A REVISION OF THE GENERA OF THE HYPODERMATACEAE[1]

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A reclassification of the genera and species of the Hypodermataceae with special emphasis on the conifer-inhabiting species is presented. The 22 genera fall into 7 groups as follows. *A*. The *Lirula* complex on *Abies* and *Picea* including 3 genera: **Virgella**, gen. nov., with rod-shaped spores segregated from *Hypoderma*, **Isthmiella**, gen. nov., with bifusiform spores from *Bifusella*, and **Lirula**, gen. nov., with clavate spores from *Hypodermella*. *B*. The *Hypodermella* complex comprising *Hypodermella* v. Tub., subcuticular on *Larix*, limited to the type species; a group of 3 subepidermal genera on *Pinus* including **Davisomycella**, gen. nov., with clavate spores, **Ploioderma**, gen. nov., with rod-like spores, and *Elytroderma* Darker with 2-celled spores; and a subhypodermal genus, *Lophodermella* v. Höhn. on *Pinus*. *C*. The *Bifusella* complex with *Bifusella* v. Höhn. on *Pinus*, *Duplicaria* Fckl. on *Empetrum*, and a new subepidermal genus, **Soleella**, on *Pinus*. *D*. The *Hypoderma* complex comprising *Hypoderma* DC. ex Saint Amans emend. De Not., **Meloderma**, gen. nov., a segregate from *Hypoderma* having *Lophodermium* affinities, *Lophodermium* Chev., and *Lophomerum* Ouellette and Magasi, a recent phragmosporous segregate from *Lophodermium*. *E*. The genus *Coccomyces* De Not. *F*. The *Colpoma* complex with *Colpoma* Wallr., *Xyloschizon* Syd., and *Bifusepta* Darker. *G*. The *Rhytisma* complex with *Rhytisma* Fr., *Placuntium* v. Höhn., and *Nymanomyces* P. Henn.

Introduction

The Phacidiales in modern classifications comprise a rather heterogeneous order of Ascomycetes with stromatic ascolocular ascocarps embedded in and connate with the host tissues above and below. Their asci are unitunicate. Three families, the Cryptomycetaceae, Phacidiaceae, and Hypodermataceae are recognized by von Arx and Müller (1954).

The Hypodermataceae differ from the other two families in several marked characteristics. In general, however, they are distinguished by their ascocarps which possess a shield-like covering layer which opens by an elongated slit, except in the genus *Coccomyces*, where the openings are or tend to be radial. A more or less definite opening mechanism is present in some species, while in others the opening is merely fortuitous, by means of a mechanical tearing of the fungus and host tissues. The hymenial layer is usually more or less cup-like and flat or tends to become so at maturity. The subhymenium is usually plectenchymatous with cells elongated, more or less parallel with the base of the apothecium and occupies the bulk of the space between the hymenium and the basal stromatic tissue. The basal stroma is pseudoparenchymatous and composed of more or less isodiametric cells which form a tissue in contact with and penetrating the inner host cells. In most species of Hypodermataceae on conifer needles the basal stroma is relatively reduced in thickness, whereas in species such as *Colpoma quercinum*, it is fairly sharply delimited and of considerable thickness. The asci of the Hypodermataceae range from broadly saccate to clavate to almost cylindrical, and may even be rather long-stalked, as in the genus *Hypoderma*. The pore of the ascus never turns blue with iodine. The ascospores vary from bacillar to fusoid or bifusiform, to clavate or cylindrical-filiform, and from one-celled to phragmosporous, and are surrounded by a gelatinous sheath. All are hyaline with the exception of *Nymanomyces*, which has brown spores.

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The pycnidia of the Hypodermataceae, where known, fall into the family Leptostromataceae.

In the older classifications of the Hypodermataceae few characters have been accepted on a primary generic basis except the gross appearance of the ascocarp. This has served merely to segregate the *Coccomyces*, *Colpoma*, and *Rhytisma* complexes from the large bulk of less conspicuous Hypodermataceae which has been further subdivided on the basis of spore shape, size, and septation. In the older schemes of classification this virtually amounted to a primary separation on spore shape alone. Consequently these species have been placed almost without exception in the four genera *Lophodermium*, *Hypoderma*, *Hypodermella*, and *Bifusella*. Many of our present difficulties may be ascribed to the continued attempts of workers to assign new species to these old genera while disregarding the morphological nature of such structures as ascocarps, asci, and pycnidia. Our present dilemma stems from the fact that, as the genera have become larger, overlapping in spore characters has occurred, and relationships between groups of species have become lost in the multiplicity of species while certain obvious similarities in other structures have been neglected or minimized. Nevertheless, the gradual accretion of knowledge has brought to light a number of relationships which it is no longer possible to ignore, and the current study has grown out of a desire to attempt the creation of more workable species groupings of the Hypodermataceae, with special emphasis on the conifer-inhabiting species. As an example, the acceptance of von Höhnel's genus *Lophodermella*, with slight emendation, appears long overdue. Furthermore, it is proposed to segregate certain other species or groups of species into new genera whose circumscriptions are based primarily on combinations of characters other than spore shape.

Historical Review

The history of the classification of the Hypodermataceae has been outlined several times in recent years. For the more detailed accounts the works of Bisby (1923), Darker (1932), Tehon (1935), and Terrier (1942) should be consulted. In review it is sufficient to recall that the species of Hypodermataceae known prior to the Friesian starting date, 1 Jan. 1821, for the Fungi Caeteri in the International Code of Botanical Nomenclature, were placed mainly in the genus *Hysterium* Fries (1823). Only three genera of the Hypodermataceae in use today were recognized during the period of Fries' Systema Mycologicum and Elenchus Fungorum, 1821–1832: *Hypoderma* DC., 1805, which was accepted by Gray, Mérat, and Saint-Amans in 1821, *Rhytisma* Fr., 1823, and *Lophodermium* Chev., 1826.

As originally defined by De Candolle in Lamarck and De Candolle in 1805, and further expanded in 1815, the genus *Hypoderma* DC. was created for those species of *Hysterium* and related forms growing under and breaking through the epidermis (used in a broad sense) at maturity. It is of interest to note that under *Hypoderma* and *Rhytisma*, which he treated under the name *Xyloma*, De Candolle had isolated fairly completely the then known species which were later to become the Hypodermataceae. Under *Hypoderma* DC. were segregated species, most of which were later transferred to *Lophodermium*, *Colpoma*, *Hypodermella*, and possibly *Duplicaria*, together with one species of *Leptostroma*, and one species of *Hysterographium*, *H. fraxini*, which tends to remain

covered during early development and thus no doubt fitted into the concept of De Candolle's genus. Chevallier (1826) established *Lophodermium* for essentially the same group of organisms treated by De Candolle under *Hypoderma* and included six still currently acceptable *Lophodermium* species, one *Hypodermella*, and two *Hypoderma* species, but according to Fries, Elenchus 2: 145, 1828, Chevallier assigned to *Lophodermium herbarum* Chev. specimens referable to *Hypoderma commune* Fr. and not to *Hysterium herbarum* Fr. Although both *Hypoderma* and *Lophodermium* were validly published during the Friesian period, 1821–1832, Fries himself continued to treat their species mainly under *Hysterium*. Unfortunately, *Lophodermium* is illegitimate (see discussion below). Two other De Candolle species, *Hypoderma quercinum* and *H. crispum*, were transferred by Wallroth (1833) to his new genus *Colpoma*.

The genera *Hypoderma* and *Lophodermium* were not clearly circumscribed until De Notaris (1847) finally segregated their species. In the same publication he established the new genus *Coccomyces* based on *Hysterium tumidum* Fr., but by a curious choice he attached three radiately dehiscing species now generally placed in *Coccomyces* to the first section of the genus *Lophodermium*. The first of these, renamed *Lophodermium phacidium* De Not., is an obligate synonym of *Phacidium coronatum* Fr. *Coccomyces tumidum* and *P. coronatum* are synonymous and the type of *Coccomyces* is considered to be *C. coronatus* (Schum. ex Fr.) De Not., thus cited later in De Not., Erbar. critt. ital. 1: 236, 1859.

During the long interval between the work of De Notaris and the studies of von Höhnel in 1917 only three more genera of Hypodermataceae were described. These comprised: *Duplicaria* Fckl., 1870, *Hypodermella* v. Tub., 1895, and *Nymanomyces* P. Henn., 1899.

Von Höhnel (1917*a*) erected a new order, the Phacidiales v. Höhn., composed of the old families Phacidiaceae and Hypodermataceae with which he united a number of genera from other families. He then arbitrarily subdivided the order into six families, primarily on the basis of the position of the fruiting body in the substratum. This resulted in the splitting of many of the old genera into two or even three genera and required the creation of a number of new names. No attempt was made to distribute all of the known species into the genera of the newly created skeletal framework although types were established for the new genera. In various papers during 1917 von Höhnel reestablished or created the following genera: *Lophodermina* and *Lophodermellina* from *Lophodermium*; *Hypodermellina* from *Hypoderma*; *Bifusella* and *Placuntium* from *Rhytisma*; and *Lophodermella* from *Hypodermella*. *Bifusella* v. Höhn. and *Placuntium* Ehrenbg. ex v. Höhn. have gained general acceptance among the Hypodermataceae by most mycologists, and it is the belief of the writer that the acceptance of *Lophodermella* v. Höhn. is long overdue. Of the remainder, Nannfeldt (1932) considered the genus *Hypodermellina* v. Höhn. to be a member of the Hemisphaeriales while von Arx and Müller (1954) treated it under the Phacidiaceae. On the other hand the genera *Lophodermina* v. Höhn. and *Lophodermellina* v. Höhn. have generally been rejected although they are both validly published taxa and as such are available in the event that someone wishes to use them with an emended circumscription. Although von Höhnel's insertion of the Hypodermataceae in the Phacidiales was adopted in a much restricted sense by Nannfeldt (1932) under the name Phacidiaceae, von Höhnel's use of the position

of the fruit-body in the host tissue as a primary basis for the separation of the Phacidiales v. Höhn. into families has not gained recognition by most mycologists.

Von Höhnel did succeed, however, in focusing attention on the need for study of this large and heterogeneous group. He, himself (1917*b*, *c*), brought further order to the Phacidiales when he removed his first family, the Schizothyriaceae, to the Thrausmatopeltineae Theissen of the Hemisphaeriaceae Theissen. During the following year, von Höhnel (1918) pointed out the sharp demarcation existing between the Hypodermataceae and the Hysteriaceae which up to that time had been treated together under the Hysteriales. In this paper he removed the Hysteriaceae to the Sphaeriales and more recently Müller and von Arx (1962) have transferred them to the Dothiorales. Petrak (1947) restricted von Höhnel's second family to *Leptopeltella* v. Höhn. and *Leptopeltis* v. Höhn. and added three new genera. This family has been accepted and revised by E. Müller and von Arx (1962) and by von Arx (1964) under the slightly modified name, Leptopeltaceae, a family which they attach to the Dothiorales also.

Tehon (1935) made the only serious attempt to apply the principles outlined by von Höhnel. Although in his studies he professed to follow von Höhnel's scheme of classification, one is left with the impression that he could not quite bring himself to accept it in its entirety. Otherwise, his key to genera would have reflected the primary splitting of the genus and the separation of its new components among three of von Höhnel's six families. Instead, he first divided the species of *Lophodermium* into two groups on the basis of the presence or absence of aliform tissue and only secondarily on the position of the hysterothecium in the host tissue and made no mention of the distribution of his genera in von Höhnel's families. An analysis of his key shows that aliform tissue is present in all subcuticular species, in some intraepidermal species, but in no subepidermal species. There is within the Hypodermataceae a rather definite correlation between the depth of insertion of the hysterothecium and its color. In general, subcuticular species are black, while certain deep-seated species are almost colorless, and apparently the ability to detect the aliform tissue is somewhat dependent on color. One subepidermal species on *Pinus strobus* which has a comparatively thin epidermis shows aliform tissue quite well developed. The question arises as to whether Tehon would have created a new genus for this had he observed it. In the 1935 publication Tehon segregated three new genera, *Dermascia* from *Lophodermium*, and *Epidermella* and *Locelliderma* from *Hypoderma*. These three genera and all new species described by him in this paper are invalid since they do not comply with article 43 of the International Code of Botanical Nomenclature which requires a Latin description for valid publication. Moreover, his new combinations under *Dermascia* are likewise invalid since they were made in an invalid genus. All of his new combinations under *Lophodermina*, *Lophodermellina*, and *Dermascia* have been treated under their original names in *Lophodermium* by most workers. His new species in these three genera, however, have been transferred by Nannfeldt (1936) and Terrier (1942) to the genus *Lophodermium* where, with the exception of *Lophodermina septata* Tehon, recently validated as *Lophomerum septatum* Ouellette, they still remain invalid awaiting Latin descriptions. The basis for

the separation of *Epidermella* Tehon from *Hypoderma* was never clearly stated by its author and as the genus is invalidly published its species should be treated under their established names in *Hypoderma*. On the other hand, the description of his monospecific genus *Locelliderma*, based on *Hypoderma ampelodesmi* Ces. on the grass, *Ampelodesmos tenax*, suggests that the fungus probably belongs outside the Hypodermataceae, possibly in or near the genus *Scirrhia*. It should be reexamined. Meanwhile, its only valid name is *Hypoderma ampelodesmi* Ces.

In a later paper, Tehon (1939) described several new species, all accompanied by Latin descriptions. One of these, however, *Epidermella hansbroughii* Tehon, is invalid because it was placed in an invalid genus. It may be called ***Hypoderma hansbroughii*** (Tehon) ex Darker sp. nov. [≡ *Epidermella hansbroughii* Tehon, Mycologia 31: 688. 1939]. Tehon's Latin description will serve to validate it in its new position.

Nannfeldt (1932), in his extensive study of the inoperculate Discomycetes, treated approximately 58 genera of von Höhnel's Phacidiales and, in addition, about 30 other related genera. After removing the discordant elements elsewhere and relegating a number of others to synonymy, the family Phacidiaceae *sensu* Nannfeldt, was reduced to 14 genera, mostly hypodermataceous in character. In a reexamination of this family, Terrier (1942) divided it into three families: the revived family Hypodermataceae composed of 10 genera and the Rhytismaceae with 3 genera together making up the order Hypodermatales, and the Phacidiaceae *sensu stricto* with 5 genera. Finally von Arx and Müller (1954) and Müller and von Arx (1962) realigned under the Phacidiales 3 families, the Phacidiaceae with 8 genera, the Cryptomycetaceae with 2 genera, and the Hypodermataceae including Terrier's Rhytismaceae with 11 genera. In the Hypodermataceae they included: *Bifusella* v. Höhn., 1917; *Clithris* (Fr.), 1822; *Coccomyces* De Not., 1847; *Duplicaria* Fckl., 1870; *Elytroderma* Darker, 1932; *Hypoderma* DC. ex Saint Amans emend. De Not., 1847; *Hypodermella* v. Tub., 1895; *Lophodermium* Chev., 1826; *Nymanomyces* P. Henn., 1899; *Placuntium* Ehrenbg. ex v. Höhn., 1917; and *Rhytisma* Fr., 1823. To these should be added *Lophodermella* v. Höhn., 1917, *Xyloschizon* Syd., 1922, known only to the writer through the original description, and two recently described genera, *Bifusepta* Darker, 1963, and *Lophomerum* Ouellette and Magasi, 1966.

The hypodermataceous fungi have been assigned over the years to various groups of Ascomycetes. If we return to De Notaris (1847) we find that he placed them in the Pyrenomycetes Ascigeri, and included them as an integral part of the Hysteriacei, which he further subdivided on the basis of color into the Phaeosporii and the Hyalosporii. Rehm (1887) elaborated the classification of the Hysteriaceae Cda., including the Hypodermieae, and again (1912) under the Hysteriineae Schröt. which he treated as synonymous with the Hysteriaceae Cda. and intermediate between the Discomycetes and the Pyrenomycetes. Von Höhnel (1917) united the Hypodermataceae with the Phacidiaceae in the Phacidiales v. Höhn. which he regarded as Discomycetes approaching the Dothideales on the one hand and the Pezizales on the other. In the following year, 1918, he made the first clear-cut distinction between the Hypodermataceae and the Hysteriaceae and united the latter with the Lophiostomaceae in a new family, the Hysterostomaceae of the Pyrenomycetes. Nannfeldt (1932)

assigned the Phacidiaceae *sensu* Nannfeldt to the Helotiales. Terrier (1942) placed his order Hypodermatales composed of the Hypodermataceae and the Rhytismaceae under the Ascohymeniales of Nannfeldt and regarded this order as being related to Nannfeldt's Drepanopezizoideae of the Dermateaceae in the Helotiales. The Phacidiaceae, on the other hand, were treated as Ascoloculares with affinities to the Dothioraceae. Gäumann (1949) suggested that the Hypodermataceae had arisen phylogenetically from the Plectascales by way of the Dermateaceae. In a distinctly different classification, Luttrell (1951, 1955) considered the Phacidiaceae to be Helotiales belonging in the series Unitunicatae, subseries Discomycetes, group Inoperculati. Von Arx and Müller (1954), while questioning the true discomycetous nature of the Phacidiales, provisionally placed the order between the Dothiorales and the Helotiales, and considered them to be unitunicate as pointed out by Luttrell but with all families belonging to the Ascohymeniales in the sense of Nannfeldt. E. Müller and von Arx (1962) treated the Phacidiales as a distinct order of the Discomycetes which like the Helotiales had arisen from a pezizaceous ancestor. Gäumann later (1964) suggested that the ancestors of the Phacidiales are to be sought among the simple Pyronemaceae or Ascocorticiaceae, that they have developed parallel with the Pezizales and Helotiales but independently, and that they do not belong in the Discomycetes. Furthermore, he noted that the ascocarps of the Phacidiales develop in a manner similar to those of the Dothiorales; yet, he believed that the two orders were not closely related because of the unitunicate asci of the former and the bitunicate asci of the latter. He believed the terms ascohymenial and ascolocular to have only descriptive value and to be unimportant in classification. In the Hypodermataceae, which he considered to be ascolocular, he noted that certain species at maturity appear to be ascohymenial. In a similar manner he considered paraphysoids and paraphyses to intergrade. In a recent publication with taxonomic implications Gordon (1966) reported the occurrence of 3 basic and 2 intermediate types of centrum ontogeny among the Hypodermataceae and in this paper discussed 2 basic and 1 intermediate type in detail.

Morphological Characters

The stromata may range from simple monoascocarpic types a fraction of a millimeter in diameter to large polyascocarpic structures up to 4 cm or more in diameter. The ascocarp itself, strictly speaking, occupies a locule within a stroma and appears as a small cupule with its associated surrounding tissues firmly attached to the stroma. For purposes of discussion reference to the ascocarp will be assumed to include the closely attached stromatic tissues as well. In the descriptive portion of this work the term hysterothecium has been used in reference to the simpler ascocarps which split open by a longitudinal slit. Although the term more properly refers to the fruit body of a member of the Hysteriaceae its use has been continued here as a matter of convenience since there appears to be no other suitable descriptive term available.

The ascocarps themselves vary in shape superficially from small, almost circular forms like *Lophodermium sphaerioides* to extremely elongated, more or less straight forms like *L. ponderosae* and the nervisequious fruit bodies on *Abies* and *Picea*, or to elongated, more or less curved or branched forms like those of certain *Colpoma* species, or to comparatively large round or polygonal

ascocarps like those of *Coccomyces*. All of these are usually considered monoascocarpous, and apparently consist of unilocular stromata. Whether these do actually represent individual ascocarps is open to question and requires more detailed study, but they are enclosed in a common stromatic structure and, to the unaided eye, show what appears to be a single hymenial surface. In the so-called polyascocarpic forms which include species of *Placuntium*, *Nymanomyces*, and *Rhytisma*, with the exception of *R. punctatum*, the large, more or less common stroma opens into numerous hymenial surfaces separated by sterile tissue. In *Placuntium* the stroma most frequently ruptures to expose a large elongated or circular hymenium with sterile islands of stromatic tissue supporting portions of the dark cover scattered through it.

In cross-sectional view the ascocarps vary from species like *Lophodermium juniperinum* which bulge outwards from the host tissue to species like *Hypodermella sulcigena* which are deeply immersed and externally show little evidence of their presence.

Length, breadth, and width of the ascocarps are characteristic in the morphology of individual species.

Color of the ascocarps is constant under fixed conditions and varies from black in the more externally situated ascocarps, such as those of *Lophodermium nitens* and *L. juniperinum*, through various shades of brown in certain nervisequious species on *Abies* to almost colorless forms in the deep-seated ascocarps of *Hypodermella concolor* and related species. Color is undoubtedly due to chemical reactions which darken the fungus tissues or the associated host tissues, and is definitely concerned with the prevention of water loss. The external parts of the ascocarp are more affected. When moisture supplies are adequate the need for this water barrier disappears. A small collection of *Lophodermium pinastri* on *Pinus resinosa* shows this very strikingly. On needles caught in a small rock depression filled with water, the upper clypeal area remained practically colorless and appeared parenchymatic, rather than pseudoparenchymatic and carbonous as in ascocarps which had developed normally on the forest floor.

The position of the ascocarp, that is, the depth of insertion in the host tissues, appears to be a constant feature for each species. Von Höhnel even made it the basis for dividing his Phacidiales into families and Tehon used it as a basis for generic separations in his treatment of the genus *Lophodermium*. It is true that in several instances groups of species show the same host position and in the present paper a few such groups have been isolated as genera but in no instance was this considered the primary factor in the separation. An excellent example of the constancy of the position of the ascocarp in the host tissues is to be found in *Hypoderma desmazierii* which maintains the same host position and other characters when transferred by inoculation from its normal North American host, *Pinus strobus*, to the hard pines, *Pinus resinosa* and *P. banksiana*.

The clypeal layer forms the upper covering of the ascocarp and on the outer side is united with the host tissue. It is variable in color, as mentioned above, apparently depending somewhat on the depth of insertion in the host tissue. At maturity the clypeus splits lengthwise to expose the hymenium. This may be very broadly exposed with the clypeus folding back, as in the nervisequious

species on *Abies* and *Picea*, or it may be very narrowly exposed by an elongated slit or pore, as in many *Hypoderma* and *Lophodermium* species. In some species, for example *Hypoderma desmazierii*, and in certain strains of *Lophodermium pinastri*, the stromatic clypeus, sometimes combined marginally with the basal tissues, may extend well beyond the area of the inner ascocarp hymenium forming a sort of shelf of dark sterile tissue. Even in species such as *Hypodermella ampla*, in which the presence of a basal layer is more difficult to demonstrate, there is a well marked subepidermal tissue extending beyond the hymenial area. Within the clypeus specialized tissues may develop which act as an opening mechanism. In their highest development these tissues are composed of a long band of parenchymatous tissue extending the length of the ascocarp. The actual opening proceeds from the outside as a notched fissure and as it develops the parenchyma cells elongate into the fissure as filaments, often septate, and extending at right angles to the line of dehiscence. Terminally these filaments, the "periphyses" of Tehon, are more or less swollen and gelatinous and form the edges of the two lips of the open ascoma. The gelatinous, parenchymatic slit band aids not only in the dehiscence of the ascocarp but also serves to seal off the hymenium under adverse conditions. There are among species of the Hypodermataceae various modifications in the structure of the opening mechanism. In some species the cover is much thickened in the lip region and as the notched fissure develops from the outside towards the inner cavity the dark exciple flattens out. This flattening may be further accentuated by areas of more or less parenchymatous tissue on the inner face of the cover on each side of the thickened lips. As these areas swell, pressure is exerted and the covering tissues are stretched further. Such extreme developments may be observed in a number of *Lophodermium* species where it aids in keeping the hymenium covered almost until maturity. On the other hand, the opening mechanism may be nothing more than a small core of parenchymatous tissue located somewhere along the middle of the covering layer. Through this parenchyma the rupture easily takes place as in *Lophodermium berberidis* illustrated by Nannfeldt (1932) or in *Hypodermella ampla*. Developmental studies may eventually show some form of preformed structure in the majority of the Hypodermataceae although at present a number of species are considered to lack any opening mechanism which foreshadows the slit and in such instances the opening takes place more or less fortuitously along the line of greatest stress. In a few species, there is a definite thinning of the exciple along the top of the ascoma, forming a sort of fault-line along which the opening occurs.

Among the characters which a fungus should possess for inclusion in the Hypodermataceae Tehon stipulated the presence of an ostiolar lining of periphyses. Unfortunately, many of Tehon's own species fail to meet this test. Furthermore, the use of the term periphyses in Tehon's meaning is unfortunate since they have nothing to do with the true periphyses occurring in the Pyrenomycetes. In the latter the periphyses develop within a perithecium as outgrowths from the perithecial wall and form a lining of the upper walls and often extend into the necks of beaked perithecia. In the Hypodermataceae the periphysis-like structures are only associated with the opening mechanism.

The basal layer formed after the splitting of the stroma during development may consist of nothing more than a thin tissue adjacent to the inner host

tissues and continuous with the fungus cells which have penetrated and more or less broken down the host cells as, for example, in *Lophodermium*. In a few genera, such as *Colpoma*, it may be highly organized. Sometimes there is a darkening of the cells of the basal layer. Close examination, however, may reveal that this darkened area is partially due to the presence of discolored host cells. The thickness of the basal layer can be most easily determined at the angles of the ascocarps at the margins at the point of union with the clypeus. The angles themselves are often filled with loose parenchymatic tissue, or collenchyma, or with prismatic tissue extending from the clypeus to the basal tissue.

The ascocarp proper lies between the clypeal and basal stromatic tissues. At the angles where these two tissues meet, the subhymenial tissues may be observed bending up along the sides of the clypeus. Terrier (1942) called special attention to the cupule nestling in the stroma of *Colpoma quercinum* and suggested that it offers the best evidence for the stromatic nature of the fruiting bodies of the Hypodermataceae. While not so obvious, the same structure is easily observed in many of the species of the family.

Ascogenous tissue develops in a flat or curved zone, usually near the lower side of the ascomal tissues between the clypeus and the basal layer, and from this zone arise the asci and paraphyses to form the hymenium. Below the hymenium is the plectenchymatous subhymenial layer composed of a compact filamentous tissue whose margins tend to curve upwards to form the wall of the ascoma. On its outer face it merges somewhat into the clypeus while inwardly it merges imperceptibly into the hymenium.

The asci are simple unitunicate structures and may be broad and somewhat saccate or clavate or rather definitely cylindrical, and without blueing of the ascus tip by iodine. In some genera they become distinctly stalked with the ascospores gathered in the upper clavate end. In size the asci of the Hypodermataceae range roughly from about 50 to 250 μ in length and about 5 to 45 μ in width. The spores are eight in number, or if four, with four aborted spores usually rather clearly evident. The scolecosporous forms are usually fascicled but there is a tendency for "sister" spores to be somewhat paired. This pairing may be observed where the pairs tend to slip down into the ascus giving the ascus tip a somewhat asymmetrical appearance. Among the shorter spored species there is often a biseriate arrangement of the spores which are again frequently in pairs although basally the arrangement may be more or less uniseriate. In *Hypoderma hedgcockii* the four spores which do not abort are arranged uniseriately while the four aborted spores are scattered about irregularly.

Ascospores may be short, rod-like, fusiform, rather broadly elliptical, clavate, bi- to trifusiform, or long needle-shaped, and are surrounded by a gelatinous sheath. In early development the spores of the long-spored species may be coiled in the ascus but these usually straighten out as the ascus matures and elongates further. The spores are usually hyaline, although in *Placuntium* and certain *Hypoderma* species they may appear slightly yellowish, and in *Nymanomyces* they are distinctly brown. Within the family, ascospores vary in size from about 20 μ in length to 160 μ or more and from about 1 μ to 18 μ in width. Most genera have simple amerospores but in *Hypoderma* the tendency is

to become two-celled, while two-celled spores are the rule in *Elytroderma*. Several genera with simple, continuous ascospores are best described as scolecosporous. Others, notably *Lophomerum*, *Bifusepta*, and *Xyloschizon*, possess phragmosporous scolescospores. Spore germination in the amerosporous and scolecosporous types is usually preceded by septation near the center of the spore. Germination then proceeds from any part of the spore as in the didymosporous and phragmosporous types. In distilled water the spores send out simple germ tubes which may form swellings into which the protoplasm gathers. These swellings may be cut off by a cell wall from the germ tube and from the swollen area another germ tube may be sent out. This may be repeated two or three times as though the spore were searching for a stomatal entrance. In *Bifusella faullii* and *Hypodermella mirabilis* the distinctive palmate structures formed at the ends of the germ tubes are probably another method for finding entrance into the host.

The paraphyses are usually simple, occasionally once branched near the tip, septate, filamentous, straight or sometimes more or less coiled at the tip or sometimes thickened, and usually surrounded by a thin gelatinous sheath which may in some species become rather prominent. Occasionally, especially near the base, anastomoses by simple bridging may take place between adjacent paraphyses. The paraphyses often appear to exceed the asci in length, although at maturity the asci usually project up through the paraphyses following a more or less rapid elongation.

The pycnidia of the Hypodermataceae are members of the Leptostromataceae and have been assigned to such genera as *Leptostroma*, *Leptothyrium*, *Leptothyrella*, *Hypodermina*, *Labrella*, *Melasmia*, *Colpomella*, and *Crandallia*, although it is doubtful that any true *Leptothyrium* or *Leptothyrella* species will be found to belong here. The pycnidia consist of simple cushions of parenchymatic tissue from which arise a palisade-like tissue of spermatiophores bearing simple bacillar spermatia. The only species at present known to possess a definite covering layer over the pycnidia are *Leptostroma berberidis* Nannf., the species of *Bifusella* as redefined below, and *Placuntium andromedae* (Pers. ex Fr.) v. Höhn. The pycnidia may be small, simple, more or less rounded, dark structures like those of *Leptostroma pinastri* Desm., or elongated, often more or less continuous, somewhat concolorous structures which sometimes tend to darken after spermatial discharge like the pycnidia of the "nervisequious" species of Hypodermataceae on *Abies*, or they may be quite numerous and tend to coalesce becoming more or less labyrinthine or effused as in the imperfect state of *Bifusella linearis* (Pk.) v. Höhn., or small, simple, elliptical and concolorous and never darkening as in the pycnidia of *Hypodermella ampla* (Davis) Dearn., or large, approaching the ascocarp in size, and shining black as in the pycnidia of *Hypoderma pini* (Dearn.) Darker. The spermatial states of *Coccomyces*, *Rhytisma*, and *Colpoma* are generally reported as falling into the form genera *Leptothyrium*, *Melasmia*, and *Colpomella* respectively. For the most part, the pycnidia have the same position in the host tissues as have their perfect states. It should be noted, however, that in *Lophodermium pinastri*, with ascocarps subcuticular in the center and subepidermal at the margins, the pycnidia are subepidermal, whereas among the "nervisequious" species on *Abies*, in certain species with ascocarps intraepidermal in the center and subepidermal at the margins, the pycnidia are intraepidermal.

The spermatiophores are borne at the tips of somewhat swollen, often pear-shaped cells at the surface of the basal parenchymatous cushion. The small spermatia are cut off acrogenously from the tips of the spermatiophores, probably in succession judging from the vast numbers produced, although this point has never been definitely established. Dispersal is usually by means of a lengthwise slit or by a rupture of the margin of the pycnidium. In certain of the "nervisequious" species on *Abies* the spermatia may emerge through the stomatal openings and effuse over the surface of the needle. Very occasionally in *Bifusella faullii*, cirrhi of spermatia may be observed standing above the stomata after maintenance in moist chambers in the laboratory. In size the spermatia vary from about 0.5–1.2 μ in width in different species and in length from about 3.0–3.5 μ in *Bifusella faullii* to 12–20 μ in *Bifusella linearis*.

The pycnidia mature 1 year after infection in the "nervisequious" species on *Abies*, whereas the ascocarps require 2 years to reach maturity. In the majority of Hypodermataceae, however, the pycnidia appear 1 or 2 years after infection and are closely followed by the ascocarps during the same season.

In addition to microscopic studies, field observations on gross morphology of the fungus, age of diseased needles, and so on, are all a helpful part in the complete circumscription of an individual species. No doubt all of the Hypodermataceae are more or less parasitic, although the degree of parasitism is extremely difficult to assess involving as it does not only the relative susceptibility of the host which may vary from plant to plant and the degree of virulence of the fungus itself but also the effects due to variation of the environmental factors as well. It is not surprising, therefore, that it is rather difficult to reproduce the diseases caused by these fungi in artificial infection experiments. Weir (1916) was successful in bringing about infection with his *Hypoderma deformans*. Darker (1932) reported satisfactory infection experiments with *Hypodermella laricis* v. Tub. and *H. concolor* (Dearn.) Darker, but with most others tested the results have proved unsatisfactory or erratic. In spite of this, most *Hypodermella* (*sensu lato*) species, indeed most of the species treated under the first nine genera below, appear to be more or less strongly parasitic and mature on young needles *in situ* on the twigs, often occurring on partially green needles or on dead needles scattered among other green needles which normally continue to remain alive for one or several seasons more. Typical of another group of Hypodermataceae are the conifer-inhabiting species of *Lophodermium* which are usually present on older needles and complete their maturation on the ground after the characteristic needle-casting, on slash, or on mechanically injured branches. Few careful observations have been made on the age of the needles involved or on the age of the needles at the time of their normal fall. It is obvious, however, that among conifer-inhabiting species there appear to be two main groups of species, one of which, comprising most of the species of the first nine genera treated below, is definitely parasitic on young needles and matures after 1 or 2 years on needles *in situ* on the twigs, and another which appears to be but weakly parasitic and usually requires 2 years to develop, often maturing more or less saprophytically on the ground after overwintering on the fallen needles or on needles weakened by some environmental facror to by mechanical injury.

One phenomenon which should be cited is the association of certain secondary fungi sometimes present on needles primarily attacked by species of Hypo-

dermataceae. These fungi, about 30 in number, occur only on host tissues killed by specific species of Hypodermataceae and apparently nowhere else. They develop only after the host food supply has been prepared for them by the primary fungus and apparently are not parasitic on either the host plant or the primary parasite. *Naevia piniperda* following after *Lophodermium macrosporum*, *Nothophacidium phyllophilum* after *Hypodermella nervata*, and *Pezizella minuta* after *Hypoderma lethale*, are typical examples. A few fungi follow after more than one species of Hypodermataceae, but for the most part the relationship is rather specific. *Lophodermium autumnale*, however, follows after *Bifusella faullii* and *Hypodermella mirabilis* in eastern North America and after *Hypoderma robustum* in the west. Several of the associated fungi may accompany the same species of Hypodermataceae although the secondary infection in any one attack is largely limited to a single species. Thus *Lophodermium autumnale*, *Stegopezizella balsameae*, or *Leptosphaeria faullii* and its imperfect state, *Coniothyrium faullii*, may be found in association with *Bifusella faullii*. From the economic viewpoint these secondary fungi are sometimes extremely important. By robbing the primary fungus of its food supply they prevent the latter from fruiting and thus act as natural biological control agents. As an example, during the height of its development in 1961, a collection (DAOM 88009) of *Hendersonia pinicola* Wehm., secondary after *Hypodermella concolor*, was so abundant that the black masses of spores hung in festoons on the needles of *Pinus banksiana* and blackened the green leaves of vegetation below. During the following year no evidence of either the primary or the secondary species could be found at the site of the earlier infection near North Onslow, Pontiac County, Quebec. Apparently the *H. concolor* infestation in this small area was completely wiped out. A related species was described on *Pinus strobus* under the name *Hendersonula pinicola* Dearn. Its pycnidia occur only on pine needles killed by *Bifusella linearis* (Pk.) v. Höhn. where they may break through the stromatic crust of the *Bifusella* species or through other points in the epidermis where the crust is absent. The original description of Dearness is obviously a composite one derived in part from a *Hendersonia* species and in part from *Bifusella linearis*. The immersed nature of the pycnidia and the absence of a stroma places this fungus in *Hendersonia* and not in Hendersonula. Since, however, the specific epithet is preempted by *Hendersonia pinicola* Wehm., ***Hendersonia dearnessii***, nom. nov. is proposed for *Hendersonula pinicola* Dearn., Mycologia 20: 236. 1928 (non *Hendersonia pinicola* Wehm., Mycologia 38: 312. 1946).

Suggested Lines of Revision

The classification of the Hypodermataceae developed slowly over the years and became more or less fixed largely along the lines of Saccardo's and Spegazzini's general scheme of classification on the basis of spore shape, color, and septation. Although other characters have been used in a broad sense to segregate *Coccomyces* and the genera of the *Rhytisma* complex from the remainder of the Hypodermataceae, it has rarely happened that spore characters have played such a primary role in the classification of a family. Usually these characters have been used secondarily and in large families may have been used over and over again. Nevertheless, as long as the number of species remained small, spore characters, especially shape, served fairly well to delimit certain

genera. Unfortunately, as the number of species mounted, the distinctions between spore shapes broke down and tended to intergrade. Moreover, when considered alone, spore shapes threw many unrelated species together and sometimes separated obviously related species rather widely. Recently, however, certain fundamental characters and relationships have come to light and it is now felt that in at least several groups certain fairly clear primary distinctions may now be made at the generic level on the basis of the morphology of the hysterothecia, asci, and pycnidia, or a synthesis of their characters. Spore shape, septation, and color may then be relegated to the position of secondary generic characters.

In the classification proposed below, the genera *Bifusella*, *Hypodermella*, and *Hypoderma* have been considerably reduced and most of their conifer-inhabiting species have been removed to new genera. It is felt that this realignment shows more accurately the relationships of the various species and genera to one another and to the other genera of the Hypodermataceae.

The Hypodermataceae, as treated below, fall into seven groups or complexes of related genera which may be designated as follows: *A*, the "nervisequia" or *Lirula* complex of 3 genera; *B*, the *Hypodermella* complex of 5 genera; *C*, the *Bifusella* complex of 3 genera; *D*, the *Lophodermium* complex of 4 genera; *E*, the genus *Coccomyces*; *F*, the *Colpoma* complex of 3 genera; and *G*, the *Rhytisma* complex of 3 genera.

The first three groups are for the most part strongly parasitic and mature on leaves which are usually *in situ* on twigs at the time of spore maturity. In contrast, the *Lophodermium* and *Coccomyces* complexes are composed largely of weakly parasitic species which in general develop on injured or weakened plants most often towards the end of the growing season or towards the end of the normal life span of the leaves. Among the species of these groups are the typical needle-casts and leaf-inhabiting species in which the diseased needles or leaves usually fall to the ground and after a sort of saprophytic existence throughout the winter produce their pycnidia and ascocarps during the following spring or summer. The *Colpoma* complex ranges from weakly parasitic species like *Colpoma quercinum* to saprophytic species which develop on dead decorticated wood. The *Rhytisma* complex is strongly parasitic, although the dark stromata which develop on green, deciduous leaves during the growing season of the host produce mature ascocarps only after overwintering on the ground while on evergreen leaves they may be produced while still *in situ* on the branch.

A. The "nervisequia" or *Lirula* complex (genera 1–3). Perhaps the most pressing problem in the taxonomy of the Hypodermataceae concerns the disposition of the nervisequious species occurring on *Abies* and *Picea*. They form a homogeneous group of closely related species which are so easily recognized that they can be segregated from all other Hypodermataceae by the unaided eye. Yet, in the older classifications, they are distributed in an anomalous fashion among the three genera *Bifusella*, *Hypoderma*, and *Hypodermella*, and at various times certain species have even been placed in the genus *Lophodermium*. In these genera they have come to rest among groups of very diverse composition composed of species exhibiting a wide variety of hysterothecial characters and parasitizing a broad range of host genera. On *Abies* and

Picea the group is characterized by long, black to brown hysterothecia often extending the whole length of the needles, which are at least 2 years in age. On *Abies* on the upper surface of 1-year-old needles the pycnidial structure which falls in the form genus *Hypodermina* v. Höhn. extends in a continuous or broken line along the sulcus or occasionally in two lines, one along each wing of the needle. The principal development of this complex is on *Abies*, but there are two species on *Picea*, *Lophodermium macrosporum* (Hart.) Rehm and *Bifusella crepidiformis* Darker, whose affinities appear to be with the nervisequious species on *Abies* rather than with any group of the remainder of the Hypodermataceae. The most logical solution is to consider all of these nervisequious species as forming a specialized complex within the Hypodermataceae. In contrast, the vast majority of the remainder have more irregularly scattered hysterothecia and pycnidia. Secondarily one may divide this nervisequious complex into three new genera on the basis of spore shape, as follows: (*a*) a short-spored genus based on *Hypoderma robustum*, (*b*) a bifusiform spored genus to accommodate *Bifusella abietis*, *B. faullii*, and *B. crepidiformis*, and (*c*) a much larger, filiform-clavate spored genus based on *Hypodermella nervisequia*.

B. The *Hypodermella* complex (genera 4–8). This group of genera is characterized by rather strongly parasitic species which fruit on needles *in situ* on the tree, sometimes on partially green needles. They possess for the most part conspicuous, usually elliptical, dark or concolorous fruiting bodies, with rather broad, clavate-saccate asci and rod-like to distinctly clavate or long fusiform or even almost filiform spores. The most striking feature of the type species, *Hypodermella laricis* v. Tub. is the shape of its ascospores, often referred to as inverted tear-shaped, that is, broadly clavate apically and tapered towards the base. The genus subsequently came to be the resting place for a large and heterogeneous group of species on *Pinus* and *Abies*, with a few on phanerogamic hosts. Darker (1932, 1935), following this old concept of spore shape, recognized 19 species on conifer needles which fall according to his key into four well defined groups of species. Lagerberg (1949) suggested that the genus should be regarded as monospecific with the name *Hypodermella* reserved for the type species only and that the other species should be relegated to the genus *Lophodermium*. This, however, in no way appears to solve our dilemma.

Perhaps no one character taken alone is sufficiently significant, but a synthesis of several enables one to define the above mentioned four groups clearly. These groups, then, may be circumscribed as distinct genera typified by the first species described in each. In addition to the *Hypodermella nervisequia* group treated under the "nervisequia" complex above, there remain three other generic aggregates of species: *Hypodermella* v. Tub., with the type-species only, subcuticular, lacking an opening mechanism, with simple, elliptic, dark colored pycnidia, on *Larix* in Eurasia and North America; the *Hypodermella ampla* group with subepidermal, dark hysterothecia, fairly deep-seated, at most with a simple immersed core of parenchyma cells foreshadowing the slit as in the type species, pycnidia when present, simple, on *Pinus*, principally in North America but with one species from Japan; and the *Hypodermella sulcigena* group for which von Höhnel established a new genus, *Lophodermella*, with deep-seated, subhypodermal, more or less concolorous hysterothecia, pycnidia unreported, on *Pinus*, in Europe and North America.

In addition to these former *Hypodermella* species, and with affinities to the *Hypodermella ampla* group are three *Hypoderma* species, *H. hedgcockii*, *H. lethale*, and *H. pedatum*, with subhypodermal hysterothecia, and short rod-like spores, on *Pinus*, in North America, which may be designated the *H. hedgcockii* group. Finally, *Elytroderma* Darker, with two-celled ascospores and subepidermal hysterothecia on *Pinus* in North America and Europe, completes the genera of this complex.

C. The *Bifusella* complex (genera 9–11). The removal of the "nervisequious" species from *Bifusella*, as proposed above, leaves among the conifer-inhabiting species only the type-species, *B. linearis* (Pk.) v. Höhn., and a rather aberrant species, *B. striiformis* Darker, which, because of its striking dissimilarities in characters other than spore form, is placed in a new genus. *B. linearis*, which occurs on soft pines, is strictly subcuticular and is characterized by an extensive, effused pycnidial state made up of numerous more or less coalesced pycnidia and a hysterothecial state in which the paraphyses disappear so early in the development that the species has come to be regarded as aparaphysate. Its closest relatives are two species of *Hypoderma* which also occur on soft pines. These species are both subcuticular, possess large conspicuous pycnidia, show a tendency towards the bifusiform condition, and possess paraphyses which disappear or tend to do so before maturity of the ascocarp. In *Hypoderma pini* (Dearn.) Darker, the paraphyses disappear so early that it too has often been regarded as aparaphysate. In *H. saccatum* Darker, the paraphyses though more persistent finally undergo lysis and at maturity may be lacking. The pycnidia of *B. linearis*, *H. pini*, and *H. saccatum* possess a definite thin pseudoparenchymatous covering above the sporulating cushion and in this respect resemble somewhat the pycnidial state of *Lophodermium berberidis* (Schleich.) Rehm described and illustrated by Nannfeldt (1932). In *Bifusella linearis* the covering layer of the pycnidium appears to consist of a single layer of dark pseudoparenchyma immediately below and attached to the cuticle. The spermatia, too, are very striking, attaining a length of 20 μ or more. In this species the effused pycnidial structure after discharge of the spermatia develops into a stroma-like crust near or through which the hysterothecia often erupt. The fact that *Hemiphacidium planum* (Davis) Korf, which develops secondarily after *B. linearis*, may also occur after *H. saccatum* on *Pinus flexilis* suggests a further relationship between the two Hypodermataceae as the secondary fungi are in general quite specific in their host relationships as well as in their associations with the primary parasites. Accordingly, for the reasons stated, these two *Hypoderma* species have been transferred below to the genus *Bifusella*.

The older genus *Duplicaria* Fckl., which is allied to *Bifusella* v. Höhn., also has bifusiform spores, but a much thicker covering layer and a moderately well developed subhymenial layer, abundant persistent paraphyses, and small, rather inconspicuous pycnidia.

An aberrant species, *Bifusella striiformis* Darker, with subepidermal hysterothecia, somewhat bi-, occasionally trifusiform spores, and with pycnidia unknown, is placed in a new genus near *Duplicaria* and *Bifusella* in the key to genera given below. It is not particularly closely allied to either or to any other member of the Hypodermataceae but is placed here because of its spore shape.

D. The *Lophodermium* complex (genera 12–15). In contrast to the foregoing

rather strongly parasitic groups is a very diverse and large complex of species which are probably only weakly parasitic. They usually complete their life cycles more or less saprophytically on fallen conifer needles, or on fallen leaves, or on twigs or on dead areas on evergreen leaves of various phanerogamic plants. The group includes the so-called "needle casts" of conifer needles. The ascocarps in the genera of this group are typically short, elliptical, dark colored, and rather sharply delimited. Their asci tend to be narrow, varying from cylindrical to more or less clavate and sometimes long-stalked, but never broadly saccate as in many of the foregoing more parasitic groups. Their paraphyses are abundant, simple, sometimes coiled or club-shaped at the tip. Ascospores vary from short fusiform or rod-shaped to needle-shaped. Pycnidia are small, circular to elliptical and fall in general into the form genus *Leptostroma*. Four genera are assigned here.

Hypoderma DC. ex Saint Amans emend. De Not., which has been a "catch-all" genus for any short-spored species, still remains one of the larger genera after removing several species elsewhere as proposed above. The genus still remains in need of study. In general it includes a mixture of species largely characterized by clavate asci which become long-stalked at maturity. As constituted at present it includes species whose ascospores vary from rod-like to fusiform and may be one-celled, pseudoseptate, or definitely uniseptate. Its ascocarps tend to be rather thin and flat. Such a definition removes from *Hypoderma* all of the conifer-inhabiting species except *H. thujae* Durrieu and *H. cunninghamiae* Teng.

A new genus is proposed below for *Hypoderma desmazierii* Duby. This species with its unstalked, subcylindrical asci resembles more closely *Lophodermium pinastri* than the other species of *Hypoderma*. Its strongly developed opening mechanism and the manner in which its developing ascocarp pushes a group of epidermal host cells to the bottom of the fruiting body are certainly reminiscent of *L. pinastri*.

Lophodermium Chev., the largest and most complex genus, though admittedly containing a widely divergent group of organisms, is the most difficult to reorganize in any satisfactory manner. The genus has been treated in a monographic study by Tehon (1935) but the generic limits applied by von Höhnel (1917*a*, *d*) and Tehon are so patently artificial that they have rarely been given recognition by other mycologists. Although certain broad divisions might be suggested it seems premature to attempt to make any worthwhile reorganization at this time.

Lophomerum Ouellette and Magasi, however, makes use of phragmosporous septation as a character to segregate certain species from the large mass of *Lophodermium* species. Care must be exercised in applying this criterion since under extremely moist conditions many of the species of this genus can be forced to form a central septum or even to germinate within the ascus.

E. The genus *Coccomyces* (genus 16). *Coccomyces* stands somewhat apart from other genera of the Hypodermataceae but it apparently has rather definite affinities to the genus *Lophodermium*. It includes subcircular to polygonal forms which tear open lacerately or open by sharply defined radiately arranged slits provided with organized opening mechanisms.

F. The *Colpoma* complex (genera 17–19). This group centers around the

genus *Colpoma* and includes forms which are erumpent through the bark or bare wood. They possess a rather well developed, sometimes more or less darkened basal layer beneath the subhymenial layer. *Colpoma* is the best known genus and consists of a number of species with scolecosporous ascospores. Included here at present are a number of species, several of which should probably be reduced to synonymy. *Xyloschizon* Syd., a somewhat doubtful genus on the basis of the description of its type species, *X. weirianum* Syd., appears to be a phragmosporous segregate from *Colpoma*. The second species, *X. stratum* Syd., on *Crataegus*, does not appear to differ markedly from the widespread *Colpoma crispum* (P. ex Fr.) Sacc., common on bark and bare wood of conifers. The third genus of this group is *Bifusepta* Darker, a phragmosporous genus with bifusiform spores.

G. The *Rhytisma* complex (genera 20–22). Finally, the seventh grouping includes the genera *Rhytisma*, *Placuntium*, and *Nymanomyces* and comprises the large stromatic types which may have several ascocarps in each stroma as in most *Rhytisma* species and in *Nymanomyces*. Often in *Placuntium andromedae* (P.) Ehrenbg. ex v. Höhn., the number of ascocarps in a stroma is reduced to one large circular ascocarp surrounding a sterile area in each stroma. The characters of *Placuntium* are those of a rather robust *Rhytisma* with large, slightly greenish-yellow clavate ascospores in contrast to the more hyaline, smaller clavulate ascospores of *Rhytisma*. In the genus *Nymanomyces* the ascospores are brown and ovoid.

The present study, then, divides the Hypodermataceae among 22 genera, including 15 hitherto validly published genera composed of the 11 genera recognized by von Arx and Müller (1954) together with *Lophodermella* v. Höhn., the somewhat doubtful *Xyloschizon* Syd., *Bifusepta* Darker, and *Lophomerum* Ouellette and Magasi. In addition seven new genera are proposed below to give a more meaningful classification, especially for the conifer-inhabiting species.

Concerning the Names of the Genera Hypoderma and Lophodermium

The nomenclature of the genus *Lophodermium* is bound intimately with that of *Hypoderma*, a genus established by De Candolle (in Lamarck and De Candolle, 1805) for 5 species segregated from *Hysterium* Pers. and *Xyloma* Pers. and to which De Candolle (1815) later added 7 more species and a number of varieties. Saint Amans (1821) established priority for *Hypoderma* and placed therein 5 of De Candolle's species including *H. arundinaceum* (Schrad.) DC. and *H. virgultorum* DC., an avowed substitute for *Hysterium rubi* Pers., both of which were destined to play leading parts in the complicated interchanges between *Hypoderma* and *Lophodermium*. Chevallier (1822) segregated from *Hypoderma* on rather questionable grounds a new genus *Lophoderma* and included *H. arundinaceum* in the former and *Lophoderma rubi* (Pers.) ex Chev. in the latter. Later, Chevallier (1826) abandoned both genera and united their species in a new genus *Lophodermium*. Clear-cut circumscriptions were not drawn up for *Hypoderma* DC. ex Saint Amans and *Lophodermium* Chev. until De Notaris (1847) revised both genera and included *Hypoderma rubi* (Pers. ex Chev.) De Not. in the former and *Lophodermium arundinaceum* (Schrad. ex Saint Amans) Chev. in the latter. Unfortunately, this treatment reversed the position taken by Chevallier in 1822. Otto Kuntze (1898) arrived at essentially

the same conclusions as Chevallier (1822) by arguing that, since 3 of the 5 species originally named by De Candolle in 1805 were congeneric, the major group of species which included *H. arundinaceum*, should have been assigned later to *Hypoderma* instead of *Lophodermium*. Accordingly, he transferred all *Lophodermium* species listed in the first 11 volumes of Saccardo's Sylloge Fungorum back to *Hypoderma* and all of the *Hypoderma* species in the same volumes to a new genus *Hypodermopsis*.

Chevallier (1822) in dividing the genus *Hypoderma* and placing *H. arundinaceum* in the *Hypoderma* entity thereby automatically fixed this species as type. *Lophodermium* Chev. (1826) in its original circumscription and in the revised, restricted circumscription of De Notaris (1847) is superfluous and therefore illegitimate (Art. 63) because it included *L. arundinaceum*, the type-species of *Hypoderma*. *Hypoderma* as treated by O. Kuntze (1898) included *H. arundinaceum* and is in accord with Chevallier's treatment of 1822.

In the *Lophoderma* entity Chevallier (1822) placed *Lophoderma rubi*, *L. scirpinum*, and *L. nervisequum*, but later he (1826) abandoned *Lophoderma* and transferred its species together with a number of *Hypoderma* species including *H. arundinaceum* to his new genus *Lophodermium*, an avowed substitute for *Hypoderma*. De Notaris (1847) revised *Hypoderma* with the type-species, *H. arundinaceum*, removed. With this revision the name would have to be ascribed to De Notaris and would be a later homonym of *Hypoderma* DC. ex Saint Amans and *Hypoderma* as revised by Chevallier, and a synonym of *Lophoderma* Chev. *Hypodermopsis* O. Kuntze is superfluous because it included in its circumscription all three species of *Lophoderma* Chev.

The current usage of *Hypoderma* and *Lophodermium* follows the treatment of De Notaris (1847) and is illegal for both genera but the revision of De Notaris has since his time been followed by practically all mycologists with the exception of O. Kuntze (1898) and to report those who have adopted this usage results in a list of all persons knowledgeable in the Hypodermataceae including Duby (1861), Fuckel (1870), Karsten (1873), Saccardo (1883), Rehm (1887), Ellis and Everhart (1892), Schroeter (1893), and among more recent workers, von Höhnel (1917a), Hilitzer (1929), Nannfeldt (1932), Tehon (1935), Terrier (1942), and others.

In keeping with the spirit of Article 14 of the International Code of Botanical Nomenclature (Lanjouw *et al.* 1961) it is highly desirable that these two genera be maintained with the circumscriptions of De Notaris to avoid the numerous confusing changes that a strict application of the rules would entail.

The simplest method of legalizing the present usage requires first, as permitted by Article 7, Note 8, of the "Code," the selection and conservation of a new type-species for *Hypoderma* DC. ex Saint Amans, a valid name at present legally typified by *H. arundinaceum*. If, however, *H. virgultorum* DC. ex Saint Amans, an obligate synonym of *H. rubi* (Pers. ex Chev.) De Not., were conserved as the type-species of *Hypoderma*, the status of the genus would then be fixed with a circumscription in keeping with that of De Notaris. *Lophoderma* Chev. (including *L. rubi*) would then become superfluous (Art. 63). *Hypoderma* in the sense of Chevallier with the type-species (*H. rubi*) removed would have to be ascribed to Chevallier (Art. 48) and would become a later homonym. *Lophodermium* Chev., because it includes *H. rubi*, would still remain superfluous

and *Lophodermium* in the sense of De Notaris with the type of *Lophodermium* Chev. removed would have to be ascribed to De Notaris and would become a later homonym of *Lophodermium* Chev. *Hypoderma* DC. ex Saint Amans, as treated by De Notaris, would then become legal and its usage would correspond to that of Saint Amans and would agree with current usage. *Hypoderma* in the sense of O. Kuntze, however, would become synonymous with *Hypoderma* Chev., while *Hypodermopsis* O. Kuntze would become illegitimate as superfluous for *Hypoderma* DC. ex Saint Amans. Unfortunately, as pointed out above, *Lophodermium* would still remain superfluous. To legalize this name it is therefore necessary to fall back on Article 14 of the "Code" and conserve *Lophodermium* Chev. with the type-species *L. arundinaceum* (Schrad. ex Saint Amans) Chev.

The formal proposals for conservation are made below for submission to the General Committee for Botanical Nomenclature. Pending the recommendations of the Committee on the proposals, the existing usage of *Hypoderma* and *Lophodermium* is being followed.

PROPOSAL 1

Proposal for the conservation of a type-species for *Hypoderma* DC. ex Saint Amans (1821) (Hypodermataceae).

LECTOTYPUS: *Hypoderma rubi* (Pers. ex Chev.) De Not. Giorn. Bot. Ital. 2(2): (37). 1847. (*typ. cons. prop.*).

[≡ *Hysterium rubi* Pers., Obs. Myc. 1: 84. 1796; ≡ *Hypoderma virgultorum* DC., Fl. Franç. 3 ed. 6: 165. 1815 (an avowed substitute); ≡ *H. virgultorum* DC. ex Saint Amans, Fl. Agen. 515. 1821; ≡ *Lophoderma rubi* (Pers.) ex Chev., J. Phys. 94: 31. 1822; ≡ *Hysterium rubi* Pers. ex Fr., Syst. Myc. 2: 587. 1823].

VERSUS LECTOTYPUS: *Hypoderma arundinaceum* (Schrad.) DC. ex Saint Amans, Fl. Agen. 516. 1821. (*typ. rej. prop.*).

DISCUSSION

When Chevallier (1822) divided *Hypoderma* DC. ex Saint Amans into two groups, he retained *H. arundinaceum* in *Hypoderma*, in effect selecting a lectotype for the name, and erected *Lophoderma* to include *L. rubi* (an obligate synonym of *H. virgultorum*). De Notaris (1847) revised the genus *Hypoderma* with the exclusion of *H. arundinaceum*, but the inclusion of *H. rubi*. This later usage has been followed in all major studies with the exception of that of O. Kuntze (1898). The proposal seeks to legalize the nomenclature of more than 140 years of reference to the genus *Hypoderma* and incidentally to eliminate any claim the rarely and always incorrectly used *Lophoderma* might have to species currently placed in *Hypoderma*.

PROPOSAL 2

Proposal for the conservation of the generic name *Lophodermium* Chevallier (1826) (Hypodermataceae).

Lophodermium Chevallier, Fl. Paris 1: 435. 1826. (*nom. cons. prop.*).

LECTOTYPUS: *L. arundinaceum* (Schrad. ex Saint Amans) Chev. (*typ. cons. prop.*).

Discussion

Whether *Hypoderma* DC. ex Saint Amans remains typified by *H. arundinaceum* in accordance with the choice of Chevallier (1822) or, through the acceptance of proposal 1, becomes typified by *H. rubi* (under the name of *H. virgultorum*), the name *Lophodermium* Chev. is superfluous and therefore illegitimate, because its original circumscription included both species. Proposal 2 serves a two-fold purpose: to conserve the name of a genus that has been in use for 140 years, and, to conserve it in the sense of De Notaris. Thus, the revision by De Notaris of both *Hypoderma* and *Lophodermium*, which is what every one is following, can be made legal.

Reasons for Conservation

According to a strict application of the rules of nomenclature, without the acceptance of the above-mentioned proposals, all *Lophodermium* species would have to be placed in the genus *Hypoderma* and all *Hypoderma* species in the genus *Lophoderma*. This is essentially what was proposed by O. Kuntze (1898) except that he erected *Hypodermopsis* O. Kuntze, an inadvertent but avowed substitute for *Lophoderma*. More than 100 species of *Lophodermium* and about 50 species of *Hypoderma*, more than one-half of the known species of the Hypodermataceae, would be involved in changes if the two genera, *Hypoderma* and *Lophodermium*, were not retained with the circumscriptions of De Notaris. With retention in this sense there would be no ambiguity attached to either name. While *Hypoderma* is validly published and legitimate there is no legitimate name for *Lophodermium* in the sense of De Notaris. Acceptance of the proposals would not involve the creation of new combinations or author citations but would merely legalize the genus *Lophodermium* and the usage of combinations under both genera in the sense of De Notaris and of current practice.

Key to Genera of Hypodermataceae

A. Stromata simple, mono-ascocarpous ..... B.
  B. Basal stromatic tissue weakly developed ..... C.
    C. Ascocarps elliptical to linear ..... D.
      D. Ascocarps mostly linear, often nervisequious, dark brown to black; pycnidia continuous or in broken lines ..... E.
        E. Ascospores rod-shaped ..... I. VIRGELLA
        E. Ascospores bifusiform ..... II. ISTHMIELLA
        E. Ascospores clavate to clavate-cylindrical ..... III. LIRULA
      D. Ascocarps mostly elliptical, concolorous to black; pycnidia scattered or unknown ..... F.
        F. Asci more or less broadly saccate to clavate ..... G.
          G. Ascospores not bifusiform ..... H.
            H. Ascocarps subcuticular, ascospores clavate ..... IV. HYPODERMELLA
            H. Ascocarps subepidermal, ascospores variable ..... I.
              I. Ascospores rod-shaped, continuous ..... V. PLOIODERMA
              I. Ascospores clavate, continuous ..... VI. DAVISOMYCELLA
              I. Ascospores elongated, fusiform, 2-celled ..... VII. ELYTRODERMA
            H. Ascocarps subhypodermal, ascospores clavate ..... VIII. LOPHODERMELLA
          G. Ascospores bifusiform ..... J.
            J. Ascocarps subcuticular ..... K.
              K. Pycnidia large, often effuse, conspicuous ..... IX. BIFUSELLA
              K. Pycnidia small, discrete, inconspicuous ..... X. DUPLICARIA
            J. Ascocarps subepidermal ..... XI. SOLEELLA
        F. Asci narrowly clavate or cylindrical ..... L.
          L. Asci clavate and typically long-stalked, ascospores rod-shaped ..... XII. HYPODERMA
          L. Asci more or less cylindrical ..... M.

M. Ascospores rod-shaped.....XIII. MELODERMA
M. Ascospores filiform.....N.
N. Ascospores continuous.....XIV. LOPHODERMIUM
N. Ascospores phragmosporous.....XV. LOPHOMERUM
C. Ascocarps subcircular to polyhedral.....XVI. COCCOMYCES
B. Basal stromatic tissue strongly developed.....O.
O. Ascospores clavate to filiform, continuous.....XVII. COLPOMA
O. Ascospores clavate, phragmosporous.....XVIII. XYLOSCHIZON
O. Ascospores bifusiform, phragmosporous.....XIX. BIFUSEPTA
A. Stromata complex, poly- and usually syncarpous.....P.
P. Ascospores hyaline, clavate to filiform.....Q.
Q. Ascocarps numerous in stroma; ascospores filiform to clavulate.....XX. RHYTISMA
Q. Ascocarps few in stroma; ascospores broadly clavate.....XXI. PLACUNTIUM
P. Ascospores brown, ovoid.....XXII. NYMANOMYCES

Genera of Hypodermataceae

I. **Virgella** gen. nov. Hypodermatacearum

Hysterothecia hypophylla, atrofusca, innata, nervisequia, longitudinali incisura aperientia, primordio incisurae conspicuo; stratum tegens atri pseudoparenchymatis; stratum basilare plectenchymaticum achroum. Asci saccato-clavati. Paraphyses simplices, filiformes. Ascosporae bacillares, muco involutae. Pycnidia simplicia continua epiphylla; stratum conidiophororum applanatum; spermatia minuta, bacillaria.

ETYMOLOGIA: *virga*, a streak or stripe of color on clothes, et *-ella*, a diminutive suffix; in reference to the appearance of the hysterothecium.

SPECIES TYPICA: *Virgella robusta* (v. Tub.) Darker

Hysterothecia hypophyllous, dark brown, innate, nervisequious, opening by a longitudinal fissure; primordium of slit conspicuous; covering layer of dark pseudoparenchyma; basal layer plectenchymatous, colorless. Asci saccate-clavate. Paraphyses simple, filiform. Ascospores rod-shaped, enclosed in gelatinous sheath. Pycnidia simple, continuous, epiphyllous; conidiophore layer flat; spermatia minute, bacillar.

1. ***Virgella robusta*** (v. Tub.) comb. nov.
≡ *Lophodermium infectans* Mayr, Die Waldungen von Nordamerika. 336. 1890 (nom. nud.).
≡ *Hypoderma robustum* v. Tub., Arb. Biol. Abth. Land- u. Forstw. kais. Gesundh. 2(1): 16. 1901.

SPECIMEN ISOTYPICUM: on *Abies concolor* (Gord.) Parry, San Bernardino Mountains, California, *H. Mayr*, in Farlow Herbarium.

In conversation Professor C. von Tubeuf informed the writer a number of years ago that Mayr's material, through serious neglect, had become worthless and had been discarded. The isotype material sent to Professor W. G. Farlow by Mayr is a part of the original collection and was apparently the basis also for von Tubeuf's later description (see Boyce, Mycologia 19: 284, 285. 1927).

II. **Isthmiella** gen. nov. Hypodermatacearum

Genus *Virgellae* subsimile, sed ascosporis bifusiformibus.

ETYMOLOGIA: *isthmus*, isthmus, et *-ella*, a diminutive suffix, in reference to the spore shape.

SPECIES TYPICA: *Isthmiella abietis* (Dearn.) Darker

A genus somewhat similar to *Virgella*, but with bifusiform ascospores.

1. ***Isthmiella abietis*** (Dearn.) comb. nov.
≡ *Bifusella abietis* Dearn., Mycologia 18: 239. 1926.

SPECIMEN HOLOTYPICUM: in Dearness Herbarium, on *Abies lasiocarpa* (Hook.) Nutt., Challis Nat. For., Bonanza, Ida., Aug. 7, 1911. *G. G. Hedgcock: 9395.*

2. ***Isthmiella crepidiformis*** (Darker) comb. nov.
≡ *Bifusella crepidiformis* Darker, Contr. Arnold Arbor. 1: 22. 1932.

3. ***Isthmiella faullii*** (Darker) comb. nov.
≡ *Bifusella faullii* Darker, Contr. Arnold Arbor. 1: 19. 1932.

III. **Lirula** gen. nov. Hypodermataceae

Genus *Virgellae* subsimile, sed ascosporis clavato-filiformibus.

ETYMOLOGIA: *lira*, a furrow, et *-ula*, a diminutive suffix; in reference to the appearance of the hysterothecium, especially when open.

SPECIES TYPICA: *L. nervisequia* (DC. ex Fr.) Darker
A genus somewhat similar to *Virgella*, but with clavate-filiform ascospores.

1. ***Lirula nervisequia*** (DC. ex Fr.) comb. nov.
≡ *Hypoderma nervisequum* DC., Fl. Franç. 6: 167. 1815.
≡ *Lophoderma nervisequum* (DC.) ex Chev., J. Phys. 94: 31. 1822.
≡ *Hysterium nervisequium* (DC.) ex Fr., Syst. Myc. 2: 587. 1823.
≡ *Lophodermium nervisequium* (DC. ex Fr.) Chev., Fl. Paris 1: 435. 1826.
≡ *Lophodermium nervisequium* (DC. ex Fr.) Rehm, in Rabh., Krypt.-Fl. II. 1(3): 44. 1887.
≡ *Hypodermopsis nervisequa* (DC. ex Fr.) O. Kuntze, Rev. Gen. Pl. 3(2): 487. 1898.
≡ *Hypodermella nervisequia* (DC. ex Fr.) Lagerberg, Medd. Stat. Skogsförsöksanst. 7: 148. 1910.
= *Hypodermella lirelliformis* Darker, Contrib. Arnold Arbor. 1: 45. 1932.

The isotype of the Friesian holotype is present in Mougeot's ample collection which is preserved in the herbarium of the Conservatoire et Jardin Botaniques (G-DC), Geneva, Switzerland. This specimen has only the small, inconspicuous, scattered pycnidia and not the broad, conspicuous kind illustrated by Hartig, von Tubeuf, and others. Not having seen the type of *Hysterium nervisequium* at the time of publication, Darker (1932) assumed the Hartig illustrations to represent the pycnidial state of *H. nervisequium*. Unfortunately this was not so and consequently *H. lirelliformis* Darker must become a synonym of *L. nervisequia*. The species wrongly determined and described as *H. nervisequia* by Darker is now proposed as a new variety.

2. *Lirula nervisequia* (DC. ex Fr.) Darker var. ***conspicua*** var. nov.

Varietas *Lirellae nervisequiae* similis, sed pycnidiis conspicuis, epiphyllis, continuis secundum sinum acus, subeffusis, 280–630 μ latis, atrobrunneis post dissipationem spermatiorum.

ETYMOLOGIA: *conspicua*, conspicuous.

SPECIMEN TYPICUM: D. Saccardo, Mycoth. Ital. No. 504. 1900. "*Lophodermium nervisequum* (DC.) Rehm—in foliis *Abietis pectinatae*. Maio 1898. Ab. A. Carestia."

Variety similar to *Lirula nervisequia* but with conspicuous pycnidia, epiphyllous, continuous along the sinus of the needle, somewhat effuse, 280–630 μ wide, dark brown after the dispersal of the spermatia.

STATUS PYCNIDICUS: *Hypodermina nervisequa* (Lk.) v. Höhn., Sitzb. k. Akad. Wiss. Wien, Math.-nat. Klasse. Abt. I. 125(1/2): 55. 1916.

≡ *Hypodermium nervisequum* Lk., Sp. Pl. 6(2): 89. 1824.

≡ *Schizoderma nervisequum* (Lk.) Duby, Bot. Gall. 2: 885. 1830.

= *Daedala nervicola* Hazslinszky, Verh. Zool.-bot. Ges. Wien 37: 154. 1887.

From von Höhnel's description of the pycnidial state it appears that he was describing the pycnidia of the variety *conspicua* when he made the new combination *Hypodermina nervisequa* (Lk.) v. Höhn. and it seems quite likely that both Link and Duby were describing the same fungus. For various reasons von Höhnel rejected both *Hypodermium* Lk. and *Schizoderma* Duby but overlooked the genus *Daedala* Hazsl. with the species *D. nervicola* Hazsl. From an examination of the type specimen, this, too, appears to be the imperfect state of the var. *conspicua*. If so, the genus has priority over *Hypodermina* v. Höhn., but unfortunately the genus name is so similar to *Daedalea* P. ex Fr., with which it has been confused by the only writers who have cited it (Hilitzer, 1929, Darker, 1932, and Tehon, 1935), that it seems best to invoke Article 75 of the International Code of Botanical Nomenclature and abandon it. In this event it may be treated as an orthographic variant of *Daedalea* Pers. ex Fr. of which it becomes a later homonym.

The pycnidial state of *L. nervisequia* var. *conspicua*, until proof is shown to the contrary, should be called *Hypodermina nervisequa* (Lk.) v. Höhn. On the other hand, the pycnidial state of *L. nervisequia* does not appear to have been named, although it was briefly described by Darker (1932) as the pycnidial state of *Hypodermella lirelliformis*.

3. ***Lirula abietis-concoloris*** (Mayr ex Dearn.) comb. nov.

≡ *Lophodermium abietis-concoloris* Mayr, Die Waldungen von Nordamerika, 336. 1890 (nom. nud.).

≡ *Hypodermella abietis-concoloris* (Mayr) ex Dearn., Mycologia 16: 150. 1924.

SPECIMEN NEOTYPICUM: in Dearness Herbarium, on *Abies concolor* (Gord.) Parry, near Whitney, Baker Co., Ore. Oct. 28, 1920. *J. S. Boyce*: 732.

Von Tubeuf (1901) stated that Mayr's material was immature and in conversation in 1932 told the writer that through lack of care Mayr's collections had become worthless and had been discarded. Dearness revived the specific epithet for several specimens which he considered to fit Mayr's description. Although doubt will always remain concerning Mayr's collection, the neotype specimen of Dearness is good and defines a distinctive species. It represents, however, but one of several closely related species or varieties of an aggregate which extends throughout the mountains of western North America.

4. ***Lirula macrospora*** (Hartig) comb. nov.
≡ *Hysterium* (*Hypoderma*) *macrosporum* Hartig, Wicht. Krankh. Waldb. 101. 1874.
≡ *Lophodermium macrosporum* (Hartig) Rehm, in Rabh., Krypt.-Fl. II. 1(3): 45. 1887.
≡ *Hypodermopsis macrospora* (Hartig) O. Kuntze, Rev. Gen. Pl. 3(2): 487. 1898.
≡ *Hypodermella macrospora* (Hartig) Lagerberg. Medd. Stat. Skogsförsöksanst. 7: 113. 1910.
= *Lophodermium filiforme* Darker, Contr. Arnold Arbor. 1: 85. 1932.

STATUS PYCNIDICUS: *Hypodermina hartigii* Hilitzer, Věd. Spisy Vyd. Československ. Akad. Zeměd. 3: 57. 1929.

On the basis of spore shape this species has always presented a problem to taxonomists, falling as it does more or less intermediately between *Lophodermium* and *Hypodermella*. Its general morphology, life cycle, and strongly parasitic nature suggest relationships with *Lirula* (the *Hypodermella* group on *Abies*) rather than with *Lophodermium* which is in agreement with Lagerberg's earlier contention. There is on *Picea* an aggregate of closely related species or varieties, and although the writer accepts for the present Terrier's placement of *Lophodermium filiforme* in the synonymy of *L. macrospora*, further study may necessitate its reestablishment as a distinct taxon.

5. ***Lirula mirabilis*** (Darker) comb. nov.
≡ *Hypodermella mirabilis* Darker, Contr. Arnold Arbor. 1: 46. 1932.

6. ***Lirula nervata*** (Darker) comb. nov.
≡ *Hypodermella nervata* Darker, Contr. Arnold Arboretum 1: 51. 1932.

7. ***Lirula punctata*** (Darker) comb. nov.
≡ *Hypodermella punctata* Darker, Contr. Arnold Arbor. 1: 48. 1932.

IV. **Hypodermella** v. Tub., Bot. Centralbl. 61: 49. 1895.

Hysterothecia black, elliptical, often in a more or less continuous row, subcuticular; covering layer dark without evident opening mechanism; hymenium flat, arising from a thin parenchymatous subhymenial layer seated on a thin basal layer of light brown pseudoparenchyma darkening below and continuous with a compact dark pseudoparenchyma occupying the epidermis and to a lesser extent the hypodermis. Asci clavate, 4-spored at maturity. Ascospores clavate. Paraphyses short, simple. Pycnidia numerous, black.

TYPE-SPECIES: *Hypodermella laricis* v. Tub.

1. *Hypodermella laricis* v. Tub., Bot. Centralbl. 61: 49. 1895.
= *Hypodermella* laricis v. Tub. var. *octospora* Dearn., Mycologia 18: 241. 1926.

PYCNIDIAL STATE:? *Leptothyrella laricis* Dearn., Mycologia 20: 240. 1928.

The type of *H. laricis* var. *octospora* Dearn. is quite immature and it is quite probable that four of the eight spores would have aborted before reaching maturity.

DISPOSITION OF SYNONYMOUS EPITHETS (HYPODERMELLA)

abietis-concoloris (Mayr) Dearn. ≡ *Lirula abietis-concoloris*
ampla (Davis) Dearn. ≡ *Davisomycella ampla*
arcuata Darker ≡ *Lophodermella arcuata*
cerina Darker ≡ *Lophodermella cerina*
concolor (Dearn.) Darker ≡ *Lophodermella concolor*
conjuncta Darker ≡ *Lophodermella conjuncta*
hiratsukae Darker ≡ *Davisomycella hiratsukae*
lacrimiformis Darker ≡ *Davisomycella lacrimiformis*
laricis v. *octospora* Dearn. = *Hypodermella laricis*
limitata Darker ≡ *Davisomycella limitata*
lirelliformis Darker = *Lirula nervisequia*
macrospora (Hartig) Lagerb. ≡ *Lirula macrospora*
medusa Dearn. ≡ *Davisomycella medusa*
mirabilis Darker ≡ *Lirula mirabilis*
montana Darker ≡ *Davisomycella montana*
montivaga (Petr.) Dearn. ≡ *Lophodermella montivaga*
montivaga v. *concolor* Dearn. ≡ *Lophodermella concolor*
nervata Darker ≡ *Lirula nervata*
nervisequia (DC. ex Fr.) Lagerb. ≡ *Lirula nervisequia*
punctata Darker ≡ *Lirula punctata*
sulcigena (Rostr.) v. Tub. ≡ *Lophodermella sulcigena*

V. **Davisomycella** gen. nov. Hypodermatacearum

Hysterothecia innata, externe atra, plerumque brevia ellipticaque usque oblonga, aut elongata, subepidermalia, primordio longitudinalis incisurae simplici parenchymatoso aut ignoto. Hymenium subcupulatum; subhymenium tenue, hyalinum. Asci clavati vel saccati. Paraphyses numerosae filiformes simplices. Ascosporae clavatae ad basin attenuatae, in maturitate non fasciculatae usque fasciculatae. Pycnidia, ubi nota, parva applanata, superficiei acus concoloria.

ETYMOLOGIA: A Dr. J. J. Davis qui primam speciem hujus generis descripsit, *mykes*, fungus, et *-ella*, a diminutive suffix.

SPECIES TYPICA: *Davisomycella ampla* (Davis) Darker

Hysterothecia innate, externally black, for the most part short elliptical to oblong, or elongate, subepidermal, with primordium of the longitudinal slit simple, parenchymatous, or unknown. Hymenium somewhat cupulate; subhymenium thin, hyaline. Asci clavate or saccate. Paraphyses numerous, filiform, simple. Ascospores clavate, at base attenuated, at maturity not fasciculate to fasciculate. Pycnidia, where known, small flat, concolorous with surface of the needle.

1. ***Davisomycella ampla*** (Davis) comb. nov.
≡ *Lophodermium pinastri* (Schrad. ex Hook.) Chev. var. *amplum* Davis, Trans. Wisc. Acad. Sci. Arts & Lett. 18: 252. 1918.
≡ *Lophodermium amplum* (Davis) Davis, l.c. 19: 695. 1919.
≡ *Hypodermella ampla* (Davis) Dearn., Mycologia 16: 152. 1924.

2. ***Davisomycella hiratsukae*** (Darker) comb. nov.
≡ *Hypodermella hiratsukae* Darker, J. Arnold Arbor. 16: 364. 1935.

3. ***Davisomycella lacrimiformis*** (Darker) comb. nov.
≡ *Hypodermella lacrimiformis* Darker, Contr. Arnold Arbor. 1: 40. 1932.

4. ***Davisomycella limitata*** (Darker) comb. nov.
≡ *Hypodermella limitata* Darker, Contr. Arnold Arbor. 1: 39. 1932.

5. ***Davisomycella medusa*** (Dearn.) comb. nov.
≡ *Hypodermella medusa* Dearn., Mycologia 16: 152. 1924.

6. ***Davisomycella montana*** (Darker) comb. nov.
≡ *Hypodermella montana* Darker, Contr. Arnold Arbor. 1: 44. 1932.

VI. **Ploioderma** gen. nov. Hypodermatacearum

Genus *Davisomycellae* simile sed ascosporis bacillaribus. Hysterothecia atra aut paene achroa, elliptica, subepidermalia. Hymenium subconcavum; subhymenium tenue, achroum. Asci clavato-saccati. Paraphyses simplices, filiformes. Ascosporae breves bacillares. Pycnidia simplicia applanata, aut ignota.

ETYMOLOGIA: *ploion*, boat, et *derma*, skin.

SPECIES TYPICA: *Ploioderma hedgcockii* (Dearn.) Darker

Genus similar to *Davisomycella* but with ascospores rod-like. Hysterothecia black or almost colorless, elliptical, subepidermal. Hymenium somewhat concave; subhymenium thin, colorless. Asci clavate-saccate. Paraphyses simple, filiform. Ascospores short, rod-like. Pycnidia simple, flat, or unknown.

1. ***Ploioderma hedgcockii*** (Dearn.) comb. nov.
≡ *Hypoderma hedgcockii* Dearn., Mycologia 18: 240. 1926.

STATUS PYCNIDICUS: *Leptostroma hedgcockii* Dearn., Mycologia 20: 240. 1928.

2. ***Ploioderma lethale*** (Dearn.) comb. nov.
≡ *Hypoderma lethale* Dearn., Mycologia 18: 241. 1926.

3. ***Ploioderma pedatum*** (Darker) comb. nov.
≡ *Hypoderma pedatum* Darker, Contr. Arnold Arbor. 1: 30. 1932.

VII. ELYTRODERMA Darker, Contr. Arnold Arbor. 1: 62. 1932.

Hysterothecia black, short elliptical to elongated, subepidermal; hymenium concave; subhymenial layer comparatively thin, colorless. Asci fusiform-clavate. Paraphyses simple, filiform. Ascospores large, fusiform, fasciculate, 2-celled. Pycnidia simple, concolorous.

TYPE-SPECIES: *Elytroderma deformans* (Weir) Darker

1. *Elytroderma deformans* (Weir) Darker, Contr. Arnold Arbor. 1: 63. 1932.
≡ *Hypoderma deformans* Weir, J. Agric. Res. 6: 277. 1916.

2. ***Elytroderma hispanicum*** (Torres Juan) comb. nov.
≡ *Hypoderma hispanicum* Torres Juan, in Benito Martinez & Torres Juan, Inst. Forestal Invest. Exper. Bol. 88: 67. 1965.

VIII. LOPHODERMELLA v. Höhn., Ber. deutsch. bot. Ges. 35: 247. 1917.

Hysterothecia more or less concolorous with needle surface, short to elongated, subhypodermal, circular to elliptical in cross-section. Hymenium cupulate; subhymenium thin. Asci clavate to subcylindric. Paraphyses simple, filiform. Ascospores clavate, subbiseriate to fasciculate. Pycnidia small, flask-like, or unknown.

TYPE-SPECIES: *Lophodermella sulcigena* (Rostr.) v. Höhn.

1. *Lophodermella sulcigena* (Rostr.) v. Höhn., Ber. deutsch. bot. Ges. 35: 247. 1917.
   = ? *Hypodermium sulcigenum* Lk., Sp. Pl. 6(2): 89. 1824.
   ≡ ? *Schizoderma sulcigenum* (Lk.) Duby, in De Candolle & Duby, Bot. Gall. 2: 885. 1830.
   = *Hypoderma sulcigenum* Rostr., Tidsskr. Skovbr. 6: 284. 1883.
   ≡ *Hypodermella sulcigena* (Rostr.) v. Tub., Bot. Centralbl. 61: 49. 1895.
   = *Hypoderma pinicola* Brunch., Bergens Mus. Aarbog 8: 6. 1892.
   ≡ *Hypodermopsis pinicola* (Brunch.) O. Kuntze, Rev. Gen. Pl. 3(2): 487. 1898.

The epithet *Hypodermium sulcigenum* Lk. was applied to a species generally thought to represent a pycnidial state. In his treatment of the genus *Hypodermium*, von Höhnel (1916) dismissed the species *sulcigenum* with the brief statement that it was considered to be an ascomycete. As the existence of a conidial state in *Lophodermella sulcigena* has never been demonstrated it seems quite possible that von Höhnel was correct and that Link and Duby had the ascocarp state before them although the description of the perfect state stems only from Rostrup's later account.

Hendersonia acicola v. Tub. was once conjectured to be the imperfect state of *Lophodermella sulcigena*, but the *Hendersonia* is only another of the numerous secondary fungi which attack needles infected by hypodermataceous species and serve in the natural biological control of the latter. In the related *Hypodermella concolor*, however, a careful search will often reveal here and there a small flask-like structure bearing minute spermatia-like spores seated in a substomatal chamber. These minute, rust-like spermatia are not inconsistent with what one might expect to find in this deep-seated subhypodermal genus. The stoma would provide a natural exit for the spermatia through the thick epidermis and hypodermis.

2. ***Lophodermella arcuata*** (Darker) comb. nov.
   ≡ *Hypodermella arcuata* Darker, Contr. Arnold Arbor. 1: 57. 1932.

3. ***Lophodermella cerina*** (Darker) comb. nov.
   ≡ *Hypodermella cerina* Darker, Contr. Arnold Arbor. 1: 61. 1932.

4. ***Lophodermella concolor*** (Dearn.) comb. nov.
   ≡ *Hypodermella montivaga* (Petr.) Dearn. f. *concolor* Dearn. Mycologia 18: 242. 1926.
   ≡ *Hypodermella concolor* (Dearn.) Darker, Contr. Arnold Arbor. 1: 59. 1932.

5. ***Lophodermella conjuncta*** (Darker) comb. nov.
≡ *Hypodermella conjuncta* Darker, Contr. Arnold Arbor. 1: 60. 1932.

6. *Lophodermella montivaga* Petr., in Petr. & Syd., Ann. Myc. 20: 191. 1922.
≡ *Hypodermella montivaga* (Petr.) Dearn., Mycologia 16: 151. 1924.

IX. BIFUSELLA v. Höhn., Ann. Myc. 15: 318. 1917.

Hysterothecia black, elliptical, subcuticular; hymenium flat, subhymenial layer thin. Asci clavate. Paraphyses wanting or tending to disappear at maturity. Ascospores bifusiform or more or less rod-like and tending towards a bifusiform condition. Pycnidia large or, if small, tending to coalesce into large areas, conspicuous, covered by a thin pseudoparenchymatous layer attached to the cuticle; spermatia relatively large, bacillar.

TYPE-SPECIES: *Bifusella linearis* (Pk.) v. Höhn.

1. *Bifusella linearis* (Pk.) v. Höhn., Ann. Myc. 15: 318. 1917.
≡ *Rhytisma lineare* Pk., N. Y. St. Mus. Ann. Rept. 25 (1871): 100. 1873.
≡ *Hypoderma lineare* (Pk.) Thüm., Diagn. Mycoth. Univ. Cent. X-XII. 12. 1878.
≡ *Lophodermium lineare* (Pk.) Ell. & Ev., N. Amer. Pyren. 721. 1892.
≡ *Hypodermopsis linearis* (Pk.) O. Kuntze, Rev. Gen. Plant. 3(2): 487. 1898.

PYCNIDIAL STATE: ?*Hypodermium effusum* Schw., Syn. Am. Bor. 297. 1822.

2. ***Bifusella pini*** (Dearn.) comb. nov.
≡ *Hypoderma robustum* v. Tub. var. pini Dearn., Mycologia 16: 149. 1924.
≡ *Hypoderma pini* (Dearn.) Darker, Contr. Arnold Arbor. 1: 35. 1932.

3. ***Bifusella saccata*** (Darker) comb. nov.
≡ *Hypoderma saccatum* Darker, Contr. Arnold Arbor. 1: 33. 1932.

DISPOSITION OF SYNONYMOUS EPITHETS (BIFUSELLA)

abietis Dearn. ≡ *Isthmiella abietis*
crepidiformis Darker ≡ *Isthmiella crepidiformis*
faullii Darker ≡ *Isthmiella faullii*
striiformis Darker ≡ *Soleella striiformis*

X. DUPLICARIA Fckl., Symb. Myc. 265. 1870.

Hysterothecia black, elliptical, subcuticular, opening irregularly; hymenium cupulate, at maturity flat, subhymenial layer colorless, grading into a thin basal layer of large brownish cells in contact with brown discolored epidermal cells occupied by dark brown hyphae. Asci clavate-saccate. Ascospores bifusiform, continuous, the lower section tending to taper basally. Paraphyses simple, filiform, as long as the asci. Pycnidia small, black.

TYPE-SPECIES: *Duplicaria empetri* (Fr. ex Fr.) Fckl.

1. *Duplicaria empetri* (Fr. ex Fr.) Fckl., Symb. Myc. 265. 1870.
≡ *Xyloma empetri* Fr., Obs. Myc. 2: 363. 1818.
≡ *Rhytisma empetri* (Fr.) Fr., Vetensk. Akad. Handl. 105. 1819.
≡ *Rhytisma empetri* (Fr.) ex Fr., Elench. Fung. 2: 127. 1828.

PYCNIDIAL STATE: *Melasmia empetri* Magnus, Ber. Deutsch. Bot. Ges. 4: 104. 1886.

XI. **Soleella** gen. nov. Hypodermatacearum

Hysterothecia nigra, elliptica usque elongato-linearia, secundum lineas stomatum, subepidermalia; hymenium applanatum; subhymenium tenue. Asci subclavati; paraphyses simplices; ascosporae bifusiformes, raro trifusiformes. Pycnidia ignota.

ETYMOLOGIA: solea, sandal, et *-ella*, a diminutive suffix.

SPECIES TYPICA: *Soleella striiformis* (Darker) Darker

Hysterothecia black, elliptical to elongated linear, along stomatal lines, subepidermal; hymenium flat; subhymenium thin. Asci somewhat clavate; paraphyses simple, filiform; ascospores bifusiform, occasionally trifusiform. Pycnidia unknown.

1. ***Soleella striiformis*** (Darker) comb. nov.
   ≡ *Bifusella striiformis* Darker, Contr. Arnold Arbor. 1: 23. 1932.

XII. HYPODERMA DC. ex Saint Amans emend. De Not., Giorn. Bot. Ital. 2(2): (35). 1847.

≡ *Hypoderma* DC., *in* Lam. & DC., Fl. Franç. 3 ed. 2: 304. 1805; 3 ed. 6: 165. 1815.
≡ *Hypoderma* DC. ex Saint Amans, Fl. Agen. 515. 1821.
≡ *Lophoderma* Chev., Journ. Phys. 94: 31. 1822.
≡ *Hypoderma* DC. ex Fckl., Jahrb. Nassau. Ver. Naturk. 23–24: 257. 1870.
≡ *Hypodermopsis* O. Kuntze, Rev. Gen. Plant. 3(2): 487. 1898.
= *Epidermella* Tehon, Illinois Biol. Monogr. 13(4): 119. 1935.
= ? *Locelliderma* Tehon, Illinois Biol. Monogr. 13(4): 122. 1935.

Hysterothecia elliptical, black; asci clavate with well developed stalk; ascospores rod-shaped or fusiform, often with a false septum or becoming one-septate at maturity.

TYPE-SPECIES: *Hypoderma rubi* (Pers. ex Chev.) De Not. (*typus cons. prop.*).

1. *Hypoderma rubi* (Pers. ex Chev.) De Not., Giorn. Bot. Ital. 2(2): (37). 1847.
   ≡ *Hysterium rubi* Pers., Obs. Myc. 1: 84. 1796; Syn. Fung. 1: 100. 1801.
   ≡ *Hypoderma virgultorum* DC., Fl. Franç. 3 ed. 6: 165. 1815 (an avowed substitute).
   ≡ *Hypoderma virgultorum* DC. ex Saint Amans, Fl. Agen. 515. 1821 [ut *virgultarum*].
   ≡ *Lophoderma rubi* (Pers.) ex Chev., J. Phys. 94: 31. 1822.
   ≡ *Hypoderma rubi* (Pers.) ex Chev., l.c. 31. *pro syn.*
   ≡ *Hysterium rubi* (Pers.) ex Fr., Syst. Myc. 2: 587. 1823.
   ≡ *Lophodermium rubi* (Pers. ex Chev.) Chev., Fl. Paris 1: 436. 1826.
   ≡ *Hypoderma virgultorum* DC. f. *rubi* (Pers. ex Chev.) Rehm, in Rabh. Krypt.-Fl. II. 1(3): 33. 1887 [ut (Pers.) DC.].
   ≡ *Hypodermopsis rubi* (Pers. ex Chev.) O. Kuntze, Rev. Gen. Plant. 3(2): 487. 1898 [ut (Pers.) OK.].

≡ *Hypoderma commune* (Fr.) Duby f. *rubi* (Pers. ex Chev.) Rehm, Bayer. Bot. Ges. München 13: 112. 1912 [ut (Pers.) DC.].

2. *Hypoderma conigenum* (Pers.) DC. ex S. F. Gray, Nat. Arrangm. Brit. Plants, 509. 1821 [ut *conigerum*].

≡ *Hysterium conigenum* Pers., Obs. Myc. 1: 30. 1796 [ut *conigerum*]; Syn. Fung. 1: 102. 1801.

≡ *Hypoderma conigenum* (Pers.) DC., Fl. Franç. 3 ed. 2: 305. 1805.

≡ *Hypodermopsis conigena* (Pers. ex S. F. Gray) O. Kuntze, Rev. Gen. Plant. 3(2): 487. 1898 [ut [P.] (DC., Cooke)].

= *Hysterium conigenum* Fr., Syst. Myc. 2: 586. 1823.

≡ *Hysterium* (*Hypoderma*) *conigenum* (Fr.) Cke., Handb. Brit. Fungi 2: 762. 1871.

≡ *Hypoderma conigenum* (Fr.) Cke., in Massee, Brit. Fungus-Flora 4: 35. 1895 [ut (Pers.) Cke.].

As originally described *Hysterium conigenum* Pers. was said to occur on *Pinus abies*, now known as *Picea abies*, whereas *Hysterium conigenum* Fr. was reported on *Pinus silvestris*. Although Fries did not refer to any previous use of the epithet, Rehm, Saccardo, and Massee all ascribed it to Persoon, but like Fries and Cooke they definitely stated the host to be *Pinus silvestris*. Until it is determined whether we are dealing with a good species or perhaps with two species, the problem of nomenclature must remain in abeyance. Meanwhile, as stated by Rehm (1887), the species remains doubtful.

3. *Hypoderma cunninghamiae* (Keissl.) Teng, Sinensia 7: 261. 1936.

≡ *Hypoderma strobicola* v. Tub. f. *cunninghamiae* Keissl., Akad. Wiss. Wien, Math.-nat. Cl. Anzeiger 61(2): 13(4). 1942.

≡ *Hypoderma handelii* Petr., Sydowia 1: 371. 1947.

4. *Hypoderma thujae* Durrieu, Sydowia Beih. 1: 356. 1957.

DISPOSITION OF SYNONYMOUS EPITHETS (HYPODERMA)

arundinaceum (Schrad.) DC. ex Saint Amans ≡ *Lophodermium arundinaceum*
brachysporum (Rostr.) v. Tub. = *Meloderma desmazierii*
brachysporum (Rostr.) O. Kuntze = *Meloderma desmazierii*
commune f. *rubi* (Pers. ex Chev.) Rehm ≡ *Hypoderma rubi*
conigenum (Fr.) Cke. = *Hypoderma conigenum* (Pers.) DC. ex S. F. Gray
deformans Weir ≡ *Elytroderma deformans*
desmazierii Duby ≡ *Meloderma desmazierii*
handelii Petr. ≡ *Hypoderma cunninghamiae*
hedgcockii Dearn. ≡ *Ploioderma hedgcockii*
hispanicum Torres Juan ≡ *Elytroderma hispanicum*
juniperinum (Fr.) O. Kuntze = *Lophodermium juniperi*
laricinum (Duby) O. Kuntze ≡ *Lophodermium laricinum*
lethale Dearn. ≡ *Ploioderma lethale*
lineare (Pk.) Thüm. ≡ *Bifusella linearis*
namyslowskii Birula et al. = *Meloderma desmazierii*
nervisequum DC. ≡ *Lirula nervisequia*
pedatum Darker ≡ *Ploioderma pedatum*

pinastri (Schrad.) DC. ≡ *Lophodermium pinastri*
pini (Dearn.) Darker ≡ *Bifusella pini*
pinicola Brunch. = *Lophodermella sulcigena*
robustum v. Tub. ≡ *Virgella robusta*
robustum var. *pini* Dearn. ≡ *Bifusella pini*
sabinae (Fautr.) O. Kuntze = *Lophodermium juniperi*
saccatum Darker ≡ *Bifusella saccata*
strobicola v. Tub. = *Meloderma desmazierii*
strobicola f. *cunninghamiae* Keissl. ≡ *Hypoderma cunninghamiae*
sulcigenum (Lk.) Rostr. ≡ *Lophodermella sulcigena*
virgultorum DC. ≡ *Hypoderma rubi*
virgultorum DC. ex Saint Amans ≡ *Hypoderma rubi*
virgultorum f. *rubi* (Pers. ex Chev.) Rehm ≡ *Hypoderma rubi*

XIII. **Meloderma** gen. nov. Hypodermatacearum

Hysterothecia elliptica, saepe in ordine, atra sed typice a cana zona circumdata, subepidermalia sed subcuticularia prope labias; labiae ochroae ordine externarum tumidarum cellularum; tegmen atrum pseudoparenchymaticum, tenue in margine; stratum basilare plectenchymaticum; hymenium applanatum; asci subcylindrici; paraphyses primo simplices filiformes denique uncinatae, afflatae, subramosae in apice; ascosporae bacillares, subclavatae usque fusiformes, muco involutae. Pycnidia simplicia, applanata.

ETYMOLOGIA: *melas*, black, et *derma*, skin.

SPECIES TYPICA: *Meloderma desmazierii* (Duby) Darker

Hysterothecia elliptical, often in a row, black but typically surrounded by a grayish zone, subepidermal, but subcuticular near the lips; lips colorless with a row of outer swollen cells; dark covering layer pseudoparenchymatous, thin at margins; basal layer plectenchymatous; hymenium flat; asci subcylindrical; paraphyses at first simple, filiform, at length hooked, swollen, somewhat branched at tip; ascospores rod-like, somewhat clavate to fusiform, with gelatinous envelope. Pycnidia simple, flat.

1. ***Meloderma desmazierii*** (Duby) comb. nov.
≡ *Hypoderma desmazierii* Duby, Mém. Soc. Phys. Hist. Nat. Genève 16: 54. 1861.
≡ *Hypodermopsis desmazierii* (Duby) O. Kuntze, Rev. Gen. Pl. 3(2): 487. 1898 [ut *desmazieri*].
= *Lophodermium brachysporum* Rostr., Tidsskr. Skovbr. 6: 281. 1883.
≡ *Hypoderma brachysporum* v. Tub. Pflanzenkrankheiten durch kryptogame Parasiten verursacht, 247. 1895 non *H. brachysporum* Speg., Bol. Acad. Nac. Cienc. Cordoba 11: 116 [repr. pag.]. 1887.
≡ *Hypoderma brachysporum* (Rostr.) O. Kuntze, Rev. Gen. Pl. 3(2): 487. 1898.
≡ *Hypoderma strobicola* v. Tub., in v. Tub. & Smith, Diseases of Plants Induced by Cryptogamic Parasites, 233. 1897.
= *Lophodermium lineatum* Smith & Ramsbottom, Trans. Brit. Myc. Soc. 6: 365. 1920.

= *Hypoderma namyslowskii* Birula et al., Roczn. Nauk Roln. Lesnych, 20: 35. 1928.

STATUS PYCNIDICUS: *Leptostroma strobicola* Hilitzer, Věd. Spisy Vyd. Českoslov. Akad. Zeměd. 3: 99, 149. 1929.

XIV. LOPHODERMIUM Chev., Fl. Paris 1: 435. 1826 (*nom. cons. prop.*)

≡ *Hypoderma* Chev., Journ. Phys. 94: 31. 1822.
= *Aporia* Duby, Mém. Soc. Phys. Hist. Nat. Genève 16: 51. 1861.
= *Lophodermina* v. Höhn., Ber. Deutsch. Bot. Ges. 35: 418. 1917.
= *Lophodermellina* v. Höhn., Ber. Deutsch. Bot. Ges. 35: 419. 1917.
= *Dermascia* Tehon, Illinois Biol. Monogr. 13(4): 60. 1935.

Hysterothecia innate erumpent, elliptical, dull to shining black, opening by a longitudinal slit, opening mechanism well developed or wanting; hymenium more or less flat. Asci narrowly cylindric to cylindric clavate, 8-spored, occasionally 4-spored with 4 aborted spores present, mostly subacute at the apex. Paraphyses simple filiform. Ascospores simple, more or less uniformly filiform, hyaline, fasciculate, unicellular, surrounded by a thin gelatinous sheath. Pycnidia simple, round or elliptical, concolorous with host or colored, or black, or unknown. Spermatia simple, bacillar.

TYPE-SPECIES: *Lophodermium arundinaceum* (Schrad. ex Saint Amans) Chev. (*typus cons. prop.*).

1. *Lophodermium arundinaceum* (Schrad. ex Saint Amans) Chev., Fl. Paris 1: 435. 1826.
≡ *Hysterium arundinaceum* Schrad., Schrad. J. Bot. 2: 68. 1799.
≡ *Xyloma arundinaceum* (Schrad.) Reb., Prod. Flor. Neomarch., 342. 1804.
≡ *Hypoderma arundinaceum* (Schrad.) DC., Fl. Franç., 3 ed. 2: 305. 1805.
≡ *Hypoderma arundinaceum* (Schrad.) DC. ex Saint Amans, Fl. Agen. 516. 1821.

2. ***Lophodermium aucupariae*** (Schleich.) comb. nov.
≡ *Hysterium aucupariae* Schleich., Plantae Crypt. Helvetiae, Exs. n. 63, 1805; Catalogus Plant. Helvetia, 58. 1821.
≡ *Hypoderma xylomoides* DC. ζ *aucupariae* (Schleich.) DC., in Lam. & DC., Fl. Franç. 3 ed., 6: 165. 1815.
= *Lophodermium tumidum* Rehm ex Nannf., Nova Acta Reg. Soc. Scient. Upsal. IV. 8(2): 237. 1932. Non *L. tumidum* (Fr.) Rehm, in Rabh., Krypt.-Fl. II. 1(3): 40. 1887, ≡ *Hysterium tumidum* Fr., Syst. Myc. 2: 591. 1823.
= *Coccomyces coronatus* (Schum. ex Fr.) De Not., Erbar. Critt. Ital. I. No. 236. 1859.

STATUS PYCNIDICUS: *Leptostroma sorbicolum* Hilitzer, Věd. Spisy Českosl. Akad. Zeměd. 3: 80, 146. 1929.

Under *Hysterium tumidum* Fries is described a fungus now generally considered synonymous with *Coccomyces coronatus* (Schum. ex Fr.) De Not. which

De Notaris had earlier called *Coccomyces tumida* (Fr.) De Not. Fuckel (1870) determined material on *Sorbus* as *C. tumida* and issued it in F. rhen. 746 under that name. Rehm accepted Fuckel's determination but having noted that the specimen was a *Lophodermium* made the combination *L. tumidum* (Fr.) Rehm. Nannfeldt pointed out that Rehm had not been dealing with the same species as Fries and dropped the name of Fries from the epithet making it read *L. tumidum* Rehm. Unfortunately the name supplied by Nannfeldt is a later homonym of *L. tumidum* (Fr.) Rehm and is based on a different type specimen. There is, however, an earlier valid epithet for this species on *Sorbus*. Schleicher called it *Hysterium aucupariae* Schleich. in 1805 and the name was also used as a varietal epithet by De Candolle as *Hypoderma xylomoides* DC. ζ *aucupariae* (Schleich.) DC. As *Lophodermium aucupariae* (Schleich.) it appears to provide an acceptable and very appropriate name for this well known species.

3. *Lophodermium cedrinum* Maire, Bull. Soc. Hist. Nat. Afr. Nord 8: 174. 1917.

PYCNIDIAL STATE: *Labrella cedrina* Dur. & Mont., L'Exploration scientifique de l'Algérie, Cryptogamie, 1: 599. 1849.

4. *Lophodermium chamaecyparisii* Sharai & Hara, Bot. Mag. Tokyo 25: 69. 1911.

5. *Lophodermium conigenum* (Brunaud) Hilitzer, Věd. Spisy Vyd. Českosl. Akad. Zeměd. 3: 76. 1929.

≡ *Lophodermium pinastri* (Schrad. ex Hook.) Chev. f. *conigena* Brunaud, Act. Soc. Linn. Bordeaux 42: 97. 1888.
≡ *Lophodermina conigena* (Brunaud) Tehon, Illinois Biol. Monogr. 13(4): 92. 1935.

6. *Lophodermium consociatum* Darker, Contr. Arnold Arbor. 1: 79. 1932.
≡ Dermascia consociata (Darker) Tehon, Illinois Biol. Monogr. 13(4): 63. 1935.

7. *Lophodermium crassum* Darker, Contr. Arnold Arbor. 1: 88. 1932.

8. *Lophodermium durilabrum* Darker, Contr. Arnold Arbor. 1: 87. 1932.

9. ***Lophodermium juniperi*** (Grev.) comb. nov.
≡ *Hysterium juniperi* Grev., Scott. Crypt. Fl. 1: tab. 26. 1822.
= *Hysterium juniperinum* Fr., Obs. Myc. 2: 355. 1818.
≡ *Hysterium pinastri* β *H. juniperinum* Fr., Syst. Myc. 2: 588. 1823.
≡ *Lophodermium juniperinum* (Fr.) De Not., Giorn. Bot. Ital. 2(2): (46). 1847.
≡ *Hypoderma juniperinum* (Fr.) O. Kuntze, Rev. Gen. Pl. 3(2): 487. 1898.
≡ *Lophodermina juniperina* (Fr.) Tehon, Illinois Biol. Monogr. 13(4): 96. 1935.
= *Lophodermium juniperinum* var. *sabinae* Fckl., Jahrb. Nassau. Ver. Naturk. 23–24: 256. 1870.
= *Lophodermium juniperinum* f. *cupressi-thyoidis* Sacc., Mich. 2: 570. 1882.

≡ *Lophodermina cupressi-thyoidis* (Sacc.) Tehon, Illinois Biol. Mongr. 13(4): 94. 1935.

= *Lophodermium sabinae* Fautrey, *in* Roum., Rev. Myc. 13: 169. 1891.

≡ *Hypoderma sabinae* (Fautrey) O. Kuntze, Rev. Gen. Pl. 3(2): 487. 1898.

10. *Lophodermium lacerum* Darker, Contr. Arnold Arbor. 1: 80. 1932.

≡ *Dermascia lacera* (Darker) Tehon, Illinois Biol. Monogr. 13(4): 68. 1935.

11. *Lophodermium laricinum* Duby, Mém. Soc. Phys. Hist. Nat. Genève 16: 58. 1861.

≡ *Hypoderma laricinum* (Duby) O. Kuntze, Rev. Gen. Pl. 3(2): 487. 1898.

≡ *Lophodermina laricina* (Duby) Tehon, Illinois Biol. Monogr. 13(4): 98. 1935.

12. *Lophodermium nitens* Darker, Contr. Arnold Arbor. 1: 74. 1932.

≡ *Lophodermina nitens* (Darker) Tehon, Illinois Biol. Monogr. 13(4): 102. 1935.

13. *Lophodermium petrakii* Durrieu, Sydowia Beih. 1: 355. 1957.

This is probably the same species described or cited earlier as follows: Teng, Contr. Biol. Lab. Sci. Soc. China, Bot. 8: 7, 1932 [ut *Lophodermium pinastri*]; Teng, Sinensia 4: 137, 1933 [ut *Lophodermium uncinatum*]; Teng, l.c., 7: 262, 1936, and Petrak, Sydowia 1: 373, 1947 [ut *Lophodermium* sp.].

14. *Lophodermium piceae* (Fckl.) v. Höhn., Sitzb. Akad. Wiss. Wien, Math.-naturw. Kl. 126(1): 296. 1917.

≡ *Phacidium piceae* Fckl., Jahrb. Nassau. Ver. Naturk. 27–28: 51. 1873.

≡ *Coccomyces piceae* (Fckl.) Rehm, in Rabh., Krypt.-Fl. II. 1(3): 80. 1888.

≡ *Coccomyces piceae* (Fckl.) Sacc., Syll. Fung. 8: 746. 1889.

= *Lophodermium abietis* Rostr., Tidsskr. Skovbr. 12: 201. 1891.

PYCNIDIAL STATE: *Leptostroma abietis* Dearn., N. Y. St. Mus. Bull. 266: 65. 1925.

≡ *Hypodermina abietis* (Dearn.) Hilitzer, Věd. Spisy Vyd. Českosl. Akad. Zeměd. 3: 60, 146. 1929.

15. *Lophodermium pinastri* (Schrad. ex Hook.) Chev., Fl. Paris 1: 436. 1826.

≡ *Hysterium pinastri* Schrad., Schrad. Journ. Bot. 2: 69. 1799.

≡ *Hypoderma pinastri* (Schrad.) DC., Fl. Franç. 3 ed. 2: 305. 1805.

≡ *Hysterium pinastri* Schrad. ex Hook., Fl. Scotia 2: 8. 1821.

≡ *Hysterium pinastri* Schrad. ex Fr., Syst. Myc. 2: 587. 1823.

≡ *Lophodermellina pinastri* (Schrad. ex Hook.) v. Höhn., Ann. Myc. 15: 311. 1917.

≡ *Lophodermium pinicolum* Tehon, Illinois Biol. Monogr. 13(4): 55. 1935.

= *Hysterium limitatum* Wibel, Prim. Fl. Werth. 329. 1799.

= *Aporia obscura* Duby, Mém. Soc. Phys. Hist. Nat. Genève 16: 51. 1861.
≡ *Schizothyrium obscurum* (Duby) Sacc., Syll. Fung. 2: 725. 1883.
= *Lophodermium baculiferum* Mayr, Die Waldungen von Nordamerika, 313. 1890 (nom. nud.).
= *Scolecodothis pinicola* Miles, Mycologia 18: 165. 1926.
= *Lophodermium australe* Dearn., Mycologia 18: 242. 1926.
= *Lophodermium laricis* Dearn., Mycologia 18: 243. 1926.

PYCNIDIAL STATE: *Leptostroma pinastri* Desm., Ann. Sc. Nat. II. 19: 138. 1843.
= *Depazea linearis* Rostr., Tidsskr. Skovbr. 6: 260. 1883.
= *Gloeosporium pini* Oud., Nederl. Kruidk. Arch. III. 2: 754. 1902.

16. *Lophodermium pini-excelsae* Ahmad, in Petr. & Ahmad, Sydowia 8: 172. 1954.

17. *Lophodermium pini-pumilae* Sawada, Bull. Govt. For. Expt. Stat., Meguro, Tokyo, 53: 151. 1952.

18. ***Lophodermium sawadae*** nom. nov.
≡ *Lophodermium thujae* Sawada, Rept. For. Expt. Stat., Tokyo, 46, 139. 1950 (non *L. thujae* Davis, Trans. Wisc. Acad. 20, 424. 1922).

19. *Lophodermium thujae* Davis, Trans. Wisc. Acad. 20, 424. 1922 [ut *thuyae*].
≡ *Lophodermina thujae* (Davis) Tehon, Illinois Biol. Monogr. 13(4): 109. 1935.

20. *Lophodermium thujopsidis* Sawada, Rep. For. Expt. Stat., Tokyo, 46: 141. 1950.

21. *Lophodermium uncinatum* Darker, Contr. Arnold Arbor. 1: 76. 1932.
≡ *Lophodermina uncinata* (Darker) Tehon, Illinois Biol. Monogr. 13(4): 110. 1935.

DISPOSITION OF SYNONYMOUS EPITHETS (LOPHODERMIUM)

abietis Rostrup = *Lophodermium piceae*
abietis-concoloris Mayr ≡ *Lirula abietis-concoloris*
agharkarii Tilak ≡ *Lophomerum agharkarii*
amplum Davis ≡ *Davisomycella ampla*
australe Dearn. = *Lophodermium pinastri*
autumnale Darker ≡ *Lophomerum autumnale*
baculiferum Mayr = *Lophodermium pinastri*
brachysporum Rostr. = *Meloderma desmazierii*
clavuligerum Speg. ≡ *Lophomerum clavuligerum*
filiforme Darker = *Lirula macrospora*
gilvum Rostr. = *Naemacyclus niveus*
infectans Mayr = *Virgella robusta*
juniperinum f. *cupressi-thyoidis* Sacc. = *Lophodermium juniperi*
laricis Dearn. = *Lophodermium pinastri*
lineare (Pk.) E. & E. ≡ *Bifusella linearis*
lineatum Smith & Ramsbottom = *Meloderma desmazierii*
macrosporum (Hartig) Rehm ≡ *Lirula macrospora*

nervisequium (DC. ex Fr.) Chev. ≡ *Lirula nervisequia*
nervisequium (DC. ex Fr.) Rehm ≡ *Lirula nervisequia*
phacidium De Not. ≡ *Coccomyces coronatus*
pinastri var. *amplum* Davis ≡ *Davisomycella ampla*
pinicolum Tehon ≡ *Lophodermium pinastri*
quercus Bose & Müller ≡ *Lophomerum quercus*
sabinae Fautrey = *Lophodermium juniperi*
septatum Tehon ≡ *Lophomerum* septatum
thujae Sawada ≡ *Lophodermium sawadae*
tumidum (Fr.) Rehm = *Coccomyces coronatus*
tumidum Rehm ex Nannf. = *Lophodermium aucupariae*

XV. LOPHOMERUM Ouellette & Magasi, Mycologia 58: 275. 1966.

Genus similar to *Lophodermium* but with phragmosporous ascospores. Hysterothecia black, elliptic, opening by a longitudinal fissure, mostly subcuticular. Covering layer black, pseudoparenchymatous. Hymenium flat; subhymenium colorless, plectenchymatous. Asci subcylindric, 8-spored. Paraphyses simple, filiform. Ascospores filiform, becoming 3 to several-septate at maturity. Pycnidia simple, flat; conidia bacillar.

TYPE-SPECIES: *Lophomerum autumnale* (Darker) Magasi

1. *Lophomerum autumnale* (Darker) Magasi, in Ouellette & Magasi, Mycologia 58: 275. 1966.
≡ *Lophodermium autumnale* Darker, Contr. Arnold Arbor. 1: 77. 1932.
≡ *Lophodermina autumnalis* (Darker) Tehon, Illinois Biol. Monogr. 13(4): 89. 1935.

2. ***Lophomerum agharkarii*** (Tilak) comb. nov.
≡ *Lophodermium agharkarii* Tilak, Sydowia 13: 28. 1959.

3. ***Lophomerum clavuligerum*** (Speg.) comb. nov.
≡ *Lophodermium clavuligerum* Speg., Bol. Acad. Nac. Cienc. Cordoba 11: 118 (reprint pag.). 1887.
≡ *Lophodermina clavuligera* (Speg.) Tehon, Illinois Biol. Monogr. 13(4): 91. 1935.

4. *Lophomerum darkeri* Ouellette, in Ouellette & Magasi, Mycologia 58: 276. 1966.

5. *Lophomerum septatum* (Tehon) ex Ouellette, in Ouellette & Magasi, Mycologia 58: 279. 1966.
≡ *Lophodermina septata* Tehon, Illinois Biol. Monogr. 13(4): 109. 1935.
≡ *Lophodermium septatum* (Tehon) Terrier, Matér. Flore Crypt. Suisse 9(2): 32. 1942.

6. ***Lophomerum quercus*** (Bose & E. Müller) comb. nov.
≡ *Lophodermium quercus* [ut *querci*] Bose & E. Müller, Indian Phytopath. 18: 340. 1965.

XVI. COCCOMYCES De Not., Giorn. Bot. Ital. 2(2): (38). 1847.
= *Coccomycella* v. Höhn., Ann. Myc. 15: 323. 1917.

Ascocarps on leaves and twigs, subcircular to polygonal, innate, connate with host tissue, black to more or less concolorous; opening lobately or radially; opening mechanism weakly or fairly well developed; hymenium flat, colorless to yellowish-orange; subhymenium thin; asci subclavate, sometimes somewhat stalked; paraphyses usually exceeding the asci, coiled or uncinate to club-shaped at the tip; ascospores continuous, cylindrical to subclavate, more or less fasciculate, surrounded by a definite narrow sheath.

TYPE-SPECIES: *Coccomyces coronatus* (Schum. ex Fr.) De Not.

1. *Coccomyces coronatus* (Schum. ex Fr.) De Not., Erbar. Critt. Ital. I. No. 236. 1859.
≡ *Ascobolus coronatus* Schum., Enum. Plant Saell. 2: 437. 1803.
≡ *Phacidium coronatum* (Schum.) Fr., Obs. Myc. 1: 167. 1815.
≡ *Phacidium coronatum* (Schum.) ex Fr., Syst. Myc. 2: 577. 1823.
≡ *Lophodermium phacidium* de Not., Giorn. Bot. Ital. 2(2): (42). 1847 (an avowed substitute).
≡ *Coccomyces coronatus* (Schum. ex Fr.) Karst., Bidr. Känn. Finlands Natur. Folk 19: 256. 1871.
= *Peziza comitialis* Batsch, Elench. Fung. Cont. 1: 217. 1786.
≡ *Coccomyces comitialis* (Batsch) ex Dearn. & House, N.Y. St. Mus. Bull. 266: 65. 1925.
= *Peziza viridis* Bolt., Hist. Fung. Halifax, 109. 1789.
= *Xyloma pezizoides* Pers., Syn. fung. 105. 1801.
= *Peziza connivens* Martius, Fl. Crypt. Erlang. 463. 1817.
= *Hysterium tumidum* Fr., Syst. Myc. 2: 591. 1823.
≡ *Coccomyces tumidus* (Fr.) De Not., Giorn. Bot. Ital. 2(2): (39). 1847.
≡ *Lophodermium tumidum* (Fr.) Rehm, in Rabh., Krypt.-Fl. II. 1(3): 40. 1887.

The genus *Coccomyces* comprises a large number of species some of which show affinities to the genus *Lophodermium* and others superficially at least to the Phacidiaceae.

XVII. COLPOMA Wallr., Fl. Crypt. Germ. 2: 422. 1833.
≡ *Cenangium* Fr. subg. [ut tribus] *Clithris* Fr., Syst. Myc. 2: 189. 1822.
≡ *Clithris* (Fr.) Endl., Gen. Plant. 32. 1836.
= *Sporomega* Corda, Icon. Fung. 5: 34. 1840.
= *Pragmoparopsis* v. Höhn., Ann. Myc. 15: 320. 1917.

Fruit-body elongated, often curved, or short, under periderm or breaking through naked wood; opening usually by a long slit; covering layer well developed; basal layer also well developed, thick, often somewhat dark colored; hymenium subcupulate; subhymenium conspicuous, hyaline; asci clavate with a narrowed basal stalk; paraphyses abundant, slender, often coiled or bent at tip; ascospores continuous, more or less fasciculate, narrowly filiform, delicately sheathed, occupying the upper swollen portion of the ascus.

TYPE-SPECIES: *Colpoma quercinum* (Pers. ex Saint Amans) Wallr.

1. *Colpoma quercinum* (Pers. ex Saint Amans) Wallr., Fl. Crypt. Germ. 2: 423. 1833.
≡ *Hysterium quercinum* Pers., Obs. Myc. 1: 83. 1796; Syn. Fung. 100. 1801.
≡ *Hypoderma quercinum* (Pers.) DC., Fl. Franç. 3 ed. 2: 306. 1805.
≡ *Hypoderma quercinum* (Pers.) DC. ex Saint Amans, Fl. Agen. 515. 1821.
≡ *Tryblidium quercinum* (Pers. ex Saint Amans) Pers., Myc. Eur. 1: 333. 1822.
≡ *Cenangium* subg. *Clithris quercinum* (Pers. ex Saint Amans) Fr., Syst. Myc. 2: 189. 1822 [ut (Pers.)].
≡ *Clithris quercina* (Pers. ex Saint Amans) Karst., Not. Fauna Flora Fenn. 11: 260. 1870; Bidr. Känn. Finl. Nat. Folk, 19: 221. 1871.
≡ *Clithris quercina* (Pers. ex Saint Amans) Schröt., Krypt.-Flora Schles. 3(2): 165. 1893.
= *Hysterium nigrum* Tode, Fungi Meckl. 2: 5. 1791.
≡ *Clithris nigra* (Tode) Keissl., Krypt. Mus. Vindob. 523.
≡ *Colpoma nigra* (Tode) v. Höhn., Ann. Myc. 15: 319. 1917.
= *Variolaria corrugata* Bull., Hist. Champ. [Ventenat Ed.] 1: 187. pl. 432, f. 4. 1809.
≡ *Colpoma corrugata* (Bull.) ex O. Kuntze, Rev. Gen. Pl. 3(2): 487. 1898.
= *Sphaeria collapsa* Sowerb., Engl. Fung. t. 373, f. 3. 1797–1809.

XVIII. XYLOSCHIZON Syd., in Syd. & Petr., Ann. Myc. 20: 192. 1922.

Hysterothecia elliptical to elongated, scattered or crowded on bare wood, at first covered, becoming erumpent and finally almost superficial, opening by a longitudinal slit, covering and basal layers well developed; asci slender and long-clavate, narrowed downwards into a long, thick stalk; ascospores elongate-cylindrical, hyaline, with 3 delicate septa; paraphyses simple, numerous, often hooked at the tip.

TYPE-SPECIES: *Xyloschizon weirianum* Sydow.

1. *Xyloschizon weirianum* Syd., in Syd. & Petr., Ann. Myc. 20: 192. 1922.

A second species, *X. atratum* Syd., l.c. p. 193, appears not to differ markedly from the wood inhabiting forms of *Colpoma crispum*.

XIX. BIFUSEPTA Darker, Mycologia 55: 816. 1963.

Hysterothecia appearing golden brown to grayish black, elliptical, subcuticular; covering layer of dark pseudoparenchyma alternating with wedges of parenchyma; hymenium flat; subhymenium thin, seated on a darkened basal layer. Asci clavate. Paraphyses simple, filiform. Ascospores bifusiform, phragmosporous. Pcynidia small, black, circular. Spermatia bacillar.

TYPE-SPECIES: *Bifusepta tehonii* Darker.

1. *Bifusepta tehonii* Darker, Mycologia 55: 816. 1963.
≡ *Bifusella vaccinii* Tehon, Mycologia 31: 678. 1939.
Non *B. vaccinii* (Schröt.) Tehon, Illinois Biol. Monogr. 13(4): 117. 1935.

XX. RHYTISMA Fr., Syst. Myc. 2: 565. 1823.
≡ *Melanosorus* De Not., Giorn. Bot. Ital. 2(2): (49). 1847.
= *Xyloma* Pers., Tent. Disp. Fung. 5. 1797; Syn. Fung. 103. 1801.
= *Pachyrhytisma* v. Höhn., Ann. Myc. 15: 317. 1917.

Ascocarps embedded in a round or elliptical stroma; stroma dark outside and white within; ascocarps opening lacerately or by elongated straight or curved slits; opening mechanism present or absent. Asci clavate, sometimes slightly stalked; ascospores fascicled, clavate to filiform-clavate, or slightly fusiform, gelatinous sheath when present not well developed; paraphyses filiform, sometimes swollen or bent at the tip.

TYPE-SPECIES: *Rhytisma acerinum* (Pers. ex Saint Amans) Fr.

1. *Rhytisma acerinum* (Pers. ex Saint Amans) Fr., Syst. Myc. 2: 569. 1823.
≡ *Xyloma acerinum* Pers., Tent. Disp. Fung. 6. 1797; Syn. Fung. 104. 1801.
≡ *Melanosorus acerinus* (Pers. ex Saint Amans) De Not., Giorn. Bot. Ital. 2(2): (50). 1847.

PYCNIDIAL STATE: *Melasmia acerina* Lév., Ann. Sc. Nat. III. 5: 276. 1846.
The synonymy of this species is much more involved than indicated and no attempt has been made to investigate it thoroughly.

XXI. PLACUNTIUM Ehrenb. ex v. Höhn., Ann. Myc. 15: 317. 1917.
≡ *Placuntium* Ehrenb., Sylv. Mycol. Berol. 17. 1818.

Fertile ascomata epiphyllous or on young stems, subcuticular, embedded in a highly developed stroma, shining black externally, opening to expose the hymenial surface, commonly with a single buff-colored hymenial surface surrounding a central sterile area or with several sterile areas in larger ascomata. Asci clavate, larger than in *Rhytisma*, up to 188–200 × 25–28 μ; ascospores broadly clavate, often basally more or less filiform, sometimes slightly greenish-yellow, up to 55–90 × 5–8 μ, with a conspicuous gelatinous sheath.

TYPE-SPECIES: *Placuntium andromedae* (Pers. ex Fr.) v. Höhn.

1. *Placuntium andromedae* (Pers. ex Fr.) v. Höhn., Ann. Myc. 15: 317. 1917.
≡ *Xyloma andromedae* Pers., Syn. Fung. 104. 1801.
≡ *Placuntium andromedae* (Pers.) Ehrenb., Sylv. Mycol. Berol. 17. 1818.
≡ *Rhytisma andromedae* (Pers.) ex Fr., Syst. Myc. 2: 567. 1823.

PYCNIDIAL STATE: A pycnidial state, apparently undescribed, was found on specimens collected in early July, 1925, Lake Timagami, Nipissing District, Ontario. In this gathering, DAOM 83512, the pycnidia are epiphyllous, dark brown to black, occasionally forming a more or less continuous zone but more frequently a broken series surrounding the ascocarps of *P. andromedae* at a distance about equal to the width of the pycnidia themselves. Pycnidial stromata up to 1.0–1.2 mm. in width and often with several pycnidial cavities in the same stroma, the cavities separated by stromatic columns; stromata with dark covering layer 2–3 cells thick, up to 4–6 μ in thickness; spermatiophores arising in vertical rows from a horizontal, often darkened layer of elongated thick walled sclerenchyma tissue 4–5 cells thick; spermatiophores 3–4 cells in length,

12–16 × 2–4 μ, terminal cell often more or less elongated and attenuated terminally and bearing one or two or perhaps more 3–5 × 1 μ spermatia; basally the spermatiophores tend to darken, and together with the basal sclerenchyna whose cell contents tend to become brownish, give the appearance of a dark basal layer in thick sections.

Little is known of the development of the pycnidia and their subsequent fate although some mature pycnidia were still present on the same leaves with mature ascocarps. It is not known, therefore, whether these pycnidia might later have been converted into ascocarps as sometimes happens in *Rhytisma* (Jones, 1925). The covered pycnidia present in this material approach rather more closely *Leptostroma berberidis* (Thüm. & Wint.) Nannf., the pycnidial state of *Lophodermium berberidis* (Schleich.) Rehm as described by Nannfeldt, than the genus *Melasmia* or the simple *Leptostroma* types such as *L. pinastri*.

XXII. NYMANOMYCES P. Henn., Monsunia 1: 28. 1899.

The five genera of the *Nymanomyces* complex have all at some time been regarded as having affinities to *Rhytisma* from which they differ through the possession of relatively short, elliptical ascospores which are said to be hyaline and 2-celled in *Synglonium* Penz. and Sacc. and 1-celled, brownish to brown in the other genera. Except in the genus *Nymanomyces* no imperfect state is known. In *Nymanomyces aceris-laurini* (Pat.) P. Henn., however, Terrier (1942) observed some structures which might conceivably represent an imperfect state, but could not, he believed, belong in the genus *Melasmia* Lév.

Certain confusion has arisen partly from the fact that *Synglonium* Penz. and Sacc., the first genus named, was described twice by the same authors, originally in 1897 and later on 1904, but the earlier description has been largely overlooked or ignored by other authors. This and later disregard for the principle of priority has resulted in an involved synonymy for such a small group of species. *Nymanomyces* P. Henn., the second genus named, was based on a specimen collected by Nyman on the same host as the type of *Synglonium*. A later homonym of the type species of *Nymanomyces* was based on a Massart specimen named by Patouillard and raised to specific rank in a publication by Raciborski. The third genus, *Phaeorhytisma* P. Henn., was described in the same paper as *Nymanomyces* but on the following page. In the second part of the same paper, the type and only species of *Phaeorhytisma* was transferred to *Criella* which up to this time had existed only as a subgenus of *Rhytisma*. Finally Saccardo, himself, raised *Rhytisma* Fr. subg. *Criella* Sacc. to generic rank as *Criella* (Sacc.) Sacc. with the type species of the subgenus as the type species of the genus to which he added three other species including *Criella lonicerae* (P. Henn. and Nym.) P. Henn. and Nym. which had been named three years previously. Whether Hennings and Nyman created the genus intentionally or inadvertently is unimportant since the genera *Nymanomyces* and *Phaeorhytisma* both have priority over *Criella*. On the other hand the status of *Synglonium* requires further study. Von Höhnel (1909) considered the type of *Synglonium insigne* Penz. and Sacc. to be a disorganized specimen of *Criella aceris-laurini* (Pat.) Sacc. and Syd. and later (1918) referred to it as an old, infected specimen of *Nymanomyces*.

In a study of the species which Saccardo treated under *Criella* (Sacc.) Sacc.

von Höhnel (1917a) was unable to state with certainty what the type species, *C. austro-caledonica* (Crié) Sacc., really represented. In the same paper and in another (v. Höhn., 1917e) he disposed of the other three species of *Criella* as follows: *C. aceris-laurini* (Pat.) Sacc. and Syd. was transferred to *Nymanomyces* which he maintained as an intraepidermal genus of the Dermopeltinaceae in the Phacidiales sensu v. Höhn.; *C. lonicerae* (P. Henn. and Nym.) P. Henn. and Nym. was returned to *Phaeorhytisma* P. Henn. which has priority over *Criella* and must be retained, and *Phaeorhytisma* was removed to the Dermateaceae near *Pseudopeziza* and *Fabraea*; and *C. rhododendri* (Rac.) Sacc. and Syd. was made the type species of a new genus, *Pseudotrochila* v. Höhn., somewhat resembling *Trochila* Fr. This new genus was also placed in the Dermopeltinaceae.

A summary of the five genera and their species is given below as an aid to anyone wishing to study the complex further. Students of the group are in agreement that at least one genus of Hypodermataceae is present here and that it should probably be called *Nymanomyces* although further elucidation of the status of the whole group is needed, but especially of the species *Synglonium insigne* and *Criella austro-caledonica*.

1. *Synglonium* Penz. & Sacc., Malpighia 11: 526. 1897.

TYPE-SPECIES: *Synglonium insigne* Penz and Sacc., l.c. 527; Icones Fung. Javan. 63. 1904.

2. *Nymanomyces* P. Henn., Monsunia 1: 28. 1899.

TYPE-SPECIES: *Nymanomyces aceris-laurini* P. Henn., l.c. 28, 170. 1899 (based on collection of Nyman).

= *Rhytisma acerinum* Fr. f. *aceris-laurini* Pat., Ann. Jard. Buitenzorg Suppl. 1: 121. 1897 (based on collection of Massart).

≡ *Nymanomyces aceris-laurini* (Pat.) P. Henn. in Racib., Parasit. Algen u. Pilze Java's 2: 23. 1900.

≡ *Rhytisma* (*Criella*) *aceris-laurini* (Pat.) P. Henn., in Racib., Hedw. Beibl. 39: (111). 1900.

≡ *Criella aceris-laurini* (Pat.) Sacc. and Syd., Syll. Fung. 16: 786. 1902.

3. *Phaeorhytisma* P. Henn., Monsunia 1: 29. 1899.

TYPE-SPECIES: *Phaeorhytisma lonicerae* P. Henn. and Nym., in P. Henn., Monsunia 1: 29. 1899.

≡ *Criella lonicerae* (P. Henn. and Nym.) P. Henn. and Nym., in P. Henn., Monsunia 1: 171. 1899.

4. *Criella* (Sacc.) Sacc., in Sacc. and Syd., Syll. Fung. 16: 786. 1902.

≡ *Rhytisma* Fr., subg. *Criella* Sacc., Syll. Fung. 8: 756. 1889.

TYPE-SPECIES: *Criella austro-caledonica* (Crié) Sacc. and Syd. Syll. Fung. 16: 786. 1902.

≡ *Rhytisma austro-caledonicum* Crié, Bull. Soc. Linn. Normandie, Caen, 8: 446. 1874.

≡ *Rhytisma* (*Criella*) *austro-caledonicum* Crié, in Sacc., Syll. Fung 8: 756. 1889.

5. *Pseudotrochila* v. Höhn., Ber. Deutsch. Bot. Ges. 35: 419. 1917.

TYPE-SPECIES: *Pseudotrochila rhododendri* (Racib.) v. Höhn., l.c. 422.
≡ *Cryptomyces* (*Criella*) *rhododendri* Racib., Parasit. Algen u. Pilze Java's 3: 18. 1900.
≡ *Criella rhododendri* (Racib.) Sacc. and Syd., Syll. Fung. 16: 787. 1902.

Discussion

The taxonomic changes proposed above involve principally species formerly assigned to the genera *Hypoderma*, *Lophodermium*, *Hypodermella*, and *Bifusella*. The revisions have been for the most part among the more parasitic species, where, as one might expect, distinctive characters are more sharply delineated. In the older classifications which were extremely artificial most of the genera were founded primarily on spore shape. In the present scheme, characters of the ascocarps, asci, and spores as well as pycnidia were more or less synthesized to arrive at more meaningful relationships. Although no modifications or additions have been incorporated into this work as the result of recent cytologic studies by Gordon (1966), it is possible that eventually certain compromises may have to be made, and further work by Gordon may result in reevaluation of certain proposals made here. In the main, however, Dr. Gordon's recent findings seem to complement those of the writer with a few minor exceptions.

In the present work it is clear, that by segregating the obviously closely related species of the "nervisequia" or *Lirula* complex from other conifer-inhabiting species, a distinctive grouping has been created. In typical species of this complex on *Abies* the epiphyllous pycnidia develop after one year and are more or less continuous along the sulcus or in two lines, one along each wing of the needle. The hypophyllous ascocarps follow the "nerve" of the needle and mature at the end of two years. The erection of three genera for the nervisequious species, i.e., *Virgella*, *Isthmiella*, and *Lirula*, brings them on a secondary basis into line with the old Saccardoan system based on spore form. The removal of the nervisequious species from *Hypodermella*, *Bifusella*, and *Hypoderma*, where they have always appeared to be discordant elements, simplifies the further taxonomic treatment of the species left in the complexes surrounding these genera.

The *Hypodermella* complex is then limited in general to species with relatively short ascocarps and scattered pycnidia which precede the appearance of the ascocarps by only a few months rather than a full year as in the nervisequious complex. After removal of *Lirula* the remaining species of the old genus *Hypodermella* fall into three very distinct groups which may be segregated into genera as follows: *Hypodermella* (type: *H. laricis*) with subcuticular ascocarps and numerous small, dark pycnidia, *Davisomycella* (type: *D. ampla*) with prominent subepidermal ascocarps and pycnidia which are inconspicuous or unknown, and *Lophodermella* v. Höhn. (type: *L. sulcigena*) with more or less concolorous, subhypodermal ascocarps. With obvious affinities to these clavate-spored genera are *Ploioderma*, segregated from *Hypoderma*, with short rod-like ascospores, and possibly also *Elytroderma* with large 2-celled ascospores.

The *Bifusella* complex with three genera is a rather heterogeneous group. The transfer of the nervisequious species to *Isthmiella* and the removal of the more or less aberrant *B. striiformis* would have left the type species, *B. linearis*, as the

sole conifer-inhabiting representative of the genus. To *Bifusella*, however, have been added two former *Hypoderma* species occurring also on soft pines. Although the spores of these two species might best be described as rod-like, they have a distinct tendency towards a bifusiform condition and in both the paraphyses tend to disappear at maturity as in the type species, *B. linearis*. Like the type species, they are also subcuticular, and have large pycnidia with a distinct covering tissue above the cushion of spermatiophores and relatively large spermatia. In *Duplicaria* the ascocarps are also subcuticular but the pycnidia are small and inconspicuous. *Soleella* is an aberrant monospecific genus with abundant subepidermal ascocarps but lacking pycnidia.

The *Hypoderma* complex with two of the older genera, *Hypoderma* and *Lophodermium*, contains by far the largest number of species. Both genera are in need of careful monographic treatment as they have become depositories for miscellanies of species. *Lophodermium*, though validly published, is illegitimate and requires conservation as proposed above. Von Höhnel's attempt to set up new genera in this complex has never met with general approval. It is quite possible that his genera *Lophodermina* and *Lophodermellina* could be redefined from their type species on a more acceptable basis to include a few species but not for a general transfer of species as was done by Tehon. The invalidly published genus *Dermascia* Tehon cannot be used without validation and subsequent redefinition and should perhaps be dropped from the literature. As accepted above *Hypoderma* and *Lophodermium* have not been reevaluated to any marked degree except to remove *Hypoderma desmazierii* to a new genus, *Meloderma*, nearer *Lophodermium*, and to accept the transfer of certain phragmosporous *Lophodermium* species to *Lophomerum* Ouellette and Magasi.

The genus *Coccomyces* is apparently a more or less mixed complex of species within itself. On the one hand are species like *C. coronatus* which tear open in a lacerate, phacidiaceous manner at maturity while others open radiately by means of organized opening mechanisms.

Colpoma, together with *Xyloschizon* and *Bifusepta*, form a small complex of species in which the basal stromatic tissue is very strongly developed. Their occurrence on dead stems and branches and even on dead wood probably accounts for the fact that the stroma in certain species has a tendency to separate laterally from the host tissue and to become somewhat erumpent. In certain species, notably *Colpoma crispum*, the ascocarps may be embedded in the bark but in the same specimen may pass over to bare wood where they originate very near the surface of the wood and appear almost completely erumpent. Von Höhnel has suggested the transfer of this and other species to a new genus *Pragmoparopsis* which he would place in the Tryblidiaceae. *Colpoma quercinum* on oak is well known but there are a number of species on conifers which do not seem to differ much from one another or from *C. crispum*. *Xyloschizon* Syd. appears to be distinct in that it possesses large, phragmosporous ascospores although unfortunately the type species has never been located by the writer. The second species, *X. atratum*, appears to be more closely related to *C. crispum*. *Bifusepta*, with a fairly thick basal stromatic layer, has some affinities with *Colpoma*. Its bifusiform, septate spores resemble somewhat those of *Bifusella* but the structure of the fruiting body is more closely related to that of *C. quercinum*.

The *Rhytisma* complex comprises three genera: *Rhytisma*, *Placuntium*, and

Nymanomyces. These genera are characterized by more highly developed stromata which are more or less sclerotic, externally dark, and internally light, with one to several ascocarps in each stroma. The ascocarps open by the rupturing of the covering layer with or without an opening mechanism. The ascospores are acicular-clavulate in *Rhytisma*, quite robust and clavate in *Placuntium*, and ovoid and brown in *Nymanomyces*.

The assignment of the Phacidiales to a position between certain of the Pyrenomycetes and the true Discomycetes as proposed by Gäumann (1964) still seems to be the most acceptable disposition of this order. This leaves the Hypodermataceae in the same relative position occupied earlier by the Hysteriaceae (treated as an order) of Rehm (1887) or the Hysteriineae (treated also as an order) of Lindau (1896). During the long interval between the classifications of Rehm and Lindau and those of more recent workers the Hypodermataceae have been variously assigned, notably by von Höhnel, Nannfeldt, Terrier, and others, in or near the Helotiales in the Discomycetes. With Gäumann's treatment the cycle is complete and the Hypodermataceae, now separated from the Hysteriaceae, are back very close to the position which they occupied seventy to eighty years ago.

While clarifying some of the problems encountered in the Hypodermataceae, the present work has merely touched upon certain of the genera and references to the species of these genera have been omitted in large part. Several of the larger genera are still in need of monographic treatment. It is hoped that this redefinition of genera may stimulate further research especially in the areas least stressed here.

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