Sarcodon imbricatus and *S. squamosus* – two confused species

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Sarcodon imbricatus has long been used to extract blue and greenish pigments for wool dyeing. We found that fruit bodies growing with *Pinus sylvestris* seemed to be superior for dyeing compared to fruit bodies growing with *Picea abies*, and macroscopical differences between the forms indicated that they are different taxa. By studying sequences of rDNA ITS and macroscopical characters, two species were recognized. *Sarcodon imbricatus* grows in association with *Picea*, and *S. squamosus* with *Pinus*. The latter species, described by Schaeffer in 1774, has been lumped with *S. imbricatus* during the past 50 years, creating great confusion among wool dyers.

Various fungi have been used as a source of pigment. North American indians used *Echinodontium tinctorium* and *Phaeolus schweinitzii* for red and golden yellow pigments. *Pisolithus arhizus* (*P. tinctorius*), *Cortinarius sanguineus* and *Hapalopilus rutilans* are used in Europe for brown, red and violet colours, and lichenized fungi such as *Roccella* and *Ochrolechia tartarea* have been used since medieval times to produce valuable purple pigments (Kok, 1966; Rice, 1974; Rice & Beebee, 1980; Lundmark & Marklund, 1989; Ye *et al*., 1996).

The basidiomycete *Sarcodon imbricatus* is also used for wool dyeing in many countries (Rice & Beebee, 1980). *S. imbricatus* is a tooth fungus which in Europe grows in ectomycorrhizal symbiosis with coniferous trees (Agerer, 1991). *Sarcodon* is sometimes referred to the Bankeraceae (Jülich, 1981; Hansen & Knudsen, 1997) but spore colour, spore shape and pigments implies a connection with Thelephoraceae (Donk, 1964; Pegler, Roberts & Spooner, 1997). The importance of pigments for fungal systematics has been discussed by several authors, e.g. Arpin & Fiasson (1971) and Gill & Steglich (1987).

S. imbricatus is appreciated for its blueish-greenish pigment, which is probably related to atromentin, thelephoric acid and dehydrogyrocyanin (Gill & Steglich, 1987). The pigment is reported to be found only in old or degraded fruit bodies of *S. imbricatus*. Lundmark in 1991 (unpubl.), however, observed that if fruit bodies were collected from stands dominated by *Pinus sylvestris* L., the blue pigment could be readily extracted from fresh fruit bodies. In contrast to this, fruit bodies collected from stands with *Picea abies* (L.) H. Karst, did not produce blue pigments at any developmental stage. These differences in pigment content, in relation to ecological and morphological differences, supported the hypothesis that *S. imbricatus sensu lato* consists of two species. In Norway, people consider *Sarcodon imbricatus* from pine forests to be more delicious than fruit bodies from spruce forests (Wiborg, 1998).

Due to the interest among wool dyers, mushroom pickers, mycologists and ecologists, we wanted to test the two-species-hypothesis by performing a molecular study based on field material of *S. imbricatus* with different geographical and ecological origin.

Sequence data in the rDNA gene subunit provide powerful information for the study of evolutionary relationships between taxa (Bruns, White & Taylor, 1991). The high level of interspecific variability, but relatively low level of intraspecific variability in the internal transcribed spacer (ITS) makes it particularly useful when working at the species level (Bruns *et al*., 1991; Kårén *et al*., 1996).

By studying the sequence of rDNA ITS, we wanted to investigate if there are two distinct taxa, and if so, whether there is evidence of gene flow for the ITS region between the two taxa. Since different ITS regions would imply two different biological species, we wanted to typify *S. imbricatus* and define the other taxon to facilitate future efforts in wool dyeing and mycological research.

MATERIALS AND METHODS

The 20 specimens used in this study are listed in Table 1. The geographic distances between some of the collected specimens are shown in Table 2.

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Table 1. Overview of *Sarcodon* fruit bodies studied and their presumed hosts. The RFLP types refer to the RFLP fragments of ITS obtained by the restriction enzyme *Taq* 1: imbricatus (174, 121, 59, 221, 120 and 57 base pairs) and squamosus (303, 59, 221, 121 and 57 base pairs)

Specimen	Origin	Collector	GenBank accession no.	ITS length (bp)/ RFLP type
From *Picea abies*				
UPS F-10712	Grödinge, Sörmland	K. Jaederfeldt	AF103885	752/imbricatus
UPS F-10711	Björklinge, Uppland	H. Johannesson	AF103886	752/imbricatus
UPS F-10708	Tuna, Medelpad	S. Muskos	AF103887	752/imbricatus
UPS F-10704	Njurunda, Medelpad	S. Muskos	AF103888	752/imbricatus
HJ1	Fiby, Uppland	H. Johannesson	AF103889	752/imbricatus
UPS F-10694	Vårdinge, Sörmland	K. Jaederfeldt	Not sequenced	752/imbricatus
UPS F-10695	Risbäck, Åsele lappmark	Unknown	Not sequenced	752/imbricatus
UPS F-10696	Garphyttan, Närke	H. Kaufmann	Not sequenced	752/imbricatus
UPS F-10699	Sollefteå, Ångermanland	L. Vessberg	Not sequenced	752/imbricatus
From *Pinus sylvestris*				
UPS F-10701	Nacka, Sörmland	O. Persson	AF103890	761/squamosus
UPS F-10700	Vårdinge, Sörmland	K. Jaederfeldt	AF103891	761/squamosus
UPS F-10703	Njurunda, Medelpad	S. Muskos	AF103892	761/squamosus
UPS F-10705	Indal, Medelpad	H. Lundmark	AF103893	761/squamosus
UPS F-10706	Tallhed, Medelpad	H. Lundmark	AF103894	761/squamosus
UPS F-10709	Timrå, Medelpad	S. Muskos	AF103895	761/squamosus
UPS F-10710	Lunsen, Uppland	L. Jonsson	AF103896	761/squamosus
UPS F-10697	Överjärna, Sörmland	K. Jaederfeldt	Not sequenced	761/squamosus
UPS F-10698	Långvattnet, Ångermanland	L. Vessberg	Not sequenced	761/squamosus
UPS F-10702	Junsele, Ångermanland	E. Engerdahl	Not sequenced	761/squamosus
UPS F-10707	Timrå, Medelpad	H. Lundmark	Not sequenced	761/squamosus

Table 2. The geographic distances and sequence variation between some of the *Sarcodon* specimens studied

Specimen	Host	Geographic distance (km)	Sequence variation (%)
UPS F-10708/UPS F-10709	*Picea/Pinus*	24	3·2
HJ1/UPS F-10710	*Picea/Pinus*	22	3·2
UPS F-10697/UPS F-10694	*Picea/Pinus*	0·3	3·2, based on RFLP
UPS F-10700/UPS F-10705	*Pinus/Pinus*	400	0
UPS F-10712/UPS F-10708	*Picea/Picea*	360	0

DNA extraction and amplification

The extraction procedure followed the method of Gardes *et al*. (1991), with minor modifications. Samples of dried fruit bodies were mixed in lysis buffer (1·4 M NaCl, 0·1 M Tris-HCl, 20 mM EDTA, 2% CTAB) with a plastic pestle. After incubating for 60–120 min at 65 °C, the suspension was centrifuged for 5 min at 2000 ***g***. The supernatant was transferred to a new tube and extracted with 1 vol. of chloroform. The aqueous phase was removed, DNA precipitated with 2 vol. of isopropanol at −20° for 30 min and harvested by centrifugation for 30 min at 13 000 ***g***. The pellet was washed with 70% ethanol and resuspended in 100 µl TE buffer (10 mM Tris-HCl, 1 mM EDTA).

PCR amplifications were performed in a Perkin-Elmer Cetus DNA thermal cycler (model GenAmp 2400) using the primer pair ITS1/ITS4 as described by White *et al*. (1990). Reaction components for the PCR were: approximately 0·01–1·0 ng μl^{-1} of total DNA, 0·1 µM of each primer, 0·025 U μl^{-1} of Taq-polymerase, 200 µM dNTP, 10 mM Tris-HCl, 1·5–3·0 mM $MgCl_2$ and 5 µM KCl. Cycling parameters were 95° for 3 min, then 35 cycles at 95° for 2 min, 53° for 22 s and 72° for 1 min, with a final extension at 72° for 10 min. Negative controls, without DNA template, were prepared in every series of amplification in order to exclude the possibility of contamination in reagents or reaction buffers. Successful PCR reactions resulted in a single band observed on a 1% agarose gel (LE-agarose, FMC BioProducts, Rockland, U.S.A.), corresponding to approximately 700 bp. PCR-products used for sequencing were cleaned using the QIAquick PCR purification kit (QIAGEN Inc., Chatsworth, U.S.A.).

DNA sequencing and restriction enzyme analysis

Twelve specimens (Table 1) were sequenced at least once using each of the primers ITS1 and ITS4 (White *et al*., 1990). Sequences were determined with an Applied Biosystems (Foster City, CA, U.S.A.) 310 sequencer using the *Taq* DyeDeoxi Terminator™ cycle system (Perkin Elmer). The alignment of the sequences was performed manually.

To facilitate the separation of the two taxa, we used sequence data to detect recognition sites for endonucleases. Aliquots of approximately 0·5 µg of amplified DNA from all samples in Table 1 were digested with *Taq* I and *Hae* III according to the manufacturers' recommendations. The

fragments were size-fractioned on 1·7% agarose gels (LE-agarose, FMC BioProducts, Rockland, U.S.A.).

Microscopical and macroscopical investigation

Fruit bodies collected from pure stands with spruce or pine, or in mixed forests, were compared with each other and herbarium material at the Botanical Museum, Uppsala University.

RESULTS

Nucleotide sequences of the ITS region were determined for the 12 specimens indicated in Table 1. No sequence variation was detected among the fruit bodies of the same host even at a distance of 400 km (Table 2), but when comparing fruit bodies from *Pinus* and *Picea* there was a 3·2% sequence variation at the shortest geographical distance between the two taxa (within the same forest). The total length between the 5′ ends of the primers ITS1 and ITS4 were 752 and 761 bp respectively for the two taxa. Sequences are available at GenBank (Table 2).

The restriction analysis of the 20 specimens in Table 1 resulted in two distinct RFLP-patterns when using *Hae* III and *Taq* 1, corresponding to each of the two taxa. The RFLP patterns of the two taxa differed even within the same forest where both pine and spruce occurred.

The pine and the spruce forms of *Sarcodon imbricatus* may easily be identified by macroscopical characteristics, from fresh or properly dried material, but we have not found any reliable microscopical differences. Both forms have hyphae with clamp connections.

The pine form has a yellow brown to vinaceous brown pileus with blackish brown scales, the margin of the pileus remains for a long time incurved, and the centre is not or only slightly depressed. When old or dried the pileus of the pine form is distinctly darker than the pileus of the spruce form. The scales are usually smaller than in the spruce form, especially near the margin of the pileus. The broad scales in the centre are not or only slightly pointed upwards. The spines are slightly decurrent, rather short and crowded, greyish and when fresh often with a tint of greyish blue. The stipe is short, usually of about the same length as the diameter of the pileus or shorter, attenuated at the base, and normally distinctly paler at the apex. The context is whitish but sometimes blackish brown in the stipe base. The smell is aromatic, spicy. The pine form can be confused with *S. scabrosus*, but *S. scabrosus* has a blue stipe base and a bitter, disagreeable taste. Under the microscope they are easily separated, the pine form of *S. imbricatus* has hyphae with clamp connections, *S. scabrosus* does not.

The spruce form has a brown pileus with brown scales, the margin of the pileus does not remain incurved for a long time, and the centre is always depressed, often even infundibuliform or hollow. The pileus of the spruce form is distinctly paler and the broad scales in the centre are usually pointed almost straight upwards. The spines are not decurrent, quite long and brown. The stipe is long, normally longer than the diameter of the pileus, cylindrical or often slightly bulbous at the base, and not paler at the apex. The context is dirty whitish-brownish, not darker in the base of the stipe. The smell is somewhat disagreeable, sour.

Sarcodon imbricatus (L.: Fr.) P. Karst. Rev. Mycol. 3: 20, 1881

Hydnum imbricatum L., *Sp. pl.* p. 1178, 1753: Fr., *Syst. mycol.* **1**: 338, 1821.

Phaeodon imbricatus (L.: Fr.) J. Schroet., *KryptFl. Schles.* **3**(1): 460, 1888.

Lectotype (selected here): Schaeffer, *Fung. Bav.* **II**, plate 140 (1767). Epitype (selected here): UPS F-10704, in old spruce forest between Mt Midskogsberget and Mt Omsberget, Njurunda par., Medelpad prov., Sweden, leg. Siw Muskos no. 97-044, 12 Oct. 1997.

Hydnum subsquamosum Batsch, Elench. fung. p. 111, 1783: Fr., *Syst. mycol.* **1**: 399, 1821. Lectotype (selected here): Schaeffer, *Fung. Bav.* **II**, plate 140 (1767).

Hydnum cervinum Pers., *Obs. mycol.* **1**: 74, 1796 (nom. illeg.). Selected icones: Breitenbach & Kränzlin (1986: pl. 275), Dähncke & Dähncke (1979: 624), Fries E (1860: pl. 33), Maas Geesteranus (1975: pl. 26a), Ryman & Holmåsen (1984: 103).

Sarcodon squamosus (Schaeff.) Quél. Enchir. Fung. p. 188, 1886

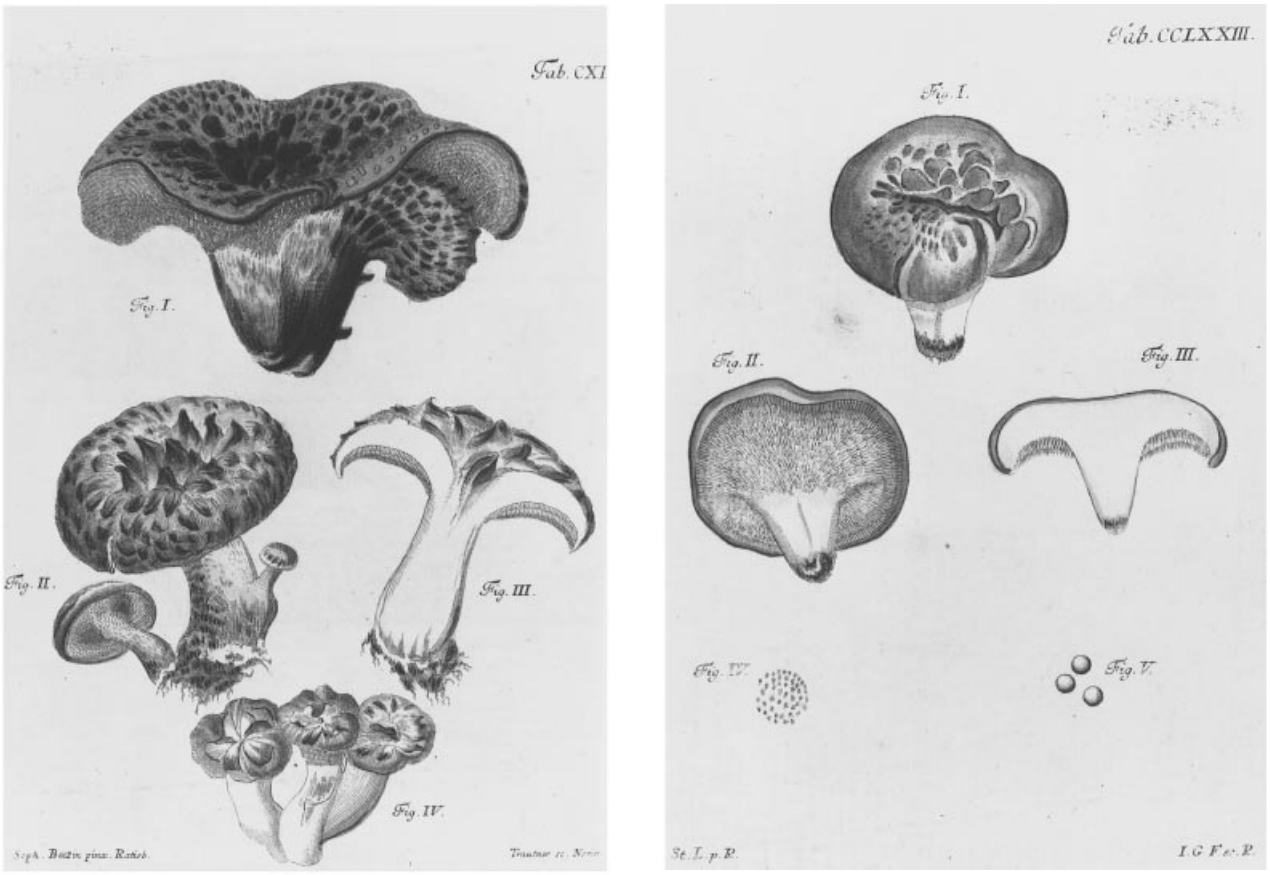
Hydnum squamosum Schaeff., *Fung. Bav.* **IV**: 99, 1774; non *Hydnum squamosum* Bull., Herb. Fr. plate 409, 1789 (= *Hydnellum* sp., fruit body with embedded vegetable debris and zonated contex).

Lectotype (selected here): Schaeffer, *Fung. Bav.* **III**, plate 273 (1770). Epitype (selected here): UPS F-10703, in pine forest on calcareous, sandy soil near the sea, Björkvik, Njurunda par., Medelpad prov., Sweden, leg. Siw Muskos no. 97-043, 12 Oct. 1997.

Hydnum badium, Pers., *Mycol. Eur.* **2**: 155, 1825 (nom. illeg.). Selected icones (all as *S. imbricatus* if not indicated): Bresadola (1932: Tab. 1038; as *Hydnum badium*), Maas Geesteranus (1975: Tafel 26b), Pegler, Roberts & Spooner (1997: 93), Phillips (1981: 242).

DISCUSSION

In this study, no variation in the ITS sequence within any individual *Sarcodon* fruitbody or taxon was detected (Table 2). This corresponds with the general assumption that concerted evolution results in the homogenization of individual repeats and produces a mostly uniform sequence in all repeats of a given species (Vogler & DeSalle, 1994). Only 20 individual fruitbodies were studied, but even in geographically separated fruitbodies (400 km) no variation in the ITS sequence within a taxon was found. Conversely, fruit bodies collected in closer proximity (0·3 km) showed a consistent difference between taxa. This fact, and their similar seasonal patterns, indicate that the differences in ITS sequence between the two taxa are unlikely to have occurred due to separation in time or due to geography. The consistent difference in sequence between the two taxa, and the consistent morphological and ecological



1 2

Figs 1, 2. Schaeffer's illustrations of *Sarcodon* from Fungorum Bavaria et Palatinatu. **Fig. 1.** *S. imbricatus* from **vol. II**, plate 140 (1767). **Fig. 2.** *S. squamosus* from **vol. III**, plate 273 (1770).

differences, indicate that a gene flow between the sampled taxa is unlikely. However, additional markers would be worth investigating. Accordingly, two biological species occur under the present *S. imbricatus* concept.

Similar species pairs associated with pine and spruce have been reported previously within the Bankeraceae *s.l.*, namely, *Bankera fuligineoalba* versus *B. violascens* (Maas Geesteranus, 1975) and *Boletopsis grisea* versus *B. leucomelaena* (Niemelä & Saarenoksa, 1989). In these cases the pine and spruce forms may be easily separated by macroscopical, but not microscopical, characteristics.

Sarcodon imbricatus was first validly described by Linnaeus (1753) as *Hydnum imbricatum*, but such a conspicuous fungus was known by many pre-*Linnaean* mycologists. According to Mass Geesteranus & Nannfeldt (1969) the epithet *imbricatus* was borrowed from Celsius' (1735) phrase name *Erinaceus pileolo amplissimo, fusco, imbricato*. There is no description of habitat by Celsius (1735), but it must have been collected in the Uppsala area, from where we now know both the spruce and the pine form, although the spruce form is decidedly more common. Two sets of Celsius' herbarium are known, one in S in four volumes, the other in UPS, in eight volumes. Both sets lack *Erinaceus … imbricato*. There is also another phrase name of our fungus in Celsius (1735), *Fungus echinatus, maximus, umbraculo amplissimo, obscuro,* & *nigricante*, which comes from Rupp (1726) where the habitat is 'sub pinus & abietibus', thus both pine and spruce.

In Linnaeus (1753) the habitat is 'in Sylvis acerosis', in his *Flora Lapponica* (1737) 'in syluis densissimis', and in *Flora Svecica* (1745 and 1755) 'in vastis sylvis Dalekarliae, Uplandiae, Norlandie'.

In the sanctioning work of Fries (1821) the habitat is 'in pinetis', but Fries' phrase 'in pinetis' means in conifer forests, not pine forests, as by that time both the spruce and the pine were referred to *Pinus*. His description seems to cover both the pine and the spruce form. The short and attenuated stipe ('Stipes uncialis, deorsum attenuatus') conforms better to the pine form, and so does the finally naval-like pileus ('Pileus … demum umbilicatus') to the spruce form.

The German mycologist Jacob Christian Schaeffer, in his *Fungorum Bavaria et Palatinatu* (1767–74) first split *Hydnum imbricatum* into two species. The habitat for *H. imbricatum* is described as in 'Tannen und Fichtenwäldern', and his illustration in **Vol. II**, plate 140 (1767) shows typical specimens of the spruce form. As this plate is also cited by Fries (1821) in the sanctioning work, and there is no original material of Linnaeus or Fries left, Schaeffer's plate is here selected as the lectotype for *Hydnum imbricatum* L.: Fr. (Fig. 1). As an epitype to that plate we at the same time select UPS F-10704.

In the same work, Schaeffer also described a segregate from *Hydnum imbricatum* L. – *Hydnum squamosum* Schaeff. – illustrated in **Vol. III**, plate 273 (1770) and furnished with a Latin name and descriptions in Latin and German in **Vol. IV** (1774). It should grow 'mit der braunen Hirschzunge (= *H.*

imbricatum) im herbste in den Wäldern'. The taxon illustrated on this plate seems to have fairly typical specimens of the pine form. Maas Geesteranus (1959) interprets it as 'a small, squat form of [*H. repandum*] var. *repandum* hampered in its growth by drought'. Maas Geesteranus' conclusion is not convincing since the pileus of the illustrated fungus is red brown with darker scales. Furthermore, Schaeffer knew and illustrated *H. repandum* (under the illegitimate name *H. flavidum*) in **Vol. IV**, plate 318. In fact, there is such great a similarity between Schaeffer's plate 278 and the colour photos of *Sarcodon imbricatus* in Phillips (1981) and Pegler *et al.* (1997), that we choose to use Schaeffer's name for the pine form. As the herbarium of Schaeffer is unknown (Stafleu & Cowan, 1985), Schaeffer's plate 273 is here selected as the lectotype for *Hydnum squamosum* (Fig. 2). As an epitype for that plate we select UPS F-10703.

There is one drawback in Schaeffer's description of *H. squamosum*. Both here and under *H. imbricatum* he has a reference to *H. imbricatum* L., which could make his new name invalid. Schaeffer's intention was, however, to split *H. imbricatum* into two species, it was indeed correct to list *H. imbricatum* of Linnaeus (e.g. *imbricatum* sensu lato) under both species and at the same time use it only for one of the species, the spruce form (Greuter *et al.*, 1994, Art. 52.1 Ex. 8). Petersen (1976) came to the same conclusion. He regarded *H. squamosum* as a validly published segregate from *H. imbricatum* and the case is also mentioned in his explanatory notes to Schaeffer's Index.

Persoon (1825) also recognized our pine form as a separate species when he described *H. badium* Pers. as a segregate from *H. cervinum* Pers. (= *H. imbricatum* L.). The name *Hydnum badium* is obviously illegitimate since Persoon includes, as a variety of *H. badium*, the older name *H. subsquamosum* Batsch.

Bresadola (1932) also split *H. imbricatum* into two species. On plate 1035, there is an illustration of *H. imbricatum* conspecific with our spruce form, and on plate 1038 he uses the illegitimate name *Hydnum badium* Pers. for our pine fungus. On plate 1036, Bresadola illustrates what he then calls *Hydnum squamosum* Schaeff., a fungus that cannot be our pine fungus, since the stem base is bluish. Maas Geesteranus (1956) examined three collections of *H. badium* from Herb. Bresadola in S. In two of the collections, the specimens have clamp connections and belong to *H. imbricatum* sensu lato. The first is labelled '*Hydnum squamosum* Schaeff. (with *squamosum* crossed out and rewritten in pencil *badium* Pers.), In pinetis, Margone, Villa Salvadori, Nov. 1898, leg. J. Bresadola'. One of the fruit bodies in this collection might, according to Maas Geesteranus, have been used for Bresadola's plate 1038. The other collection is labelled '*Hydnum squamosum* Schaeff. = *Hydnum badium* Pers., Sopramonte, sub *Pino sylv.*, Oct. 1899, Leg. J. Bresadola'.

It is thus clear that Bresadola, from the beginning, used the name *Hydnum squamosum* for our pine form, but later changed it to *H. badium* and then used *H. squamosum* for a *Sarcodon* with blue colour in the stem base.

Another name which must be considered is *Hydnum subsquamosum* Batsch: Fr. This name has been used for different hydnaceous fungi. In Fries (1821) at least some elements refer to a *Hydnellum*, namely the zonated context and the reference to *H. squamosum* Bull. Later Fries (1838) changed his mind, and used the name *H. subsquamosum*, at least in part, for our pine associated taxon, since he had a reference to *H. badium* Pers., and at the same time excluded the reference to Bulliard which he then cited under *H. ferrugineum* (= *Hydnellum ferrugineum*). There is no herbarium material of *H. subsquamosum* left from Batsch or Fries. The only original material are the three illustrations cited by Batsch (1783) or by Fries (1821).

The first illustration in Schaeffer, pl. 140 (1767) cited by Batsch. This illustration is in fact *Sarcodon imbricatus*.

The second illustration is Batsch, pl. 10, fig. 43 (1783) cited by both Batsch and Fries. This illustration can not be identified with certainty, but the possibility that it might represent a weathered specimen of *S. imbricatus* can not be eliminated. Alternatively, it may not even represent a *Sarcodon* species.

The third illustration is Bulliard, pl. 409 (1789), cited by Fries. This plate illustrates a *Hydnellum*, and Bulliard's plate was excluded already by Fries (1838).

It is evident that the epithet *subsquamosum* was introduced as a counter-part to Schaeffer's epithet *squamosum* and was an unnecessary change of the epithet *imbricatum*. We therefore select Schaeffer's pl. 140 as the lectotype of *Hydnum subsquamosum* Batsch. *H. subsquamosum* is, therefore, a synonym of *H. imbricatum*.

Sarcodon imbricatus is probably absent from countries where spruce does not occur naturally, e.g. Scotland and the Netherlands. Instead, *S. squamosus* is expected in pine forests. Since there seem to be no microscopical differences between the two species, all *Sarcodon* with clamp connections and coarse scales on the pileus have for the last fifty years been lumped under the name *S. imbricatus* (or *H. imbricatum*). Since it appears that *S. imbricatus* and *S. squamosus* contain different amounts of pigment, the grouping under the same name may explain the difficulties experienced by wool dyers in reproducing pigment extraction.

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REFERENCES

Agerer, R. (1991). Ectomycorrhizae of *Sarcodon imbricatus* on Norway spruce and their chlamydospores. *Mycorrhiza* **1**, 21–30.

Arpin, N. & Fiasson, J.-L. (1971). The pigments of basidiomycetes: Their chemotaxonomic interest. In *Evolution in the Higher Basidiomycetes* (ed. R. H. Petersen), pp. 63–99. University of Tennessee Press: Knoxville.

Batsch, J. G. C. (1783). *Elenchus Fungorum*. Magdeburg.

Breitenbach, J. & Kränzlin, F. (1986). *Pilze der Schweiz, Band 2, Nichtblätterpilze*. Verlag Mykologia: Luzern.

Bresadola, J. (1932). *Iconographia Mycologica* **Vol. XXI**. Milano.

Bruns, T. D., White, T. J. & Taylor, J. W. (1991). Fungal Molecular systematics. *Annual Review of Ecological Systematics* **22**, 525–564.

Bulliard, J. B. F. (1789). *Herbier de la France. Tome* 9. Paris.
Celsius, O. (1735). Plantarum circa Upsaliam sponte nascentium Catalogus. *Acta literaria et scientiarum Sueciae* **3**, 9–44.
Dähncke, R. M. & Dähncke, S. M. (1979). *700 Pilze in Farbfotos*. AT Verlag: Aarau.
Donk, M. A. (1964). A conspectus of the families of Aphyllophorales. *Persoonia* **3**, 199–324.
Fries, E. (1821). *Systema Mycologicum* **Vol. 1**. Lund.
Fries, E. (1838). *Elenchus fungorum*. Lund.
Fries, E. (1860). *Sveriges ätliga och giftiga svampar*. Stockholm.
Gardes, M., White, T. J., Fortin, J. A., Bruns, T. D. & Taylor, J. W. (1991). Identification of indigenous and introduced symbiotic fungi in ectomycorrhizae by amplification of nuclear and mitochondrial ribosomal DNA. *Canadian Journal of Botany* **69**, 180–190.
Gill, M. & Steglich, W. (1987). *Pigments of fungi* (*Macromycetes*). Progress in the Chemistry of Organic Natural Products 51. Springer Verlag: Wien, New York.
Greuter, W., Barrie, F. R., Burdet, H. M., Chaloner, W. G., Demoulin, V., Hawksworth, D. L., Jørgensen, P. M., Nicolson, D. H., Silva, P. C., Trehane, P. & McNeill, J. (ed. 1994). International Code of Botanical Nomenclature (Tokyo Code). *Regnum Vegetabile* **131**.
Hansen, L. & Knudsen, H. (1997). *Nordic Macromyctes*, **vol. 3**. Nordsvamp: Copenhagen.
Jülich, W. (1981). Higher Taxa of Basidiomycetes. *Bibliotheca Mycologica* **85**, 1–485.
Kok, A. (1966). A short history of the orchil dyes. *Lichenologist* **3**, 248–272.
Kårén, O., Högberg, N., Dahlberg, A., Jonsson, L. & Nylund, J.-E. (1997). Inter- and intraspecific variation in the ITS region of rDNA of ectomycorrhizal fungi in Fennoscandia as detected by endonuclease analysis. *The New Phytologist* **136**, 313–325.
Linnaeus, C. (1737). *Flora Lapponica*. Amsterdam.
Linnaeus, C. (1745) *Flora Svecica*. Stockholm.
Linnaeus, C. (1753). *Species Plantarum*. Stockholm.
Linnaeus, C. (1755). *Flora Svecica*. Ed. 2. Stockholm.
Lundmark, H. & Marklund, H. (1989). *Färga garn med svamp*. Utbildningsförlaget brevskolan: Stockholm, Sweden.
Maas Geesteranus, R. A. (1956). The stipitate Hydnums of The Netherlands – 1. *Sarcodon* P. Karst. *Fungus* **26**, 44–60.
Maas Geesteranus, R. A. (1959). The stipitate Hydnums of The Netherlands – IV. *Auriscalpium* S. F. Gray, *Hericium* Pers. ex S. F. Gray, *Hydnum* L. ex Fr., and *Sistotrema* Fr. em. Donk. *Persoonia* **1**, 115–147.
Maas Geesteranus, R. A. (1975). Die terrestrischen Stachelpilze Europas. *Verhandelingen der Koninklije Nederlandse Akademie van Wetenschappen, afd. Natuurkunde, Tweede reeks* **65**, 1–127.
Maas Geesteranus, R. A. & Nannfeldt, J. A. (1969). The genus *Sarcodon* in Sweden in the light of recent investigations. *Svensk Botanisk Tidskrift* **63**, 401–440.
Niemelä, T. & Saarenoksa, R. (1989). On Fennoscandian polypores 10. *Boletopsis leucomelaena* and *B. grisea* described and illustrated. *Karstenia* **29**, 12–28.
Pegler, D. N., Roberts, P. J. & Spooner, B. M. (1997). *British Chanterelles and Tooth Fungi*. Royal Botanic Gardens: Kew.
Persoon, C. H. (1825). *Mycologia Europaea 2*. Erlangen.
Petersen, R. H. (1976). An annotated index for J. C. Schaeffer's 'Bavarian Fungi'. *Mycotaxon* **4**, 145–154.
Phillips, R. (1981). *Mushrooms and Other Fungi of Great Britain and Europe*. Pan Books Ltd: London.
Rice, M. (1974). *Let's Try Mushrooms for Color*. Thresh Publications: Santa Rosa.
Rice, M. & Beebee, D. (1980). *Mushrooms for Color*. Mad River Press: Eureka.
Rupp, H. B. (1726). *Flora Jenensis*. Frankfurt & Leipzig.
Ryman, S. & Holmåsen, I. (1984). *Svampar, en fälthandbok*. Interpublishing: Stockholm.
Schaeffer, J. C. (1767). *Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur*. **Vol. II**. Regensburg.
Schaeffer, J. C. (1770). *Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur*. **Vol. III**. Regensburg.
Schaeffer, J. C. (1774). *Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur*. **Vol. IV**. Regensburg.
Stafleu, F. A. & Cowan, R. S. (1985). Taxonomic literature. **Vol. V**. Regnum Vegetabile **112**.
Vogler, A. P. & DeSalle, R. (1994). Evolution and phylogenetic information content of the ITS-1 region in the tiger beetle *Cicindela dorsalis*. *Molecular Biology and Evolution* **11**, 393–405.
White, T. J., Bruns, T., Lee, S. & Taylor, J. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In *PCR protocols: a guide to methods and applications* (ed. M. Innis, D. Gelfand, J. Sninsky & T. White), pp. 315–322. Academic Press: San Diego.
Wiborg, E. R. (1998). Skjellpiggsopp og skjellpiggsopp fru Blom! *Blekksoppen* **26**, 10.
Ye, Y., Josten, J., Arnold, N., Steffan, B. & Steglich, W. (1996). Isolation of a fluorone pigment from the indian paint fungus. *Echinodontium tinctorum* and *Pyrofomes albomarginatus*. *Tetrahedron* **52**, 5793–5798.

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