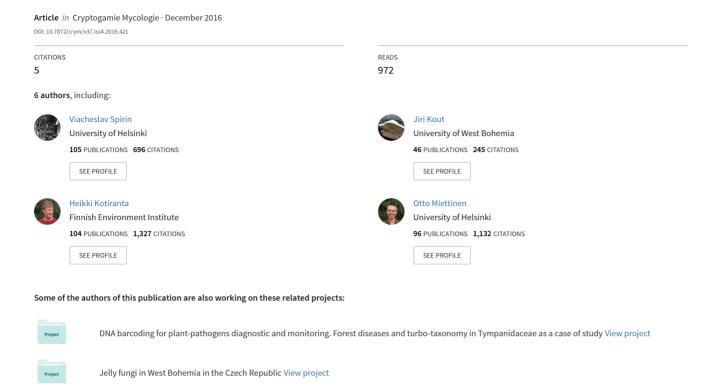
Studies in the Ceriporia purpurea Group (Polyporales, Basidiomycota), with Notes on Similar Ceriporia Species



Studies in the *Ceriporia purpurea* group (Polyporales, Basidiomycota), with notes on similar *Ceriporia* species

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Abstract – Taxonomy of the *Ceriporia purpurea* group is revised based on morphological and DNA data. Neotype is selected to settle current species concept of *C. purpurea* s.str. *Ceriporia bresadolae* is reinstated as a good species, and four new species from subtropical and temperate forests of Europe (*C. torpida*, *C. triumphalis*) and North America (*C. manzanitae*, *C. occidentalis*) are described. In addition, diagnostic features of other red-colored *Ceriporia* species are discussed, including *C. punicans*, spec. nov.

Neotypification / new species / Polypores / phylogeny / taxonomy

INTRODUCTION

Ceriporia Donk is a genus of the basidiomycetes, with about 70 species currently referred to. It embraces predominantly resupinate polypores with monomitic, ephemeral basidiocarps, often with a rather brightly colored hymenial surface. Hyphae lack clamp connections (except a few species with clamps scattered on basal hyphae) and basidiospores are hyaline, thin-walled, inamyloid, and mostly cylindrical to oblong ellipsoid (Ryvarden 1991). In the current scope, Ceriporia is polyphyletic,

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although most species studied by DNA methods cluster together with the genus type, *C. viridans* (Berk. & Broome) Donk and thus constitute the *Ceriporia* clade (Jia *et al.* 2014, Miettinen *et al.* 2016).

In the present paper, we revise taxonomy of *Ceriporia purpurea* (Fr.) Donk and its close relatives in the temperate northern hemisphere. The neotype for *Ceriporia purpurea* is selected in order to re-establish its extant concept. In addition, several morphologically similar but phylogenetically more distant *Ceriporia* species are treated.

MATERIAL AND METHODS

Morphological study. Type specimens and collections from herbaria H, S, O, PC, PRM, LY, KBI, BRNM, PH, TU, as well as from private herbarium of the author JV, were studied. Herbarium acronyms are given according to Thiers (2016). Morphological study follows Miettinen *et al.* (2006, 2012). At least 20 pores, 30 basidiospores and 10 subicular / tramal hyphae were measured from each specimen studied. For presenting these measurements, 5% of extreme values for basidiospores and 20% of them for hyphae are given in parentheses.

Phylogenetic study. DNA was isolated, amplified and sequenced as in Spirin et al. (2013). ITS and nLSU sequences were prepared using ITS5/ITS4 and LR0R/LR5 primers and concatenated in the region of overlapping primers ITS4 and LR0R, yielding one dataset for analysis. The sequences were aligned with Clustal X using default parameters except of "Gap opening penalty" which was set at 10, and "Gap extension penalty" set at 5, and adjusted manually. After removing unalignable regions, the ITS-LSU dataset contained 1637 characters of which 439 variable and 350 parsimony informative. The maximum likelihood analysis was conducted in MEGA6 (Tamura et al. 2013) using Jukes-Cantor substitution model, which was tested as the best one, using models of evolution testing program incorporated in MEGA6.

Specimens examined (sequenced collections are provided with GenBank numbers): C. aurantiocarnescens. Czech Republic. South Bohemia: Novohradské Hory, Fagus sylvatica, May 2001, Novotný (JV 0105/10) (GenBank KX236482). Finland. Uusimaa: Helsinki, Mustavuori, Betula sp., 28 October 2006, Niemelä 8348 (H). France. Rhône: Orliénas, Padus avium, 17 May 2008, Rivoire 3383 (LY, H). Germany. Berlin, Botanical Garden, Populus sp., November 1897, Hennings (S F211396, lectotype). Poland. Mazovia: Siedlce, Populus tremula, July 1900, Eichler 33 (S F249305). Russia. Buryatia: Fertik Bay, P. tremula, 10 September 2000, Kotiranta 17881 (H). Nizhny Novgorod Reg.: Lukoyanov Dist., Panzelka, P. tremula and dead Phellinus tremulae, 9 August 2007, Spirin 2676 (H); Sharanga Dist., Kilemary Nat. Res., P. tremula, 28 September 1999, Spirin (H). St. Petersburg: Volkovka, Quercus robur, 20 July 2006, Spirin 2448 (H), Spirin 2451 (H). USA. Arkansas: Franklin Co., Buffalo Nat. River, hardwood, 25 October 2013, Miettinen 17460 (H). California: Tulare Co., Sequoia Nat. Park, hardwood, August 2001, Vlasák 0108/85 (JV, H).

C. bresadolae. Canada. Alberta: Yellowhead Co., William A. Switzer Provincial Park, Picea mariana, 24 July 2015, Spirin 8849 (H) (GenBank KX236468), 8857 (H). Finland. Inarin-Lappi: Inari, Lemmenjoki Nat. Park, Pinus sylvestris, 1 September 1982, Kotiranta 3988 (H). France. Aveyron: Causse Noir, P. sylvestris,

3 November 1911, Galzin (ex herb. H. Bourdot #8197) (S F249306, isotype). Aude: Fleury d'Aude, Pinus halepensis, 30 November 2009, Rivoire 3701 (LY, H) (GenBank KX236467), 1 November 2010, Rivoire 3944 (LY, H). Bouches-du-Rhône: Barbentane, P. halepensis, 26 October 1995, Rivoire 1199 (LY, H). Hautes-Alpes: Châteauroux, P. svÎvestris, 3 March 2011, Rivoire 3999 (LY, H). Poland. Mazovia: Siedlee, P. sylvestris, Eichler 6, 96 (S). Russia. Buryatia: Tankhoy, Larix sibirica, 1 October 2000, Kotiranta 17470 (H), P. sylvestris, 1 October 2000, Kotiranta 17476 (H). Irkutsk Reg.: Talzi, L. sibirica, 20 August 2000, Kotiranta 17042 (H) (GenBank KX236465), Emeralda Lake, Picea sp., 12 September 2000, Kotiranta 17999 (H), Oto-Khushun, Pinus sp., 14 September 2000, Kotiranta 18071 (H) (GenBank KX236469). Nizhny Novgorod Reg.: Lukoyanov Dist., Panzelka, P. sylvestris, 12 September 2010, Spirin 3476 (H), Razino, P. sylvestris, 18 August 2015, Spirin 9491 (H). Omsk Reg.: Tara Dist., Tara, conifer, October 1929, Krawtzew 289 (PRM 491160). Spain. Canary Islands: Gran Canaria, Pinar de Tamadaba, *Pinus* canariensis, 16 April 1973, Torkelsen 18/73 (O F-501124). Málaga: Mijas, P. halepensis, 16 November 2012, Miettinen 15873, 15874 (H).

C. aff. bresadolae. USA. Arizona. Pima Co.: Coronado Nat. Forest, Pinus ponderosa, 29 January 1970, Budington 1487 (O F501116). Russia. Khabarovsk Reg.: Komsomolsk Dist., Boktor, Quercus mongolica, 8 August 2011, Spirin 3969 (H) (GenBank KX236470); Solnechnyi Dist., Chalba, Ulmus laciniata, 9 August 2011, Spirin 4018 (H) (GenBank KX236466).

C. griseoviolascens. Czech Republic. Ústí nad Labem: České Středohoří, Milá, hardwood, 13 March 2011, Kout (JV 1103/2, KBI, H) (GenBank KX236486). Lanžhot: Ranšpurk NPR, hardwood, 19 August 1998, Vágner (BRNM 642705, JV 0110/26) (GenBank KX236487). France. Rhône: Chaussan, *Quercus petraea*, 11 October 2010, Rivoire 3897 (LY, H); Orliénas, *Salix* sp., 27 October 1996, Rivoire 1391 (PC – holotype, H – isotype). Poland. Mazovia, rotten wood, Eichler 3 (S F43515), *Pinus* (?), Eichler 86 (S F43513).

C. manzanitae. USA. California: Tulare Co., Sequoia Nat. Park, Arctostaphylos glauca, 20 March 1984, Ryvarden 21832 (O – holotype, H – isotype) (GenBank KX236478).

C. mellita. Czech Republic. Lanžhot: Ranšpurk NPR, Quercus sp., October 2001, Vlasák 0110/20 (JV) (GenBank KX236484). France. Ain: Brégnier-Cordon, Populus nigra (?), 29 August 2013, Rivoire 5104 (LY, H). Aveyron, 6.I.1906, Galzin 1558 (P C0085716, lectotype). Isère: Les Avennières, Q. robur, 20 September 2012, Rivoire 4589 (LY, H) (GenBank KX236485). Rhône: Mornant, Aesculus (?), 15 November 2010, Rivoire 3943 (LY, H); Orliénas, Alnus glutinosa, 16 August 2012, Rivoire 4545 (LY, H); Sérézin, P. nigra, 24 September 1995, Rivoire 1160 (LY, H); St. Laurent d'Agny, Quercus petraea, 3 October 2009, Rivoire 3651 (LY, H). Savoie: Grésy sur Isère, Fagus sylvatica, 27 October 2010, Rivoire 3814 (LY, H). Slovakia: Bratislava, Rusovce, Salix sp., 20 June 2004, Hagara & Vampola (H ex MJ 182).

C. occidentalis. USA. California: Los Angeles Co., Santa Ynez Canyon, *Platanus racemosa*, 7 February 1981, Gilbertson 12986 (O), Malibu Creek State Park, hardwood, April 2012, Vlasák 1204/14 (JV) (GenBank KX236472); Siskiyou Co., Castle Crags State Park, hardwood, September 2007, Vlasák 0709/140 (JV) (GenBank KX236474); Sonoma Co., Santa Rosa, *Umbellularia californica*, May 2011, J. Vlasák Jr. 1105/12 (JV, H) (GenBank KX236473); Tulare Co., Sequoia Nat. Park, hardwood, 20 March 1984, Ryvarden 21839 (O). Washington: Pend Oreille Co., Slate Creek, *Corylus cornuta*, 15 October 2014, Spirin 8548a (H), 8558 (H, holotype) (GenBank KX236475).

C. punicans. USA. Pennsylvania: Montgomery Co., Schwenksville, Swamp Creek, hardwood, August 2008, Vlasák 0808/30 (H – holotype, JV – isotype) (GenBank KX236479).

C. purpurea. Czech Republic. Lanžhot: Ranšpurk NPR, hardwood, October 2001, Vlasák 0110/19 (JV) (GenBank KX236460). Estonia, Valgamaa: Otepää, Trommi, Corylus avellana, Populus tremula, 12 September 2012, Spirin 5799, 5800 (TU, H). Finland. Uusimaa: Helsinki, Patola, Alnus incana, 6 November 2011, Miettinen 15066.3 (H); Kirkkonummi, Sundsberg, Salix caprea, 24 October 2012, Miettinen 15855 (H). Etelä-Häme: Hämeenlinna, Lammi Biological Station, S. caprea, 13 September 2013, Spirin 6722 (H), France, Haute Savoie: Sallanches, hardwood, 27 August 2007, Rivoire 3203 (LY, H). Isère: Les Avennières, *Ouercus robur*, 9 May 2012, Rivoire 4408 (LY, H). Rhône: Orliénas, Quercus petraea, 25 July 2002, Rivoire 2119 (LY, H), rotten wood, 18 April 2004, Rivoire 2379 (LY, H), Fraxinus excelsior, 7 November 2009, Rivoire 3677 (LY, H); Sérézin, rotten wood (Populus nigra?), 19 May 2012, Rivoire 4413 (LY - neotype for Polyporus purpureus, duplicate in H) (GenBank KX236461). Poland. Mazovia: Siedlee, Alnus, October 1900. Eichler 84 (S F-249301). Russia. Irkutsk Reg.: Talzi, Populus sp., 20 August 2000, Kotiranta 17003 (H). Khabarovsk Reg.: Khabarovsk Dist., Malyi Niran, Acer mono, 5 August 2012, Spirin 4881 (H) (GenBank KX236463), Malyi Kukachan, Populus tremula, 19 August 2012, Spirin 5415 (H) (GenBank KX236462). Leningrad Reg.: Tikhvin Dist., Ur'ya, P. tremula, 25 September 2011, Spirin 4624 (H). Nizhny Novgorod Reg.: Lukoyanov Dist., Razino, P. tremula, 8 August 2008, Spirin 2800 (H), Q. robur, 8 September 2011, Spirin 4490 (H), Sanki, Corylus avellana, 9 September 2011, Spirin 4524 (H). Primorie Reg.: Krasnoarmeiiskii Dist., Melnichnoe, P. tremula, 23 August 2013, Spirin 6277 (H); Ternei Dist., Maisa, Tilia amurensis, 11 September 1990, Parmasto (O ex TAAM 150846). USA. Pennsvlvania: Montgomery Co., Hatfield, hardwood, August 2001, Vlasák 0108/58 (JV) (GenBank KX236464).

C. spissa. USA. Massachusetts: Essex Co., Salem, Schweinitz 418 (PH, lectotype). Pennsylvania: Montgomery Co., Hatfield, hardwood, August 2005, Vlasák 0508/18 (JV, H), Norristown, hardwood, August 2001, Vlasák 0108/6 (JV) (GenBank KX236483), *Pinus* sp., September 2004, Vlasák 0409/39 (H, JV).

C. torpida. Czech Republic. Plzeň Reg.: Klatovy, Čepičná NR, Fagus sylvatica (fallen branch), 14 July 2012, Kout (H, KBI). Finland. Satakunta: Nakkila, dead *Trametes* sp. on *Salix caprea*, 8 October 2004, Murdoch 90 (H, holotype) (GenBank KX236477).

C. triumphalis. Spain. Canary Islands: Anaga Mts., on deciduous wood in laurisilva forest, 18 January 1974, Ryvarden 12396 (O, H), 14 December 2013, Kout-18 (H – holotype, KBI – isotype) (GenBank KX236476).

C. viridans. Finland. Uusimaa: Vantaa, Tammisto, dead P. tremulae on P. tremula, 1 June 2013, Spirin 5909 (H) (GenBank KX236481). Russia. Nizhny Novgorod Reg.: Lukoyanov Dist., Panzelka, Padus avium, 12 September 2010, Spirin 3483 (H) (GenBank KX236480).

RESULTS

Ceriporia purpurea was first introduced by Fries (1821: 379) as *Polyporus purpureus*. The protologue deals with a resupinate, purple polypore which was growing on

rotten wood of *Fagus*, and it contains a reference to the species (as "*Hall. helv.* 2274!") described earlier by Haller from Switzerland (1768: 139). In turn, Haller's diagnosis, which Fries referred to, literally repeats the species description published 24 years earlier (Haller 1742: 28). However, Haller did not use a binomial name in either of the cases, and he labelled his species as "*Agarico-polyporus crustaceus purpureus*" (Haller 1742) and "*Polyporus crustaceus purpureus*" (Haller 1768). It means that Fries' description was the first valid one (Code Art. 23.1).

The species concept of *P. purpureus* currently persisting in mycological literature comes from Bresadola (1897, 1903, as *Poria purpurea* Fr.) who coined Fries' epithet to a resupinate, reddish-colored polypore with cylindrical basidiospores 5–7 × 2 µm. However, his views on identity of this species, as well as other, similarly looking resupinate polypores (treated as *Poria rhodella* Fr., *P. violacea* Fr. and *P. sanguinolenta* (Alb. & Schwein.) Fr. – Bresadola 1897, 1903) varied considerably, as we can judge from his descriptions and specimens kept in Stockholm. Höhnel (1907) tried to define species concepts of red-colored porioid fungi properly but he left this work without making plain taxonomic conclusions.

Bourdot & Galzin (1925, 1927) accepted Bresadola's interpretation of *Poria purpurea* and described another species, *Poria bresadolae* Bourdot & Galzin, in order to give a name to *P. sanguinolenta* sensu Bresadola (1903). *P. bresadolae* was recognized as a species by Donk (1933) and Bondartsev (1953) while Baxter (1939) and Pilát (in Kavina & Pilát 1936–1942) considered it conspecific with *P. purpurea*. After that *P. purpurea* was dealt with by most authors in Baxter's broad sense (Lowe 1966, Gilbertson & Ryvarden 1986, Ryvarden & Gilbertson 1993, Pieri & Rivoire 1997, Ryvarden & Melo 2014).

Lowe (1966) studied Fries' authentic specimen of *P. purpureus* from Uppsala and concluded that it represents another species, which he called *Poria rhodella* (see discussion to *Ceriporia aurantiocarnescens*). Selecting this specimen as a lectotype would undermine the current concept of *C. purpurea* and cause some confusing name changes. In order to avoid this unfavourable situation, we propose to conserve *P. purpureus* with a newly selected type specimen (see below), in accordance with the Code Art 57.1.

For the present revision of *Ceriporia purpurea* s.l., 28 combined ITS-LSU sequences of *Ceriporia* specimens were newly generated and deposited in GenBank. The species of the *Ceriporia* clade have a highly variable ITS region, more so than in hardly any other polypore genus. For instance, two closely related species, *C. viridans* and *C. aurantiocarnescens*, show difference in about every tenth ITS base and compared to more distant species in about every third. Long, unique insertions are also present in some species. Accordingly, proper alignment of sequences is sometimes problematic and phylogenies are dependent on the selection of specimens and alignment conditions. LSU sequences of *Ceriporia* spp., however, are much more conservative, being easier aligned under different conditions. Thereafter, we have used concatenated ITS-LSU sequences for the present analysis.

The Ceriporia purpurea group is well delineated. According to our data, six closely related species exist (Fig. 1). Our study shows that C. purpurea in the present sense is closely related to C. bresadolae, reinstated here as a good species, as well as to four other species described as new. Among these, C. torpida and C. triumphalis are found in Europe, and C. manzanitae and C. occidentalis in North America. Morphological differences between species are small, and most important characters include pore and basidiospore sizes, in combination with hosts and geographic data. DNA data confirm that C. purpurea and its kin are related to the genus type of Ceriporia, C. viridans. For now, we see no reasons for splitting

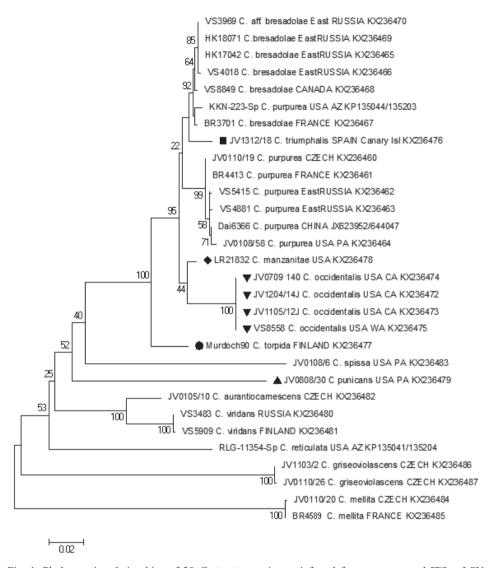


Fig. 1. Phylogenetic relationships of 30 *Ceriporia* specimens inferred from concatenated ITS-nuLSU sequences. Topology from Maximum Likelihood (ML) analysis. Support values along branches from ML bootstrap (500 replicates). Branch lengths are drawn proportional to the number of substitutions per site. Graphic symbols indicate specimens of new species. Three combined GenBank numbers indicate sequences retrieved from GenBank and ITS/LSU concatenated; other GenBank numbers (KX) refer to newly prepared sequences.

Ceriporia into smaller, more homogeneous genera, although we do not preclude possible generic revision in the future. Other red- or violet-coloured species, such as *C. aurantiocarnescens* (P. Henn.) Pieri & Rivoire, *C. griseoviolascens* Pieri & Rivoire, *C. mellita* (Bourdot & Galzin) Bondartsev & Singer, *C. punicans* Vlásak &

Spirin, and *C. spissa* (Schwein.) Ryvarden, are not closely related to the *C. purpurea* group but are spread among several separate lineages within the genus. These species are briefly discussed below.

The Ceriporia purpurea group

Basidiocarps annual, resupinate or rarely effused-reflexed, soft, waxy to rather tough. Hymenophore poroid, pink, reddish or violet; pores mostly angular, 2-8 per mm. Margin non-rhizomorphic. Hyphal structure monomitic, hyphae clampless, of approximately the same diameter in subiculum and trama, thin to only slightly thick-walled. No differentiated cystidia. Basidia clavate, four-spored, without clamp connection, $9\text{-}19 \times 4\text{-}6~\mu\text{m}$, usually not glued together. Basidiospores allantoid to cylindrical, $4\text{-}8.5 \times 1.7\text{-}2.7~\mu\text{m}$. Causes white rot of deciduous trees and conifers.

Ceriporia bresadolae (Bourdot & Galzin) Donk

Figs 2, 3

Holotype. France. Aveyron: Causse Noir, *Pinus sylvestris*, 3 November 1911, Galzin (ex herb. H. Bourdot #8197) (S – isotype, studied).

Basidiocarps annual, resupinate or effused-reflexed, first small-sized, orbicular, later fusing together and up to 5 cm in widest dimension. **Pilei** small-sized, fingernail-like, projecting up to 5 mm; upper surface greyish white, indistinctly fibrillose, sometimes with a few uncertain zones; margin sharp, fertile. **Margin** of resupinate parts first white, strongly contrasting with pore surface, floccose, up to 1 mm wide, later more or less concolorous with pore surface. **Pore surface** even, first pinkish, later dark pinkish red, in herbarium specimens and senescent basidiocarps dark reddish brown to almost black; **pores** angular, 2-4 per mm, with thin, entire or uneven dissepiments. **Section:** subiculum / context whitish, floccose, 0.1-0.2 mm thick, tubes concolorous with hymenial surface, waxy, 0.2-0.5 mm thick.

Hyphal structure monomitic; hyphae simple-septate. **Subicular hyphae** loosely interwoven, with distinct walls, branched at sharp angles, some in subparallel bundles, (3.2-) 3.3-5.0 (-5.1) μm (n = 30/2). **Tramal hyphae** subparallel, thin- or only slightly thick-walled, (2.1-) 2.2-4.0 (-4.5) μm (n = 70/4), abundantly encrusted by oily matter. **Dissepiment edges** sterile, consisting of evenly outlined thin-walled hyphae 2-3 μm in diam. **Cystidioles** rarely present, poorly differentiated, bottle-shaped to hyphoid, located mostly close to dissepiment edges, $18-21 \times 4-5$ μm. **Basidia** clavate, 4-spored, (11.8-) 13.0-18.6 (-19.3) × (4.1-) 4.2-5.3 (-5.6) μm (n = 38/5). **Basidiospores** allantoid, slightly or distinctly curved, (5.5-) 5.9-8.2 (-8.8) × (1.7-) 1.8-2.3 (-2.6) μm (n = 210/7), L = 6.90, W = 2.06, Q = 3.14-3.65.

Notes. Ceriporia bresadolae was described as a conifer-dwelling relative of C. purpurea (Bourdot & Galzin 1925, as Poria bresadolae). DNA data show that specimens of "C. purpurea" collected on gymnosperms in Europe (= C. bresadolae) are surely different from those recorded on deciduous hosts (= C. purpurea in the strict sense). Morphological differences between these species are subtle, however. Ceriporia bresadolae possesses slightly wider pores than C. purpurea; its basidiocarps often produce large, white margin, strongly contrasting with the pore surface, while in C. purpurea tubes and margin are normally concolorous. In Siberia C. bresadolae is often found in effused-reflexed condition; all European collections studied by us are totally resupinate.

Ceriporia bresadolae is reported here from North America as well, based on two specimens from Alberta, Canada. Gilbertson & Lowe (1962) described this species as inhabiting ponderosa pine in Arizona. We studied one effused-reflexed



Fig. 2. Basidiocarps of *Ceriporia* species. **A.** *C. purpurea* (*Miettinen 15066.3*), **B.** *C. purpurea* (young basidiocarp) (*Spirin 2800*), **C.** *C. occidentalis* (holotype), **D.** *C. triumphalis* (holotype), **E.** *C. punicans* (holotype), **F.** *C. bresadolae* (*Miettinen 15873*).

collection from Arizona (*Budington 1487* – see under *C.* aff. *bresadolae* in Specimens examined). For now we refrain to interpret it as conspecific with typical specimens of *C. bresadolae*, due to smaller pores and shorter basidiospores. Identity of *C. bresadolae* from the American South-West should be checked by DNA methods.

There are two more deviating collections related to this species from East

Asia (*Spirin 3969*, 4018 – treated under *C.* aff. *bresadolae*). DNA data show that they are more or less identical to *C. bresadolae*; although both appear to represent separate species in morphological terms. More specimens are needed to clarify their identity.

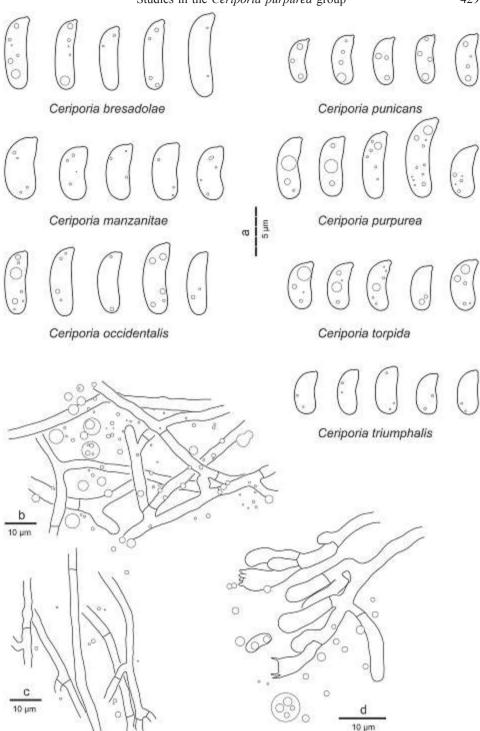


Fig. 3. Microscopic structures of *Ceriporia species*: **a.** basidiospores; **b.** subicular hyphae; **c.** tramal hyphae; **d.** hymenial cells (b, c, d – from neotype of *C. purpurea*).

According to our data, *C. bresadolae* is widely distributed in temperate and boreal zones of the northern hemisphere. It inhabits recently fallen, tough branches and logs of coniferous trees (*Pinus, Larix, Picea*), especially hard, decorticated pine twigs. *Ceriporia bresadolae* is rather tolerant to environmental conditions, and it often grows in rather young forests and even in open places if suitable substrate is available.

Ceriporia manzanitae Spirin & Vlasák, spec. nov.

Fig. 3

Holotype. USA. California: Tulare Co., Sequoia Nat. Park, *Arctostaphylos glauca*, 20 March 1984, Ryvarden 21832 (O, isotype – H).

Mycobank: MB 817344

Basidiocarps annual, resupinate, small-sized, up to 2 cm in widest dimension. **Margin** white, floccose, up to 0.5 mm wide. **Pore surface** even, bright brick-red; **pores** angular, 4-5 per mm, with thick, entire dissepiments. **Section:** subiculum whitish, floccose, 0.05-0.1 mm thick, tubes concolorous with hymenial surface, waxy, 0.1-0.2 mm thick.

Hyphal structure monomitic; **hyphae** simple-septate. **Subicular hyphae** loosely interwoven, thin-walled or with distinct walls, branched at sharp angles, some in subparallel bundles, (3.3-) 3.6-5.3 (-5.2) μm (n = 20/1). **Tramal hyphae** subparallel, thin- or only slightly thick-walled, (2.7-) 2.8-3.4 (-3.6) μm (n = 20/1), abundantly encrusted by oily matter. **Dissepiment edges** sterile, consisting of evenly outlined thin-walled hyphae 3-4 μm in diam. **Basidia** clavate, 4-spored, (12.1-) 12.8-18.4 (-18.8) × (4.2-) 4.5-5.8 (-6.1) μm (n = 20/1). **Basidiospores** cylindrical, distinctly curved, (5.0-) 5.1-6.2 (-6.3) × (2.1-) 2.2-2.7 (-2.8) μm (n = 30/1), L = 5.56, W = 2.36, O = 2.37.

Notes. This species is introduced here based on the single collection from California. Morphologically, it is similar to *C. torpida* and *C. triumphalis* from Europe. *Ceriporia occidentalis*, another member of the *C. purpurea* group from the Western USA, differs in having more light-colored basidiocarps (at least in fresh condition) and in average narrower basidiospores.

Ceriporia occidentalis Spirin & Vlasák, spec. nov.

Figs 2, 3

Holotype. USA. Washington: Pend Oreille Co., Slate Creek, Corylus cornuta, 15 October 2014, Spirin 8558 (H).

Mycobank. MB 817345

Basidiocarps annual, resupinate, up to 7 cm in widest dimension. **Margin** white, floccose, up to 0.5 mm wide. **Pore surface** even, first almost white or pinkish, later pinkish red, in herbarium specimens vinaceous-brown to almost black; **pores** angular, 4-6 per mm, with thin, entire dissepiments. **Section:** subiculum first whitish, floccose, later more or less concolorous with tubes, 0.05-0.1 mm thick, tubes concolorous with hymenial surface, waxy, 0.2-0.5 mm thick.

Hyphal structure monomitic; **hyphae** simple-septate. **Subicular hyphae** loosely interwoven, thin- or slightly thick-walled walls, branched at sharp angles, some in subparallel bundles, (3.2-) 3.3-4.8 (-5.2) μm (n = 20/1). **Tramal hyphae** subparallel, thin-walled, (2.2-) 2.4-3.8 (-4.2) μm (n = 40/2), abundantly encrusted by oily matter. **Dissepiment edges** sterile, consisting of evenly outlined or slightly swollen, thin-walled hyphae 3-5 μm in diam. **Basidia** clavate, 4-spored, (11.0-) 11.4-17.2 (-18.4) × (4.0-) 4.1-5.2 (-5.3) μm (n = 20/2). **Basidiospores** allantoid, distinctly curved, (5.0-) 5.1-7.1 × 1.8-2.2 (-2.3) μm (n = 120/4), L = 5.97, W = 2.01, Q = 2.86-3.11.

Notes. In microscope, C. occidentalis is almost indistinguishable from C. purpurea. However, these species are strikingly different macroscopically. Young

and vigorously growing basidiocarps of *C. occidentalis* are almost white or pale pink, with distinct, white margin, but strongly darkening if bruised or dried (field notes of R.L. Gilbertson, our own observations). In turn, basidiocarps of *C. purpurea* are first bright orange or pink, becoming pinkish red or sometimes violaceous red in herbarium (Fig. 2). ITS sequences of these species are clearly different.

Ceriporia occidentalis seems to be widely distributed in the Western USA (California and Washington), and probably also occurs in the neighboring areas of Canada. It inhabits recently fallen or moderately decomposed branches and logs of deciduous trees and shrubs.

Ceriporia purpurea (Fr.) Donk

Figs 2, 3

Neotype for Polyporus purpureus Fr. France. Rhône: Sérézin, île de la Table Ronde, rotten wood (*Populus nigra?*), 19 May 2012, Rivoire 4413 (**neotypus hic designatus**, LY, duplicate in H).

Basidiocarps annual, resupinate, first small-sized, orbicular, later fusing together and up to 5 cm in widest dimension. **Margin** pinkish to reddish, as a rule concolorous with or slightly paler than pore surface, floccose, up to 1 mm wide. **Pore surface** even, pink or orange, later dark pinkish red, in herbarium specimens sometimes with violet tints, in senescent basidiocarps dark reddish brown; **pores** angular, normally 4-6 per mm (3-4 on sloping substrates), with thin, entire or uneven dissepiments. **Section:** subiculum first whitish, floccose, later more or less concolorous with tubes, 0.05-0.1 mm thick, tubes concolorous with hymenial surface, waxy, 0.2-0.5 mm thick.

Hyphal structure monomitic; **hyphae** simple-septate. **Subicular hyphae** loosely interwoven, with distinct walls, branched at sharp angles, some in subparallel bundles, (3.1-) 3.2-5.4 (-5.8) μm (n = 40/4). **Tramal hyphae** subparallel, thin- or only slightly thick-walled, (2.2-) 2.3-4.4 (-4.5) μm (n = 80/5), abundantly encrusted by oily matter. **Dissepiment edges** first fertile, covered by basidioles, in older specimens becoming sterile, consisting of sinuous or irregularly inflated, sometimes dichotomously branched hyphae 3-5.5 μm in diam. **Cystidioles** present in a few collections, rare, poorly differentiated, hyphoid, located mostly close to dissepiment edges, $16-20 \times 3.5-6$ μm. **Basidia** clavate, 4-spored, (9.0-) 9.1-15.2 (-16.3) × (3.8-) 3.9-5.6 (-5.8) μm (n = 49/5). **Basidiospores** allantoid, distinctly curved, (4.8-) 5.0-8.4 (-8.7) × (1.6-) 1.7-2.3 (-2.4) μm (n = 150/5), L = 6.11, W = 1.99, Q = 2.88-3.43.

Notes. Ceriporia purpurea is morphologically most similar to *C. bresadolae* and *C. occidentalis* (see notes to these species). It is widely distributed in the temperate zone of Eurasia and occurs exclusively on moderately or strongly decomposed wood of deciduous trees. Our data confirm its presence in the American North-East.

Ceriporia torpida Spirin & Miettinen, spec. nov.

Fig. 3

Holotype. Finland. Satakunta: Nakkila, dead *Trametes* sp. on *Salix caprea*, 8 October 2004, Murdoch 90 (H).

Mycobank: MB 817346

Basidiocarps annual, resupinate, small-sized, up to 2 cm in widest dimension, extremely thin. **Margin** pink, floccose, up to 0.3 mm wide. **Pore surface** even, first pink, in older basidiocarps dark vinaceous-red; **pores** roundish to angular, 6-8 per mm, with thin, entire dissepiments. **Section:** subiculum reddish, floccose, up to 0.05 mm thick, tubes concolorous with hymenial surface, first waxy, then rather tough, about 0.1 mm thick.

Hyphal structure monomitic; **hyphae** simple-septate. **Subicular hyphae** loosely interwoven, with distinctly thickened walls, branched at sharp angles, (2.9-) 3.0-4.2 (-4.3) μm (n = 20/1). **Tramal hyphae** subparallel, with distinctly thickened walls, (2.2-) 2.3-4.2 (-4.3) μm (n = 20/1), tightly glued together; oily matter scanty, present as small globules or amorphous substance on or between hyphae. **Dissepiment edges** fertile, covered by basidioles and normally developed basidia, or sterile. **Basidia** clavate, 4-spored, (9.0-) 9.4-11.9 (-12.8) × (3.7-) 3.9-4.5 (-4.8) μm (n = 20/1), often glued together. **Basidiospores** short cylindrical, slightly to moderately curved, (4.1-) 4.3-5.7 (-5.8) × (1.8-) 1.9-2.3 (-2.5) μm (n = 30/1), L = 4.93, W = 2.05, Q = 2.42.

Notes. Ceriporia torpida differs from other relatives of the *C. purpurea* complex in having very thin, small-pored basidiocarps. Hyphae and hymenial cells in mature basidiocarps of *C. torpida* are so densely glued together that it is difficult to squeeze the microscopic slide. The latter feature is also characteristic for *C. spissa* which, however, is not closely related to this group. Basidiospores of *C. torpida* are distinctly wider than in *C. spissa* and its European look-alike, *C. mellita* (see below).

Ceriporia triumphalis Spirin & Kout, spec. nov.

Figs 2, 3

Holotype. Spain. Canary Islands: Tenerife, Anaga Mts., on deciduous wood in laurisilva forest, 14 December 2013, Kout-18 (H – holotype, KBI – isotype).

Mycobank: MB 817347

Basidiocarps annual, resupinate, small-sized, up to 3 cm in widest dimension, very thin. **Margin** first whitish, floccose, up to 1 mm wide, later pink or reddish orange. **Pore surface** even, bright yellow-orange in fresh condition, red to dark brick-red when dry; **pores** roundish to angular, 5-7 per mm, with thin, entire dissepiments. **Section:** subiculum white to pale pink, floccose, up to 0.05 mm thick, tubes dark vinaceous-red, waxy, in older specimens rather tough, up to 0.2 mm thick.

Hyphal structure monomitic; **hyphae** simple-septate. **Subicular hyphae** loosely interwoven, thin-walled, branched at sharp angles, (3.1-) 3.2-5.4 (-5.7) μm (n = 30/2). **Tramal hyphae** subparallel, thin-walled, (2.4-) 2.5-4.0 (-4.1) μm (n = 31/2), glued together; oily matter abundant, present as small globules or amorphous substance on or between hyphae. **Dissepiment edges** sterile, consisting of hyphal endings 2.5-4 μm in diam. **Basidia** clavate, 4-spored, (9.3-) 9.4-12.3 (-12.9) × (3.8-) 3.9-4.7 (-5.1) μm (n = 20/2). **Basidiospores** short cylindrical, distinctly curved, (4.0-) 4.1-5.0 (-5.1) × (1.7-) 1.8-2.1 (-2.2) μm (n = 30/1), L = 4.50, W = 1.92, O = 2.34.

Notes. Ceriporia triumphalis is so far known from two localities in Canary Islands, both of them are relict laurisilva forests. In fresh condition, its basidiocarps are orange, but this colour is changing to bright red or dark brick-red once dried. C. triumphalis possesses the smallest basidiospores in the C. purpurea group, which are more similar to those of C. aurantiocarnescens in the C. viridans complex. However, the latter species has paler basidiocarps (pink in herbarium), and its subicular hyphae are thick-walled and considerably wider than tramal ones.

Notes on some other reddish Ceriporia species

Ceriporia aurantiocarnescens (P. Henn.) Pieri & Rivoire

Lectotype. Germany. Berlin, Botanical Garden, *Populus* sp., November 1897, Hennings (S F211396, studied) (selected by Lowe 1966).

Macroscopically, *C. aurantiocarnescens* is confusingly similar to *C. purpurea*. Its young and intensively growing basidiocarps are egg-yellow or bright orange in fresh condition, and these colours rapidly change to pink or pinkish-red during drying. Pore size is also the same as in *C. purpurea*. However, these species are easily distinguishable in microscope. Basidiospores of *C. aurantiocarnescens* are bean-shaped and much smaller than in *C. purpurea*, (3.1-) 3.2-4.8 $(-4.9) \times (1.6-)$ 1.7-2.2 $(-2.3) \mu m$ (n = 150/5), L = 3.79, W = 1.92, Q = 1.84-2.07. Moreover, subicular hyphae of *C. aurantiocarnescens* are distinctly thick-walled, often swollen at septa, and much wider than subhymenial ones $(5-10 \mu m \text{ vs. } 3-5 \mu m \text{ in diam.})$. As stated above, members of *C. purpurea* group have hyphae of approximately the same diameter in the whole basidiocarp.

According to DNA data, *C. aurantiocarnescens* is the closest relative of *C. viridans* with which it shares all principal morphological features. Differences between these species are listed by Pieri & Rivoire (1997) and Ryvarden & Melo (2014).

Lowe (1966) used a collective name *Poria rhodella* (Fr.) Cooke for *C. viridans*, *C. aurantiocarnescens* and its sibs. Bresadola's concept of *P. rhodella* at least partly implies *C. aurantiocarnescens* (Bresadola 1903, authentic material from S seen). However, Lundell & Nannfeldt (1946) showed that *P. rhodella* is an ambiguous name due to absence of specimens so named in Fries' herbarium, and therefore it cannot be applied to a certain pink- or red-colored *Ceriporia* species.

Ceriporia griseoviolascens Pieri & Rivoire

Holotype. France. Rhône: Orliénas, *Salix* sp., 27 October 1996, Rivoire 1391 (PC – holotype, H – isotype, studied).

Basidiocarps of *C. griseoviolascens* have colours similar to those of *C. purpurea*, possessing pinkish-violet tints (photo in Pieri & Rivoire 1997) and then changing to greyish-violet. Microscopically, however, *C. griseoviolascens* is a very distinct species, having cystidia and rather large, bean-shaped basidiospores, (4.9-) 5.0-6.1 (-6.8) \times (2.4-) 2.5-3.1 (-3.2) μ m (n = 30/1), L = 5.38, W = 2.71, Q = 1.99, often with a large central oil drop. *Poria violacea* sensu Bresadola (1903) from Poland is in fact *C. griseoviolascens*.

Ceriporia mellita (Bourdot & Galzin) Bondartsev & Singer

Lectotype. France. Aveyron, 6 January 1906, Galzin 1558 (P C0085716) (selected here).

Ceriporia mellita was placed to the synonyms of *C. purpurea* by Ryvarden & Gilbertson (1993). However, it is a good species morphologically similar to the North-American *C. spissa*. Macroscopically, tough basidiocarps with dark-colored, reddish brown, resinous tubes and much paler margin are characteristic. Hyphal structure is reminiscent of *C. purpurea* because all hyphae are thin-walled and of more or less the same diameter. However, hymenial cells of *C. mellita* are very densely packed and strongly glued by resinous matter, and basidiospores are narrow, (4.1-) 4.2-5.8 (-6.1) × 1.5-1.9 (-2.0) µm (n = 60/2), L = 4.93, W = 1.70, Q = 2.84-2.98. We agree with Pieri & Rivoire (2005) that *C. herinkii* is a synonym of *C. mellita*.

Ceriporia punicans Vlasák & Spirin, spec. nov.

Figs 2, 3

Holotype. USA. Pennsylvania: Montgomery Co., Schwenksville, Swamp Creek, hardwood, August 2008, Vlasák 0808/30 (H).

Mycobank: MB 817348

Basidiocarps annual, resupinate, small-sized, up to 1 cm in widest dimension, later fusing together. **Margin** first whitish, floccose, up to 1 mm wide, later pink to pinkish orange. **Pore surface** even, white or pale pink in fresh condition, orange to pinkish orange when dry, with vinaceous red stains when bruised; **pores** angular, 5-7 per mm, with thin, entire dissepiments. **Section:** subiculum white to pale pink, floccose, up to 0.05 mm thick, tubes dark vinaceous-red, waxy, up to 0.3 mm thick.

Hyphal structure monomitic; **hyphae** simple-septate. **Subicular hyphae** loosely interwoven to subpallel, slightly thick-walled, branched at sharp angles, (4.6-) 4.8-7.4 (-8.1) μm (n = 20/1). **Tramal hyphae** subparallel, thin-walled, (2.8-) 3.0-3.9 (-4.0) μm (n = 20/1), rather loosely arranged; oily matter abundant, present as small droplets on or between hyphae. **Dissepiment edges** sterile, consisting of hyphal endings 3.5-5 μm in diam. **Basidia** clavate, 4-spored, 10.3-12.2 × 4.1-5.9 μm (n = 7/1). **Basidiospores** short cylindrical, not or only slightly curved, (4.0-) 4.1-5.3 (-5.4) × (1.6-) 1.7-2.1 (-2.2) μm (n = 30/1), L = 4.57, W = 1.86, Q = 2.46. **Crystals** prismatic or stellate, abundant among tramal hyphae, up to 20 μm in diam.

Notes. Relatively wide subicular hyphae of *C. punicans*, as well as orange tints of its dried basidiocarps, are reminiscent of *C. aurantiocarnescens*. However, the latter species is differently coloured in fresh condition and never shows distinct colour changes when bruised. Moreover, basidiospores of *C. punicans* are longer than in *C. aurantiocarnescens* and not so distinctly curved. Large prismatic or stellate crystal agglomerations are also characteristic for *C. punicans*. DNA data confirm that *C. punicans* has a rather isolated position within *Ceriporia* and close relatives have not been detected so far.

Ceriporia punicans is still only known from the type locality but could be widely distributed in the North-Eastern USA.

Ceriporia spissa (Schwein.) Ryvarden

Lectotype. USA. Massachusetts: Essex Co., Salem, Schweinitz 418 (PH, studied) (selected by Overholts 1923).

Ceriporia spissa is distributed in the American North-East. Morphologically, it is most similar to *C. mellita* from Europe. These species share tough basidiocarps with dark-colored, sometimes indistinctly stratified tubes and rather pale margin; hyphae are of more or less the same width in subiculum and tube trama. Nevertheless, pores of *C. spissa* are smaller than in *C. mellita* (6-8 per mm versus 4-6 per mm), and basidiospores of *C. spissa* are distinctly smaller, (3.6-) 3.7-4.4 (-4.5) × 1.2-1.6 (-1.8) μ m (n = 60/2), L = 4.03, W = 1.36, Q = 2.89-3.08. Moreover, DNA data do not confirm that these species are closely related (Fig. 1).

Ceriporia spissa was earlier reported from Canary Islands (Ryvarden & Gilbertson 1993). We studied this specimen (Ryvarden 12396, O), and it belongs to C. triumphalis. Previous records of C. spissa from different geographic areas of the world should be re-checked.

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