**Phaeocalicium** (Mycocaliciaceae, Ascomycetes) in Northern Europe

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The taxonomy, distribution and ecology of eight species of *Phaeocalicium* A. F. W. Schmidt (Mycocaliciaceae, Ascomycetes) occurring in the Nordic countries and Greenland are described. They are parasitic or saprophytic mainly on thin twigs of trees and shrubs such as Alnus, Betula, Populus and Salix and are often quite host-specific. A key to the species is supplied. Two new species, *Ph. boreale* Tibell and *Ph. flabelliforme* Tibell are described. A lectotype is selected for *Calicium praecedens* Nyl., *Mycocalicium pusiolum* (Ach.) Räsänen var. *macrospora* Räsänen and *Stenocybe tremulicola* Norrl. ex Nyl., and a neotype is selected for *Phaeocalicium populneum* (Brand. ex Duby) A. F. W. Schmidt. The new combination *Ph. tremulicola* (Norrl. ex Nyl.) Tibell is proposed.

**Key words:** Ascomycetes, Caliciidae, Mycocaliciaceae, *Phaeocalicium*, taxonomy

**INTRODUCTION**

The ascomycete genus *Phaeocalicium* belongs to Mycocaliciaceae in Caliciidae *s. lat.* (Tibell 1984). The North European species occur as saprobes and/or weak parasites mostly on thin, decaying branches of deciduous trees or shrubs. The genus occurs mainly in cool temperate to temperate areas of the Northern Hemisphere, with one species each occurring in Australasia and South America. *Phaeocalicium* was described by Schmidt (1970) and in that paper *Ph. compressulum*, *Ph. populneum* and *Ph. praecedens* were dealt with in detail. As conceived there *Phaeocalicium* includes species in Mycocaliciaceae with rather large, simple or 1-septate spores, large asci and a strongly and evenly thickened ascus apex. As noted earlier (Tibell 1984, 1995), the generic relationships between *Phaeocalicium*, Chaenothecopsis, Mycocalicum and Stenocybe, as conceived by Schmidt (1970), are unsatisfactory and in need of revision. Thus as an example spore septation does not seem to be consistent evidence for generic delimitation. In the present paper a group of similar and presumably closely related species has provisionally been accommodated in *Phaeocalicium* pending a detailed analysis based on macromolecular evidence in progress. Notwithstanding a regional revision of *Phaeocalicium* in the USSR by Titov (1986), the genus is still incompletely known. In this paper eight species occurring in Northern Europe are treated, two of which are previously undescribed.

**MATERIAL AND METHODS**

The study has been based on field studies and material collected by the author (kept in UPS), additional material from
the herbaria at C, H, LD, O, S, UPS, as well as the private herbaria of S. Hultgren (Stenungsund), A. Nordin (Uppsala), M. Karström (Vuollerim), L.-E. Muhr (Karlskoga), and D.-O. Övstedal (Bergen).

Estimates of the size of ascomata height, capitulum width, stalk width, ascus length, ascus width, spore length \((l)\) and spore width \((w)\) are given as \(l\pm l\times w\pm w\) where \(l\) and \(w\) represent the arithmetic mean minus 1 standard deviation and \(l\) and \(w\) the arithmetic mean plus 1 standard deviation. If the measurements have been estimated by statistical methods they are followed by a parenthesis in which the arithmetic mean \((X)\), the standard deviation \((s)\), the number of observations \((n)\) and the number of collections measured \((co)\) are given. If statistical estimates are not given the sizes indicated represent common ranges.

### PHAEOCALICIUM A. F. W. SCHMIDT


Saprophytic or parasitic. Ascomata well stalked, black to blackish brown. Capitulum obvoid to lenticular or strongly compressed. Excipulum well developed, consisting of dark brown, periclinally arranged or isodiametric hyphae. Hymenium covered by a thin epithecium. Stalk consisting of dark brown to aeruginose or pale, periclinally arranged hyphae. *Asci* narrowly cylindrical, with uniseriately arranged spores, 70–100 \(\mu\)m long, formed singly from ascogenous hyphae with hooks. Asci with strongly and uniformly thickened apex or the apex is penetrated by a short and blunt canal persisting until the spores are ejected. No mazaedium. Spores 10–18 \(\times\) 4–6 \(\mu\)m, non-septate or 1–3-septate, ellipsoidal, with rounded apices or fusiform. Spore wall rather thick, dark brown, smooth or with a verrucose ornamentation, not rupturing at maturity. Conidiomata unknown.

**Chemistry.** No secondary substances identified. Some species contain pigments which change colour with a change of pH yielding reactions with KOH and HNO\(_3\) observable under the microscope.

### Key to the species

1. Spores non-septate ........................................... 2
   — Spores 1–(3)-septate ....................................... 5
2. Capitulum strongly flattened ............................... 3
   — Capitulum lenticular ....................................... 4
3. Excipulum with an outer layer of small, isodiametric cells, spores pale brown, smooth ..... 1. *Ph. betulinum*
   — Excipulum consisting of periclinally arranged hyphae, without isodiametric cells, spores dark brown, with a minute ornamentation .......... 3. *Ph. compressulum*
4. Excipulum edge not thickened, ascomata 0.6–0.9 mm high, on *Populus* ................................. 7. *Ph. praecedens*
   — Excipulum edge strongly thickened, ascomata 0.3–0.4 mm high, on *Populus* and *Salix* .................. 5. *Ph. interruptum*
5. Capitulum strongly flattened ............................. 4. *Ph. flabelliforme*
   — Capitula not strongly flattened ........................................... 6
6. Ascomata 0.4–0.7 mm high, excipulum consisting of periclinally arranged hyphae, on *Populus* .................................................. 6. *Ph. populinum*
   — Ascomata 0.3–0.4 mm high, excipulum consisting of isodiametric or periclinally arranged cells, on *Alnus*, *Betula*, *Populas* and *Salix* .............................. 7
7. Excipulum edge strongly thickened, spores 9–11 \(\times\) 4–4.5 \(\mu\)m .................................................. 5. *Ph. interruptum*
   — Excipulum edge not strongly thickened, spores 11–17 \(\times\) 4–6 \(\mu\)m ........................................... 8
8. Excipulum and stalk reddish in section, K+ intensified reddish, stalk finally dark reddish grey .... 2. *Ph. boreale*
   — Excipulum and stalk pale, brownish or greenish brown in section, K– ........................................... 9
9. Mature spores with heavily pigmented septa, excipulum consisting of a single layer of isodiametric cells with thick walls 5–6 \(\mu\)m wide ..................... 8. *Ph. tremulicola*
   — Mature spores with poorly pigmented septa, excipulum consisting of 2–3 layers of sclerotized, periclinally arranged hyphae .......................... (Stenocybe pullatula)

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1. *Phaeocalicium betulinum* (Nyl.) Tibell (Fig. 1)


Saprophytic or parasitic on *Betula.* Ascomata 0.27–0.36 mm high \((X = 0.31\) mm, \(s = 0.05\) mm, \(n = 20, co = 3)\), shiny. *Capitulum* blackish brown, strongly flattened, 0.08–0.13 mm wide \((X = 0.11\) mm, \(s = 0.03\) mm, \(n = 20, co = 3)\), epruinose. Epithecium brown, 6–8 \(\mu\)m thick. Hypothecium c. 75 \(\mu\)m high, hyaline, consisting of mainly periclinally arranged, winding and sparsely branched, thin-walled hyphae, 1.5–2 \(\mu\)m diam. Excipulum medium brown, 14–25 \(\mu\)m thick, composed of two layers. The outer layer is formed by isodiametric to irregular, slightly sclerotized cells with strongly thickened walls and lumina only 1–2 \(\mu\)m diam. The inner part of the excipulum consists of 2–4 layers of periclinally arranged hyphae 1–1.5 \(\mu\)m diam. Excipulum and epithecium HNO\(_3\)– and K–. *Stalk* pale, olivaceous brown, 0.04–0.05 mm diam., K–, HNO\(_3\)–, in section very pale olivaceous brown,
Fig. 1. Phaeocalicium betulinum (Nyl.) Tibell. — A: Longitudinal section of ascoma. — B: Longitudinal section of ascoma stalk with gelatinous coat. Stalk moderately pigmented, consisting of periclinally arranged, short-celled, slightly intertwined hyphae. — C: Excipulum consisting of two layers. The outer layer (o) is formed by isodiametric to irregular, slightly sclerotized, thick-walled cells, the inner part (i) by 2–4 layers of periclinally arranged, sclerotized hyphae. — D, E: Mature asci. Phase contrast micrograph. — F–H: Mature spores. Under the light microscope the spores appear smooth. In TEM the almost mature spores have a wall consisting of three layers: an outermost, thin layer with a very electron-dense lining (L); a thick middle layer with irregularly distributed pigment granules (M); and an electron-lucent innermost layer (i). Surface of the spore only very slightly and irregularly uneven. In SEM the spore surface with a very minute and irregular ornamentation partly consisting of longitudinally arranged wrinkles. — A–D, F: Lectotype; E, G, H: isotype. — Scales: A: 50 µm; B: 25 µm; C–F: 20 µm; G–H: 2 µm.

Asci 47.6–70.7 × 4.4–5.1 µm (X = 59.2 µm, s = 11.5 µm, n = 25; X = 4.9 µm, s = 0.5 µm, n = 25, co = 3). Spores non-septate, rather pale brown, el-

consisting of periclinally arranged, short-celled, slightly intertwined hyphae, 1.5–2 µm diam., surrounded by a 2–5 µm thick hyaline gelatinous coat.
lipsoidal, 10.2–13.1 \times 4.4–5.4 \mu m (X = 12.1 \mu m, s = 0.96 \mu m, n = 28; X = 4.9 \mu m, s = 0.5 \mu m, n = 29, co = 3), appearing smooth under the light microscope. In TEM the almost mature spores have a wall consisting of three layers: The outermost layer is rather thin (0.13–0.20 \mu m) and covered by a very electron-dense lining; the middle layer is rather thick (0.33–0.47 \mu m) strongly pigmented from minute, irregularly distributed granules; the innermost layer rather thick (0.26–0.40 \mu m) and completely electron-lucent. Surface of the spore only very slightly and irregularly uneven. In SEM the spores are seen to be provided with a very minute and irregular or- namentation partly consisting of longitudinally arranged wrinkles.

**Distribution and ecology.** Very poorly known. Known from bark of *Betula* from a few 19th century collections from Southern Finland. Present status unknown.

**Remarks.** Characterized by the non-septate spores, the strongly flattened capitula, the excipulum anatomy, the smooth spores, the K– reaction of the ascomata and the occurrence on *Betula*. Similar to *Phaeocalicium flabelliforme*, but has a different excipulum anatomy and non-septate spores.

**Specimens examined.** — **Finland.** Tavastia australis, Padasjoki, Vieru, 1872 Lang (H-NYL 40.694); Padasjoki, Nyystölä, 1872 Lang 261 (H-NYL 40.729); Asikkala, 1866 Norrlin (type material).

2. *Phaeocalicium boreale* Tibell, n. sp. (Fig. 2)

*Saprophyticum* ver parasiticum in ramis *Alni, Betulae et Salicis. Ascomata 0.37–0.70 mm alta, olivacea ad cinereobrunnea vel fere nigra, nitida. *Capitulum* obconicum ad anguste lenticulare. *Excipulum* e 2–4 stratis cellularum membranis crassis scleroideis texturam epidermoideam formantium. Stipes in sectione pallide violaceoruber ad atroviolaceus. Asci anguste cylindrici, 63–75 \times 4.5–6 \mu m, apex saepe tumidus subshphaericus praeepiciue in ascis seminaturis. *Sporae* vulgo 1–3-septate, 12–16 \times 4.5–6 \mu m.

**Type:** Sweden. Torne Lappmark, Jukkasjärvi par., 3.5 km SW of Abisko, at junction between Abiskojäkka and Nissanjäkka, 68°20'N, 18°46'E. 26.V.1989 *Tibell* (holotype, UPS).

*Saprophyticum* or parasitic on branches of *Alnus, Betula* and *Salix*. *Ascomata* 0.37–0.70 mm high (X = 0.53 mm, s = 0.17 mm, n = 15, co = 3), olivaceous to greyish brown or almost black, shiny. *Capitulum* obconical to narrowly lenticular, 0.12–0.23 mm wide (X = 0.18 mm, s = 0.05 mm, n = 15, co = 3), epruinose. Epithecium reddish brown, 6–10 \mu m high, amorphous. Hypothecium 55–65 \mu m high, pale brown, consisting of largely periclinally arranged, intricately interwoven branching and thin-walled hyphae. *Excipulum* yellowish to reddish brown, 6–14 \mu m thick, formed by 2–4 layers of irregularly intertwined, sclerotized and thick-walled cells, 2–3 \mu m diam., forming a mosaic pattern in surface view. *Excipulum* and epithecium K+ intensified reddish, HNO₃– or turning more yellowish red. *Stalk* 0.04–0.07 mm diam., black, in section pale to deep violet red, HNO₃+ intensified, violet-red, consisting of largely periclinally arranged, slightly intertwined hyphae, 1–2 \mu m diam., with swollen walls. Stalk K+ dark reddish grey, strongly swelling. Stalk without or surrounded by a very thin or up to 6 \mu m thick, hyaline gelatinous coat. *Asci* 62.5–75.1 \times 4.4–6.2 \mu m (X = 71.6 \mu m, s = 9.1 \mu m, n = 15, co = 3; X = 5.3 \mu m, s = 0.9 \mu m, n = 16, co = 3), with uniserially or sometimes overlapping and almost biseriately arranged spores. Ascus apex often swollen, subspherical, particularly in semi-mature asci. *Spores* usually 1-septate, medium brown, ellipsoidal to narrowly ellipsoidal, 11.9–15.6 × 4.3–5.8 \mu m (X = 13.8 \mu m, s = 1.8 \mu m, n = 17, co = 3; X = 5.1 \mu m, s = 0.8 \mu m, n = 17, co = 3), with poorly pigmented septum, smooth under the light microscope or with a very minute ornamentation of small dots. The septation of the spores is irregular insofar that 2–3-septate spores occur regularly, although in low frequencies. Spore septa formed early in the asci.

In TEM the nearly mature spores have a wall consisting of two layers: The outermost layer is thick (0.67–0.79 \mu m), heavily pigmented by mostly fused minute pigment granules; the inner layer rather thin (0.11–0.20 \mu m) and electron-lucent. There is a differentiation into two sublayers delineated by a slightly darker zone in this part of the wall, and both sublayers contribute to the septum, which has an electron-lucent mid-lamella. The surface of the spore is only very slightly and irregularly uneven. In SEM the spores are seen to be provided with a very minute and irregular ornamentation.

**Distribution and ecology.** Overlooked or rare, growing on twigs of *Alnus incana* and *Salix (S. caprea)* in low, shrubby stands, on trunks of *Betula* in subalpine situations in altitudes up to 500 m, and on *Ribes rubrum*. Only known from a
few localities in northernmost Norway and Sweden and westernmost North Russia.

Remarks. Characterized by the 1–3-septate spores, the violet red colour of the well-pigmented stalk (section), the K+ dark greyish red reaction of the stalk, the well defined, reddish brown excipulum consisting of irregularly arranged cells, and the swollen ascus apex.
3. Phaeocalicium compressulum (Nyl. ex Szatala) A. F. W. Schmidt (Fig. 3)


Saprophytic or parasitic on twigs of *Alnus*. Ascomata 0.25–0.34 mm high (*X* = 0.29 mm, *s* = 0.04 mm, *n* = 28, *co* = 3). *Capitulum* blackish, stalk olivaceous to dark brown, shiny. Capitulum of young ascomata obconical, but in mature ascomata strongly flattened, 0.08–0.15 × 0.02–0.05 mm (*X* = 0.11 mm, *s* = 0.03 mm, *n* = 28, *co* = 3; *X* = 0.04, *s* = 0.02 mm, *n* = 28, *co* = 3), epruinose. Epithecium brown, sclerotized. Hypothecium obconical, c. 0.02 mm high, hyaline to medium brown, consisting of 3 layers: The outermost layer, the pigment occurring as minute, irregularly shaped elevations forming a transverse line across the widest part of the spore.

**Distribution and ecology.** On thin, decaying branches of *Alnus* known from Greenland (on *Alnus crispa*) where it seems to be not uncommon in some parts. Also known from Central and Southern Europe, Russia to the Far East and North America.

**Remarks.** Characterized by the non-septate spores, the strongly flattened capitula, the excipulum anatomy, the ornamented spores, the K– reaction of the ascomata and the occurrence on *Alnus*. Similar to *Phaeocalicium betulinum* and *Ph. flabelliforme*, but differs from the latter in having non-septate spores and from the former in excipulum anatomy. Also known from Eastern and Central Europe, Asia and North America.

**Specimens examined.** — Greenland. Godthåbsfjord, Ilulialik, 1976 Alstrup 76234, 76497, 76571, 765915 (C); Karra, 1976 Alstrup 76637 (C); Sagedlersuaq, 1976 Alstrup 76725 (C); Ivnajuagtoq, 1976 Alstrup 76282 (C); Isortoq, Igdlut kangiidiit, 1977 Alstrup 77932b (C); Pingoo, 1977 Alstrup 77119a (C); Quvernup qaqa, 1977 Alstrup 77026a (C).

4. Phaeocalicium flabelliforme Tibell, *n.* sp. (Fig. 4)

*Species in Betula saprophytica vel parasitica.* Ascomata 0.25–0.29 mm alta, capitulo nigro stipite olivaceobrunneo, nitido. *Capitulum* ascomatum juvenium obconicum sed valde complanatum in ascomatibus maturis. Excipulum *e* 3–4 stratis hypharum pericinaliter dispositarum. Asci anguste cylindrici, 76–96 × 4–5.5 μm. Spore semper septatae septo uno vel raro septis duobus, 11.5–14.0 × 4–5 μm.

**Type:** Sweden. Norrbotten. Korpilombolo par., 15 km SSE of Kainulasjärvi, Vinsanlehto, along Kurkijoki, 66.52N, 22.35E, 17.VII.1977 Tibell 6820 (holotype, UPS).

Saprophytic or parasitic on *Betula*. Ascomata 0.25–0.29 mm high. *Capitulum* black, stalk paler, olivaceous brown, shiny. Capitulum of young ascomata obconical, but in mature ascomata strongly flattened, 0.14–0.24 × 0.05–0.07 mm, epruinose. Epithecium brown, sclerotized, 5–8 μm thick. Hypothecium obconical, ca. 55 μm high, hyaline, consisting of more or less isodiametric cells. Excipulum medium brown, 11–13 μm thick, consisting of 3–4 layers of pericinically arranged, moderately sclerotized hyphae 2–3 μm diam. Excipulum and epit-
Fig. 4. *Phaeocalicium flabelliforme* Tibell. — A: Longitudinal section of ascoma. — B: Longitudinal section of ascoma stalk. Stalk with heavy pigmentation in the central part, consisting of periclinally arranged hyphae, surrounded by a thin gelatinous coat. Phase contrast micrograph. — C: Excipulum consisting of 3–4 layers of periclinally arranged, moderately sclerotized hyphae. Phase contrast micrograph. — D, E: Mature asci. — F–H: Mature spores. Under the light microscope the spores appear smooth. In TEM the almost mature spores have a wall consisting of three layers. The outermost layer (o) is thin and strongly pigmented, has no electron-dense lining and is poorly delineated; the middle layer (M) moderately thick, less homogeneously pigmented than the outermost layer; innermost layer (i) thin and electron-lucent. Spore septum not pigmented. The surface of the spores is somewhat uneven. In SEM the spores have a minute ornamentation of low, polygonal to rounded elevations. — A–E, G, H: Holotype. F: *Tibell 6796* (UPS). — Scales. A: 25 μm; B, D–F: 20 μm; C: 30 μm, G–H: 2 μm.

hecium K−. *Stalk* 0.03–0.04 mm diam., K−, medium brown in the central part, consisting of periclinally arranged, slightly intertwined hyphae, 2–3 μm diam., surrounded by an up to 8 μm thick gelatinous coat. *Ascii* 76.1–95.6 × 4.5–5.3 μm, with uniseriately arranged spores. Ascus apex strongly thickened with the ascus plasma cut off horizontally. *Spores* consistently septated, 1-septate or rarely with two septa,
medium brown, ellipsoidal, 11.6–14.0 × 4.1–5.1 µm, appearing smooth under the light microscope or with a very minutely ornamented surface. Spore septum not pigmented. In TEM the almost mature spores have a wall consisting of two layers: The outer layer is thick (0.55–0.92 µm) and well pigmented by irregularly distributed pigment granules concentrated towards the surface of the spore; inner wall layer thin (0.10–0.16 µm) and electron-lucent. The surface of the spores is somewhat uneven, with the outermost spore wall layer being interrupted by minute invaginations. In SEM the spores are seen to be provided with a minute but distinctive ornamentation of low, polygonal to rounded elevations forming the structural elements. In the central part of the spore there are some 5–7 structural elements along a transversal line across the widest part of the spore.

**Distribution and ecology.** Overlooked or rare, growing on thin, decaying branches of *Betula* along streams in mixed *Picea abies*–*Betula* forests. Only known from one locality in Northern Sweden.

**Remarks.** Characterized by the one-septate spores, the strongly flattened capitula, the excipulum anatomy, the K- reaction of the ascomata and the occurrence on *Betula*. Similar to *Phaeocalicium asciiforme*, which occurs in New Zealand, but *Ph. flabelliforme* differs in having a thinner excipulum, in section a brown rather than aeruginose coat. *Asci* 46.1–57.4 × 3.4–4.3 µm (*X = 51.8 µm, s = 5.7 µm, n = 20, co = 4; X = 3.9 µm, s = 0.5 µm, n = 20, co = 4*), with uniseriately or sometimes overlapping and almost biseriately arranged spores. Ascus apex uniformly and not strongly thickened. Spores usually non-septate, but often 1-septate, medium brown, ellipsoidal to narrowly ellipsoidal, 8.8–10.8 × 3.7–4.5 µm (*X = 9.8 µm, s = 1.0 µm, n = 22, co = 4; X = 4.1 µm, s = 0.4 µm, n = 22, co = 4*), smooth under the light microscope or with a very minute ornamentation of small dots. Spore septa not pigmented. The spores continue to grow after having left the asci, eventually measuring up to 15 × 6.5 µm, 1–3-septate and with a coarse, areolate ornamentation. In TEM the almost mature spores have a wall consisting of two layers: The outermost layer is thick (0.40–0.53 µm), heavily pigmented by rather coarse (0.06–0.12 µm), partly fusing, pigment granules and with a more or less distinctive, very electron-dense thin surface layer; inner layer thinner (0.23–0.37 µm) and electron-lucent. There is a differentiation into two sublayers in this part of the wall with the innermost layer being slightly darker, and both sublayers contributing to the septum, which has a wide electron-lucent mid-lamella. The surface of the spore is provided with irregular invaginations breaking the outermost electron-dense layer. In SEM the spores have a minute but distinctive ornamentation.

5. *Phaeocalicium interruptum* (Nyl.) Tibell (Fig. 5)


Saprophytic or parasitic on branches of *Populus* and *Salix*. *Ascomata* 0.24–0.44 mm high (*X = 0.32 mm, s = 0.08 mm, n = 21, co = 4*). *Calicium* campanulate, dark brown to black, 0.08–0.15 mm wide (*X = 0.10 mm, s = 0.04 mm, n = 20, co = 4*), epruinose, with thickened excipular edge. Epithecium poorly developed. Hypothecium poorly developed, 20–30 µm high, hyaline, consisting of largely periclinaly arranged, short-celled hyphae, 2–3 µm diam. Excipulum thin at the base, 7–15 µm thick, consisting of 1–2 layers of isodiametric to irregular, sclerotized cells, 2–5 µm diam., forming a mosaic in surface view. Upper part of excipulum strongly widened, 38–44 µm thick, consisting of an outer layer of the same structure as further down and an inner part which widens strongly towards the top. The inner layer consists of largely periclinaly arranged or somewhat intertwined, hyaline hyphae 2–4 µm diam. All parts of the excipulum and epithecium K-. *Stalk* 0.03–0.05 mm diam., olivaceous brown, rather pale, glossy, in section pale violet red, consisting of largely periclinaly arranged, slightly intertwined hyphae with swollen walls, 2–4 µm diam. Stalk K+ intensified violet red, strongly swelling. Stalk surrounded by a 5–8 µm thick hyaline gelatinous coat. *Asci* 46.1–57.4 × 3.4–4.3 µm (*X = 51.8 µm, s = 5.7 µm, n = 20, co = 4; X = 3.9 µm, s = 0.5 µm, n = 20, co = 4*), with uniseriately or sometimes overlapping and almost biseriately arranged spores. Ascus apex uniformly and not strongly thickened. Spores usually non-septate, but often 1-septate, medium brown, ellipsoidal to narrowly ellipsoidal, 8.8–10.8 × 3.7–4.5 µm (*X = 9.8 µm, s = 1.0 µm, n = 22, co = 4; X = 4.1 µm, s = 0.4 µm, n = 22, co = 4*), smooth under the light microscope or with a very minute ornamentation of small dots. Spore septa not pigmented. The spores continue to grow after having left the asci, eventually measuring up to 15 × 6.5 µm, 1–3-septate and with a coarse, areolate ornamentation. In TEM the almost mature spores have a wall consisting of two layers: The outermost layer is thick (0.40–0.53 µm), heavily pigmented by rather coarse (0.06–0.12 µm), partly fusing, pigment granules and with a more or less distinctive, very electron-dense thin surface layer; inner layer thinner (0.23–0.37 µm) and electron-lucent. There is a differentiation into two sublayers in this part of the wall with the innermost layer being slightly darker, and both sublayers contributing to the septum, which has a wide electron-lucent mid-lamella. The surface of the spore is provided with irregular invaginations breaking the outermost electron-dense layer. In SEM the spores have a minute but distinctive ornamentation-
tion of low, polygonal to rounded elevations forming the structural elements. In the central part of the spore there are 7–8 structural elements along a transverse line across the widest part of the spore.

Fig. 5. Phaeocalicium interruptum (Nyl.) Tibell. — A: Ascoma. SEM micrograph. — B: Longitudinal section of ascoma. Stalk with weak pigmentation, consisting of intertwined hyphae surrounded by a gelatinous coat. — C: Excipulum thin at the base, consisting of 1–2 layers of isodiametric to irregular, thick-walled, sclerotized cells. Upper part of excipulum strongly widened, consisting of an outer layer of the same structure as at the base and an inner part of periclinally arranged or somewhat intertwined, hyaline hyphae, which widens strongly upwards (arrow). — D: Mature asci. Phase contrast micrograph. — E–G: Mature spores. Under the light microscope the spores have a minute verrucose ornamentation. In TEM the spore wall two-layered with outer thick layer (o) heavily pigmented by coarse, partly fusing, pigment granules and with an electron-dense surface layer; inner layer (i) thinner and electron-lucent. Septum non-pigmented, with a wide electron-lucent mid-lamella. The surface of the spore is provided with irregular invaginations. In SEM the spores are seen to be provided with a minute ornamentation of low, polygonal to rounded elevations. — A, B, G: Finland, Kuusamo, 1937 Laurila (H); C: isotype (UPS); D, E: Sweden, Värmland, Sundell 1922 (UPS); F: lectotype. — Scales: A: 50 µm; B: 100 µm; C: 20 µm; D, E: 10 µm; F–G: 2 µm.
Distribution and ecology. On twigs of Salix and Populus tremula. Has been found on Salix caprea, S. glauca, S. nigricans, S. pentandra and S. phyllicifolia x S. nigricans. Known from only a few localities in Finland, Russia, Norway and Sweden, but probably overlooked.

Specimens examined. — Finland. Ostrobotnia borealis, Simo (type of Mycocicum pusiolum var. macrosspora); Regio kuusamoensis, Sovajoki, Kaita-Tervajärvi, 1937 Laurila (H, UPS); Lapponia kitilensis, Muonio, 1867 Norrlin (type). Norway. Hedmark, Vinger par., E of Foskersjøen, 1948 Ahlner (S); Finnmark, Varanger, Nyborg, 1857 Th. M. Fries (UPS). Sweden. Lule Lappmark, Gällivare par., 15.5 km NE of Malmerget, 4 km NNE of Muorjevaare, Kutsajoki, 1995 Tibell 21014 (UPS); Värmeland, Östra Ämtervik par., Bössvik, 1960 Sundell (UPS); Uppland, Danmark par., Karlso, 1945 Svenonius (UPS); Skogstibble par., Friberg, 1946 Degelius (UPS); Gästrikland, Valbo par., between Järvesta and Lärkbo, 1948 Ahlner (S); Jämtland, Revsund par., Gröttingen, 1951 Ahlner (S). Russia. Regio kuusamoensis, River Tuntsa, Hassersokka, 1938 Laurila (Räätänen, Lich. Fenn. exs. 685, together with Ph. boreale; H, UPS; not exsiccata: H); Paanajärvi, Kornetta, Verilammet, 1938 Laurila (H).

Note. This species is not easily accommodated either in Phaeocalicium or in Stenocybe in a traditional sense, and a revision of the generic delimitation is needed. The situation is further complicated by the fact that Stenocybe as now conceived seems to consist of several natural groups. A thickening of the excipular edge akin to that met with in Ph. interruptum is found in some Stenocybe species, but the spore size and spore shape of Ph. interruptum is much more similar to that of Phaeocalicium. The spores of Stenocybe have 3–9 transverse septa, whereas in Phaeocalicium as traditionally conceived the spores are non- or 1-septate. In Ph. interruptum the spores are either non-septate or 1-septate with an unpartitioned septum. In old spores, however, additional septa are formed and 3-septate spores are rather common. In this respect Ph. interruptum is similar to Ph. boreale, which it also resembles in ascoma size and ecology. Phaeocalicium interruptum is recognized by the thickened excipulum edge, the thin apical ascus wall and smaller spores. Differs from Stenocybe pulatula in not having branched stalks, the apical thickening of the excipulum and in having shorter spores.

6. Phaeocalicium populneum (Brond. ex Duby) A. F. W. Schmidt (Fig. 6)


1830. — Type: France. Paris, St. Cloude, 1861 Pelvet (neotype, proposed here, UPS).

Saprophytic or parasitic on branches of Populus. Ascomata 0.46–0.70 mm high (X = 0.58 mm, s = 0.12 mm, n = 27, co = 4), olivaceous to greyish brown or almost black, shiny. Capitulum lenticular, 0.18–0.28 mm wide (X = 0.23 mm, s = 0.04 mm, n = 27, co = 4), epruinose. Epithecium brown to reddish brown, 5–12 µm thick, consisting of layers of anticlinally arranged, sclerotized hyphae. Hypothecium 30–60 µm high, hyaline, consisting of largely periclinally arranged, thin-walled hyphae with occasional branches at right angles. Excipulum brown to reddish brown, with an aeruginose tinge in the inner part, 6–19 µm thick, formed by 3–6 layers of periclinally arranged, sclerotized hyphae. Excipulum and epithecium HNO3– and K– or slightly intensified reddish. Stalk 0.04–0.06 mm diam., the surface often with a slightly reddish tinge in section, K+ first darker and then strongly swelling and unchanged or slightly reddish brown, HNO3+ slightly reddish brown, consisting of largely periclinally arranged, slightly interwoven, sclerotized, dark hyphae, 2 µm diam., with a reddish brown or aeruginose tinge. Stalk surrounded by a 2–5 µm thick hyaline gelatinous coat. Asci 74.1–86.2 × 4.3–5.2 µm (X = 80.1 µm, s = 6.1 µm, n = 27, co = 4; X = 4.7 µm, s = 0.5 µm, n = 27, co = 4). Spores 1-septate, moderate brown, ellipsoidal and with a poorly pigmented septum which forms rather late, 11.6–13.2 × 4.2–4.9 µm (X = 12.6 µm, s = 1.2 µm, n = 27, co = 4; X = 4.8 µm, s = 0.5 µm, n = 27, co = 4), young spores appearing smooth under the light microscope, ageing spores with a minute ornamentation. In TEM the almost mature spores have a wall consisting of two layers: The outermost layer is moderately thick (0.38–0.46 µm), heavily pigmented by minute, partly fusing, pigment granules and with a distinctive, very electron-dense thin surface layer; inner layer thinner (0.29–0.33 µm), electron-lucent. Septum pigmented in an narrow, central zone. The surface of the spores is somewhat uneven, with the outermost spore wall layer being interrupted by slight invaginations. In SEM some spores appear nearly smooth whereas some have an ornamentation of low, polygonal to rounded elevations forming the structural elements. In ageing spores the ornamentation is coarser, with deep cracks.

Rare in Finland. Also known from cool temperate and temperate areas of the Northern Hemisphere: the British Isles, continental Europe, Western Russia, Siberia and the Far East of Russia and North America.
Remarks. Characterized by the 1-septate spores with poorly pigmented septum, the olivaceous or greyish brown colour of the stalks, the smooth spores, the K– or faint K+ reddish reaction of the stalk and the occurrence on twigs of *Phaeocalicium* Indicator species of long forest continuity.

I have not been able to locate any original material, and a neotype from France is proposed.


7. *Phaeocalicium praecedens* (Nyl.) A. F. W. Schmidt (Fig. 7)


Saprophytic or parasitic on branches of *Populus*. *Ascomata* 0.56–0.85 mm high (*X* = 0.70 mm, *s* = 0.15 mm, *n* = 27, *co* = 4), dark greyish to black, shiny. *Capitulum* lenticular, 0.18–0.28 (*X* = 0.23 mm, *s* = 0.05 mm, *n* = 27, *co* = 4) mm diam., epruinose. Epitheicum brown, 7–17 μm thick, consisting of anticlinally arranged, sclerotized hyphae. Hypothecium 75–110 μm high, medium brown or with a yellowish or aeruginose tinge, consisting of largely periclinally arranged, slightly-walled hyphae with occasional branches at right angles. Excipulum brown, with an aeruginose tinge in the inner part, 11–31 μm thick, formed by 5–12 layers of periclinally arranged, sclerotized hyphae. Excipulum and epithecium HNO₃+ intensified reddish. *Stalk* 0.04–0.07 mm diam., reddish in section in the outer part and often in the inner part with hyphae filled by an oily, yellowish red pigment; K–, only turning slightly darker or usually K+ intensely aeruginose, HNO₃+ intensified reddish brown, consisting of largely periclinally arranged, slightly intertwined hyphae with strongly swollen walls, 3–4 μm diam. Stalk usually without but sometimes surrounded by a 4–6 μm thick hyaline gelatinous coat. *Asci* 61.6–75.4 × 4.1–5.3 μm (*X* = 68.5 μm, *s* = 6.9 μm, *n* = 27, *co* = 4; *X* = 4.7 μm, *s* = 0.6 μm, *n* = 27, *co* = 4). *Spores* non-septate, medium brown, ellipsoid, 10.1–12.8 × 4.3–5.6 μm (*X* = 11.5 μm, *s* = 1.3 μm, *n* = 27, *co* = 4; *X* = 5.0 μm, *s* = 0.7 μm, *n* = 27), young spores appearing smooth under the light microscope, ageing spores with a minute ornamentation. In TEM the almost mature spores have a wall consisting of two layers. Outer layer moderately thick (0.43–0.53 μm), heavily pigmented by minute, partly fusing, pigment granules and with a very electron-dense thin surface layer; inner layer thinner (0.13–0.20 μm). Surface of the spores somewhat uneven, with outermost spore wall layer interrupted by slight invaginations. In SEM some spores appear nearly smooth whereas some have an ornamentation of low, polygonal to rounded elevations forming the structural elements. In ageing spores the ornamentation is coarser, with deep cracks.

Distribution and ecology. Uncommon on thin, decaying branches of *Populus tremula*. Scattered or possibly overlooked in Finland and Sweden. Endemic to Northern Europe and also known from Scotland.

Remarks. Characterized by the non-septate smooth spores, the K+ aeruginose reaction of the stalk,
the brown hypothecium, the strongly swollen hyphae of the stalk and the occurrence on twigs of *Populus*.

*Specimens examined.* — **Finland.** Satakunta, Kankaanpää, Venesjärvi, 1936 *Laurila* (UPS); Tavastia australis, Evois (lectotype, H-NYL 40719); Hollola, 1882 *Norrlin* (H-NYL 40717, UPS); Tavastia borealis, Pihlajavesi, 1871 *Norrlin* (H, H-NYL 40693). **Norway.** Rogaland, Forsand par., the Frafjord Valley, 1947 *Degelius* (UPS). **Sweden.** Dalsland, Edsleskog par., Klöverudsbranten, 1994 *Kennesten* (UPS); Nössemak
par., Grä Kulle, 1994 *Hultengren 951* (Hb. Hultengren); Bokullen, 1994 *Hultengren 671* (Hb. Hultengren); Gästrikland. Hille par., Iggön, 1946 *Ahliner* (UPS); Lule Lappmark, Jokkmokk par., 9 localities (Hb. Karström, UPS); Norrbotten, Hietaniemi par., 9 km SW of Övertorneå, 1995 *Tibell 20096* (UPS); Övertorneå par., 7.5 km SW of Juoksengi, 1995 *Tibell 21001* (UPS); Närke, Göltuna par., Torpstäng, 1869 *Blomberg* (LD); Södermanland, Dunker par., Dunker, 1891 & 1894 *Blomberg* (LD, UPS, S); Örnö par., Mörby, 1951 *Ahliner* (S); Nacka, Störängen, 1920 *Vestergren* (Magnusson, Lich. sel. scand. exs. 331, UPS, S); Uppland, Åland par., E of Fallet, 1945 *Hasselrot & Svenonius* (UPS); Balingsta par., Kumlaborg, 1975 *K & L. Holm 422c* (UPS); Danderyd par., Danderydsberget, 1949 *Ahliner* (S); Ekeby par., Högberrsmossen, 1995 *Hermansson 4757* (UPS); Skogstibble par., Friberga, 1946 *Degelius* (UPS); Vaksala par., Högтомt, 1946 *Ahliner* (S); Vänge par., Fibi, 1981 *Anderberg 615* (S); Ålkvarleby par., Harön, 1988 *Tibell 88142* (UPS); Värmland, Degerfors par., Krontorp, 1978 *Muhr 882* (Hb. Muhr); Ölsdalen, 1981 *Muhr 3569* (Hb. Muhr); Holmedal par., Gröttins, 1968 *Sundell 6506* (LD); Järmiskog par., Kronan, 1965 *Sundell 4496* (LD); Munkfors, SE of Småpottorna, 1957 *Sundell 970* (UPS); Kronan, 1969 *Sundell 7115a* (S); Fiskevik, 1956 *Sundell 879* (LD); Västerbotten, Vindeln par., Kullbäcksliden, 1989 *Tibell 18625* (UPS); Västmanland, Järnboäs, Erikaberget, 1994 *Hermansson 3770* (UPS); Kungsör, 1878 *Blomberg* (LD).

8. Phaeocalicium tremulicola (Norrl. ex Nyl.) Tibell, comb. nova (Fig. 8)

*Stenocybe tremulicola* Norrl. ex Nyl., Flora 66: 531. 1883.

— Type: Finland. Tavastia australis, Hollola, 1882 *Norrlin* (H-NYL 40571, lectotype, designated here).

Saprophytic or parasitic on branches of *Populus*. **Ascomata** 0.25–0.33 mm high (X = 0.29 mm, s = 0.04 mm, n = 40, co = 4), black, shining, often with olivaceous to greyish brown stalk. **Capitulum** obovate to narrowly lenticular, 0.04–0.13 mm wide (X = 0.09 mm, s = 0.05 mm, n = 40, co = 4), epruinose. Epithecium medium brown, 7–10 μm high, consisting of small cells with partly melanized walls. Hypothecium 35–45 μm high, hyaline, consisting of largely periclinally arranged, intricately interwoven branching and thin-walled hyphae. **Exciptulum** medium brown, 9–13 μm thick, formed by an outer layer of large, sclerotized and thick-walled cells, 4–7 μm diam. covering a thin layer of periclinally arranged hyphae, 1–3 cells thick. Exciptulum and epithecium K–, HNO₃–. **Stalk** 0.02–0.04 mm diam., in section pale brown, K–, HNO₃–, consisting of largely periclinally arranged, somewhat intertwined hyphae, 1–2 μm diam., with swollen walls. Stalk enclosed in a 5–8 μm thick, hyaline layer. **Ascii** 75.0–91.0 × 4.5–5.7 μm (X = 83.0 μm, s = 8.0 μm, n = 40, co = 4; X = 5.1 μm, s = 0.6 μm, n = 40, co = 4), with unisierately arranged spores. Ascus apex with uniformly thickened apical wall. **Spores** when mature 3-septate, brown, narrowly ellipsoid, 14.4–17.3 × 4.8–5.5 μm (X = 15.9 μm, s = 1.4 μm, n = 40, co = 4; X = 5.4 μm, s = 0.6 μm, n = 40, co = 4), smooth under the light microscope. The spores often remain unseptated or have one septum only. Spore septa strongly pigmented. In TEM the almost mature spores have a wall consisting of three layers. Outermost layer thin (0.11–0.17 μm) and less electron-dense than the middle layer; middle layer rather thick (0.39–0.50 μm) strongly pigmented, pigment granules large, sometimes nearly as wide as the middle wall layer; innermost layer rather thick (0.28–0.39 μm) and completely electron-lucent. Septum strongly pigmented in a central zone around an electron-lucent mid-lamella. Surface of the spores only very slightly and irregularly uneven. In SEM the spores appear nearly smooth.

**Distribution and ecology.** On thin and decaying twigs of *Populus tremula*. Only known from a few localities in Central and Northern Finland and adjacent parts of Russia. Also recorded from Central Europe.

**Remarks.** Characterized by the small size of the ascomata, the 3-septate spores, the anatomy of the excipulum, the often pale stalk and the occurrence on *Populus*.

**Specimens examined.** — Finland. Tavastia australis, lectotype; Korpihahti, 1874 *Lang* (H-NYL 40569); Evois, 1866 *Norrlin* (H-NYL 40568); Ostrobotnia borealis, Turtola, 1867 *Norrlin* (H); Regio kuusamoensis, Kitkajoki, Juuma, Jäkkälävuoma, 1938 *Laulira* (H). *Russia. Regio Kuusamoensis, Salla, Auktiäärvi, 1937 *Laurira* (H); Kutsajoki, Niluntijärvi, 1937 *Laurira* (H); Alimmainen-Kursujärvi, 1937 *Laurira* (H); Paanajärvi, Kyökkäysvaara, 1937 *Laurira* (Råsänen, Lich. fenn. exs. 544, UPS; not exsiccata: H).

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**Phaeocalicium in Northern Europe**
Fig. 8. Phaeocalicium tremulicola (Norrl. ex Nyl.) Tibell. — A: Longitudinal section of ascoma. — B: Longitudinal section of ascoma stalk. Stalk with weak pigmentation, consisting of largely periclinally arranged, intertwined and rather short-celled hyphae. Phase contrast micrograph. — C: Excipulum in longitudinal section consisting of an outer layer (ol) of large, isodiametric sclerotized and thick-walled cells (arrows), 4–7 µm diam. covering a thin layer (il) of periclinally arranged hyphae, 1–3 cells thick. Phase contrast micrograph. — D: Longitudinal section of excipulum with an outer lining of isodiametric cells. — E: Mature asci. — F–H: Mature spores. In TEM the almost mature spores have a wall consisting of three layers: Outermost layer (o) thin and less electron-dense than the middle layer; middle layer (M) rather thick, strongly pigmented, pigment granules large, sometimes nearly as wide as the middle wall layer; innermost layer (i) rather thick and completely electron-lucent. Septum quite strongly pigmented in a central zone around an electron-lucent mid-lamella. Surface of the spores only very slightly and irregularly uneven. In SEM the spores appear nearly smooth. — A–C: Finland, Turtola, 1867 Norrlin (H); D, F, G: Russia, Paanajärvi, 1937 Laurila (H); E, H: Russia, Auktijärvi, 1937 Laurila (H). — Scales: A: 50 µm; B–D, E: 30 µm; F: 20 µm; G, H: 2 µm.
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