THE GASTEROMYCETES OF AUSTRALASIA. X.

THE PHALLALES, PART I.

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(Plates i-ii.)

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This Order comprises a group of fungi characterized as a rule by the bizarre shape, bright colour and fetid odour of the spore-bearing receptacle. Two essential groups of tissues are common to all of them: (1) the peridium, a membrane enclosing the receptacle until maturity is reached; and (2) the receptacle, a pseudoparenchymatous structure upon which is borne the gleba or spore-mass. The fact that the hymenium is enclosed until maturity has led to the Order being placed in the Gasteromycetes.

Morphology of the Mature Plant.

Peridium.—In immature plants this structure appears as a globose or obovate structure of three layers (two in *Claustula*): an outer, furfuraceous or smooth, usually white membrane (the exoperidium); a middle, thick and gelatinous layer (the mesoperidium); and an inner, thin and tough white membrane (the endoperidium). Collectively these layers form in the unexpanded plant the outer layer of the "egg", and enclose the receptacle and gleba. At maturity the peridium ruptures from the apex downwards, splitting into several lobes, exposing the receptacle, and remains at the base of the latter, forming a stellate supporting cup or "volva". The receptacle is always free within the volva (save in *Claustula*, where it is at first attached by a fine basal strand), being held in position in expanded plants by lateral pressure of the receptacle against the cupulate base and edges of the lobes. The peridium is practically identical in all genera, consequently it is upon the diversity of structure exhibited by the receptacle that the numerous genera and species have been erected.

Receptacle.—In essentials this structure consists of a pseudoparenchymatous, usually coarsely chambered tissue, upon some modified portion of which is carried the gleba. It develops within the peridium, and as it approaches maturity, the receptacle is thrown into folds, the cells become strongly turgescent, and pressure is exerted upon the apex of the peridium, causing its rupture. The receptacle continues to expand, until finally it assumes a size considerably in excess of the peridium. Expansion is rapid, for in *Aseroe rubra* the plant is fully developed within one or two hours after rupture of the peridium. The gleba, borne on some portion of the receptacle, appears as a mucilaginous, olivaceous, fetid mass containing countless numbers of exceedingly minute, smooth, elliptical spores.

The most primitive type of receptacle occurs in the genus *Claustula*, and consists of a cellular, hollow, apparently indehiscent structure, not unlike an inverted hen's egg, bearing the gleba on its inner surface. As it is a somewhat anomalous genus (being apparently indehiscent), discussion concerning it will be deferred until the systematic portion of this work. The next most primitive type of receptacle occurs in the genus *Mutinus*, and consists of a cylindrical hollow stem, upon the modified apical portion of which is borne the gleba. In the related genus *Floccomutinus*, the gleba is carried upon a loose network (the forerunner of the pileus) at the apex of a similar stem; and in *Ithyphallus* and *Dictyophora* it is borne upon an additional structure, the pileus. This is a campanulate, pseudoparenchymatous tissue attached to the apex of a stem similar to that of *Mutinus*, and may be rugulose or reticulated. *Dictyophora* possesses an additional structure in the form of a pendent, pseudoparenchymatous membrane termed an indusium, which hangs beneath the pileus around the stem; and its presence would show that this is the most highly developed genus of those present in the family Phallaceae, to which these genera (save *Claustula*) belong.

In many genera of a second family included in the Order (the Clathraceae) a stem is present as in *Mutinus*, but the apex is modified to form various arms, which may be organically united apically, as in *Anthurus*; united by a membrane, as in *Mycopharus*; apically free but connivent, as in *Lysurus*; or horizontally expanded, as in *Aseroe*. In other genera the stem may be modified apically to support a small spherical latticed structure, as in *Simblum*; reduced to a small basal cylinder supporting several columns, in turn supporting a latticed structure, as in *Colus*; suppressed altogether, the receptacle then appearing clathrate, as in *Clathrus*, or as several simple columns apically united, but basally free, as in *Linderia*, *Blumenavia* and *Laternea*.

The receptacle is usually coloured in some conspicuous manner. Thus in *Mutinus* the stem-like receptacle may be yellow, orange, or red; in *Clathrus* the latticed receptacle may be red or white; and in *Dictyophora multicolor* the stem is lemon-yellow, the pileus orange, indusium and volva pink, and mycelium purple.

The bright colours, bizarre shape of the receptacle, strongly fetid odours and mucilaginous nature of the gleba are obviously developed to attract insects and thus secure rapid dispersal of the spores. This is supported by the fact that flies and other insects are readily attracted to expanded plants, and that the faeces of insects fed on the gleba contain numerous spores which germinate readily (Fulton, 1889).

The economic importance of the Order is slight. Cobb (1906) reported that *Ithyphallus rubicundus* was the cause of a root-rot of sugar-cane in Hawaii; and Carne (1922) recorded *Aseroe rubra* upon roots of *Cynodon Dactylon* L. Occasional records have been published showing that certain species possess poisonous properties. Thus Farlow (1890) recorded that *Linderia columnata* killed pigs within 12 or 15 hours after eating; and Colenso (1883) claimed that *Aseroe rubra* destroyed cats in the Woodville (N.Z.) district. But one species, *Clathrus cibarius*, has been claimed to be edible. But this is open to doubt, as I have shown elsewhere (1922).

The Order is usually divided into two families, the Phallaceae and the Clathraceae, differing in details of development and in the structure of the receptacle. Opinions are divided as to which is the more primitive family. Lohwag (1924) and others considered that the Phallaceae were derived from the

Clathraceae. This is supported by the fact that in the Phallaceae there are present in certain genera additional structures (as the pileus in *Ithyphallus* and *Dictyophora*; indusium in *Dictyophora*) not found in the Clathraceae; but is negatived by the fact that genera such as *Mutinus* are obviously more primitive than any occurring in the Clathraceae, and by the more complex nature of the receptacle of many genera of the latter family. It is probable that each has had a separate origin in time from some *Mutinus*-like ancestor, and that development has proceeded on the one hand to considerable alteration of the receptacle, leading to the evolution of the higher genera of the Clathraceae (as represented by *Laternea*, *Aseroe* and *Clathrus* of the tribes Columnateae, Stellateae and Clathrateae respectively); and on the other to the production of the characteristic pileus (and indusium) of the Phallaceae.

To these two families, I would add a third, the Claustulaceae, to contain the interesting genus *Claustula*.

The following diagram illustrates my views on the probable origin of the known genera, and shows, too, the possible evolution of the three tribes of the Clathraceae.

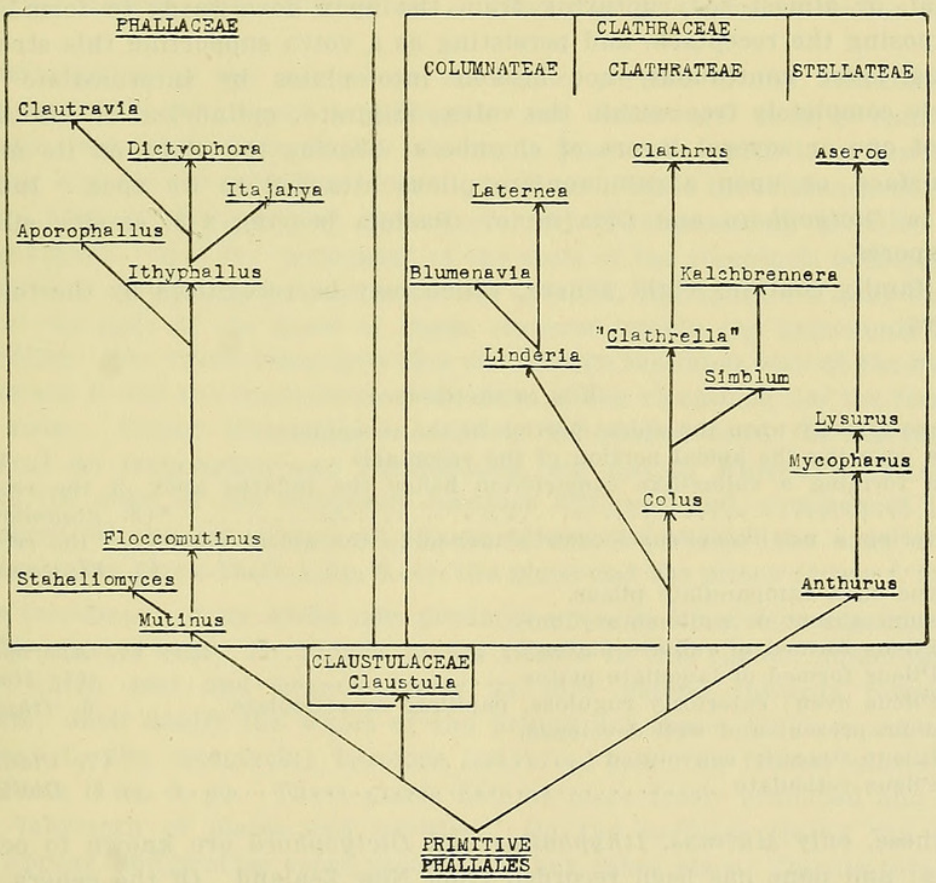

Diagram showing the probable evolution of the Phallales.

Order Phallales.

Plant at first consisting of a 2- or 3-layered peridium enclosing the receptacle and gleba. Peridium rupturing apically, remaining at the base of the receptacle as the volva. Receptacle pseudoparenchymatous, bearing the gleba on some portion of its surface. Gleba at maturity mucilaginous, olivaceous and usually fetid.

I have emended the Order to contain the three following families:

I. Family PHALLACEAE: Receptacle stipitate; cylindrical or fusoid, with or without an apical campanulate pileus and an indusium; gleba borne on the exterior of the pileus, or directly upon the modified apical portion of the stem.

II. Family CLATHRACEAE: Receptacle stipitate or sessile; clathrate, of simple columns united at their apices but basally free, or stipitate and divided apically into several arms which may be apically united or free; gleba borne on the interior, exterior of or between the arms.

III. Family CLAUSTULACEAE: Receptacle sessile; an obovate or spherical, apparently indehiscent hollow sphere; gleba lining the inner surface.

There would appear to be twenty genera in the Order, containing in all some sixty species; but the number is uncertain owing to differences of opinion held by different workers as to the generic and specific value of many characters.

Family I. PHALLACEAE.

Peridium of three layers, obovate or subglobose, at first submerged, becoming superficial, or almost so; rupturing from the apex downwards to form several lobes, exposing the receptacle and persisting as a volva supporting this structure; gelatinous layer continuous, not broken into plates by intermediate tissue. Receptacle completely free within the volva; stipitate; cylindrical or fusoid, stem hollow, of one or several layers of chambers; bearing the gleba on its modified upper surface, or upon a campanulate pileus attached to its apex. Indusium present in *Dictyophora* and *Clautravia*. Basidia bearing 4–8, sessile, elliptical, smooth spores.

The family contains eight genera, which may be recognized by the following characters:

Key to the Genera.

Gleba borne directly upon the apical portion of the receptacle.
- Gleba covering the apical portion of the receptacle ..... 1. *Mutinus*
- Gleba forming a collar-like constriction below the inflated apex of the receptacle ..... *(2. *Staheliomyces*)

Gleba covering a net-like pileus loosely attached to the apical portion of the receptacle ..... (3. *Floccomutinus*)

Gleba borne on a campanulate pileus.
- Indusium absent or rudimentary only.
  - Pileus formed of radiate plates ..... (4. *Aporophallus*)
  - Pileus formed of lamellate plates ..... (5. *Itajahya*)
  - Pileus even; exteriorly rugulose, papillate or reticulate ..... 6. *Ithyphallus*
- Indusium present and well developed.
  - Pileus strongly convoluted ..... (7. *Clautravia*)
  - Pileus reticulate ..... 8. *Dictyophora*

Of these, only *Mutinus*, *Ithyphallus* and *Dictyophora* are known to occur in Australia; and none has been recorded from New Zealand. Of the genera placed under the Phallaceae, *Staheliomyces* (Fischer, 1921) has been found in British Guiana and Surinam (Malay Archipelago); *Floccomutinus* is confined to West Africa; *Aporophallus* is confined to Brazil; *Itajahya* is not uncommon in South America; and *Clautravia* has a distribution through Java, Ceylon, East Indies and probably New Guinea. *Aporophallus* and *Itajahya* resemble *Ithyphallus*, and

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* Genera not occurring in Australia are in brackets.

Clautravia resembles *Dictyophora*, but these are separated principally on account of the different structure of the pileus.

Development.

The development of species of the genera *Mutinus*, *Ithyphallus* and *Dictyophora* has been investigated by Burt (1896, with *Mutinus caninus*), Fischer (1886; 1890, with *Ithyphallus impudicus*), and Atkinson (1911, with *I. impudicus*, *I. Ravenelii* and *Dictyophora duplicata*); and from their accounts the following particulars have been derived.

The primordium of the fructification arises as a terminal inflation on the end of the rhizomorph. Each is seen to consist of a cortical layer of loosely-woven hyphae enclosing a central medullary layer of hyphae arranged more or less parallel with the long axis of the primordium. The hyphae of this central tissue are expanded apically into a sheaf-like head, and at a very early stage exhibit between them a quantity of gelatinized tissue. The cortical layer at maturity becomes the outer layer of the peridium, and the medullary layer gives rise to all other tissues. The primordium at this stage is shown in section in fig. 1, Plate i.

Gelatinization of the hyphae of the upper portion of the medullary layer follows, and this progresses centrifugally and downward until a campanulate gelatinous tissue (which is thicker above) is produced, which later becomes the gelatinous layer of the peridium (Plate i, fig. 2, *f*). While this tissue is developing, and soon after its development commences, the fundaments of the other tissues begin to appear. Thus the fundament of the stem of the receptacle becomes noticeable first as a delicate columnar structure (Plate i, fig. 2, *a*), its apex extending nearly to the apex of the dome of tissue enclosed within the gelatinous layer of the peridium. The tissue lying next this later forms the inner wall of the peridium. And between it and the fundament of the stem of the receptacle lies the fundament of the gleba. Within this again is another bell-shaped zone, the fundament of the pileus (in *Ithyphallus* and *Dictyophora*, but not in *Mutinus*). Thus about the time the stem of the receptacle becomes differentiated, commences likewise development of the inner wall of the peridium (or rather the zone at which separation takes place, Plate i, fig. 2, *d*), the gleba and the pileus (Plate i, fig. 2, *p*).

The fundament of the gleba now produces upon its inner face a palisade layer of slender clavate cells. By growth of the tissues in this region, numerous plates develop which fold and branch freely as they extend inwards towards the receptacle; until finally the whole of the primordial tissue (save a narrow zone contiguous to the receptacle) becomes converted into the tramal plates of the gleba (Plate i, fig. 3, *g*). These plates become more freely branched and shortly form a labyrinth of plates and cavities. On the surfaces lining the cavities basidia appear, and profuse spore production then takes place. During this period, formation of the stem of the receptacle is progressing. Opinions differ as to the manner in which it is formed. Fischer (1890) considered the wall was formed from the outer portion of the medullary strand (which passes up from the rhizomorph as a slender cylinder and expands apically to form the capitate head of the medullary layer); whereas Burt (1896) believed that this strand played no part in the formation of the receptacle, but that all tissues (save the outer layer of the peridium) are derived from the capitate apex of the medulla. Atkinson (1911) was inclined to support Burt's interpretation.

The wall of the receptacle finally becomes pseudoparenchymatous and strongly folded. The central portion is filled with undifferentiated tissue which later becomes gelatinized and ultimately disappears (being utilized in giving the necessary turgescence to the expanding receptacle) to leave the mature and expanded receptacle hollow.

In *Mutinus* the apex of the receptacle becomes modified, according to the species, appearing as a smooth surface, covered with loosely arranged pseudoparenchymatous cells, or of digitate processes. As the tissue of the gleba continues to develop, the tramal plates press against the remaining primordial (undifferentiated) tissue lying between it and the receptacle apex, causing the gleba to become adnate at maturity. The stem of the receptacle during this later stage of development is only slightly compressed where in contact with the gleba, but much convoluted basally. Finally the tramal plates become gelatinized and the gleba becomes attached to the apical portion of the receptacle as a viscid mass. Owing to increased turgidity of the cells of the receptacle (partly due to enlargement of the whole through growth, but principally due to the pressure exerted through increased turgescence owing to absorption of the gelatinous matrix of the central core of the receptacle), pressure is exerted upon the apex of the peridium. This ruptures and remains as a cup (the volva) at the base of the receptacle. The convolutions in the latter flatten out, causing the receptacle to elongate, when it appears as a mature plant, the apex coated with the viscid, now fetid, gleba, the base held loosely within the volva.

In *Ithyphallus* and *Dictyophora*, however, development proceeds further, for the gleba, instead of being carried on the apex of the stem of the receptacle, is borne upon a well-developed pileus. This additional structure is formed in the primordial tissue situated between the fundaments of the gleba and receptacle, being separated from the latter by undifferentiated tissue. As development progresses it becomes converted to pseudoparenchyma and assumes a form characteristic of the species. The pileus is bell-shaped, and occupies a considerable portion of the area of the unexpanded plant, extending from near the apex (within the gelatinous layer of the peridium) to the base. Throughout its whole surface it is in intimate contact with the gleba, and serves effectively to prevent the gleba from coming in contact with the stem of the receptacle, which until rupture of the peridium is compressed within the pileus. The section (Plate i, fig. 4) of *Ithyphallus impudicus* shows the manner in which the gleba comes in contact with the reticulated pileus of this species. Between pileus and receptacle persists a residuum of fundamental tissue, to form at maturity the evanescent veil (and basal "collar") which may be noted in many species immediately following rupture of the peridium.

In *Dictyophora* (and *Clautravia*) there is an additional tissue, the indusium. This develops within the primordial tissue lying between pileus and receptacle, utilizing the residuum which, in *Ithyphallus*, forms the veil. The indusium is composed of chambered pseudoparenchyma of a similar nature to that of the receptacle, and, like the latter, is much convoluted during development, and remains in this condition until the peridium is ruptured, when the folds flatten out, causing it to appear from beneath the pileus as a delicate, pendent, campanulate, latticed tissue.

In *Ithyphallus impudicus*, Atkinson (1911) recorded a rudimentary indusium which had not advanced beyond the condition of a more densely compacted

primordium. This rudiment occupied the position in which the indusium develops in *Dictyophora*, and was composed of the same fundamental tissue which, undifferentiated, gives rise to the veil of *Ithyphallus*; differentiated, produces the indusium of *Dictyophora*.

1. Mutinus Fries.

Syst. Veg. Scand., ii, 1849, p. 434.—*Phallus*§*Cynophallus* Fr., *Syst. Myc.*, ii, 1822, p. 284.—*Cynophallus* (Fr.) Cda., *Icon. Fung.*, vi, 1854, p. 19.—*Corynites* Berk. et Curt., *Trans. Linn. Soc.*, xxi, 1855, p. 149.—*Jansia* Penz., *Ann. Jard. bot. Buit.*, xvi, 1899, p. 139.—*Phallus* Auctt.

Receptacle a hollow, simple, cylindrical or fusiform, coloured stem, closed below, pervious or impervious above; wall chambered, cavities usually opening to the exterior below, to the interior in the glebiferous region. Gleba mucilaginous, olivaceous, fetid, borne upon the apical portion of the receptacle, which may be externally smooth or covered with pseudoparenchymatous pulvinate or digitate processes.

Habitat.—Growing upon the ground, or on decayed wood.

Type Species, *Mutinus caninus* (Huds. ex Pers.) Fr.

Distribution.—Europe; Asia; North and South America; Africa; India; Ceylon; Java; Australia.

The genus is the most primitive of those in the family, consisting as it does of plants with a receptacle in the form of a simple hollow stem with the apical portion modified to carry the gleba. There would appear to be nine valid species in the genus, the numerous others which have been described being synonyms or forms of these. Of the generic synonyms *Jansia* alone is used by certain recent workers in a valid sense. Fischer (1900, p. 556) reduced it to a subgenus of *Mutinus*, characterized by the hollow digitate processes developed upon the wall of the apical part of the receptacle. Petch (1908, p. 143) has shown that the Ceylon *Mutinus proximus* is intermediate between *M. borneensis* ("Jansia rugosa") and *M. Penzigii* Fisch. ("Jansia elegans"), as it has the blunt anastomosing ridges of the former mixed with the appendages of the latter. It is evident therefore that *Jansia* cannot be maintained.

Mutinus may be divided into three sections upon the nature of the glebiferous region of the receptacle, thus:

I. Section *Glabrosi*: apical portion of the receptacle glabrous, either tuberculate or regularly reticulated with raised bands. (*M. caninus*; *M. curtus*; *M. elegans*; *M. Fleischeri*; *M. xylogenus.*)

II. Section *Granulosi*: apical portion of the receptacle covered with irregular pseudoparenchymatous processes, appearing granular or pseudo-reticulate. (*M. bambusinus*; *M. borneensis.*)

III. Section *Tuberculosi*: apical part of the receptacle covered with digitate processes. (*M. Penzigii*; *M. proximus.*)

Apparently but two species are known to occur with certainty in Australia, the numerous other records being based upon synonyms or misdeterminations of these.

1. Mutinus curtus (Berkeley) Fischer. Plate i, fig. 6.

Sacc., *Syll. Fung.*, vii, 1888, p. 13.—*Phallus curtus* Berk., in Hook. *Lond. Jour. Bot.*, iv, 1845, p. 69.—*Mutinus papuasius* Kalchbr., *Grev.*, iv, 1875, p. 74.—*Phallus* (*Cynophallus*) *papuasius* Kalchbr., *Ber. Nat. Akad. Wiss.*, x, 1880, p. 19.—*P. annulatus* Bailey ex Lloyd, *Phall. Aus.*, 1907, p. 13.—*Jansia annulata* (Bailey)

Lloyd, *Syn. Phall.*, 1909, p. 34.—*Mutinus annulatus* Bailey, *Comp. Cat. Queensland Pl.*, 1910, p. 745.

Peridium subglobose, white, to 15 mm. diameter. Receptacle to 3 cm. tall, 5–8 mm. diameter, hollow, fusiform, white below, pallid-red beneath the gleba, yellowish towards the sterile and pervious apex, finely but obscurely transversely rugulose throughout its length. Gleba sage-green in mass, arranged in an irregular zone around the upper portion of the receptacle, but not on the prominent sterile apex, fetid. Spores smooth, tinted, elliptical, 3·5 × 1·8 μ.

Type locality.—Swan River, Western Australia.

Distribution.—Australia: W. Aust.: Swan River (Berkeley, *l.c.*). Queensland: Rockhampton (as *M. papuasius*, Kalchbr., *l.c.*); Brisbane (as *M. annulatus*, Bailey, *l.c.*). N.S.W.: Mt. Wilson; Kurrajong Heights (Cleland and Cheel, 1915).

Cleland and Cheel (1915) have suggested that *Mutinus curtus* as illustrated by Corda (*Icon. Fung.*, vi, 1854, Pl. 3, f. 47) and *M. papuasius* as illustrated by Kalchbrenner (*l.c.*, 1880, Pl. 3, f. 1) are the same species, and that both figures refer to the species here considered as *M. curtus*. The illustrations show totally different plants, but as Berkeley's original description agrees very closely with the Mt. Wilson plant, it is evident Corda's drawing is largely diagrammatic, and, as Cleland and Cheel have suggested, constructed from an unexpanded plant. According to the same workers, Kalchbrenner's figure, if the greatly elongated stem were considerably shortened, resembles closely the two collections they recorded. From the particulars they have given, there can be little doubt but that such is the case, and that *M. papuasius* is a synonym of *M. curtus*. As an additional synonym I would add *Mutinus annulatus*, as it appears from the illustration to possess the same transversely-rugose receptacle, although the attenuate apex appears to be considerably exaggerated, and to suggest it to be a plant Fischer named as *M. boninensis* (which in turn is a synonym of *M. bambusinus*).

The minute size and transversely-rugose nature of the receptacle appear to characterize the species, and to separate it from the four other species which occur in the tropic or subtropic regions.

2. Mutinus borneensis Cesati. Plate ii, fig. 7.

Atti. Acc. d. Sci. Napoli, viii, 1879, Pl. 1, fig. 1.—*Phallus Watsoni* Berk., *Journ. Linn. Soc.*, Bot., xviii, 1881, p. 387.—*Mutinus? Watsoni* (Berk.) Fisch., in Sacc. *Syll. Fung.*, vii, 1888, p. 13.—*Floccomutinus nymenianus* P. Henn., *Monsunia*, i, 1899, p. 22.—*Jansia nymeniana* (P. Henn.) Penz., *Ann. Jard. bot. Buit.*, xvi, 1899, p. 139.—*J. rugosa* Penz., *l.c.*, p. 142.—*J. truncata* McAlp., in Lloyd's *Myc. Notes*, 1910, p. 484.

Peridium white, obovate, to 2 × 1·5 cm., splitting into 3–4 blunt and irregular lobes. Receptacle to 8 × 3 cm., fusiform, hollow, acuminate above and below, pervious at the apex, white at the base, becoming salmon-pink at the glebiferous region. Gleba borne on an irregular, fragile, raised network of variable meshes, olivaceous, fetid. Spores elliptical, hyaline, smooth, 3–3·5 × 1–1·8 μ.

Type locality.—Matang, Borneo.

Distribution.—East Indies. Australia: Queensland: Burnett River (Berkeley, *l.c.*, as *Phallus Watsoni*); Victoria: Melbourne (McAlpine, *l.c.*, as *Jansia truncata*); N.S.W.: Rookwood, Sydney, Mosman Bay (Cleland and Cheel, 1915, p. 203), Bradley's Head, North Dorrigo (Cleland and Cheel, 1923, p. 72).

This is separated from the preceding species by the larger size, and especially by the delicate structure bearing the gleba, which appears in the form of a raised

network corresponding to the polygonal depressions of the chambers of the receptacle.

Lloyd (*Myc. Notes*, 1923, p. 1215) examined the type specimen and drawing of *M. borneensis* in the herbarium of Cesati and found it to be identical with *Jansia rugosa* Penz. Fischer, as a result of examination of the type at Berlin, considered *Floccomutinus nymenianus* was also identical with *J. rugosa.* I have examined part of the type collection of *Jansia truncata*, and agree with Lloyd (*Myc. Notes*, 1910, p. 485) that it, too, is the same as *J. rugosa*, differing only in the somewhat larger size. And the description of *Phallus Watsoni* given by Berkeley shows it to belong to the same species. From this it becomes evident that the prior name for the species is *M. borneensis*, and that *Phallus Watsoni*, *Floccomutinus nymenianus*, *Jansia rugosa* and *J. truncata* are synonyms.

In a recent paper Petch (1926) described the microscopic structure of the pseudoparenchymatous processes upon the glebiferous portion of the receptacle of *M. bambusinus.* From this it would appear that *M. borneensis* in this particular closely resembles *M. bambusinus*, differing in that these processes are more strongly developed and arranged in an irregular network. His account and illustrations show *M. bambusinus* to differ in this and in the pervious chambers of the non-glebiferous portion of the receptacle (closed and polygonal in *M. borneensis*), and for this reason I consider *M. borneensis* a valid species. Petch has shown that *M. boninensis* and *M. Muelleri* are synonyms of *M. bambusinus*; that the apex may or may not be sterile, pervious or truncate, and that plants vary considerably in size. The odour of this species has been described by McAlpine (*l.c.*) as resembling scorched linen; by Cleland and Cheel (1923, p. 72) as musty but not fetid.

2. Ithyphallus (Fries) Fischer.

Ann. Jard. bot. Buit., vi, 1886, p. 4.—*Hymenophallus* Nees, *Syst. Pilz. u. Schw.*, 1817, p. 251.—*Phallus*§*Ithyphallus* Fr., *Syst. Myc.*, ii, 1822, p. 283.—*Phallus* §*Leiophallus* Fr., *l.c.*, p. 284.—*Dictyophallus* Cda., *Icon. Fung.*, vi, 1854, p. 19.—*Kirchbaumia* Schulzer, *Verh. k. Wien. Zool.-Bot. Gesell.*, xvi, 1866, p. 798.—*Omphalophallus* Kalchbr., *Flora*, xlvi, 1883, p. 95.—*Phallus* Auctt.

Receptacle a hollow, cylindrical or fusoid stem bearing an apically attached campanulate pileus, which may be smooth, rugulose or reticulate; apex usually pervious; indusium absent, but an evanescent veil often present. Gleba olivaceous, mucilaginous, usually fetid, covering the exterior of the pileus.

Type species, *Ithyphallus impudicus* (L. ex Fr.) Fisch.

Distribution.—Europe; Asia; North and South America; Africa; Australia; East and West Indies.

The presence of an additional structure, the pileus, borne apically on the receptacle, separates this genus from *Mutinus*; and from *Dictyophora* it is separated by the absence of an indusium. In several species is present a veil which has by many workers been confused with the indusium. But, as Atkinson (1911) has shown, the veil consists of a membranous, delicate layer of fundamental tissue lying between pileus and apex of the receptacle in unexpanded plants. As the stem of the receptacle elongates this is torn and fragments are left as a veil on the surface of the stem of the receptacle and the inner surface of the pileus, and as a collar at the base of the receptacle. It is seen as a rule only in freshly expanded plants, for it quickly disappears after exposure. It

is evident, therefore, that the veil is merely undifferentiated tissue, structurally different from the pseudoparenchymatous indusium of *Dictyophora*.

There are about eight valid species in the genus, which may be separated into two sections on the surface markings of the pileus:

I. Section *Reticulati*: pileus with raised reticulations.
(*I. costatus*; *I. impudicus*; *I. paucinervis*; *I. tenuis*.)
II. Section *Rugulosi*: pileus finely rugulose or smooth.
(*I. glutinolens*; *I. Ravenelii*; *I. rugulosus*; *I. rubicundus*.)

Ithyphallus impudicus is the common European species, and extends to North America (as *I. imperialis*). It has a white receptacle and pileus. (*I. imperialis* is a colour form with a pink volva and base of the receptacle.) *I. costatus* is a Javan form with more strongly developed reticulations; and *I. paucinervis* a form from Surinam (Malay Archipelago) with scantily developed irregular reticulations. *I. tenuis* is a distinct tropic species, found in Java, Ceylon and Japan, characterized by its small size, yellow pileus and receptacle, and reticulated pileus. The rugulose section contains three well defined species. *I. Ravenelii* possesses a white receptacle and is confined to North America; *I. rubicundus* has a red receptacle and pileus and is common in India, southern North America, West Indies, Africa and Australia; and *I. glutinolens*, characterized by the depressed globose shape of the pileus, is confined to Brazil. *I. rugulosus*, confined to Japan, is a form of *I. rubicundus* differing only in the colour of the pileus. The many others which have been described are but synonyms of these, or of species of *Dictyophora*.

The genus is represented in Australia by the following solitary species, though many others have been recorded.

1. Ithyphallus rubicundus (Bosc.) Fischer. Plate ii, fig. 8.

Jahrb. bot. Gart. u. Mus. Berlin, iv, 1886, p. 50.—*Satyrus rubicundus* Bosc., *Mag. Ges. nat. Freunde Berlin*, v, 1811, p. 86.—*Phallus*§*Leiophallus rubicundus* Fr., *Syst. Myc.*, ii, 1822, p. 284.—*Phallus canariensis* Mont., *Phyto. Canariensis*, 1840, p. 84.—*P. aurantiacus* Mont., *Ann. Sci. Nat.*, ser. 2, xvi, 1841, p. 277.—*Dictyophallus aurantiacus* Cda., *Icon. Fung.*, vi, 1854, p. 19.—*Phallus aurantiacus* var. *discolor* Kalch., *Grev.*, ix, 1880, p. 2.—*Cynophallus Cayleyi* Berk., ex F.v.M., *Fragm. Phyto.*, xi, 1880, p. 119.—*Omphalophallus Muellerianus* Kalch., *Flora*, xlvi, 1883, p. 95.—*Phallus libidinosus* Cayley ex Cke., *Grev.*, xi, 1883, p. 57.—*Omphalophallus retusus* Kalch., *Ungar. Akad. Wiss. Budapest*, xiii, 1884, p. 6.—*Ithyphallus retusus* (Kalch.) Fisch., *Jahrb. bot. Gart. u. Mus. Berlin*, iv, 1886, p. 49.—*I. aurantiacus* (Mont.) Fisch., *l.c.*, p. 51.—*I.* ? *canariensis* (Mont.) Fisch., in Sacc. *Syll. Fung.*, vii, 1888, p. 10.—*I. retusus* (Kalch.) Fisch., *l.c.*, p. 11.—*Phallus novae-hollandiae* Cda. ex Fisch., *Denks. Schweiz. nat. Gesell.*, xxxii, 1890, p. 88.—*Mutinus* ? *discolor* (Kalch.) Fisch., *l.c.*, p. 93.—*Omphalophallus calvescens* Kalch. ex Fisch., *Denks. Schweiz. nat. Gesell.*, xxxiii, 1893, p. 34.—*Ithyphallus Muellerianus* (Kalch.) Fisch., *l.c.*, p. 34.—*Phallus celebicus* P. Henn., *Monsunia*, i, 1899, p. 21.—*P. sanguineus* P. Henn., Engl. *Bot. Jahrb.*, xxx, 1901, p. 57.—*Ithyphallus celebicus* (P. Henn.) Sacc. et Syd., in Sacc. *Syll. Fung.*, xvi, 1902, p. 225.—*I. sanguineus* (P. Henn.) Sacc., *Syll. Fung.*, xvii, 1905, p. 212.—*I. coralloides* Cobb, *Exp. Stn. Hawaii* Bull. 5, 1906, p. 208.—*Phallus discolor* (Kalch.) Lloyd, *Phall. Aus.*, 1907, p. 10.—*P. gracilis* (Fisch.) Lloyd, *Syn. Phall.*, 1909, p. 14.—*Ithyphallus discolor* (Kalch.) Sacc. et Trav., in Sacc. *Syll. Fung.*, xix, 1910, p. 987.—*I. atrominiatus* Bailey, *Comp. Cat. Queensland Pl.*, 1910, p. 746.—*I. operculatus* Bailey, *l.c.*

Peridium ovate or subglobose, to 3 cm. diameter, solitary or in small groups of 2–6. Receptacle variable in size and shape, fusiform or cylindrical, to 18 × 3 cm., scarlet, wall several chambers in thickness; pileus conical, slightly rugulose, scarlet, apex perforate. Gleba covering the exterior of the pileus, mucilaginous, fetid, olivaceous. Spores smooth, elliptical, tinted, 3·5–5 × 1·5–2 μ.

Type locality.—South Carolina, North America.

Distribution.—Southern North America; West Indies; Africa; India; Hawaii; Australia.

Queensland: Burnett District (Herb. Brit. Mus., Fischer, 1893, p. 37); Brisbane (Bailey, *l.c.*, as *I. atrominiatus* and *I. operculatus*); Toowoomba; Darling Downs (Herb. Kew, Fischer, 1893, p. 37).—N.S.W.: Mosgiel (Herb. Berol., Fisch., 1893, p. 35, as *I. Muellerianus*); Illawarra (Kalchbrenner, *l.c.*, as *Omphalophallus Muellerianus*); Mudgee (Herb. Berlin, Fischer, 1890, p. 88 as *I. aurantiacus* f. *gracilis*); Campbelltown; Richmond River; Grafton (Nat. herb., Sydney, Cleland and Cheel, 1915, p. 200).—Victoria: Melbourne; Yarra Yarra.—S. Aust.: Kingston (Cleland, 1924, p. 251, in herb. Cleland).—Tasmania: No locality (herb. Delessert, Fischer, 1890, p. 88).

This species appears to be common in the tropic and subtropic regions. In Australia it has been collected fairly frequently, as the records show, and recorded under *Ithyphallus aurantiacus* f. *gracilis*, *I. Muellerianus*, *I. retusus*, *I. novae-hollandiae*, *I. atrominiatus*, *I. operculatus*, *Mutinus discolor*, *Phallus rubicundus* var. *gracilis* and *P. gracilis*, all of which are synonyms of the same species, for there is no character (other than size) by which one form may be separated from another; and size in a variable species where so many intermediate forms are known, has no specific value. The scarlet colour of the pileus and receptacle, and finely rugulose pileus, characterize the species.

3. Dictyophora Desvaux.

Jour. de Bot., ii, 1809, p. 88.—*Hymenophallus* Nees, *Syst. Pilz. u. Schw.*, 1817, p. 251.—*Phallus*§*Hymenophallus* Fr., *Syst. Myc.*, ii, 1822, p. 282.—*Sophronia* Gaud., *Voy. aut. Monde*, 1826, p. 178.—*Phallus* Auctt.

With the characters of *Ithyphallus* and in addition a definite indusium. This is a campanulate, latticed, pseudoparenchymatous, pendent membrane, apically attached to the apex of the receptacle beneath the pileus, and basally free, extending to a position midway between volva and pileus.

Type species, *Dictyophora indusiata* (Vent. ex Pers.) Fisch.

Distribution.—Africa: North and South America; East and West Indies; India; Ceylon; China; Cook Islands; Australia.

As has been shown, the indusium characterizes the genus, and is a very different structure from the veil. The function of this distinctive membrane is unknown, but it possibly aids in attracting insects to the plant to assist in spore dispersal.

There would appear to be but four valid species in the genus, the many others described being synonyms of this or *Clautravia*, or at most colour forms. *D. indusiata* apparently has a wide distribution through the tropic and subtropic regions, and is characterized by the white indusium and receptacle, and by the rugulose-reticulate nature of the pileus. *D. duplicata*, confined to North America, closely resembles the preceding (and by many workers is considered to be identical), but is separated by the more definite nature of the reticulations of the pileus. *D. Farlowii*, which is confined to Brazil, differs in the structure of the

indusium and reticulations of the pileus. *D. multicolor* is similar to *D. indusiata* in form, but differs considerably in colour. It has a limited distribution in Australia and Java.

1. Dictyophora indusiata (Vent. ex Pers.) Fischer. Plate ii, fig. 9.

Unter. Phall. Surinam, 1928, p. 28.—*Phallus indusiatus* Vent. ex Pers., *Syn. Meth. Fung.*, 1801, p. 244.—*Dictyophora phalloidea* Desv., *Jour. de Bot.*, ii, 1809, p. 88.—*Hymenophallus indusiatus* (Vent.) Nees, *Syst. Pilz. u. Schw.*, 1817, p. 252.—*Sophronia braziliensis* Gaud., *Voy. aut. Monde*, 1826, p. 178.—*Dictyophora campanulata* Nees ex Lev., *Mem. Soc. Linn. Paris*, v, 1827, p. 499.—*D. speciosa* Meyen, *Nov. Acad.*, xix, 1843, p. 239.—*D. bicampanulata* Mont., *Ann. Sci. Nat.* ser. 3, x, 1848, p. 120.—*D. radicata* Mont., *Ann. Sci. Nat.*, ser. 3, iii, 1855, p. 137.—*Phallus speciosus* Schlecht., *Linnaea*, xxxi, 1862, p. 121.—*P. braziliensis* Schlecht., *l.c.*, p. 124.—*P. tahitiensis* Schlecht., *l.c.*, p. 126.—*P. radicatus* (Mont.) Schlecht., *l.c.*, p. 129.—*Dictyophora nana* Berk. ex Cke., *Grev.*, xi, 1882, p. 39.—*Phallus collaris* Cragin, *Bull. Washborn Coll.*, i, 1885, p. 33.—*Dictyophora braziliensis* (Schlecht.) Fisch., *Jahrb. bot. Gart. u. Mus. Berlin*, iv, 1886, p. 32.—*D. tahitiensis* (Schlecht.) Fisch., *l.c.*, p. 37.—*Hymenophallus alboindusiatus* Loth. ex Fisch., in Sacc. *Syll. Fung.*, vii, 1888, p. 469.—*Phallus diplopora* Mont. ex Fisch., *Denks. Schweiz. nat. Gesell.*, xxxii, 1890, p. 81.—*Dictyophora callichroa* A. Moell., *Braz. Pilz.*, 1899, p. 129.—*D. Lilloi* Speg., *An. Mus. Nac. Buenos Aires*, xvi, 1906, p. 30.—*Phallus callichrous* (A. Moell.) Lloyd, *Phall. Aus.*, 1907, p. 6.—*P. rochesterensis* Lloyd, *Syn. Phall.*, 1909, p. 20.—*P. Moelleri* Lloyd, *l.c.*

Peridium ovate or subglobose, to 4 cm. diameter, white. Receptacle fusiform or cylindrical, to 20 × 3·5 cm., white, hollow; pileus campanulate, dingy-yellow when the gleba is removed, reticulate-rugulose, the reticulations being even and with rounded edges, apex perforate, collar raised and distinct. Indusium coarsely net-like, white, pendent, campanulate, apertures large, bars elliptical. Gleba olivaceous, spread between the reticulations over the pileus, fetid, mucilaginous. Spores elliptical, smooth, tinted, 3·5–4·5 × 1·5–2 μ.

Type locality.—Dutch Guiana.

Distribution.—Africa; North and South America; Asia; East and West Indies; India; Ceylon; Australia.

Queensland: Daintree River (Fischer, 1890, p. 81); Brisbane (Herb. Kew, Fischer, 1893, p. 31); Endeavour River (Herb. Kew, Fischer, 1893, p. 31).—N.S.W.: Neutral Bay; Booyong (Nat. Herb., Sydney, Cleland and Cheel, 1915, p. 200).—Cook Islands: Samoa (Lloyd, 1909, p. 18).

This species varies considerably in size, structure of the indusium, and especially in the sculpturing of the pileus. Shortly after a plant has emerged from the peridium the pileus appears rugulose, but as it ages the pileus becomes more clearly reticulated, the reticulations becoming thinner and more sharply defined.

2. Dictyophora multicolor Berkeley and Broome. Plate ii, fig. 10.

Trans. Linn. Soc. Lond., ser. 2, ii, 1883, p. 66.—*Phallus quadricolor* Berk. et Br., *l.c.*—*P. calyptratus* B. et Br., *l.c.*—*Ithyphallus quadricolor* (B. et Br.) Fisch., *Jahrb. bot. Gart. u. Mus. Berlin*, iv, 1886, p. 45.—*I. calyptratus* (B. et Br.) Fisch., *l.c.*, p. 46.—*Phallus multicolor* (B. et Br.) Lloyd, *Phall. Aus.*, 1907, p. 6.

Receptacle fusiform, to 16 × 3 cm., white below, pink above, hollow, of three layers of fine chambers; pileus conical, irregularly reticulate, orange, pervious,

thin and tough. Indusium pendent, to 4 cm. below the pileus, salmon-pink, with fine meshes. Gleba olive-brown, spread between the reticulations of the pileus. Spores tinted, elliptical, smooth, 3·5 × 1·8 μ.

Type locality.—Brisbane, Queensland.

Distribution.—Australia; Java.

Queensland: Brisbane (Herb. Brit. Mus., Fisch., 1893, p. 33).—N.S.W.: Ballina (Cleland and Cheel, 1915, p. 200); National Park (Cleland and Cheel, 1923, p. 72).

This is a strongly marked colour form of *D. indusiata*. The colour is not always constant, for in the type collection the receptacle was stated to be pallid-yellow (or cream coloured), the indusium bright lemon-yellow and the pileus orange. The type of "*Phallus quadricolor*" was stated to possess a lemon-yellow stipe, orange pileus, white volva and purple mycelium. Cleland and Cheel (1923, p. 72) have described a specimen from National Park (N.S.W.) in which the receptacle was white below, shading from orange to pink above, pileus orange, indusium salmon-pink, and volva tinted lilac. As *D. rosea* (Ces.) Fisch. (Fisch., 1886, p. 35), which was described from Borneo, possessed a pink indusium it is possible it may be the same species; if so this name has priority, the species being described in 1879 (*Hymenophallus roseus* Ces. *Atti Reale Acc. sci. nat. Napoli*, viii, p. 12). But as it is not possible from Cesati's description to determine to what plant he was referring, and as no type exists, I prefer to use a name which is associated with a known plant.

D. multicolor, *Phallus quadricolor* and *P. calyptratus* were based on specimens collected near Brisbane by Bailey, now in the herbarium of the British Museum (South Kensington). All three possess a reticulated pileus, which suggests that they are collections of the same species. And this belief is strengthened by the fact that the two former agree in all particulars (even to the unusual colouring) save that "*Phallus quadricolor*" has no indusium, and *P. calyptratus* lacks an indusium and possesses a portion of the volva accidentally attached to the apex of the pileus (Lloyd, 1909, p. 22, stated that this was a mass of dried gleba). As all three possess the reticulated pileus and colouring of no other known species, it is evident all are collections of the same species (particularly as they were taken from the same locality), the absence of an indusium being accounted for by loss, since this membrane is delicate and readily detached.

Doubtful and Excluded Species.

a. Dictyophora merulina Berk.—This was recorded in error from Australia by Cooke (1892, p. 212), the plant he has illustrated being *D. indusiata*, collected at Brisbane by F. M. Bailey, and the one which Lloyd (1907, p. 6) named *Phallus rochesterensis.*

b. Ithyphallus impudicus (L. ex Fr.) Fisch.—At Kew is a specimen labelled *I. impudicus*, collected by Bailey from Fringiburra Creek, Queensland. As it possesses a white receptacle and reticulated pileus, and as no other specimen has been found in this region, it is probable that this is a specimen of *D. indusiata* which had lost its indusium.

c. Phallus vitellinus Muell., *Phyt. Aust.*, 1880, p. 122.—This was listed, but not described, among a collection of fungi recorded by von Mueller. Consequently as it is a *nomen nudum*, it should be deleted from our records. Lloyd (1907, p. 8) suggested it was a synonym of *I. rubicundus.*

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Literature Cited.

Atkinson, G. F., 1911.—The origin and taxonomic value of the veil in *Dictyophora* and *Ithyphallus*. *Botanical Gazette*, li, pp. 1-20.

Burt, E. A., 1896.—The development of *Mutinus caninus* (Huds.) Fr. *Annals of Botany*, x, pp. 343-372.

Carne, W. M., 1922.—In Lloyd's *Mycological Notes*, 1922, p. 1117.

Cleland, J. B., 1924.—Australian fungi: Notes and descriptions, No. 5. *Trans. Roy. Soc. S. Aust.*, xlviii, pp. 236-252.

Cleland, J. B., and Cheel, E., 1915.—Notes on Australian Fungi, No. 2. Phalloids and Geasters. *Journ. Proc. Roy. Soc. N.S.W.*, xlix, pp. 199-232.

————, 1923.—Australian Fungi: Notes and descriptions, No. 4. *Trans. Roy. Soc. South Aust.*, xlvii, pp. 58-78.

Cobb, N. A., 1906.—Fungus maladies of the sugar cane with notes on associated insects and nematodes. *Rept. Exp. Stn. Hawaii Sugar Pl. Assn.*, Bull. 5, 134 pp.

Colenso, W., 1883.—*Aseroe corrugata*, n. sp. *Trans. N.Z. Inst.*, xvi, p. 362.

Cooke, M. C., 1892.—Handbook of Australian Fungi, 458 pp.

Cunningham, G. H., 1922.—*Clathrus cibarius*, or "Bird-cage" fungus. *N.Z. Jour. Sci. Tech.*, v, pp. 247-250.

Farlow, W. G., 1890.—Poisonous action of *Clathrus columnatus*. *Botanical Gazette*, xv, pp. 45-46.

Fischer, Ed., 1886.—Versuch einer systematischen Uebersicht ueber die bischer bekannten Phalloideen. *Jahrbuch bot. Gartens u. botan. Museums Berlin*, iv, pp. 1-92.

————, 1890.—Untersuchungen zur vergleichenden Entwicklungsgeschichte und Systematik der Phalloideen. *Denks. Schweiz. naturf. Gesellschaft*, xxxii, pp. 1-103.

————, 1893.—*Ibid*, xxxiii, pp. 1-51.

————, 1900.—Phalloideen, in Engler and Prantl, *Natürlichen Pflanzenfamilien*, i, pp. 276-296; 555-556.

————, 1921.—*Staheliomyces cinctus*, ein neuer Typus aus der Gruppe der Phalloideen. *Mitteil. Naturf. Gesell. Bern im Jahre* 1920, pp. 1-6 (Separate).

Lloyd, C. G., 1907.—The Phalloids of Australasia, 26 pp.

————, 1909.—Synopsis of the known Phalloids, 94 pp.

Lohwag, H., 1924.—Der Uebergang von *Clathrus* zu *Phallus*. *Archiv. f. Protistenk.*, xlix, pp. 237-259.

Petch, T., 1908.—The Phalloideae of Ceylon. *Ann. Roy. Bot. Gard. Peradeniya*, iv, 139-184.

————, 1926.—Mutinus bambusinus (Zoll.) Ed. Fischer. *Trans. Brit. Myc. Soc.*, x, pp. 272-282.

EXPLANATION OF PLATES I-II.

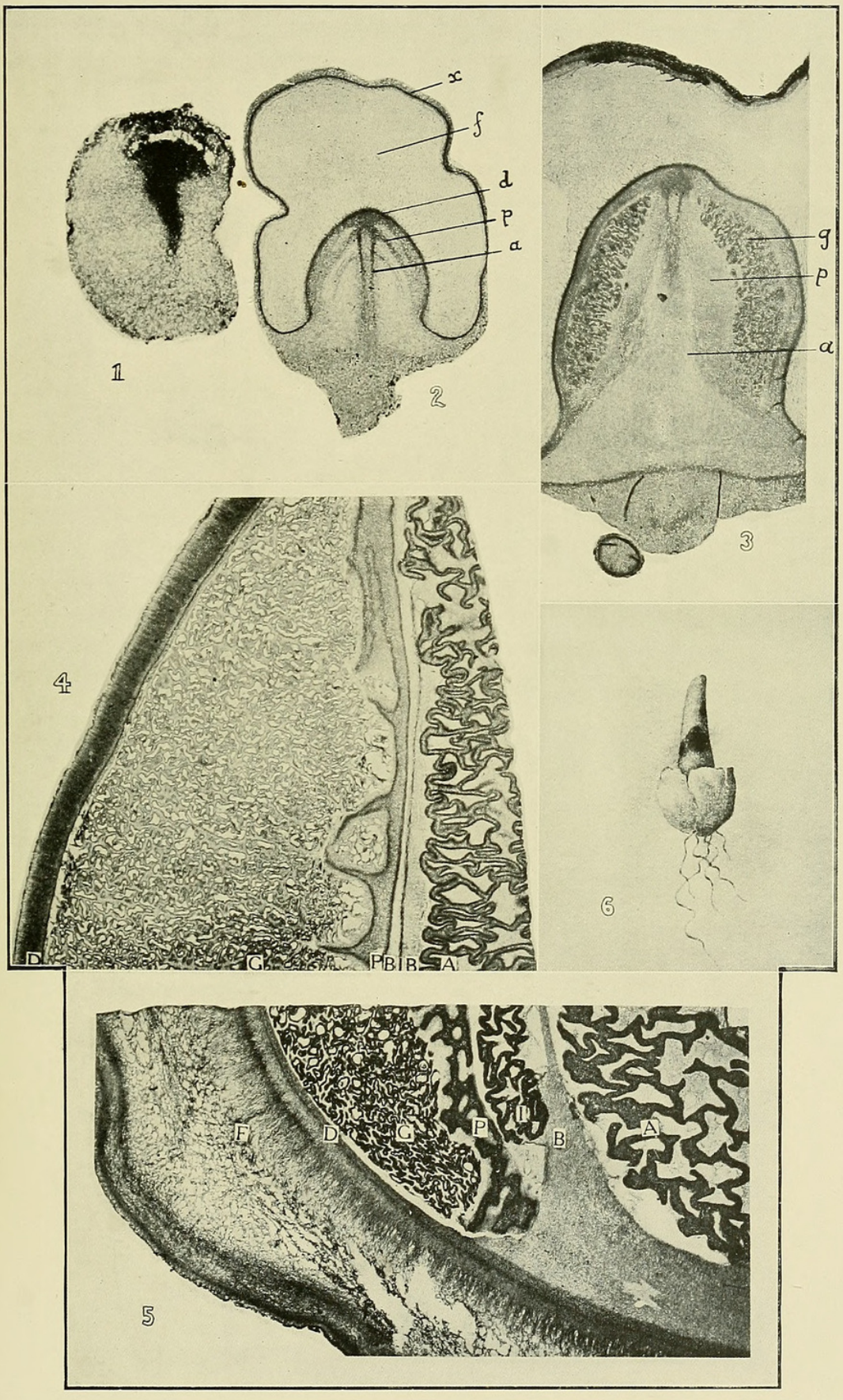
Plate i.

1.—Development of *Ithyphallus impudicus*. Young plant shortly after commencement of development. Commencement of gelatinization of tissue to form the middle layer of the peridium (mesoperidium); the dark area is the fundament of the fruit body. × 17·5. (After Atkinson, 1911.)

2.—Older stage of the same species. *a*, rudiment of the stem of the receptacle; *p*, of the pileus; *d*, the endoperidium; *f*, gelatinous layer of the peridium (mesoperidium); *x*, exoperidium. × 7. (After Atkinson, 1911.)

3.—Later stage showing development of the gleba, *g*; pileus, *p*; and stem, *a*. × 7. (After Atkinson, 1911.)

4.—Plant shortly before the rupture of the peridium. *a*, strongly convoluted stem of the receptacle; *b*, fundamental tissue lying between stem and pileus which gives rise to the veil (the dark line marked *i* is the rudimentary indusium of this species); *p*, reticulated pileus; *g*, chambered gleba before deliquescence; *d*, endoperidium. × 7. (After Atkinson, 1911.)



Gasteromycetes of Australasia—Phallales.