1.15-1.3 |
| ellipsoid | | 1.3 -1.6 |
| elongate | | 1.6 -2.0 |
| cylindrical | | 2.0 -3.0 |
| bacilliform | | > 3.0 |

In general the shape of the spores of *Amanita* is fairly regular. Cylindrical to bacilliform spores are sometimes slightly curved. Rarely the spores are somewhat constricted in the middle (Figs. 203, 365); quite often they are slightly ovoid or obovoid.

In a number of species of subsection *Vittadiniae* (Figs. 82, 86, 91, 93) the apiculus of the spores is conspicuously tapering and projecting. In the same group the walls of the spores are sometimes distinctly thickened, a character thus far not found elsewhere in *Amanita*. I have been unable to distinguish layers in these thickened walls, even after colouring them in Melzer's reagent, Congo Red, and Cresyl Blue. The amyloid reaction of the thick-walled spores is, however, somewhat more pronounced than in thin-walled spores.

The walls of the spores of *Amanita* are nearly always smooth. Exceptions are the above mentioned spores with amyloid warts of *A. roanokensis* and the minutely asperulate spores of *A. princeps* in section *Vaginatae*.

The contents of the spores of the species treated here have been described because there is a general trend towards granular-refractive contents in section *Lepidella*. The contents of the spores of any specimen, however, may vary considerably; moreover those of spores taken from the gills sometimes look different from those of spores taken from a sporeprint. The more or less dextrinoid contents of the spores of a few species of section *Lepidella* have been mentioned above.

The colour of the spore print is usually white to pale cream, but in *A. solitaria* (= *A. echinocephala*, see p. 394) it is greenish cream and in *A. pelioma* (see p. 465) cream to olive-buff. More information on the colour of fresh spore prints is badly needed.²⁸

BASIDIA

Except for the presence or absence of clamps at their basal septa, as treated in the discussion on clamp connections (p. 318), the characters of the basidia are of little taxonomic importance.

²⁸ It is not sufficient simply to file a spore print with the dried material because the print often turns yellowish with age. The colour of the print must be noted while it is fresh.

Size and shape vary considerably, even in the same fruit-body. In general, however, there seems to be a certain correlation between the structure of the subhymenium and the shape of the basidia. In species with a ramose subhymenium, which often occurs in section *Lepidella*, the slender, tapering base tends to make the basidia relatively long and slender (Fig. 11). In species with a cellular subhymenium, found frequently for instance in section *Validae* but more rarely also in section *Lepidella*, the fairly abrupt, broad base makes the basidia relatively short (Fig. 132); intermediate forms are frequent.

Although the basic number of spores per basidium is nearly always four, species with many aberrant basidia are not rare. In one fruit-body of a species close to *A. virosa*, from Michigan (*Bas* 3761), 48 % of the basidia proved to be 4-spored, 30 % 3-spored, 20 % 2-spored and 2 % 1-spored. In species of the *A. vaginata*-complex aberrant basidia are even fairly common. Uniformly 2-spored taxa are rare (*A. bisporigera!*).

In a few species with more or less dextrinoid contents of the spores (see above), the basidia have similar contents, though mostly less conspicuously so (*A. westii*, p. 486; *A. mutabilis*, p. 542). In *A. sculpta* many elements of the young hymenium turn red-brown in Melzer's reagent, but this has not yet been investigated in mature basidia and spores.

CYSTIDIOID BODIES

Thus far no true hymenial cystidia have been found in *Amanita*, unless the marginal cells are reckoned among them (see below).

In *A. xanthogala* (p. 488) laticiferous hyphae penetrate from the trama of the gills into the hymenium, there forming a very simple type of tramal cystidia, which in agreement with Singer (1962: 41) are here called pseudocystidia (Figs. 250, 255). They have yellow, refractive contents and show no special reaction in the usual reagents (see p. 333).

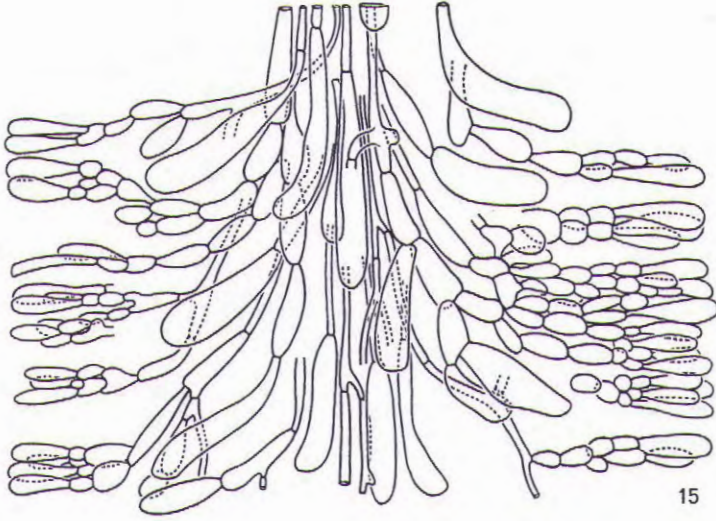
In the hymenium of *A. borneensis* (p. 477) scattered basidium-like cells with one rather thick apical appendix were found, and in that of *A. codinae* a few ventricose-fusiform cells (Figs. 33). Both cases probably represent incidentally abortive basidia.

THE MARGINAL TISSUE OF THE GILLS

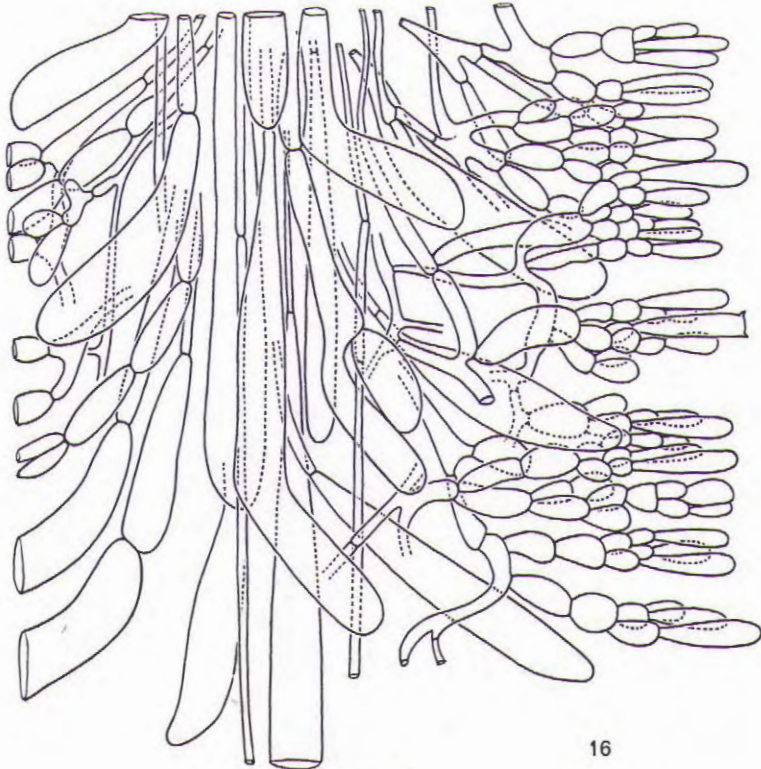
Because of the schizohymenial type of development of the hymenophore in *Amanita* (see p. 300) the edges of the gills are attached to the partial veil until the expansion of the cap tears them loose. The elements found along the edges of the

EXPLANATION OF FIGURES 15,16

Figs. 15, 16. Cross-sections of gills of *A. citrina*. — 15. Gill from button of which cap is still closed and stem starts to elongate. — 16. Gill from almost completely expanded fruit-body (both figs. $\times 325$; from *Bas* 4528a; L).



15



16

Figs. 15, 16

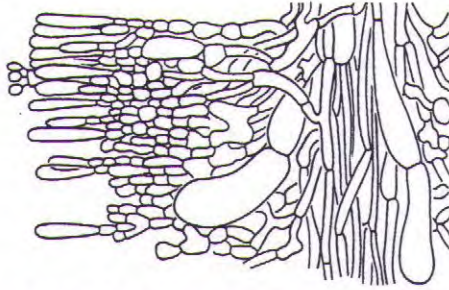


Fig. 17. Cross-section of gill of *A. volvata*; gill from fruit-body of which cap is partly expanded; sporulation just starting ($\times 325$; from *Bas 3799*; L).

gills of just-opened caps are the remnants of a cleavage layer formed between the edges of the cap and the main tissue of the ring or its rudiments on the stem (see p. 317). This means that the elements of the marginal tissue of the gills of *Amanita* are probably not homologous with any type of cheilocystidia found in other genera of the agarics.

In many cases the marginal tissue consists almost entirely of small to large inflated cells, attached terminally or in short terminal rows to hyphae of the trama of the gills. Usually the inflated cells vary considerably in size and shape, even in the same fruit-body.

It is also not unusual to find loose hyphae or fragments of hyphae, whether connected with inflated cells or not, along the edges of the gills. Apparently the outer hyphae of the main tissue of the ring are then borne upwards by the gills. This is the usual course in *A. muscaria*.

In one case, viz. in *A. crassa* (p. 402), I found the edges of the young gills cut off cleanly, viz. completely devoid of any marginal tissue. Here the outer layer of the ring turned out to consist merely of hyphae.

In species of subsection *Vittadini* the marginal tissue is mostly very scanty.

Because in dried material the elements along the edges of the gills are sometimes completely collapsed or disintegrated, data on the marginal tissue are lacking in several of my descriptions.

THE TRAMA OF THE GILLS

Thus far the trama of the gills of *Amanita* has appeared to be bilateral²⁹ in all the species in which it was studied. This means that in a cross-section of a gill the

²⁹ Singer (1962: 50) called any trama of a gill bilateral if the lateral hyphae diverge outward and downward. Reijnders (1963: 260) on the other hand made a distinction between (i) a permanently divergent trama in which the structure is merely a continuation of the initial divergent trama found in the primordial gills in the majority of the agarics, and (ii) a bilateral trama in *Amanita*, a secondary structure, since in this genus the trama of the primordial gills is regular.

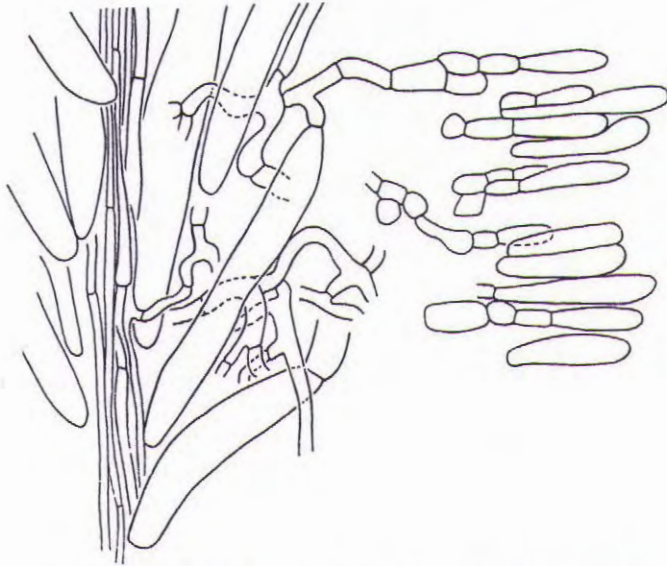


Fig. 18. Cross-section of gill of *Pluteus petasatus* (Fr.) Gill.; gill from expanding fruit-body with 40 mm wide cap ($\times 500$; from Bas 4509; L).

mediostratum of parallel hyphae, which run from the cap above to the edge of the gill below, is flanked on both sides by a lateral stratum of elements curving outward and downward towards the subhymenium (Figs. 15, 16, 31, 51). Usually the main direction of the diverging elements is obliquely downward towards the subhymenium but occasionally, especially near the attachment of the gill to the cap and in young gills, it is perpendicular to the subhymenium (Fig. 17).

In most species of *Amanita*, e.g. in *A. citrina* (Fig. 15, 16) the trama of the gills is composed of two types of elements.

First there are diverging hyphae, consisting of narrow cylindrical to rather inflated but relatively small cells, which continue into the subhymenium and are actually connected with the cells of the subhymenium. For convenience these diverging hyphae are referred to as 'feeding hyphae'.

Secondly there are large, elongate, inflated cells, single or in short rows, which are not connected with the cells of the subhymenium but simply terminate with free tips in the trama or the subhymenium. These are provisionally called 'pressure cells'.³⁰

³⁰ 'Feeding hyphae' and 'pressure cells' correspond with Fayod's (1889: 219) 'connective tissue' and 'fundamental tissue', but in my opinion his terms are so misleading that I prefer to avoid them.

In a cross-section of a mature gill of *Amanita* the 'pressure cells' often fill the whole picture and make the 'feeding hyphae' difficult to distinguish.

Apparently in the majority of the species of *Amanita* the increase in bulk of the trama of the gills succeeding the differentiation of its elements is caused mainly by inflation of the 'pressure cells'.

In several species of section *Lepidella*, however, 'pressure cells' are lacking or very scarce (Figs. 31, 51). In that case the increase in bulk of the trama is caused by inflation of the 'feeding hyphae'. It would seem to me evident that this is more primitive than the differentiation of the trama into a feeding and an inflating system such as is found in the majority of the species of *Amanita* (see also the discussion on the trama of the stem).

Where 'pressure cells' are lacking in the trama of the gills in species of *Amanita* the trama is still unmistakably bilateral. Moreover in very young gills of *A. rubescens* and *A. citrina* I found that the trama of the gills is distinctly bilateral even when the 'pressure cells' are still inconspicuous. Reijnders (1963: 262) stated that the only important difference between the structure of the trama of the gills in *Amanita* on the one side and the inverse trama of the gills in *Pluteus* (Fig. 18) and *Volvariella* on the other is that in *Amanita* the 'pressure cells' curve outward and in *Pluteus* and *Volvariella* inward. My own observations, however, suggest that the hymenophoral trama of *Amanita* is bilateral and of *Pluteus* and *Volvariella* regular before the 'pressure cells' develop.

Another dissimilarity is that in *Amanita* differentiation into a feeding and an inflation system in the trama of the gills is part of a phenomenon occurring in many tissues of the fruit-body (see below discussion on trama of stem) but that in *Pluteus* and *Volvariella* this differentiation is restricted to the gills (Reijnders, 1963: 262). I am not completely convinced that the 'pressure cells' in *Amanita* are homologous to the inflated cells in the trama of the gills of *Pluteus* and *Volvariella*.

In the gills of dried specimens it is difficult to ascertain the presence or absence of 'pressure cells'. Information on this character is therefore often lacking in my descriptions, even though it may be of taxonomic value.

THE SUBHYMENIUM

In *Amanita* the subhymenium is usually well developed and about one to two times thicker than the hymenium. Sometimes, however, delimitation of it against the trama proper is rather difficult as its cells usually gradually increase in size inward.

In section *Lepidella* the shape of the subhymenial cells appears to be rather variable. The following main types are distinguished but intermediate types are common.

Ramose: cells relatively narrow and branching (Figs. 11, 12).

Inflated-ramose: cells inflated and branching (Fig. 13).

Coralloid: cells shaped very irregularly, with more projections than connections with other cells (Figs. 14, 178).

Cellular: cells ellipsoid to more or less isodiametric (Fig. 132).

The young stages of the inflated-ramose and coralloid types are probably always ramose. Apart from section *Lepidella*, the cellular subhymenium type seems to be the common one in *Amanita*. When young basidia are formed by proliferation of the clamps at the base of older basidia (see p. 319) irregularly shaped subhymenial cells are formed, each carrying a number of differently aged basidia (Fig. 12).

That at least in some species of *Amanita* there is a kind of thickening hymenium³¹ is demonstrated in the illustration of a 'subhymenial tree' of *A. subsolitaria* (Fig. 11), where basidia are found to arise from the subhymenium at four to five levels.

Apparently the long, clamped basidium on the ramose, somewhat thickening subhymenium belongs at the incipience of a phyllogenetic trend towards a short, clampless basidium on a scarcely thickening, cellular subhymenium.

THE PILEIPELLIS

In many recent publications on Agaricales the term 'cuticle' or 'cuticula', introduced into mycology by Fayod (1889: 241), is still used to indicate the cortical layer(s) of the cap. This term has, however, a distinct meaning in the anatomy of the phanerogams: a non-cellular layer covering the epidermis. Therefore it should not be used in mycology for cellular cortical layers in general. This was already pointed out by Lohwag & Peringer (1937: 301), Lohwag (1941: 95), and Jossierand (1952: 190).

For this reason I propose the Latin term 'pellis', for the cortical layers of the basidiomycetous fruit-body not belonging to the veils; consequently 'cuticle' is replaced by 'pileipellis'. This opens the way for the introduction of such terms as 'stipitipellis' and 'bulbipellis'.

It should be emphasized that these terms are purely topographical; in descriptions they would have to be followed by terms describing their structure, such as 'trichoderm', 'ixocutis', etc.

It is evident that the meaning of the terms proposed is no more precise than that of 'cuticle' in mycology. It is frequently difficult to indicate the lower (or inner) limit of a pellis because this often passes gradually into the trama underneath. Sometimes there is the same difficulty with the upper limit when there is an adnate volva, which is not rare in the species of *Amanita* treated here.

Singer (1951: 58; 1962: 59) pointed out that Lohwag, in introducing a detailed nomenclature for different parts and types of cortical layers in fungi, failed to make a sufficient distinction between topographical and descriptive terms. But Singer did not accept the consequences. If Lohwag's descriptive terms for cortical layers are admitted along general lines (as is done by Singer) 'derm' must be used for

³¹ Might 'thickening subhymenium' perhaps not be a better name?

(layers of) the pellis in which the elements are arranged in an anticlinal position (e.g. hymeniderm, trichoderm, etc.) and 'cutis' for (layers of) the pellis consisting of periclinal elements. It is then simply not practicable to use 'hypoderm' or 'subcutis' for a layer following downward on the 'epicutis'. The last three terms are topographical and should be free from conspicuous, etymological connections with descriptive terms.

Disregarding their structure I therefore propose the division of a pellis of two layers into an outer 'suprapellis' and an inner 'subpellis' and a pellis of three layers into a 'suprapellis', a 'mediopellis' and a 'subpellis'. It goes without saying that use of the same topographical terms for different fungi does not imply homology.

The pileipellis of *Amanita* is a cutis or ixocutis. When a cutis it is sometimes so slightly developed as to be difficult to distinguish from the volval tissue above and the trama of the cap underneath.

When the pileipellis is an ixocutis it is especially the suprapellis that gelatinizes (often so strongly that its hyphae disintegrate completely), whereas the subpellis gelatinizes only slightly and comprises the hyphae in which the pigment, if present, is usually localized.

The hyphae of the pileipellis are usually narrow and radial to interwoven. The type of hyphal arrangement found often depends on which part of the pileipellis is examined. Nevertheless there are indications that study of the diameter and disposition of the hyphae in the pileipellis of certain groups of species of sections *Vaginatae* and *Phalloideae* will produce valuable results.

THE TRAMA OF THE STEM AND THE CAP

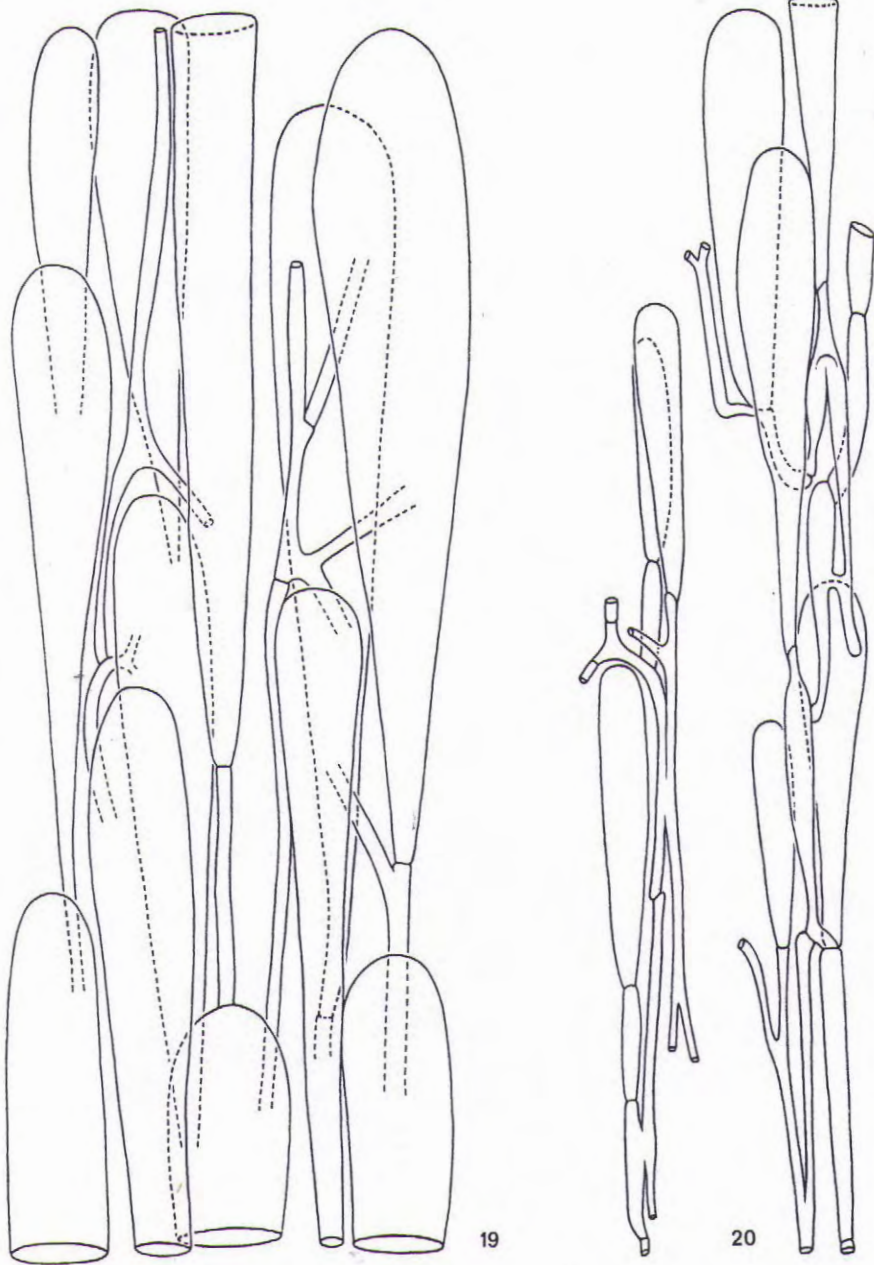
THE TRAMA OF THE STEM.—Hoffmann (1861: 11) was probably the first to describe, and Boudier (1886: pl. 1 fig. 8) the first to illustrate clearly the curious type of tissue in the stems of species of *Amanita*.

Under the microscope the tissue at first sight often seems to consist merely of large, longitudinally disposed, slenderly clavate cells. More careful examination reveals that the enormous clavate cells are usually the terminal members of short side-branches of a diffuse system of narrow, branching, predominantly longitudinal hyphae (Figs. 19, 20). Here again (compare the discussion above on the trama of the gills) the elements of the tissue are clearly differentiated in 'feeding hyphae' (connective tissue) and 'pressure cells' (fundamental tissue).

In several species of section *Lepidella* the 'feeding hyphae' and 'pressure cells' are less perfectly differentiated than those in the species of other sections of *Amanita*. Not only are the 'pressure cells' often in rows, with the intercalary cells less inflated than the terminal ones, but the 'feeding hyphae' are also wider, so less easy to

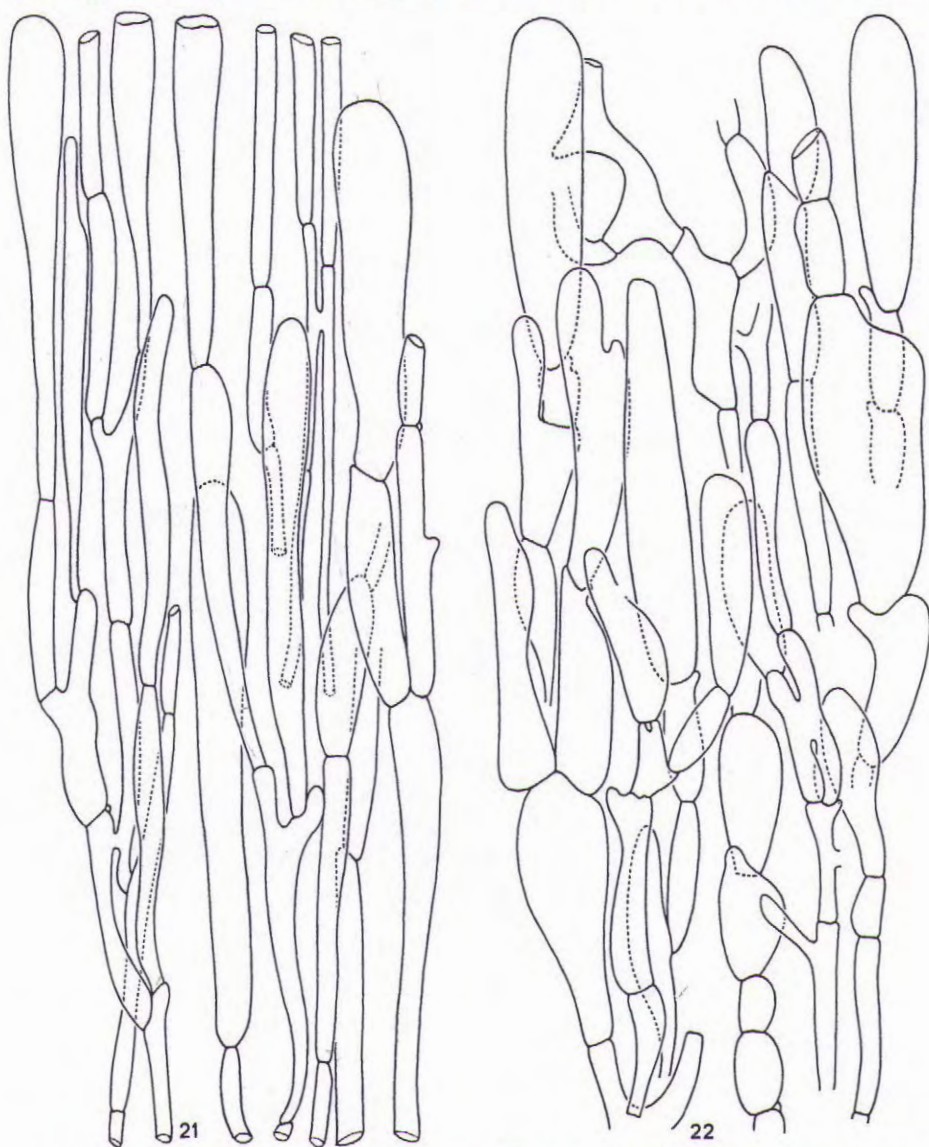
EXPLANATION OF FIGURES 19, 20

Figs. 19, 20. Longitudinal sections of trama of stem. — 19. *A. citrina* ($\times 325$). — 20. *A. porphyria* ($\times 250$).



Figs. 19, 20

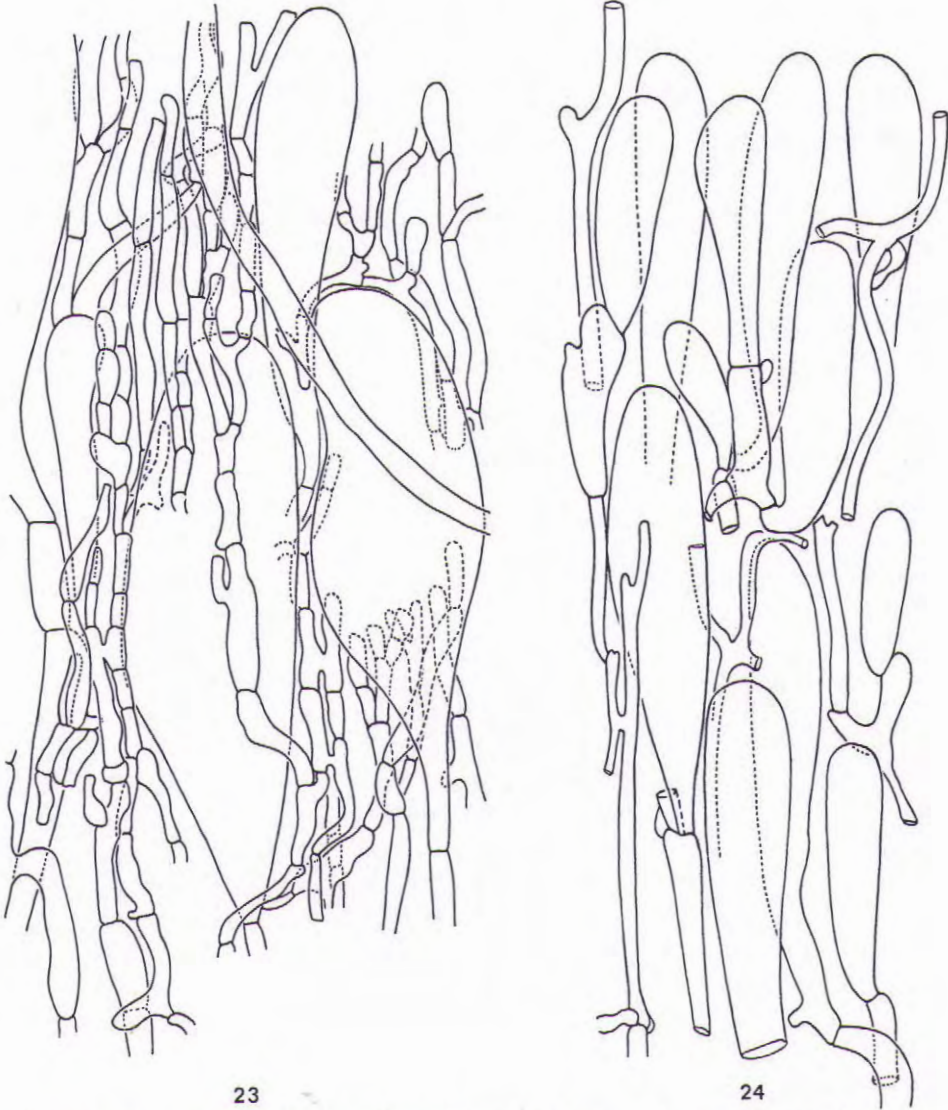
distinguish from the 'pressure cells' (Fig. 21). In *A. bubalina* (Fig. 22) the tissue of the stem is even so irregular that it barely reveals the typical 'Amanita-structure'. Aside from the genus *Amanita* this structure is known only in the genus *Limacella*, which is generally considered to be closely related to *Amanita*. In *L. guttata*



Figs. 21, 22. Longitudinal sections of trama of stem. — 21. *A. silvifuga*. — 22. *A. bubalina* (both figs. $\times 325$; from type).

I found the structure of the stem much the same as that described above for some species of section *Lepidella*.

In my opinion the low degree of differentiation of the elements of the tissue of the stems in some species of section *Lepidella* and in the genus *Limacella* must be



Figs. 23, 24. — Longitudinal sections of trama of stem of *A. timida*. — 23. Upper part of clavate base of stem. — 24. Apical half of stem (both figs. $\times 325$; from type).

regarded as primitive compared with the highly differentiated tissue in the stems of most of the species of *Amanita*.

THE TRAMA OF THE BULB.—Very early the tissue of the primordial bulb of *Amanita* is made up of a dense tissue of interwoven, branching, narrow hyphae with scattered, large, globose cells (Brefeld, 1877: 123; Reijnders, 1963: 123). When the lower part of the bulb does not participate in the process of elongation of the young fruit-body this primordial tissue can be found, only slightly altered, in the basal bulb of the mature fruit-body. If, on the other hand, the bulb does participate in the elongation the inflated cells also become more or less elongate, like, for instance, in the upper part of the clavate base of *A. timida* (Fig. 23). In that case the tissue surrounding the inflated cells preserves its primordial character to some extent. In the upper part of the stem of *A. timida* the tissue has the normal '*Amanita*-structure' (Fig. 24).

THE TRAMA OF THE CAP.—The trama of the cap in *Amanita* does not differ fundamentally from that in the stem (Boudier, 1866: pl. 1 fig. 9). It is only more difficult to analyze because of its more irregularly disposed elements, the more variable shape and size of the 'pressure cells', and local inflations of the 'feeding hyphae'.

PIGMENTATION

In *Amanita* when pigment is present and discernible under the microscope, it (nearly) always turns out to be vacuolar. This agrees with previous observations by Kühner (1934: 367). The only exception is the brown pigment in the thickened walls of volval elements of dried specimens of *A. borneensis*. As in this case, however, the colour of the fresh fruit-bodies was described as much paler than that of the present dried fruit-bodies, it is possible that the brown colour was caused here by necropigment.

Not yet localized necropigment also occurs in dried specimens of many species of section *Amidella* in which the gills take a peculiar brownish grey to greyish purple-brown colour after drying. In *A. subalbida* (p. 510) of section *Lepidella* the originally white to pale cap and gills have turned conspicuously dark chocolate brown in the dried type-collection.

It is noteworthy (i) that sections *Lepidella* and *Amidella* comprise so many poorly pigmented species, (ii) that when in species of these sections pigment is abundant it is either concentrated in the volva, or in both the volva and the pileipellis, and (iii) that in these sections the pigment is very rarely bright.

In the other sections of *Amanita* (i) poorly pigmented species are relatively rare, (ii) the pigment is often concentrated in the pileipellis, more rarely in both the pileipellis and the volva (e.g. in several species of section *Validae* and in *A. rubrovolvata* of section *Amanita*), and (iii) bright pigment occurs fairly frequently.

VASCULAR HYPHAE

Oleiferous hyphae are present in the trama of cap and stem of nearly every species of *Amanita* and fairly often also in the trama of the gills and in the volval tissue. Sometimes, however, they seem to be completely lacking, e.g. in *A. silvicola* (p. 526).

In a few cases the characters of oleiferous hyphae may offer some help in distinguishing stirpes or species. In the two species of stirps *Perpasta* (p. 409), for instance, they form characteristic, large, brown, radiating vessels on the base of the volval warts on the cap. One of the differences between *A. onusta* and *A. atkinsoniana* is the scantiness of oleiferous elements in the volval tissue of the former and their abundance in the volval tissue of the latter. Such characters, however, should be carefully used, as it is my impression that the frequency of oleiferous hyphae may be rather variable within a single species. Moreover this type of hyphae is sometimes more than normally abundant in places where the fruit-body has been damaged.

The refractive contents of oleiferous hyphae are usually yellowish in alkaline solution; in the few cases tested they were inactive in Melzer's reagent, Congo Red, Sulfovanillin, and Cresyl Blue.

Laticiferous hyphae have thus far been found only in *A. xanthogala* (p. 490), where they contain yellow latex. Probably they are modified oleiferous hyphae. Their contents turn a fairly bright yellow in alkaline solution but for the rest have the same set of negative reactions as mentioned above for oleiferous hyphae. It is curious, however, that the laticiferous hyphae in *A. xanthogala* penetrate into the hymenium (see p. 322); this has not been observed in oleiferous hyphae.

CHEMICAL CHARACTERS

SMELL

Most species of *Amanita* have no manifest smell. In some cases, however, particular smells have been observed which are characteristic of species or groups of species and sufficiently constant to be of taxonomic value. The smell like that of raw potatoes of *A. citrina* and *A. porphyria* and the sweetish-nauseating smell of *A. phalloides* and *A. virosa* are good examples of this.

It is useless to enumerate all the types of smells recorded for species of *Amanita*. One type of smell, however, needs a few words of explication. It is that which is often indicated as 'like chloride of lime' and recorded in American literature for several species of section *Lepidella*. The problem is that chloride of lime itself has no particular smell. I have been told, however, that the smell referred to is that caused by its use as a disinfectant for old-fashioned toilets. At any rate the smell is disagreeable and pungent; it combines an unpleasant, chemical component with a foetid component of deteriorating proteins. Sometimes it is also described as the smell of old ham, i.e. of the outside of the rind of old ham.

This particular smell is probably a character of importance in section *Lepidella*, where it occurs in about half the species. In view of the new delimitations given here for several species of *Lepidella*, especially North American ones, new and more precise records of the smell of many species is needed.

TASTE

The taste of fresh specimens of *Amanita* is rarely recorded. Where it is known it is often indistinct. The great collector, Mrs. M. Goossens-Fontana (see Beeli, 1927, 1931, and 1935), however, described several species from the Congo as being acrid (e.g. *A. rhodophylla*) or bitter (e.g. *A. odorata*, *A. amanitoides*). Dr. H. D. Thiers described *A. silvifuga* and *A. thiersii* as being bitter.

POISONOUS AND EDIBLE SPECIES

The genus *Amanita* comprises both deadly poisonous species and species highly appreciated as delicate food.

From the taxonomic point of view it is important that, at least on occasion, certain poisonous properties be registered as characteristic of groups (series?) of closely related species, e.g. the *A. muscaria*—*A. pantherina*-complex and the *A. phalloides*—*A. verna*—*A. virosa*-complex.

Unfortunately for many species information on these qualities is lacking, especially for those more recently described. For species of section *Lepidella* I met with the following records:³²

Poisonous: *A. ameghinoi* (p. 358), *A. preissii* (p. 536), *A. robusta* Bouriquet (p. 563), and *A. robusta* var. *spinosa* (p. 565).

Suspected: *A. solitaria* (see Konrad & Maublanc, 1948: 68, under *Aspidella echinocephala*).

Edible: *Amanita vittadinii* (p. 349) and *A. strobiliformis* (see Konrad & Maublanc, 1948: 67, under *A. solitaria*). *Amanita praegraveolens* (p. 375) is reported as not toxic to guinea-pigs.

There is a vast amount of literature on the poisonous agents in *Amanita*. By way of introduction I refer to Heim (1963) and the publications of Th. Wieland and his school.

CHEMICAL TESTS

Thus far macrochemical tests have played no part in the infrageneric classification of *Amanita*. On several species I have tested the chemicals used by Bataille (1948: 9) on specimens of *Amanita* and found the results very unsatisfactory. The only test I found useful is that of 10 % KOH on the cap of *A. virosa* (dried as well

³² A number of reports on edibility or poisonous properties of species of section *Lepidella* are unreliable because the names used are probably misapplied. This is especially the case with names like '*A. solitaria*' and '*A. chlorinosma*' in American literature.

as fresh); it gives a bright yellow colour, in contrast to *A. verna* and *A. citrina* var. *alba*, which barely discolour with the same chemical. This reaction is not specific; it also occurs in *A. bisporigera*.

Sections of dried fruit-bodies of species of section *Lepidella* often turn yellow in 10 % KOH. Perhaps this reagent will give useful results when tested on fresh fruit-bodies of these species.

The only microchemical test of importance in *Amanita* is that of Melzer's reagent on the walls and sometimes the contents of the spores (see discussion on spores on p. 320).

ECOLOGY AND DISTRIBUTION

The large majority of species of *Amanita* are terrestrial, forest-inhabiting fungi. Syntheses have proved that a number of them (e.g. *A. caesarea*, *A. frostiana*, *A. muscaria*, *A. rubescens*) are able to form ectotrophic mycorrhizas with trees (Doak, 1934; Hacskeylo & Palmer, 1955; Hatch & Hatch, 1933; Melin, 1923, 1925, 1936 etc.). From general field-experience it may be concluded that practically all the forest-inhabiting species of *Amanita* are obligate mycorrhizal. A number of species, especially of section *Vaginatae*, venture into treeless boreal and alpine regions, but there they are almost certainly associated with dwarf-shrubs.

In section *Lepidella*, particularly in its subsection *Vittadiniae*, however, several species are reported to grow in meadows, on fields, on lawns, on prairies, on pampas, etc. It seems very probable that these species are non-mycorrhizal.

In this connection it is interesting that in large areas of South America ectomycorrhizal forest is absent or rare (Singer, 1964: 8; Moser, 1967: 363), and that six species of subsection *Vittadiniae* and one of subsection *Solitariae* (viz. *A. crassa*) are the only indigenous species of *Amanita* known from these regions.

In contrast to the tropical South American forests, those of south-eastern Asia are relatively rich in species of *Amanita* (see Corner & Bas, 1962); judging by their relationship these are probably mostly mycorrhizal.

See also the notes on habitat and distribution of the genus on p. 340 and of section *Lepidella* on p. 344.

It is regrettable that scarcity of data makes it so difficult to obtain a picture of the ecology of the species from study of herbarium material of agarics.

From literature and my own experience it would seem that species of the following genera of trees are potential mycorrhizal partners for species of *Amanita*:

Gymnospermae:

Abies
Cedrus
Larix
Picea
Pinus

Pseudotsuga
Tsuga

Angiospermae:

Alnus
Betula
Carpinus
Castanea
Castanopsis

Corylus
Eucalyptus
Fagus
Lithocarpus
Nothofagus

Populus
Quercus
Salix
Shorea
? Tilia

RELATIONSHIP

The taxonomic affinities within the genus *Amanita* that are recognized here are founded on degrees of similarity. The sequence, however, in which the taxa are treated is also determined by the assumption that certain characters are primitive and others derived. The following hypothetical lines of development³³ have played their part:

1. Friable volva → Limbate volva → Saccate volva.
2. Volva composed mainly of rows of large, elongate, inflated cells → Volva composed either of hyphae and variously shaped inflated cells, or of relatively broad inflated cells only.
3. Volva adnate to cap → Volva separating from cap because of well-developed pileipellis.
4. Base of stem elongating → Base of stem remaining bulbous and apex of stem elongating → Totally elongating stem without bulbous base.
5. Excentric initiation of fruit-body in primordial bulb → Central initiation of fruit-body in primordial bulb.
6. Inflated elements and hyphae in trama of gills, cap, and stem poorly differentiated → Inflated elements and hyphae in trama strongly differentiated.
7. Subhymenium ramose and somewhat thickening → Subhymenium cellular and scarcely thickening.
8. Clamps abundant → Clamps locally present → Clamps absent.
9. Margin of cap appendiculate → Margin of cap not appendiculate.
10. Margin of cap smooth → Margin of cap sulcate.
11. Saprophytic → Mycorrhizal.
12. Thin-walled spores → Thick-walled spores.
13. Globose to ellipsoid spores → Bacilliform spores.

Judging by the large number of supposedly primitive characters in *Lepidella*, this would be the most primitive section in *Amanita*. Within section *Lepidella* the *Vittadiniae* would be the most primitive subsection.

Even with all the characters listed above it was not easy to find a reasonably satisfactory arrangement of the stirpes in the subsections. In the scheme given here (Fig. 25) the sequence finally adopted is elucidated by indicating which stirpes are placed together because they may represent side-lines deviating from the main line drawn from subsection *Vittadiniae* towards subsection *Limbatulae* and probably running from there to section *Amidella*.

³³ Most of the characters involved have been mentioned in the foregoing chapters.

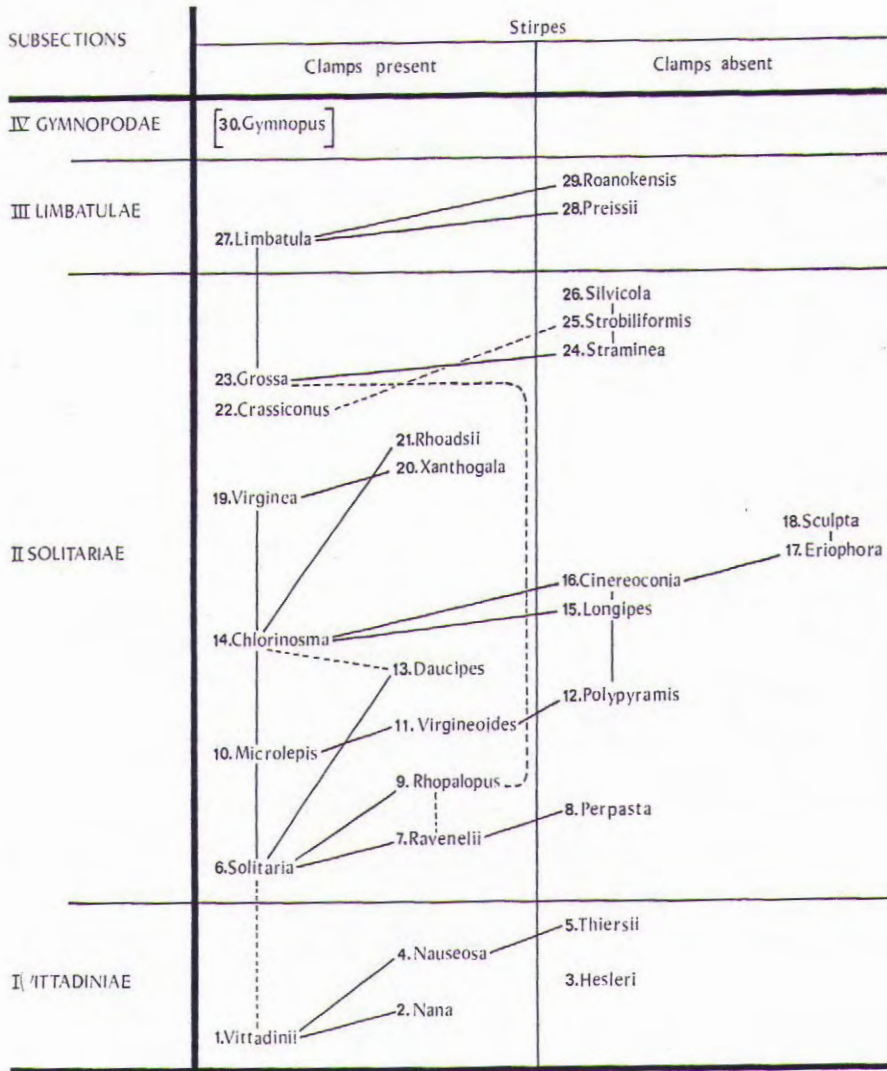


Fig. 25. Scheme of classification of subsections and stirpes of section *Lepidella*; numbers indicate sequence adopted; continuous lines and broken lines connecting names symbolize great and fairly great similarities.

Subsection *Gymnopodae* is probably a side-line of subsection *Limbatulae* from which it differs mainly in the reduction of the lower part of the volva. It should be borne in mind, however, that a similar reduction of the volva is also found in some stirpes of subsection *Vittadiniae*.

It seems probable that somewhere in subsection *Solitariae* there is a connection with section *Validae*, but it is still too early to place it.

The relationship of the genus *Amanita* and the scope and relationship of the family Amanitaceae will be discussed when I have more information on certain structures in the other genera.