First report of a *Sirobasidium* species in Austria, and a survey of the *Sirobasidiaceae*

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Abstract: Based on a recent collection from Austria, *Sirobasidium rubrofuscum* (formerly *S. sanguineum*) is described and illustrated. A survey of the family *Sirobasidiaceae* with special emphasis on the exceptional arrangement of the basidia in chains or clusters and on the ecological association with *Diatrypales* and *Sphaeriales* is given. All *Sirobasidium* species described so far are known from only one or a few localities world-wide. For a clear delimitation of the species still more collections will be required.

Zusammenfassung: Ein Fund von *Sirobasidium rubrofuscum* (früher *S. sanguineum*) aus Niederösterreich wird vorgestellt und ausführlich dokumentiert. Die Gattungen *Sirobasidium* und *Fibulobasidium* (*Sirobasidiaceae*) und ihre Vertreter werden überblicksartig diskutiert, besonders in Hinsicht auf die außergewöhnliche Entwicklung und ketten- bzw. clusterförmige Anordnung der Basidien und die substratökologische Vergemeinschaftung mit *Sphaeriales*- und *Diatrypales*-Arten. Alle bisher beschriebenen Arten der *Sirobasidiaceae* sind weltweit nur von einem oder wenigen Fundorten bekannt, und ihre taxonomische Abgrenzung ist daher noch ungenügend geklärt. Der vorliegende Fund aus Niederösterreich ist der zweite Nachweis einer *Sirobasidium*-Art in Mitteleuropa.

Fructifications of *Sirobasidium* species (*Tremellales*, *Heterobasidiomycetes*) typically appear as a number of small gelatinous pustules which coalesce to a few centimeters across, or can become cerebriform or even foliaceous and macroscopically very similar to well known jelly fungi, e.g., *Tremella* species.

The most striking character of the genus *Sirobasidium* is the serial arrangement of the basidia on the end of the hyphal threads, as already pointed out by LAGERHEIM & PATOUILLARD (1892) in the protologue of this genus ("… in catenulas disposita") and in their introductory comments ("… se distinguant nettement de tous les Basidiomycètes connus par ses sporophores placés bout à bout comme les grains d'un chapelet").

The mature basidia are divided by usually oblique, sometimes also vertical or horizontal septa into two or four cells. From each cell fusiform structures are born which eventually become detached (deciduous). In the original description (LAGERHEIM & PATOUILLARD 1892), as well as in many papers published later on, these structures were regarded as basidiospores, until BANDONI (1957) identified them as epibasidia (protosterigmata) from which true sterigmata grow and the true basidiospores (ballistospores) are differentiated.

During the last 110 years, several theories, ideas and speculations have been published in the mycological literature, all of which acknowledge the exceptional systematic position of the genus *Sirobasidium* somewhere within the *Auriculariales*, *Tremellales*, or *Tulasnellales*.

In 1994, a *Sirobasidium* species was found in Lower Austria that corresponds well with descriptions of *S. sanguineum* LAGERHEIM & PATOUILLARD (1892), hitherto reported from Australia, Brazil, Ecuador, India, and the United States. According to ROBERTS & MEIJER (1997), this name has to be replaced by *Sirobasidium rubrofuscum* (BERK.) P. ROBERTS, based on *Dacrymyces rubrofuscus* BERKELEY (1845), described from Australia.

Colour codes in the following description are according to KORNERUP & WANSCHER (1975).

***Sirobasidium rubrofuscum* (BERK.) P. ROBERTS**, Mycotaxon **64**: 262; 1997. (Colour fig. I; Figs. 1, 2)

Description: Young basidiomes composed of separate pustules, which coalesce and build up "colonies" up to 12 x 3.5 mm, the individual pustules around 1.0-1.5 mm in diameter and up to 1.0 mm high. Basidiome surface uneven, undulating, with shallow depressions, partly cerebriform and convoluted. Young pustules greyish-hyaline, soon becoming reddish-brown (8D8) in the centre, dark red-brown to dark brown (8E8-8E5) at the margin, finally blackish (8EF2). Consistency soft, gelatinous, easily damaged and detached from the substratum.

Microscopic characters: Probasidia: 22-35 x 12-16 µm; some elongated, more often inflated, ellipsoid to globose; at first single-celled, finally divided into four cells by oblique septa; somewhat thick-walled in parts; young cells contain one large drop, older ones two smaller drops. The probasidia are arranged in chains, 2-4 probasidia per chain (J. HECHLER, in litt., observed chains of 5 probasidia); the proximal/inferior probasidia (next to the basidiogenous hyphal segment) with a distinct clamp connection; the distal/superior ("uppermost") probasidia inverted-ovate; mature probasidia with attached epibasidia very rare.

Epibasidia: separated from the probasidia in mounts, numerous; (13.0-)14.5-23.0 (-25.5) x 4.5-5.5 µm, mean length = 17.8 ± 3.9 µm, mean width = 5.0 ± 0.5 µm, length/width ratio (Q) = (2.6-)3.0-4.6; mean Q = 3.6 ± 0.6; variable in shape, in general fusiform, but often asymmetric and irregular, the proximal end as a rule tapering, more or less truncate, the distal end shortly rounded; often one of the ends slightly bent or the entire cell somewhat S-shaped; hyaline; containing two or more drops; the cell wall neither remarkably thin nor thick. Germinating epibasidia: rare (seen only by J. HECHLER, in litt., Fig. 2 a), with one or two sterigmata arising from the long side at about half the length of the epibasidia, sterigmata around 5 µm long, tubular.

Basidiospores: rare (seen only by J. HECHLER, in litt., Fig. 2 b), subglobose, around 4.5-6.5 µm in diameter, with distinct apiculus, germinating by a tubular excrescence (repetitive?). - Cystidia: not present. - Subhymenial hyphae: 1.5-3 µm wide, slightly to distinctly thick-walled, in the latter case appearing yellowish, hyphal surface partly rough; with distinct clamp connections.

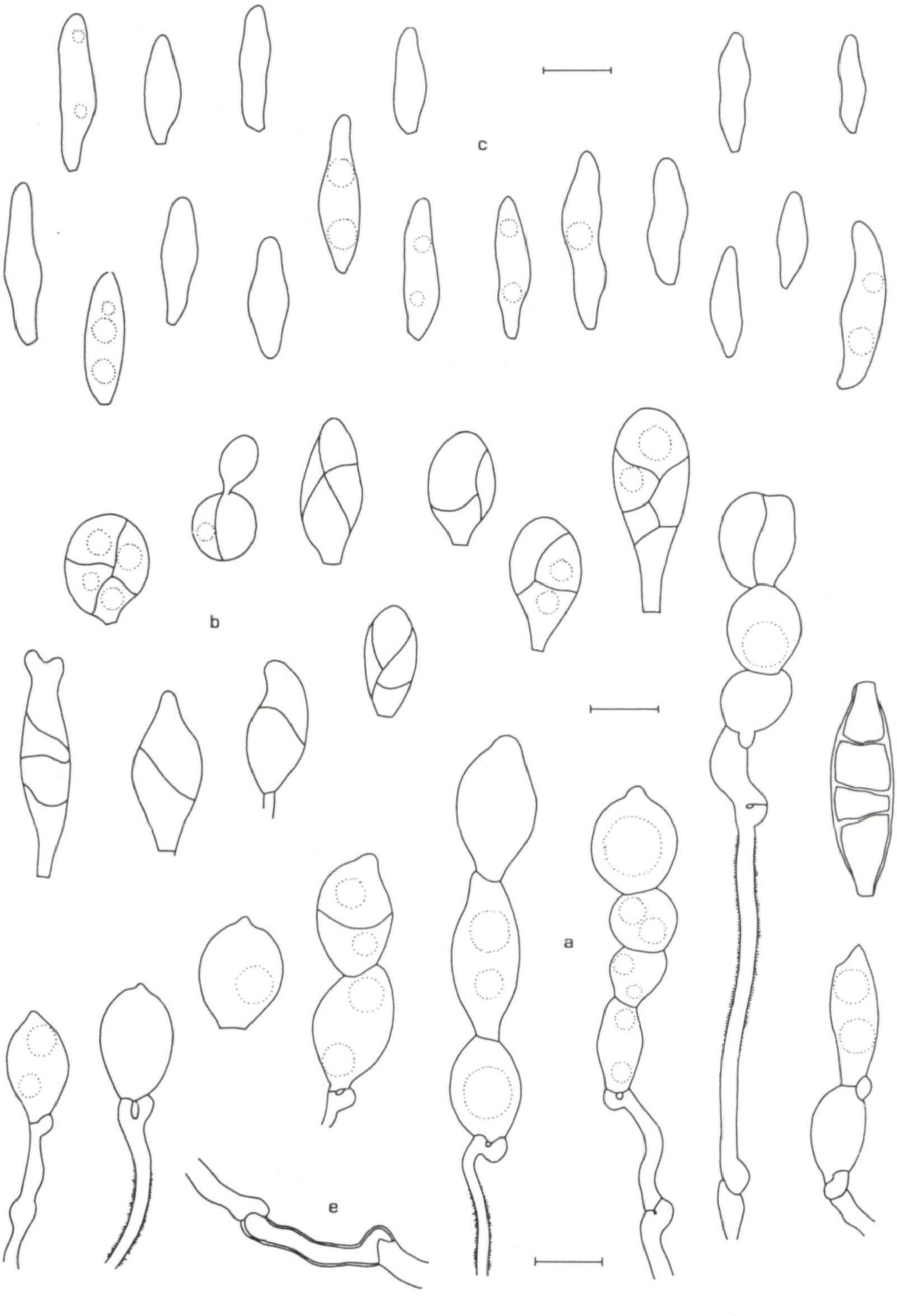


Fig. 1. *Sirobasidium rubrofuscum* (Herb. WU 12771). *a* Serially arranged probasidia (up to four per chain). *b* Bud-shaped probasidia, mostly from the top of the basidia chains, divided by oblique septa in usually four cells. *c* Detached epibasidia. *e* Hyphal system. – Bar: 10 µm.

Ecology: On wood of fallen branch of a deciduous tree; associated with *Eutypa maura* (FR.: FR.) FUCKEL (Syn. *E. acharii* TUL. & C. TUL.; *Diatrypales*, *Ascomycota*).

Specimen examined: Austria: Lower Austria, Lilienfeld, Hohenberg, Hinterbergtal, 500-600 m s. m.; 47° 54' N, 15° 38' E, map grid: 8059/4; Herbarium WU 12771, 10. 5. 1994 (leg. A. HAUSKNECHT, det. J. HECHLER as *Sirobasidium sanguineum*).

Sirobasidiaceae LINDAU 1897

When MÖLLER (1895) introduced the *Sirobasidiaceae* and the name was published validly by LINDAU two years later (see CABI 2000), this family comprised only three species. Today the *Sirobasidiaceae* include the genera *Sirobasidium* and *Fibulobasidium* with about 10 species altogether. As to the outline and definition of the family, hardly any discussions have arisen. BANDONI (1979) once proposed to place *Sirobasidium* and *Tremella* in a single family, while in his later papers the author still retains the traditional systematic concept.

Sirobasidium LAGERHEIM & PATOUILLARD 1892

The original description (LAGERHEIM & PATOUILLARD 1892: 468-469) is as follows: „*Sirobasidium* LAG. et PAT. nov. gen. – Fungi gelatinosi, pulvinati, ubique hymenio vestiti. Basidia ex apice hypharum oriunda, globosa vel ovoidea, longitudinaliter quadripartita, in catenulas disposita, quarum articuli inferni juniores; e quacumque parte basidii spora unica, continua, fusiformis, acrogena, sessilis, exoritur. Germinatio sporae ignota."

LAGERHEIM & PATOUILLARD (1892) already observed the development of the serially arranged basidia by basipetal succession: the first and oldest basidium remains on top (next to the hymenial surface), whereas the subsequent basidia are below, the youngest one next to the segment of the hyphal thread. Starting at the uppermost end of the basidia chain, the basidia form "spores", but usually only one basidium at a time. After the "spores" are detached, the basidia collapse and disintegrate. MÖLLER (1895) believed this mode of basidial development must have been a very early one, while in higher organized basidiomata the spores formed from the inferior basidia would stay inclosed; consequently, during phylogeny the number of basidia per hyphal thread was reduced to one. Actually, in some species of *Auriculariales* and *Tremellales* two serial basidia have still occasionally been observed.

Only three years after the genus had been published, MÖLLER (1895) presented in-depth studies on the ontogeny of *Sirobasidium*, namely on the newly described *S. brefeldianum* MÖLLER. He especially investigated the germination of the "spores" and the yeast-like stages of the fungus growing in a moist chamber. MÖLLER (1895) was the first to observe not only the detached epibasidia (so called "fusiform spores"), but also true (globose) basidiospores. Unfortunately he did not find the "missing link" (i.e. epibasidia bearing sterigmata and sporulating), so he explained the globose type of spores as deformed fusiform spores which had been shed and hurtled through the air ("... werden abgeschleudert und gehen, während sie durch die Luft fliegen, von der länglichen zur kugelrunden Gestalt über"). Nevertheless, MÖLLER (1895) documented the microscopical details of *S. brefeldianum* very thoroughly (Fig. 4). The quality of MÖLLERs work on tropical tremelloid species was praised by LLOYD (1917) as follows: "... his work was so well done that the species may be recognized, which is something that can rarely be said about mycological work".

BOEDIJN (1934) amended the genus concept when including the new foliaceous species *Sirobasidium magnum* BOEDIJN.

Even in one single *Sirobasidium* fructification extreme variations in basidial types can occur (some basidia longitudinally divided as in the *Tremellales*, some laterally divided as in the *Auriculariales*). This induced OLIVE (1946) to point out the intermediate systematic position of *Sirobasidium* within the *Heterobasidiomycetes*. OLIVE (1946) still considered the detached epibasidia to be basidiospores, though his description of their development expressed some doubt as to their true nature ("... budded out directly from the basidial cells or produced on short protrusions, which, however, do not appear to be true sterigmata").

The complete sexual reproduction procedure was eventually researched by BANDONI (1957) when re-examing specimens of *Sirobasidium sanguineum*: "Eleven hours after soaking, large numbers of fusiform spores were observed in various stages of germination through formation of tubular extensions of variable lengths tipped with sterigmata upon which were produced typical basidiospores". As these spores differ conspicuously from the fusiform structures in terms of shape, size, and bearing an apiculus, their development can not simply be a case of repetition, the author argues. Furthermore, BANDONI (1957) gives reasons why the fusiform structures, even though they are detached from the serial basidia, are obviously homologous with the epibasidia of, e.g., *Tulasnellales*. This interpretation was confirmed by KOBAYASI (1962) in his cytological studies on *Sirobasidium* and is generally accepted to this day.

The re-characterized description of the genus *Sirobasidium* by BANDONI (1957) was adopted without major adjustments by PILÁT (1957), DONK (1966), LOWY (1971), WOJEWODA (1981), JÜLICH (1984), FLORA FUNGORUM SINICORUM (1992), WELLS (1994), and others.

When BANDONI (1979) proposed *Fibulobasidium*, the second genus of the *Sirobasidiaceae*, he used the terms "mature basidia", "primary basidiospores", and "ballistospores", instead of, or synonymously with the terms probasidia, epibasidia, and basidiospores, respectively. In the opinion of the author "these (primary basidiospores, detached epibasidia) represent the most primitive form of basidia", and "the ballistospore ... must originally have been an asexual spore".

FLEGEL (1976, 1981) carried out intensive morphological and physiological studies on *Sirobasidium magnum* BOEDIJN. The life cycle of this species (with special emphasis on the yeast stage) is described in detail and documented with many photographs. As a result, the author stresses the close relationship between the *Sirobasidiaceae* and the *Tremellaceae*. Also WELLS (1994) concluded from his investigations on the septal pore apparatus (SPA) in the *Heterobasidiomycetes* that the *Sirobasidiaceae* are best placed in the *Tremellales* (*Tremellomycetidae*). INGOLD (1995, 1998) focused on *Sirobasidium* when comparing the range of reproductive structures and spore production processes in *Basidiomycota*.

Morphological characters of *Sirobasidium rubrofuscum* (*S. sanguineum*)

So far, no more than ten records of *Sirobasidium rubrofuscum* have been reported and documented world-wide (see Tables 1, 2), most of them under the name *S. sanguineum*. Since the type specimen of *Dacrymyces rubrofuscus* BERKELEY (1845) has proved to be conspecific with *Sirobasidium sanguineum* (MCNABB 1973, ROBERTS & MEIJER 1997), the current name is *S. rubrofuscum*. Further synonyms are *S. indicum* RAMAKR.

& SUBRAM. (P. ROBERTS, in litt.) and *Tremella fusca* LLOYD (BANDONI 1957, 1958; LOWY 1971; ROBERTS & MEIJER 1997).

The original description of *Dacrymyces rubrofuscus* (BERKELEY 1845: 61-62) is as follows: "pusillus rubro-fuscus; stromate sinuato gyroso; sporis magnis globosis ovalibusve simplicibus vel uni-bispetatis."

The original description of *Sirobasidium sanguineum* (LAGERHEIM & PATOUILLARD 1892: 468-469) is: „acervuli sparsi vel omnino confluentes, innato-erumpentes, gyroso-cerebriformes, rubri, e coriaceo gelatinosi, 4-20 mm. longi; hyphis filiformibus, valde ramosis, rufis; catenulis basidiorum 2-4 vel plus articulis compositis; articulum (scilicet basidium) saepe oblique 4-septatum, 18-20 μ longum, 10-12 μ latum, ovoideum, apice attenuatum, rufescens; sporis hyalinis, fusiformibus (17-20 x 6-8 μ)".

Table 1. Comparison of some characters of *Sirobasidium rubrofuscum*, as reported in eight publications since 1892.

Reference, locality and year of record	Size of fructifications	Serial basidia	Size of basidia	Size of Epibasidia	Basidiospores
LAGERHEIM & PATOUILLARD (1892), Ecuador, 1892 *	4-20 mm	2-4	18-20 x 10-12 µm	17-20 x 6-8 µm	not observed
LLOYD (1917), Brazil, before 1917 **	20-30 mm	1(-3)	x 12 µm	10-12 x 4-5 µm	7-9 x 5.5-8 µm
COKER (1928), USA, North Carolina, 1920	3-20 mm, 1-5 mm high	?	24 x 12-15 µm	(12.2-)15-23 x 5.5-7.7 µm	not observed
MARTIN (1936), Australia, before 1936	(twice that of earlier reports)	1-3	?	14-17 x 7-9 µm, 22-26 x 5-7 µm	not observed
OLIVE (1946), USA, Maryland, 1945	?	1-4	12.5-20(-32.5) x 11-12.5 µm	(11-)12-23.3 x 5-8 µm	not observed
LOWY (1956), USA, Louisiana, 1955	10 x 5 mm, 4 mm high	1-4	(13.4-)14.2-16.6 (-18) x (14.5-)15-17.5 µm	(14.2-)15.1-18.5(-24) x (5.4-)6.1-6.8(-7) µm	9-11 x 7-9 µm
ROBERTS & MEIJER (1997), merged description ***	10 mm across, 5 mm high	2-4	x 10-12 µm	15-20 x 5-7.5 µm	7-7.5 x 8-8.5 µm
this report Austria, 1994	12 x 3.5 mm, 1 mm high	2-4	22-35 x 12-16 µm	(13-)14.5-23(-25.5) x 4.5-5.5 µm	observed

* type of *Sirobasidium sanguineum*
** type of *Tremella fusca*
*** including type of *Dacrymyces rubrofuscus*
Basidiospore size values partly from BANDONI (1957)

The original description of *Tremella fusca* (LLOYD 1917: 683) is: "cerebrine, reddish brown, 2-3 cm in diameter. Basidia globose, with brownish contents, mostly cruciately divided, 12 mic in diameter. Spores narrow, obovate, tapering to the base, hyaline, 4-5 mic broad at upper end, 10-12 mic long."

As in other *Heterobasidiomycetes*, the size of the fructifications (pustular masses) is a taxonomical criterion of minor reliability as it evidently depends on growing conditions (humidity, above all) and on the moisture content of the basidiomata. Nevertheless, the measurements given for *S. rubrofuscum* are all within a range of 10-20 x 3-5 mm (by 1-5 mm height), except for the Australian collections with a maxium size "nearly twice that given in the earlier accounts cited" (MARTIN 1936).

In typical cases, the species is well characterized by the blood-red to reddish-brown colour which was eponymous not only for the name "rubrofuscum", but also for the synonymous epithets "fuscum" and "sanguineum". The colour becomes even deeper and darker on aging and on drying, and finally the fructifications turn almost black (as already described by BERKELEY 1845). Remarkably, the colour codes given by ROBERTS & MEIJER (1997) are almost identical to those in our description of the Austrian collection. LAGERHEIM & PATOUILLARD (1892), LLOYD (1917) and COKER (1928) report a somewhat reddish pigmentation of hyphal and basidia cell walls, whereas LOWY (1956) explicitly notes the "lack of red pigment in any part".

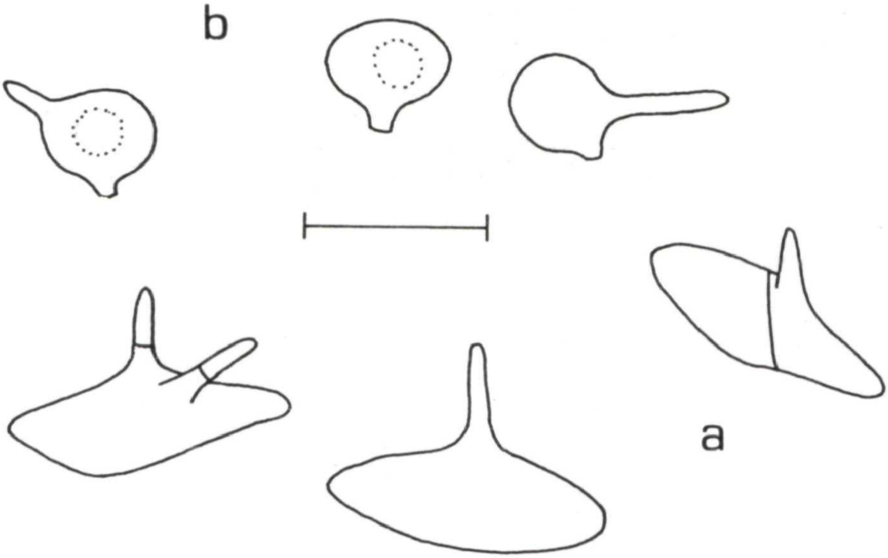


Fig. 2. *Sirobasidium rubrofuscum* (Herb. WU 12771), after sketches by J. HECHLER. *a* Epibasidia with one or two sterigmata. *b* Basidiospores, partly germinating by repetition. – Bar: approximately 10 µm.

However, young fructifications are described as "pale amber" (COKER 1928), "light tan to reddish amber" (OLIVE 1946), "whitish like chewed bread" (MARTIN 1936), or even "greyish hyaline" (in the Austrian collection). Likewise, a large, obviously old fructification from Australia (MARTIN 1936) appeared "pallid to light ochraceous buff". This, the author states, "may well be due to the fact that the colour has been washed out, as not infrequently happens in case of tremellaceous fungi with red or yellow tints".

In none of the reported collections does the maximum number of serial probasidia exceed four per chain (see Table 1), while in younger stages, or under unfavourable growth conditions, many chains with less than four probasidia can be seen. Thus, if in extreme cases only one basidium per hyphal end has been differentiated, a *Sirobasidium* could be mistaken for a *Tremella* species, as demonstrated by the type specimen of "*Tremella fusca*" (see above comments on the synonymy). However, even LLOYD (1917) himself was not sure about the systematic position of the species which he named *Tremella fusca*: "In fact this is the only *Tremella* I have met with narrow, obovate spores".

The size of the probasidia (width) given in the literature ranges from 10-12-15 µm, wheras the data for the length diverge considerably (with 22-35 µm in the Austrian collection among the longest probasidia). Presumably many of the data include different development stages. This makes a comparison difficult and invalid, as the shape and proportions of the probasidia change from elongated to subglobose or ovate during their maturity process.

In *Sirobasidium rubrofuscum* the probasidia are in the end predominantly divided into four cells, which separates it from other species of this genus (see below).

Another interesting distinguishing criterion concerning the probasidia was emphasised by ROBERTS & MEIJER (1997): "Unlike most other *Sirobasidium* species, the sterigmata develop apically and it is quite common to find some basidia with all four sterigmata still attached". Unfortunately, mature probasidia with still attached epibasidia are rarely observed and must be scarce in *S. rubrofuscum*. No illustrations exist, but those in LAGERHEIM & PATOUILLARD (1892) and BANDONI (1957) each show only one probasidium with indeed apically positioned sterigmata (even though there are just two sterigmata, instead of four).

The length and width of the detached epibasidia of a given specimen vary within a wide range, but the data obtained from different collections (see Table 1) are surprisingly homogenous and can be summarised as (12-)15-23(-26) x 5-8 µm. It has to be noted that in the Austrian collection the mean epibasidia width (5.0 ± 0.5 µm) is considerably lower than in the other collections of *S. rubrofuscum* reported so far. The shape of the epibasidia is commonly described as "fusiform" or, more precisely, as "subelliptic, pointed and bent at one end" (COKER 1928).

When looking at the early drawing with which LAGERHEIM & PATOUILLARD (1892) illustrated the type specimen of *S. sanguineum*, one may conclude that the species lacks clamp connections and that the probasidia are septated longitudinally. However, both the presence of clamp connections and the predominantly oblique septation of the probasidia are described correctly in the text („hyphes … munies de boucles; … souvent ces cloisons ne sont pas longitudinales, mais plus ou moins obliques").

True basidiospores of *S. rubrofuscum* have been observed and documented only by BANDONI (1957); in the type specimen of *Tremella fusca*, and in a collection reported by LOWY (1956), and by ROBERTS & MEIJER (1997). During a previous study of the collection from Lower Austrian J. HECHLER (in litt.) demonstrated basidiospores and epibasidia bearing sterigmata (Fig. 2), while our own attempts to search for basidiospores when re-examing the material have not been successful. Remarkably, some of the basidiospores are typically "depressed" (broader than long), with the apiculus seemingly positioned "laterally", as also can be seen in other *Sirobasidium* and *Tremella* species (VAN DE PUT 1994, VAN DE PUT & ANTONISSEN 1995).

COKER (1928) found "spores" (detached epibasidia) of *S. rubrofuscum* sprouting in a yeast-like way and the resulting cells budding repeatedly, thus becoming smaller and smaller in each generation (from 8.2 to finally 1.5 µm), whereas MARTIN (1936) and LOWY (1956) observed the "spores" germinating by a germ tube. One of the germinating epibasidia illustrated in MARTIN (1936) seemingly bears a sterigma.

Picture photographs of *Sirobasidium rubrofuscum* are provided by LLOYD (1917) and COKER (1928).

Distribution of *Sirobasidium rubrofuscum*

Sirobasidium rubrofuscum has been reported from North America, South America, Asia, and Australia (see Table 2, Fig. 3). In addition to the data in the table, there are further records in the USA (Louisiana, OLIVE 1951; New Jersey, P. ROBERTS, in litt.), and in Brazil (LOWY 1971).

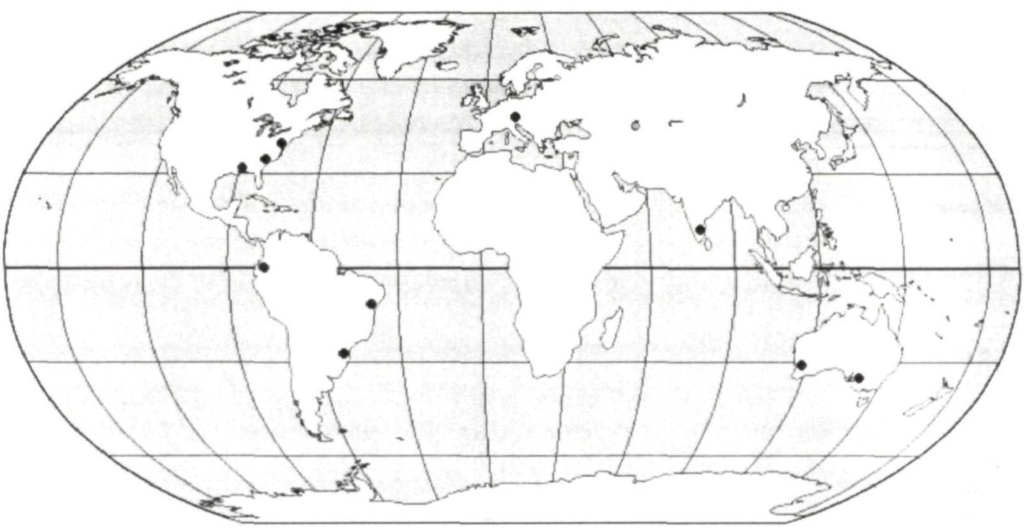


Fig. 3. Distribution of *Sirobasidium rubrofuscum* in the world based on collection localities reported so far (North America, South America, Australia, Asia, Europe). The line indicates the equator.

Table 2. Distribution and ecology of *Sirobasidium rubrofuscum*. The geographical co-ordinates (latitude, longitude) and the climate data (average annual mean temperature, average annual total precipitation) are obtained from various sources in the World Wide Web (e.g., WEBMET 2001).

Locality	Co-ordinates	Climate	Date	Ecology	Reference
North America					
USA, Maryland, Beltsville	39° 03' N 76° 56' W	12.1 °C 1060 mm	winter 1944/45	decorticated frondose limb on the ground	OLIVE (1946)
USA, North Carolina, ?	35° 49' N 78° 39' W (Raleigh)	15.3 °C 1180 mm (Raleigh)	December 1920	emerging from the unbroken bark of *Ligustrum* spec.	COKER (1928)
USA, Louisiana, Baton Rouge	30° 27' N 91° 08' W	19.6 °C 1540 mm	November 1955	dead, about 1 m long branch of *Fraxinus nigra* MARSH.	LOWY (1956)
South America					
Ecuador, Pichincha, Pululahua *	0° 04' N 78° 46' W	13.0 °C 1250 mm (Quito)	February 1892	dead branch of *Barnadesia* spec., soc. *Eutypella* spec.	LAGERHEIM & PATOUILLARD (1892)
Brazil, Bahia State, unlocalized **	12° 58' S 38° 29' W (Salvador)	21-26 °C 600-1500 mm (Bahia State)	?	?	LLOYD (1917)
Brazil, Paraná State, Curitiba	25° 30' S 49° 15' W	16.5 °C 1500 mm	February 1987	on dead wood	ROBERTS & MEIJER (1997)
Australia					
Australia, Western Australia, Swan River ***	31° 56' S 115° 58' E (Perth Airport)	18.2 °C 790 mm (Perth Airport)	?	decayed branches, on the wood itself, or from some *Sphaeria*	BERKELEY (1845)
Australia, South Australia, Mt Lofty	34° 59' S 138° 42' E	13.2 °C 1120 mm (Stirling)	?	?	MARTIN (1936)
Asia					
India, Madras, Jambaran****	13° 04' N 80° 15' E (Madras)	28.7 °C 1400 mm (Madras)	Sept. 1951	on dead twig, soc. *Eutypa* spec.	(P. ROBERTS, in litt.)
Europe					
Austria, Lower Austria, Hohenberg	47° 54' N 15° 38' E	7.2 °C 1240 mm (Schwarzau)	May 1994	decorticated branch of a frondose tree, soc. *Eutypa acharii*	this report

* type of *Sirobasidium sanguineum*
** type of *Tremella fusca*
*** type of *Dacrymyces rubrofuscus*
**** type of *Sirobasidium indicum*

Pululahua, the peculiar type locality of "*S. sanguineum*" (LAGERHEIM & PATOUILLARD 1892), is worth mentioning briefly. The 3356 m high volcano in Ecuador, located just a few kilometers from the equator and the famous "Middle of the World Monument", was declared the first National Park in South America and is now a Geobotanical Reserve that houses and protects more than 50 plant and 20 animal endemic species. The interior of the 4 km wide crater of Pululahua (the biggest in South America) has its own micro-climate (EÄ FOUNDATION 1999, SHANNON 2000). The high richness of *Heterobasidiomycetes* species in Ecuador in general was already pointed out by LAGERHEIM & PATOUILLARD (1892).

Sirobasidium rubrofuscum is distributed from 39° N to 35° S. The localities are characterized by a very warm, humid climate (annual mean temperature 13-21(-29) °C, annual precipitation as a rule higher than 1000 mm) and are situated more or less nearby a coastline, thus at a low elevation (near the sea level), and more under the influence of oceanic climate types than continental ones.

The locality in Austria (47° N) does not fit well in this distribution pattern. It is situated in the centre of the European continent, far from the coast, the climate is comparatively cold (7 °C), but nevertheless not typically continental due to the high precipitations at the Northern frontiers of the Alps (1200 mm) and thereby also rather balanced temperature conditions.

For sure, a single deviating record of a rare, insufficiently known species can not be accepted as a valid argument in a general discussion of fungal chorology. However, myco-distributional investigations will have to keep in view probable changes (extent) of species distribution patterns related to global warming. For further comments on this topic (on the occasion of an "atlantic" corticioid fungus occuring in Bavaria), see DÄMON (2002).

Phenology, ecology, and the association of *Sirobasidium* with *Diatrypales* and *Sphaeriales*

In Austria, *S. rubrofuscum* produced basidiomes in spring (May), as it was reported from North America (February to March). OLIVE (1946) found basidiomes not producing epibasidia during the winter months, while at the beginning of March they were "sporulating" abundantly.

Basidiomes have been observed on dead, fallen, decorticated branches of frondose trees and shrubs (see Table 2), namely on *Barnadesia* (*Asteraceae*), *Fraxinus* and *Ligustrum* (both *Oleaceae*). COKER (1928) reports the fungus "emerging from the unbroken bark of a privet shoot".

Actually, the wood pieces from which *S. rubrofuscum* has been collected might not be the true substratum (in regard to the nutrition of the fungus), as "the species is associated with, and possibly parasitic on, pyrenomycetes" (ROBERTS & MEIJER 1997). This association with *Sphaeriales* was demonstrated for the type specimen of *Dacrymyces rubrofuscus* ("... growing from some *Sphaeria*"; BERKELEY 1845), for the type specimen of *S. sanguineum* (with *Eutypella* spec., LAGERHEIM & PATOUILLARD 1892, ROBERTS & MEIJER 1997), and was very obvious also in the Austrian collection (with *Eutypa maura*).

Other species of *Sirobasidium* have proved to be associated with *Diatrypales* and *Sphaeriales* as well (e.g., MAIRE 1945; BANDONI 1979; GILBERTSON & ADASKAVEG 1993; VAN DE PUT 1994; VAN DE PUT & ANTONISSEN 1995; ROBERTS & SPOONER 1998; KRIEGLSTEINER 1999, 2000; BMSFRD 2000). Surprisingly, this fungal association has not been given much attention in the past. Only a few years ago GILBERTSON & ADASKAVEG (1993) stated: "None of the described species of *Sirobasidium* is reported to be associated with fruiting structures of other fungi". Further records will show if *Sirobasidium* species are perhaps specialized on certain host taxa and whether these relationships are of taxonomic relevance.

Survey of *Sirobasidium* species

The genus *Sirobasidium* currently comprises nine species. General works on *Heterobasidiomycetes* (e.g., LOWY 1956, 1971; WOJEWODA 1981, FLORA FUNGORUM SINICORUM 1992) have attempted a key to some of these species. KOBAYASI (1962) tabulates important characters of six species and provides a distribution map for the genus. In the popular key to the *Aphyllophorales* (incl. *Heterobasidiomycetes*) of Europe by JÜLICH (1984) only one species is considered (*S. brefeldianum* MÖLLER). A monographic revision of the genus is not yet available, and most of the species are still known only from one or a few localities. So in order to determine a *Sirobasidium* specimen, it is essential to study the original descriptions.

Sirobasidium albidum LAGERHEIM & PATOUILLARD (1892: 469)

Fructifications 2-4 mm, pustulate, gelatinous, white. Probasidia 15 x 12 µm, divided into 4 cells, arranged in serial chains of up to 8 probasidia, epibasidia 24-26 x 6-10 µm (LAGERHEIM & PATOUILLARD 1892). The species was described from the same type locality as *S. sanguineum* (Ecuador, Pichincha, Pululahua volcano crater, February 1892) and has never been reported for about 100 years.

Only a few years ago, two *Sirobasidium* collections from Europe were assigned to *S. albidum* (VAN DE PUT & ANTONISSEN 1995): Belgium, Antwerp District, Schilde [51° 13' N, 04° 34' E]; December 1993; Antwerp District, Sint-Katelijne-Waver [51° 05' N, 04° 33' E]; December 1994; both collections were made after a frost and a subsequent period with heavy rainfalls on twigs of *Acer pseudoplatanus* L., associated with *Diatrype stigma* (HOFFM.) FR. (*Diatrypales*, *Ascomycota*).

The Belgian specimens match the original description very well, especially in regard to the macroscopic characters and the probasidia. In addition, VAN DE PUT & ANTONISSEN (1995) were able to demonstrate the basidiospores (ballistospores) which are 7-9 x 6-7 µm and germinate by repetition (after preserving a specimen in a moist chamber for some hours).

According to LAGERHEIM & PATOUILLARD (1892), the epibasidia of *S. albidum* are significantly larger than the epibasidia of *S. rubrofuscum* (*S. sanguineum*), while in the Belgian collection the size ranges between 15-23(-25) x 5.5-8(-10) µm (VAN DE PUT & ANTONISSEN 1995) and merges with the data given for *S. rubrofuscum*. Consequently, *S. albidum* differs from *S. rubrofuscum* (S. *sanguineum*) only by the higher number of serial basidia per chain and by the lack of pigmentation of the fructifications. It should be noted that pallid fructifications of *S. rubrofuscum* have been reported (see above). Furthermore, both the type specimens of *S. albidum* and "*S. sanguineum*" are from the same locality, and LAGERHEIM & PATOUILLARD (1892) mentioned only macroscopic characters to distinguish these two species.

Differences between *S. albidum* and *S. brefeldianum* are more obvious and have been scrutinised by VAN DE PUT & ANTONISSEN (1995), as the authors know both species from their own experience (VAN DE PUT 1994): In *S. albidum* (as well as in *S. rubrofuscum*), the microscopic structure within the basidiomata is clearly divided in two sharply delimited layers, viz. the basal layer with rarely septate generative hyphae, and the "upper" layer with the chains of elliptic to globose basidia. In *S. brefeldianum*, the 4-celled generative hyphae are regularly septate, resulting in short segments that gradually become broader towards the top and, near the end of the hyphal thread, form the elongated to fusiform 2-celled basidia.

Following these distinguishing criteria, two collections of "*S. albidum*" reported from India by KUNDALKAR & PATIL (1986) appear to be *S. brefeldianum*. In the article, the records are documented only by a drawing, which clearly shows elongated, 2-celled probasidia. Furthermore, the specimens examined by KUNDALKAR & PATIL (1986) were collected at the same site and even on the same date as specimens of *S. brefeldianum*.

***Sirobasidium brefeldianum* MÖLLER (1895: 165), and *S. brefeldianum* f. *microsporum* MAIRE (1945: 38)**

Fructifications of *S. brefeldianum* MÖLLER (1895) up to 3 mm, hyaline, whitish. Probasidia arranged in serial chains of up to 12 and more, divided into two cells, epibasidia 22-24 x 7-8 µm, germination yeast-like. Type locality: Brazil, Santa Catarina state, Blumenau [26° 55' S, 49° 07' W], on the bark of branches lying on the ground; March 1892 ("and re-collected many times"). The excellent drawings by MÖLLER (1895) are reproduced in Figure 4. An additional specimen from Brazil is documented in LLOYD (1922).

The species was also reported from North America (USA, COKER 1920), Asia (Ceylon, T. PETCH, cited in BOEDIJN 1934; India, KUNDALKAR & PATIL 1986; Brunei, ROBERTS & SPOONER 1998), Africa (Canary Islands, P. ROBERTS, in litt.), and Europe (France, MAIRE 1945; Belgium, VAN DE PUT 1994; Germany, KRIEGLSTEINER 1999, 2000; England, BMSFRD 2000).

Both the specimens from North America and from France are characterized by minute, hyaline, inconspicuous fructifications and small epibasidia, viz. 13-14 x 7.5-8 µm (COKER 1920) and 13-16 x 6.5-8 µm (MAIRE 1945). Based on the deviant size of the epibasidia, the French collection was named *S. brefeldianum* f. *microsporum* (MAIRE 1945). Later, DONK (1966) even supposed that it may be distinguished from the type of *S. brefeldianum* on species level, while P. ROBERTS (in litt.) does not consider "f. *microsporum*" as a distinct taxon. VAN DE PUT (1994) believes that the description is based on immature basidiomata.

Anyway, this collection from France was the first, and, for a long time, the only record of a *Sirobasidium* species in Europe. MAIRE (1945) himself concluded that the species evidently must be very rare, otherwise its characteristic serial basidia would have attracted the attention of European mycologists before: "Le *S. Brefeldianum* ... doit être rare en Europe, car une espèce si caractérisée ne serait pas restée inaperçue des mycologues si elle était fréquente". The detailed information on the site and ecology are: France, [Lorraine], Lunéville [48° 36' N, 06° 33' E]; erupting from the epidermal tissue of a fallen branch of *Laburnum vulgare* GRISEB., associated with a *Sphaeriales* or *Diatrypales*, probably "*Diatrype* [*Diaporthe*] *medusaea* NITSCHKE" (MAIRE 1945).

In Devon and Cornwall, U. K., several specimens of *S. brefeldianum* have been recorded between 1994 and 2000 (BMSFRD 2000; P. ROBERTS, in litt.). The species was collected on branches of *Acer* and *Ulmus*, almost always associated with *Euty-*

pella leprosa (PERS.: FR.) BERL., resp. with *Diatrype* spec. (both *Diatrypales*, *Ascomycota*).

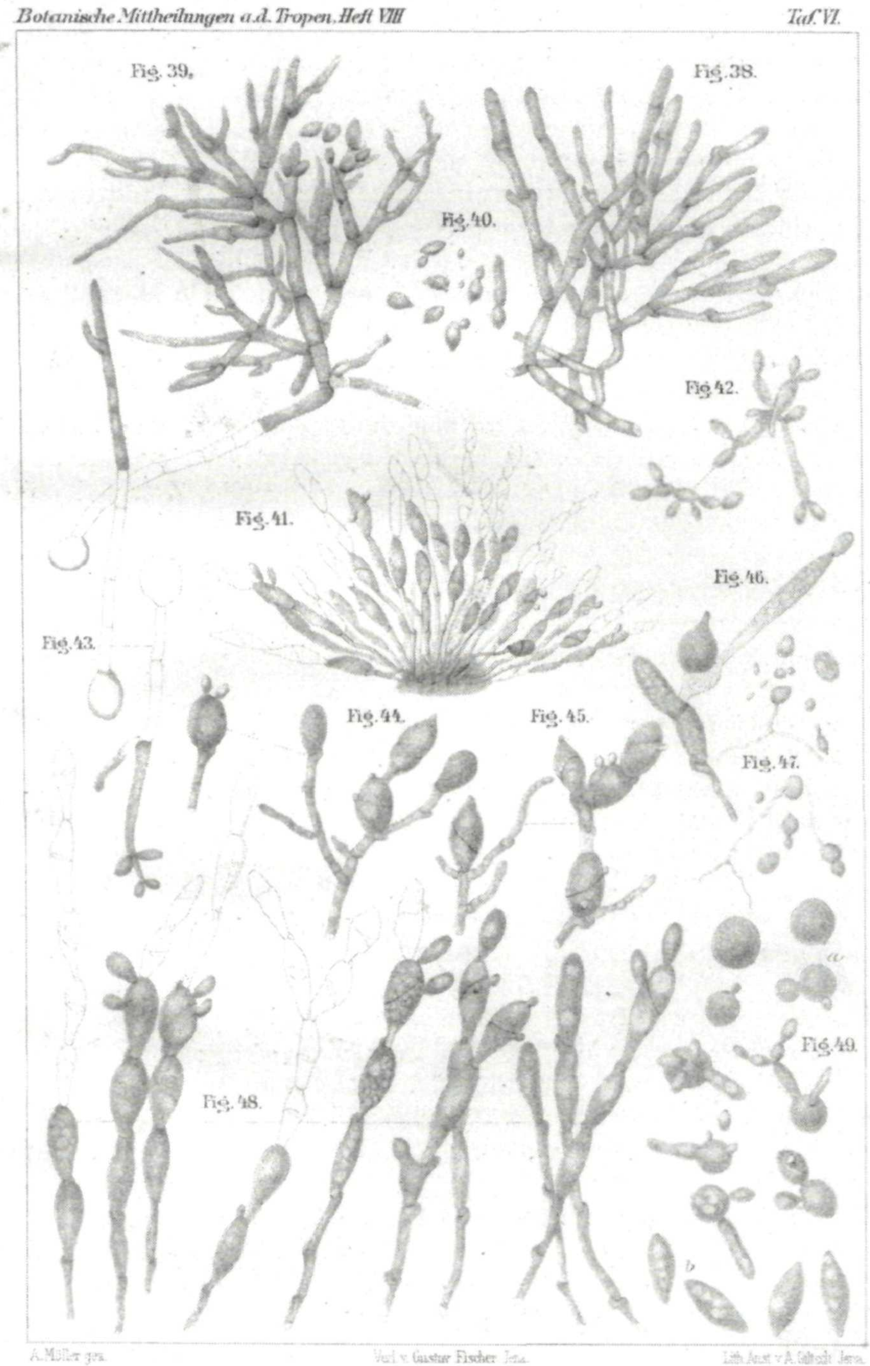
In the winter 1990-1991, *S. brefeldianum* f. *microsporum* occurred in Belgium, Antwerp District, Zoersel, on three places within the "Zoerselbos" area [51° 15' N, 04° 45' E], on roots of fallen (wind-blown) *Picea abies* (L.) KARST. (VAN DE PUT 1994). The pustulate, hyaline fructifications were growing in small depressions caused by pyrenomycete species and previously filled by their stromata. Though the specimens were fully developed, the pustules did not exceed 1-4 mm in diameter and 2 mm in height.

The probasidia in the Belgium collections are described as typically elongated (19-50 x 10-12 µm), almost all of them divided into two cells (exceptionally three cells) by predominantly (80-90%) horizontal, otherwise (10-20%) slightly oblique septa. VAN DE PUT (1994) considers these characters which fully correspond with the drawings of the probasidia in MAIRE (1945) as the most striking features of "the European forma of *S. brefeldianum*". Clamp connections are very distinct in all parts of the basidiomata and in all stages (even in the unstructured layer consisting of old, collapsed basidia). The detached epibasidia, somewhat larger than in MAIRE (1945), were germinating by conidia or germ-tubes after being cultured in a moist chamber for ten hours.

For the first time, VAN DE PUT (1994) demonstrated the basidiospores (ballistospores) of *S. brefeldianum*, which are 7.5-10.0(-11.0) x 6.0-8.5(-9.0) µm, typically "depressed" (broader than long) and repetitive. However, the author succeeded in observing basidiospores only in one specimen, collected at the end of February and preserved in a moist chamber for twelve hours.

Another collection of a *Sirobasidium* was recorded recently in Germany: Baden-Württemberg, Schwarzwald, Baiersbronn [48° 31' N, 08° 22' W]; on a dead, rain-soaked branch of *Acer platanoides* L. lying on the ground, May 1997 (KRIEGLSTEINER 1999, 2000; description and drawings by H. MASER). The collection was determined according to JÜLICH (1984) who keys out only *S. brefeldianum* (H. GROSSE-BRAUCKMANN, in litt.). Indeed, the fructifications completely lacked red colours, and H. MASER observed chains with mostly 4-8 serial probasidia, the longest chain with 13 probasidia (U. SAUTER, in litt.), which supports the determination as *S. brefeldianum*.

Fig. 4. *Sirobasidium brefeldianum*. Drawings by MÖLLER (1895). All figures 500 : 1 (but 220 : 1 in fig. 41). Legend translated literally from German: "Plate VI: All figures from *Sirobasidium Brefeldianum* nov. spec. Fig. 38. Part of the hyphal branchings and hyphal ends of a very young primordium of the fungus. Fig. 39. A germinated spore of the fungus, from which a mycelium developed that at some of its tips forms conidia. Fig. 40. Yeast budding, as an exception hyphal germination of the resulting conidia. Fig. 41. Part of the hyphae bearing the basidia chains in the mature stage of the fungus. Fig. 42. Exceptionally high number of contiguous yeast conidia. Fig. 43. Germination of two basidiospores. Fig. 44. Basidia development. One of the basidia exceptionally with a longitudinal septum. Fig. 45. Singular and partly irrregular basidia development. Fig. 46. Irregularities in basidia development. Fig. 47. After many budding germinations, yeasts germinate with fine capillary hypha. Fig. 48. The regular basidia development in different stages and forms of appearance. Fig. 49. a) Shadded globose spores. b) Detached ovoid spores. In between variations of spore germination."


Botanische Mittheilungen a.d. Tropen. Heft VIII
Taf. VI.
Fig. 39.
Fig. 38.
Fig. 40.
Fig. 42.
Fig. 41.
Fig. 46.
Fig. 43.
Fig. 44.
Fig. 45.
Fig. 47.
a
Fig. 49.
Fig. 48.
b
A. Möller gez.
Verl. v. Gustav Fischer, Jena.
Lith. Anst. v. A. Giltsch, Jena.

On the other hand, the probasidia in the German collection are subglobose when mature and finally divided into four cells, which is typical for, e.g., *S. albidum* or *S. rubrofuscum*. The size of the epibasidia is 13-16-24 x 6.5-8 µm (KRIEGLSTEINER 1999, but data evidently obtained from the literature), respectively 15-20(-23) x 6-7.5 µm (measurements by H. MASER; U. SAUTER, in litt.). The fructifications were growing on *Acer* (as in the Belgian collections of *S. albidum*) and were associated with *Eutypa maura* (as in the Austrian collection of *S. rubrofuscum*).

Sirobasidium intermediae **KUNDALKAR & PATIL (1986: 357)**
Fructifications minute, 1-4 mm, coalescent, white to pale yellow. Probasidia arranged in serial chains of 1-2(-4), but also in clusters; divided into 2(-4) cells by oblique to transverse septa. Epibasidia 15-32 x 3.2-4.6 µm. Basidiospores (ballistospores) 6.4-9.6 µm. Type locality: India, Kolhapur, August 1979, re-collected in August 1981 (KUNDALKAR & PATIL 1986).

The species was originally characterized by the occurrence of basidia partly arranged in clusters as a result of sparse ramifications within the hymenium and named with regard to its intermediate position within the genera *Sirobasidium* and *Fibulobasidium* (see below). However, irregularities of basidial development have been observed in *S. brefeldianum* (MÖLLER 1895, VAN DE PUT 1994). What KUNDALKAR & PATIL (1986) considered to be the typical character of their new species *S. intermediae* (as shown in the drawings), is nearly identical to irregular basidial structures which MÖLLER (1895) documented in "Fig. 45" of his excellent early drawings (see Fig. 4). Moreover, the specimens of "*S. intermediae*" were collected at the same location in India (and one of them even on the same day) as specimens of *S. brefeldianum* (KUNDALKAR & PATIL 1986).

The type collection of *S. intermediae* is not available for examination, but the species appears to be synonymous with *S. brefeldianum* (P. ROBERTS, in litt.).

A European record of *S. intermediae* was reported from U. K., Devon, on twig of *Ulmus*, associated with *Eutypella leprosa*, 1997 (NCYC 2000). INGOLD (1995, 1998) used *S. intermediae* in his investigations on the reproduction structures in *Sirobasidium*.

Sirobasidium japonicum **KOBAYASI (1962: 1)**
Fructifications effused, surface tuberculate, pale yellow to salmon colour. Probasidia arranged in serial chains of 2-4, divided into 2-4 cells by predominantly horizontal (transversal) septa, epibasidia 10-15 x 3.5-5 µm, germination yeast-like. Type locality: Japan, Yaku Island, October 1961, underside of a fallen tree, on the bark (KOBAYASI 1962, including photographs and many drawings). Out of all *Sirobasidium* species, *S. japonicum* is closest to the *Auriculariales* due to the transversally septate basidia.

Sirobasidium magnum **BOEDIJN (1934: 267)**
Fructifications large, 40-70 x 20-45 mm, 10-25 mm high, foliaceous, *Tremella*-like, brown to orange, tawny to ochraceous tawny. Probasidia arranged in serial chains of up to 8, divided into two cells by oblique septa, epibasidia 15-19 x 4-5 µm. Type locality: Borneo, Eastern part, West Koetai, on dead wood, November 1925; Java, Res. Bantam, Pasir Waringin, on dead wood, December 1922; Java, Res. Batavia, Buitenzorg, on bark and wood, February and April 1924 (BOEDIJN 1934). However, the

author's strange observation of basidia that "originate within the hyphae" and consequently are surrounded by the hyphal wall of the mother cell (reminiscent of asci), was objected to by BANDONI (1957) and explained as an artificial appearance of thick and seemingly laminated basidia walls.

Sirobasidium magnum serves as a popular research organism in morphology, physiology, cell biology, biochemistry, and genetics to study the principles of reproduction, mating and compatibility patterns, conjugation processes, growth and yeast stages, and also molecular structures in the *Basidiomycota* (e.g., FLEGEL 1976, 1981; WELLS 1994, with excellent drawings of the microstructures; CHEN 1998). For laboratory purposes, cell and yeast cultures are available (e.g., NCYC 2001, DSMZ 2002). Cultures have been derived, for instance, from collections from Japan, November 1968 (FLEGEL 1976), the Philippines, February 1969 (FLEGEL 1976), and Louisiana, USA, 1993 (NCYC 2001).

Sirobasidium minutum **KISIMOVA-HOROVITZ, OBERWINKLER & GÓMEZ (2000: 540)**
Fructifications pustulate, white-greyish, 0.5-1.5 mm. Probasidia divided into two cells, differentiated intercalary, epibasidia 15-20 x 5-6 µm, basidiospores 5-5.4 µm. Type locality: Costa Rica, Puntarenas, Coto Brus, Las Alturas [08° 57' N, 82° 50' W]; on a small branch on the ground (KISIMOVA-HOROVITZ & al. 2000).

The species is characterized by its small size and the probasidia developed intercalary (within the generative hyphal segments), as partly also seen in *S. magnum* (BOEDIJN 1934).

Sirobasidium sandwicense **GILBERTSON & ADASKAVEG (1993: 390)**
Fructifications 1-2 mm, whitish. Probasidia arranged in serial chains of two (to four), divided into two cells by oblique septa (a few with 3-4 cells), epibasidia 20-30 x 5-6 µm, hyphae with obvious clamp connections at all septa, basidiospores 6-9 µm („near *S. sanguineum*"). Type locality: Hawaii, Hilo, June 1990; on fallen branches of *Trema orientalis* (L.) BLUME (*Ulmaceae*); on perithecial stromata of *Diatrypella favacea* (FR.) SACC. (GILBERTSON & ADASKAVEG 1993).

In the drawings by GILBERTSON & ADASKAVEG (1993) the most eye-catching structure are the collapsed probasidia that appear cerebriform or like intestines. By mistake, in the original description, as well as in the English one, the size values of basidia and epibasidia are identical. The epithet is chosen after the old name for Hawaii (Sandwich islands).

The species was originally distinguished by growing on or with pyrenomycetes, and appears to be synonymous with *S. brefeldianum* (P. ROBERTS, in litt.).

Synonyms and excluded species
Sirobasidium indicum is a synonym of *S. rubrofuscum*. While *S. indicum* originally was characterized by 2-celled probasidia, re-examination of the isotype by P. ROBERTS (in litt.) confirmed the presence of 3-4-celled probasidia.

"*Sirobasidium cerasi* BOURD. & GALZIN" is *Coryne albida* (BERK.) KORF & CAND., the anamorph of *Ascocoryne solitaria* (REHM) DENNIS (GAIGNON 1993). The species was already excluded from *Sirobasidium* by BOEDIJN (1934).

"*Sirobasidium brunneum* LLOYD" is an ambiguous species and should also be excluded from the genus (KOBAYASI 1962).

The genus *Fibulobasidium*

The genus *Fibulobasidium* BANDONI (1979) is closely related to *Sirobasidium*, and has therefore been placed in the *Sirobasidiaceae*. In this genus, the basidia develop through expansion of clamp loops and are typically grouped in clusters as a result of repeated clamp formations (the basal clamp connection of the first basidium swells to become the second, and so on).

Fibulobasidium inconspicuum BANDONI (1979), the type species, was found in New Orleans (Louisiana, USA), where it was collected from March to May 1974 many times on windblown branches of *Quercus virginiana* MILL. The fructifications developed subcortically (under the bark) and were associated with unidentified stromata.

Fibulobasidium sirobasidioides BANDONI (1998) is characterized by superficially *Sirobasidium*-like chains of basidia. The type specimen was found in British Columbia (Canada) under the bark of recently dead branches and trunks of *Acer macrophyllum* PURSH.

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Colour fig. I. *Sirobasidium rubrofuscum* (WU 12771). – Phot. A. HAUSKNECHT.

Fig. en couleur II. *Entoloma brunneoserrulatum* (holotype). – Phot. A. EYSSARTIER