ANNALS OF NATURAL HISTORY.

VIII.—On the Fructification of the Pileate and Clavate Tribes of Hymenomycetous Fungi. By the Rev. M. J. BERKELEY, M.A., F.L.S.

IN the sixth volume of the New Series of the Annales des Sciences Naturelles, p. 336, in the Number dated Dec. 1836, but not published till some months later, M. Montagne has the following observation under Gomphus rutilus: "Elle m'a donné occasion de faire des observations précieuses pour le mémoire que j'ai eu l'honneur de lire devant l'Académie des Sciences sous le titre de Recherches anatomiques et physiologiques sur l'hyménium des Agaricinées." This attracted special notice, as my attention had been directed for some time to the real structure of the hymenium in Agarics, which I had reason to believe had been altogether misunderstood. It appeared highly probable that the result of his investigations was in substance the same as that to which I had myself arrived, from a series of observations on the supposed asci of Agarics; but at the same time I felt that, if this were the case, it would not be useless, in a matter of such difficulty and obscurity, to publish an account of my own perfectly independent researches. I was however desirous before doing so of following up the matter in as many genera as could be procured of Pileate Fungi, and this led to an examination of the Clavate group also, which, from their very close affinity, I could scarcely believe, notwithstanding the received notions of mycologists, to differ essentially in organization. The facts which presented themselves appeared to me not only interesting from their novelty, but of such importance, that I considered it expedient, as far as possible, to trace the history of the present state of knowledge on the point in question, and it was curious to observe that the earlier notions were the more correct.

Since almost the whole of my observations were made, and the greater part of the present memoir drawn up, I have had Ann. Nat. Hist. Vol. 1. No. 2. April 1838.

the good fortune to meet with the Comptes Rendus des Séances de l'Académie for the Session January 2, 1837, in which there is a report of M. Montagne's paper by MM. Mirbel, Turpin and Richard, from which it appears that there is a great difference between our observations, though at the same time there is a strong confirmation in what is there adduced of the correctness of the views which are now offered. He understands the evolution of the reproductive bodies in a very different way from myself, though it is quite clear that his observations, as far as they go, are substantially the same as my own, and he appears to have altogether overlooked the very important fact that their arrangement is very generally quaternary as in *Coprini*. His observations appear not to have been extended at all to the Clavate Fungi.

I should perhaps feel more diffidence with respect to my own correctness, on finding such discrepancy in the account given by so eminent an observer as M. Montagne, if I were not in the first place sure that the facts as stated by him are such as will eventually lead him to similar results with my own, and were I not in the second place supported by the testimony of accurate observers, to whom I have communicated the facts, who have seen precisely the same appearances as myself. When once any notion is very generally received and supported by high authority, it is very difficult even in matters of much less obscurity than minute microscopic analysis where there is so much room for the exercise of imagination, to divest oneself entirely of preconceptions. A fortunate moment sometimes puts one in possession of truths which it would have taken a long and tedious process to arrive at in the ordinary routine of investigation. Nothing can more clearly show that we are both in the right track, than the fact that while M. Montagne has been led to see the perfect analogy between the spores of Botrytis Bassiana and the reproductive bodies of Agarics, I have myself recognised the same fact as regards the spores of Botrytis curta, a species nearly allied to Botrytis parasitica, an analogy which would by no means be suspected.

In 1729, Micheli* first, I believe, attempted an analysis of

^{*} Nova Genera Plantarum juxta Tournefortii methodum disposita. Florentiæ, 1729.

the hymenium of pileate Fungi. Indeed Dillenius* so late as 1719 denies that Fungi possess seeds. At tab. 65 B is a representation of a portion of a gill of some dimidiate Agaric referred to his genus Agaricum, which consists of lateral Polypori, Agarici, Hydna, &c. It is fringed with cylindrical shortly pedicellate bodies which are called flowers, and separate seeds at D. "Harum flores," he says, p.117, "sunt apetali monostemones, seu unico filamento constantes, steriles, et nudi, nempe calyce, pistillo, atque staminibus destituti, et vel in lacunarum vel in foraminulorum ore nascentes. Semina autem rotunda vel subrotunda." The flowers are evidently cells fringing the margin of the gills or cavities of the hymenium. The seeds are said to be hid in tubes as in Fistulina, or to adhere to the external processes as in Hydnum. Again at tab. 68, under the genus Suillus, which is the modern Boletus, are representations of similar bodies; and at O the so-called seeds are very clearly shown in situ adhering to the interior surface of the tube with their longer axis perpendicular to it, which, as far as it goes, is perfectly consistent with the facts I have to bring forward.

The same appearances are described in his genus Polyporus, consisting of central-stemmed Polypori. In Erinaceus, which consists of mesopous Hydna, the seeds are said to adhere to the prickles. In his genus Fungus (Agaricus of authors) the same things are described p. 133, with slight differences: "In earundem lamellarum margine nascuntur flores apetali, nudi, constantes ex mero filamento cylindrico, in nonnullis speciebus solitario seu inter se distincto, in aliis vero in massam seu floccum digesto. In superficie autem utriusque partis supradictarum laminarum undique nascuntur semina rotunda vel subrotunda et minutissima, in aliquibus sigillatim dispersa, in aliis quaterna sibi contigua." He also describes and figures the utricles of the Coprini, whose office he believes to be the prevention of the gills coming in contact. The flowers are here again very evidently short single hair-like cells, or fascicles of them. No definite information is given with respect to the fructification of the clavate Hymenomycetes.

On the whole then Micheli clearly considered the seeds as

^{*} Appendix ad Catalogum Plantarum sponte circa Gissam nascentium, 1719, p. 72.

superficial, and he described the quaternate arrangement and utricles in the Coprini.

In 1753 the same things were confirmed by Gleditsch*, his figures being copied from those of Micheli. He professes, however, p. 5, not to have servilely copied Micheli, but to have certified himself of his correctness.

In 1762 Schmidel+ described the gills of Agaricus comatus as furnished with seeds, "qui utrumque parietem dense vestiunt." Analyses of certain Clavaria are also given, which, though very incomplete, are as far as they go correct.

In 1763 Gleichen ‡ figured a portion of the gill of an agaric with an appearance described as "vaisseaux de poussière avec leurs filets noires et tachetés de blanc," which must have arisen from optical deception. The so-called "filets" are of considerable size, swelling upwards and supporting lobed masses of naked reproductive bodies. He appears to consider these imaginary bodies as the same with the utricles described by Micheli and Gleditsch in Coprini, who, he says, have well observed them; but Schaeffer & denies their existence. The reproductive bodies themselves are well figured.

In 1780 Müller || gave an excellent figure of a portion of a gill of Ag. comatus, in which not only is the quaternate arrangement of the spores very well expressed, but towards the edge they are accurately represented as naked and supported by little peduncles.

In 1783 Bergeret¶ noticed the large utricles in Ag. micaceus (Ag. farinaceus, Berg.), but appears to have been unacquainted with the quaternary arrangement.

In 1784 Hedwig published his Theoria Plantarum Cryptogamicarum, a second edition of which appeared in 1790. In this four plates are devoted to pileate Fungi. At tab. 41, fig 2, the gills of some Cortinaria, and at tab. 42, fig. 2, a prickle of Hydnum imbricatum, are represented as covered with project-

* Methodus Fungorum, &c. Berolini, 1753.

† Icones Plantarum et analyses partium. Nuremberg, 1762.

Supplément d'observations mêlées, tab. 4, in Observations Microscopiques. Nuremberg, 1763.

§ Vorläufige Beobachtungen der Schwämme um Regensburg. Regens-

burg, 1759.

fi Flora Danica. Fasc. XIV. Hafniæ.

[¶] Bergeret, Phytonomatotechnie Universelle. Paris, 1783.

ing spiculæ, but without any reproductive bodies. The spores which had fallen on the veil were considered by him as male organs, an error pointed out by Bulliard in 1791.

In 1791 Bulliard* distinguished two different kinds of bodies in the hymenium of Agarici, Boleti, and Thelephoræ by the name of spermatic vessels and seeds. The utricles on the gills of Coprini are an instance of the first; and though analogous bodies, as will be seen hereafter, exist in Boleti, &c., he appears often to have called the true reproductive bodies by the same name, and sometimes perhaps the fringes noticed by Micheli. The true sporidia, or more properly speaking spores, he figures as superficial, tab. 1. fig. iii. 10. 11, tab. 2. fig. xi. p; and at fig. ix. k the spores of Auricularia phylacteris are represented (under the name however of spermatic vessels) as seated four together upon a common peduncle. The same structure is also given under Auricularia caryophyllea, tab. 483. 6 & 7. S. Indeed, he says, "Les champignons dont nous venons de parler ont presque toutes leurs graines inserées à des filets extrêmement courts." (p. 50.) Such are represented tab. 2. fig. 1. F. G. In fig. vii. and viii., which represent the structure of Boletus and Fistulina, superficial grains are figured, which in the former case probably consist partly of the spores and spore-bearing cells, in the latter possibly of the spores only. No analysis is given of Clavaria. The remarks about spermatic vessels in that genus apply principally to Sphæria and Hypoxylon.

In 1796 Persoon† described the quaternary arrangement of the reproductive bodies of *Corticium cæsium* (*Thel. cæsia*, Nees), comparing it with the similar arrangement in *Coprini*. It is highly probable that he considered them as superficial.

Up to this time all seem agreed that the reproductive bodies are superficial. Müller and Bulliard figured them as supported by peduncles; and Bulliard and Persoon detected the quaternary arrangement in *Thelephora*. Modern notions of the structure of the hymenium appear to have arisen from two important memoirs of Link, to which we have now to call at-

^{*} Histoire des Champignons de la France, vol. i. p. 44. &c. Paris, 1791. † Observationes Mycologicæ. Pars prima. Lipsiæ, 1796.

tention. In 1809 Link* first described and figured the reproductive bodies as contained in thecæ, in the genus Agaricus. Merulius, Cantharellus, Xylophagus, Dædalea, Boletus (fig. 59), Fistulina, Sistotrema, Hydnum (fig. 61), Thelephora, Stereum, Merisma, Clavaria are also described as thecigerous. "Omnibus fere series unica sporidiorum in theca excepto Coprinus et paucis aliis." Of Coprinus, he says, "Ab omnibus fere Fungis charactere singulari thecarum differt. Hæ enim non juxta positæ sunt ut in Agaricis, nec unicâ sporidiorum serie farctæ, sed segregatæ majores quadruplici sporidiorum serie refertæ. Hinc sporidia dum effunduntur quaternatim disposita sunt, donec nimia prodeuntium copia ordo turbatur." The figures, it should be observed, are by Ditmar. The same year produced another memoir on the same subject from the same pent. The analyses of Hymenomycetous genera are upon the whole more clearly made out. In Amanita bulbosa tab. 1, fig. 14, the sporidia are represented as contained at first in the thecæ and then escaping. Of Coprinus he says, "Thecæ magnæ sporam regulariter emittentes in frustulis segmenti parum obliqui apparent, unde satis patet quamlibet thecam quaternam sporarum seriem amplecti, et hanc ob causam, sporam ad quatuor orificii latera excutere." It is clear from this that his figure of the contents of the thecæ in Coprinus is ideal, representing what was supposed to be the structure, and not what was actually seen. The united authority of Link and Ditmar has prevailed to hand down this notion almost to the present moment.

In the same year, however, Mr. Sowerby ‡ figured the spores in Merulius lamellosus (Ag. panuoides, Fr.) as naked and seated upon short hairs. The same appearance is represented in the figure of Hydnum membranaceum published in 1801. In both cases the bodies are called glands in the text.

In 1813 Ditmar & ascribed thecæ to Agaricus phlebophorus.

† Nova Plantarum genera e classe Lichenum, Algarum, Fungorum; in Schrader's Neues Journal für die Botanik, vol. iii. Erfurt, 1809.

^{*} Der Gesellschaft naturforschender Freunde zu Berlin Magazin. Dritten Jahrgangs, erstes Quartal. Berlin, 1809. Observationes in Ordines Plantarum Naturales. Dissertatio prima.

[†] Coloured figures of English Fungi, tab. 403. Supplement. London, 1809. § Deutschlands Flora. 3te Abtheilung. Nurnberg, 1813.

He has not however represented sporidia within them. 1814 he represented sporidia within the thecæ in Ag. pluteus, and, amongst the thecæ, urn-shaped bodies crowned with two or three spicules. This was, in more modern times, the first step, however distant,-for he does not consider them as having any immediate connexion with the sporidia, but compares them with the utricles in Coprini, -towards a knowledge of the true arrangement of the spores in the rest of the Agarics. Under Cantharellus villosus, Pers., thecæ are also represented as containing from one to three globose sporidia.

Nees von Esenbeck's* important work appeared in 1817. His original designs of analyses of various pileate and clavate genera are on the whole in perfect accordance with those copied from Link. Under Thelephora cæsia, the figure of which is copied from that of Persoon alluded to above, it is remarked that the quaternary arrangement of the sporidia forms as it were a prelude to that in Coprini. From this it should seem that he regarded them as contained in thecæ (asci).

Fries† in 1821 describes the asci generally in his Hymenomycetes evoluti as "in superficie collocati immersi. Sporidia in ascis seriatim disposita." Under Thelephora, & Phylacteria, he writes, "Sporidia quaterna serie Coprinorum instar disposita."

Dr. Greville t commenced his great work in 1823. Twenty pileate and clavate Fungi are there more or less analysed; the figures according entirely with the observations of Link, Ditmar, and Nees von Esenbeck. In 1825 Fries & separated Thelephora from Auricularia on account of the quaternary arrangement of the sporidia. Dr. Greville followed him in this separation, but apparently did not understand Fries correctly, as the asci of Thel. laciniata are figured as containing a single row of four sporidia, whereas Bulliard figured to a certain degree correctly their quaternary arrangement on a peduncle, a fact which Fries could not have overlooked. Indeed experience has clearly shown that Dr. Greville must have been

^{*} System der Pilze und Schwämme. Wurzburg, 1817. † Systema Mycologicum, vol. i. p. 1. Gryphiswaldiæ, 1821. † Scottish Cryptogamic Flora. Edinburgh, 1823, &c. § Systema Orbis Vegetabilis, p. 1. Lundæ, 1825.

misled by a confidence in Fries' correctness, who however appears not to have had himself a very clear perception on the point. Fries' real notion, though nowhere expressed very distinctly, is perhaps sufficiently clear from the expression* "Hymenium e setulis quaternatis," under the subtribe *Phylacteria* of *Thelephora*.

In 1828 M. Desmazières† described the sporidia of Ag. radians just as Link had done those of the Coprini, "les sporules sont, comme dans les Coprini avant la déstruction de l'hyménium, disposées sur quatre rangs dans des thèques distantes les uns des autres."

In 1830 Fries‡ still described and figured Favolus Brasiliensis and Cyclomyces fusca as ascigerous. In the latter sporidia are figured in the asci.

In 1831 Krombholz § published figures by Corda of the fructification of Agaricus, &c. I have not seen the work myself, but from the account of it in the Linnæa I conclude that it accords with the observations of Link and Ditmar. Articulations are figured in the fruit-cells of Ag. alutaceus, but evidently from incorrect observation, though he is borne out by Nees v. Esenbeck. See fig. 199 B.

In 1833 Klotzsch || figured in Favolus Boucheanus clavate asci containing sporidia. Wallroth's Flora Crypt. Germaniæ published in the same year follows the views of Link.

In the third volume of Nouv. Ann. du Muséum are some observations on Fungi by Dutrochet, republished in the collected Memoirs, vol. ii. in 1837, with the author's latest corrections. Turpin there figures the reproductive bodies of Cantharellus Dutrochettii, Mont., (which is apparently a state of Ag. panuoides, Fr.) as attached to the walls of the filaments of which the gills are composed. There is also a memoir on the same Fungus by M. Turpin, vol. xiv. des Mém. de l'Ac. des Sciences Naturelles, which I much regret that I have not seen.

The second part of the fifth volume of the English Flora

^{*} Elenchus Fungorum sistens Commentarium in Systema Mycologicum, vol. i. p. 170. Gryphiswaldiæ, 1828.

[†] Annales des Sciences Naturelles, vol. xiii. p. 215.

[‡] Linnæa, vol. v. p. 511, 512.

[§] Krombholz naturgetreue Abbildungen der essbaren, schädlichen und verdächtigen Schwämme. Heft I. Prag. 1831.

|| Linnæa, vol. viii. p. 316.

was published in 1836. Under Ag. prunulus, p. 76, I have given the following description: "Gills covered with very minute conical papillæ, ending in four spiculæ. Sporules often seated upon the spiculæ." The fructification of Ag. cernuus, Ag. bifrons, Ag. gracilis, and Ag. disseminatus is described as quaternate. In Ag. semiovatus the reproductive bodies are described as quaternate, the major axis perpendicular to the gills. Under Ag. panuoides it is remarked that "the gills are beset with minute hairs, upon which the sporules are often seated, as in Ag. prunulus."

A paper by M. Montagne* was read before the Academy of Sciences at Paris on January 2, 1837, in the report of which are the following observations: "Des planches dessinées à la chambre claire du microscope composé de M. Charles Chevalier sont destinées à montrer tous les degrés par lesquels passe une sporidie avant de se détacher de l'utricule où elle a pris naissance. Avant sa chute, cette sporidie est ordinairement supportée par un pédicelle plus ou moins long, qui se forme peu à peu, quoique d'une manière très prompte en égard à la vie éphémère de ces végétaux, aux dépens du sommet de l'utricule, qu'elle chasse devant lui." The latter sentence is so confused that the reporter's meaning is not clear; but judging from the observations on the evolution of Botrytis Bassiana+, with which it is expressly compared, it should seem that M. Montagne considers the reproductive bodies as essentially internal; in other words, as sporidia and not spores. "Les sporidies," he says, speaking of Bot. Bassiana, "se forment à l'intérieur des filaments, et en sortent et se groupent symmétriquement à l'extrémité des ramules par un mécanisme que nous avons tenté d'expliquer. Elles s'échappent de l'extrémité des filaments et des rameaux par un mécanisme particulier qui consisterait en ceci. Chaque seminule arrivée à l'extrémité du tube, avant de s'en séparer, en emprunterait une seconde enveloppe qu'elle conserverait."

It is clear that when the notices given above from the English Flora were published, I was not satisfied with the cha-

^{*} Recherches anatomiques et physiologiques sur l'Hymenium, &c. † Expériences et Observations sur le Champignon Entomoctone, ou histoire botanique de la Muscardine. Par M. Montagne, Aug. 16, 1836.

racters assigned to the hymenium of Agarics; but the great body of authority in favour of the received notions prevented my doing more than recording such isolated observations, which indeed are accompanied in the text with other circumstances which are not always perfectly correct. The acquisition of a more powerful doublet than I before possessed determined me to examine accurately the structure in Coprinus, in Link's account of which I did not feel confidence; and the result was such as to lead to a more extended examination of species of the genus Agaricus belonging to different tribes, and those of other pileate genera. The clavate Hymenomycetes were then reviewed, and the investigation has ended in a conviction that, notwithstanding the vast body of authority and evidence which existed on the point, the structure has been almost uniformly mistaken since the publication of Link's observations, and that in true pileate and clavate Fungi asci do not exist, but that the reproductive bodies are naked, and consequently are, properly speaking, neither sporules nor sporidia, but spores, and that with very few exceptions they are quaternate as in the Coprini. In proof of this position I will begin by stating what I find to be the structure in Coprini, in which it is most easy to form a correct estimate; and then, in order, give the result of my observations in other tribes of the genus Agaricus, and as many genera as I have been able to examine of pileate and clavate Fungi.

It is perhaps right that I should state that, with the exception of the few similar facts published in the English Flora, all my observations have been made subsequently to the presentation of Montagne's Memoir, though without a knowledge of its existence.

The agaric first examined was a form of Ag. micaceus, differing from the ordinary state of that species in having the pileus minutely pilose instead of being sprinkled with mealy particles. As it grew in dense clusters consisting of individuals in every stage of growth, it afforded me a good opportunity of tracing the development of the hymenium. In very young specimens it consisted of oblong, obtuse, transparent cells, disposed side by side like the pile of velvet with their tips all level. It was not possible with a magnifying power of

600 diameters to trace the cellular texture of the substance interposed between the two layers of the hymenium, though in an extremely thin slice cut in the direction of the gill there was a faint trace of lines running in the direction of the section. There was scarcely any change so long as the margin of the pileus was not detached from the stem; but in an individual a little more advanced some of the cells were found to have acquired a more cylindrical form, having grown faster than the others, and in consequence to project beyond them. The intermediate substance was now seen to consist of elongated, somewhat anastomosing cells, coated on either side by a layer of shorter ones, which are subglobose. The contents of the cells of the hymenium are grumous. As the pileus expands, the tips of some of the more elongated cells, or, if I may so call them, sporophores, show four minute points disposed nearly in a square, which rapidly increase in length till they are about half as long as the portion of the sporophore which is emersed. In this stage of growth they are slightly curved inwards. On the tip of each of these a minute globule is soon developed, which is at first perfectly pellucid. This rapidly increases, acquiring an oval form, though more gibbous on the side which is turned from the axis of the sporophore, so that the position of the perfect spores upon the spicules is oblique. The apex becomes minutely papillate, and at the base there is a very short peduncle. The grumous contents of the spores, which were at first almost colourless, acquire in the perfect fruit a rich purple brown. The contents of the sporophores as they increase become more distinctly granular, and are attracted towards the apex as the spores are developed, which appear to be nourished by them. When the spores are perfected the sporophores are nearly empty.

It is to be observed that the sporophores in the mature plant are not all of the same height. In looking down upon a thin slice from the surface of the gill, the lowest, which are frequently without spores, appear like circles; others are observed to be furnished with four spiculæ; and it is not uncommon, when the gill has not acquired its deepest tint, to see the spores themselves in various stages of development. The large utricles so conspicuous in most Coprini were here extremely few. The arrangement of the sporophores appears to be by no means vague. Link figures the spaces between the sori as square. This does not accord with my own observations. I find them triangular in Ag. striatus, Bull., five or six being arranged around each sporophore, so that the sporophores are arranged round a central one in pentagons or hexagons. In Aq. macrocephalus, Berk., the sporophores are urnshaped and supported upon long peduncles. The cellular layer beneath the hymenium is here exceedingly obscure, and the central stratum very thin and consisting of filaments much more slender in proportion than in Ag. micaceus. In that species there are about three layers of subglobose cells between the hymenium and the central stratum. In Ag. momentaneus the sporophores are similar; and the utricles large as in Ag. macrocephalus.

The quaternary arrangement of the spores has been recognised from the time of Micheli, but no one appears to have suspected how general it is in Agarics. It may, however, be very readily seen with a good doublet, if a thin slice from the surface of the gill be examined; and a thin transverse section will show them to be arranged on the spiculæ of the sporophores exactly as in the *Coprini*.

Taking the tribes as they stand in Fries, I will mention the species which I have had under observation, making occasional notes where requisite.

The quaternary arrangement then has been verified in

Ag. phalloides, Fr.	Ag. Columbetta, Fr.
vaginatus, Bull.pantherinus, Dec.	- emeticus, Schaeff.
— rubescens, Fr.— muscarius, Linn.	— fætens, Pers.
- procerus, Scop.	— volemum, Fr. — theiogalus, Bull.
- erubescens, Fr.	— rufus, Scop. — pyrogalus, Bull.
— hypothejus, Fr.	— fuliginosus, Fr. — piperitus, Bolt.
— luridus, Schaeff.	

In most, if not in all the Galorrhei, the spores are minutely echinulate. In Ag. flexuosus, Fr. alone, the arrangement of

the spores appears to be uniformly binary, the one being exactly opposite to the other. The other pair appears to be suppressed.

The arrangement is quaternary again in

Ag. nebularis, Batsch.
— grammopodius, Bull.
— ceraceus, Wulf.

Ag. pelianthinus, Fr. — balaninus, Berk.

In the two latter, which belong to the section *Calodontes*, besides the fertile sporophores, there are barren ones or utricles, which are coloured, and give the peculiar character to the section.

Ag. radicatus, Relh.

Ag. pudens, Pers.

The gills are studded with cells much longer than the sporophores, which in some states are surmounted by a large pellucid globule. This at length vanishes and leaves the tip of the utricle denticulate.

- Ag. velutipes, Curt.
- peronatus, Bolt.
- oreades, Bolt.
- tenacellus, Pers. The gills have utricles like those of Ag. radicatus.
- Rotula, Scop.
- ostreatus, Jacq.

Ag. prunulus, Scop.

- fertilis 3. intybaceus, Fr. Occasionally in this species there appear to be only three spiculæ and three spores.
- rhodopolius, Fr.
- chalybeus, Pers.
- asprellus, Fr., or an allied species.

In most of the *Hyporrhodia* the spores are very irregular in form, with a globose central nucleus (sporidium) which is small in proportion to the spore itself.

- Ag. gentilis, Fr.
- scaurus, Fr. In this species there are sometimes five spores together.
- rimosus, Bull.
- cucumis, Pers.
- tener, Schaeff.
- trechisporus, Berk. The spores have little granules upon them. The utricles are like those of Ag. pudens.
- involutus, Batsch. Gills with large pointed transparent utricles many times longer than the sporophores.

- Ag. pusillus, Dec. Cylindrical utricles.

 Spores occasionally reduced to two.
- campestris, Linn.
- lateritius, Schaeff.
- stipatus, Pers.gracilis, Fr.
- semiovatus, Sow.
- titubans, Bull.
- disseminatus, Pers.
- (Gomphus) rutilus, Schaeff.
 Spores elongated; grumous,
 contents disposed in two masses.

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In all these species it will be observed the reproductive bodies are naked spores, and that, except in Ag. flexuosus, the arrangement is almost uniformly quaternary. The exceptions are very rare, and no more invalidate the general rule than occasional additions or suppressions of parts in phænogamous plants. In all, the major axis of the spores is vertical to the gills, and in general they are placed rather obliquely upon the spicules.

But this description of the spores and their arrangement applies with slight modifications to other pileate Hymenomycetes. In all, the reproductive bodies are naked spores seated upon spicules which crown the sporophores, and in the genera which most abound in species the arrangement appears to be in general quaternary, though in some genera the number four does not prevail. It must be confessed, however, that a sufficient number of species have not yet been examined to warrant any general conclusion.

In Cantharellus cibarius, Fr., and C. tubæformis, Fr., the spores are six, seated upon rather long spicules disposed in pairs so as to form an ellipse, two pairs forming a square in the narrow part of the ellipse, and the other seated at the apices of the major axis ·:··; or five by the suppression of one of the spores belong to the single pair. In Canth. cornucopioides, Fr., there is only a single pair, apparently from the suppression of the four which form a square. In Canth. fissilis, Fr., the spores are solitary, but still seated on spicules. Polyporus squamosus, Fr., has quaternate spores.

Boletus subtomentosus, Linn. pachypus, Fr.

Boletus luridus, Schaeff. —— scaber, Bull.

Have the spores quaternate. There are also acuminate utricles, generally furnished with an articulation towards the tip.

In Hydnum repandum, L., the spores vary from three to five. In Hydnum farinaceum, Pers., they are solitary, which is probably the case in most of the lower resupinate Fungi.

Thelephora laciniata, Pers. cristata, Fr.

Thelephora purpurea, Pers.

The arrangement is in these quaternate. In the latter there are cylindrical utricles, and probably the bristles in *Thel. rubi-ginosa*, &c. are of the same nature.

Phlebia vaga, Fr., has quaternate sporidia.

We have now to inquire what is the arrangement in the clavate Fungi which are clearly very closely related to the Pileati. In point of structure the hymenium is just like that of the pileate species. In Clavaria cristata, Pers., the spores are binary, or occasionally ternary. In Clav. crispula, Fr., ternary or quaternary. In Clav. vermicularis, Swartz., binary. Calocera viscosa, Fr., has solitary spores curved like those of some Tremellæ. In Typhula gyrans, Fr., the spores are quaternate.

In Geoglossum, Spathularia, and Mitrula it is well known that the reproductive bodies are not spores, but sporidia contained in distinct asci. In Geoglossum they are curved and septate. Spathularia has very long and slender sporidia, which are filled with sporidiola, thus approaching very near to Leotia, in which they are cylindrical, containing four globose sporidiola. At present I have not seen perfect sporidia in Mitrula. It is clear then that these genera, which differ so essentially in their fructification, are not properly associated with the clavate Hymenomycetes.

The essential character of hymenomycetous Fungi appears then to consist in a hymenium composed of closely packed sporophores, which support on spicules a generally determinate number of spores. If this be deemed of the importance I am inclined to attribute to it, the elvellaceous Fungi, as also the Cupulati, cannot be included in the same primary division. The Tremellini, on the contrary, appear to me to be true Hymenomycetes. In Tremella albida the curved spores are superficial, vertical with regard to the hymenium, and seated obliquely upon spicules, almost exactly as in Calocera viscosa. At present I have not had sufficient leisure to examine their structure attentively, and there are some peculiarities in it which I do not understand. The Sclerotiacei I consider another tribe of true Hymenomycetes, though very imperfectly organized. I have stated in the English Flora that I believe the true "ideal notion" of their structure is that of highly condensed Hyphomycetes, which, if the analogy of the spores in Botrytis be taken into consideration, confirms greatly the present view. The abbreviated flocci of Botrytis curta, Berk., with their two or three spiculæ-form branchlets, each bearing a spore, resemble very closely the sporophores of pileate and clavate Hymenomycetes. The notion that they are condensed Coniomycetes arises from the consideration of one or two obscure epiphyllous species, which are scarcely more than abortive Uredos.

We have then, as the typical group of Hymenomycetes, Agaricus and allied genera. The subtypical consists clearly of the clavate genera Clavaria, Calocera, &c. The Tremellini and Sclerotiacei form two aberrant groups. The third aberrant group consists, if I mistake not, of Isaria and certain allied genera. It is only necessary to compare the prickles of one of the resupinate Hydna with the fruit-bearing hairs of Isaria citrina, or, what is better, some of the more obscure Pistillariæ and Typhulæ, to be convinced of the propriety of such an arrangement. Anthina, with its subgenus Pterula, is still more evidently allied. Ceratium again has spores disposed on short bristles, altogether reminding us of the Hymenomycetes. The sporidia, of the second order mentioned by Greville and Fries, are merely the tips of the spicules from which the spores have fallen. It is remarkable that these spicules are distinctly disposed in quincunxes. The spores too, when seen with high powers, are much narrower at one end, and have their longer axis vertical to the hymenium.

The pileate Fungi pass evidently into the Tremellini by means of *Phlebia mesenterica*, which scarcely differs generically from *Exidia Auricula Judæ*. The Tremellini are connected with Sclerotiacei by means of *Pyrenium*, and these again with Isariacei by means of *Periola*.

If we now turn to the cupulate and mitrate Fungi excluded* from Hymenomycetes, we have in them, if I mistake not, the typical and subtypical groups of another grand division characterized by the presence of true asci; Peziza and its allied genera forming the first, and Helvella, Leotia, &c., exactly analogous to Clavati, forming the second. We shall then have as the aberrant groups the Scleromycetes, Perisporiacei, and that part of Angiogastres comprising the truffles, Carpoboli, and Nidulariæ.

^{*} In the new Systema Fungorum, the twelve first sheets of which I have received from the author since the above was printed, these are, in fact, now separated by Prof. Fries from Hymenomycetes, under the title of Discomycetes. The Hymenium in the former is still described as ascigerous.

We cannot doubt the very close relation of the cupulate and scleromycous groups. The Scleromycetes evidently pass into the Perisporiacei by means of some of those epiphyllous species whose asci are reduced to the form of sporidia, and the sporidia in consequence mere sporules. This makes way through Perisporium for a new form of free asci, the socalled sporidia of Erysiphe. The transition from thence to Angiogastres is very easy through Polyangium. The Carpoboli, as Fries has admirably pointed out, are Perisporia with a volva. The circle returns to Mitrati through Tuber and Rhizina. The Hymenomycetous and Uterine circles are connected by Tremella and Tuber. I have reason to think that this will appear much more evident than it does at first sight, when the structure of Tremella shall have been more perfectly studied.

The intimate structure of the Phalloid Fungi, as I hope to show at some future opportunity, is exactly that of Trichogastres, as appears from the examination of both before maturity. Indeed the transition from them through Battarea and Geastrum is far from abrupt.

I am inclined then to think that the typical and subtypical groups of the Gasteromycetes consist of Trichogastres and Phalloidei; two of the aberrant groups being Myxogastres and Trichodermacei.

The phalloid group is connected with Trichodermacei by Spadonia and the curious fungus figure by Battara, tab. 40, A-E, a Phallus, without a volva. The gasteromycous circle is evidently connected with the uterine by Ægerita.

The group Myxogastres, as Fries remarks, differ in their singular vegetation * from all other Fungi, and have but few and remote analogies. The old notion of their connexion with Hypodermii is, I believe, correct, and by means of these they pass either into Coniomycetes, or through them to Trichodermacei. At present, however, I dare not venture to remove them from Coniomycetes. The fifth group, therefore, is left blank in the diagram.

I do not attempt to indicate the groups of Hyphomycetes

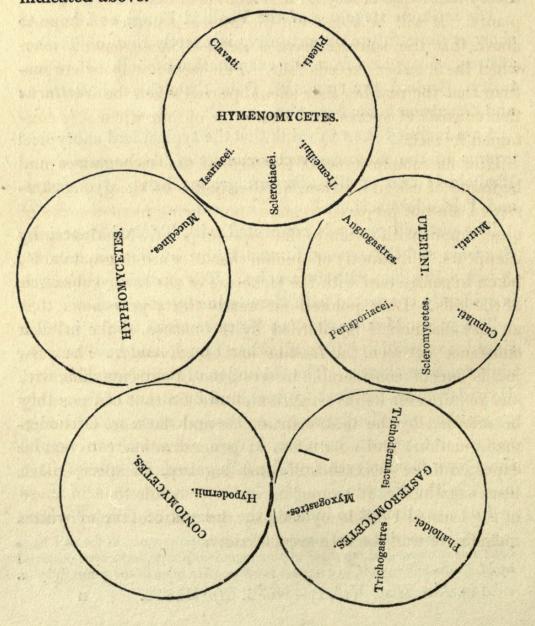
Ann. Nat. Hist. Vol. 1.—No. 2. April 1838.

^{*} It is curious that spiral vessels, differing in no respect, as far as I have been able to discover, from those of phænogamous plants, have been observed by M. Corda and myself, to compose the flocculent mass in the genus *Trichia*.

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or Coniomycetes, as so much uncertainty still exists with regard to many of them. Indeed, notwithstanding all the attention that has been paid to Fungi, it may be asserted without fear of giving offence, that the modern improvements of microscopes have opened quite a new field to the mycologist. All the genera require an accurate revision, and in such case, I am sure from my own experience, that the structure of many would be found to differ much from received notions. If it had not been from the imperfection of instruments, it is quite impossible that it should have fallen to the lot of any one at the present day to describe the true structure of the hymenium in Agarics, or that the quaternary arrangement should have been scarcely recognised except in the *Coprini*.

The annexed is a tabular view of the affinities of Fungi as indicated above.



I am by no means positive as to its correctness in all points. I have probably in some instances confounded analogies with affinities; but they are thrown out at least as hints. It would carry me to greater length than is desirable to state fully the grounds on which they are indicated. My object is principally to call the attention of students to the room which still remains for investigation, even in the field which has been so successfully trod by Fries. Too much attention cannot well be paid to any of his suggestions, to which every mycologist must acknowledge the deepest obligations. It seems, however, almost impossible that any system can be right in all its parts which is founded on false notions of the structure of the group of highest importance.

The facts stated above confirm in a striking degree the theory that a quaternary arrangement prevails in Cryptogamic plants. It will be seen from the anomalous cases mentioned above that the spicules have a definite arrangement, even when the number exceeds four. Few facts are more curious than that the number four should prevail when the fructification consists of spores, and a multiple of four when it is contained in asci.

How far modifications of the form of the sporophores may be found of use in distributing the species of the genus Agaricus I am not prepared to state, not having made a series of observations with a view to that especial point. M. Montagne, it appears, is distinctly of opinion that they are of great value, taken in connection with the structure of the inner substance of the gills. Link pointed out nearly thirty years since that an easy distinction is afforded by the nature of the cellular substance between the Russulæ and Ag. Russula. The subject is one of considerable interest, but of extreme difficulty, and requires for its investigation all the aid that can possibly be afforded by the best instruments and the most dexterous manipulation; and no attempt at generalization can well be expected to be successful till some hundreds of species have been examined. It cannot be in better hands than in those of the learned French mycologist, the publication of whose memoir we wait for with great anxiety.

EXPLANATION OF PLATES.

PLATE IV.

- Fig. 1. Section of gill from a very young specimen of a var. of Ag. micaceus, showing the young sporophores not yet distinct from the other cells of the hymenium.
 - 2. Ditto, in a specimen rather more advanced. The sporophores have become more cylindrical, and are longer than the other cells. The central cellular substance of the gill is distinctly marked.

3. The sporophores have acquired four spicules.

4. Section very highly magnified, showing the spores just beginning to be developed, and a sporophore with four spores more advanced. 5. Tip of sporophore, with four infant spores, magnified 600 diameters.

6. Ditto, with four mature spores. 7. A spore seen from one side.

8. Ditto seen from behind.

- 9. Portion of gill of Ag. momentaneus, with two sporophores and an utricle.
- 10. Ditto of Ag. macrocephalus, showing an utricle, with sporophores and spores in various stages of growth.

11. A form sometimes assumed by the utricles in very young plants.

12. Utricle.

13. Part of a gill of Ag. striatus, showing the disposition of the sporophores, each of which is marked with four dots, which are the tips of the spicules.

14. Sporophores in Ag. Phalloides.

15. Tip of sporophore, with its four spores in Ag. nebularis.

- 16. Portion of gill of Ag. velutipes, from a sketch by Mr. Cornelius Varley, very highly magnified.

 17. Tip of sporophore of Ag. flexuosus, with its two echinulate spores.

18. Sporophore of Ag. Volemum with its four echinulate spores.

19. Spore of the same.

20. Portion of hymenium of Ag. pudens. Two of the utricles are crowned with a transparent globule; in one the globule has vanished, and another is obtuse without any crown.

21. Portion of hymenium of Ag. balaninus, with its coloured utricles. The structure of Ag. pelianthinus is similar.

22. Sporophores of Ag. fertilis, var. intybaceus.

23. Spores.

24. Spores of Ag. chalybeus and Ag. asprellus with their nuclei.

25. Portion of hymenium of Ag. tener.

26. Portion of hymenium and pileus of Ag. rimosus.

27. Hymenium of Ag. involutus, with utricles.

28. Spores of ditto.

PLATE V.

29. Hymenium of Ag. pusillus, with an utricle and a sporophore bearing two spicules.

30. Hymenium of Ag. semiovatus.

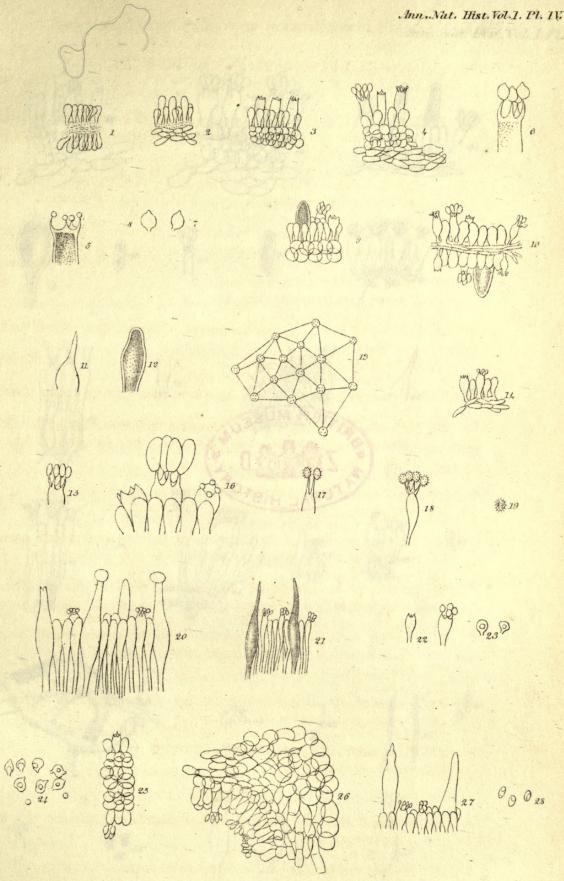
31. Hymenium of Gomphus rutilus, with utricles.

32. Sporophore of ditto.

33. Spore.34. Tip of sporophore of Ag. ostreatus.

35. Spore.

36. Portion of hymenium of Cantharellus cibarius. 37. Ditto of Cantharellus cornucopioides.



Fructifications of Hymenocetous Fungis

M.J. Berkeley Del!



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