CHAPTER IV

A SYSTEMATIC ACCOUNT AND ARRANGEMENT OF THE PILOBOLIDAE

CONTRIBUTED BY W. B. GROVE

Introductory Remarks—Historical Account—Systematic Arrangement—Bibliography

Introductory Remarks.—The section of the Mucorini entitled Pilobolidae includes only two genera, Pilobolus and Pilaira. In 1884 the writer of this chapter published a *Monograph of the Pilobolidae*, in which he gave a systematic arrangement of the ten species which had been up to that time described. This arrangement was followed by Saccardo in the seventh volume of his Sylloge Fungorum, pp. 184–189, and has since been revised by Palla and Morini.[1]

The writer's personal knowledge of the Pilobolidae in England is based upon the forms called *Pilobolus crystallinus*, *P. Kleinii*, *P. sphaerosporus*, *P. oedipus*, and *Pilaira anomala*, and in addition he has seen *Pilobolus longipes* and *P. umbonatus*, which have been found in Canada as shown by Professor Buller in preceding chapters of this volume. The six forms of Pilobolus just mentioned, as well as *Pilaira anomala*, *P. nigrescens*, *P. Saccardiana*, and *P. Moreaui*, may probably be regarded as definitely established species; in regard to most of the others there remains a certain doubt which can only be removed when some one has devoted to the group

[1] This account of the Pilobolidae, written at the request of my friend Professor Buller, may be considered to be a revision of the systematic part of the *Monograph of the Pilobolidae* which I published in the Midland Naturalist exactly fifty years ago. Professor Buller has been good enough to give me the benefit of his assistance in defining the group and the genera, in revising the descriptions of certain species, and in preparing the illustrations.—W. B. G.

a large amount of time and patience. The account of those species which I have not seen is of course compiled from the published sources.

The drawings of the earlier authors were but free-hand sketches, inaccurate in certain details. For instance, Bolton's figure of *Pilobolus roridus* (Fig. 98) makes the subsporangial swelling appear nearly twice as broad as it is high (seemingly in an attempt at perspective); Zopf and Klein represent the subsporangial swelling of *P. Kleinii* (their *P. crystallinus*) as hardly or not at all wider than the sporangium; van Tieghem makes the same error in his figure of *Pilobolus nanus* (Fig. 106, p. 212), while in *Pilobolus longipes* (Fig. 100, p. 203) he draws the spores in the sporangium out of all proportion to the sporangium in which they are enclosed. By future workers pure cultures of each so-called species should be obtained and their special characteristics should be fully illustrated by photographs and *camera-lucida* drawings.

The Historical Account which follows is founded, with many emendations and the necessary later additions, on that given in the Monograph of 1884.

Historical Account.—The earliest record I have been able to find of a species belonging to Pilobolus is in the works of the famous British botanist, John Ray. In his Historia Plantarum (1688) occurs the following passage which, on account of its importance, shall be quoted in full :—

"E Catalogo huc tranſmiſſo *Anno* 1680, quem compoſuit eruditiſſimus Vir et conſummatiſſimus Botanicus D. *Johannes Baniſter* Plantarum à ſeipſo in Virginia obſervatarum.

"Fungus (ex ſtercore equino) capillaceus capitulo rorido, nigro punctulo in ſummitate notato. Ex recenti fimo noctu exoritur cauliculis erectis, vix digitum longis, capillorum inſtar tenuibus nec minùs denſis ſeu confertis. Singuli Cauliculi parvulo globulo aqueo coronantur, qui in ſumma ſui macula parva nigra Limacis oculi ſimili inſignitur."

The same species of Pilobolus was then mentioned and figured by Plukenet (1691) as "*Fungus Virginianus* ex ſtercore equino capillaceus canus capitulo rorido, nigro punctulo in ſummitate notato, D. Baniſter." Plukenet did not merely copy what Ray had

published, for he adds the correct descriptive word "canus," of which Ray says nothing, as well as a small but characteristic figure (Fig. 97). Both these additions he obtained from Banister's MS. From Ray's description and Plukenet's figure, it is evident that the species they had in view was similar to that which was afterwards called *Mucor roridus*.

These two notices stimulated observation, for a few years later the first British record was published in Ray's Synopsis (1696), in a list of plants communicated by Mr. James Petiver, who remarks "*This I have observed on Horse-dung about* London," and refers to Plukenet's figure. This record, therefore, may be considered to belong to *Pilobolus roridus*. It is repeated by Ray in his Historia Plantarum in 1704, and again in his Synopsis in 1724, and by Petiver in his Gazophylacium (1711), where he gives a figure similar to that of Plukenet.

FIG. 97.—The first illustration of a Pilobolus. Banister's drawing, reproduced by Plukenet (1691).

Another mention of a fungus belonging to this genus (the earliest known to Coemans in his review, 1861, of the literature of the subject up to his time) is due to Henry Baker, who, in his Natural History of the Polype Insect (1744), described a number of small vase-like plants, filled with a clear liquid and crowned by a black ball; these, which he had found on mud brought from the river Thames, were undoubtedly a species of Pilobolus, presumably *Pilobolus oedipus*.

In 1764 Otto Müller discovered and afterwards (1782) described and figured a Pilobolus under the name of "Kristallschwämmchen"; he imagined it was in part an animal, in part a plant, and even in part a crystal, thus partaking of all the three kingdoms of nature. He thought he saw a slender worm-like body residing within the organism, which, he says, "crawled round in the crystal globe and seemed to swim at its ease in a tiny ocean." This was no doubt a species of Anguillulidae, but outside, not within, the subsporangial swelling. The singularity of this view accounted for the widespread attention which was given to his discovery.

It was not till 1772 that Scopoli in his Flora Carniolica first

gave to the plant a name which showed a recognition of its true affinities. He called it *Mucor obliquus*, from the oblique manner in which the stipe frequently sprang from the side of the basal reservoir, but his description, though very interesting, is insufficient to enable us to identify the species.

Withering, in his Botanical Arrangement (1776), quoted Petiver's plant from Ray's Synopsis and bestowed upon it the name *Mucor roridulus*.

In Wiggers' Primitiae Florae Holsaticae (1780) Scopoli's plant was placed in a new genus, under the name *Hydrogera crystallina* suggested by his tutor Weber.

But the first good description of the genus was given by Tode, who imposed upon his species the name of *Pilobolus crystallinus* by which it is now known. The generic name is a translation of the title "Hutwerfer," which he used in the Schrifte der Berlinsche Gesellschaft naturforschenden Freunde (1784); his account was repeated in his Fungi Mecklenburgenses selecti in 1790.

FIG. 98.—*Pilobolus roridus* (Bolton) Pers. A cluster of fruit-bodies on horse dung, about natural size, and two fruit-bodies much enlarged. Reproduced by photography from Bolton's *History of Fungusses* (1789).

Species of Pilobolus were then mentioned successively: by Dickson (1785), who figured one under the name *Mucor urceolatus*; by Bulliard, under the same name, in his Herbier de la France (1784), with a figure added in 1789; by Bolton (1789), who, besides figuring under that name a form resembling a badly grown *Pilobolus Kleinii*, added another supposed to be identical with Petiver's as *Mucor roridus* (Fig. 98); and by Vahl, in the Flora Danica (1792), who figured one as *Pilobolus crystallinus*.

Persoon gives an excellent description of *P. crystallinus* in his Observationes Mycologicae (1796), accompanied by an imperfect figure; and in his Synopsis methodica Fungorum (1801) he mentions both that and *P. roridus*, but considers the latter as doubtfully distinct.

Sowerby, in his English Fungi (1803), gives a figure of *Mucor urceolatus* which seems to represent *P. crystallinus*.

Link, in his First Dissertation (1809), attributed for the first time the projection of the sporangium to its true cause, namely the tension of the swelling below the sporangium. His words are: "Explosio fieri mihi videtur, dum suprema pars stipitis bullata, sporangium inferne ambiens, contrahitur."

Relhan, in his Flora Cantabrigiensis (1820), maintained that *Pilobolus roridus* was distinct from *P. crystallinus*; but Purton, in his Midland Flora (1821), recorded both of them under one name *Pilobolus urceolatus*, giving detailed reasons from experiment to show that they are not distinct, and accompanying his account with "a very beautiful and accurate drawing" by his niece, "taken from the fresh plant."

In 1823 Ehrenberg published in Kunze u. Schmidt's Mykologische Hefte an account of some observations he had made upon *P. crystallinus*, in which, while searching for Otto Müller's "worm," he noticed a curious movement of yellowish particles arranged in a snake-like form in a drop of water which occupied the summit of the sporangium. This, he thought, might be the "worm," because it moved with a "slow, steady, circling motion" which excited his wonder.

All the authors mentioned so far correctly placed the genus in the immediate vicinity of Mucor. Fries, however, in 1823, considered it as nearly allied to Sphaerobolus and placed it in the Gasteromycetes in the section Carpoboli, but in 1829 he discovered his mistake and restored it again to the Mucorini. Nevertheless Berkeley, in Smith's English Flora (1836), incautiously repeated Fries' error, and in his Outlines of British Fungology (1860), perhaps by reason of this confusion, he omitted Pilobolus altogether.

Up to this time only the two species already mentioned, called *P. crystallinus* and *P. roridus*, were generally known, but in 1828 Montagne had already described a third, to which he gave the name of *P. oedipus* (*cf.* Fig. 104, p. 209) on account of the swollen basal reservoir which is so conspicuous a feature in that species. He repeated this in his Sylloge generum specierumque cryptogamarum in 1856.

In 1837 Corda instituted in his Icones Fungorum the group Pilobolidae to contain Pilobolus and Chordostylum; in 1842 he

added to the group Pycnopodium and Caulogaster, placing in the former genus, as *Pycnopodium lentigerum*, a species which he had formerly included in Pilobolus and which would seem to be merely an abnormal state of *P. Kleinii*. After Corda's lamented early death, Zobel published (1854) from his friend's manuscript notes a sixth volume of the Icones, in which he gives a long account of *Pilobolus crystallinus* containing numerous errors. In his drawing (f. 32) he represents the interior of the subsporangial swelling as lined with reticulations of orange-coloured granules such as no other author has seen, and which are probably only the meridional streams, occasionally met with but rarely figured,[1] disturbed by the pressure to which the preparation had been subjected.

When Cohn published, in 1851, his celebrated monograph "Die Entwicklungsgeschichte des Pilobolus crystallinus," he had before him, not that species with which he was really unacquainted, but the species of Montagne. He figures the characteristic yellow, spherical, thick-walled spores of *Pilobolus oedipus*, and then remarks with naïve surprise that Corda had represented the spores of *P. crystallinus* as elliptic and colourless "in contradiction to nature."

Cesati discovered, in 1850, a species which he published the next year in Klotzsch's Herbarium vivum mycologicum under the name *Pilobolus anomalus*, now known as *Pilaira anomala* Schröt.

Bonorden, in his Handbuch (1851), described a species under the name of *P. crystallinus*, which on account of its round spores Coemans referred to *P. oedipus*, but which I think there is greater reason for considering as *P. Kleinii*, forma *sphaerospora*.

In 1857 Currey wrote a note "On a species of Pilobolus" which he thought to be *P. roridus*, but his plate and description clearly show that the species he had in view was *P. Kleinii*; according to van Tieghem, Léveillé in 1826 had fallen into the same error, giving the name of *P. roridus* to a form of *P. Kleinii*. Currey also attributed the projection of the sporangium to the eversion and upward pressure of the columella, which he believed not to be thrown off with the sporangium.

In 1861 Coemans issued his "Monographie du genre Pilobolus," in which he summarised what he had read about this subject, and

[1] I figured them in my Monograph (1884), pl. 4, f. 12.

gave a list of all the species referred by other authors to this genus. He considered *P. crystallinus* and *P. oedipus* (Fig. 104, p. 209) to be the only certain species; *P. roridus* he regarded as doubtful, *P. lentiger* he refers, wrongly, to *P. oedipus*, and *P. anomalus* he places in the genus Ascophora by the name of *A. Cesatii*.

In 1871 Cooke published the Handbook of British Fungi, but, though he mentions the two conventional species, *P. crystallinus* and *P. roridus*, it is impossible to recognise exactly what he means by the names.

It was in 1872 that Klein (after a short note in 1870) gave to the world his monograph "Zur Kenntniss des Pilobolus," a monument of patient and minute investigation. In this he describes two species, "*P. crystallinus*" and "*P. microsporus*"; under the former name he says that he unites the *P. crystallinus* and *P. oedipus* of former authors. But, though he records his painstaking observations with great accuracy, in respect of the identification of his specimens Klein was peculiarly unfortunate. His *P. microsporus* is identical with *P. roridus*, and he was unacquainted with either the true *crystallinus* or the true *oedipus*. He had before his eyes, without knowing it, another species hitherto undistinguished, to which van Tieghem afterwards gave in his honour the name of *Pilobolus Kleinii*. The spores of *P. oedipus* are yellow, nearly spherical, and surrounded by a thickened epispore; those of *P. crystallinus* are ellipsoidal and nearly colourless. Now those of *P. Kleinii* are also ellipsoidal, but of an orange-yellow colour and twice as long as those of *P. crystallinus*; in certain circumstances, however, *P. Kleinii* bears sporangia containing nearly spherical spores of the same colour but without a thickened epispore. It was this abnormal state, to which I gave in my monograph of the Pilobolidae the name *forma sphaerospora*, that led Klein erroneously to imagine that he had met with forms intermediate between *oedipus* and *crystallinus*. The credit of clearing up this mistake was due to van Tieghem (1876).

In my own cultures, on many occasions, I found that the first two or three days' crops of *P. Kleinii* bore small sporangia, containing roundish spores, of unequal size in the same sporangium. These, however, could be distinguished at once by the want of the thickened

epispore from those of *P. oedipus*, and, moreover, the fungus agreed in all other respects but its minuteness with the true *Kleinii* into which it gradually passed on the following days. It would seem likely that the inequality of the spores in the same sporangium, together with the dwarfed size, was due to the fact that the fungus had not yet established itself, and was of weak and uncertain growth, like some of the dwarf forms of Coprinus.

Brefeld, in 1872, in his Untersuchungen über Pilze mentions and figures a species which he assigns to the genus Pilobolus, under the name *P. Mucedo*, but afterwards (1881) he discovered this to be, in part at least, the same as that previously called by Cesati *P. anomalus*. In the same work (1881) he gives a short account of the other species assigned by him to Pilobolus, but not one of the names he uses is that to which the species is entitled, as will be seen by the following list: his

P. crystallinus (Fig. 99, A)	= *P. Kleinii* van Tiegh.
P. oedipus (Fig. 102)	= *P. Kleinii*, forma *sphaerospora* Gr.
P. microsporus (Fig. 99, B)	= *P. crystallinus* Tode.
P. roridus	= *P. longipes* van Tiegh. (Fig. 100)

Brefeld, however, like van Tieghem, observed zygospores in *Pilobolus anomalus* (= *Pilaira anomala*). He found them on horse dung.

It will be seen that in "this strange eventful history" nearly every author seemed to be fated to misunderstand in some degree the opinions of those who had preceded him. It was not until 1875 that van Tieghem succeeded in clearing up the confusion in which the subject had been plunged, especially in relation to the *Mucor roridus* of Bolton. Bolton expressly describes his species (Fig. 98, p. 193), which he had found in the neighbourhood of Halifax, as "four lines high, pellucid and white, sustaining a small globular head, like a minute pearly drop, with a black spot on its upper part, which gives to the globe the resemblance of an eye in miniature." No other author but Klein had been able, up to this time, to meet with a species answering to this description, and hence it was doubted by some, as by Persoon, Coemans, Greville, and Purton, whether it was really distinct; Klein, as has been said, failed to recognise it in his *microsporus*, and it was reserved for van Tieghem

to describe and figure (Fig. 101, p. 204) a form which possibly is that which Bolton had found, and which is as similar as may be to Klein's *microsporus*. The long slender stem, the rounded subsporangial swelling, the minute sporangia, and the want of colour of van Tieghem's species, all point in this direction and agree pretty well with Bolton's figure. But it must be admitted that, since Bolton does not describe the spores, a certain amount of doubt must always attend any identification of his species; it would, perhaps, be better to quote *P. roridus* van T. rather than *P. roridus* (Bolt.).

In the same memoir (1875) van Tieghem also instituted the new genus Pilaira for the reception of the old *Pilobolus anomalus* of Cesati, and added a new species *Pilaira nigrescens* (Fig. 108, p. 218). He also discovered the zygospores of *P. anomala* (Fig. 107, p. 217).

In 1876 van Tieghem completed his work by publishing the descriptions of two new species, *P. longipes* (Fig. 100, p. 203) and *P. nanus* (Fig. 106, p. 212), while at the same time he pointed out the error which Klein had made and bestowed the name of *P. Kleinii* on the species with which Klein had worked. He also described the chlamydospores of *P. nanus* (Fig. 106, p. 212), a mode of reproduction which had already been signalised by Roze and Cornu (1871) in *P. crystallinus*.

Bainier, in 1882, published his "Étude sur les Mucorinées," in which he described specimens he had met with of *P. longipes*, *P. oedipus*, *P. Kleinii*, *P. roridus*, as well as a supposed new species, *P. exiguus*; he also confirmed van Tieghem's account of *Pilaira nigrescens*.

In 1884 my "Monograph of the Pilobolidae" was published in the Midland Naturalist, Birmingham, in which there was added to the hitherto known species the curious form of *Pilobolus Kleinii* to which, as already mentioned, the name forma *sphaerospora* was affixed. A new species of Pilaira was also described, to which the name *P. dimidiata* (Fig. 109, p. 218) was given on account of its possessing an apophysis nearly as large as its sporangium; unfortunately this has never been met with since, although at the time of publication such a sequel was not imagined possible.

Dewèvre, in 1894, included a good account of the species of Pilobolus in his "Contribution à l'Étude des Mucorinées." He

emphasised the distinction of *P. crystallinus* from *P. Kleinii*, with both of which he was personally acquainted.

Palla, after that date, issued a long account "Zur Kenntniss der Pilobolus-Arten" (1900), in which he classified the known species in a novel way, but without adding much to what was previously discovered; he also invented a new name, *Pilobolus heterosporus* (Fig. 103, p. 208), which was my *P. Kleinii*, forma *sphaerospora*, under a different designation.

In the same year (1900), Morini gave a short description, without a name, of a new species of Pilobolus, to which afterwards (1905) Saccardo added the name *P. Morinii*. In 1906, Morini described another species of Pilobolus, *P. Borzianus*, of which he also discovered the zygospores, and in 1904 he had figured a new species of Pilaira, *P. Saccardiana* (Fig. 110, p. 219). But *Pilobolus Morinii* and *P. Borzianus* seem to be involved in a cloud of doubt, as do many of the others, like those of Spegazzini and Massee, which are placed towards the end of the following systematic lists.

In 1926 Ling Yong, working in France, described a new species of Pilaira, which he named *P. Moreaui* (Fig. 111, p. 220), distinguished from *P. anomala* by its larger spores.

The latest addition to our knowledge of the species of Pilobolus has been made by Buller who, in the preceding chapter of this volume, has described *P. umbonatus*, a new species distinguished by the possession of a remarkably umbonate sporangium (Fig. 105, p. 210).

This long story of the observations made on the systematics of Pilobolus during nearly two hundred and fifty years is deeply interesting to the mycologist; it shows how slowly and painfully a little accurate knowledge has been accumulated. From now on, with the modern technique of pure cultures and the art of photography at our disposal, progress should be more rapid. It is to be hoped that some younger mycologist may be stimulated by this presentation of the subject to make a life-study of the genus and give us a comparative description of all the species that can be gathered together from different parts of the world.

Systematic Arrangement.—An attempt will now be made to arrange systematically all the species of the Pilobolidae and to give

to the group itself and to the two genera Pilobolus and Pilaira included within it more precise definitions than have yet appeared.

PILOBOLIDAE

A family of the Mucoraceae having a sporangium which contains a mass of dense jelly around its base between the sporangium-wall and the spore-mass. At maturity the mass of jelly swells up and causes the sporangium to dehisce near its base, so that the jelly protrudes between the sporangium-wall and the columella. The sporangium-wall is usually intensely black and is persistent when immersed in water.

Pilobolus Tode, in Schrift. d. Berl. Gesell. naturf. Fr., vol. v, p. 46 (1784).

Fruit-body consisting of a sporangiophore and a sporangium. Sporangiophore seated on a main mycelial hypha, from which it is separated by one or two septa. From below upwards, it is composed of a basal swelling or trophocyst, a cylindrical stipe, and a more or less ovoid subsporangial swelling, and when young it is generally ornamented by beads of moisture. Sporangium usually jet-black, seated on the apex of the subsporangial swelling, separated from it by a columella, and having its wall highly cutinised and persistent when immersed in water. When mature the sporangium and columella are violently projected. The species usually occur on the dung of herbivorous animals.

A. *Sporangium black when mature ; no apophysis.*

1. P. crystallinus.
2. P. longipes.
3. P. roridus.
4. P. Kleinii
5. P. sphaerosporus.
6. P. heterosporus.
7. P. oedipus.
8. P. umbonatus.

B. *Sporangium yellow when projected ; provided with an apophysis.*

9. P. nanus.

All these species have been adequately described and figured, and (whether they are truly distinct from one another or not) may

be recognised with certainty. After them are placed others which have been insufficiently or negligently described, and which are possibly nothing but variants of some of the preceding species :

Doubtful Species

10. P. Morinii.
11. P. Borzianus.
12. P. argentinus.
13. P. roseus.
14. P. minutus.
15. P. pullus.
16. P. Schmidtii.

Key to the Species of Pilobolus

	Sporangium decidedly umbonate . . .	*umbonatus*
	Sporangium rounded above	1
1	Trophocyst much elongated . . .	*longipes*
	Trophocyst ovoid or turnip-shaped . .	2
2	Spores globose and ellipsoid in the same sporangium	*heterosporus*
	Spores globose or subglobose only . .	3
	Spores ellipsoid only	5
3	Spores with two coats	*oedipus*
	Spores with only one coat	4
4	Sporangium yellow when projected . .	*nanus*
	Sporangium black when projected. . .	*sphaerosporus*
5	Spores from 10 μ upwards in length . .	*Kleinii*
	Spores averaging less than 10 μ in length .	6
6	Spores 5–10 × 4–6 μ ; sporangium large .	*crystallinus*
	Spores 6–8 × 3–4 μ ; sporangium small .	*roridus*

(Probably *crystallinus* and *roridus* are merely forms of one species.)

A. *Sporangium black when mature ; no apophysis.*

1. **Pilobolus crystallinus** Tode, *l.c.* p. 46, pl. 1 (1784). Van Tieghem, *Trois. Mém.* in Ann. Sci. Nat. ser. 6, vol. iv, pp. 335–8, pl. 10, f. 4, 5, repeated from Bull. Soc. Bot. Fr. vol. xxii, pp. 283–4

(1875). Coemans, *Monographie*, pp. 57–8, pl. 2, f. 1–20. Sacc. Syll. vii. 185. Grove, *Pilobolidae*, p. 333 (p. 33 of Reprint), pl. 4, f. 16. Palla, *Zur Kenntniss der Pilobolus-Arten*, p. 399.

Mucor urceolatus Dickson, *Fasc. Pl. Crypt.* part 1, p. 25, pl. 3, f. 6 (1785). Sowerby, *English Fungi*, pl. 300. Bolton's figure under this name (*Fung. Halif.* pl. 133, f. 1) is doubtful.

Pilobolus urceolatus Purton, *Midland Flora*, vol. iii, p. 323, pl. 31 (1821).

P. microsporus Brefeld, *Botan. Untersuch.*, part 4, p. 70, pl. 4, f. 16, 19–22 (1881).

Not *P. crystallinus* of Bonorden, or of Cohn, or of Klein, or of Brefeld, or of many others.

Sporangiophore 5–12 mm. high, or even up to 2 cm., rising usually from a single, more or less erect, terminal, ovate trophocyst, which is often concealed in the substratum; occasionally the trophocyst may be intercalary. Subsporangial swelling ovoid or elliptic-ovoid, about 1 mm. high, 600–800 μ broad. Sporangium convex above, from half as wide to nearly as wide as the subsporangial swelling, usually 350–500 μ in width; columella conical, faintly blackish-blue; spores ellipsoid, pale yellowish or quite colourless, 5–10 μ long (8–10 × 5–6 μ, van T.; 5–12 × 3–6 μ, Palla; 6 × 4·7 μ, Brefeld; 7–11 × 4·5–7, Dewèvre).

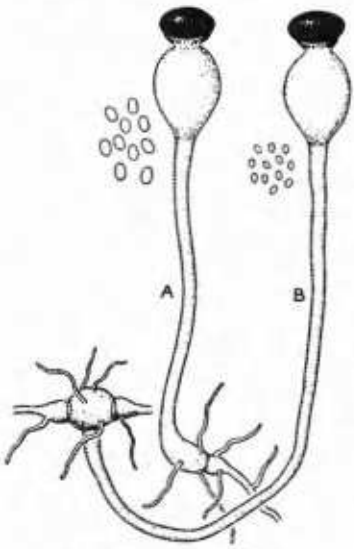

FIG. 99.—Ripe fruit-body and spores: A, *Pilobolus Kleinii* (= Brefeld's *P. crystallinus*); B, *Pilobolus crystallinus* (= Brefeld's *P. microsporus*). Copied by A. H. R. Buller from Brefeld's *Untersuchungen*. Magnification: fruit-bodies, 20; spores, 200.

Zygospores subglobose, 140–200 μ in diameter, nearly smooth, faintly coloured, filled with oil-drops (Krafczyk. in Ber. d. D. Bot. Gesell. 1931, p. 145, f. 2). Apparently not quite mature.

On dung of cows, horses, and the like. Reputed common. Europe, North and South America, Porto Rico, etc. Not seen by Buller at Winnipeg.

The upper cutinised part of the sporangium, when it is dried up, is sometimes marked with a few polygonal reticulations (one central);

but the reticulations are not always so geometrical as van Tieghem represents them, and they can be found also in other species.

Illustration : 99, B.

2. **Pilobolus longipes** van Tiegh. *Trois. Mém.* in Ann. Sci. Nat. ser. 6, vol. iv, pp. 338–340, pl. 10, f. 11–15 (1876), repeated from Bull. Soc. Bot. Fr. vol. xxii. pp. 283–4 (1875). Grove, *Pilobolidae*, p. 335, pl. 6, f. 1. Sacc. Syll. vii. 185. Palla, *l.c.* p. 399.

P. roridus Brefeld, in Bot. Zeit. 1875, p. 852 ; *Botan. Untersuch.* part 4, p. 70, pl. 4, f. 17.

Sporangiophore 2–3 cm. high, sometimes 4–5 cm. or even 6–7 cm. ; trophocyst usually external to the substratum, elongated horizontally, 1·5–2 mm. long, golden-yellow, almost cylindrical or slightly tapering, giving rise to the stipe at one end. Subsporangial swelling oval, rather less than 1 mm. broad. Sporangium globose, black, about 500 μ across ; columella broadly conical, tinged with bluish-black ; spores globose or ovoid, 12–15 × 10–12 μ, the wall rather thick and tinged (often very faintly) with bluish-black, contents yellow-orange.

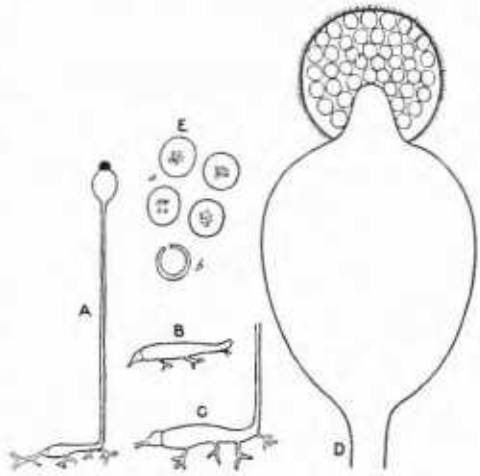

FIG. 100.—*Pilobolus longipes* v. Tiegh. A, whole fruit-body. B, trophocyst. C, basal swelling and part of stipe. D, upper part of fruit-body enlarged. E, spores : *a*, intact ; *b*, broken open. Reproduced by photography from van Tieghem's *Troisième Mémoire*.

On dung of horses. Europe, Canada, U.S.A.

Distinguished by its large roundish spores, its elongated trophocyst, and its height.

Illustration : Fig. 100. Other illustrations in this volume : Figs. 18, 24, 40, 57, 70, 82, 83, 85, 91, and 96.

3. **Pilobolus roridus** (Bolt.) Pers. *Syn. meth.* p. 118 (1801). Coemans. *Monographie*, pp. 61–2, pl. 2, f. B. (copied from Bolton). Van Tiegh. *Nouv. Rech.* Nat. in Ann. Sci. ser. 6, vol. i, pp. 46–50, pl. 1, f. 7–13. Grove, *Pilobolidae*, p. 336. Sacc. Syll. vii. 185. Palla, *l.c.* p. 398.

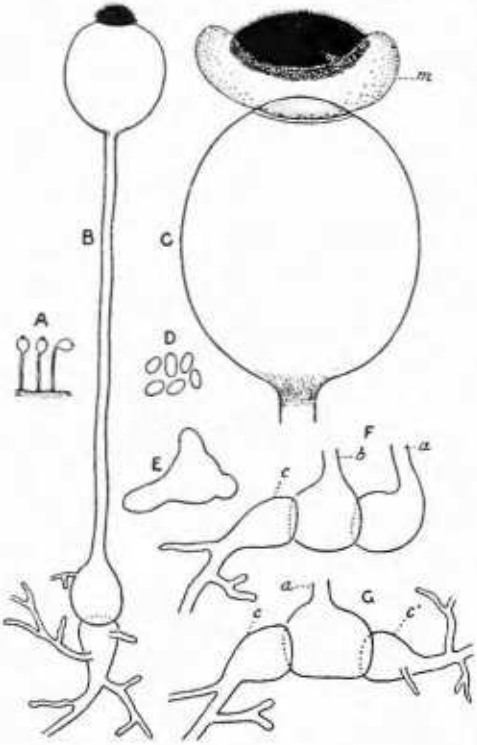

FIG. 101.—*Pilobolus roridus* (Bolt.) Pers. A, three fruit-bodies. B, whole fruit-body, shortened. C, upper part of fruit-body after sporangium has dehisced in water; *m*, mucilage. D, spores. E, germinating spore. F, two basal swellings, *a* and *b*, inserted successively on the same apophysis *c*. G, an intercalary basal swelling *a* formed between two apophyses, *c* and *c'*. Copied by A. H. R. Buller from van Tieghem's *Nouvelles Recherches*. Magnification: A, natural size; B, 25; C, 65; D and E, 380; F and G, 50.

Mucor roridus Bolton, *Fung. Halif.* vol. iii, pl. 132, f. 4 (1789).

Pilobolus microsporus Klein, *Zur Kenntniss des Pilob.* in Jahrb. f. wiss. Bot. vol. viii, p. 360, pl. 27, 28, f. 53–67 (1872).

Not *P. roridus* of Brefeld, or of Currey, or of many others.

Sporangiophore 1–2 cm. high, nearly colourless, the trophocyst often intercalary between two (or even three) mycelial swellings. Subsporangial swelling oval or almost globose, up to 600 or 700 μ diam. Sporangium very much less in diameter, even as little as 200 μ; columella flatly convex or conical, tinged with bluish-black; spores ellipsoid, nearly colourless, 6–8 × 3–4 μ (van T.).

On dung of herbivorous animals, including rabbits. Not common. Distribution uncertain.

This species shows generally much less of the yellow colour

(carotin) than its allies; but there has been in most cases considerable doubt whether the plants entered under this name were anything but forms of *P. crystallinus*. The chief points which are supposed to characterise the species are the smallness of the spores and of the sporangium. The "dew-drops" which are implied in the name *roridus* are to be found in suitable circumstances in equal abundance on other species. It tends to excite our suspicions when we find authors recording the occurrence of *P. roridus* in company with *P. crystallinus*.

Illustration: Fig. 101.

4. **Pilobolus Kleinii** van Tiegh. *Trois. Mém.* in Ann. Sci. Nat. ser. 6, vol. iv, pp. 337–8, pl. 10, f. 6–10 (1876), repeated from Bull. Soc. Bot. Fr. vol. xxii, pp. 282–3 (1875). Grove, *Pilobolidae*, p. 335, pl. 4, f. 1–8, 10–13, and in Journ. Bot. 1884, p. 131, pl. 245, f. 4. Sacc. Syll. vii. 185. Bainier, *Étude*, p. 43, pl. 2, f. 14, 15. Palla, *l.c.* p. 399.

P. roridus Currey, in Journ. Linn. Soc. Lond. Bot. vol. i, pp. 162–7, pl. 2, f. 1–10 (1857). Not *M. roridus* Bolton.

P. crystallinus Klein, *Zur Kenntniss des Pilobol.* in Jahrb. f. wiss. Bot. vol. viii, p. 360, pl. 23–7, f. 1–52. Brefeld, *Botan. Untersuch.* part 4, p. 70, pl. 4, f. 15. Zopf, *Zur Kenntniss der Infectionskrankheiten*, p. 354. Not of Tode.

P. Kleinii var. *minor* Dewèvre, in Grevillea, vol. xxii, p. 74 (only 1 mm. high).

Sporangiophore 2–5 mm. high, varying up to 10–12 mm. high, rising singly from a turnip-shaped trophocyst which is often buried in the substratum. Subsporangial swelling obovoid or subellipsoid, 400–800 μ high. Sporangium black, more or less depressed or subglobose, about two-thirds as wide as the swelling to nearly as wide; columella sometimes with a faint blackish tinge, generally colourless, broadly conical below, but occasionally narrowed in the middle so that the apex resembles a papilla; spores in varying shades of orange-yellow, ellipsoid, 11–20 × 6–10 μ, with a thin smooth colourless cell-wall.

Zygospores thick-walled, spherical, nearly smooth, about 200 μ diam. (Zopf, *l.c.* pl. 6, f. 8–19).

On all kinds of dung. Very common. Europe, E. Africa, Canada, U.S.A., etc.

This appears to be the commonest species in Europe, and perhaps in most countries where Pilobolus occurs. It has often been confounded with *P. crystallinus*, but is not so high, is more tinged with yellow, the thickened band of protoplasm at the top of the stipe is more brightly orange, and its spores, although of the same shape, are perceptibly larger. Trophocysts usually with a single apophysis, rarely with two.

Illustration: Fig. 99, A. Other illustrations in this volume: Figs. 2, 12, 13, 22, 27, 28, 29, 32, 39, 42, 46, 61, 62, 83, 86, 91, 94, and 95.

5. **Pilobolus sphaerosporus** Palla, *Zur Kenntniss der Pilobolus-Arten*, in Oesterr. Bot. Zeitschr. vol. 50, p. 400, pl. 10 (1900).

Pilobolus lentiger Corda, *Icon. Fung.* vol. i, p. 22, pl. 6, f. 286 (1837), including var. *macrosporus* Berl. & de Toni, in Sacc. Syll. vii. 188 (1888).

Pycnopodium lentigerum Corda, *ibid.* vol. v, p. 18 (1842), an ill-nourished form.

Pilobolus crystallinus Bonord. *Handb.* p. 128, pl. 10, f. 203 (1851).

P. oedipus, var. *intermedia*, Coemans, *Spic. Mycol.* in Bull. Acad. Belg. ser. 2, vol. xvi, p. 71 (1863).

P. crystallinus (*P. oedipus*, forms *b* and *c*) Klein, *Zur Kenntniss des Pilobol.*, p. 360, pl. 26, f. 40 *b*, 46–8; pl. 27, f. 49, 50 (1872).

P. intermedius (Coem.) Karst. *Myc. Fenn.* part 4, p. 71 (1879).

P. oedipus Brefeld, *Botan. Untersuch.* part 4, p. 69, pl. 3, f. 1–10; pl. 4, f. 11–14 (1881).

P. exiguus Bainier, *Étude*, p. 47, pl. 2, f. 17 (1882).

P. Kleinii, forma *sphaerospora*, Grove, in Journ. Bot., vol. xxii, p. 132, pl. 245, f. 5 (1884); *Pilobolidae*, p. 335, pl. 4, f. 9.

Similar to *P. Kleinii*, but usually smaller. Spores yellow or orange, more or less globose, 10–20 μ in diam., varying greatly in size, often with granular contents, diffusing very easily in water, and having a thin wall composed of only one coat.

On dung of man, horse, cow, etc. Europe.

The spores vary considerably in size. I have always found this in company with *P. Kleinii* at the beginning of its growth in a culture, but changing and passing gradually into the normal form.

Palla (*l.c.*) says that this appearance is due to the growth of the two species in a mixed (impure) culture, but that *P. sphaerosporus* produces its fruit-bodies from one to several days before those of *P. Kleinii* show themselves. I do not entirely agree with this; it does not explain the transition stages, which may always be found on looking for them, like those represented by Coemans' *intermedia* and Klein's variety *c* of his *P. crystallinus*, where both ellipsoid and round spores may be seen in the same sporangium.

Illustration: Fig. 102. The figure here given, from Brefeld's Untersuchungen, is called by him *P. oedipus*; it is not that species, but exactly represents my *P. Kleinii* forma *sphaerospora*.

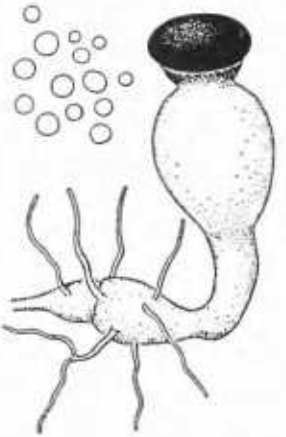

FIG. 102.—*Pilobolus sphaerosporus* Palla. Fruit-body and spores. Copied by A. H. R. Buller from Brefeld's *Untersuchungen* (his *P. oedipus*) and enlarged by one-third. Magnification, 40 and 400.

6. **Pilobolus heterosporus** Palla, *Zur Kenntniss der Pilobolus-Arten*, in Oesterr. Bot. Zeitschr. vol. 50, p. 349, pl. 10, f. 1–5 (1900); a *Résumé* of this article, with plates and descriptions, is given by R. Ferry in Revue Mycologique, 1904, pp. 19–33.

Sporangiophore 2–3 mm. high; trophocyst usually buried in the substratum, ellipsoid, rarely globose, 300–400 μ long. Subsporangial swelling ovoid or ellipsoid, 500–600 μ high, provided at the insertion of the columella with a thin narrow annular zone. Sporangium shaped like a convex cap, deep-black, 400 μ broad; columella more or less deeply constricted in the middle, rounded at the apex, reaching nearly to the top of the sporangium; spores yellow or orange-red, varying in form and size in the same sporangium, narrow- or roundish-ellipsoid, with all intermediate forms, 8–20 (or even 25) μ long, and 6–12 μ broad.

On cow dung, Graz (Styria).

I have drawn up this description from Palla's rambling and diffuse account as given in his article. Palla says that he

cultivated his species, and found that it retained its characters up to fifteen generations. But it is in no way different from my forma *sphaerospora* of *Pilobolus Kleinii*. The irregularity of the spores is exactly what I found in my cultivations, and the retention of the characters may be due merely to the persistence of similar conditions throughout the whole series of his fifteen generations. If I am right in my opinion, the three species here numbered 4, 5, and 6 are all identical, and the variations in form are dependent upon the surrounding circumstances.

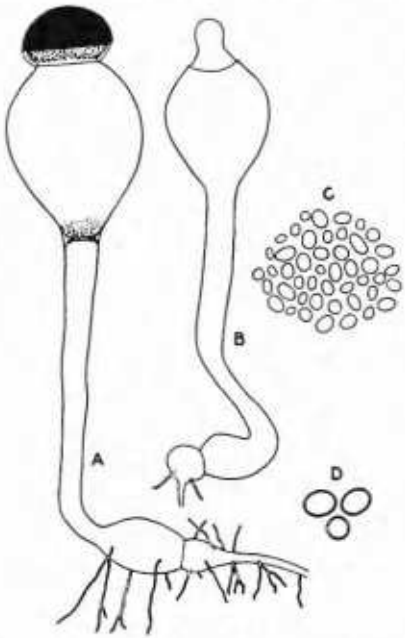

FIG. 103.—*Pilobolus heterosporus* Palla. A, fruit-body, after dehiscence of the sporangium. B, fruit-body, after removal of the sporangium, showing the columella. C and D, spores. Copied by A. H. R. Buller from Palla's *Zur Kenntniss der Pilobolus-Arten* and reduced to two-thirds. Magnification: A and B, 30; C, 214; D, 434.

Illustration: Fig. 103.

7. **Pilobolus oedipus** Mont. *Mémoire sur le genre Pilobolus*, in Ann. Soc. Linn. de Lyon, pp. 1–7, f. *a–i* (1828). Coemans, *Monographie*, pp. 59–60, pl. 1, f. 1–20. Grove, *Pilobolidae*, p. 308, pl. 4, f. 14–15; and in Journ. Bot. vol. xxii, p. 131, pl. 245, f. 3. Sacc. Syll. vii. 186. Palla, *l.c.*, p. 400. Bainier, *Étude*, pp. 43–4, pl. 2, f. 1–10.

P. crystallinus Cohn, *Entwicklungsgeschichte des Pilob. crystallinus*, with pl. 51, 52 (1851).

P. reticulatus van Tiegh. in Ann. Sci. Nat. ser. 6, vol. iv, p. 336.

Not the *P. oedipus* of Brefeld or of Klein, nor perhaps that of van Tieghem (*Nouv. Rech.* 1875, p. 43).

Sporangiophores yellow or reddish, usually short and thick, about 2–3 (or even 5) mm. high, rising singly from a roundish

trophocyst which projects somewhat above the substratum, but several of these are often so closely aggregated together that they form little tufts. Sporangium about 500 μ broad, not quite so broad as the ovoid subsporangial swelling, almost hemispherical, black; columella conical or subcylindrical, slightly narrowed in the middle, sometimes so high that it reaches almost to the top of the sporangium; spores globose, yellowish-red, 9–16 μ diam.; with a wall composed of two distinct layers, of which the outer (epispore) is thick and often bluish.

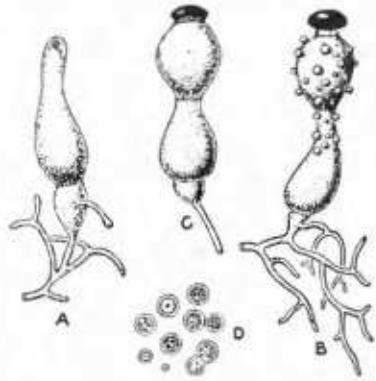

FIG. 104.—*Pilobolus oedipus* Montagne. A, young fruit-body. B, mature fruit-body. C, another mature fruit-body, with the sporangium more flattened than usual. D, spores. Copied by A. H. R. Buller from Coemans' *Monographie* and reduced to two-thirds. Magnification: A, 53; B and C, 40; D, 200.

On dung of horses, cows, pigs, goats, and mules; it has also been found on human excrement, and it often occurs on decaying vegetable substances such as Algae (Spirogyra, Conferva, Oscillaria, and so on), and therefore also on the mud of river-banks (Thames, Oder, Red River of Winnipeg, etc.). It has been suggested that perhaps its spores do not require to pass through the alimentary canal of an animal, but this seems unlikely, since in a discharged sporangium they adhere together just as in other species of Pilobolus. They germinate, however, easily in water. The name of this species should be spelled *oedipus* (adjectival), not *OEdipus*.

Europe, E. Africa, N. America. Its round thick-walled spores are characteristic, also the deep colour which it displays owing to the crowded visible trophocysts. Chlamydospores (*Mycogone anceps* Coem.), lying in the mycelium, globose or ovoid, orange-yellow, oily-granular, 20–30 μ in diameter, are assigned to this species by Coemans, and by Ellis, North American Fungi (no. 3360); these may be azygospores (*cf.* Fig. 106, G.).

Illustration: Fig. 104.

8. **Pilobolus umbonatus** Buller, in his Researches on Fungi, vol. VI, pp. 177–178, figs. 81–84, 87–91 (1934).

Fruit-body 3–9 mm. high, arising from an oval to turnip-shaped

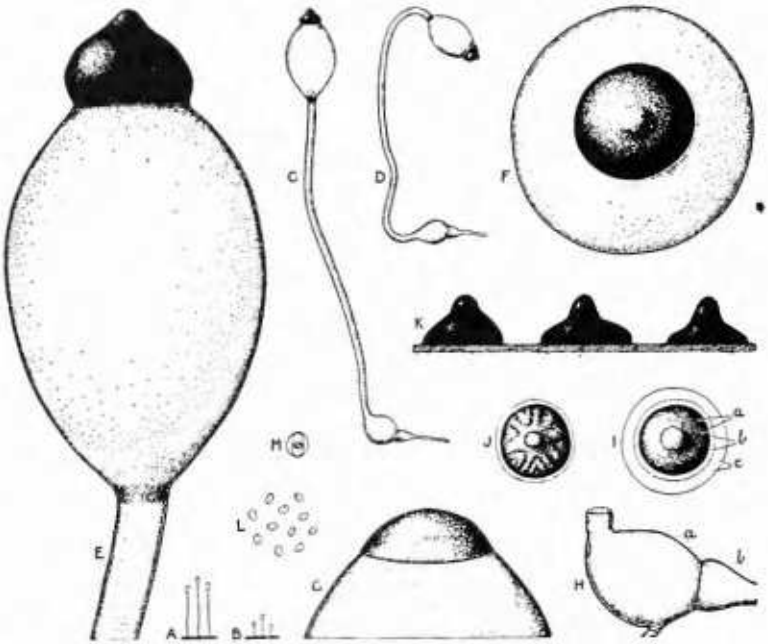

FIG. 105.—*Pilobolus umbonatus* Buller. A, well-grown fruit-bodies 7–8 mm. high. B, less well-grown fruit-bodies 1·5–3·0 mm. high. C and D, whole fruit-bodies, showing sporangium, subsporangial swelling, stipe, and basal swelling attached to an apophysis; C was 4 mm. high, and D 3·5 mm. high. E, the upper part of a fruit-body, showing the umbonate sporangium, the barrel-shaped subsporangial swelling, and part of the stipe. F, the same seen from above; ratio of width of sporangium to width of subsporangial swelling = $\frac{1}{2}$. G, the greyish columella, seen after removal of the sporangium from the top of the fruit-body. H, a basal swelling *a*, attached to an apophysis *b*. I, a discharged sporangium: *a*, the black sporangium-wall; *b*, the colourless fringe of the sporangium-wall; and *c*, adhesive jelly. J, a similar sporangium, but jelly is not shown: the surface of the sporangium-wall in I was smooth, in J wrinkled. K, three discharged and dried-up sporangia seen in lateral view. L, spores. M, diagram showing a spore of *P. umbonatus* enclosed by a spore of *P. Kleinii*, in turn enclosed by a spore of *P. longipes*. Drawn by A. H. R. Buller from material obtained at Winnipeg. The drawings C and D reproduced from pencil drawings made by Hans Ritter. Magnification: A and B, natural size; C and D, 15; E–K, 75; L and M, 255.

basal swelling or trophocyst which may be terminal or intercalary, single or dispersed at intervals along a coarse stolon-like main hypha.

Stipe increasing slightly in diameter from below upwards, until just beneath the subsporangial swelling it is about 0·1 mm. in diameter. Subsporangial swelling ellipsoid, its maximum diameter being about midway between the base of the sporangium and the top of the stipe, 0·65 mm. long and 0·46 mm. broad; a pale orange-red band of protoplasm at the junction of the stipe and the subsporangial swelling. Sporangium decidedly umbonate and more or less conical, 0·21–0·23 mm. in diameter or about one-half the diameter of the subsporangial swelling, shrinking on drying after discharge and becoming acutely pointed; columella very bluntly conical or rounded (when removed from a discharged sporangium its edge is turned inwards towards the axis), greyish, distinctly darker than the subsporangial swelling. Spores ellipsoid, singly almost colourless, but yellow in mass, 5·0–6·0 × 3·0–3·8 μ.

On horse dung, Winnipeg, Canada, and, according to a communication from the late Dr. Roland Thaxter (who observed the species forty years ago but did not describe it), more frequently on sheep dung, at Boston, U.S.A.

Easily distinguished from all other species of Pilobolus by its decidedly umbonate sporangium and its minute ellipsoidal spores. With a hand-lens one can readily make out the acutely-pointed umbonate shape of the dried discharged sporangia when these are seen in lateral view.

Illustration: Fig. 105. Other illustrations in this volume: Figs. 81, 82, 83, 84, 87, 88, 89, 90, and 91.

B. *Sporangium yellow when projected; provided with an apophysis.*[1]

9. **Pilobolus nanus** van Tiegh. *Trois. Mém.* in Ann. Sci. Nat. ser. 6, vol. iv, pp. 340–2, pl. 10, f. 16–22 (1876). Grove, *Pilobolidae*, p. 336, pl. 6, f. 2. Sacc. Syll. vii. 186. Palla, *Lc.*, p. 398.

[1] In most Piloboli, the subsporangial swelling is not constricted below the level of its attachment to the columella and the wall of the sporangium. In *P. nanus*, according to van Tieghem, the subsporangial swelling is constricted a short way below that level so that it is divided into two unequal parts, a lower globular subsporangial swelling proper and an upper shallower swelling—the so-called *apophysis*.

Sporangiophores erect, not more than 1 mm. high, collected into groups of two or three (even four or five), all rising from contiguous buried intercalary trophocysts. Subsporangial swelling subglobose, colourless. Sporangium globular, about as wide as the subsporangial swelling, with the membrane of the upper part cutinised and

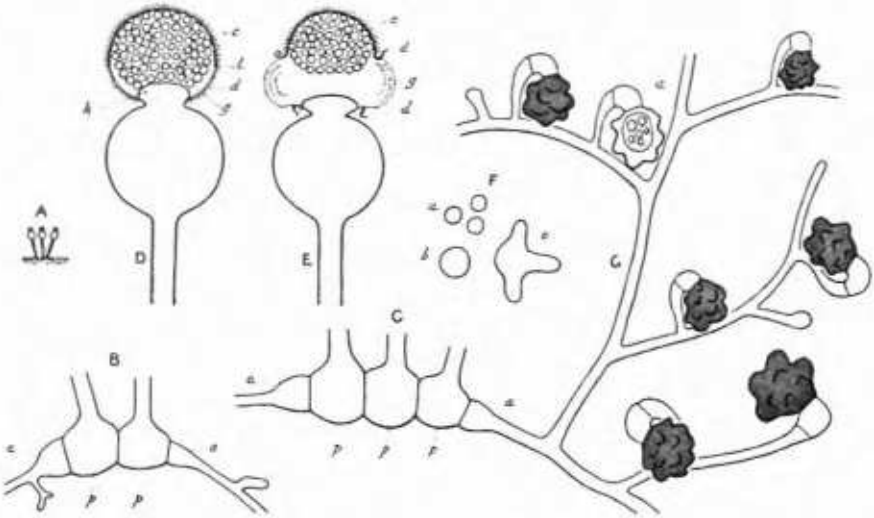

FIG. 106.—*Piloboluus nanus* v. Tiegh. A, three fruit-bodies. B, two basal swellings *p p*, and C, three basal swellings *p p p*, between two apophyses *a a*. D and E, optical sections through the upper part of a fruit-body, before and after dehiscence of the sporangium respectively; *c*, yellow cuticularised wall of the sporangium; *d*, diffluent region; *l*, limiting ring of cuticularisation; *g*, jelly; *k*, columella. F, spores: *a*, resting; *b*, swollen; *c*, germinating. G, resting spores (azygospores), with tuberculate membranes, on a mycelium; *a*, in section to show the thick cell-wall. Copied by A. H. R. Buller from van Tieghem's *Troisième Mémoire*. Magnification, not given.

yellow; columella depressed-convex; spores globose, colourless, 3·5–4 μ in diameter.

On excrement of rat. France.

Not observed by anyone but van Tieghem. The protoplasm of the sporangiophores is said by him to be colourless, as is also that of the mycelium. On the mycelium grew oblong-roundish, faintly yellow, coarsely verrucose chlamydospores, 15–20 μ in diameter, resting on short curved pedicels; these are probably azygospores. The sporangia were shot off as in other Piloboli and stuck to the surrounding objects, while still yellow. When the explosion took

place, the rupture occurred at the constriction between the apophysis and the subsporangial swelling.

There is a possibility that this species is an abnormal form due to the unfavourable environment in which it was growing. Sporangia with defective black pigment in their walls have been observed by van Tieghem himself in his *P. oedipus* and by Buller in *P. longipes* (*vide* these *Researches*, vol. iv, p. 9, and this volume, p. 54).

Illustration : Fig. 106.

Insufficiently known Species

10. **Pilobolus Morinii** Sacc. Syll. xvii. 505 (1905).

Pilobolus sp. Morini, in Mem. Accad. Sci. Ist. Bologna, ser. 5, vol. viii, p. 85, with plate (1899–1900).

Sporangiophores solitary, 600–800 μ high, each rising from an erect ovoid trophocyst. Subsporangial swelling subglobose or ovoid, somewhat narrowed above, and attenuated below into the sporangiophore, almost colourless when mature. Sporangium globular, somewhat flattened above, black, 130–200 μ in diameter ; columella obtusely conical, colourless, rounded above ; spores globose, orange-yellow (not colourless), 4·5–6 μ in diameter.

On dry human excrement. Montese, Bologna, Italy. Resembling *P. manus* van Tiegh., except for its black sporangium and its sporangiophores not arising in groups.

11. **Pilobolus Borzianus** Morini, in Mem. Accad. Sci. Ist. Bologna, ser. 6, vol. iii, p. 126 (or 396), f. 3–10 (1906). Sacc. Syll. xxi. 827.

Sporangiophores 2·4–5 mm. high, growing two or three together from one trophocyst, which is ovoid and often imperfectly developed. Subsporangial swelling globose or shortly ovoid, 200–360 μ high, almost colourless or quite hyaline. Sporangium globose, very much flattened from above, 160–250 μ wide, intense bluish-black ; columella hemispherical or shortly conical, without apophysis ; spores spherical, deep yellow, 16–23 μ in diameter. Oval chlamydospores are developed in the mycelium.

Zygospores black, globose, about 180 μ across, with a thick and glabrous epispore (Morini, *l.c.* f. 3, 9).

On dung in the north of Italy.

Morini (in Mem. Accad. Sci. Ist. Bologna, ser. 6, vol. vi, pp. 123–4, f. 6–8, 1909) describes a var. *geminata* of this species. He says that the trophocyst may produce two hyphae at a time or, if one only, the one may branch into two above. He asserts that these forms remained constant in repeated artificial cultures. I suspect that the var. *geminata* is nothing more than an abnormal form; for, since normally a Pilobolus sporangiophore collapses at the moment of discharging its sporangium, a forked sporangiophore can shoot away only one of its sporangia and not both. Abnormal branched sporangiophores are occasionally met with in other species, and are figured by Coemans in *P. crystallinus*, by Klein in *P. Kleinii* (his *P. crystallinus*), and have been seen by Zopf and Grove also in *P. Kleinii*.

12. **Pilobolus argentinus** Spegazzini, *Fung. Argent.* I, p. 176 (1880). Sacc. Syll. vii. 187.

Sporangiophores "immersed," here and there densely gregarious, 5–6 mm. high, at first cylindric-clavate, then filiform below, with a trophocyst and an ellipsoid subsporangial swelling, the whole plant entirely yellow. Sporangium globose, 100–125 μ diam., olive-black above, greenish-yellow below; spores spherical, 12–15 μ diam., thick-walled, filled with a greenish-yellow granular protoplasm.

On horse dung, in grassy places alongside the Rio de la Plata. Judging by the description, one would consider this only a form of *P. oedipus*.

13. **Pilobolus roseus** Speg. *Fung. Argent.* I, p. 175 (1880). Sacc. Syll. vii. 187.

Sporangiophores densely gregarious, 2–4·5 mm. high, at first clavate, rosy-orange, truncate at the rounded apex, then filiform below, ellipsoid or ventricose-spheroid above, very beautifully rosy-hyaline. Sporangium black, hemispherical, 300–400 μ diam.; spores ellipsoid, obtusely rounded at the ends, granular within, rosy-hyaline, 12–16 × 7–8 μ.

On cow dung, near the Rio de la Plata. This species might well be merely a form of *P. Kleinii*; its chief distinction seems to reside in its colour, but a rosy hue is not unknown in some other species of Pilobolus.

14. **Pilobolus minutus** Speg. *Fung. Argent.* I, p. 176 (1880). Sacc. Syll. vii. 186.

Sporangiophores superficial, loosely gregarious, 2–5 mm. high, at first filiform-clavate, then ventricose and ellipsoid above, always hyaline, more or less elongated and filiform below. Sporangium black, lenticular, 125–145 μ diam.; spores spherical or ellipsoid, granular, hyaline or faintly greenish-yellow, 7–8 μ diam.

On cow dung, in shady places near the Rio de la Plata. This species may well be only *P. Kleinii* var. *minor* Dewèvre.

15. **Pilobolus pullus** Massee, in Kew Bulletin, 1901, p. 160. Sacc. Syll. xvii. 506.

Sporangiophore about 1 mm. high, nearly colourless, inflated and ventricose above. Sporangium depressed-hemispherical, black, smooth, 250–300 μ broad; columella convex, often constricted in the middle; spores ellipsoid, 10–12 × 8–9 μ, with an orange epispore.

On cow dung. Tasmania (Rodway). Perhaps akin to a form of *P. Kleinii*.

Petch, in recording a species under this name in Annals Roy. Gard. Peradeniya, vol. vii, part 4, p. 297, says: "Scattered; total height 0·6–0·8 mm., clavate, expanding almost from the base, 0·3 mm. diameter above. Sporangia oval, black, 0·25 × 0·15–0·2 mm.; wall black-brown, smooth, not areolated. Spores oval, pale-yellow, 8–10 × 5–6 μ.

"On cow dung, Hakgala, Ceylon, December, 1917."

16. **Pilobolus Schmidtii** Sacc. Syll. xxiv. 11 (1926). *Pilobolus* sp. Alf. Schmidt, in Jahresber. d. Schles. Gesell. xc. 19 (1912).

Sporangiophores standing singly; trophocyst ovoid, yellowish, 560–720 × 340–400 μ. Stipe 4 mm. high; subsporangial swelling ovoid, up to 1 mm. high, 640–800 μ broad; columella colourless, 250–370 μ high. Sporangium hemispherical, black, 430–510 μ broad; spores ellipsoid, thin-walled, yellow or yellowish, 6·5–8·5 × 5–6 μ, not diffusing readily in water.

On dung of mules. Reared at Breslau, Germany, on mule dung

brought from Amani, German East Africa. Allied to *P. Kleinii*, but differing in the dimensions of its parts.

Pilaira van Tieghem, *Nouv. Rech.* in Ann. Sci. Nat. ser. 6, vol. i, p. 51 (1875).

Fruit-body consisting of a sporangiophore and a sporangium. Sporangiophore arising from the mycelium without a septum at its base. It is evenly cylindrical and has no basal or subsporangial swelling. Sporangium black, separated from the sporangiophore by a columella, and having its wall highly cutinised and persistent when immersed in water. When mature the sporangiophore collapses and there is no projection of the sporangium. The species are all coprophilous.

Pilaira differs from Pilobolus in that its sporangiophore has no septum at the base, no basal swelling, and no subsporangial swelling, and in that its sporangium is not violently projected.

In 1930 Fitzpatrick, in his book on the Phycomycetes, suggested that the genus Pilaira is "based on abnormal material of Pilobolus." There can be no doubt that this view is erroneous. Not only van Tieghem and Brefeld but also Buller, I myself, and others have observed and cultivated the type of the genus, *Pilaira anomala*, and have found it to be quite distinct from any abnormal form of Pilobolus.

Five species of Pilaira are known. The key to them, given below, is founded on that of Ling Yong.

Key to the Species of Pilaira

1	Spores round	*nigrescens*
	Spores oval or elongated	1
	Sporangiophores branched	*Saccardiana*
	Sporangiophores simple	2
2	Sporangiophores only about 1 mm. high . .	*dimidiata*
	Sporangiophores up to 10 cm. high . . .	3
3	Spores oval, up to 10 μ long	*anomala*
	Spores elongated, up to 22 μ long . . .	*Moreaui*

1. **Pilaira anomala** (Ces.) Schröter, *Pilze*, in Cohn's Kryptogamen-Flora von Schlesien, vol. iii. p. 211 (1889). Sacc. Syll. vii. 188.

Pilobolus anomalus Cesati, in Klotzsch, *Herb. viv. mycol.*, no. 1542 (1851). Brefeld, *Botan. Untersuch.* part 4, pp. 60–5, pl. 4, f. 18, 23–28.
Ascophora Cesatii Coemans, *Monographie*, p. 63, pl. 2, f. E (1861).
Pilobolus Mucedo Brefeld, *Botan. Untersuch.* part 1, p. 27, pl. 1, f. 25, 26 (1872).
Pilaira Cesatii van Tiegh. in Ann. Sci. Nat. ser. 6, vol. i, p. 52, pl. 1, f. 14–24 (1875). Bainier, *Étude*, pp. 29–32, pl. 1, f. 16–18. Grove, in Journ. Bot., vol. xxii, p. 132, pl. 245, f. 6; *Pilobolidae*, p. 337, pl. 6, f. 7, 8.

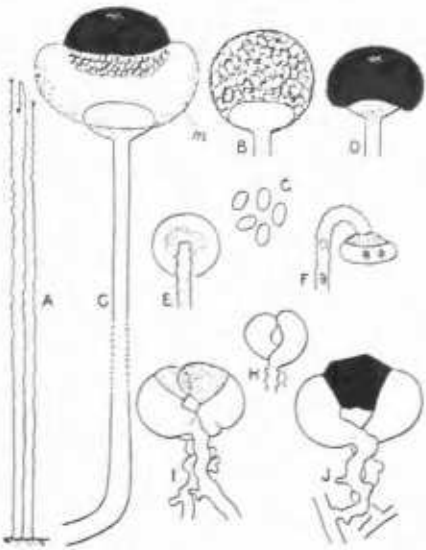

FIG. 107.—*Pilaira anomala* (Ces.) Schröter. A, three fruit-bodies, collapsing. B, longitudinal optical section of a sporangium. C, upper and lower part of a fruit-body, after the dehiscence of the sporangium; *m*, protruding mucilage. D, sporangium in air, before dehiscence. E, columella, seen from below, after the fall of the sporangium. F, a similar columella, in lateral view; there are crystalloids in both the stipe and columella. G, spores. H, I, and J, three successive stages in the formation of a zygospore. Copied by A. H. R. Buller from van Tieghem's *Nouvelles Recherches*. Magnification: A, natural size; B–F, 90; G, 380; H–J, 200.

Sporangiophore cylindrical, colourless, at first erect, 1–2 cm. high, then growing to a height of 9–12 (or even 20) cm., at length shrivelling and falling down on the substratum. Sporangium at first yellow, black when mature, more or less globular, 120–250 μ diam., then hemispherical with a small granular apophysis below; columella colourless, hemispherical, but somewhat depressed; spores ovoid, nearly colourless (but yellowish in mass), 8–12 × 6–7 μ.

Zygospores black, globose or ovoid, up to 115 μ diam., epispore covered with numerous minute papillae (Brefeld, *l.c.* part 4, f. 26–28).

On dung of sheep, goats, gazelles, hares, rabbits, goose, pig, ass, and horse. Europe, U.S.A. (Pennsylvania). Rather uncommon.

The zygospores were found by Brefeld on horse dung which had borne luxuriant crops of fruit bodies (*cf.* Fig. 107, H–J).

Illustration : Fig. 107.

2. **Pilaira nigrescens** van Tiegh. in Ann. Sci. Nat. ser. 6, vol. i, p. 60, pl. 1, f. 25–8 (1875). Grove, *Pilobolidae*, p. 337. Sacc. Syll. vii. 189.

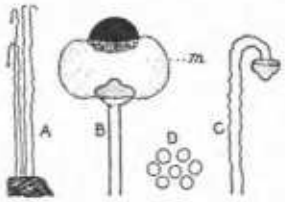

FIG. 108.—*Pilaira nigrescens* v. Tiegh. A, four fruit-bodies, collapsing. B, upper part of a fruit-body after dehiscence of the sporangium; *m*, protruding mucilage. C, upper part of a fruit-body after the fall of the sporangium. D, spores. Copied by A. H. R. Buller from van Tieghem's *Nouvelles Recherches*. Magnification : A, natural size; B and C, 90; D, 380.

Sporangiophore shorter than in the preceding species (1·5–2 cm.) and more slender. Sporangium also smaller, but having a similar granular apophysis ; columella blackish-violaceous or bluish, hemispherical, and ending in a conical papilla. Spores globose, colourless, 5–6 μ in diameter.

On dung of rabbit. France ; rare. Distinguished by its size, its spores, and its conical and coloured columella.

Illustration : Fig. 108.

3. **Pilaira dimidiata** Grove, in Journ. Bot. vol. xxii, p. 132, pl. 245, f. 7 *a–d* (1884) ; *Pilobolidae*, p. 338, pl. 6, f. 10 *a–c*. Sacc. Syll. vii. 189.

Sporangiophore slender, cylindrical, and while erect not more than 0·5–1·0 mm. high, then bending down towards the substratum and becoming 3–4 mm. long. Sporangium at first yellow, then black, hemispherical, 100–120 μ diam. ; immediately beneath it the sporangiophore is widened somewhat

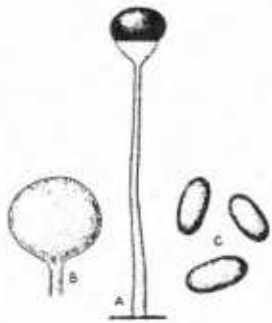

FIG. 109.—*Pilaira dimidiata* Grove. A, mature fruit-body. B, columella. C, spores. Drawn by A. H. R. Buller from sketches made by W. B. Grove in 1883 without the use of a *camera lucida*. *Cf.* Plate 245, Fig. 7, *a–d*, in Grove's *New or Noteworthy Fungi*, 1884. Magnification : A, 116 ; B, 240 ; C, 660.

like the apophysis of a moss-capsule (Funaria). Spores ellipsoid, almost colourless, 12–14 × 5–6 μ.

On dog's dung. England (Worcestershire); found only once, March and April. Distinguished from *Pilaira anomala* not only by its much smaller size, but also by its peculiar apophysis, which is almost as large as the sporangium, but slightly less in diameter, and not granular. It was growing luxuriantly on a rich substratum.

Illustration: Fig. 109.

4. **Pilaira Saccardiana** Morini, first mentioned in Rendic. Sess.

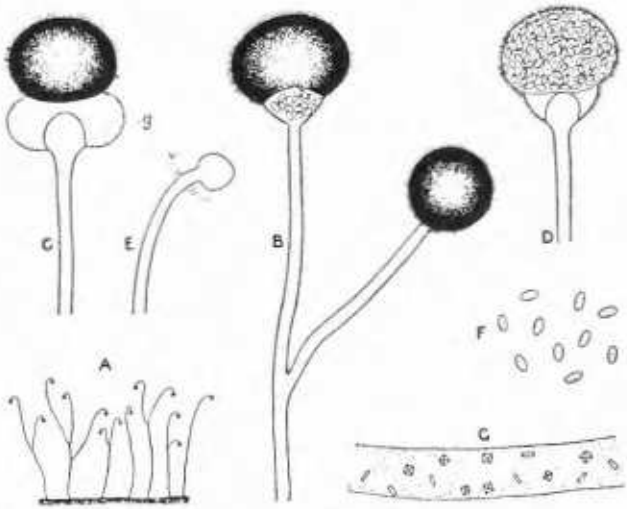

FIG. 110.—*Pilaira Saccardiana* Morini. A, fruit-bodies, sporangiophores branched: sporangia mature and now hanging down. B, a branched sporangiophore bearing two sporangia, one in side view and the other seen from above. C, a sporangium after dehiscence; *g*, swollen jelly. D, optical longitudinal section of a sporangium, showing the spores and the columella. E, the sporangium has gone; the columella remains and, about its base, can be seen a gelatinous substance derived from the liquefaction of the inferior zone of the sporangial membrane. F, spores. G, part of a sporangiophore whose sporangium had not yet ripened; in the protoplasm are numerous crystalloids of mucorine. Copied by A. H. R. Buller from Morini's *Ricerche intorno ad una nuova forma di Pilaira*. Magnification: A, natural size; B–G, not stated.

R. Accad. Sci. Ist. Bologna, 1904, with plate, and then named *P. Saccardiana* in Mem. R. Accad. Sci. Ist. Bologna, ser. 6, vol. iii, p. 128 (1906). Sacc. Syll. xxi. 827.

Sporangiophore rarely emerging from a rudimentary trophocyst (which is usually wanting), slender, simple or branched, with at most two branches. Sporangium globose, faintly depressed from above, 90–130 μ in transverse diameter, brown above, then blackish, lower zone not cutinised and forming a broad annulus of the membrane by the gelatinisation of which the spores are afterwards set free; columella shortly conical, deep-violet in colour; spores oval, 7–10 μ long, hyaline, but with a smooth pallid violaceous membrane.

On dung, in the north of Italy.

Illustration: Fig. 110.

5. **Pilaira Moreaui** Ling, in "Étude morphologique, cytologique

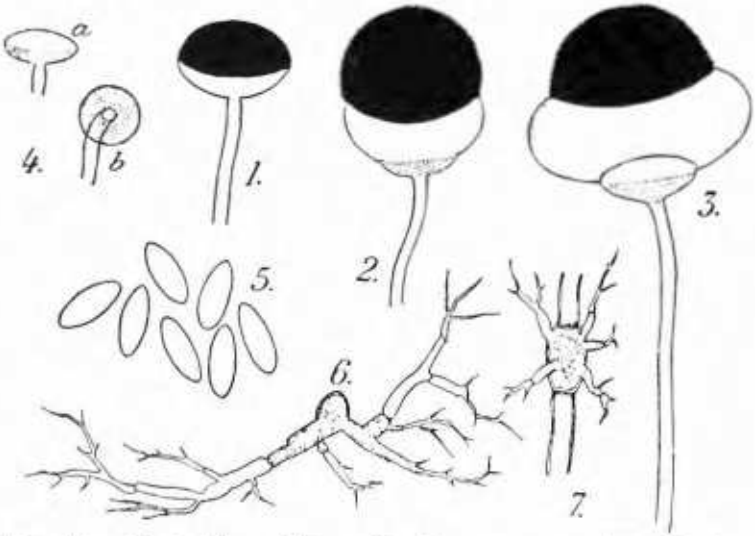

FIG. 111.—*Pilaira Moreaui* Ling. No. 1, young sporangium. No. 2, mature sporangium, seen in moist air. No. 3, the dehiscence of the sporangium under the influence of water which swells its lower part. No. 4, columellae after the fall of the sporangium: *a*, in profile; *b*, from below. No. 5, spores. No. 6, a germinating spore. No. 7, a germinating chlamydospore. From Ling Yong's *Étude*. Magnification: nos. 1–4, 60; no. 5, 300; nos. 6 and 7, 70.

et microchimique d'une nouvelle Mucorinée, Pilaira Moreaui" (1926). See also Rev. générale de Botanique, xlii. 743.

Sporangiophores lax, hyaline, not branched, erect, soon decumbent, 10–12 cm. high, 30 μ broad. Sporangia at first yellow, depressed, when mature globose, intensely bluish-black, 300–400 μ

in diameter (in dwarfed specimens only 80 μ), membrane encrusted, the upper zone cutinised, persistent, the lower gelatinous, deliquescent; columella flattened, broadly adnate, 150–180 × 90–100 μ. Spores cylindric-ellipsoid, smooth, hyaline, 18–20 × 8–10 μ (sometimes as much as 24 μ long), granular within, agglutinated; chlamydospores few, intercalary in the submerged mycelium; zygospores not seen.

On dung of horses and rabbits. France. Allied to *P. anomala*, from which it differs chiefly in its larger spores. It forms a gall with *Chaetocladium Jonesii*.

Illustration: Fig. 111.

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