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WAWELIA EFFUSA LUNDQVIST, SPEC. NOV. (XYLARIACEAE)

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Wawelia effusa Lundq., spec. nov. is described, a stromatic pyrenomycete with 8-spored, deliquescing, non-amyloid asci without apical apparatus and with limoniform spores with a germ slit. It is found on dung of hare and roe-deer in Sweden and Hungary respectively, and differs from the two other species of the genus, *W. regia* Namysłowski and *W. octospora* Minter & Webster, by a basal, effused stroma, equilateral spores and probable lack of an anamorph. The stromatic nature of *W. effusa* is discussed, as well as the taxonomic position of the genus and the ecology of its species. The author joins those who argue for *Wawelia* being xylariaceous.

Some fungi are extremely rare, seemingly without reason. The stromatic pyrenomycete *Wawelia regia* Namysłowski (1908a, b) is a striking example. It was discovered growing on rabbit dung in Cracow, Poland, in 1908 and found there again by Guminska in 1957 on the same kind of substrate. There are also a few later records but only on rabbit dung from this very locality.

When interest in coprophilous fungi boomed in the 1860–90's several European mycologists of the time focussed their investigations on the mycoflora of leporid dung, for example B. Auerswald, G. von Niessl, G. Winter, and C.A.J.A. Oudemans, not to mention scores of other students up to the present days. I have investigated 41 collections of rabbit dung from Sweden using moist chamber cultures, but *W. regia* always baffled me. Like some other big coprophiles it may not thrive in such cultures, but, on the other hand, except from the finds in Cracow, it has never been discovered in the field either, so it must be extraordinarily rare. A large characteristic fungus like this could hardly have escaped detection.

Recently Minter & Webster (1983) published a new species of the genus, *W. octospora,* on rabbit dung from near Exeter in England. This fungus is even larger than *W. regia* with an up to 25 mm long, filiform stroma. Where has *W. octospora* been hiding all the time? The British Isles are mycofloristically well-known, and a number of renowned mycologists have for more than a century collected and studied also the minor coprophiles there.

In 1969 I received a real thrill when a new species of *Wawelia* turned up in my cultures, showing a spreading, *Hypoxylon*-like stroma totally different from that of *W. regia.* In my mycology courses in Uppsala I always used coprophilous fungi in moist chamber cultures as paramount objects for demonstrating living specimens of different groups and various phenomena. For three years my colleague, Dr. Erik Gunnerbeck, had gathered hare droppings for incubation from a single locality near Uppsala. After the courses I always checked the material for possible interesting finds. In the third year the unknown *Wawelia* species appeared after six weeks, when the culture was almost forgotten and partly dried out.

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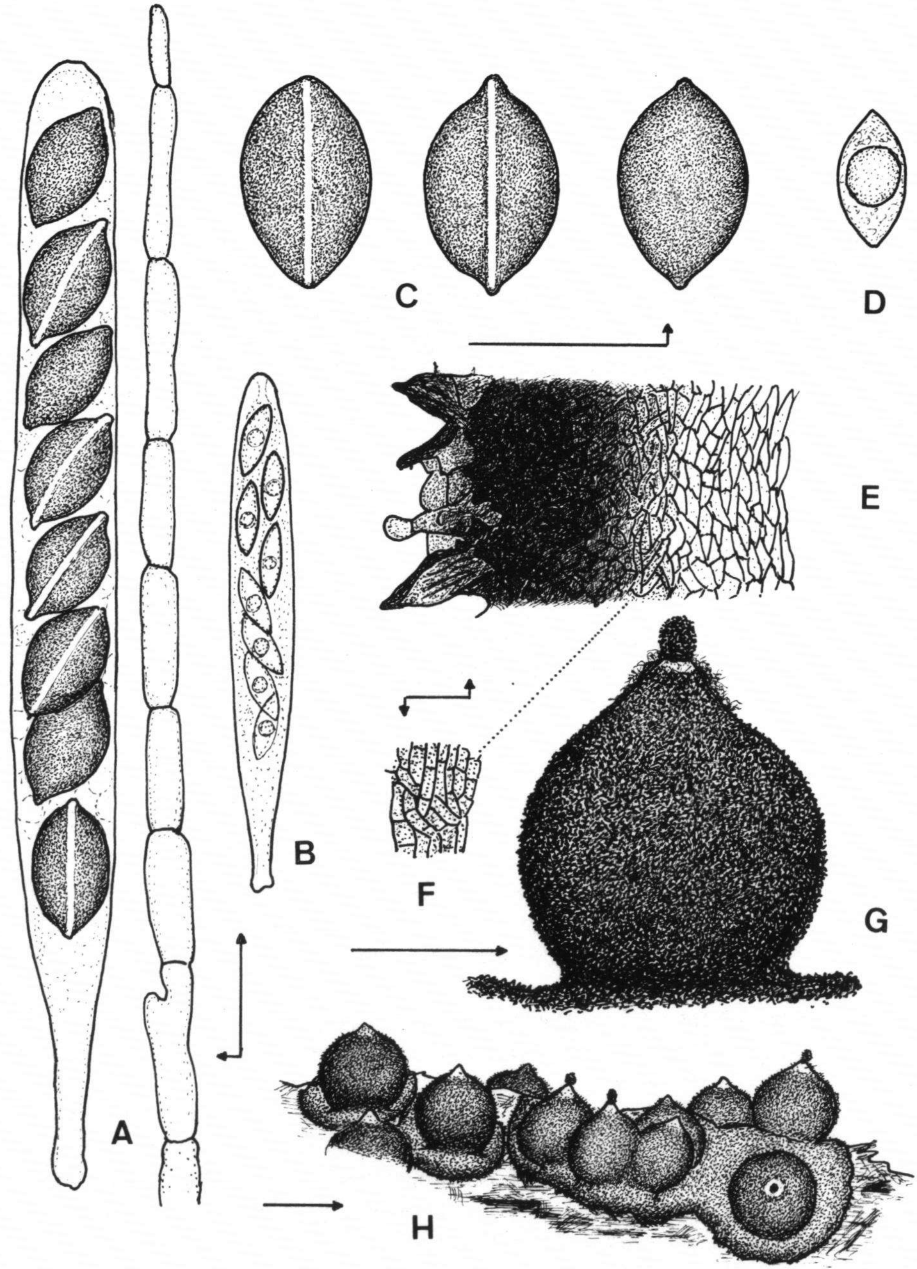
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It is notable that I had at the time investigated 69 collections of hare dung (*Lepus europaeus* and *L. timidus*) from Sweden with the moist chamber technique, each one for about a month or more, without seeing the fungus. After the discovery and up to 1987 another 27 Swedish samples of hare droppings were studied with negative result in this respect. In addition another 42 collections of leporid droppings from other countries and hundreds of dung samples from other animals investigated in the same way failed to yield any *Wawelia*. I considered it so rare that the publishing of it was shelved for more urgent tasks. Recently, however, I investigated a Hungarian collection of deer dung with the moist chamber method—and there it was again! Sandor Tóth, the foremost explorer of coprophilous fungi in Hungary, has repeatedly studied cervine droppings in his country without observing the species. It is undoubtedly rare, and the time is now ripe to present it.

Wawelia effusa[1] Lundq., *spec. nov.*—Figs. 1, 2

Stroma basale effusum, nigrobrunneum, superficie rugosa, textura angulari compositum. Ascomata 650–960 × 615–720 µm, ostiolata, globosa vel ovoidea, collo conico breve, normaliter cum uno perithecio. Peridium externum stromaticum, 45–55 µm crassum, stromati basali simile et eodem cohaerens, textura angulari compositum. Paraphyses filiformi-ventricosae, 5–12 µm crassae. Asci cylindrici, 110–140 × 13–15 µm, octospori, non-amyloidei, sine annulo apicali, postremo dissolventes. Sporae unicellulares, oblique uniseriatae, 15–19 × 9–10 µm, nigrobrunneae, limoniformes, aequilaterales, fissura germinali longitudinali, unilaterali instructae, gelatino carentes.

Basal stroma spreading on the substrate, black-brown, firm but not brittle with a rough surface and an opaque, partly indistinct textura angularis. Ascomata 650–960 × 615–720 µm, ostiolate, globose to ovoid with a short, conical neck, black-brown, often with white, agglutinate hyphae on the neck, stromatic, containing one, rarely two perithecia. Stromatic layer external, 45–55 µm thick with a rough surface of brown outgrowths, a middle part of opaque, indistinct, black, angular, thick-walled cells, and an inner, transitional part of light brown cells mixed with hyphae. Perithecial wall 25–40 µm thick, semitransparent, hyaline, composed of angular, more or less flattened, thin-walled cells. Perithecial contents hyaline to light ochraceous. Paraphyses filiform-ventricose, 5–12 µm thick, mixed with and longer than the asci. Asci 8-spored, 110–140 × 13–15 µm, cylindrical, short-stiped, non-amyloid with a rounded tip lacking apical apparatus, finally dissolving. Spores at first fusiform, biseriate with a central oil drop, then obliquely uniseriate, ranging from hyaline, olive brown to black brown, limoniform, equilateral, 15–19 × 9–10 µm, with a broad, distinct, longitudinal, unilaterally placed germ slit reaching from end to end. Gelatinous equipment lacking.

Specimens studied. SWEDEN: Uppland, Haga parish, Åtorpet, on hare dung (*Lepus*), 6.IV.1969, *E. Gunnerbeck 1832-d* (UPS, holotype; K, S, isotypes). — HUNGARY: Bács-Kiskun, 20 km W. of Kecskemet at Fülöphaza, on roe-deer dung (*Capreolus capreolus*), 26.V.1987, *Lundqvist 1649-q* (S).

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[1] Etymology: From Latin, effusus, spread out, referring to the basal stroma.

Fig. 1. *Wawelia effusa* Lundq. (*Gunnerbeck 1832-d*, holotype, UPS). — A. Mature ascus, spores, and paraphysis. — B. Immature ascus and spores. — C. Three mature spores, one in ventral view with germ slit not visible in this position. — D. Immature spore. — E. Peridium in median vertical section; the dark, stromatic part to the left. — F. Surface view of transitional layer of peridium between the stroma and the perithecial wall. — G, H. Ascomata and basal stroma. (A–F, bars 15 µm; G, H, bar 800 µm.)

MORPHOLOGY AND ANATOMY

Anatomy, cytology, and perithecial development are well-known in *Wawelia* thanks to studies by Namysłowski (1908a) and Doguet (1961a, b, c) on *W. regia,* which they cultured on agar media. An account of the results is beyond the scope of my presentation, but one point demands a commentary. The perithecia of both *W. regia* and *W. octospora* are, with one exception, stated to be placed *on* the stroma: 'Perithecia non sunt infixa in stromate, sed semper superficiei supercedent' (Namysłowski, 1908a: 602); 'perithecia superficial' (Minter & Webster, 1983: 371); 'Les périthèces adultes sont extérieurs au stroma' (Doguet, 1961c: 200).

These statements are partly misleading and are contradicted by the descriptions and illustrations by these authors, which show that at least the outermost layer of the ascomata is continuous with the main stroma. In *W. octospora* even the middle layer is 'merging with the textura intricata of the stroma' (Minter & Webster, 1983: 371). In *W. regia* Namysłowski mentions a 'couche corticale' that undoubtedly alludes to the outer stromatic layer. In the Stockholm herbarium we have a slide of the species made by Namysłowski with sections of ascomata and stromata, and they clearly reveal that this stratum merges with the main stroma. The same phenomenon occurs in *W. effusa,* and it is even possible to peel off the stromatic layer with a needle like in *Hypocopra* (Xylariaceae). Only one author unequivocally described the ascomata as stromatic, namely Müller (1959: 518): 'Sie [die Fruchtkörper] bleiben aber dauernd von der Stromakruste umschlossen'. The transitional zone between the peridial stroma and the perithecial wall is of problematic origin. I have here interpreted this layer as the innermost part of the peridial stroma.

In *W. effusa* the basal stroma may bear hundreds of ascomata as well as a few or single ones. Occasionally two perithecia are fused to form a double body with two necks within a single stromatic cover. The ascus wall is thin and difficult to see, and the asci apparently finally deliquesce. On some ascomata a spore mass gathers on the ostiolum or smears the whole body indicating a passive spore release. There are no long ostiolar hairs, however, to promote the spore dispersal as in the case of the two other species of the genus. It is also remarkable that all three Waweliae, although coprophilous, lack gelatinous equipment on the spores.

Wawelia effusa seems to be the only member of the genus lacking an anamorph, but conclusive proof about it can be obtained only by culturing the species on agar media.

TAXONOMY

Several opinions have been voiced as to the taxonomic position of *Wawelia.* Namysłowski was convinced that the genus belonged in the 'family' Hypocreales between the Melanosporaceae and the Nectriaceae, forming a new subfamily Wawelioideae ('Waweliaceae'). Vincens (1918), Chenantais (1920), von Arx & Müller (1954) and Müller & von Arx (1973) placed it among the Xylariaceae, i.a. because of its spore characters, whereas Doguet (1961c) and Müller (1959) connected it with the Melanosporaceae owing to the ciliate ostiolum and non-amyloid, dissolving asci without apical apparatus. Doguet (1961c: 216) meant that the resemblance with the *Xylaria* kind of ontogeny is a convergence. A whole-sale analysis of his conclusions and very detailed investigations on ascomatal development remains, however, to be

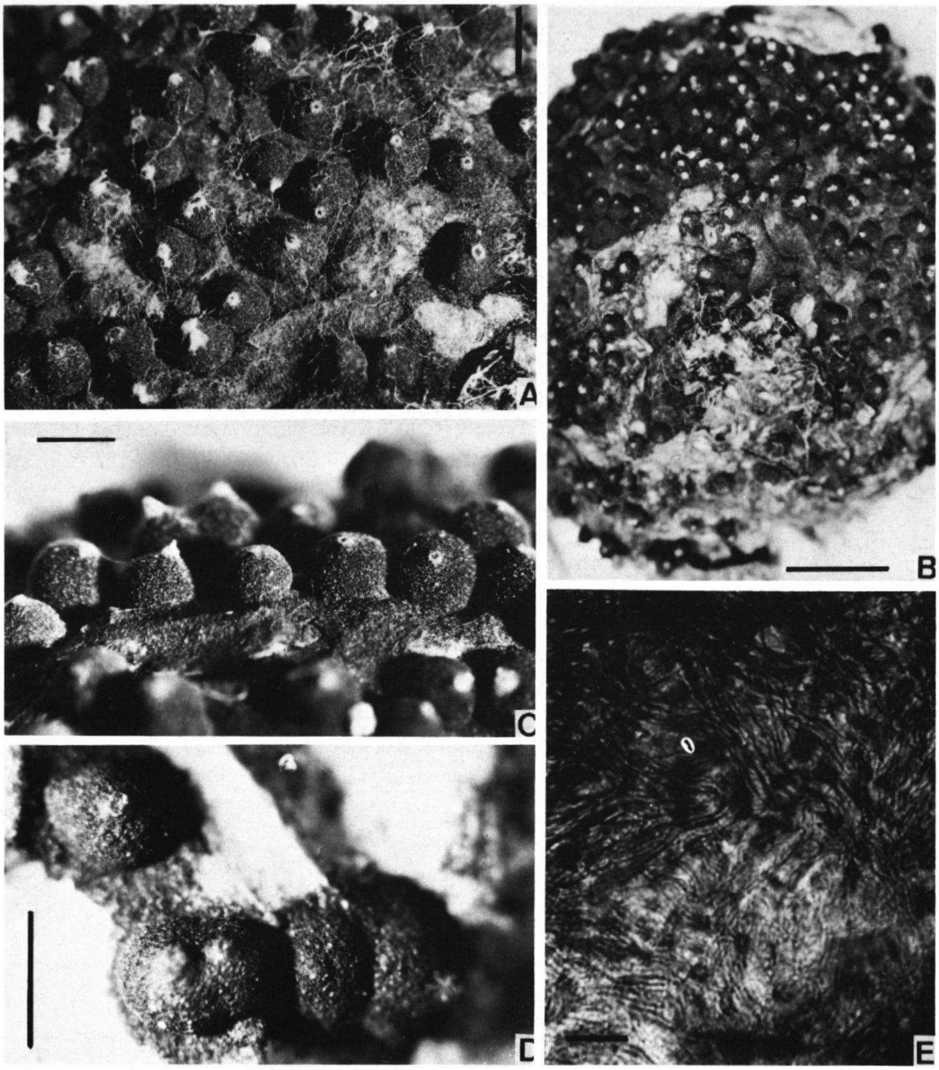

Fig. 2. *Wawelia effusa* Lundq. (*Gunnerbeck 1832-d*, holotype, UPS). — A–D. Ascomata on dung pellet. — D. Stroma with two perithecia (bottom left). — E. Surface view of transitional peridial layer between the stroma and the perithecial wall. (A–D, bars 800 µm; E, bar 4 mm.)

made. Minter & Webster (1983) also advocate a xylariaceous affinity pointing to the dark stroma, the spore type with a germ slit and kind of anamorph. Non-amyloid, dissolving asci without apical apparatus are not unique characters in the Xylariaceae, nor is a rope-like stroma as in *W. octospora*.

Oddly enough, nobody but Barr (1990: 99) has compared *Wawelia* to groups other than the Xylariaceae, having one-celled, dark spores with a germ slit. The Coniochaetaceae offer a possible alternative, although they lack a stroma and most of them have setose perithecia, persistent asci with apical ring and more or less flattened spores. But if non-amyloid, dissolving asci without apical apparatus are considered exceptional characters in the Xylariaceae and yet no hindrance for including *Wawelia* there, one may with the same logic argue that occurrence of a stroma, non-setose perithecia, and dissolving asci without an apical ring are exceptional but not impossible features in the Coniochaetaceae. However, this comparison concerns ostiolate species only. Dissolving asci connected with cleistocarpy, which exists in both the Coniochaetaceae and the Xylariaceae are irrelevant characters in this case. On the other hand, deliquescent asci are found in some ostiolate members of the Xylariaceae, and both families in question have different dominating spore symmetries with a bilateral flattening in the Coniochaetaceae and a unilateral flattening in the Xylariaceae. The anamorphs are also dissimilar: phialidic and holoblastic respectively. I agree with those who favour a xylariaceous relationship with *Wawelia*. Its species are in many respects very similar to *Xylaria, Hypoxylon,* and *Rosellinia.*

ECOLOGY

There are too few records of the *Wawelia* species to allow a definite judgement about their choice of environment. *Wawelia effusa* was found in coniferous forest and on sand dunes with steppe vegetation. *Wawelia regia* was collected repeatedly in a botanical garden, whereas *W. octospora* also occurs on sand dunes. Leporid droppings seem to be the favoured substratum. Occurrences in dry habitats are certainly not accidental in the species. Minter & Webster (1983) have demonstrated that *W. octospora* can stand a low relative humidity of the air and yet develop ascomata. It is also striking that the Swedish specimens of *W. effusa* appeared on dried-out substratum.

The time of development of the ascomata is several months long in *W. octospora,* 1–2 months in *W. effusa,* and 6–7 weeks in *W. regia* Namysłowski, 1908a: 598). Under natural conditions the maturation period may be even longer than in a moist chamber. Possibly also the anamorphic state promotes the longevity of the stroma.

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