THE GENUS PARAGYRODON

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Paragyrodon sphaerosporus was extremely abundant in the autumn of 1965 in various counties of Michigan, U.S.A. The author therefore had ample opportunity not only to study many fresh specimens, in different stages of development from a large number of localities but to compare it directly with *Gyrodon merulioides* (Schw.) Singer a fungus it is said to be related to. The findings were supplemented later with the results from the examination of dried material received from several national herbaria.

It quickly became evident during the study that either some discrepancies exist in those descriptions by recent authors or else there is some argument in favour of there being two distinct taxa. It was therefore decided necessary to review and reassess the information available and compare this with a full description of the fungus made from fresh and dried material. Such a description reads:—

Paragyrodon sphaerosporus (Peck) Singer in Ann. Myc. 40:25 (1942). Plate 4 and fig. 1, A–C.

Basionym: *Boletus sphaerosporus* Peck in Bull. Torrey Bot. Club 12:33 (1885).

Synonym: *Suillus sphaerosporus* (Peck) Smith & Thiers in A contribution towards a monograph of North American species of *Suillus*, 1964.

Pileus up to 340 mm, convex to plano-convex almost sub-globose at first expanding to become plane or shallowly depressed particularly about the disc in age or the margin becomes sometimes uplifted and then often wavy, glabrous, viscid to glutinous, but when first appearing above the soil surface not truly glutinous, rapidly becoming spotted or streaked with patches of dried gluten, ochre to golden yellow when young becoming ochraceous tawny and finally dingy yellow-brown often with rust coloured stains which become more prominent on handling; *margin* incurved, sterile and entire. *Stipe* 30–150 × 10–30 mm, equal or nearly so, pale yellow to pale mustard, pruinose to glabrous above the heavy, tough, gelatinous more or less median annulus; apex sometimes reticulate with wings from the decurrent tubes and lower stipe either completely covered in veil or simply rust brown streaky fibrillose and becoming more so with age. *Tubes* shallow in relation to the pileus tissue but soon elongating, adnate to subdecurrent to even decurrent or with lines extending down the stipe, canary yellow when first exposed although pallid ochraceous when very young and protected by veil, becoming golden yellow and finally brown; *pores* large up to 4 mm broad or even greater in fully mature carpophores, yellow, angular staining brown when bruised, finally red brown at maturity. *Flesh* well-developed, up to 20 mm thick under the disc, whitish to yellowish changing brownish with a distinct vinaceous tint on cutting and exposing to the air, more yellowish in the stipe and becoming red brown particularly towards the base; green then olive with $FeSO_4$ and greyish buff about yellow spot with NH_4OH. *Veil* consisting of two adhering, thick, tough elastic membranes which becomes gelatinised, at first straw yellow or slightly rust then dark rust and staining red brown on handling.

Spore-deposit aniline yellow. *Basidiospores* 6–9 × 6–8 μ globose or subglobose, to broadly elliptic, smooth, hyaline to faintly flushed yellow but more ochraceous in KOH and more tawny in Melzer's reagent, wall slightly thickened. *Basidia* 4-spored, 18–22 × 9–11 μ, hyaline in KOH, or faintly yellowish in Melzer's reagent. *Pleurocystidia* scattered to abundant 20–32 × 8–12 μ, fusoid ventricose with subacute apices and with dingy brown content when revived in KOH, similarly coloured in Melzer's reagent and ammoniacal solutions; *cheilocystidia* abundant and similar to the pleurocystidia. *Caulocystidia* similar in all respects to cheilocystidia or possibly more variable particularly as to neck length. *Hymenophoral trama* gelatinous and consisting of divergent hyphae with a central strand which is brownish in KOH and tawny in Melzer's reagent. *Context hyphae* loosely interwoven, slightly brownish when revived in KOH, in mass non-amyloid. *Clamp-connections* present, variable as to number from one population to another.

Solitary to gregarious under hardwoods, especially Oak (*Quercus* spp.)

Material examined: Herbaria after Lanjouw and Stafleu (1959).
(E): Waterloo Res. Area, Washtenaw Co., 20 vi 1940, legit *A. H. Smith* 15138, *Wat.* 4059; Michigan University, Botanic Garden, Dixboro, near Ann Arbor, Washtenaw Co., 30 viii 1965, *Watling* A1575/C1834; Saginaw Forest, Washtenaw Co., 2 ix 1965, legit *T. Burge*, *Watling* A1852/C2268; Ann Arbor Hills, Ann Arbor, Washtenaw Co., 2 ix 1965, *Watling* A470/C1819; Saginaw Forest, Washtenaw Co., 3 ix 1965, *Watling* A1579/C839: Picrol Lake, Livingston Co., legit *S. Mazzer*, 11 ix 1965, *Watling* A446/C1857; Saginaw Forest, Washtenaw Co., 13 ix 1965, *Watling* 500A/C1945; Ann Arbor, Washtenaw Co., 3 ix 1966, *Watling* 2768; Ann Arbor, Washtenaw Co., legit *A. H. Smith*, *Wat.* 4060 (all Michigan localities, U.S.A.).
(MICH): Wisconsin localities:—along lakeside, Madison, Dane Co., 1902, *C. H. Kauffman* (from type locality); Dane Co., viii 1907, *Kelly*; Madison, Dane Co., *Kelly* 2010: Michigan localities:—West of Chelsea, Washtenaw Co., 19 x 1907, *C. H. Kauffman*; cemetry, Chelsea, Washtenaw Co., 21 vii 1917, *C. H. Kauffman*; on sandy soil, George Reserve, Washtenaw Co., 15 ix 1936, *Smith* 6067; Whitmore Lake, Washtenaw Co., 29 viii 1937, legit *Smith*; Saginaw Forest near Ann Arbor, Washtenaw Co., 15 viii 1938, *Smith* 9612; roadside, Waterloo near Chelsea, Washtenaw Co., 26 vii 1940, *Smith* 15138; on low wet ground, Cascade Glen near Ann Arbor, Washtenaw Co., 19 vii 1940; on soil along road, Waterloo, Jackson Co., 11 vii 1942; on sandy soil along roadside, Waterloo, Washtenaw Co., 6 viii 1942, *Smith* 18571; Cascade Glen, near Ann Arbor, Washtenaw Co., 15 viii 1942, *Smith* 18375; scattered in open oak woods, Waterloo, Washtenaw Co., 9 vii 1957, *Thiers* 4508; under oak, Ann Arbor, Washtenaw Co., vi 1961, *Nancy Smith*; roadside, Waterloo Project, Washtenaw Co., *Smith* 18663; Meader's Yard, Glenwood Road, Ann Arbor, Washtenaw Co., 7 ix 1961, *Smith* 64130; Oakland Co., 24 ix 1961, *Smith* 64513; Ann Arbor, Washtenaw Co., 27 ix 1961, *Smith* 64482; on ground by logging road, Vestabury, Montcaba Co., 8 x 1961, *Potter* 13521; Ann Arbor, Washtenaw Co., 10 x 1962, *Smith* 66448; on soil in deciduous woods, Saginaw Wd., Washtenaw Co., 30 viii 1964; Saginaw Forest, Washtenaw Co., 31 viii 1964, *Homola* 1049; Washtenaw Co., 27 ix 1965, *Hoseney* 33; *Hoseney* 33 second collection; Saginaw Forest,

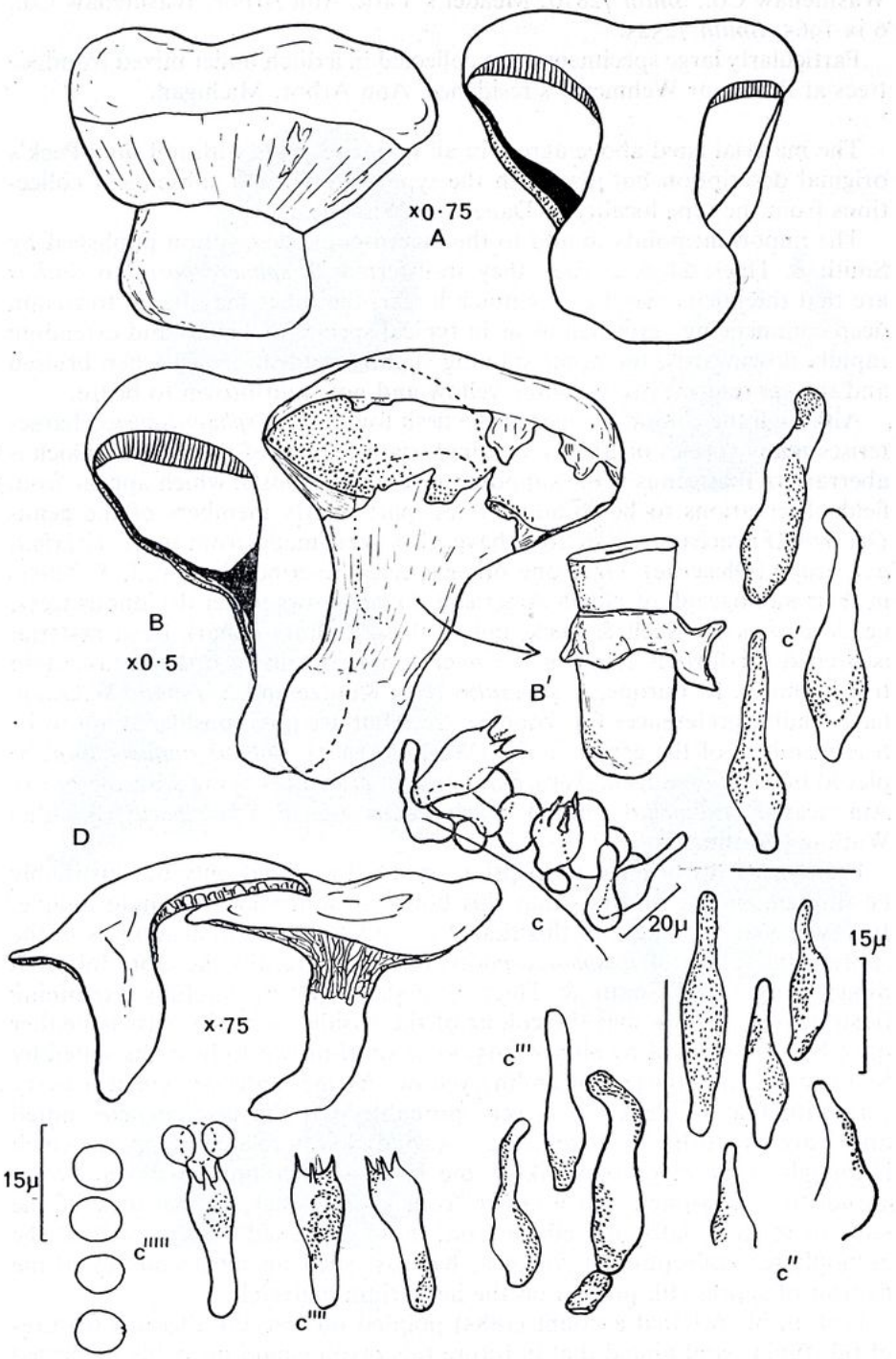

FIG. 1. A. B. & C. *Paragyrodon sphaerosporus* (Peck) Singer: A. Habit sketch, A470/C1819; B. Habit sketch, A500A/C1945. B′ shows collapsing ring; c–c′′′′′, microscopic characters of A1579/C839, c. part of caulohymenium, c′ caulocystidia, c″ pleurocystidia, c‴ cheilocystidia, c′′′′ basidia, c′′′′′ basidiospores. D. *Gyrodon merulioides* (Schw.) Singer. A1693/C1871. Magnifications as indicated.

Washtenaw Co., *Smith* 72870; Meader's Yard, Ann Arbor, Washtenaw Co., 6 ix 1965, *Smith* 72525.

Particularly large specimens were collected in a ditch under mixed frondose trees at Professor Wehmeyer's residence, Ann Arbor, Michigan.

The material cited above agrees in all major respects with not only Peck's original description but also with the type material and subsequent collections from the type locality in Dane Co., Wisconsin.

The important points to add to the macroscopic description published by Smith & Thiers (1964), when they transferred *B. sphaerosporus* to *Suillus* are that the pileus may be very much larger, the tubes may be up to 20 mm deep commencing very shallow as in typical species of *Suillus* and extending rapidly downwards, the pores staining slightly reddish brown when bruised and the spore-print being aniline yellow and not snuff-brown to bistre.

Although the colour changes of the flesh found in *B. sphaerosporus* characterises many species of *Suillus*, one important feature of this fungus which is aberrant in that genus is the supposed mycorrhizal hosts, which appear from field observations to be frondose trees, particularly members of the genus *Quercus* (Fagaceae); collections have also been made from under *Fraxinus americana* (Oleaceae). Only one other species described by Smith & Thiers in their monograph of North American *Suillus* grows under deciduous trees, i.e. *S. castanellus* Snell & Dick, but as these authors remark fresh material is needed for further study of the microscopic details in order to ascertain true affinities. In Europe, *S. piperatus* (Fr.) Kuntze and *S. rubinus* W.G.Sm. have similar preferences for frondose trees but are now considered not to be true members of the genus *Suillus* (Watling, 1963); *Boletus ruinus* should be placed in *Boletus* subgen. *Xerocomus* and *B. piperatus*, along with the North American *B. rubinellus*, should be placed in subgen. *Chalciporus* (Bataille) Watling (Watling, 1967).

Peck based his original description on dried material only but justifiably he thought on the grounds that this bolete to him appeared quite unique. It was probably because of this that Peck could give no indication as to the spore-print colour of *B. sphaerosporus*: one has naturally therefore followed Singer (1951) and Smith & Thiers (1964). However, carefully examining fresh material shows that the colour of the basidiospores in mass is neither olive brown as stated by Singer (1951) nor snuff-brown to bistre as stated by Smith & Thiers (1964), but aniline yellow. As the material agreed in every way with that of Peck's it is very probable that the discrepancies noted above are either due to there being a second closely related taxon or, which is thought to be much more likely, the spore-print colour was taken by the authorities mentioned above either from spores stuck to the apex of the stipe or to the gelatinous veil, or from those deposited on leaves about the carpophore; collection A1579/C839 has just such an olivaceous to citrine deposit of spores still present on the herbarium material.

Peck in his original account (1885) pointed out certain aberrant features of this fungus and hinted that in future this taxon would probably be placed in a separate genus. Singer (1942) took up this opinion and erected the genus *Paragyrodon* to accommodate it. As Singer so rightly says the distinct cystidia and membranous veil when taken in conjunction with the subglobose to broadly elliptic spores are sufficient to keep this fungus separate from all

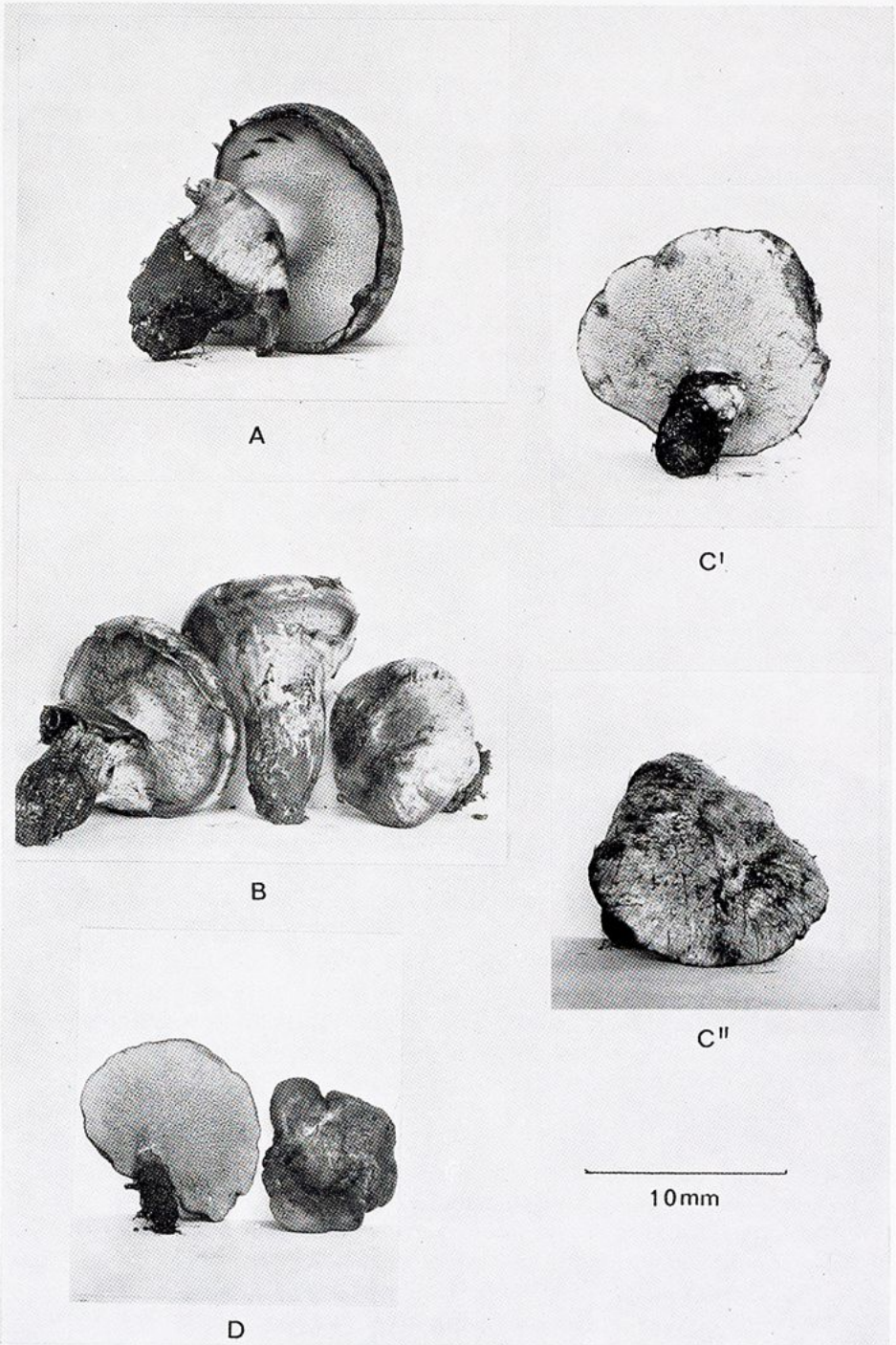

PLATE 4. A. B. & C.: *Paragyrodon sphaerosporus* (Peck) Singer: A. *Smith* 62557; B. *Smith* 1960; C′ & C″ *Smith* 6067; D. *Gyrodon merulioides* (Schw.) Singer.

other members of the Boletaceae. This is particularly important when these characters can now be correlated with the colour of the spore-print and habitat. The tough double veil and the cystidia, which are not fasciculate as they are in typical *Suillus* spp., also tend to place *B. sphaerosporus* out on a limb in bolete classification, in much the same way that *Boletus piperatus* (Watling, 1963) cannot be considered typical of the genus *Suillus*.

I am certain therefore that *Paragyrodon* should be retained as an autonomous genus although due to configuration of the hymenophoral tissue placed close to *Suillus*; the hymenophore is not really *Gyrodon*-like i.e. thin and gyrose, but frequently quite thick and composed of independent tubes up to 15 mm long (Plate 4 & fig. 1 A, B & D).

However, like the spores of *Gyrodon*, those of *P. sphaerosporus* are not typically boletoid being subglobose to elliptic. This is itself not a factor to support or reject the placing of Peck's fungus in or close to any of the existing bolete genera, for in studying exotic boleti which appear to be otherwise typical members of the genus *Boletus* (i.e. *Tubiporus* of Paulet) similar shaped spores have been observed. They also appear in some members of the badly confused genera *Boletochaete* and *Pulveroboletus*. In fact during the preparation of this paper, Horak (1967) has used spore shape etc. to separate *Boletochaete* into two separate genera.

The development as far as can be judged from the examination of the smallest of primordia collected to date (primordia a few centimetres high) indicate the carpophores to be possibly pseudoangiocarpic (pilangiocarpic of Reijnders, 1963); more observations are, however, required for it has already been found in members of the Bolbitiaceae (Watling, 1963) that even primordia just visible to the naked eye can undergo very sudden and drastic changes so obscuring the true identity of the developmental type.

The veil in *P. sphaerosporus* appears to consist of two adhering, thick, tough, elastic membranes, the outermost, or primary, is confluent with the pileus 'cuticle', whilst the second (inner layer) appears to develop from the inner surface of the inrolled margin; the hymenophore forms within the cavity between the second membrane and the pileus trama. On expansion, the veil splits irregularly at the margin of the pileus; it may be also attached to either the base of the stipe or up to half way towards the apex. Some specimens appear superficially volvate, the gelatinous membrane being attached very near the stipe base and thus below ground level. Peck's comments are pertinent and once again show that he was a very perceptive observer. The tissue of the veil is not truly part of the stipe, although just before the hymenophore commences to elongate some inter-weaving of the hyphal elements of both veil and stipe takes place.

The cuticle of *P. sphaerosporus* may be over 180 μ thick and consists of a layer of appressed, narrow, gelatinous, hyaline hyphae lying over a subcutis. The thick cuticle, an epicutis, is in all ways structurally similar to the 'veil' on the stipe, in fact it is in every way homologous thus resembling that described for *Suillus luteus* by Disbrey & Watling (1967). The tissue beneath the pileus 'surface' is modified probably by pressure from the 'universal veil' but it also appears to be somewhat gelatinised; it is brown in colour even in water mounts but contains no amyloid elements. It does not appear to be a true ixotrichoderm although more fresh material in very young stages of development is required to see how this layer originates,

for drastic changes take place as the pileus 'cortex' matures as indicated by Disbrey & Watling (1967) for *Boletus piperatus* and by Watling (1968) for *Leccinum* spp. The outermost layer of the veil forms the 'cuticle' and overlies floccose, interwoven, non-amyloid hyphae of the body of the pileus tissue.

The innermost (second) layer of the veil appears to be much more jelly-like than the outer zone (primary); it is really the latter which gives to the pileus and the lower parts of the stipe their typical macroscopic characters and appears thus in the species-diagnosis. The true outer layer of the pileus and lower stipe are hidden from view for a very long period.

A certain amount of confusion exists in the literature concerning the placing of *P. sphaerosporus* in any one subfamily of the Boletaceae. Singer (1951 & 1962) placed this species in the Boletaceae subfamily Gyrodontoideae and recognised a close correlation between it and *Gyrodon merulioides* (= *Paxillus porosus* Berk.) whilst in a more recent account Smith & Thiers (1964) placed it in the genus *Suillus*; this last genus is the type of the subfamily Suilloideae according to Singer (1962). Gilbert was of a similar opinion to Smith & Thiers and as early as 1931 placed this same fungus in the genus *Ixocomus* (= *Suillus*).

Because of this conviction of a relationship with *Gyrodon lividus*, *Gyroporus* and *Phaeogyroporus*, Singer derived the generic name *Paragyrodon* from *Gyrodon*, the bolete genus, and the prefix 'para' meaning beside i.e. close to 'Gyrodon'. The emphasis on *Gyrodon* is unfortunate and far too great, firstly because *P. sphaerosporus* does not have a Gyrodon-like hymenium and secondly *Gyrodon* is based on a monstrosity; *Uloporus* is adopted here as the legitimate name for *Boletus lividus* because of factors laid down by Donk (1955) and Watling (1964). The usage of *Uloporus* also tries to separate *B. lividus*, type of the genus, from the other so-called *Gyrodon* spp., many of which may later prove to be quite unrelated to *B. lividus* and possibly more related to the Paxillaceae. Heim's (1966) general remarks on 'Les Meiorganes' and their relationships are pertient here and worthy of further consideration in the light of the above information even if not all the proposals on phylogeny expressed in the same paper are acceptable.

Gyroporus spp. differ from *P. sphaerosporus* in having much paler spores, lemon yellow in mass, and carpophores of quite different structure; both *G. castaneus* and *G. cyanescens* are probably quite unrelated either to *P. sphaerosporus* or to *Uloporus lividus*. The infrastructure of the spore of *G. castaneus* figured recently by Mme. J. Perreau (1967) may support this view.

P. sphaerosporus is here assigned to the Suilloideae of the Boletaceae to fall in line with current classification but because of the necessity for a drastic reassessment of the value of clamp-connections in the taxonomy of the boleti it cannot be over emphasised that the definition of the subfamilies of the Boletaceae need critical reviewing.

Many collections of *Gyrodon merulioides* have been examined in the field and the following herbarium material has been examined:—

(E) Under *Fraxinus*, Ann Arbor, Washtenaw Co., Michigan, ix 1965 *Watling* 4064; on soil on upturned *Fagus grandifolia*, Proud Lake, Oakland Co., Michigan, *Watling* 837; as *Paxillus porosus*, Ohio ex Herb. Hookerianum.

Acknowledgment

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