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Chemosystematics of *Suillaceae* and *Gomphidiaceae* (suborder *Suillineae*)*

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Abstract: The chemotaxonomic findings relating to the genera *Boletinus*, *Suillus*, *Gastroboletus*, *Gomphidius*, and *Chroogomphus* are summarized and discussed, using published data as well as our own hitherto unpublished evidence of pigments and chromogens. The study confirms repeatedly made claims that these genera are closely related. In addition to the presence of pigments which are typical for most members of the *Boletales* (e.g., pulvinic acid derivatives, terphenyl quinones, cyclopentenones), prenylated phenols and quinones can also be constantly detected here (with the exception of *Boletinus*), just as in *Rhizopogon*. Accordingly, *Suillus* is more closely related to the *Gomphidiaceae* and *Rhizopogonaceae* than to the remaining boletes. It is therefore necessary to establish a new family (*Suillaceae* which include *Boletinus*, *Suillus*, and *Gastrosuillus*) and a new suborder (*Suillineae* which include *Suillaceae*, *Gomphidiaceae*, and *Rhizopogonaceae*) within the *Boletales*.

The investigation of pigments within *Boletales* s. l. supports hitherto accepted interrelationships which have been established on the basis of none-chemical features. On the other hand, some more or less unexpected records of chemical constituents make a new evaluation of possible interrelationships necessary. The evidence for a new suborder and family within the *Boletales* (*Suillineae*, *Suillaceae*) will be discussed in the present paper.

A wide range of characteristics suggests that the *Gomphidiaceae* and the genus *Suillus* are closely related. ARPIN & KÜHNER (1977) therefore grouped the genus *Gomphidius* (including *Chroogomphus*) together with *Suillus* within the *Boletaceae*. HØILAND (1987) provides another alternative in which the genus *Suillus* is incorporated into the *Gomphidiaceae*, a hypothesis which is widely accepted in Scandinavia (e.g., KORHONEN & al. 1993). However, in most of the systematic

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* Chemosystematics of *Boletales* **2**. For part 1 see BESL & al. (1986). Dedicated to emer. Univ.-Prof. Dr FRIEDRICH EHRENDORFER on the occasion of his 70th birthday

overviews, *Suillus* is considered to be linked to the *Boletaceae*, not to the *Gomphidiaceae*. According to SINGER (1986), this genus, together with several others, forms the subfamily *Suilloideae*. Yet, the incorporation (PEGLER & YOUNG 1981) into the *Strobilomycetaceae*, a family with variable circumscription, is difficult to understand.

An extensive compilation of the chemical and biosynthetic aspects of macromycete pigments by GILL & STEGLICH (1987) as well as the results from our hitherto unpublished research incited us to analyse and evaluate the chemosystematic data concerning the previously mentioned taxa within the *Boletales*.

Important compounds for systematics of *Boletales*

The chemosystematically relevant components from *Suillus* and the *Gomphidiaceae* and their relatives are briefly characterized as follows. Structural formulae and further references can be found in the review of GILL & STEGLICH (1987).

1. Terphenyl quinones. These compounds are derived from the amino acid tyrosine and are produced through a double condensation of two activated esters of the corresponding phenylpyruvic acid. In particular, the atromentin holds a key position for the biosynthesis of additional colouring substances like hydroxypulvinic acids and cyclopentenones. Simple oxidation products under the preservation of the central quinone ring include cyclovariegatin and thelephoric acid. All of the terphenyl quinones in the above mentioned fungi only appear sporadically and represent phylogenetic relicts. This explains the basal position of these pigments in the biosynthetic pathway.

2. Cyclopentenones. Cyclopentenones are formed by ring contractions of terphenyl quinones and appear almost as frequently as terphenyl quinones. The substances found here include chamonixin, involutin, and the more highly oxidized gyroporin. They occur in *Paxillaceae* and *Omphalotaceae*, as well as in the genera *Leucogyrophana*, *Gyrodon*, *Gyroporus*, *Leccinum*, *Albatrellus*, *Chamonixia*, and *Melanogaster*, i.e. taxa beyond the scope of the present paper. Thus, cyclopentenones can be detected in fungi at every organizational level (from corticioid to gastroid) within the *Boletales*.

3. Pulvinic acid derivatives. Hydroxypulvinic acids are formed through lactone formation, after the quinone ring of atromentin has been oxidized and opened. Xerocomic and variegatic acid play the most important role in *Boletales*. They can be detected in *Coniophoraceae*, which are the presumably most primitive representatives of the *Boletales*. For this reason, these compounds represent a kind of indicator pigments for this order. In contrast, the *Thelephorales*, which are probably related to the *Boletales* through a common ancestor (AGERER 1991, BESL & al. 1986), remain at the level of terphenyl quinone accumulation. Special developments among pulvinic acid derivatives include: gomphidic acid (which replaces isomeric variegatic acid in *Gomphidius*), methyl bovinate (in *Suillus bovinus*), and methyl variegatate (in cultures of *Suillus collinitus*). The presence of badiones in *Suillus* and related genera has not yet been confirmed.

4. Grevillins. During the biosynthesis of atromentin (see above) a benzoquinone ring is produced by forming two C-C bonds. If, however, only one C-C bond is formed, then the resulting lactonization yields grevillins. This kind of pigment virtually appears only in the genus *Suillus*. The necessary rearrangement which is needed for the transition from grevillin B to grevillin D suggests the existence of a higher evolutionary level.

5. 1.2.4-Trihydroxybenzene. This colourless, but easily oxidized substance is responsible for the red and black discolouration in species from the genus *Gomphidius*. The oxidation products are the red gomphilactone and the corresponding biphenyls (JÄGERS & al. 1981).

6. Prenylated phenols. Derivatives of the above mentioned trihydroxybenzene commonly appear in *Suillus* and *Gomphidiaceae*. The aromatic ring found in these compounds bears an additional farnesyl or geranylgeranyl side chain. These kinds of structures are otherwise unknown in *Boletales*. Certain colourless phenols are stabilized by O-acetylation of the readily oxidizable hydroquinone system. Suillin and bolegrevilol serve as examples for this. Moreover, several additional prenylated phenols were isolated. Oxidation products of these chromogens produce gray to brown shadows in the upper half of the thin-layer chromatogram. Together with the occasional presence of benzoquinones (see below), they are characterized as the so-called "lipophilic pigments". Oxidation products from suillin are also responsible for the caps' brown colour (JÄGERS & al. 1986).

7. Prenylated benzoquinones. Benzoquinones corresponding to the mentioned phenols most commonly appear as boviquinones. Dimeric compounds, such as diboviquinone, are present as well. Tridentoquinone and rhizopogone are quite interesting and special in that the outer end of the geranylgeranyl side chain becomes attached to the quinone system to form an intramolecular ring closure. This kind of macrocyclic ansa-compound is unique in nature.

8. Cavipetins. These five anti-fungal diterpenesters were isolated from *Boletinus cavipes* (TOYOTA & HOSTETTMANN 1990). They are esters of 16-hydroxy-geranylgeraniol and mesaconic or fumaric acid. Some further derivatives of farnesol and geranylgeraniol have been found more recently in chemotypes of the same species (WADA & al. 1995).

9. Carotenoids. CZECZUGA (1977) claimed to have detected carotenoids in certain species of *Suillus*. Since then, no one has been able to verify this claim. Thus, their existence in this genus is rather unlikely.

Material and methods

Origin of fruit-bodies. *Boletinus asiaticus*: 5.9.83, Mt Fuji, Japan, leg. A. BRESINSKY, det. H. BESL. – *Boletinus cavipes*: 20.9.88, Matting, Oberpfalz, Germany, leg. et det. H. BESL. – *Chroogomphus rutilus*: 9.9.86, Siegenburg, Niederbayern, Germany, leg. et det. H. BESL. – *Gastroboletus subalpinus*: 15.9.83, Yuba Pass, California, USA, leg. et det. H. THIERS et A. BRESINSKY. – *G. valdivianus*: 26.3.88, near Contulmo, Chile, leg. et det. A. BRESINSKY et N. GARRIDO. – *Gastrosuillus laricinus*: 25.9.75, Olcott, New York, USA, leg. A. CLIPPINGER, det. R. SINGER et E. E. BOTH. – *Gomphidius glutinosus*: 7. 9. 94, Ellbachtal, Oberpfalz, Germany, leg. et det. H. BESL. – *G. maculatus*: 28.8.94, Girnitztal, Oberpfalz, Germany, leg. et det. A. REISINGER. – *G. roseus*: 5.10.94, Offenstetten, Niederbayern, Germany, leg. et det. H. BESL. – *Suillus acidus*: 3.9.86, Cliffside Lake, North Carolina, USA, leg. et det. A. BRESINSKY et B. MEIXNER. – *S. americanus*: 18.7.81, Blacksburg, Virginia, USA, leg. et det. W. E. HORNER. – *S. bellinii*: 24.1.96, La Esperanza, Tenerife, Spain, leg. et det.

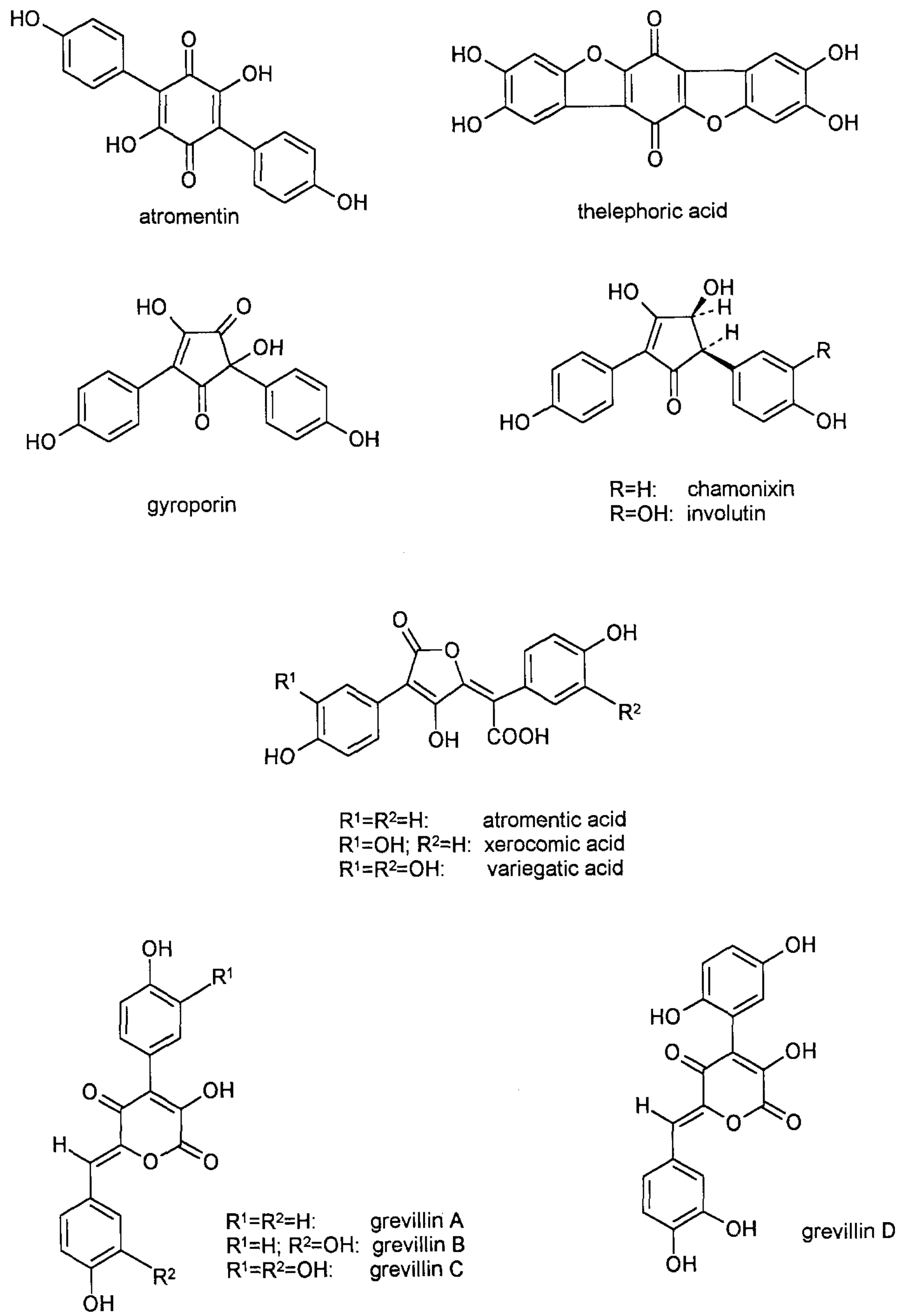

Fig. 1. Important compounds from *Suillus* and *Gomphidiaceae*, biogenetically linked to the terphenylquinone atromentin

M. BEISENHERZ. – *S. bovinus*: 20.9.80, Etterzhausen, Oberpfalz, Germany, leg. et det. H. BESL. – *S. borealis*: 16.9.77, Lake Itasca, Minnesota, USA, leg. et det. A. BRESINSKY (M). – *S.* cf. *bresadolae*: 1.8.81, Bergmatting, Oberpfalz, Germany, leg. et det. H. BESL. – *S. brevipes*: 14.8.88, border between Placer Co. and Nevada Co., California, USA, leg. et det. A. BRESINSKY et M. FISCHER. – *S. clintonianus*: 16.9.77, Lake Itasca, Minnesota, USA, leg.

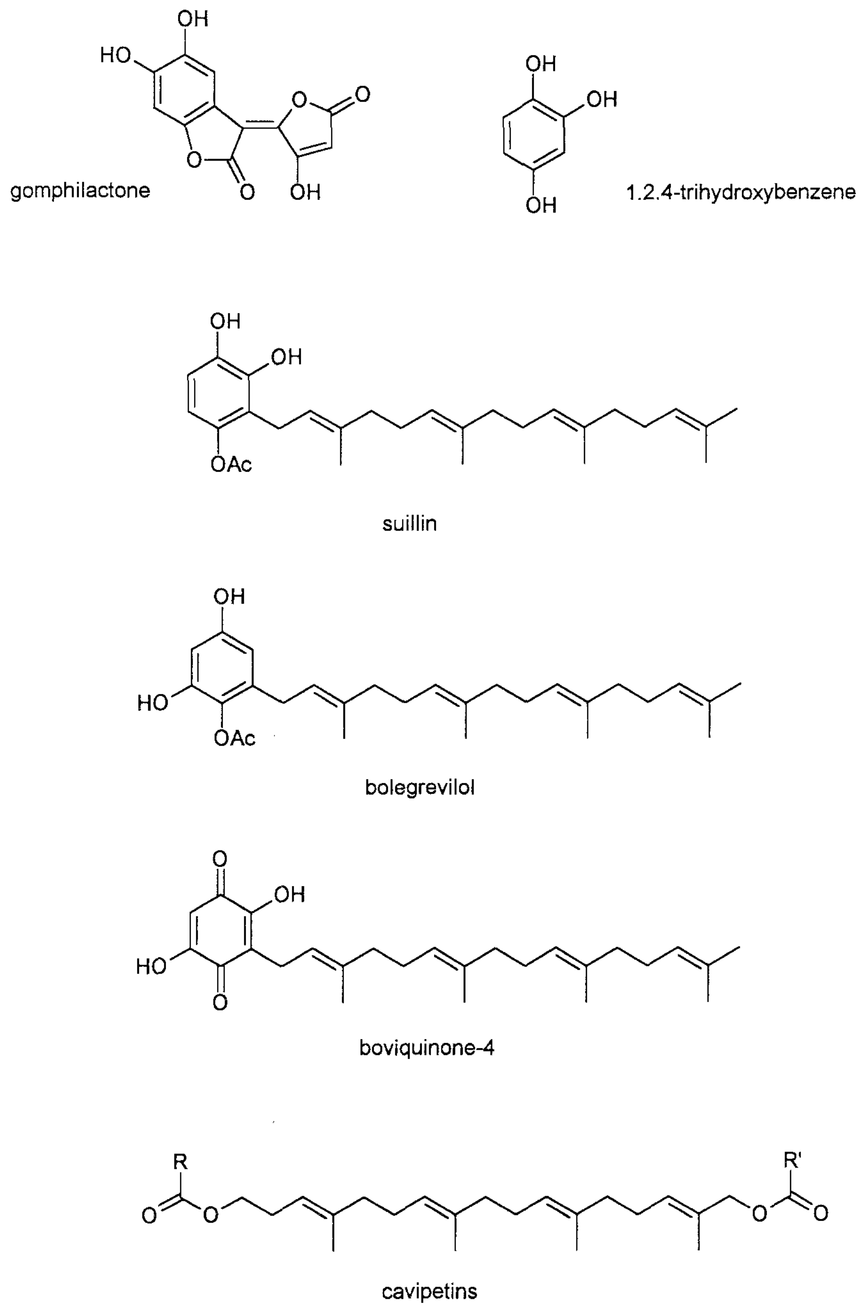

Fig. 2. Compounds from *Suillus* and *Gomphidiaceae*, related to benzoquinones or cavipetins

et det. A. Bresinsky. – *S. collinitus*: 12.9.88, Botanical Garden, Regensburg, Germany, leg. et det. H. Besl. – *S. cothurnatus*: 29.8.86, Great Smoky Mts Natl. Park, Tennessee, USA, leg. et det. A. Bresinsky. – *S. flavidus*: 1.10.89, Neubäu, Oberpfalz, Germany, leg. et det. A. Bresinsky. – *S. glandulosus*: Sept. 88, Univ. Forest, Oreno, Maine, USA, leg. et det. A. Bresinsky. – *S. granulatus*: 20.9.76, Etterzhausen, Oberpfalz, Germany, leg. et det. H. Besl. – *S. grevillei*: 2.8.84, Bruckdorf, Oberpfalz, Germany, leg. et det. N. Luschka. – *S. hirtellus* subsp. *hirtellus*: 19.9.83, Great Smoky Mts Natl. Park, Tennessee, USA, leg. et det. A. BRESINSKY. – *S. luteus*: 22.10.80, Botanical Garden, Regensburg, Germany, leg. H. VARNECKE, det. H. BESL. – *S. neoalbidipes*: 23.9.77, Cascades, Oregon, USA, leg. et det. A. BRESINSKY (as *S. albidipes*). – *S. placidus*: 5.10.80, Parksteinhütten, Oberpfalz, Germany, leg. et det. H. BERGMANN. – *S. plorans*: 15.8.91, Schachen, below Alpengarten, Oberbayern, Germany, leg. et det. A. BRESINSKY. – *S. pseudobrevipes*: 6.3.91, Auburn, California, USA, leg. M. FISCHER, det. T. D. BRUNS. – *S. punctipes*: 21.9.83, Highlands, North Carolina, USA, leg. et det. A. BRESINSKY. – *S. pungens*: 15.3.91, Pt. Reyes, California, USA, leg. M. FISCHER, det. T. D. BRUNS. – *S. riparius*: Sept. 1977, Cascade Range near Corvallis, Oregon, USA, leg. et det. A. BRESINSKY (M). – *S. serotinus*: 16.9.77, Lake Itasca, Minnesota, USA, leg. et det. A. BRESINSKY (M). – *S. sibiricus*: 22.8.87, Davos, Switzerland, leg. et det. A. BRESINSKY. – *S. spectabilis*: 5.9.83, Shojin-guchi, Mt Fuji, Yamanashi, Japan, leg. A. BRESINSKY, det. H. BESL. – *S. spraguei*: 19.9.83, Knoxville, Tennessee, USA, leg. et det. A. BRESINSKY. – *S. tomentosus*: 15.9.83, Yuba Pass, California, leg. et det. H. THIERS et A. BRESINSKY. – *S. umbonatus*: 15.9.83, Yuba Pass, California, leg. et det. H. THIERS et A. BRESINSKY. – *S. variegatus*: 17.9.88, Regenstauf, Oberpfalz, Germany, leg. et det. A. BRESINSKY. – *S. viscidus*: 1.8.81, Bergmatting, Oberpfalz, Germany, leg. et det. H. BESL.

Voucher specimens are deposited in the herbarium of the University of Regensburg (REG), unless otherwise stated.

Origin of mycelial cultures. *Suillus acerbus*: CBS 211.76. – *S. acidus*: CBS 209.76. – *S. americanus*: TDB 577 – *S. bellinii*: no. 862, 26.1.96, La Esperanza, Tenerife, Spain, M. BEISENHERZ. – *S. brevipes*: CBS 107.57. – *S. caerulescens*: CBS 208.76. – *S. collinitus*: no. 724, 12.9.88, Regensburg, Botanical Garden, H. BESL. – *S. cothurnatus*: no. 590, 29.8.86, Cades Cove, Great Smoky Mountains Natl. Park, USA, A. BRESINSKY. – *S. neoalbidipes*: J. M. TRAPPE no. 6361 (as *S. albidipes*). – *S. ochraceoroseus*: CBS 233.67. – *S. pictus*: CBS 214.76. – *S. pungens*: CBS 237.76. – *S. subluteus*: CBS 212.76. – *S. tomentosus*: no. 629, J. M. TRAPPE no. 7644, Oregon, USA.

Methods for cultivation of mycelia, extraction, and use of thin-layer chromatography are described in BESL & al. (1989). The fruit-bodies (fresh, freeze-dried or from herbaria) were extracted using acetone which was slightly acidified with hydrochloric acid. The crude extract was treated in the same manner as the mycelial extract.

Bolegrevilol was isolated from fruit-bodies of *Gomphidius glutinosus* by extraction with slightly acidified acetone and subsequently repeated column chromatography on acetylated polyamide using acetone and petroleum ether respectively. Bolegrevilol was identified by means of spectroscopy.

Results and discussion

In addition to recording and evaluating previously published data, we were able to examine a considerable number of fungi (fruit-bodies and/or mycelial cultures) either for the first time or in greater detail. These results are labelled "new" in the following surveys. The chemotaxonomic data regarding individual genera and species are summarized in the chronological order of their publication and briefly discussed. The nomenclature largely conforms to BOTH (1993) and KREISEL (1987).

The genus *Suillus* S. F. GRAY (including *Fuscoboletinus* POMERLEAU & A. H. SM.)

Metabolites from fruit-bodies. *Suillus acidus* (PECK) SINGER: BRESINSKY & BESL (1979): grevillin D; new: "lipophilic pigments".

Suillus amabilis (PECK) SINGER [= *S. lakei* (MURRILL) A. H. SM. & THIERS]: BRESINSKY & BESL (1979): grevillins B and C, variegatic acid.

Suillus americanus (PECK) SNELL in SLIPP & SNELL: BRESINSKY & BESL (1979): grevillins B, C and D; JÄGERS (1981): diboviquinone-4,4; JÄGERS & al. (1986): suillin; STEGLICH, STEFFAN & HOVENBITZER (in GILL & STEGLICH 1987: 6): grevillin D, anhydrogrevillin D; new: additional grevillin A, "lipophilic pigments".

Suillus bellinii (INZENGA) WATLING: new: grevillins B, C, and D, suillin, "lipophilic pigments".

Suillus borealis A. H. SM., THIERS & O. K. MILLER: BRESINSKY & BESL (1979): no identified pigments; new: "lipophilic pigments".

Suillus bovinus (L.) KUNTZE [= *Mariaella bovina* (L.) ŠUTARA]: GABRIEL (1965): "boletol" (= variegatic acid); MINAMI & al. (1968): methylenediboviquinone-4,4 (amitenone); BEAUMONT & EDWARDS (1969): atromentin, variegatic acid, boviquinone-4 (bovinone); BRESINSKY & ORENDI (1970): variegatic acid; SCHMITT (1970): variegatic acid; BEAUMONT & EDWARDS (1971): additional diboviquinone-4,4; JÄGERS (1981): bovilactone-4,4; SCHMIDT (1990): atromentin, atromentic acid, xerocomic acid, variegatic acid, variegatorubin, methyl bovinate, boviquinone-4; new: "lipophilic pigments"; grevillins absent.

Suillus bresadolae (QUÉL.) GERHOLD: BRESINSKY (1974): pigment type E (grevillins B and C); BESL & al. (1975a): additional grevillin A; new (*S.* cf. *bresadolae*): additional variegatic acid, "lipophilic pigments".

Suillus brevipes (PECK) KUNTZE: BRESINSKY & BESL (1979): grevillins B and D; new: "lipophilic pigments".

Suillus caerulescens A. H. SM. & THIERS: BRESINSKY & BESL (1979): no identified pigments.

Suillus clintonianus (PECK) KUNTZE [= *Suillus grevillei* var. *badius* (SINGER) WATLING]: EDWARDS & GILL (1973): grevillin B, cyclovariegatin, thelephoric acid, "pulvinone", pigment A [probably artefact from grevillin B (GILL & STEGLICH 1987: 12)]; EDWARDS & GILL (1975): cyclovariegatin, thelephoric acid from cap skins; new: grevillins B and C, "lipophilic pigments".

Suillus collinitus (FR.) KUNTZE [= *Suillus fluryi* HUIJSMAN]: SCHMITT (1970): xerocomic acid; BRESINSKY (1974): pigment type E (grevillins); BESL & al. (1975a): grevillin D; JÄGERS (1981): bovilactone; JÄGERS & al. (1986): suillin; SCHMIDT (1990): xerocomic acid, variegatic acid; the grevillins probably destroyed by prolonged storage!; new: additional grevillins B and C, "lipophilic pigments".

Suillus cothurnatus SINGER: BRESINSKY & BESL (1979): no identified pigments; new: "lipophilic pigments".

Suillus flavidus (FR.: FR.) PRESL: GABRIEL (1965): "boletol" and "pseudoboletol" absent; BRESINSKY (1974): pigment type E (grevillins); BESL & al. (1975a): grevillin D; new: "lipophilic pigments".

Suillus glandulosus (PECK) SINGER [= *Fuscoboletinus glandulosus* (PECK) POMERLEAU & A. H. SM.]: new: "lipophilic pigments".

Suillus granulatus (L.) KUNTZE: GABRIEL (1965): "boletol" and "pseudoboletol" absent; SCHMITT (1970): variegatic acid (perhaps misidentified grevillin D); BRESINSKY (1974): pigment type E (grevillins); BESL & al. (1974): grevillins B and D, anhydrogrevillin D; BESL & BRESINSKY (1977): additional grevillin C; BRESINSKY & BESL (1979): grevillins B, C and D (in fruit-bodies of North American origin); JÄGERS & al. (1986): suillin; GARRIDO (1988): grevillins B, C and D (in fruit-bodies of South American origin); TRINGALI & al. (1989a,b): suillin and other prenylated phenols; new: "lipophilic pigments", bolegrevilol (trace).

Suillus grevillei (KLOTZSCH: FR.) SINGER: GABRIEL (1965): "boletol" and "pseudoboletol" absent; SCHMITT (1970): xerocomic acid (probably confusion); STEGLICH & al.

(1972): grevillins A, B and C; EDWARDS & GILL (1973): cyclovariegatin (pigment C2), pigment A, 3′,4′,4-trihydroxypulvinone (pigment B3), grevillin B (pigment B1), 3,4-dihydroxybenzoic acid; EDWARDS & GILL (1975): cyclovariegatin; BRESINSKY & BESL (1979): grevillins B and C (in fruit-bodies of North American origin); GARRIDO (1988): grevillins B and C (in fruit-bodies of South American origin); HAYASHI & al. (1989): bolegrevilol (isomeric to suillin); SCHMIDT (1990): grevillins B and C, variegatic acid, cyclovariegatin, thelephoric acid; new "lipophilic pigments"; grevillin D absent.

Suillus grisellus (PECK) ENGEL & KLOFAC [= *Fuscoboletinus grisellus* (PECK) POMERLEAU & A. H. SM.]: BRESINSKY & BESL (1979): xerocomic acid, variegatic acid, variegatorubin.

Suillus hirtellus (PECK) KUNTZE subsp. *hirtellus*: new: variegatic acid, "lipophilic pigments".

Suillus hirtellus subsp. *thermophilus* SINGER: BRESINSKY & BESL (1979): xerocomic acid, variegatic acid, variegatorubin.

Suillus leptopus (Pers.) MARCHAND: BESL & BRESINSKY (1977): grevillin D.

Suillus luteus (L.) S. F. GRAY: GABRIEL (1965): trace of "boletol" (= variegatic acid); GILL (1973): xerocomic acid, variegatic acid; BRESINSKY (1974): pigment type E (grevillins); BESL & al. (1974): grevillins B and D; BRESINSKY & BESL (1979): no identified pigments (fruit-bodies of North American origin; pigments destroyed?); JÄGERS & al. (1986): suillin; SCHMIDT (1990): atromentic acid, xerocomic acid, variegatic acid; grevillins probably destroyed; GARRIDO (1988): grevillins B and D, xerocomic acid (in fruit-bodies of South American origin); new: additional grevillins A and C, "lipophilic pigments".

Suillus neoalbidipes PALM & STEWART [= *Suillus albidipes* (PECK) SINGER ss. auct.]: BRESINSKY & BESL (1979): grevillin D; new: "lipophilic pigments".

Suillus placidus (BONORD.) SINGER: GABRIEL (1965): "boletol" (= variegatic acid), trace of "pseudoboletol" (= xerocomic acid); BRESINSKY (1974): pigment type E (grevillins); BESL & al. (1974): grevillins B, C and D; new: additional grevillin A, atromentic acid, xerocomic acid, variegatic acid, "lipophilic pigments".

Suillus plorans (ROLLAND) KUNTZE: BRESINSKY & ORENDI (1970): variegatic acid; BRESINSKY (1974): variegatic acid, variegatorubin; BESL & al. (1975a): additional atromentic acid, xerocomic acid; new: "lipophilic pigments".

Suillus pseudobrevipes A. H. SM. & THIERS: BRESINSKY & BESL (1979): grevillin D; new: "lipophilic pigments".

Suillus punctatipes (SNELL & DICK) SNELL & DICK: BRESINSKY & BESL (1979): grevillins A, B, C and D.

Suillus punctipes (PECK) SINGER: new: variegatic acid, variegatorubin, "lipophilic pigments".

Suillus pungens THIERS & A. H. SM.: new: "lipophilic pigments".

Suillus riparius THIERS: BRESINSKY & BESL (1979): grevillin D; new: "lipophilic pigments".

Suillus serotinus (FROST) KRETZER & BRUNS [=*Fuscoboletinus serotinus* (FROST) A. H. SM. & THIERS]: BRESINSKY & BESL (1979): xerocomic acid, variegatic acid, gyroporin; new: chamonixin, involutin.

Suillus sibiricus (SINGER) SINGER: BRESINSKY (1974): pigment type E (grevillins); BESL & al. (1975a): grevillin D; new: additional grevillins B and C, "lipophilic pigments".

Suillus spectabilis (PECK) KUNTZE [= *Fuscoboletinus spectabilis* (PECK) POMERLEAU & A. H. SM.]: BRESINSKY & BESL (1979): xerocomic acid, variegatic acid, variegatorubin; new: "lipophilic pigments".

Suillus spraguei (BERK. & M. A. CURTIS in BERK.) KUNTZE [= *Suillus pictus* (PECK) KUNTZE]: BRESINSKY & BESL (1979): variegatic acid; LANG & STEGLICH (in GILL & STEGLICH 1987: 6 and 99): grevillins B, C and D, boviquinone-4; new: "lipophilic pigments".

Suillus tomentosus (KAUFFM.) SINGER, SNELL & DICK: BRESINSKY & BESL (1979): xerocomic acid, variegatic acid, variegatorubin; new: "lipophilic pigments".

Suillus tridentinus (BRES.) SINGER: GABRIEL (1965): "boletol" and "pseudoboletol" absent; STEGLICH & al. (1972): grevillins A, B and C; BESL & al. (1975b): grevillins B and C, tridentoquinone; SCHMIDT (1990): grevillins A, B and C, cyclovariegatin; new: further "lipophilic pigments", thelephoric acid.

Suillus umbonatus DICK & SNELL: new: grevillin D, anhydrogrevillin D, "lipophilic pigments".

Suillus variegatus (SWARTZ: FR.) KUNTZE: GABRIEL (1965): "boletol" (= variegatic acid); EDWARDS & ELSWORTHY (1967): variegatic acid; BEAUMONT & al. (1968): variegatic acid; BRESINSKY & ORENDI (1970): variegatic acid, variegatorubin; JÄGERS & al. (1986): suillin; SCHMIDT (1990): variegatic acid, traces of atromentic acid and variegatorubin; new: "lipophilic pigments"; grevillins absent.

Suillus viscidus (FR. & HÖK) RAUSCHERT [= *Suillus aeruginascens* (SECR.) SNELL; *Fuscoboletinus aeruginascens* (SECR.) POMERLEAU & A. H. SM.; *Suillus laricinus* (BERK.) KUNTZE]: GABRIEL (1965): "boletol" (= variegatic acid); BRESINSKY & RENNSCHMID (1971): variegatic acid in young fruit-bodies; BRESINSKY (1974): trace of variegatic acid, pigment type E (grevillins); BESL & al. (1975a): grevillins B and C, variegatorubin; BESL & BRESINSKY (1977): additional thelephoric acid; BRESINSKY & BESL (1979): grevillin C in fruit-bodies of North American origin; new: xerocomic acid, grevillin A, chamonixin, "lipophilic pigments".

Pigments of pulvinic acid and/or grevillin types could be found in the fruit-bodies of all examined species with the exception of *S. borealis*, *S. caerulescens*, *S. cothurnatus*, *S. glandulosus*, and *S. pungens*. These negative indications were most likely caused by the fact that the amount of the examined material was not large enough or because the pigments have already decomposed. Upon examining mycelial cultures, pulvinic acids (mostly xerocomic acid) were detected at least for *S. caerulescens*, *S. cothurnatus*, and *S. pungens*. Because variegatorubin is produced through the spontaneous oxidation of variegatic acid, no peculiar taxonomic significance can be attributed to its frequent presence.

Three different types of pigmentation within the genus *Suillus* can be discerned with respect to the distribution of pulvinic acids and grevillins (Table 1). Type I: Species with pulvinic acids, without grevillins; Type II: Species with grevillins A, B, and/or C, sometimes with small amounts of pulvinic acids; Type III: Grevillin D appearing in addition to or instead of previously mentioned pigments. Because an oxidative rearrangement is necessarily involved here, fungi with grevillin D represent a higher level of development.

Additional pigments of the atromentin metabolism could be detected only sporadically: atromentin in *Suillus bovinus*; cyclovariegatin and/or thelephoric acid in *S. clintonianus*, *S. grevillei*, *S. tridentinus*, and *S. viscidus*; cyclopentenones in *S. serotinus* and *S. viscidus*; methyl bovinate in *S. bovinus*. The terphenylquinones as well as the cyclopentenones can be regarded as relicts indicating that the corresponding *Suillus* species may be primitive. In contrast, the presence of methyl bovinate suggests a special position for *S. bovinus*, which, in connection with the anatomical characteristics (ŠUTARA 1987a), clearly supports the creation of the genus *Mariaella* ŠUTARA.

Prenylated phenols and quinones, including their oxidation products, are pooled under the heading "lipophilic pigments" and considered to be indicator

Table 1. Distribution of pulvinic acids and grevillins in fruit-bodies of *Suillus* species; *Pa* pulvinic acids (atromentic, xerocomic, or variegatic acid respectively); *ABC* grevillins A, B, and/or C; *D* grevillin D

Type	Taxon	Pa	ABC	D
Type I	*S. bovinus*	+	–	–
	S. grisellus	+	–	–
	S. hirtellus	+	–	–
	S. plorans	+	–	–
	S. punctipes	+	–	–
	S. serotinus	+	–	–
	S. spectabilis	+	–	–
	S. tomentosus	+	–	–
	S. variegatus	+	–	–
Type II	*S. amabilis*	+	+	–
	S. bresadolae	+	+	–
	S. clintonianus	–	+	–
	S. grevillei	+	+	–
	S. tridentinus	–	+	–
	S. viscidus	+	+	–
Type III	*S. acidus*	–	–	+
	S. americanus	–	+	+
	S. bellinii	–	–	+
	S. brevipes	–	+	+
	S. collinitus	+	+	+
	S. flavidus	–	–	+
	S. granulatus	+	+	+
	S. leptopus	–	–	+
	S. luteus	+	+	+
	S. neoalbidipes	–	–	+
	S. placidus	+	+	+
	S. pseudobrevipes	–	–	+
	S. punctatipes	–	+	+
	S. riparius	–	–	+
	S. sibiricus	–	+	+
	S. spraguei	+	+	+
	S. umbonatus	–	–	+

substances for the genus *Suillus* (and for the *Gomphidiaceae/Rhizopogonaceae*). Only phenols and quinones with a diterpene (geranylgeranyl) side-chain appear within the genus *Suillus*. Unfortunately the feature "lipophilic pigments" has not yet been under consideration in earlier observations. For this reason, it has only been found in 26 of the 37 species studied up to now. In one case, however, these substances were detected in a mycelial culture (*S. caerulescens*, see below). Thus far, such "lipophilic pigments" have not been found in any single bolete species (i.e. *Boletales* with tubulate hymenophore) outside the genus *Suillus*. These are clearly the substances that form the characteristic encrustation on the fasciculated cystidia which are coloured by KOH. A comparison of these results with those of *Boletinus* proves to be interesting (see chapter *Boletinus*).

Metabolites from mycelial cultures. *Suillus acerbus* A. H. Sm. & Thiers: Regner (unpubl.): atromentic acid, xerocomic acid; "lipophilic pigments" absent.

Suillus acidus: Regner (unpubl.): trace of xerocomic acid, "lipophilic pigments".

Suillus amabilis: Bresinsky (1974): xerocomic acid.

Suillus americanus: new: xerocomic acid, "lipophilic pigments".

Suillus bellinii: new: "lipophilic pigments".

Suillus bovinus: Bresinsky (1974): xerocomic acid, variegatic acid, variegatorubin; Besl & al. (1989): methyl bovinate (mentioned as "Bovinsäure"), variegatic acid; "lipophilic pigments" dominating (e.g., boviquinones).

Suillus brevipes: Regner (unpubl.): atromentic acid, xerocomic acid, "lipophilic pigments".

Suillus caerulescens: Regner (unpubl.): atromentic acid, xerocomic acid, "lipophilic pigments".

Suillus collinitus: Bresinsky (1974): variegatic acid; Besl & Bresinsky (1977): additional xerocomic acid, variegatorubin; new: methyl variegatate, grevillins B and D, "lipophilic pigments".

Suillus cothurnatus: new: xerocomic acid, "lipophilic pigments".

Suillus flavidus: Bresinsky (1974): xerocomic acid, trace of atromentic acid.

Suillus granulatus: Bresinsky (1974): xerocomic acid, trace of atromentic acid, pigment type E (grevillins); Besl & al. (1989): grevillin B, "lipophilic pigments".

Suillus grevillei: Bresinsky (1974): xerocomic acid; Besl & al. (1989): xerocomic acid, trace of variegatic acid, "lipophilic pigments".

Suillus luteus: Bresinsky (1974): xerocomic acid, pigment type E (grevillins); Besl & al. (1989): grevillin B, "lipophilic pigments".

Suillus neoalbidipes: new: xerocomic acid, "lipophilic pigments".

Suillus ochraceoroseus (Snell) Singer [= *Fuscoboletinus ochraceoroseus* (Snell) Pomerleau & A. H. Sm.]: Regner (unpubl.): atromentic acid, xerocomic acid, grevillins B and C, "lipophilic pigments" (trace).

Suillus placidus: Bresinsky (1974): atromentic acid, xerocomic acid; Besl & al. (1989): atromentic acid, "lipophilic pigments".

Suillus plorans: Bresinsky (1974): xerocomic acid, trace of atromentic acid.

Suillus pungens: Regner (unpubl.): xerocomic acid, "lipophilic pigments".

Suillus sibiricus: Besl & Bresinsky (1977): xerocomic acid.

Suillus spraguei: Regner (unpubl.): atromentic acid, xerocomic acid, "lipophilic pigments".

Suillus subluteus (Peck) Snell in Slipp & Snell: Regner (unpubl.): atromentic acid, "lipophilic pigments".

Suillus tomentosus: new: atromentic acid, xerocomic acid, "lipophilic pigments".

Suillus tridentinus: Bresinsky (1974): xerocomic acid, trace of variegatic acid; Besl & al. (1989): additional tridentoquinone and further "lipophilic pigments".

Suillus variegatus: Bresinsky (1974): xerocomic acid; Besl & al. (1989): traces of variegatic acid and xerocomic acid; "lipophilic pigments".

Suillus viscidus: Bresinsky (1974): xerocomic acid; Besl & al. (1989): "lipophilic pigments".

Thus far, hydroxypulvinic acids, which are quite commonly found in *Boletales* (the most common of those being xerocomic acid), have been detected in 25 of 26 screened mycelial cultures taken from *Suillus* species. Grevillins seldom appeared, and when they did, only in small amounts: grevillin B in *S. granulatus* and *S. grevillei*; grevillin B and C in *S. ochraceoroseus*; grevillin B and D in *S. collinitus*. "Lipophilic pigments" were detected in all cultures except in one single strain from *S. acerbus*. At present, there is still no explanation for the absence of "lipophilic pigments" in this species.

The genus *Fuscoboletinus* POMERLEAU & A. H. SMITH

The genus *Fuscoboletinus* unites fungi which are related to *Suillus*. The only feature which distinguishes them from typical representatives of *Suillus* is the red to chocolate brown spore print (POMERLEAU & SMITH 1962). We support SINGER (1986) and others, who claim that the exclusive consideration of the colour of spore print establishes artificial groups within the relatives of *Suillus* (*Suilloideae*). Thus, we do not recognize *Fuscoboletinus* as an independent genus (see also SINGER & al. 1963).

Preliminary investigations of pigments in the spores from boletes (BESL & REGNER, unpubl.) demonstrate that the spores possess the same pigments as the fruit-bodies or the hymenophore respectively. There are many colours of spore prints which cover a rather large spectrum, ranging from olive to ochre as well as to all other imaginable brown tints. This, however, is not surprising when one considers the various pigmentations (type A, B, and C) in *Suillus* and the possibility of quantitative differences. Because the colour of the spore print cannot be easily established in terms of chemical compounds, it seems more appropriate to use the composition of the pigments in the fruit-bodies or the hymenophore as taxonomic characteristics. Because in this case pigment characters do not correspond to other characteristics in an apparent way, it is better to use chemistry for infrageneric ordering, and not to define different genera.

In addition to the findings of chemical compounds, investigations on the characteristics of mycelial cultures (HUTCHISON 1991) and of mycorrhizae (e.g., SAMSON & FORTIN 1988) as well as comprehensive DNA-analytical investigations (BRUNS & al. 1988, BRUNS & PALMER 1989) revealed no gap between *Suillus* and *Fuscoboletinus*.

The genus *Boletinus* KALCHBR.

Metabolites from fruit-bodies. *Boletinus asiaticus* SINGER: new: variegatic acid, variegatorubin; "lipophilic pigments" absent.

Boletinus cavipes (FR.) KALCHBR.: GABRIEL (1965): "boletol" (= variegatic acid); BRESINSKY & ORENDI (1970): atromentic acid, xerocomic acid, variegatic acid, variegatorubin; SCHMIDT (1990): 5 lipophilic substances with absorption <200 nm; TOYOTA & HOSTETTMANN (1990): cavipetins A to E (16-hydroxygeranylgeraniol esters); WADA & al. (1995): two chemotypes with either geranylgeraniol or farnesol derivatives; new: "lipophilic pigments" absent.

Boletinus paluster (PECK) PECK [= *Fuscoboletinus paluster* (PECK) POMERLEAU & A. H. SM.]: BRESINSKY & BESL (1979): xerocomic acid, variegatic acid, variegatorubin.

Metabolites from mycelial cultures. *Boletinus cavipes*: BRESINSKY (1974): xerocomic acid; BESL & al. (1989): additional atromentic acid and variegatic acid; "lipophilic pigments" absent.

The genus *Boletinus* in the restricted sense of SINGER (1986) is generally considered to be closely related to *Suillus* and has, therefore, been placed either next to this genus in subfam. *Suilloideae* (e.g., SINGER 1986), or is even thought to be a subgenus of *Suillus* (e.g., SMITH & THIERS 1964, ARPIN & KÜHNER 1977). Because of the clamps, the hollow stipe and the decurrent hymenophore in *Boletinus*, PEGLER & YOUNG (1981) and JÜLICH (1982) offer an opposing view, and group this genus within the *Gyrodontaceae*. HØILAND (1987) placed *Boletinus* even more closely to the true boletes (e.g., *Boletus*, *Xerocomus*) than to *Suillus*. However, new evidence confirms the placement of *Boletinus* next to *Suillus*, as mentioned above. DNA analyses (BRUNS & al. 1988, BRUNS & PALMER 1989) as well as morphological and physiological examinations of mycelial cultures (HUTCHISON 1991) demonstrate a close association of *Suillus* and *Boletinus*.

The following conclusions can be drawn on the chemical findings: all three species of the genus *Boletinus* maintain hydroxypulvinic acids, namely xerocomic and variegatic acid, which are typical for *Boletales* in general. Upon first glance, they seem to resemble pigment type I from *Suillus*. A more careful examination reveals, however, that there is indeed a marked difference: nearly all investigated *Suillus* species (except *S. acerbus*) synthesize lipophilic prenylated phenols or benzoquinones ("lipophilic pigments"). Such compounds had not been previously detected in any other genus of boletes. At least in *Boletinus asiaticus* and *B. cavipes* these substances were absent. This correlates with the absence of redbrown (in KOH) encrusted, fasciculated cystidia. The regular appearance of clamps and the sterile stipe covering (ŠUTARA 1987b) reveals a clear gap between *Boletinus* (sensu stricto) and *Suillus*. The *Suillus* species from sect. *Solidipedes* (e.g., *S. spectabilis*) are quite similar in many respects to the genus *Boletinus*. However, for the reasons just given, they are to be left within *Suillus*.

The previously mentioned morphological and physiological examinations of the mycelial cultures, the morphology of the mycorrhiza, and the DNA-analytical investigations all support to group *Boletinus* and *Suillus* closely to one another. From a chemosystematic point of view, it is interesting to note the presence of cavipetins (i.e. esters of 16-hydroxy-geranylgeraniol) and other derivatives of farnesol and geranylgeraniol in *Boletinus cavipes*. In contrast to *Suillus*, where the geranylgeranyl residue is bound to trihydroxybenzene, the terpenes in *Boletinus* are found in another bond; this is due to the absence of phenols. In preliminary investigations (BESL & LANGE, unpubl.), cavipetins were not detected in *Suillus*. Thus, *Boletinus* can be considered to be a genus on its own which is closely related to *Suillus*.

The genera *Gastroboletus* LOHWAG and *Gastrosuillus* THIERS

The species of *Gastroboletus* (sensu lato) exhibit certain reductions in adapting to environmental conditions. Loss of the active spore discharge, loss of gravitropic alignment of the tubes, and partial reduction of the stipe are typically observed. *Gastroboletus* is an artificial form-genus of a polyphyletic origin and its division has been long overdue. Because some of its representatives are closely connected to *Suillus* (e.g., *G. laricinus*, see SINGER & BOTH 1977), the genus *Gastrosuillus* was established (THIERS 1989).

In the following outline all the chemically analyzed representatives of *Gastroboletus* (sensu lato) have been arranged for comparison.

Metabolites from fruit-bodies. *Gastrosuillus laricinus* (SINGER & BOTH) THIERS [= *Gastroboletus laricinus* SINGER & BOTH]: new: grevillin B; pulvinic acids absent.

Gastroboletus ruber (ZELLER) CÁZARES & TRAPPE [= *Truncocolumella rubra* ZELLER]: BRESINSKY & BESL (1979): xerocomic acid, variegatic acid, variegatorubin.

Gastroboletus subalpinus TRAPPE & THIERS: new: variegatic acid; grevillins absent.

Gastroboletus turbinatus (SNELL) A. H. SM. & SINGER: BRESINSKY & BESL (1979): xerocomic acid, variegatic acid.

Gastroboletus valdivianus HORAK: new: atromentic acid, xerocomic acid, variegatic acid.

Gastroboletus xerocomoides TRAPPE & THIERS: new: variegatic acid, trace of xerocomic acid, "lipophilic pigments" (?).

The appearance of hydroxypulvinic acids in five out of six analyzed representatives of *Gastroboletus* shows their expectedly close relationship to true boletes. *Gastrosuillus laricinus* contains grevillin B, which associates this species with the pigmentation type B of *Suillus*. In addition to morphological, anatomical and DNA similarities of *G. laricinus* to *S. grevillei* (SINGER & BOTH 1977, BAURA & al. 1992), the chemical findings serve as an additional confirmation.

While the close relationship between the boletes and the corresponding secotioid fungi has never been doubted (for phylogenetic progression in *Boletales* see also BRESINSKY & WITTMANN-BRESINSKY 1995), the direction of evolution has been strongly debated. The hypothesis that secotioid fungi developed from the boletoid ancestors loosing active spore discharge is receiving increasing support. Recent DNA-analytical investigations (BAURA & al. 1992) seem to indicate that this is indeed the case.

The genus *Gomphidius* FR.

Metabolites from fruit-bodies. *Gomphidius glutinosus* (SCHAEFF.: FR.) FR.: GABRIEL (1965): "pseudoboletol" (= xerocomic acid); FURTNER (1969): atromentic acid; STEGLICH & al. (1969): xerocomic acid, gomphidic acid; BRESINSKY & ORENDI (1970): atromentic acid, xerocomic acid, gomphidic acid; SCHMITT (1970): xerocomic acid, gomphidic acid; ARDENNE & STEGLICH (1974): 1,2,4-trihydroxybenzene; BRESINSKY & BESL (1979): atromentic acid, xerocomic acid, gomphidic acid (in fruit-bodies of North American origin); JÄGERS & al. (1981): gomphilactone, 2,2′,4,4′,5,5′-hexahydroxybiphenyl; new: bolegrevilol.

Gomphidius maculatus FR.: BRESINSKY & ORENDI (1970): xerocomic acid, gomphidic acid; ARDENNE & STEGLICH (1974): xerocomic acid, 1,2,4-trihydroxybenzene; BESL & al. (1975a): atromentic acid; gomphidic acid lacking; JÄGERS & al. (1981): gomphilactone, 2,2′,4,4′,5,5′-hexahydroxybiphenyl; new: bolegrevilol.

Gomphidius roseus (FR.) FR.: ARDENNE & STEGLICH (1974): 1,2,4-trihydroxybenzene; BESL & al. (1975a): atromentic acid; new: bolegrevilol.

Gomphidius subroseus KAUFFM.: BRESINSKY & BESL (1979): xerocomic acid, variegatic acid, trace of variegatorubin.

Within *Gomphidius*, only the fruit-bodies have been investigated so far, due to unsuccessful attempts to cultivate mycelia. On one hand, hydroxypulvinic acids, which indicate a link to boletes, appeared in the few species which have been investigated. On the other hand, the phenol 1,2,4-trihydroxybenzene and its oxidation products (e.g., gomphilactone) are unique to *Gomphidius*. These substances are responsible for the fruit-body's red and black discolourations and certainly for the almost black colour of the spore deposit. The presence of bolegrevilol in three *Gomphidius* species strongly supports the claim that *Gomphidius* is indeed closely related to *Suillus*, because this substance also appears in some species of *Suillus*.

The genus *Chroogomphus* (Singer) O. K. Miller

Metabolites from fruit-bodies. *Chroogomphus helveticus* (Singer) Moser in Gams: Gabriel (1965): "pseudoboletol" (= xerocomic acid); Bresinsky & Orendi (1970): xerocomic acid; Schmitt (1970): xerocomic acid; Steglich & al. (1971): xerocomic acid, boviquinone-3 ("helveticone"), boviquinone-4.

Chroogomphus rutilus (Schaeff.: Fr.) O. K. Miller: Gabriel (1965): "pseudoboletol" (= xerocomic acid); Schmitt (1970): xerocomic acid; Beaumont & Edwards (1971): xerocomic acid, boviquinone-3, boviquinone-4, diboviquinone-3,4, diboviquinone-4,4, methylenediboviquinone-3,3, methylenediboviquinone-3,4, methylenediboviquinone-4,4; Steglich & al. (1971): boviquinone-3, boviquinone-4; Bresinsky & Besl (1979): xerocomic acid, boviquinones (in fruit-bodies of North American origin); new: trace of atromentic acid.

Chroogomphus tomentosus (Murr.) O. K. Miller: Bresinsky & Besl (1979): xerocomic acid, boviquinones.

Chroogomphus species, as *Gomphidius* spp., could not be successfully cultured. *Chroogomphus* differs from *Gomphidius* in that trihydroxybenzene and its oxidation products are absent. However, it can be assumed that this phenol appears as an intermediary product during biosynthesis of boviquinones (Gill & Steglich 1987: 108). In addition to other characteristics, the presence of prenylated benzoquinones in *Chroogomphus* is an evident difference to *Gomphidius*. Hence, we accept the independence of these two genera.

Boviquinones also appear sporadically in *Suillus*. However, they are primarily replaced by prenylated phenols (e.g., suillin, bolegrevilol), which are biogenetically related. Thus, there is hardly any doubt that *Suillus* and *Chroogomphus* are closely related.

Position of the treated genera within the *Boletales*

Based on the evidence shown above, the close relations between the genus *Suillus* and *Gomphidiaceae* (and *Rhizopogon*) cannot be disputed. The chemotaxonomic (see above; see also Agerer 1991) and DNA-analytical results (Bruns & Szaro 1990) confirm this as well. The taxa mentioned are considered to be more closely related to each other than to the remaining boletes. This additional information makes a re-evaluation of their taxonomic position necessary.

Arpin & Kühner (1977) classify *Gomphidius* (including *Chroogomphus*) within the *Boletaceae* (sensu lato). Høiland (1987) grouped *Suillus* within the

Gomphidiaceae. Due to the chemical (STEGLICH & al. 1971, BRESINSKY & STEGLICH 1989) and DNA-analytical findings (BRUNS & al. 1989), the genus *Rhizopogon* is considered to be closely related to the *Gomphidiaceae* as well.

In contrast to ARPIN & KÜHNER (1977) as well as to HØILAND (1987), however, we support a definition of a family which also takes the morphological organizational levels into consideration. Representatives with lamellae appear quite frequently within the *Boletales*. These are mostly regarded to be primitive like the lamellar fungi within the *Paxillaceae* (*Paxillus*, *Tapinella*, *Hygrophoropsis*; e.g., BRESINSKY & WITTMANN-BRESINSKY 1995, PEGLER & YOUNG 1981). In some cases, a secondary regressive metamorphosis of a tubulate to a lamellate hymenophore could have occurred. In such a case, the remaining characteristics could still be unaffected (e.g., chemical pathways). For this reason, it is appropriate to classify such fungi next to the boletoid relatives within one and the same family (e.g., *Phylloporus* and *Xerocomus* within the *Boletaceae*). Similarily, the secotioid fungi can hardly be isolated from their boletoid ancestors.

Despite many similarities with *Suillus*, the two genera *Gomphidius* and *Chroogomphus* display other differences in addition to the dissimilar hymenophore types. The possibility that these are primarily lamellate fungi cannot be ignored. Therefore, leaving these fungi in the family *Gomphidiaceae* is justifiable. However, it is consequently necessary to create a separate family, *Suillaceae*, for the boletoid species (and for those secotioids which are closely related) and to leave the gastroid species (*Rhizopogon*) in the family *Rhizopogonaceae*. The close relationship between these three families can best be expressed through the creation of a new suborder, *Suillineae*, within the *Boletales*.

Synopsis of the order *Boletales*

Order *Boletales* GILBERT (including *Rhizopogonales* KREISEL)
- Suborder *Paxillineae* FELTGEN
  - Family *Coniophoraceae* ULBR.
  - Family *Paxillaceae* MAIRE (including *Hygrophoropsidaceae* KÜHNER)
  - Family *Gyrodontaceae* (SINGER) HEINEM. (excl. *Gyroporaceae* LOCQ.)
  - Family *Omphalotaceae* BRESINSKY
- Suborder *Boletineae* REA emend. GILBERT
  - Family *Boletaceae* CHEV. s. str. (including *Xerocomaceae* PEGLER & YOUNG)
- Suborder *Strobilomycetineae* GILBERT
  - Family *Strobilomycetaceae* GILBERT
- Suborder *Suillineae* BESL & BRESINSKY
  - Family *Gomphidiaceae* SINGER [*Gomphidius*, *Chroogomphus*]
  - Family *Suillaceae* (SINGER) BESL & BRESINSKY [*Boletinus*, *Suillus* (including *Fuscoboletinus*, *Mariaella*), *Gastrosuillus*]
  - Family *Rhizopogonaceae* DODGE [*Rhizopogon*]

Concerning the boletes, this synopsis of the order *Boletales* corresponds to the ideas of THIERS (1971): "I believe that there are three major groups of boletes today – the *Suillus* and *Fuscoboletinus* group which possibly represent a distinct family, ... the *Strobilomycetaceae* ... and the large family *Boletaceae* ..."

New taxa

Suillaceae **(SINGER) BESL & BRESINSKY, comb. et stat. nov.**
Basionym: *Boletaceae* subfam. *Suilloideae* SINGER, Farlowia **2**: 250 (1945).
Typus: *Suillus* S. F. GRAY 1821, in: Nat. Arr. Brit. Pl. 1: 646.

Boletales **subordo** ***Suillineae*** **BESL & BRESINSKY, subordo novus**
Typus: *Suillaceae* (SINGER) BESL & BRESINSKY

Diagnosis latina: Carposomata agaricoidea vel boletoidea vel secotioidea vel gasteroidea. Sporae levigatae, pigmentatae, ellipsoideae ad fusiformes. Hic subordo metabolitibus terpenoideis exemplaris Cavipetini vel Suillini vel Bovichinonis a Boletalibus ceteris differt. *Suillineae* semper mycorrhizam cum coniferis ineunt.

Description: Fruit-bodies agaricoid, boletoid, secotioid or gastroid. Spores smooth, pigmented, elliptical to fusiform. In contrast to the remaining *Boletales*, compounds of type cavipetin, suillin and/or boviquinone can be found. Mycorrhizae are only formed with conifers.

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