Lauderlindsaya, a new genus in the Verrucariales for *Sphaerulina chlorococca* (LEIGHTON) R. SANT.

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The new generic name *Lauderlindsaya* is introduced for the lichenicolous parasite of *Normandina pulchella* (BORRER) NYL., previously known as *Sphaerulina chlorococca* (LEIGHTON) R. SANT. The biology and systematics of the new genus are discussed, and it is referred to the Verrucariales. It is compared with other multiseptate-spored members of that order.

The presence of perithecia associated with the squamules of *Normandina pulchella* (BORRER) NYL. has been known since BORRER (1829: tab. 2602, fig. 1) described it as *Verrucaria pulchella* BORRER but the precise nature of that association has been a source of considerable problems, both nomenclaturally and systematically. The nomenclatural problems were resolved (HENSSEN, 1976: 129), when *N. pulchella* was lectotypified on a specimen of BORRER's from Sussex, preserved in his herbarium at K, which lacked the pyrenomycete.

The systematic confusion derives from the fact that *N. pulchella* is now known to be a sterile lichen of uncertain affinity. The presence of the parasite gives the impression that *N. pulchella* is fertile, as for the most part the parasite does no apparent damage. The illustration in BORRER (1829) of *N. pulchella* includes one specimen from Sussex which lacks the parasite (the lectotype; see above), and one from Bantry in Eire which clearly is infected. His text also includes a reference to the perithecia of the parasite as an integral part of his description of *Verrucaria pulchella.* This was followed by subsequent lichenologists, so that HOOKER (1833) treated it as a species of *Endocarpon* HEDW. DELISE, in DESMAZIÈRES' exsiccata, Plantes Cryptogames du Nord de la France, fasc. 23, no. 1144 (1841), described a new genus, *Lenormandia* based on material of *N. pulchella,* but his name must be rejected as a later homonym of *Lenormandia* SONDER nom. cons. [Rhodophyceae]. The type of *Lenormandia* DELISE, *L. jungermanniae* DELISE, was considered identical to *N. pulchella* by KÖRBER (1855: 101). NYLANDER (1855: 191) described

the genus *Normandina,* again including descriptions of the parasite's ascomata as if they were the perithecia of the lichen. However TULASNE (1852: 128), commenting on DELISE's description of the genus *Lenormandia,* said that the "fruits" which had been illustrated as part of the lichen in BORRER (1829) and by LEIGHTON (1851) were those of a parasite to which he gave the name *Sphaeria borreri* TULASNE. KÖRBER (1855) noted the similarity between *Lenormandia* and TULASNE's parasitic fungus. LINDSAY (1869: 54) states, in his notes on *Normandina jungermanniae* (DELISE) NYL. [i. e. *N. pulchella*], that the spores found in the thallus belong to the parasitic fungus *Sphaeria borreri,* thus demonstrating that he also was aware of the allochthonous nature of the perithecia described for *N. pulchella.*

Unfortunately the contributions of TULASNE and LINDSAY went unnoticed by later lichenologists (LEIGHTON, 1879; VAINIO, 1890; SMITH, 1926; FINK, 1935; SWINSCOW, 1963) who included *Normandina* as a member of the Verrucariaceae, on the assumption that the presence of the parasite represented its ascomata. VAINIO (1921: 231), however, treated *Normandina* pro parte as a synonym of *Coriscium* VAINIO, as a sterile lichen but did include a reference to the description of "apothecia" by LEIGHTON (1851, 1879). He left the actual position of the lichen as uncertain.

LEIGHTON (1879: 484) described *Verrucaria chlorococca* with exactly the same features as the "fertile *Normandina*" except in the thallus which he gave as, "green, thickish, granulate, somewhat areolato-diffract". This has subsequently been referred to informally as the "free-living form". SMITH (1926) transferred *V. chlorococca* to *Arthopyrenia* MASSAL., emending LEIGHTON's description to include, "paraphyses slender, mucilaginous, disappearing", as opposed to LEIGHTON's, "paraphyses none".

SWINSCOW (1963) realised that LEIGHTON's *V. chlorococca* was the same as the fungus on *N. pulchella* but continued to regard the fungus as being the fertile state of *Normandina.* The problem was not considered again until HENSSEN (1976: 128) confirmed the view that the squamulose part of the association is a sterile lichen. Although she drew comparisons with *Coriscium,* she concluded, due to the absence of dolipore septa in the hyphae, that *Normandina* could not be a basidiomycete. The identity of the parasite was dealt with by SANTESSON (in HENSSEN 1976: 129), who considered it faute de mieux, "to be a species of *Sphaerulina* (a somewhat heterogenous assembly . . .)", and transferred it to that genus as *Sphaerulina chlorococca* (LEIGHTON) R. SANT., LEIGHTON's epithet being lectotypified by LARBALESTIER's specimen in BM, which is *S. chlorococca* not associated with *N. pulchella.*

Materials and Methods

Specimens examined were from BM, E, UPS and IMI. The specimens were sectioned using a freezing microtome and mounted in lactophenol or Lugol's iodine. Squash preparations of the perithecia were made, mounted in 10% KOH or Lugol's iodine. Slides were examined using a Zeiss Universal microscope with Nomarski and phase optics.

Biology

The rediscovery of "free-living" material prompted an investigation to determine, (a) whether *Sphaerulina chlorococca* really was free-living in association with algae, and, (b) if this morph represented a separate new species. Examination of sections of material from bark and mosses showed the ascomata surrounded by algae, with brownish hyphae spreading out from the ascomata into the algal mass. Sections of the *"Sphaerulina"* immersed in the thallus of *Normandina* show that the ascomata protrude on the underside of the squamules, but are not attached at the base to the substrate on which the *Normandina* is growing. The algae of *Normandina* and those found associated with the "free-living" ascomata were chlorococcalean. Initially, the presence of the ascomata have no apparent effect on the algae or the thallus of *Normandina,* but later on the thallus can become bleached or even degenerate to a powdery mass. The ascomata and ascospore sizes were recorded and the peridial structure was examined in both the "free-living" and the "parasitic" collections in order to determine whether there were any differences between them (Tab. 1, Fig. 1).

Tab. 1. – Range and average (with standard deviations) in length and width of spores of *Lauderlindsaya borreri* on different substrata

substrate	length µm range	length µm average	width µm range	width µm average
Sambucus (COPPINS 4009)	31.1 – 37.8	33.6 ± 2.2	5.9 – 8.4	7.0 ± 0.9
Quercus (COPPINS 11223)	26.9 – 38.6	31.9 ± 3.2	6.7 – 8.4	7.4 ± 0.7
with *Parmeliella* (COPPINS 4165)	26.9 – 36.1	32.1 ± 2.7	6.7 – 8.4	7.6 ± 0.7
Salix (COPPINS 2574)	31.5 – 38.4	35.3 ± 2.2	6.9 – 8.8	8.0 ± 0.5
Moss (indet.) (COPPINS 9905)	26.0 – 31.9	29.3 ± 1.8	6.7 – 8.4	7.6 ± 0.4
Normandina (a) (IMI 196191)	35.3 – 41.6	38.5 ± 2.3	6.3 – 8.2	7.5 ± 0.6
Normandina (b) (IMI 296945)	27.7 – 42.0	34.7 ± 4.0	6.7 – 9.2	7.8 ± 0.9

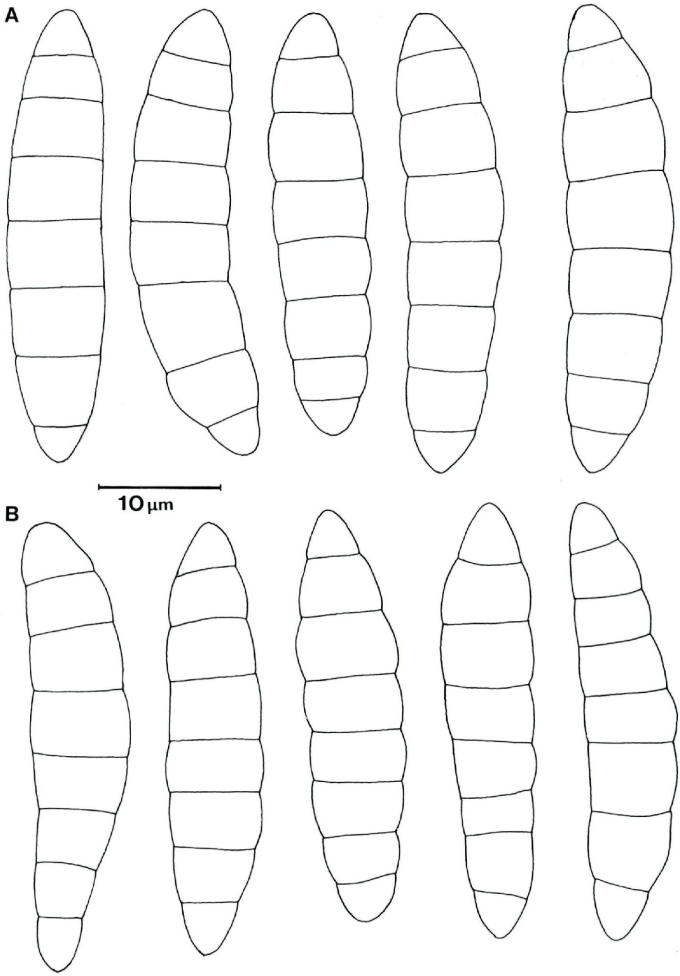

Fig. 1: Ascospores. – A. *Lauderlindsaya borreri*, from perithecia on *Normandina pulchella*. – B. From perithecia on *Salix*.

The "free-living" material of *Sphaerulina chlorococca* proved to be almost identical to that found on *Normandina* thalli (Tab. 1). The only noticeable difference was in the ascomatal wall; when "free-living" the perithecia are more heavily thickened than when "parasitic" (see Plate 2, b & c), to the extent that the ascomatal wall of "free-living" material shows a distinct tendency to break up into plates (in squash preparations) (Plate 3, a). This is probably a phenotypic response to their different ecologies. It seems unlikely that the "free-living" type represents an independently lichenized morph of *S. chlorococca,* and it is probably best to consider it as weakly pathogenic or commensalistic (HAWKSWORTH, 1988). The similarity of the host algae suggests that the relationship is a specific one; indeed the difference between the attachment of the ascomata of *S. chlorococca* suggests that the "free-living" material is not a result of the degeneration of *Normandina* thalli.

Taxonomy

Examination of both "free-living" and "parasitic" material confirmed the suspicion of HAWKSWORTH (1983: 15) that the fungus did not belong to *Sphaerulina* SACC. It was therefore necessary to determine where its affinities lay. The asci have such delicate walls that there were difficulties in examining them in detail. The walls of the asci were seen to have more than one layer (Plate 1, fig. d) and are similar to *Dermatocarpon* ESCHW., as SANTESSON (in HENSSEN 1976: 129) noted: "The ascus type is difficult to recognize on account of the very easily bursting walls . . . have a similar structure to the bitunicate ascus of *Dermatocarpon*". JANEX-FAVRE (1970) and ERIKSSON (1981: 55) however, state the *Dermatocarpon* asci have a distinct ocular chamber, which *S. chlorococca* does not. *S. chlorococca* was compared with several similar genera, using data from direct observations and available literature, and was found to have the most characters in common with the Verrucariales, a placement supported by its ascus features. That it is not a *Sphaerulina*, a genus in the Dothideales, is clear as it has prominent periphyses (Plate 1, figs b & c) and a different peridial structure (Plate 2, figs b & c); the ascomata are also much larger than in any accepted *Sphaerulina* species, and the asci lack the apical nasse seen in *Sphaerulina.*

The Verrucariales contains almost entirely lichenized taxa, but also a few lichenicolous fungi such as *Muellerella* species and lichenicolous lichens, particularly species of *Verrucaria* (ZEHETLEITNER, 1978; MCCARTHY, 1988). Whilst the Verrucariales have mainly non-septate spores, all the basic spore septation types can be found; trans-septate genera are *Thelidium* MASSAL, *Macentina* VĚZDA, *Placidiopsis* BELTR. and *Heterocarpon* MÜLL. ARG. and muriform ones also occur, in *Agonimia* ZAHLBR., *Polyblastia* MASSAL.,

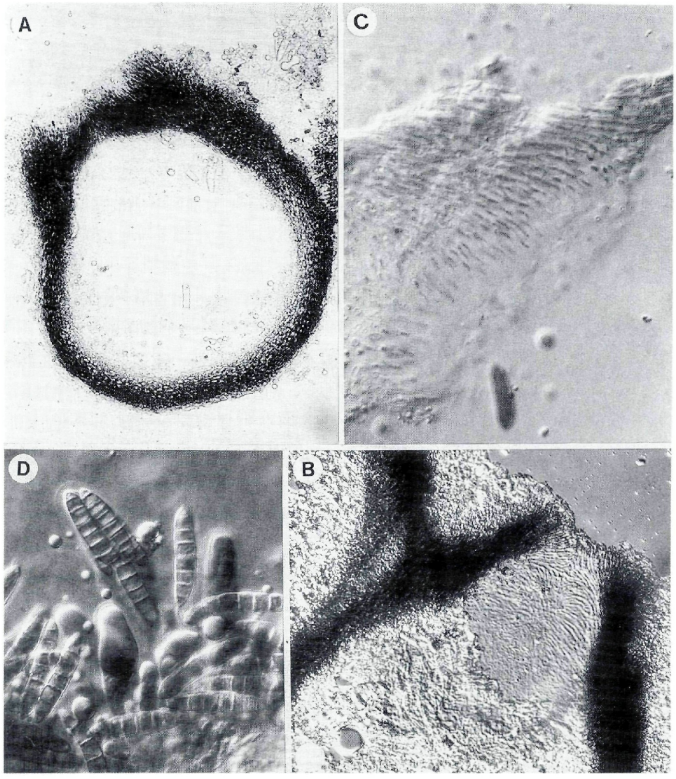

Plate 1: *Lauderlindsaya borreri*. – A. Ascoma (× 250). – B. Ostiole of ascoma showing arrangement of periphyses (× 650). – C. Detail of periphyses (x 650). – D. Asci and ascospores (× 650).

and *Leucocarpia* VĚZDA. Compared with the septate genera, *Macentina* differs from *S. chlorococca* in having small pellucid perithecia. The squamulose/foliose genera *Placidiopsis* and *Heterocarpon* usually have 1-septate ascospores but may have up to 3-septate spores. Thallus morphology, insofar as the perithecia do not project below the lower surface of the thalli, precludes further consideration here. The differentiation between *Thelidium* and *S. chlorococca* is more problematical. ZSCHACKE's (1934) account of *Thelidium* includes a number of taxa which occur on substrata considered unusual for *Thelidium* and also with a degree of spore septation which similarly is not typical of that genus. A number of these taxa have been examined in order to be able to more clearly define the separation between *Thelidium* and *S. chlorococca*, and some of them have indeed proved to be identical to the latter as anticipated. Further work is needed to determine the nature of these taxa. A. ORANGE (pers. comm.) has noted that the ascus dehiscence in *Thelidium* s. str. is quite different, in that there is an extrusion of the endotunica after the release of spores. ERIKSSON (1981: 158) observed that the type species of *Thelidium*, *T. amylaceum* MASSAL. has a "distinct, low, broad ocular chamber" which *S. chlorococca* does not. *Pocsia* VĚZDA, a genus of foliicolous lichens currently treated as a member of the Trichotheliaceae (ERIKSSON & HAWKSWORTH, 1987), was suggested by VĚZDA (1975) to be possibly related to the Verrucariales, particularly through the absence of paraphyses, the presence of periphyses and the perithecium structure; the asci also appear to be Verrucarialean. *Pocsia* differs from *S. chlorococca* in having perithecial walls which are not black in colour and are covered by a thalline layer.

Thus it is clear that a new genus is necessary to accommodate *S. chlorococca*.

Lauderlindsaya J. C. DAVID & D. HAWKSW., gen. nov.

Genus lichenicola aut algicola, ad Verrucariales pertinens. Ascomata perithecia subglobosa aut conoido-globosa, nigra, pseudoparenchymatica, quaeque ostiolo punctiformi terminali induta. Paraphyses non manifestae, et periphyses faciles visae, simplices aut ramosae. Centrum iodo fusco-rubescens. Asci clavati ad lati-clavati, muris tenuibus sed ad apicem incrassatis, 8-spori. Ascosporae ellipsoideo-fusiformes, plerumque 7-septatae, ad septa constrictae, primum decolores, dein pallide fuscae, laeves.

Species holotypica, adhuc unica, est *Lauderlindsaya borreri* (TULASNE) J. C. DAVID & D. HAWKSW. (syn. *Sphaeria borreri* TULASNE).

Lichenicolous or algicolous ascomycete, belonging to the Verrucariales. – Ascomata perithecioid subglobose or conical-globose, black, pseudoparenchymatous with a terminal punctiform ostiole. – Paraphyses not seen, periphyses well developed, branched or unbranched. Centrum turning red-brown with iodine. – Asci clavate

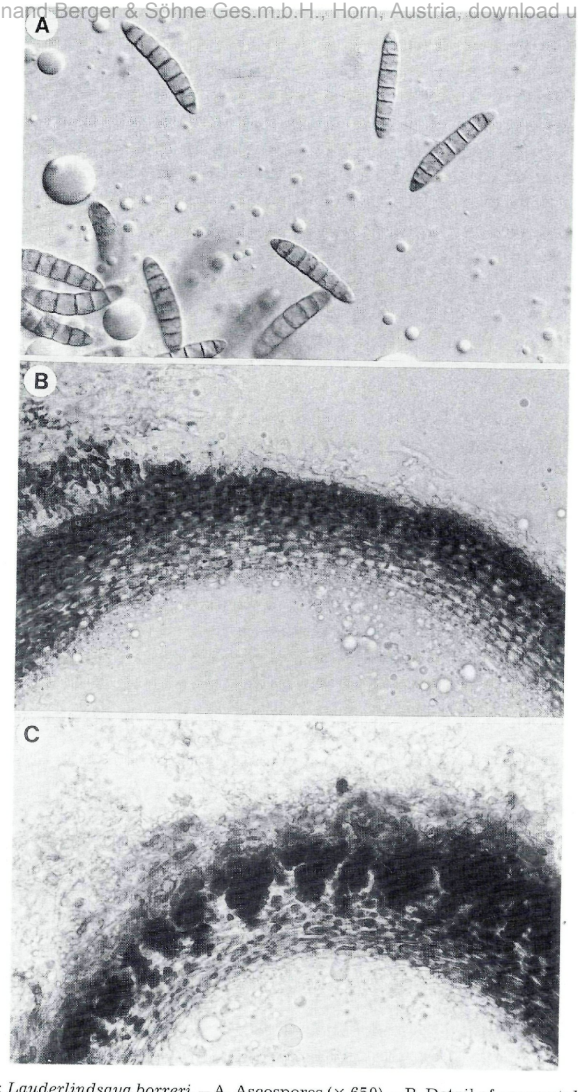

Plate 2: *Lauderlindsaya borreri*. – A. Ascospores (× 650). – B. Detail of ascomatal wall of *L. borreri* on *Normandina pulchella* thallus. – C. Detail of ascomatal wall in "free-living form" (× 650).

or broadly clavate, with thin walls but thickened at the apices, 8-spored. – Ascospores ellipsoid-fusiform, usually 7-septate (immature spores 3-5-septate), constricted at the septa, at first colourless then becoming pale brown (with age), smooth walled.

This genus is named in honour of WILLIAM LAUDER LINDSAY (1829–1880) one of the foremost pioneers of studies of lichenicolous fungi.

The generic name *Normandinomyces* CIFERRI & TOMASELLI (1953: 30), was also considered as a possible earlier name for *Lauderlindsaya*. The former name can be excluded as nomenclaturally illegitimate; being based on the same type as *Normandina* it is automatically typified by the lectotype of BORRER's name, thus rendering it superfluous under Article 63 of the Code.

Lauderlindsaya borreri (L. R. TULASNE) J. C. DAVID & D. HAWKSW., comb nov.

Bas.: *Sphaeria borreri* L. R. TULASNE, Ann. Sci. nat., Bot., sér. 3, 17: 128, 1852.

Syn.: *Verrucaria chlorococca* LEIGHTON, Lich. Fl. Br., edn 3: 484, 1879.
Arthopyrenia chlorococca (LEIGHTON) A. L. SMITH, Br. Lich., edn II, 2: 361. 1926.
Thelidium chlorococcum (LEIGHTON) KEISSLER, Rabenh. Krypt. Fl. edn 2: 9, 1(2): 191. 1938.
Sphaerulina chlorococca (LEIGHTON) R. SANT., in HENSSEN, apud BROWN et al., Lichenology: Progr. Probl.: 129, 1976.

= *Thelidium erichsenii* KEISSLER, Revue mycol., 1: 179. 1936.

= *Polyblastia armericola* W. WATSON, J. Bot., Lond., 77: 42. 1939.

Typification. – TULASNE (l. c.) cites BORRER's illustration (2602 fig. 1) as showing *Sphaeria borreri*, the parasite of *Normandina;* the specimens used for this illustration are kept in BORRER's herbarium at Kew. One of the specimens was used to lectotypify *Normandina pulchella* (HENSSEN, 1976: 129). The other two are from Ireland, of which one collected by Miss HUTCHINS from Bantry was the other specimen used for the drawings, and is the top right specimen figured. The other Irish specimen was collected by Dr. T. TAYLOR and was used for LEIGHTON's (1851) plate 3 fig. 1. Since TULASNE in his protologue cites BORRER's illustration, the top right-hand specimen on the sheet must be considered as the lectotype material of the name *Sphaeria borreri*. VOUAUX (1913) considered TULASNE's name to be "trop hypothétique", but whilst TULASNE did not give a description as such, it was clear from his protologue what he intended when he said, "simul et Sphaeriam (*S. Borreri* Nob.) hospitem sparsim suis in penetralibus immersam exhiberet", and in his citation of relevant literature.

Illustrations. – *Lauderlindsaya* has been illustrated by BORRER (1829: tab. 2602 fig. 1), LEIGHTON (1851: Plate 3 fig. 1), SMITH

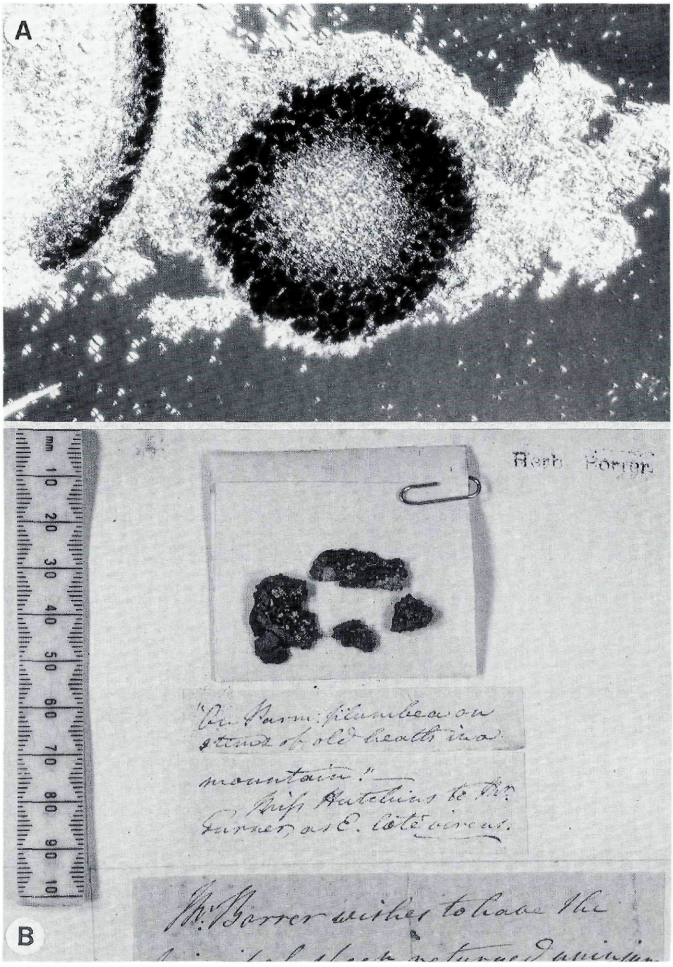

Plate 3: *Lauderlindsaya borreri*. – A. Squash preparation of ascomatal wall of "free-living form", under phase contrast (× 250). – B. Lectotype of *Sphaeria borreri* TULASNE, in Herb. K.

(1926: Plate 40), Swinscow (1963: 168, fig. 1) and Henssen (1976: Plates XVII, XVIII & XIX).

Description. – Fungus occurring on *Normandina pulchella* or on free-living chlorococcalean algae, not forming an independent thallus. – Ascomata perithecioid, solitary, immersed in the host thallus, protruding through the underside of host squamules, or not on a distinct thallus and surrounded by an algal mass; black, matt, with a distinct apical ostiole, entire, globose at the base, becoming conical at the apex; peridium *textura angularis* with fairly elongated cells composed of 10–15 cell layers, 30–45(–55) µm thick, the outer cells having densely pigmented walls, the inner layers ± colourless, (160–)200–300(–350) × (150–)170–250(–330) µm diam. – Centrum I+ red–brown. – Hamathecium lacking interascal filaments, periphyses well developed at the ostiole, septate, branched or unbranched. – Asci clavate to broadly clavate, short stalked, with delicate walls, ascus apex lacking any apparatus, but clearly showing the 2-layered nature of the walls, I–; (15–)17–23 × 85–95 (–115) µm, 8-spored. – Ascospores elongate-ellipsoid, ends pointed, (5–)7-trans-septate, colourless, becoming brown with age (usually after discharge), initially not constricted at the septa but becoming so with age, smooth-walled, 25–35(–45) × 6–9 µm, after discharge the spores tend to remain clustered together. – Anamorph not observed.

Distribution. – In the British Isles the fungus occurs along the western coasts, and is also present in continental Europe (Diederich, 1986), in Chile, W. Australia, the Philippines and Madeira. This distribution tends to indicate that *Lauderlindsaya* will be found where its host occurs.

The distribution of *Normandina pulchella* is temperate – subtropical to tropical, mainly occurring in damp woodlands/rainforests. It is recorded from all five continents. North America (Culberson & Hale, 1966); South America (eg. Degelius, 1935; Figueiras, 1986; Xavier Filho & Toledo Rizzini, 1976); Central America (Pluntke, 1984); Africa (eg. Almborn, 1966; Swinscow & Krog, 1988); Australia (Filson & Rogers, 1979); New Zealand (Galloway, 1985); Papua New Guinea (Shaw, 1984); Japan (Yoshimura, 1974); USSR (Oxner, 1956); Europe (Degelius, 1935).

Many records of the host in floras tend to include a description of the parasite (usually as the fertile perithecia), but this may not always mean that they had recorded it with the parasite themselves.

Specimens examined. – EIRE: Co. Cork, on a mountain near Bantry, on stems of a heath, Miss Hutchins (K-Borrer – Lectotype of *Sphaeria borreri* Tul.). [Plate 3, b]. – UK: Buckinghamshire: Stokenchurch, on mossy bark of Ash *(Fraxinus excelsior)*, ii. 1876, C. Larbalestier, (BM-Lectotype of *Verrucaria chlorococca* Leighton). – V. C. 1, Cornwall: Lizard, on *Armeria maritima*, 1928, H. H. Knight & D. A.

JONES (BM-Holotype of *Polyblastia armericola* W. WATSON). – V. C. 3, Devon: Newton Abbott, Bradley Manor, on *Normandina pulchella*, 15. viii. 1975, J. FILDES (IMI 196191). – Holne Chase below the Hotel, on *N. pulchella* on *Salix* branch, 3. viii. 1985, D. L. HAWKSWORTH 5519 (IMI 296945). – V. C. 68, Northumberland: Easington, Spindlestone Haugh, on *Sambucus* bark, 9. iv. 1979, B. J. COPPINS 4009 (E). – V. C. 96, Easterness: Glen Cannich, by R. Cannich south west of Muchrachd, on *Populus*, 22. vi. 1976, B. J. COPPINS 3226 (E). – V. C. 97, Westerness: north side of Loch Sunart, c. 4 km, east of Salen, Resipole ravine, on *N. pulchella*, with *Capronia* sp., 10. iii. 1983, B. J. COPPINS & P. M. JØRGENSEN 9405 (E). – V. C. 98, Argyll: Seil, Ballachuan, wood south of Port Mor, on *Salix*, 30. vi. 1976, B. J. COPPINS 3226 (E). – V. C. 103, Mid-Ebudes: Coll, west side of Loch Fada, on a horizontal branch of *Salix*, iv. 1983, B. J. COPPINS 9637 (E); Coll, Arinagour, The Lodge, on *Acer* with, but not on *N. pulchella*, 16. iv. 1983, B. J. COPPINS 9666 (E). – V. C. 104, Skye: Dunvegan Castle woods, over (not in) thallus of *Parmeliella atlantica* on *Fraxinus*, 26. vi. 1979, B. J. COPPINS 4165 (E). – V. C. 105, West Ross: Loch Maree, Talladale oakwood, on *Quercus*, 19. v. 1984, B. J. COPPINS et al. 11223 TE). – V. C. 108, West Sutherland: Bettyhilll, Invernaver NNR, over mosses amongst *Dryas*, 22. viii. 1983, B. J. COPPINS et al. 9823 (E) & B. J. COPPINS et al. 9905 (E). – EIRE: V. C. H 1 or 2, Co. Kerry: sine loc., on *N. pulchella*, Dr. MOORE (E). – GERMANY: Schleswig-Holstein, near Ackerum on Föhr island (Nordfriesische Inseln), on bark of *Populus tremula*, 22. v. 1929, C. F. E. ERICHSEN (HBG-Lectotype of *Thelidium erichsenii* KEISSLER). – CHILE: Prov. Chiloé: Isla Chiloé, Peninsular Lacui, Punta Corona, on *N. pulchella*, on *Berberis buxifolia* in a dense forest near the seashore, 20. x. 1940, R. SANTESSON No. 4078 (UPS). – AUSTRALIA: W. Australia: 15 km W. of Pemberton, Beedelup National Park, at Beedelup Falls, 34° 26′ S, 115° 53′ E, on *N. pulchella* on bark of *Eucalyptus* sp., 10. x. 1983, L. TIBELL No. 14001 (UPS). – PHILIPPINES: Luzon Island, Benguet subprovince, Baguio "and vicinity", on *N. pulchella* growing with isotype specimen of *Anaptychia propagulifera* (PERS.) VAIN. var. *propagulifera* VAIN., in BM (UPS). – MADEIRA: Concelho da Santana: Ribiero Frio, by the "levada" E. of Ribiero Frio, alt. 850–870 m, on *N. pulchella*, 6. v. 1978, R. SANTESSON No. 28096 (UPS).

Acknowledgments

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