ISSN 1450-7153

*Mycologia Montenegrina*

*(Separatum)*

# THE DISTRIBUTION AND OCCURRENCE OF COPROPHILOUS *ASCOBOLACEAE*

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*Mycol. Monten.* X: 211-227, 2007

ISSN 1450-7153
UDK 582.282.16

# THE DISTRIBUTION AND OCCURRENCE OF COPROPHILOUS *ASCOBOLACEAE*

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**Abstract**

The occurrence of coprophilous members of the *Ascobolaceae* (Pezizales) developing on over 1000 samples of herbivore dung from various parts of the world, from 65°N to 52°S, after incubation in damp chambers, is reviewed and discussed. Relative abundance and occurrence of different species in different geographical regions or on the dung of different animals is reported, the commonest species are identified and notes are given on the distribution of some of the less frequent species. Approximately 11% of fungi developing on dung on incubation in damp chambers are species of *Ascobolaceae*. They are more prevalent on cattle, sheep and goat dung, with over 1.5 species per sample, while dung of hare and tetraonid birds is relatively unsupportive, with less than 0.5 species per sample.

## INTRODUCTION

The core genera of the *Ascobolaceae* are *Ascobolus*, *Saccobolus* and *Thecotheus*, all with species that are predominantly coprophilous. Three others are *Cubonia*, *Cleistoiodophanus* and *Ascophanus*; the position of the first two is uncertain, but it is suggested by some authorities that they may be placed in the *Ascobolaceae*, and many species of the old *Ascophanus* have been reclassified as *Coprotus* species in the *Pyronemataceae*, and the position of those that remain is uncertain. This paper reviews the occurrence and distribution of coprophilous *Ascobolus, Saccobolus* and *Thecotheus* species worldwide, particularly with respect to substrate and latitudinal preferences. Passage of the spores through the gut of an animal is often necessary to facilitate spore germination of coprophilous fungi. They are adapted to the coprophilous habitat by having asci that forcibly discharge their spores at around midday towards the sun, to increase the chances of being widely dispersed into the airstream. Ascospores often have gelatinous appendages, or a complete or partial sheath, that enables them to stick to vegetation to increase the chances of being consumed by grazing animals, and the exospores are often pigmented, to provide protection against UV exposure.

Depending on the source, the number of 'species' in these genera varies considerably. The *Index Fungorum* database (www.speciesfungorum.org) lists approx. 220 species names in total for the three genera, excluding synonyms and varietal taxa, but many of these lack a taxonomic opinion as to their standing, and there are errors. Kirk *et al.* (2001) list 52, 26 and 22

*Ascobolus*, *Saccobolus* and *Thecotheus* spp. respectively, but these numbers were not updated from the earlier edition of the *Dictionary of the Fungi* (Hawksworth *et al.*, 1996). The most recent and authoritative monographs are Brummelen (1967) for *Ascobolus* and *Saccobolus* and Aas (1992) for *Thecotheus*. Aas's thesis is not generally available and Yao & Spooner (2000) provide a summary of the main characters of the 17 species treated by Aas and 3 additional species, and Nagao *et al.* (2003) provide a key to 21 species. Doveri & Coué (in press) added *T. neoapiculatus* and provide a key to all 22 species of *Thecotheus*. Doveri (2004) also provides an update on species of all three genera described subsequently.

*Ascobolus* is the largest genus with 67 species [48 accepted by Brummelen (1967), and 19 species subsequently described], the majority of which are coprophilous. *Saccobolus* has 27 species [18 accepted by Brummelen (1967), and nine species subsequently described], all of which are all coprophilous, and differ mainly from *Ascobolus* in having the ascospores aggregated more or less firmly into a group of usually eight, but occasionally four, spores. The other three genera are *Thecotheus* [17 species accepted by Aas (1992), and 5 described subsequently, most coprophilous], *Cubonia* (three species in Kirk *et al.*, 2001, five in *Index Fungorum*, some coprophilous, all poorly known and of uncertain identity) and *Cleistoiodophanus*, with one coprophilous species (Bezerra & Kimbrough, 1976). The latter authors considered *C. conglutinatus* to be closely related to *Iodophanus*, at the time considered to be in the *Ascobolaceae*, but no longer so.

Since 1993 I have collected, or had sent to me, over 1000 samples of dung from, mainly, herbivorous mammals and birds from various parts of the world. These samples have been incubated in damp chambers (Fig. 1) and observed at intervals over periods of up to several months, until additional species were no longer found. The fungi that developed over a period have been identified and recorded (see, e.g., Richardson, 2001a). These collections have yielded 1115 records of species of *Ascobolaceae*, and in this paper their occurrence and distribution are reviewed, particularly with respect to substrate preferences and latitudinal preferences.



## Results and discussion

The country of origin of samples and the animals from which they came are summarized in Tables 1 and 2. As with most communities, a few species of fungi were relatively abundant, while the majority were infrequent. For those that were abundant it has been possible to statistically analyse their occurrence on different types of dung and to examine their distribution. Members of the *Ascobolaceae* comprised 11% of all coprophilous fungi developing in damp chambers, with species of *Ascobolus* the most frequent (680 records of approx. 20 species), with 4 species present on some samples. *Saccobolus* occurrence was approx. 60% that of *Ascobolus*, which is perhaps to be expected, since the genus has about half as many species, with 413 records of approx. 15 species. *Thecotheus* was the least frequent of the 'main stream' members of the family, with only 22 records (incidence 2%) of five, possibly six, species.

In *Ascobolus*, *A. albidus*, *A. immersus* and *A. stictoideus* were the most frequent, comprising 74% of all *Ascobolus* records. They showed two different patterns of distribution (Table

3, Fig. 2), with *A. immersus* occurring at higher frequencies on cattle, sheep and goat dung from lower latitudes, while *A. albidus* and *A. stictoideus* occurred more frequently at higher latitudes, with *A. albidus* widespread on a variety of dung types, but especially on horse, deer and sheep, and *A. stictoideus* particularly frequent on goose dung. These findings add to the observations of BRUMMELEN (1967), who commented that " *with our rather poor and one-sided knowledge it appeared impossible to form ...conclusions on distribution*" and confirm the cosmopolitan nature of *A. immersus* and *A. stictoideus*, but with a tendency to tropical and temperate occurrence respectively. They also show that *A. albidus*, with records from the southern hemisphere, is cosmopolitan but with a preference for temperate regions.

The most frequent *Saccobolus* species were *S. versicolor* and *S. depauperatus*, accounting for 80% of all *Saccobolus* records. *S. versicolor* was present on 51% of the rabbit samples, while it was less frequent on dung of sheep (29%), cattle, deer and hare (15-18%), and scarce on other dungs. It is widely distributed, with a tendency to occur at higher latitudes (Fig. 2). *S. depauperatus* was more frequent on goat dung at 35%, and much less frequent on any other substrate. There was a significant tendency for the frequency to be higher at lower latitudes, but this may be in part an artefact, since relatively few goat samples were collected, and the majority of those were from lower latitudes (< 40° N/S).

Species of *Thecotheus* occurred most frequently on horse and cattle dung, at a frequency of approx. 10 %, compared to ca 2.5% on other substrates. *T. holmskjoldii* was the most frequent, accounting for just over half the records. There were insufficient samples to come to any conclusions about global distribution, but the impression is that the genus is widespread, with relatively high incidence in some samples from widely separated places – e.g., the Aegean islands of Greece (13% of samples), Tenerife (13%) and Iceland (6%).



Members of the *Ascobolaceae* were much more frequent on bovine dung (cattle, sheep and goat), and much less frequent on dung of hare and tetraonid birds (grouse and ptarmigan) (Table 3).

## NOTES ON SELECTED SPECIES

### ASCOBOLUS

***A. albidus*** P. Crouan & H. Crouan (Fig. 3).

This was the most frequent species observed, recorded from most substrates, but most often on deer, horse and sheep, and less commonly on rabbit, hare and cattle, and rarely or not at all on bird and other substrates examined (Table 3). These findings confirm the observations of BRUMMELEN (1967) who, from his studies of both fresh and herbarium material, suggested that *A. albidus* was mainly a north temperate species. Only one northern hemisphere occurrence south of 40°N was recorded, and from the southern hemisphere only four records from 105 samples (4%), compared to 24% occurrence in northern hemisphere samples.

***A. brantophilus*** Dissing (Fig. 4).

This was described by DISSING (1989) from a large number of collections of goose dung from Canada, Greenland and Norway, and subsequently collected from three out of five

samples of goose dung from Iceland (Richardson, 2004), and Yell, one of the northernmost U.K. Shetland Islands (Richardson, 2007). I also have a record from the Southern Ocean area (Falkland Islands, Stanley, near Yorke Bay, goose dung, 51.70°S, 57.77°W, 14 May, 2000 (MJR 26/00, E), so this species is of interest both in its occurrence at high latitudes and in its, so far, exclusive occurrence on goose dung. This distribution is similar to that of another goose-associated, high latitude species, *Saccobolus quadrisporus* (q.v.).

***A. brassicae*** P. Crouan & H. Crouan (Fig. 5).

One of the few species in sect. *Sphaeridiobolus*, with globose spores, and relatively infrequent in my collections with only nine records, all from Scotland, mostly on rabbit, and all from samples collected from late November to early March, in keeping with the observation of Paulsen & Dissing (1979). There are records from small mammal droppings from the UK (Bramley, 1985), from Nordic countries (Hansen & Knudsen, 2000), and Brummelen (1967) only lists material studied from Europe and N. America so, apart from Bell's (2005) record from Macquarie Island in the Indian Ocean (55°S), *A. brassicae* would appear to be a mainly northern hemisphere species.

***A. carletonii*** Boud.

This species was first collected in 1912 from capercaillie (*Tetrao urogallus*) dung collected by Charles Macintosh from Inver Woods, Dunkeld, Scotland (Coates, 1923). He sent it to Carleton Rea, who forwarded it to Boudier, who described it (Boudier, 1913). It was subsequently recorded in 1937 from Yorkshire (no details of this record have been found), by the author from grouse (*Lagopus lagopus*) dung in Scotland in 1966 and 1967, and from capybara dung from near Rio de Janeiro, Brazil, in 1989 (Brummelen, 1990). It occurs frequently on grouse or ptarmigan (*Lagopus mutus*) droppings in Scotland and England, and I have 14 records from 36 samples (39%) collected since 1993. It was not, however, recorded from 10 samples from ptarmigan I collected in Iceland in 2002 and 2006. Given that ptarmigan migrate from Iceland to breed in the UK it might be expected that *A. carletonii* might also occur there, and further Icelandic samples should be collected. It was also recorded by Piia Juntunen (personal communication, unpublished thesis) from two samples from Finnmark, Norway, out of 24 collections of rock ptarmigan (*Lagopus mutus*) dung from northern Finland and Norway (69-70°N), from capercaillie dung from northern Italy by Doveri (2004), and by Prokhorov & Raitviir (1991) from two Russian localities, goose dung from the Chegitun River Basin, Chukotka (66°N) and polar partridge (?) dung from Kolguyev Island (69°N), so its distribution would seem to be distinctly northern and closely related to that of the *Tetraonidae*, with whose dung it is almost exclusively associated, and mostly in high latitudes, apart from the occurrence in Brazil.



***A. cervinus*** Berk. & Broome

This appears to be a rare species. Only the type, from deer dung (?) from Sri Lanka, was known when Brummelen (1967) monographed the genus. Subsequently Brummelen & Kristiansen (1998) were able to study some good collections from both north and south Norway, all on elk (*Alces*) dung, and provide a complete description. My samples have pro-

vided 6 collections, from the UK and France (2 each), and from Finland and Spain (Tenerife), four on deer dung, the others on rabbit and goat.

***A. crenulatus*** P. Karst.

This appears to be an infrequent but cosmopolitan species that occurs on a variety of dung types, but it is mainly recorded from the temperate north, with 20 of my 24 collections from > 50°N, all from the UK and Finland, and only four from latitudes between 50°N and 50°S (Florida, USA, and Australia), although BELL (2005) lists 12 records from Australia, from between 16-20°S, and it was the fourth most frequent *Ascobolus* found in her records, after *A. immersus*, a new species in sect. *Dasyobolus*, and *A. dadei*. The majority of my records are from the dung of various deer and lagomorphs.

***A. furfuraceus*** Pers.: Fr.

Possibly one of the best known *Ascobolus* species, because it has larger and more conspicuous apothecia than the commoner *A. albidus* and *A. immersus*, which require microscopic examination of dung for their discovery. It is cosmopolitan and frequently observed in the field on cattle and horse dung. Its occurrence in my moist chambers, 37 records from 1025 samples, of which 98 were from cattle or horse, is perhaps less frequent than may have been expected on the basis of its perceived commonness. It may be that the conditions of the moist chambers do not favour the development of *A. furfuraceus* on incubation, but the ratio of occurrence of *A. furfuraceus* : *A. immersus* from my moist chambers (81:172 = 2.1) is of a similar order to that found in the extensive studies of DOVERI (2004) (21:37 = 1.8), so it is possible that its position as only the fourth most frequent *Ascobolus* species in my collections is a true indication of its relative occurrence. It occurred on 24% of cattle samples, and at a much lower frequency on other dung types (7% on deer, 3% on all others).



***A. hawaiiensis*** Brumm.

Since its description from Hawai'i by BRUMMELEN (1967), *A. hawaiiensis* has been recorded from New Zealand (BELL, 1983), Australia (BELL, 2005), Spain (VALLDOSERA & GUARRO, 1985), Pakistan (BRUMMELEN, 1990), various Central Asian and Transcaucasian states of the old USSR (PROKHOROV & RAITVIIR, 1991), Scotland (RICHARDSON, 1998), Denmark (PAULSEN & DISSING, 1979), Iceland (RICHARDSON, 2004), and I have unpublished records from France, Greece, Australia, Chile and the Falkland Islands, and a total of 36 records from over 1000 samples. Clearly, while it is not a common species, it can be considered to be cosmopolitan in its distribution. It occurred most frequently on sheep (11%) and marsupial dung (15%), and very infrequently on that from deer, horse, rabbit and goose (1-4%). Most of the material I have seen has spores which are slightly smaller than those described by BRUMMELEN (1967), but otherwise the apothecial characters, spore ornamentation and a complete gel are all characteristic of the species. The apothecia are hyaline, very small, often only about 200 µm diam, and so easily overlooked, which may partly explain its apparent rarity.

***A. immersus*** Pers.

The second most frequent *Ascobolus* species, after *A. albidus*, with 172 records from 1025 samples (25% of all *Ascobolus* observed). It is clearly cosmopolitan, with Brummelen (1967) examining numerous specimens from all continents except Antarctica, from Iceland to Argentina, and my collections coming from Iceland to Australia, Chile and the Falkland Islands. It does, however, tend to be more frequent in samples from lower latitudes (Fig. 2), and occurs more frequently on cattle, sheep and goat dung (Table 3).

***A. roseopurpurascens*** Rehm

*A. roseopurpurascens* is distinguished from the related *A. furfuraceus* by the densely aggregated apothecia that are dark pink-purplish brown due to the presence of amorphous pigment amongst the paraphyses. It appears to be infrequent, but widespread in western and central Europe (Brummelen, 1967), with more recent records from Israel and Saudi Arabia (Doveri, 2004), Belgium and France [Ann Bogaerts, National Botanic Garden of Belgium (BR), pers. comm.]. I have five records from Scotland and N. England, on horse, rabbit and cattle dung.

***A. sacchariferus*** Brumm.

Described from deer dung by Brummelen (1967) from material collected from the same locality in the Netherlands in two successive years, there seem to be few later records, apart from a collection on roe-deer dung from Belgium (BR). My records are all from north temperate areas (>42°N), five each from France and Scotland, and one each from the USA (Alaska) and Canada (Yukon). Both N. American collections were on dung of Dall's sheep, and two of the French collections were from mouflon sheep. Five of the other eight collections were from deer.



***A. scatigenus*** (Berk. & M.A. Curtis) Brumm. (Fig. 6).

This is the largest species in the genus, and quite spectacular, with mature apothecia reaching 3 cm diam, with the mature disc changing instantaneously from dark purple to buff with the simultaneous discharge of spores. Its distribution is distinctly tropical, and I have two records, from Dominica and Puerto Rico, both from cattle.

Brummelen (1967) examined many specimens from pantropical locations, all except one from dung. Valldosera & Guarro (1985) recorded it, however, from Spain, (ca 42°N and at an elevation of approx. 1000 m a.s.l.), and Prokhorov & Raitviir (1991) also report an unusual non-coprophilous and relatively northern and high elevation occurrence on stems of *Ligularia*, a perennial composite from Tajikistan (approx. 39°N and 2750 m a.s.l.).

***A. stictoideus*** Speg.

This is a common species that appears to be cosmopolitan, with records from the Falkland Islands in the southern hemisphere to Iceland in the north, but significantly lower frequency at lower latitudes. The records are from a wide range of substrates, but by far the highest proportion is from goose droppings, with it occurring on 55% of the 29 samples studied, and

much lower frequencies on rabbit, cattle and sheep (10-20%). Five records of *A. degluptus* Brumm. are included with those for *A. stictoideus*, as the two species are very similar in both morphology and ecology. Spores with the peeling exospore that defines *A. degluptus* have been found in the same apothecium, and even in the same ascus, as spores that are more typical of *A. stictoideus*. BOOTH (1982) recorded it on snow goose dung collected from Devon Island, north east of Greenland at 75-76°N. PAULSEN & DISSING (1979) recorded it for the first time in Denmark, from rabbit, hare and deer dung and, interestingly illustrate, as spores of *A. stictoideus*, spores that are very similar to those of *A. degluptus* as described by BRUMMELEN (1967).

SACCOBOLUS

***S. caesariatus*** Renny

A rare species, with the type represented only by a drawing in the British Museum, and two collections from Netherlands and Austria studied by BRUMMELEN (1967). There have been few records since then, but DOVERI (2004) described five collections from rabbit, goat and cattle dung from Italy. An additional collection was identified by BRUMMELEN (pers. communication) from rabbit pellets collected from SW Scotland (MJR 53/00). Interestingly, this collection yielded *A. albidus*, *S. versicolor* and *Ascozonus woolhopensis* from material incubated by the author in Scotland, while a sample of pellets from the same collection sent to J. van Brummelen yielded *A. sacchariferus*, *S. caesariatus* and *Ascozonus monascus*.



***S. citrinus*** Boud. & Torrend (Fig. 7)

The commonest of the species in sect. *Saccobolus*, which have spores arranged in a regular 4 x 2 pattern (Pattern I) and yellowish apothecia. The 31 records I have are from Australia to Iceland, and come from a wide range of dung types:- sheep (8), horse (6), rabbit and cattle (5 each), goat (3), deer (2), and wallaby and capybara (1 each).

***S. depauperatus*** (Berk. & Broome) Rehm

The second most frequent *Saccobolus*, but much less so than *S. versicolor*, which it resembles in all respects except size, with smaller apothecia, asci, spore clusters and spores. There would also appear to be an ecological or biogeographical difference, since it occurred much more frequently in low latitude samples (Fig. 2) than in samples from temperate regions.

***S. dilutellus*** (Fuck.) Sacc. and ***S. globuliferellus*** Seaver

From the few collections available for study BRUMMELEN (1967) considered these to be vicarious species, i.e. different species strikingly close to each other with one, *S. dilutellus*, occurring in Europe (Germany, France and Czech Republic) and being replaced in North and South America (Canada, USA and Argentina) by *S. globuliferellus*. LARSEN (1970) found both species in Denmark, on several samples of dung from deer, and one of hare. Similarly, PROKHOROV & RAITVIIR (1991) also found both species in Russia, and S. *globuliferellus* in Belarus. On the basis of the descriptions of BRUMMELEN (1967) and LARSEN (1970) I identified a collection from W. Australia as *S. globuliferellus* and two from Canada (Yukon) and USA (California) as *S. dilutellus*. It is possible, therefore, that these two fungi are syn-

onymous, since they are not geographically isolated, as originally supposed. Careful morphological and molecular study could perhaps confirm that suggestion.

Material examined: *S. dilutellus*. USA, California, Sonora Pass, white tailed (?) jack rabbit (*Lepus townsendii*) dung, 18.28°N, 65.85°W, 2940 m, 1 Sep., 2001 (MJR 53/01). Canada, Yukon Territory, Kluane Lake Res. St., arctic ground squirrel (*Spermophilus parryii*) dung, coll. Aimee Pelletier, 61°N, 138°W, ca 1000 m, 10 Aug., 2004 (MJR 97/04, E). *S. globuliferellus*. Australia, WA, Pemberton, on rabbit dung, 34.44°S, 116.05°E, 29 Sep., 1999 (MJR 36/99, E).

***S. glaber*** (Pers.) Lambotte

A cosmopolitan species, with many specimens examined by Brummelen (1967) from many countries worldwide. Relatively infrequent in my collections, with nine records from Finland, UK, Puerto Rico, Costa Rica and Australia, mostly on cattle or sheep dung.

***S. minimus*** Velen.

Brummelen (1967) noted that because this fungus has such small apothecia, it is only collected rarely, and will probably have a worldwide distribution. He studied material from Europe, Canada, USA, Thailand, Hawai'i, and Ecuador (Galapagos), and Doveri (2004) reported 11 collections from Italy, so most collections are from temperate regions. Redressing the balance, 6 of my collections are tropical in origin, from Puerto Rico, St Lucia and the US Virgin Islands, between 13° and 19°N, and the seventh is from W. Australia (35°S).



***S. portoricensis*** Seaver

At the time of Brummelen's(1967) monograph this was known only from the type collection, described by Seaver from the dung of an unidentified animal from Puerto Rico. As there are no native land mammals in Puerto Rico, or most of the other Caribbean islands, it is possible that the dung would have been from an introduced domestic mammal – horse, cattle, sheep or goat. There are few subsequent records so the species must be considered rare, and with a tropical distribution. Ebersohn & Eicker (1997) recorded it from the dung of game animals in the Kruger National Park, South Africa, Bell (2005) illustrates material from Northern Territory, Australia, there is a record from India (Anonymous, 2001-07), and details are given below of three collections, all from cattle dung, from Puerto Rico and two Lesser Antillean islands.

Material examined: Puerto Rico, Canovanas, Caribbean National Forest, Route PR 186, 18.28°N, 65.85°W, 640 m, 13 March, 1997 (MJR 4/97, E). Dominica, St Paul, Springfield, 15.34°N, 61.38°W, 380 m, 18 March, 2000 (MJR 3/00, E). St Lucia, Mamiku Valley, Praslin, 13.87°N, 60.91°W, 2 March 2004 (MJR 5/04).

***S. quadrisporus*** Massee & E. S. Salmon

Although originally described from goose dung in the London Zoo this species is characteristically found on goose dung from high latitudes. It has been recorded from goose

dung from Spitsbergen (78°N) (Eckblad, 1968), from Churchill (59°N) and Devon Island (75°N) in NE Canada (Booth, 1982), from Kolguyev Island in the Barents Sea, northern Russia (69°N) (Prokhorov & Raitviir, 1991), and from Iceland (64°N) (Richardson, 2004). Dissing (1987, 1989) obtained three records of *S. quadrisporus* from eastern Greenland (72°N), in addition to numerous records of related 4-spored *Saccobolus* spp. from Greenland, Norway and Arctic Canada. I also have two records of *S. quadrisporus* on goose dung from the Falkland Islands in the Southern Ocean (51-52°S). The lowest northern hemisphere latitude record (51°N) would appear to be that of De Sloover (2002), from duck dung in Belgium.

***S. truncatus*** Velen.

A widespread species, probably underrecorded because of its small size, but Doveri (2004) provides an extensive bibliography of records worldwide. Thirteen of the fourteen records from my samples are from low latitudes (20°S – 30°N), and one is from the UK, from a wide range of dung types, but mostly from cattle, sheep and horse.

***S. verrucisporus*** Brumm.

Described by Brummelen (1967) from New Guinea, it was recorded from Spain by Valldosera & Guarro (1988), and Prokhorov (1989) suggested that it is widely distributed but rarely reported and cited records from India, Japan, Venezuela, Czechoslovakia and Poland, and described three records from Estonia. There were few subsequent records of this small, rough-spored species until Bell (2005), reported 42 records from Australia, where it comprised over 50% of all *Saccobolus* records, and from New Zealand (Anonymous, 2001-07), and it has been reported from South Africa (Ebersohn & Eicker, 1997), and Brazil (Richardson, 2001b) and I have one unpublished record each from Malaysia and Guadeloupe.



Material examined: Malaysia, Pantai Cherating, Terrengannu, on goat dung, coll. A.J. Whalley, 5°N, 103°E, 10 April, 2001 (MJR 10/01). France, Guadeloupe, Grande Terre, St Anne, Plage Bois Jolan, 16.23°N; 61.35°W, 11 Feb., 2007 (MJR 4/07, E).

***S. versicolor*** (P. Karst.) P. Karst.

Brummelen (1967) observed that *S. versicolor* is the commonest species of the genus, with a worldwide distribution, although his studies did not include any material from the southern hemisphere. It was also, by far, the commonest in my collections, accounting from almost two thirds of all *Saccobolus* occurrences, and included records from Australia and the Falkland Islands (3 each), and Chile (2). There was a slight, but non-significant tendency for occurrences to be more frequent at higher latitudes.

THECOTHEUS

***T. crustaceus*** (Starbäck) Aas & N. Lundq.

*Thecotheus crustaceus* is widespread but, from published data, less frequent than *T. holmskjoldii* and *T. pelletieri*, and reported mostly from temperate regions, so it is interesting to

note that Bell's (2005) record from Australia is from Mt Kosciusko. It occurs mostly on horse dung, and can be locally very frequent, as exemplified by its occurrence on four out of eight collections made in 2006 over an area of ca 5000 km$^2$ in the valleys of the adjacent Hvítá and Þhórsá rivers in SW Iceland (Richardson, in press).

***T. holmskjoldii*** (E.C. Hansen) Chenant. (Fig. 8).

Aas (1992) found this to be one of the two most frequent species, and about half the collections he studied occurred on cattle dung, with a distinctly north temperate to arctic distribution, with only occasional records from south of the Mediterranean area or from the southern hemisphere. It was also the most frequent species recorded in Italy by Doveri (2004), with 13 of his records coming from cattle or deer dung. This is confirmed by the current observations, with 12 collections all from the northern hemisphere, over the range 28°N (Tenerife) to 62°N (Finland), but mostly from sheep (6), sheep/goat (3), horse (2) and deer (1).

***T. lundqvistii*** Aas

A rare north temperate species, apparently only recorded from Sweden and Spain (Aas, 1992) and Italy (Doveri, 2004). My collections have yielded one record, from France, which is a new record for that country so details of the collection are given below. It was originally thought to be a large spored collection of *T. keithii,* which is more frequent, but the combination of larger spores and asci, and the very minute granulation of the spores at maturity, agree more with the description of *T. lundqvistii*.



Material examined: France, Aude/Pyrénées-Orientales, Pic Dourmidou, 42.47°N, 2.26°E, 1843 m, 21 April, 2004 (MJR 20/04).

**Apothecia** ca 2.5 mm diam, pale, almost white, with scurfy exterior. **Asci** KI +ve, cylindrical, 225-290 µm (<350 µm when mature) x 21-29 µm. **Paraphyses** densely packed, hyaline, slightly swollen at the tips to 3-4 µm. **Spores** ellipsoid, 22.5-25.5 x 12.5-13 µm, with polar apiculi ca 3 x 3 µm and perisporal gel.

***T. pelletieri*** (H. Crouan & P. Crouan) Boud.

This, with *T. holmskjoldii,* is one of the most frequent species, particularly characterised by its 32-spored asci. Aas (1992) notes that it is cosmopolitan, occurs on a wide range of dung types, but most frequently on cattle, and is probably the most frequently collected *Thecotheus* species. My collections yielded only two records, both from cattle, from Costa Rica and Queensland, Australia.

Material examined: Costa Rica, San Luis, 10.28°N, 84.78°W, 13 Feb., 1997 (MJR 2/97, E). Australia, Queensland, Lamington NP, O'Reilly's, 28.19°S, 153.09°E, 27 Oct., 1999 (MJR 76/99, E).

Table 1. Origin of samples by country and latitude*

| Latitude | Country (no. of samples) |
|---|---|
| > 60°N | Iceland (70), Scotland (26), Finland (30), Sweden (19), Faeroe Islands (20), Canada, Yukon (11), USA, Alaska (3). Total = 179 |
| 60-57.6°N† | UK (174). Total = 174 |
| 57.6-55.6°N | UK (172). Total = 172 |
| 55.6-50°N | UK (166), UK, Scilly Is. (3), Republic of Ireland (3). Total = 172 |
| 50-40°N | France (63), France, Corsica (5), USA (10), Spain (6). Total = 84 |
| 40-25°N | Italy, Sicily (8), Greece, Aegean Is. (39), Morocco (14), Tunisia (4), Egypt (1), Spain, Canary Is. (16), USA (32). Total = 114 |
| 25-25°N/S | Puerto Rico (5), US Virgin Is. (2), France, Guadeloupe (5), Dominica (4), St Lucia (5), Costa Rica (3), Brazil (7), St Helena (6), Malaysia (1). Total = 38 |
| 25-40°S | Australia (45). Total = 45 |
| 40-50°S | France, Kerguelen Is. (9). Total = 9 |
| 50-60°S | Falkland Is. (36), Chile (2). Total = 38 |

* Regional associations have been maintained, so that a sample just out of the latitudinal class for most of a collection has been considered a part of that group.

† The large number of samples from between 50-60°N has been split into 3 groups to allow more data points to be plotted in Fig. 2.



Table 2. Number of records of *Ascobolaceae* from dung of different animal groups and no. of samples of that substrate examined.

| Main group | Sub-group | No. of samples | No. of Ascobolaceae records | (no. per sample) |
|---|---|---|---|---|
| Lagomorpha | Rabbit (*Oryctolagus* & *Sylvilagus* spp.) | 278 | 303 | (1.1) |
| | Hare (*Lepus* spp.) | 145 | 75 | (0.5) |
| Ungulates | Sheep and goat (Bovidae spp.) | 237 | 365 | (1.5) |
| | Horse, ponies, asses (*Equus* spp.) | 55 | 67 | (1.2) |
| | Cattle (*Bos* spp.) | 46 | 87 | (1.9) |
| | Deer (Cervidae spp.) | 126 | 134 | (1.1) |
| Other mammals | *e.g.* marsupials, rodent, vole, fox, camel | 56 | 36 | (0.6) |
| Aves | Grouse, ptarmigan, capercaillie (*Lagopus* and *Tetrao* spp.) | 53 | 18 | (0.3) |
| | Geese (Anatidae spp.) | 29 | 30 | (1.1) |

Table 3. Substrate preferences of the six commonest *Ascobolus* and three commonest *Saccobolus* spp. recorded from 1025 samples of dung - % of dung samples from different animal sources with the species (blank cells are substrates with an incidence of <1%). The highest incidences of species on a particular substrate are indicated by **bold** type.

| | *N* | rabbit | hare | cattle | sheep | goat | deer | horse | goose | tetraonid |
|---|---|---|---|---|---|---|---|---|---|---|
| *A. albidus* | 222 | 21 | 20 | 17 | **30** | | **33** | **35** | 7 | 2 |
| *A. immersus* | 172 | 7 | 4 | **52** | **38** | **32** | 12 | 26 | 7 | 2 |
| *A. stictoideus* [inc. | 105 | 10 | 3 | 11 | 20 | 3 | 6 | 4 | **55** | 2 |
| *A. degluptus*] | | | | | | | | | | |
| *A. furfuraceus* | 37 | 3 | | **24** | 3 | 3 | 7 | 2 | | |
| *A. hawaiiensis* | 36 | 3 | | | **11** | | | 2 | 3 | |
| *A. crenulatus* | 24 | 3 | 1 | | | 3 | **8** | | | 2 |
| *S. versicolor* | 261 | **51** | 16 | 18 | 29 | 6 | 17 | 9 | | |
| *S. depauperatus* | 63 | 3 | 2 | 4 | 7 | **35** | 6 | 13 | 3 | |
| *S. citrinus* | 31 | 2 | | **11** | 4 | 9 | 2 | **11** | | |



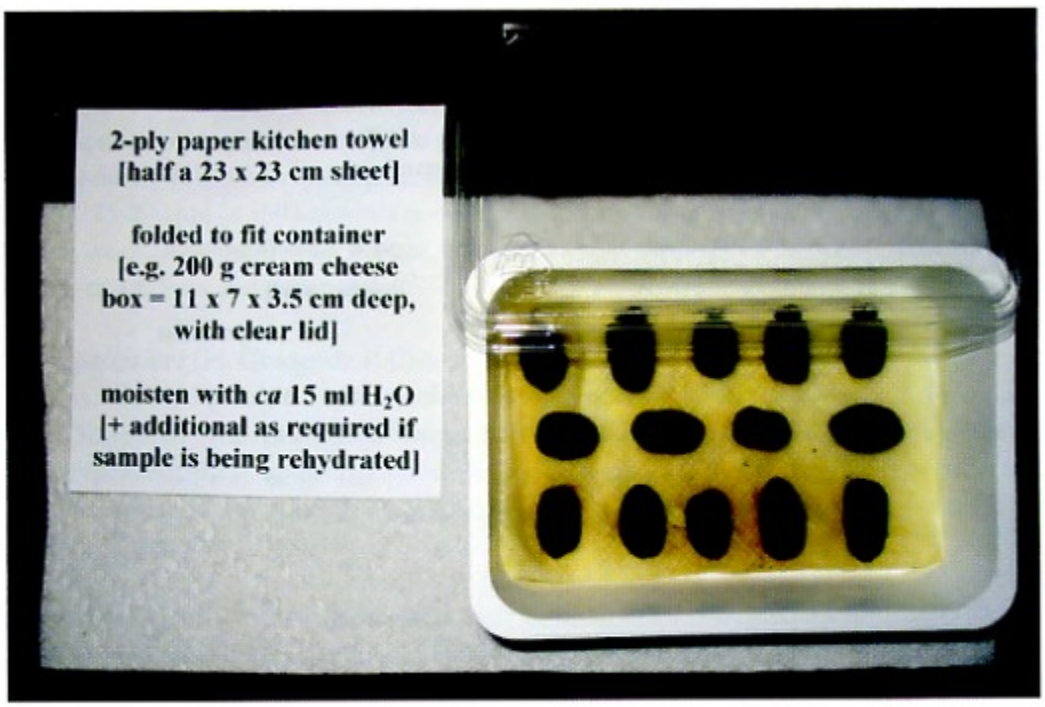



Fig. 1. Details of damp chamber incubation. During incubation the box is covered with its transparent lid.

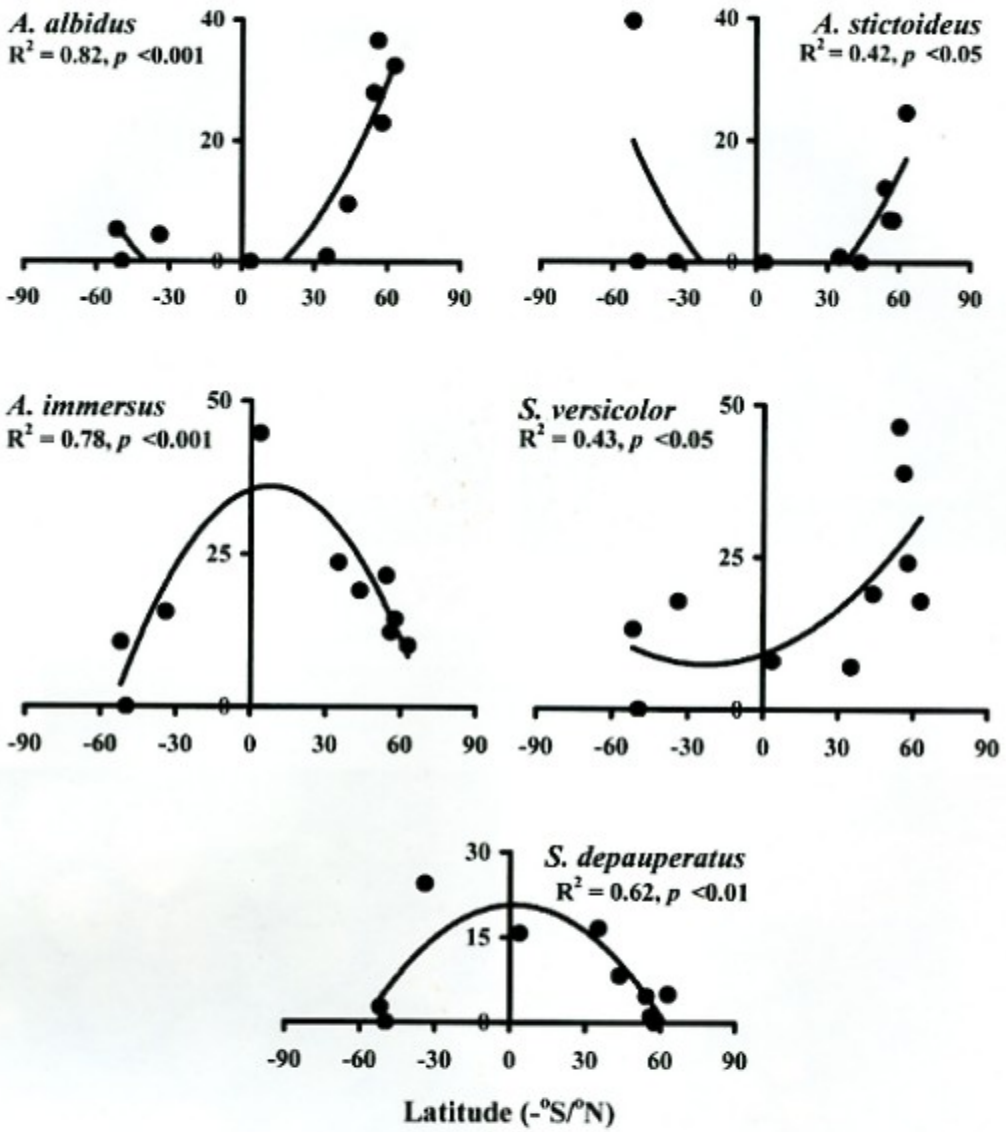



Fig. 2. Frequency of occurrence (%) of the commonest *Ascobolus* and *Saccobolus* species from 1025 samples of dung collected from different latitudinal ranges.

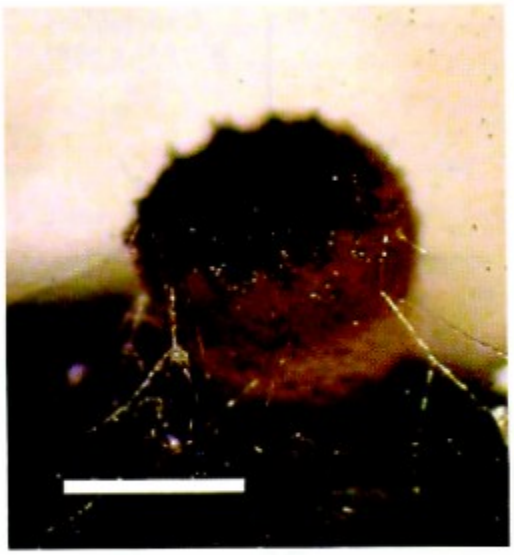


Fig. 3. Apothecium of *Ascobolus albidus*. Scale bars: fig. 3 = 500 µm;

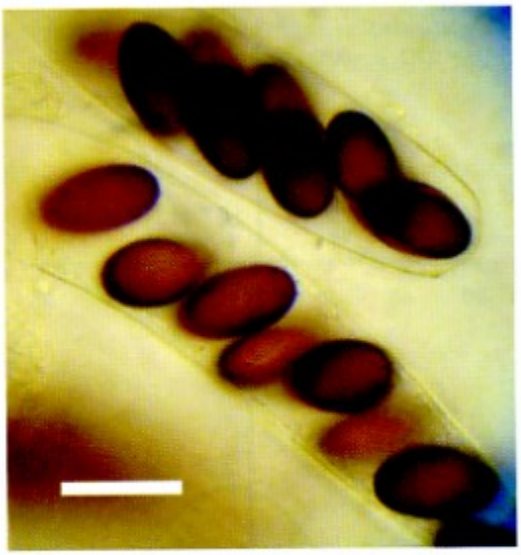
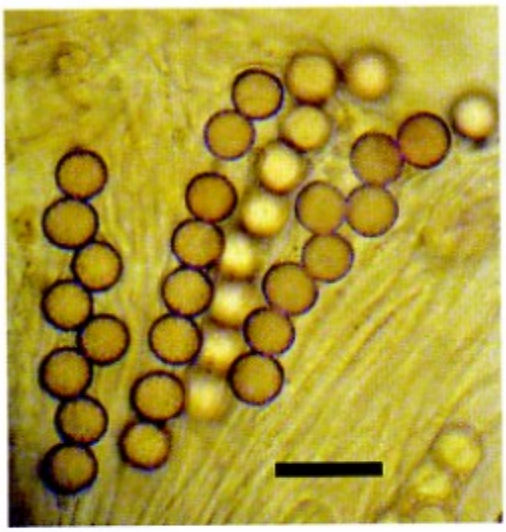


Fig. 4. *Ascobolus brantophilus*, spores in ascus, showing smooth exospore with only occasional and faint cracks. Scale bars: fig. 4 = 20µm.





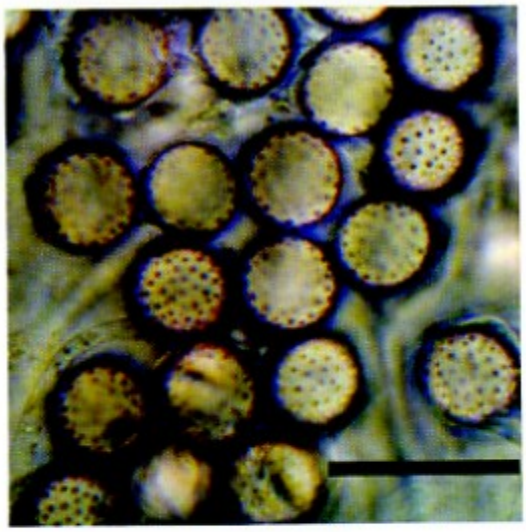


Fig. 5. Asci and spores of *Ascobolus brassicae*. Scale bars = 20 µm.

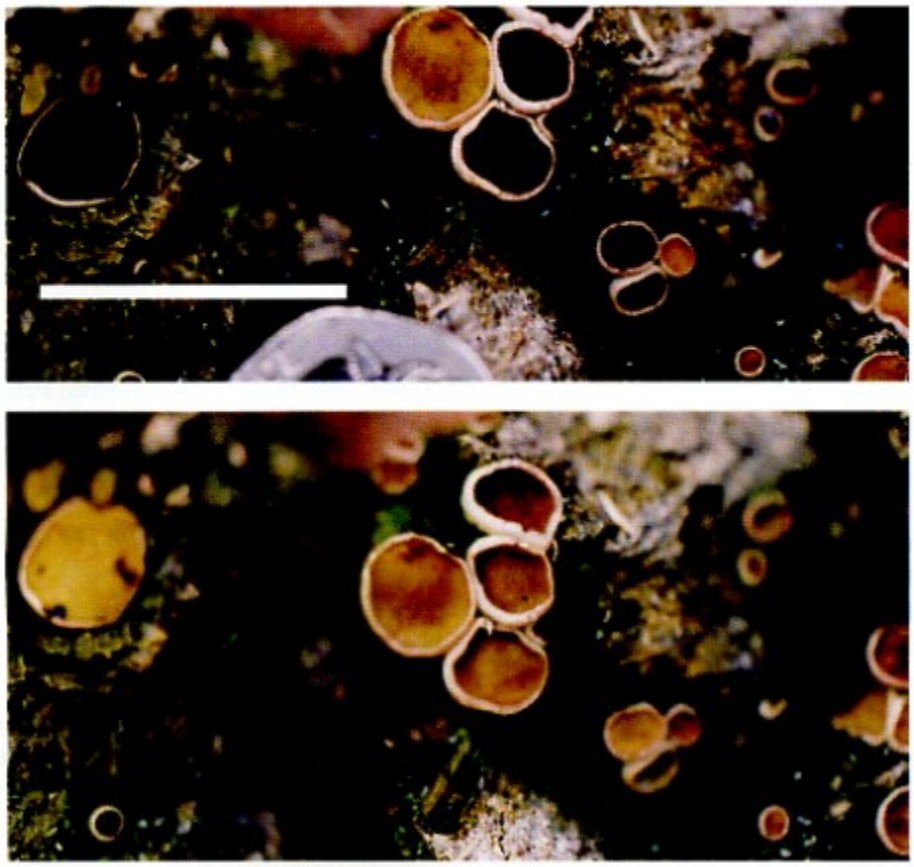




Fig. 6. Apothecia of *Ascobolus scatigenus*, before (above) and after (below) spore discharge. Scale bar = 20mm.

Fig. 7. *Saccobolus citrinus* asci, showing characteristic 4 x 2 (pattern 1) arrangement of spores. Scale bars: fig. 7 = 50 µm

Fig. 8. *Thecotheus holmskjoldii* apothecia. Scale bars: fig. 8 = 1mm.

Acknowledgements

I am grateful to my wife Barbara, Roy Watling, Kathleen Birchall, and to many other friends who have been quite happy to pack a supply of paper envelopes on their travels to provide me with samples for study, or to wait while I searched for pearls, and to Ann Bell, Francesco Doveri, and Joop van Brummelen for many interesting discussions and much encouragement.

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