

SQUAMANITA PARADOXA, A NICE ADDITION TO THE BELGIAN MYCOFLORA

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Summary

Squamanita paradoxa (A.H. Sm. & Singer) Bas has been collected for the first time in Belgium. The specimen is described and illustrated. The main characters of the species are summarized and its distribution in Western Europe revised. A phylogenetic tree is provided, which includes two sequences of the ribosomal ITS of the specimen, one obtained from the cap, one from the stipe.

Samenvatting

In dit artikel bespreken we de eerste vondst van *Squamanita paradoxa* (A.H. Sm. & Singer) in België. De specimens worden beschreven en geïllustreerd. De belangrijkste kenmerken van deze soort worden besproken en een overzicht van de verspreiding in West-Europa wordt gegeven. Op basis van ribosomale ITS sequenties (hoed en steel) wordt de fylogenetische positie van het materiaal gegeven.

Introduction

During an excursion in La Hulpe (Belgium, prov. Walloon Brabant) on November 1st, 2014, the lawns situated near the hotel Dolce (site formerly occupied by IBM) were explored in search of mushrooms. The place is known to host many species of fungi, a.o. *Hygrocybe* and *Geoglossum* species.

The visit of the site allowed one of us (AL) to discover a few specimens of a strange fungus, slightly emerging from the mosses. The macroscopic aspect was very peculiar: a violet scaly cap and a very scaly stem whose color abruptly changes from violet on the top to fulvous orange in the lower part (fig. 1). These macroscopic features are very typical and point towards *Squamanita paradoxa* (A.H. Sm. & Singer) Bas.

The genus *Squamanita*

Squamanita paradoxa has been described from Oregon (USA) by Smith & Singer (1948), under the name *Cystoderma paradoxum* A.H. Sm. & Singer. Given its original characteristics, in particular the fact that the cap of the young specimens is covered with a "cuticle found to be similar to that of the typical form of *C. amianthinum*", these authors also created the subg. *Dissoderma* to accommodate the species. This subgenus has been subsequently erected at the generic rank and the species named *Dissoderma paradoxum* (A.H. Sm. & Singer) Singer. Finally, in his revision of the genus, Bas (1965) included the species in *Squamanita* Imbach.

The genus *Squamanita* currently contains 12 species. It is very unique within the Agaricales, because it is composed of biotrophic parasites living on a range of agarics including *Hebeloma*, *Galerina*, *Kuehneromyces*, *Cystoderma*, *Phaeolepiota* and *Amanita* species. The

parasitic nature of these species remained unknown for years although several authors have had some doubts about this. In the original description of the species, Smith & Singer (1948) already mention the fact that a collection of *S. paradoxum* (sub *Cystoderma*) "gave some evidence of having come from a decayed fruiting body of a fleshy fungus" but they apparently did not realize that the labile covering of the cap is made up of remains of a parasitized sporophore. When describing the first British collection of the species, Watling (1974) cites the collector, P. James, who already indicated "Curious and anomalous: base seems to be *Lepiota amianthina* with a mutant cap". J. Pitt, another collector, noted "it seems as if another agaric has been grafted onto the stem of *Cystoderma amianthinum*." The particular aspect of the species and the fact that it is often collected among healthy sporophores of the *Cystoderma* led Reid (1983) to clearly put the question "could it be that *S. paradoxa* might represent *C. amianthinum* parasitized by another agaric". Finally, the observation of three sporophores of *S. contortipes* (A.H. Sm. & D.E. Stuntz) Heinem. & Thoen growing on an exceptionally well preserved sporophore of *Galerina* sp. allowed Redhead *et al.* (1995) to demonstrate the true parasitic nature of this species. Afterwards, the parasitism of *S. paradoxa* on *Cystoderma amianthinum* has also been demonstrated by molecular analysis (Matheny & Griffith 2010)

Description and identification of the collection

Cap convex, nearly hemispherical, reddish violet, not hygrophanous, with appressed scales and a few small remnants of the *Cystoderma* pileipellis; margin exceeding gills. Gills pale violaceous, arcuate-adnate,



Fig. 1. *Squamanita paradoxa*, specimens collected in La Hulpe, Belgium (photo R. Notte).

rather distant, quite thick, and sometimes forked. Stem above “bulb” cylindrical, reddish violet, with appressed scales. « Bulb » cylindrical, broader than stem, bright ochraceous-orange, scaly to granulose.

Spores 7.0-8.1-9.0 (-10.0) × (4.0-) 4.5-4.9-5.5 (-6.0) μm, Q = (1.4-) 1.50-1.65-1.89 (-2.00) [20 spores measured], ellipsoid, rarely somewhat phaseoliform, sometimes a bit irregular and angular, hyaline, with slightly thickened wall, dextrinoid (mostly visible on the spores remaining on the gills), metachromatic. Basidia 4-spored, 8-10 μm wide. Hyphae in the trama of the gills composed of fusoid inflated cells, which are 18-25 μm wide in their middle part, clamped, thin-walled and hyaline.

The macroscopic appearance of the sporophores (fig. 1) is very typical of *Squamanita paradoxa* and the microscopic characters described above are in good agreement with those of this species. Phylogenetic analysis of the ITS sequences obtained from the stem and the cap confirmed this identification. The data set included 8 ITS sequences of four *Squamanita* species, totalizing 728 positions. Analysis was performed using the maximum likelihood (ML) methodology. Maximum likelihood (ML) searches were conducted with RAxML 7.0.4 (Stamatakis 2006) and involved 500 replicates under the GTRGAMMA model. In addition, 500 bootstrap (BSML) replicates were run with the same model. The tree (fig. 2, phylogeny) represents the best ML tree (best log likelihood -2205.1311).

Squamanita pearsonii Bas is another species suspected of growing on *Cystoderma amianthinum* (although this has never been demonstrated). However, the scales on its cap and stem are recurvate (appressed in *S. paradoxa*). Its stem is claviform, gradually enlarged towards base (“bulb”), which is smooth and yellowish (in *S. paradoxa*: “bulb” cylindrical, granulose-scaly and orange, being the base of the *Cystoderma* stem).

Specimen examined: Belgium, prov. Walloon Brabant, La Hulpe, lawns near the hotel Dolce, 01.XI.2014, among mosses (*Rhytidiadelphus squarrosus*), herb. A. Leclerque s.n. (BR). GenBank Accession number: pileus: GenBank MK377323, stipe: GenBank MK408620.

Synthetic description of *Squamanita paradoxa*

Cystoderma paradoxum A.H. Sm. & Singer, *Mycologia* **40** (4): 454 (1948). – *Squamanita paradoxa* (A.H. Sm. & Singer) Bas, *Persoonia* **3** (3): 348 (1965). – *Dissoderma paradoxum* (A.H. Sm. & Singer) Singer, *Beih. Sydowia* **7**: 69 (1973).

?= *Squamanita basii* Harmaja, *Karstenia* **27** (2): 73 (“1987”, publ. 1988). – *Dissoderma basii* (Harmaja) Bon, *Doc. mycol.* **29** (n°115): 34 (1999).

?= *Squamanita umbilicata* Harmaja, *Karstenia* **27** (2): 73 (“1987”, publ. 1988). – *Dissoderma umbilicatum* (Harmaja) Bon, *Doc. mycol.* **29** (n°115): 34 (1999).

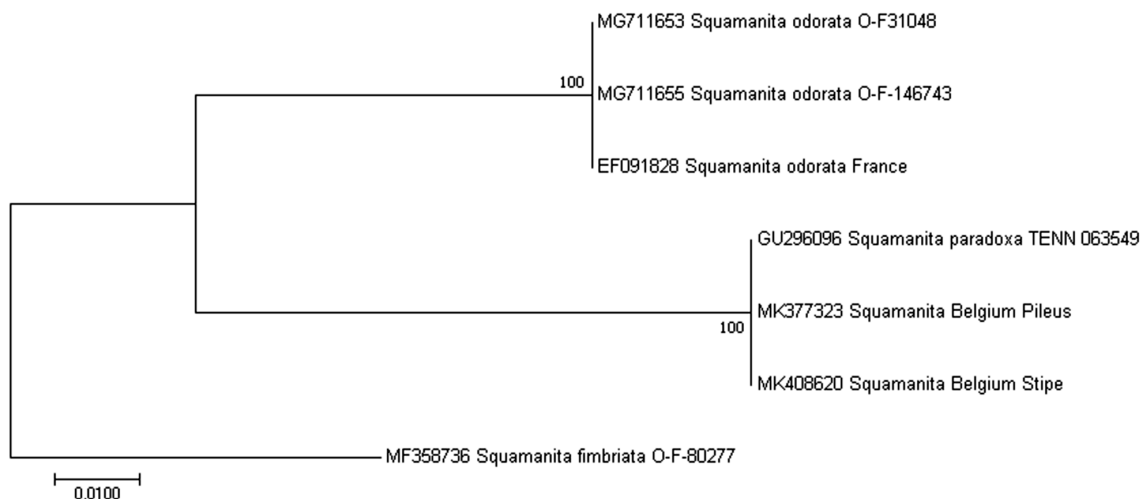


Fig. 2. Maximum likelihood (ML) tree (best log likelihood - 2205.1311).

Descriptions

Smith & Singer (1948), Bas (1965), Watling (1974), Trimbach (1975), Romagnesi (1980), Reid (1983), Torrent & Pérez-De-Gregorio (1996), Bon & Massart (1997), Bon (1999), Ludwig (2001), Roux (2006), Arauzo (2008), Pérez-De-Gregorio *et al.* (2009), Eyssartier & Roux (2011), Laessøe (2012).

Illustrations

(d=drawings, p=photo): Bas (1965, d), Watling (1974, d), Trimbach (1975, d), Romagnesi (1980, d), Reid (1983, d), Lange & Laessøe (1989, p), Bas (1991, d), Torrent & Pérez-De-Gregorio (1996, p), Bon & Massart (1997: pl. 3C, p and d), Massart *et al.* (1998, p), Ludwig (2000, aquarelle), Bingham & Bingham (2005, p), Roux (2006, p), Moser & Jülich (1985-2007, p), Arauzo (2008, p), Wulbaut (2008, p), Kibby (2009, p), Pérez-De-Gregorio *et al.* (2009, p), Matheny & Griffith (2010, p), Eyssartier & Roux (2011, p), Henrici (2013, p).

Cap (7-) 10-30 (-35) mm wide, convex to broadly-convex, sometimes with a slightly depressed disc and sometimes with a low broad umbo, with an appendiculate margin; not hygrophanous, pallid lilac to dark violaceous drab or reddish brown (the colour of the cap of *Amanita porphyria*); young buttons entirely covered with a brownish orange, granulose veil (remains of the host), which is only loosely connected to tissue of pileus and disappears quickly. **Gills** subdistant to distant, arcuate-adnate to subdecurrent, sometimes adnexed with a small tooth, pallid brownish drab to pale greyish violet. **Stem** (8-) 10-30 × 2.5-6 mm, cylindrical to slightly clavate, pale lilac or violaceous, lacerate-scaly as well as longitudinally striate. **"Bulb"** (remains of the host) often slightly wider than the stem, cylindrical or slightly clavate, 26-54 × 6-8 mm, sheathed by a granulose cinnamon buff to clay colour veil which is broken up into more or less concentric rings of tufts or scales. **Flesh** pale brownish drab to greyish violaceous in cap, lilac to violaceous in stem, yellowish to clay colour in bulb. Smell usually strong and aromatic

or perfumed, sometimes weak, faintly fruity like oranges or of fresh laundry (Laessøe 2012), or unpleasant as that of *Lactarius porninsis*, becoming unpleasant on aging; it is likely that the young carpophores produce a fragrant smell, which becomes unpleasant when they get older. Taste mild, not distinctive, or (after Herinck 1954) metallic astringent like a solution of potassium permanganate. **Spore print** white.

Spores (6.5-) 8.5-9.5 (-11.5) × (4.0-) 4.5-6.0 (-6.4) μm, Q = (1.4-) 1.5-1.9 (-2.0), ellipsoid, sometimes cylindrical or slightly angular (fide Brandrud *et al.* 1997), with thin to slightly thickened wall (up to 0.6-0.9 μm thick after Arauzo 2008), hyaline to subhyaline, smooth, non-amyloid, slightly dextrinoid (sometimes difficult to see), metachromatic, slightly accumulating Congo red, cyanophilous, binucleate. **Basidia** 4-spored, (25-) 29-42 (-55) × (6-) 7-10 μm, sometimes with thickened wall (sclerobasidia, fide Arauzo 2008). **Cystidia** absent. **Trama** of **gills** sub-regular, metachromatic, hyphae 12.5-30 μm wide. **Scales** on bulb consisting of chains of oval, ellipsoid or globose cells with yellowish-brown to rusty vinaceous walls in KOH. **Clamps** present.

Ecology

Parasitic on *Cystoderma amianthinum*, occasionally also on *C. carcharias* (Eriksen 1997), among mosses (often *Rhytidiadelphus*) or decaying needles, in woods of conifers (*Pinus*, *Picea*, *Larix*), eventually mixed with broadleaved trees (*Betula*, *Quercus*), or in grassy places but then usually near scattered trees or close to a forest edge. On acid as well as on calcareous soils. Quite often among healthy sporophores of *Cystoderma amianthinum*.

Phenology

Sporophores produced in autumn (11 Sept. - 24 Nov.).



Fig. 3. *Squamanita paradoxa*, specimens collected in Liessies, France (photo J.-J. Wuilbaut).

Note 1

In his revision of *Squamanita*, Bas (1965) mentions several differences between the type specimen of *S. paradoxa*, collected in the U.S.A., and the two European specimens he had in hands. He however concludes that “these slight discrepancies seems not to warrant the description of the European form as a distinct taxon”. For his part, Harmaja (1988) considers these differences as significant. He consequently describes a new species, *S. basii*, to accommodate the European collections of *S. paradoxa*. Many authors (a.o. Redhead *et al.* 1994: 1817 and Laessøe 2012) believe the two taxa are probably synonyms. The problem is that if quite a large number of descriptions are available for the European collections, a single description has been published on the American material (Smith & Singer 1948), which does not allow getting an idea of the variability of the species on this continent.

We made a careful screening of that literature and give the results hereafter. The main differences suggested by Harmaja between American and European specimens are the following:

1) The odour of the sporophores was “not distinctive” in the American material when many European authors mention a strong sweet odour which may become foetid in old sporophores (Herinck 1954, Harmaja 1988, Lange & Laessøe 1989, Torrent & Pérez-De-Gregorio 1996, Arauzo 2008, Pérez-De-Gregorio *et al.* 2009). However, some French authors perceived only a rather weak smell: “odeur faible, plutôt désagréable, spermatique” (Trimbach 1975), “odeur légère (un peu de persil ?)” (Romagnesi 1980), “odeur faible ou pholitoïde” (Bon & Massart 1997), odeur “faible mais agréable, un peu aromatique” (Roux 2006).

2) Harmaja also mentions the fact that European specimens usually have confluent stipe bases. This is also not a good character to separate both species. Smith & Singer (1948) indicate “solitary or in small clusters from a fleshy basal mass of tissue” and the European collections can be single or confluent by 2 or several sporophores.

3) Spores would be slightly dextrinoid on the American material and not or perhaps very faintly so on European collections. Here also, this is not a significant difference between the two taxa. Smith & Singer (1948) describe the spores of *Cystoderma paradoxa* as “yellowish to pale tawny (hence slightly pseudoamyloid) in iodine (most coloration obtained when plunged in alcohol, then in water, and finally stained with Melzer’s reagent; least coloration obtained with ammonia followed by Melzer’s reagent)”. European authors describe the spores either as dextrinoid (Herinck 1954, Trimbach 1975, Lange &

Laessøe 1989, Bas 1991, Torrent & Pérez-De-Gregorio 1996, Pérez-De-Gregorio *et al.* 2009) or as not or only slightly dextrinoid (Bas 1965, Watling 1974, Bon & Massart 1997, Roux 2006, Arauzo 2008).

In conclusion and while awaiting more data (including DNA sequence data), we consider *S. basii* a synonym of *S. paradoxa*.

Note 2

In the same publication, Harmaja (1987) also describes *Squamanita umbilicata*, a second new species close to *S. paradoxa*. According to Harmaja, the main differences between the two species are that, in *S. umbilicata*, the pileus is pronouncedly umbilicate (vs. convex-plane in *S. paradoxa*), the granules of the basal part of the stipe are smaller and +/- diffuse (vs. larger and tending to be arranged in distinct horizontal rows), and the gills are narrower and short-decurrent. These differences are probably not significant enough to warrant the creation of a new species; for example, the attachment of the gills to the stipe is very variable in the genus. Many authors (a.o. Redhead *et al.* 1994: 1817 and Laessøe 2012) consider the two species as probable synonyms and we agree with this point of view.

Distribution

NORTH AMERICA: U.S.A., Canada; EUROPE: UK, Spain, Italy, France, Switzerland, Belgium, Netherlands, Germany, Denmark, Norway, Sweden, Finland, Poland, Czech Republic, Slovakia, Ukraine; ASIA: Russia.

A first observation of the species in the **United Kingdom** was made in 1969, on the Isle of Mull (Dennis 1986). The British Mycological Society website contains 40 mentions of the species, most of them being located in the southern third of the country. This relatively high number is perhaps due to an intensive survey of waxcap grasslands. Southern Sweden is another place where the species is relatively less rare than elsewhere in Europe. In **the Netherlands**, four localities are known, all of them after 1989 and located near the coast: Velsen (Noord-Holland, first collection for the country: 1990), Stellendam or Havenhoofd (Zuid-Holland) and island of Ameland (Friesland, two collections). In **France**, the species has been first discovered in Le Porge (Gironde) in 1972 (Romagnesi 1980). Since then, it has been observed in several places. The closest to Belgium are Liessies (départ. Nord, collected on 01.11.2008 by J.-J. Wuilbaut, see fig. 3, and on 21.10.2011 by C. Lécureu) and Saint-Gobain (Aisne 2010). We are also aware of the following sites: Var-Neige (Var, 1973), Col de Bleine (Alpes-Maritimes, 1973), Saint-Brieuc (Côte d’Armor, 1983), Lapte (Haute-Loire, 1992), Mont-de-Marsan (Landes, 1996), Tréglamus (Côtes d’Armor, 2009). In **Germany**, 6 localities are mentioned by the Deutsche Gesellschaft für Mykologie website. The closest to Belgium is Mannheim-Feudenheim, Wingertsbuckel (Baden-

Württemberg 1990). The species has not been observed yet in the **Grand-Duchy of Luxembourg**, fide M.-T. Tholl and M. Garnier-Delcourt (pers. comm.). In **Belgium**, it seems that the collection described here is the only one known for the country.

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