Sutorius: a new genus for *Boletus eximius*

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**Abstract:** *Sutorius* is described as a new genus of Boletaceae to accommodate *Boletus robustus* originally named illegitimately by C.C. Frost from eastern North America. The legitimate name, *Boletus eximius*, provided by C.H. Peck, has been used since for a dark purple to chocolate brown bolete with finely scaly stipe and reddish brown spore deposit. This iconic taxon has been documented on five continents. Despite the straightforward species identification from morphology, the interpretation of stipe macro-morphology and spore color has led to equivocal generic placement. Phylogenetic analyses of genes encoding large subunit rRNA and translation elongation factor 1α confirm *Sutorius* as a unique generic lineage in the Boletaceae. Two species are recognized based on multiple accessions: *S. eximius*, represented by collections from North America, Costa Rica, Guyana, Indonesia and Japan (molecular data are lacking for only the Guyanan and Japanese material); and *S. australiensis*, represented by material from Queensland, Australia. Additional collections from Zambia and Thailand represent independent lineages, but sampling is insufficient to describe new species for these entities.

**Key words:** biogeography, boletes, Boletineae, phylogeny, ribosomal DNA

**INTRODUCTION**

*Boletus eximius* Peck was proposed as a new name by Peck (1887) for *Boletus robustus* Frost (1874) non Fries (1851). Since then, this idiosyncratic bolete from northeastern North America has been placed in *Ceriomyces* (Murrill 1909), *Tylopilus* (Singer 1947) and *Leccinum* (Singer 1973). Because Murrill’s concept of *Ceriomyces* can be discounted as a mixture of several modern genera, placement of *B. eximius* has been based primarily on either color of the spore deposit or the type of surface ornamentation of the stipe. Thus, Smith and Thiers (1971) were inclined to consider the spore color (reddish brown) more nearly like that of a *Tylopilus* whereas Singer (1973, 1986) judged that the stipe ornamentation was of a scabrous nature as in a *Leccinum*.

To anchor the name to a specimen, Halling (1983) designated a lectotype from among original Frost specimens and noted that descriptions published by Snell and Dick (1970), Smith and Thiers (1971) and Grund and Harrison (1976) adequately describe and illustrate the characters of the taxon. Treatments by Bessette et al. (2000) and Roody (2003) as a *Tylopilus* and Halling and Mueller (2005) as a *Leccinum* provide color photographs and updated descriptions. The latter publication extended the distribution to Central America. Fulgenzi et al. (2007) reported *T. eximius* from Guyana in northeastern South America.

*Boletus eximius* has been described from collections beyond the Americas, specifically Papua New Guinea (Hongo 1973, as *B. nigroviolaceus* Heim), Japan (Hongo 1975, 1979, 1980; Imazeki and Hongo 1989), China (Teng 1996) and Australia (Bougher and Thiers 1991, as *L. australiense*; Watling and Li 1999). Corner (1972) placed Heim’s taxon as a questionable synonym of *Boletus alboater* (= *Tylopilus alboater*). Corner’s description might circumscribe *T. alboater*, but Horak (2011) maintains that those interpretations are still in doubt.

Obvious patterns of amphi-Pacific disjunction of bolete morphotaxa have been cited and documented by Halling et al. (2008). Among these, four species of *Tylopilus* (*alboater, balloui, eximius* and the *chromapes*-group) were noted as particular examples of boletes.
exhibiting this disjunction. Those authors limited their study to the phylogeography of the *T. ballouei* consortium and further suggested such disjunctions deserved additional examination from a molecular perspective. Critical morphological and molecular analyses of Chinese materials supported recognition of a new genus, *Zangia*, in the *T. chromapes* group (Li et al. 2011). Our study of specimens morphologically identifiable as *Boletus eximius* from the Americas, eastern Asia, Indonesia, Africa and Australia with support from phylogenetic inference suggests recognition of a new genus, *Sutorius*, to accommodate that species plus *S. australiensis* from Queensland. Sufficient accession data is lacking to diagnose lineages properly from Thailand (*Sutorius* sp. 1) and Africa (*Sutorius* sp. 2).

**MATERIALS AND METHODS**

*Morphological datasets.*—Macromorphological data were derived from fresh specimens. General color terms are approximations, and the color codes (e.g., 7D8) are page, column and grid designations from Kornerup and Wanscher (1983). All microscopic structures were observed with an Olympus BHS compound microscope equipped with Nomarski differential interference contrast (DIC) optics and measured from dried material revived in 3% KOH. The abbreviation *Q* refers to the mean length/width ratio measured from *n* basidiospores, and *x* refers to the mean length × mean width. Herbarium codes (Thiers 2011) are cited for all collections from which morphological features were examined.

*Molecular datasets.*—Eighteen sequences from 15 collections (Table 1) that have been identified morphologically as *B. eximius* were newly generated, including nuclear large subunit ribosomal DNA (nuc-lsu) and translation elongation factor 1 (tef1) based on taxa having affinities to *B. chromapes* group (Li et al. 2011). Our study of specimens morphologically identifiable as *Boletus eximius* from the Americas, eastern Asia, Indonesia, Africa and Australia with support from phylogenetic inference suggests recognition of a new genus, *Sutorius*, to accommodate that species plus *S. australiensis* from Queensland. Sufficient accession data is lacking to diagnose lineages properly from Thailand (*Sutorius* sp. 1) and Africa (*Sutorius* sp. 2).

**RESULTS**

*DNA extraction and PCR.*—Obtaining high quality DNA and PCR products was straightforward except for the *B. eximius* samples. The crude *B. eximius* DNA was heavily pigmented, which interfered with PCR; as a result LR0R-LR7 and *tef1* products were successfully
<table>
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<th>Location</th>
<th>Date</th>
<th>Collector</th>
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Fig. 1. Phylogenetic relationships and placement of *Sutorius eximius* within the Boletaceae inferred from a combined nuc-lsu + tef1 dataset (2245 bp) using RAxML and PhyloBayes. The tree topology corresponds to the optimal maximum likelihood tree calculated by RAxML. Support values ≥ 50% BS and 0.95 PP are shown.
Boletaceae is poorly resolved. The genus *Boletus* without support as sister group of a larger clade. The phylogenetic placement of *tef1* alignments were combined without additional characters of 0.053864 in RAxML. The nuc-lsu and patterns and a proportion of gaps and undetermined characters of 0.112345 in RAxML. The full length LR0R-LR5 sequences were trimmed to fit the majority of LR0R-LR5 sequences. The *tef1* alignment is 1250 nucleotides long including introns and third positions, with 607 distinct alignment patterns and a proportion of gaps and undetermined characters of 0.053864 in RAxML. The nuc-lsu and *tef1* alignments were combined without additional modifications. PhyloBayes analyses were run on the combined nuc-lsu + *tef1* with four MCMC chains, sampling data every 100th cycle. The maximum difference in split frequency between runs dropped to zero after approximately 37000 per chain, and the analyses were stopped. The chains were analyzed with the readpb program, removing 10% of the samples as burn-in. A total of 37 144 trees were used to estimate posterior probabilities. The tree inferred from the combined dataset and the support values estimated with RAxML and PhyloBayes is illustrated (Fig. 1).

**Alignments and phylogenetic analyses.**—The final nuc-lsu alignment included 995 positions with 335 distinct alignment patterns and a proportion of gaps and undetermined characters of 0.112345 in RAxML. The full length LR0R-LR7 sequences were trimmed to fit the majority of LR0R-LR5 sequences. The *tef1* alignment is 1250 nucleotides long including introns and third positions, with 607 distinct alignment patterns and a proportion of gaps and undetermined characters of 0.053864 in RAxML. The nuc-lsu and *tef1* alignments were combined without additional modifications. PhyloBayes analyses were run on the combined nuc-lsu + *tef1* with four MCMC chains, sampling data every 100th cycle. The maximum difference in split frequency between runs dropped to zero after approximately 37000 per chain, and the analyses were stopped. The chains were analyzed with the readpb program, removing 10% of the samples as burn-in. A total of 37 144 trees were used to estimate posterior probabilities. The tree inferred from the combined dataset and the support values estimated with RAxML and PhyloBayes is illustrated (Fig. 1).

**The phylogenetic placement of *Boletus eximius*.**—The Boletaceae received maximum support in all analyses (BS = 100%, PP = 1), but the backbone of the Boletaceae is poorly resolved. The genus *Boletus* is not monophyletic, as has been shown with nuc-lsu (Binder 1999) and multilocus data (Binder and Hibbett 2006, Dentinger et al. 2010), and splits into at least three groups: the *B. edulis*, the *B. eximius* and a group of weakly resolved *Boletus* species termed “residual.” *Boletus eximius* is not closely related to the genera *Tylopilus* or *Leccinum*, which earlier served as alternative placements for *B. eximius*. The phylogenetic tree inferred from nuc-lsu data places *B. eximius* without support as sister group of a larger clade including *Xerocomus*, *Phyloporus*, *Aureoboletus*, *Boletellus* pro parte and *Hemileccinum* species. This result is consistent with Binder (1999) and Binder and Hibbett (2006). The *tef1* phylogeny places *B. eximius* close to the “residual” *Boletus* species outside the *B. edulis* group. This relationship is not supported by bootstrap but holds up in the combined nuc-lsu + *tef1* phylogenetic analyses. The *B. eximius* clade, including ECV3603 from Thailand, is supported in all analyses and receives 68% and 100% BS from nuc-lsu and *tef1* analyses respectively and 100% BS and 1.0 PP in the combined analyses (Fig. 1).

**Taxonomy**

*Sutorius* Halling, Nuhn & Fechner gen. nov.

A generibus Boletacearum sporis in cumulo rubrobunneis, inamylodeis, oblongis, levibus; contexto pallido, lilaceo vel roseobrunneo collirubro; fibulis nullis; pileo (i.e. cobbler; specifically Charles C. Frost, a Vermont shoemaker, who described the species *Boletus robustus* non Fr.

MycoBank: MB563942

*Sutorius eximius* (Peck) Halling, Nuhn, & Osmundson. comb. nov.

*Boletus robustus* Fr. for *S. eximius* non Fr.

Figs. 2–3


MycoBank: MB563943

As noted above, *S. eximius* has been sufficiently described and well illustrated. Variations in spore dimensions are given (Table II).

*Habit, habitat, distribution:* Reported or observed among litter, on soil in forests associated with *Dicymbe*, *Dipterocarpus*, *Fagus*, *Hopea*, *Quercus*, *Shorea*, *Tsuga*. North America: eastern Canada to Georgia, west to


Commentary: Based on the phylogram (Fig. 1), a true S. eximius clade is well supported by molecular data and geography (Java, USA, Costa Rica). The Japanese material was not placed based on molecular inference, but it could be either S. eximius (consistent with other patterns of Laurasian disjunctions) or an Asian group near Sutorius sp. 1 (Thailand). It is not clear where the Guyanan entity would place in a molecular analysis, even though it occurs in north-eastern South America, but mycorrhizal partnership with legumes might be consistent with an African grouping near Sutorius sp. 2 (Zambia). Except for variation of spore dimensions (Table II), there is little if any morphological difference in the specimens examined. The differences between the Costa Rican and USA measurements probably represent a clinal variation well documented by Halling and Mueller (2002, 2005) and Osmundson and Halling (2010) for many agarics and boletes.

Sutorius australiensis (Bougher & Thiers) Halling & Fechner comb. nov. Fig. 4


Pileus (3–)7.5–9–(11) cm broad, convex to plano-convex to plane, dry or viscid (in wet weather), finely matted to matted subtomentose, sometimes finely velutinous with a subtle to distinct hoary bloom at first, brown (7E6-5), dark (chocolate) brown (7,8F8,7), reddish brown (8E8), violet brown
(10D4-11E4) to lilac brown (11D4) (especially toward margin), to nearly black in some, becoming brown (7E6,5), even at margin or sometimes with a slight sterile extension. Flesh white to pale lilac, with pinkish brown to brownish lilac marbleling/mottling, with mild odor and flavor that is mild to slightly unpleasant, slightly bitter. Tubes adnexed to deeply depressed, lilac whitish when young, soon flesh (6A-B3) to light brown (6D4), with pores stuffed and violet brown (11F5) when young, becoming brown (7E6,5) to cocoa brown (6E7) with age, bruising a cinnamon brown. Stipe (2.5–)4–6(–8.5) cm long, 1–2 cm broad, strict or curved, equal to subclavate, dry, finely subquamulose to finely scabrous-scissurate on a pale lilac ground (16D3) or very nearly white, with white basal mycelium or occasionally mixed with lilac brown to grayish lilac and mottled, becoming or a dull brown (7E6,5,8E3), with interior whitish to a pale lilac ground (16D3) or very nearly white, with finely subsquamulose to finely scabrous-scissurate on 2 cm broad, strict or curved, equal to subclavate, dry, cinnamon brown. Stipe (2.5–)4–6(–8.5) cm long, 1–5(7E6,5) to cocoa brown (6E7) with age, bruising a dull brown (6D4), with pores stuffed and unpleasant, slightly bitter. Tubes adnexed to deeply depressed, lilac whitish when young, soon flesh (6A-B3) to light brown (6D4), with pores stuffed and violet brown (11F5) when young, becoming brown (7E6,5) to cocoa brown (6E7) with age, bruising a cinnamon brown. Stipe (2.5–)4–6(–8.5) cm long, 1–2 cm broad, strict or curved, equal to subclavate, dry, finely subquamulose to finely scabrous-scissurate on a pale lilac ground (16D3) or very nearly white, with scales a pinkish brown to pinkish lilac to violet brown or a dull brown (7E6-5, 8E3), with interior whitish to lilac brown to grayish lilac and mottled, becoming streaked with pale brown or light brownish orange staining, white and matted to tomentose at base with white basal mycelium or occasionally mixed with a short brown, ocher tomentum, sometimes “brownish tomentose” (Hongo 1973, PNG).

Spores red brown in deposit, 11.9–15.4(–16.8) × 3.5–4.9 μm (n = 15, x = 13.9 × 4.1 μm, Q = 3.58), light brown in KOH, smooth and thin-walled, ellipsoid to subfusoid to fusoid, inamyloid. Basidia 20–34 × 8–11 μm, clavate, hyaline, four-stereigmate. Hymenial cystidia 20–40 × 6–8 μm, scattered and uncommon, thin-walled, with hyaline to granular and golden to pale brown contents, narrowly fusoid. Tube trama boletoid and divergent, with central stratum brown to golden yellow; the lateral strata elements hyaline, 3.5–8.4 μm wide, subgelatinous with age, often with amorphous dark lilac to pinkish orange-brown pigment deposits. Pileipellis hyphae a trichodermium, in KOH yellow ochraceous, inamyloid; elements 3.3–6 μm wide, elongated to cylindrical or obtuse, encrusted with pigment (but dissolving in KOH), thin-walled, not gelatinized. Pileus trama interwoven, hyaline, inamyloid, thin-walled. Stipitipellis hyphae vertically oriented, parallel, giving rise to clusters of caulocystidia, 20–30 μm × 5–15 μm wide, cylindrical to clavate to subfusoid, hyaline to brown contents, with encrusting pigment present (with dark brown or lilac to purple acerose crystals dissolving in KOH). Stipe trama hyphae parallel, cylindrical, hyaline, inamyloid, often with amorphous dark lilac to pinkish orange-brown pigment deposits. Clamp connections absent.

Specimens examined: AUSTRALIA. QUEENSLAND: Koombooloomba area, [label data: “Red Road, Tully Falls area”], 4 May 1988, Bougher & Mulajczuk E4010 (ACIAR E4010, BRIP 17542, Holotype: Leccinum australiense, BRI). Davies Creek Road, 5 Apr 1991, M. Castellano E4095 (Paratype: Leccinum australiense, BRIP 17543, BRI). Wide Bay District, Great Sandy National Park, Cooloola section, Freshwater Road, 25°56’37”S, 153°7’24”E, 154 m, 20 Feb 2011, Halling 9441 (BRI, NY), 23 May 2011, Halling 9543 (BRI, NY); Fraser Island, road from Central Station to Eurong, 25°29’6”S, 153°5’18”E, 75 m, 11 Feb 2009, Halling 9056 (BRI, NY); road from Wanggoolba Creek Ferry landing to Central Station, 25°27’39”S, 153°1’26”E, 90 m, 7 Jun 2009, Halling 9190 (BRI, NY); Ungowa Road 25°27’31”S, 153’0’40”E, 24 m, 9 Jun 2009, Halling 9205 (BRI, NY); road from Eurong to Central Station, about 1 km W of Eurong, 25°29’9”S, ± 153°6’5”E, 26 Mar 2010, Halling 9280 (BRI, NY); road from Eurong to Central Station, 25°30’1”S, 153°6’19”E, 51 m, 17 May 2011, Halling 9485 (BRI, NY); 4 km along Woralie Road, at Knifeblade Sandblow car park, 25°13’25”S, 153°13’46”E, 121 m, 18 May 2010, Halling 9315 (BRI, NY).

Habit, habitat, distribution: Reported or observed among litter, on soil or sand in forests associated with Allocasuarina, Corymbia, Eucalyptus, Lophostemon, Syncarpia. Queensland, Australia. Reported from Victoria and the Australian Capital Territory (Watling and Li 1999 as T. eximius). Possibly in Papua New Guinea with Fagaceae.

Commentary: As near as we can tell, R. Heim’s specimen of B. nigroviolaceus from Papua New Guinea is not available from PC. The original description of B. nigroviolaceus (Heim 1963) and color illustration in Heim (1965) portray a deeply pigmented Sutorius recalling material collected in Queensland. Hongo’s (1973) report of B. nigroviolaceus from PNG was decreed by him (Hongo 1975) to be nothing more than S. eximius (a Tylopilus). Additional material from PNG could add support for the Austral lineage. For the specimens supporting the description of Leccinum australiense (Bougher and Thiers 1991), a spore print is included with the holotype specimen along with a Kodachrome transparency showing three, intensely colored basidiomes (one cut lengthwise), a bit on the young side and just approaching maturity. The paratype also includes a Kodachrome illustrating a Sutorius. The microscopic features presented by Bougher and Thiers (1991) sufficiently show those features. At present, an Australian indigenous Leccinum in the classical/typical sense of Lannoy and Estades (1995) or Den Bakker and Noordeloos (2005) is still unknown.

A geographical structuring (Fig. 1) recalls some-what the one observed for Boletus sect. Boletus (Dentinger et al. 2010, fig. 4). This latter is based on material with morphological differences and using mostly different gene loci from localities comparable to ones in this study. The spore dimensions and statistics of the Australian material are most nearly like those from the USA (TABLE II), but the support from the molecular inference and geographic structuring
lend weight to our hypothesis that the Australian lineage is distinct. In the description above there is notice of different colors and morphology on the exterior of the stipe base. These features sometimes are not easy to discern because of adhering or embedded substrate but might be useful for finer distinctions when additional material is available.

In general, one feature specifically mentioned in the field description of Vellinga 3603 and in the protolog (Heim 1963) and French description (Heim 1965) of B. nigrovioleaeus is the nature in which the stipe ornamentation manifests itself. The protolog states “... transverse scissuris albis et acuminatus striatus ...”; in French, “... formant à la loupe une sorte de tigrure complex, ...”, and Vellinga noted “... upper part [of stipe] surface breaking up and becoming fine tiger-patterned.” In fact, this manifestation has been overlooked or perhaps not properly described in documenting the macroscopic features of this taxon (Figs. 2–4). These transversely scissurate scales can be found in the freshest, well preserved material and are present in such specimens cited above (including those of the senior author). An image showing this feature also can be found on Mushroomobserver.org (Image 95315 of Observation 49122 by Damon Brunette). This manner of appearance of the surface ornamentation is fundamentally different from that of a Leccinum in the strict sense (Fig. 5).

**DISCUSSION**

*Sutorius eximius* is one of a number of boletes having a combination of morphological characteristics that have led to alternative classifications depending on character-weighting judgments by different authors; other prominent examples include *Tylopilus chromapes* (which has also been placed in *Leccinum*), *Tylopilus balloui* (also placed in *Rubinoboletus* and *Gyroporus*) and *Bothia castanella* (also placed in *Boletinus*, *Boletinellus*, *Chalciporus*, *Gyrodon*, *Suillus*, *Xerocomus*). Molecular data recently have proven useful in resolving these taxonomic quandaries. In the case of *T. ballouii*, molecular data support placement in *Tylopilus* despite its basidiospore morphology that is uncharacteristic for the genus (Osmundson and Halling 2011). In the case of *B. castanella* and the *T. chromapes*-like *Zangia* spp. (Li et al. 2011) and now *Sutorius eximius* these taxonomic enigmas are shown to be phylogenetically distinct from all genera in which they were formerly placed. Aligned with *Tylopilus* on the basis of spore deposit color (Smith and Thiers 1971), *S. eximius* is an uneasy match to the former due to having reddish brown instead of truly pinkish spores in deposit. Here we present morphological evidence that the nature of the stipe ornamentation of *S. eximius* superficially resembles *Leccinum* but appears to lack developmental homology in the genus. The molecular data presented here confirm what we therefore can conclude (if with some degree of uncertainty) from morphology: that *S. eximius* should not be placed in *Tylopilus or Leccinum; Sutorius* does not share a recent common ancestor with either of these genera in our phylogenetic analysis. Specimens sharing the unique morphology of *Sutorius* from North America, Asia, Africa and Australia form a monophyletic clade; however, the broader phylogenetic affinity of this group is as yet unknown due to poor backbone resolution, a problem observed in both single-gene (e.g. Halling et al. 2007) and multilocus (Binder and Hibbett 2006) analyses of the Boletineae (sensu Binder and Bresinsky 2002). Despite lacking this broader phylogenetic context, both the morphological and molecular distinctiveness of these fungi warrant generic recognition.

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![Fig. 5. Habit image, Leccinum versipelle, REH8498, Valday District, Russia (×0.5).](image-url)
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