AGONIMIA Zahlbr. (1909)

**Thallus** crustose, composed of aggregations of goniocysts-like units, or minutely squamulose to coralloid, in one species more or less foliose with fragile lobes up to 5 mm wide; in squamulose species surface cells forming a pseudocortex, sometimes with brown pigment, cells often with one or more small papillae per cell; in one species papillae greatly elongated and adhering to form stiff hairs; epinuclear absent, or present in one species as isodiametric cell remains with refractive contents; squamules often fragile and disintegrating into granules or irregular fragments, sometimes producing blastidia, or isidia-like or soredia-like propagules. **Prothallus** inapparent or rarely present. **Photobiont** chlorococcoid, cells 4–13 × 3.5–7.5 µm. **Ascomata** perithecia, black, sometimes grey-brown due to a very thin unpigmented surface layer, subglobose to barrel-shaped, often situated between squamules or granules, surface smooth to strongly roughened. **Involucrellum** absent (or at least not distinguishable from the exciple). **Exixple** thick, ± layered, outer part of ± rounded cells which are densely pigmented, middle layer of similarly shaped but unpigmented cells, innermost layer of compressed, colourless cells; pigments dark brown, K+ grey-brown or reddish-brown or greenish. **Hymenial gel** hemiamyloid: I+ red (I+ blue at low concentrations of iodine), K/I+ blue. **Hamathecium** of periphyses and periphysoids; interascal filaments absent. **Asci** fissitunicate, 2- or 8-spored, I−, K/I−. **Ascospores** colourless (sometimes slightly browned when over-mature), muriform. **Conidiomata** pycnidia, absent in most species. **Conidia** colourless, bacilliform. **Chemistry**: no lichen substances detected. **Ecology**: on neutral or slightly basic soil, bark, and rock, often associated with mosses. **Distribution**: currently 17 species in temperate and tropical areas.

The genus as currently defined is apparently non-monophyletic, with Agonimia repleta occurring in a different clade to the others, but few species have been sequenced (Muggia et al. 2010). Other genera of Verrucariaceae with muriform ascospores differ in characters including an involucrellum present as a separate structure from the exciple, ascospores brown when mature, exciple colourless, or perithecia forming pits in rock. The ‘layered’ exciple of Agonimia is a less distinctive character if it is interpreted as an entire involucrellum surrounding an exciple. Protothelenella and Thelenella differ in the presence of abundant interascal filaments.

In the squamulose species, ‘squamule size’ is not a very useful character, as squamules are of indeterminate growth and soon lose their individuality; measuring the width of the ultimate lobes is more useful.

**Literature:**


1 Thallus with a distinct epinecral layer of dead, more or less isodiametric cells, resulting in a pale to dull mid-grey colour and a faint pruina to the lobes; lobes often with minute stiff projecting hairs up to 40 µm long, which are visible with a 10× hand lens ....................... *opuntiella*
   Thallus crustose or squamulose, but without a distinct epinecral layer, and never with stiff projecting hairs ................................................................. 2

2(1) Ascospores (25–)29–55 µm long; thallus crustose and finely verrucose, or squamulose-coralloid with narrow lobes up to 40 µm wide; asci 8-spored ................................................................. 3
   Ascospores (42–)57–120 µm long; thallus squamulose, with lobes 30–160 µm wide; asci (1–)2-spored or 8-spored ................................................................. 8

3(2) Perithecia rough, upper part with vertical cracks or furrows .................................................. *repleta*
   Perithecia smooth, uncracked ........................................................................................................ 4

4(3) Perithecia small, 120–220 µm diam.; ascospores (25–)29–35–(-44) µm long; usually on bark .............. 5
   Perithecia small or large, 140–600 µm diam.; ascospores 31–55 µm long; on soil or on mosses over soil and rock ................................................................. 6

5(4) Thallus a thin, slightly uneven and faintly roughened crust ...................................................... *allobata*
   Thallus with narrow branched lobes in one plane or in coralloid clusters .................................. *flabelliformis*

6(4) Perithecia 140–230 µm diam., asci 2-spored ............................................................................. *vouauxii*
   Perithecia 250–600 µm diam., asci 8-spored ............................................................................. 7

7(6) Glossy, sterile, black globules 70–240 µm usually present on thallus, thallus grey-green, cortical cells without pigment .............................................................. *globulifera*
   Sterile black globules absent; thallus brown, cortical cells brown-pigmented ....................... *gelatinosa*

8(2) Asci (1–)2-spored; squamules with the lobes usually distinctly flattened, 30–160 µm wide, brownish green to brown .......................................................... *tristicula*
   Asci 8-spored; squamules with the lobes terete (or rarely slightly flattened when poorly developed), 40–100 µm wide, grey-green ........................................ *octospora*

*Agonimia allobata* (Stizenb.) P. James, in Coppins, James & Hawksworth (1992) LC

Thallus crustose, thin, uneven and minutely roughened, grey-green to brown, sometimes with minute granules c. 20 µm diameter visible; thallus composed of goniocysts c. 14–30 µm diameter, surface cells isodiametric, without papillae. Perithecia 120–220 µm diam., more or less globose or taller than wide, occasionally collapsed when dry, two-thirds immersed in the thallus to almost superficial; grey-brown when young, later often black, surface smooth, matt. Asci 8-spored. Ascospores (25–)29–35–(-44) × 10–15 (–16.5) µm, ellipsoid. BLS 1149.

On bark, often amongst mosses, on trunks of old trees, particularly *Quercus*, *Ulmus* and *Fraxinus*, in long-established woodlands, sheltered gullies, rarely on wayside trees; local. S. & W. and N. England, Wales, Scotland, Ireland. Europe (widespread),
N. America. *Agonimia flabelliformis* differs in the coralloid thallus. *Agonimia vouauxii* differs in the 2-spored asci, larger ascospores, and it usually grows on soil. *Agonimia borysthenica* Dymytrova, Breuss & S.Y. Kondr. differs in the more coarsely granular thallus and the larger ascospores (33–)40–55(–75) × (15–)18–24 µm; it is reported from bark in Ukraine and Switzerland (Dymytrova et al. 2011, 2012).

**Agonimia flabelliformis** Halda, Czarnota & Guzow-Krzemińska (2012)

Thallus pale green-grey to brown-green, of repeatedly-branched, very narrow terete lobes 20–40 µm wide, branched either in one plane (thallus flabelliform-squamulose) or in more than one plane (thallus coralloid), squamules or coralloid clusters up to 300 µm wide or tall, comprising photobiont cells completely enclosed by more or less isodiametric fungal cells 4–7.5 m wide, surface cells without papillae; older parts of lobes composed of goniocyst-like units, pale brown-green. Perithecia globose, rarely ovoid to pyriform, 150–250 µm diam., smooth, superficial or partly immersed in thallus. Ascii 8-spored. Ascospores ellipsoid, 31–55 × 15–20 µm, with 16–30 cells visible in optical section. Pycnidia rare, small, ovoid, 70 × 40 µm, black; conidia bacilliform, 2.3–3 × 0.7–0.8 µm. **BLS 2588.**

On bark. S. England, Wales. Czech Republic, Germany, Poland, Lithuania.

Differs from *A. allobata* in the coralloid thallus.

**Agonimia gelatinosa** (Ach.) M. Brand & Diederich, in Sérusiaux et al. (1999)

Thallus dark brown, composed of rounded goniocysts 20–40 µm diam., or lobed goniocysts 70–120 µm long; surface cells brown, papillae absent; sterile globules absent; prothallus sometimes visible, of dark hyphae. Perithecia almost superficial, 300–500 µm diam., surface smooth, black, matt; exciple 40–70 µm thick, of more or less rounded cells. Ascii 8-spored. Ascospores ellipsoid, 31–55 × 15–20 µm, with 16–30 cells visible in optical section. Pycnidia rare, small, ovoid, 70 × 40 µm, black; conidia bacilliform, 2.3–3 × 0.7–0.8 µm. **BLS 1155.**

Over mosses or on soil in calcareous habitats, limestone, mortar, mica-schist and on dunes; from sea-level to at least 700 m altitude. Distribution uncertain; most confirmed records are from submontane and montane habitats in the British Isles. Widespread in Europe; N. America, Asia, subantarctic islands, most frequent in arctic-alpine situations.

Data on pycnidia are from Sérusiaux et al. (1999). This species has been confused with *Agonimia globulifera*, which differs in the unpigmented thallus, the presence of distinctive, black, sterile globules, and the more strongly muriform ascospores. *Polyblastia philaea* differs in the perithecia two-thirds to almost completely immersed in soil (not merely in thallus), the densely pigmented, unlayered exciple, and the thallus not composed of goniocysts.

**Agonimia globulifera** M. Brand & Diederich, in Sérusiaux et al. (1999)

Thallus grey-green to greenish, of minute granules or short finger-like lobes 20–50 µm long, surface cells without pigment, often with papillae 1–2.5 µm high; prothallus indistinct; sterile globules frequent, subspirhedral to oblong, 70–240 µm long, black, glossy, superficial, or lower third immersed in thallus, composed of thin-walled colourless to pigmented cells each containing a large oil drop. Perithecia rare, superficial or partly immersed, 250–600 µm diam., black, matt. Ascii 8-spored. Ascospores ellipsoid, (32–)37–50 × (15–)16–26 µm, with (22–)35–60 cells visible in optical section. Pycnidia unknown. **BLS 26.**

Overgrowing mosses, lichens, sand, or rarely rocks, in calcareous habitats; possibly locally frequent but overlooked. Scattered records in England, Wales & Scotland. Europe (widespread).

Distinguished by the conspicuous, glossy, black, sterile globules scattered over the thallus. See also *A. gelatinosa.*
**Agonimia octospora** Coppins & P. James (1978)  
Thallus minutely squamulose, squamules up to 250 µm long, of narrow lobes 40–100 µm wide, lobes sparingly to repeatedly branched, fragile, terete, or slightly flattened (especially when thallus poorly developed), irregularly slightly constricted, matt, pale grey-green; surface cells with papillae which are easily seen under a 40× objective. Photobiont cells 6–10 × 5–8 µm. Perithecia occasional, scattered amongst squamules, 460–800 µm, one-quarter- to half-immersed, globose or more or less pear-shaped, black, matt or more or less glossy, surface smooth or slightly roughened or shallowly fissured above; exciple 120–160 µm thick. Asci 8-spored. Ascospores 60–75 (–85) × 20–26 (–30) µm. **BLS 37.**  
On bark of trunks of aged *Quercus* and *Fagus*, often amongst mosses, in somewhat sheltered situations in old woodlands; rare. S. & W. England & the Lake District, Wales, W. Scotland (Kintyre), S. and W. Ireland, Europe, Macaronesia, S. America.  
The perithecia sometimes occur near to, but not contiguous with, the squamules. Sterile specimens can be confused with *Agonimia tristicula*, which has distinctly flattened lobes. The isidioid lobes of *Rinodina isidioides* can look very similar in size and shape: they are paler, grey rather than grey-green, and are **K+** yellow (though testing these rare species in the field is scarcely recommended); the surface of the lobes is of isodiametric to shortly oblong cells, but is distinctly hyphal in squashes, unlike the apparently non-hyphal surface of *Agonimia*; some of the surface cells project, giving a knobbly outline under the microscope, but they are smooth, without papillae; the photobiont cells are 7–14.5 µm long.

**Agonimia opuntiella** (Buschardt & Poelt) Vězda (1997)  
Thallus of squamules, these subglobular at first, rapidly becoming flattened and lobed, lobes convex, 100–260 µm wide, sometimes concave below when well-developed, pale grey in shade to dull greenish grey when well-illuminated, minutely roughened and more or less pruinose, often with numerous stiff, straight hairs up to c. 40 µm long, blastidia often produced on the underside or also the upper side of the lobes, visible as granules c. 30–40 µm wide at first. Thallus of isodiametric cells throughout, with intercellular spaces; a brown pseudocortex is present, overlain by a very distinct epinecral layer of isodiametric cells c. 6–10.5 µm diameter, bearing several conspicuous papillae mostly 1.5–3.3 × 1.5 µm, and sometimes very long hairs up to c. 40 µm, comprising very long papillae adhering in bundles; the cells of the epinecral layer are hyaline, with refractive contents; in **K** the epinecral layer becomes indistinct, with broken remains of cells without refractive contents. Photobiont distributed throughout the squamule, cells isodiametric to irregularly oblong, 4–13 × 3.5–7.5 µm. Perithecia (unknown in the region) pyriform, 200–250 µm diam., rough around the ostiole. Asci (1–)2-spored. Ascospores 60–80 × 25–30 µm. **BLS 2449.**  
Among mosses on *Quercus* and in crevices in siliceous rocks in open or lightly shaded habitats, sometimes beside streams on mosses including *Andreaea rothii*. Scotland (Argyll, Stirlingshire), Wales (rare). Europe, Macaronesia, North America, Africa (Madagascar), Eastern Asia, Australia.

In many collections the lobes have very distinctive stiff hairs which are visible with a 10× hand lens, but these are sometimes rare or absent. In well-lit habitats the dull grey colour and (under the dissecting microscope) faintly pruinose surface are distinctive, and are due to the presence of a remarkable layer of dead, refractive cells overlying the brown pseudocortex. The hairs were depicted by Harada et al. (2016) and Poelt (1980). *Agonimia tristicula* has lobes of a similar size, and the two species can grow together; it differs in the green to brown, non-pruinose thallus surface, and slightly less convex lobes without a distinct epinecral layer.
**Agonimia repleta** Czarnota & Coppins (2000)

Thallus dull green, rarely brownish, granular, granular-verrucose or minutely squamulose; granules (30–)40–120 µm diam., often coalescing; squamules sometimes present, elongate, to 240 × 100 µm; cortex often with papillae to 1.7 µm high on a few cells. Perithecia mostly half to three-quarters immersed in the thallus, 140–200 µm diam., globose when young, later pear-shaped, upper part roughened with vertical cracks or grooves. Ascii 8-spored. Ascospores 20–46 × 12–20 µm, mainly ellipsoid, sometimes globose.

On bark, often where mossy, and on mossy rocks in upper flood zone of a river; local. S.W. England (W. Cornwall, S. Devon), Wales (Radnorshire). Europe.

Distinguished from *A. allobata* by the roughened surface of the perithecia.

**Agonimia tristicula** (Nyl.) Zahlbr. (1909)

Thallus minutely squamulose, squamules to (100–)1600 × 100–300 (–500) µm, but soon becoming confluent or losing their identity and then impossible to measure, scattered or crowded and overlapping, with mostly short lobes 30–160 µm wide, gently convex, smooth to very faintly pruinose-roughened, grey-green to brown; the larger lobes slightly concave below; lower surface pale, uneven; some narrow-lobed squamules readily disintegrating into granules. Upper surface with a pseudocortex, unpigmented to brown, with or without papillae up to 2.5 µm high, epinecral layer absent; remainder of thallus with photobiont throughout, with intercellular spaces; lower surface rather lax, sometimes producing blastidia. Perithecia 240–500 µm diam., sparse to frequent, often in-between or overgrown by squamules, barrel-shaped, surface black, matt, roughened and furrowed; exciple thick. Asci (1–)2-spored. Ascospores (42–)57–120 (–150) × 26–50 µm, elongate-ellipsoid, densely muriform.

On calcareous soil and dunes, or on mosses and lichens in crevices of more or less calcareous rocks and walls, including limestone, mortar, basalts and serpentine, more rarely on bark of base-rich trees, especially *Acer, Ulmus* and *Fraxinus*, also amongst bryophytes on periodically inundated siliceous rocks by rivers and lakes; frequent. Throughout the British Isles. Europe, Azores, N. America, Asia, Australia, Pacific Islands.

Sterile corticolous specimens are distinguished from *A. octospora* by their larger, more distinctly flattened lobes which are brown when well-illuminated. There is evidence that material on siliceous rocks is not conspecific with material on calcareous rocks, but no firm morphological differences have been found.

**Agonimia vouauxii** (de Lesd.) M. Brand & Diederich (1999)

Thallus crustose, thin, green to green-brown, composed of aggregations of goniocyst-like units with brown pigment in the surface cells. Perithecia 140–230 µm diam., smooth, sometimes collapsed when dry, half- to two-thirds immersed, or a few almost superficial. Asci 2-spored. Ascospores colourless, or becoming brownish when over-mature, narrowly oblong-ellipsoid, (42.5–)49–72 (–65.5) × (14–)16–25 (27) µm, length/width ratio (2.2–)2.5–3.4 (–3.6).

On mossy soil on disturbed ground, old metal mines, calcareous dunes, and on stones or bone; occasional, overlooked. Scattered records throughout Britain, Ireland, Europe.

This species has been recorded in the British Isles as *Polyblastia agraria* Th. Fr.; if the two prove to be conspecific then the name *P. agraria* has precedence.