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A TALE OF TWO SPECIES—POSSIBLE ORIGINS OF RED TO PURPLE-COLOURED *GYMNOPILUS* SPECIES IN EUROPE

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Abstract

Reports of exotic purple-coloured *Gymnopilus* species from separate locations in Europe have sparked interest in whether the species are native to the areas where they are found, or have been introduced recently with wood or with plants. Four of these collections have been investigated by morphological and also molecular means where possible, and compared with similar species from the Southern Hemisphere. Although some variation in character states is present, both sets of data confirm the presence of two separate, but closely related species *Gymnopilus dilepis* and *Gymnopilus purpuratus* both of which are also found in Australia. *Gymnopilus mullaunius* from Australia is reduced to synonymy with *Gymnopilus purpuratus*.

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Introduction

Gymnopilus is easily recognised in the field by its bright, golden to rust-brown colour resulting from the presence of styrylpyrone pigments. The occurrence of wine-red to purple colours masking the rich gold colour is not frequently encountered, but numerous species exhibiting these colours, sometimes in association with blue-green colours have been described from most continents.

In Europe, *Gymnopilus purpuratus* (Cooke & Massee) Singer was originally described from tree-fern stems in a glass house at Kew Gardens, Great Britain (Cooke & Massee 1890), where it was regarded as exotic. A red-coloured *Gymnopilus intermedius* (Singer) Singer was later reported from birch and chestnut logs in the Caucasus Mountains (1929), but no other red to purple-coloured *Gymnopilus* were described in the intervening 60 years until a succession of reports of the presence of *Gymnopilus purpuratus* from continental Europe, including Kreisel & Lindquist (1988), Gsell (1995), and also *Gymnopilus dilepis* from Great Britain by Tantram (1998), Watling (1998), Kokobun, Farrow and Leech (Henrici 2002). In all cases the species were described growing under warm conditions, initially from pigsty woodchip litter and decomposing fibreboard, and later in glasshouses, potplants and woodchip piles. More recently *Gymnopilus igniculis* Deneyera, P.-A. Moreau & Wuilbaut has been recorded from smouldering coal slag heaps in Belgium (Deneyera *et al.* 2002) and *Gymnopilus luteofolius* (Peck) Singer from an area of geothermal activity (Bon & Roux 2002).

These reports indicate a preference for warm growing conditions not consistently found in Northern Europe, and are suggestive of tropical to warm temperate origins for these species. *Gymnopilus dilepis* (Berk. & Broome) Singer, first described from Sri Lanka (Berkeley & Broome 1871) is widespread in S.E. Asia and is commonly found growing on coconut stumps (Treu 1998, Watling 1998). *Gymnopilus purpuratus* has been redescribed from Chile (Singer 1969), and may have been brought recently to Europe on grain from neighbouring Argentina.

Gymnopilus purpureo-nitens (Cooke & Massee) Pegler, *Gymnopilus mullaunius* Grgurinovic and *Gymnopilus moabus* Grgurinovic have been described from Australia, all of which are wine-red to purple at maturity, as well as *Gymnopilus megasporus* Grgurinovic which exhibited red to purple colours during development (Grgurinovic 1997). The presence of a further scaly, wine-red coloured species with smaller spores was detected by Rees

(1996) and provisionally named *Gymnopilus vinaceus*. Its microcharacters did not match those illustrated by Pegler (1986) for *Gymnopilus dilepis*, but were similar to *Gymnopilus norfolkensis* B.J.Rees & Lepp (2000) described from the Australian Federal Territory Norfolk Island. This species had a pronounced densely fibrillose to membranous annulus which disappeared shortly after the expansion of the pileus.

The presence of a membranous, more or less persistent annulus has been used to group *Gymnopilus* species into two subgenera (Hesler 1969, Romagnesi 1942, Singer 1951) although Singer was of the opinion that it 'might not be a character of primary importance'. Recent findings (Rees *et al.* 2002) have indicated that species with a persistent annulus are independant phylogenetically from those in which the annulus is not persistent. Problems with identification arise when the annulus and colours of a collection are ephemeral, and provision must be made for this possibility when keys to species are constructed. Size and shape of spores and cystidia (and the location of the latter) are regarded as important characters for species identification. Additional characters, including the arrangement of cells in the subhymenium and the orientation of pileus tramal hyphae, are also useful according to Guzmán-Dávalos (2003).

The concentration of yellow to rust-coloured styrylpyrone pigments, *bis*-noryangonin and hispidin, is highest in young fruit bodies of purple-coloured *Gymnopilus* species and very low in mature fruit bodies (Rees & Ye 1999). The margins and faces of lamellae in small fruit bodies (in which the veil is still present or has just separated from the pileus margin), bear numerous heavily pigmented cells, variously labelled as pseudoparaphyses by Singer (1969), or pseudocystidia (or cystidia) by Thomas *et al.* (2003) and Guzmán-Dávalos (2003). At maturity or under dry growing conditions or strong sunlight, purple colours may disappear completely from all parts of the fruit body as well as from pigmented cells microscopically. In Australia, collections which have lost all colour may then be mistaken for the common Australian species *Gymnopilus crociphyllus* (Cooke & Massee) Pegler. Many synonyms for *Gymnopilus dilepis* have been described from Sri Lanka for this reason (Pegler 1986).

Line diagrams, so essential for the differentiation of *Gymnopilus* species, are not available for either the type or Chilean collections of *Gymnopilus purpuratus*. Many Australian collections appear to exhibit features which are not consistent with, or are missing from existing descriptions of *Gymnopilus dilepis* and *Gymnopilus purpuratus*. In order to check the accuracy of identifications of Australian species, a comparison is presented of important morphological and molecular characters which may shed some light on the relationships of collections found in Great Britain and Switzerland with other parts of the world where similar species occur.

The Internal Transcribed Spacer (ITS) region of ribosomal DNA has been used to generate a preliminary phylogeny of Australian and related Northern Hemisphere species of *Gymnopilus* (Rees *et al.* 2002). In this and other phylogenies (Rees *et al.* 2003), *Gymnopilus picreus* (Fr.) P. Karsten and *G. austropicreus* B.J. Rees always emerged basal to the remainder of the species, confirming the view that these species may be ancestral to other species in the genus (Høiland 1990). The isolation of these species from other members of the genus has prompted their use as an outgroup for exploring relationships with other more closely related species in the genus.

Materials and Methods

A total of 16 red to purple-coloured collections of *Gymnopilus*, which had been assigned a variety of names were collected from as wide a geographic range as possible including most States of Australia, and its Federal Territories, Norfolk and Christmas Islands (Table 1). They included collections in which purple colour had been recorded from different parts of the fruit body, a collection with similar microcharacters but no purple colour whatsoever, one emerging after fire, and a species displaying red colours during development.

These were compared morphologically with collections of *Gymnopilus dilepis* from Sri Lanka and Great Britain, *Gymnopilus purpuratus* from Great Britain, Chile and Switzerland, and *Gymnopilus luteofolius* (Peck) Singer from N. America, a species reported to be present in Australia (Fuhrer pers. comm.). Other *Gymnopilus* species with a persistent, membranous annulus, *Gymnopilus junonius* (Fr.) P.D. Orton and *Gymnopilus allochrous nom. prov.* from Australia were included to confirm their independance from species with a fugacious membranous annulus as described by Rees *et al.* (2002). Regrettably no recently dried collections were available of *Gymnopilus dilepis* from the type locality in Sri Lanka, or of *Gymnopilus purpuratus* from Chile for DNA extraction. *Gymnopilus picreus* (Fr.) P. Karsten from Sweden was included as out group for a phylogenetic analysis.

Morphological examination

Tissue was examined microscopically in 5% KOH with the later addition of 1% Congo Red for contrast as described previously (Rees *et al.* 2002). Measures for spore sizes do not include ornamentation or apiculus and basidia sizes do not include length of sterigmata. Terminology for spore and cystidia shapes follows Vellinga (1988). Spore size range is given and *E*, the ratio of the sum of the lengths divided by the sum of the widths for a sample of spores. Where possible young and mature fruit bodies were examined from each collection, as some structures tend to be obscured by a heavy spore load at maturity. Hand-cut transverse sections of lamellae were examined for pleurocystidia as these structures can often be overlooked in squashes. Spore size ranges quoted for *Gymnopilus* species can often be very wide due to the presence of unusually large spores. These are often accompanied by the presence of two- or three-spored basidia. These will be recorded in brackets at the end of the spore size range as their inclusion often masks differences between species.

Table 1. *Gymnopilus* species with red to purple colouring and/or a well-developed fibrillose to membranous annulus.

Species name	Collection No.	Location	GenBank No
G. dilepis (spirit colln)	K. Sivapalan 1984	Jaffna District, Sri Lanka	DNA not obtainable
G. dilepis (purple foot)	UNSW 89/311a	Lismore, N.S.W., AUS	AY386830
G. dilepis (wine red)	UNSW 89/12	Hunters Hill, N.S.W., AUS	AY386825
G. dilepis (Xmas Island)	CANB HL 70329	Xmas Island, AUS protect.	AY386828
G. dilepis (no purple)	UNSW 99/3	Ourimbah, N.S.W., AUS	AY386826
G. dilepis (pine chips)	BA5	Nelson, VIC., AUS	AY386823
G. dilepis (U.K.)	Leech AR 982	Beeston Common, U.K.	AY219594
G. dilepis (U.K.)	Leech AR 406	Holt Lowes, U.K.	AY386824
G. dilepis (after fire)	UNSW 95/2	Ryde, N.S.W., AUS	AY386827
G. dilepis (Queensland)	BRI O'Leary 5	Banyo, QLD, AUS	AY386829
G. junonius (NSW)	UNSW 98/24	Bradley's Head, N.S.W., AUS	AY386831
G. junonius AS 98	AS 25690	Vittlycke, SWEDEN	AF501549
G. junonius (slender)	IB 70/320	Bremen, GERMANY	AF501561
G. junonius (Victoria)	BRV 99/1	Yarra Ranges N. Pk, VIC., AUS	AY219597
G. junonius (S. Aust.)	BRSA 99/29	Parra Wirra , Rec. Pk, S.A., AUS	AY219598
G. luteofolius	JFA 12367	Shelton, Wash., U.S.A.	AY219599
G. megasporus	BRSA 02/02	Victor Hbr, S.A., AUS	AY219601
G. moabus	UNSW 99/38	Audley, N.S.W., AUS	AY219602
G. norfolkensis	CANB HL 1283	Norfolk Is., AUS (protect)	AF 501553
G. picreus	AS 97/103	Karl-Ols, SWEDEN	AF 501557
G. purpuratus (Chile)	SGO 92549	Llanquihue, CHILE	DNA not obtainable
G. purpuratus (U.K.)	K (M)32888	Kew Gdns, G.B.	DNA not obtainable
G. purpuratus (Zurich)	ZT 02/01	Zurich Gdns, Switzerland	AY 386818
G. purpuratus (purple form)	UNSW 99/35	Audley, N.S.W., AUS	AF501552
G. purpuratus (pink form)	UNSW 99/40	Audley, N.S.W., AUS	AY386819
G. purpuratus (S.A.)	BRSA 02/01	Belair N. Pk, S.A., AUS	AY386820
G. purpuratus (W.A.)	BRWA 99/14	Tunney, W.A., AUS	AY386822
G. purpuratus (S.A. shiny)	BRSA 02/11	Mambrey Ck, S.A., AUS	AY386821
G. allochrous	UNSW 02/02	Mt Wilson, N.S.W., AUS	AY386832

Molecular studies

Methods of DNA extraction, and determination of ribosomal ITS sequences, have been described previously (Rees *et al.* 2002). Sequences were aligned with Clustal (Thompson *et al.* 1997) and refined by eye. The length of the aligned sequences, including inserted gaps is 594 bases, of which 51 are parsimony-informative. The alignment is deposited in TreeBase (http://www.treebase.org/treebase/). Phylogenetic relationships were inferred with PAUP* (Swofford 2001). In all analyses gaps were considered as missing data. Trees were rooted using the outgroup taxon *Gymnopilus picreus*, an isolated species within *Gymnopilus* on morphological, chemical and molecular grounds (Rees *et al.* 2002). All sequences are deposited at GenBank (see Table 1).

Results

Morphology

Written descriptions are available for all of the species studied, some more detailed than others, and are not repeated here. Line diagrams are included where none exist, or for comparison of important features in similar species. As microcharacters of *Gymnopilus* can often be very variable within the same species, diagrams display the predominant character states observed in proportion to their frequency, while at the same time illustrating some of the less frequently seen variations. Commentary will be reserved for those features that add to, or differ from existing knowledge. Abbreviations for herbaria follow Holmgren *et al.* (1990) with the exception of the following: BR collections are currently housed at UNSW; private collections—BA (Bruce Fuhrer), Leech (material held at K), AS (Åke Strid), and JFA (material held at UNSW).

1. *Gymnopilus purpuratus* (Cooke & Massee) Singer, *Lilloa* 22: 561 (1951). Fig. 1 [1–4]
Type: K(M) 32888, from tree-fern stems in a glasshouse at Kew Gardens.

Agaricus purpuratus Cooke & Massee, *Grevillea* 18: 73 (1889).
Flammula purpurata (Cooke & Massee) Sacc., *Syll. Fung.* 9: 107 (1891).
Gymnopilus mullaunius Grgurinovic, *Larger Fungi of South Australia*, p. 120 (1997).

Illustrations: Cooke (1888); Massee (1893).

The type collection consists of two small, rust-coloured fruit bodies 10–12 mm in diameter, which probably represent only part of the original collection illustrated as 30–55 mm by Cooke (1888) and 76 mm by Massee (1893). Macroscopic features such as colour and pileal surface texture included in the original description are not visible in these small fruit bodies. Their *pilei* are low convex with an irregular decurved margin (reflexed in some places) which has a striate appearance in a few small areas, and they appear more tomentose than squamulose. *Lamellae* are adnate with tooth in the dry state, and are rich rust-coloured without being paler at the margin. *Stipes* 8–15 × 1 mm are very dark, upcurved above the pileus margin in both cases, and longitudinally striate. There are no obvious velar remains. Flesh is illustrated as purple in Cooke's illustration (1888).

Basidiospores 7.5–8.7 (–9.3) × 4.8–5.7 µm, *E* = 1.64, ellipsoid to amygdaliform, bright rust against a golden-yellow, strongly coloured background, moderately verrucose with darker rust ornamentation forming occasional small ridges, with a small plage, inamyloid at first, and weakly dextrinoid at 24 hours. *Basidia* 17–21 × 5–7 µm, broadly clavate with a short pedicel, mostly hyaline with occasional dull gold pigmented forms, four-spored, sterigmata to 4 µm, accompanied by dark-rust, pigmented basidioles of the same overall size. *Cheilocystidia* are of two different types, (i) cylindrical to ventricose, 18–26 × 4.0–4.5 µm, with a gradually sloping 'neck' section surmounted by a capitellum 3 µm wide with occasional terminal thickening, mostly hyaline, occasionally pigmented, (ii) narrowly saccate cystidia 14–16 × 7–8 µm which are also pigmented. Although pigmented *basidioles* are present on lamella faces, *pleurocystidia* were not seen. *Caulocystidia* 33–42 × 7–8 µm. lecythiform, all hyaline. *Pileipellis* a disrupted cutis consisting of radially parallel, dull melleous, lightly encrusted hyphae with rounded to finger-like terminal cells which would not reinflate to the point where they could be accurately measured. *Spore print* bright rust. 5% KOH on pileus surface turns black (+ve). Golden, rust-coloured pigment diffusing in 5% KOH mounting fluid.

Growth habit and habitat: On tree-fern stems of unknown origin in a glasshouse at Kew Gardens, where it has always been regarded as exotic to Great. Britain.

Material examined: **Great Britain**. Type collection (K).

Chile collections Fig. 1 [5–6]
Three collections identified as the same species were comprehensively described and compared with the type collection of *Gymnopilus purpuratus* by Singer (1969) from several locations near Santiago and Valdivia in Chile. The collections are fully mature, and field characters, especially colour, are extensively described. The presence of an evanescent, purple context and bluish spots on the pileus surface are noteworthy macroscopically. Discrete squamules and a striate margin can be seen in some of these collections, and there is a tendancy for the pileus to become very darkly coloured and almost shiny-smooth looking after drying. Lamellae are also very dark in colour, especially towards the base and may be seen to bear sulphur-coloured granules on their faces. Microscopically spores are similar in size and shape, 7.5–8.7 (–9.6) × (4.5–) 5.1–5.7 µm and fit the range for the type collection, but are slightly wider in general, with *E* values ranging from 1.51–1.56. Spore colour and the colour of the ornamentation are also similar to the type collection. They have a small plage. Basidia and cheilocystidia are similar to the type in shape, but are marginally larger and pigmented, although hyaline forms are present. Vesciculate to saccate pigmented cystidia are present at the lamella margin and on the faces as well, compared to the margin only in the type material. Singer has described these as pseudoparaphyses. The pileipellis consists of much compressed, lightly encrusted, radially parallel hyphae above tramal hyphae which are also radially parallel. Once again surface hyphae are difficult to inflate. Some pigment-filled hyphae are also present in the subpellis. The Singer collections of the species correspond broadly with the type from Kew, bearing in mind that the type collection is of very immature fruit bodies in which spores are frequently more elongate than those shed in nature or in a spore print.

Material examined: **Chile**. Llanquihue: Ensenada, 11.v.1967, *R. Singer* M7080 (SGO); Colaco, 9.v.1967, *R. Singer*. M 6808 (SGO). Valdivia: Hueycolla, 1–4.v.1967, *R. Singer* M6580 (SGO).

Gymnopilus mullaunius Grgurinovic, *Larger Fungi of South Australia*, p.120 (1997). (Botanic Gardens of Adelaide and State Herbarium and the Flora and Fauna of South Australia Handbooks Committee: Adelaide). Type: New South Wales. Neutral Bay, Sydney. Plate 1 (A, C).

Flammula purpurata auct. non Cooke & Massee: Cleland & Cheel, *Trans. Roy. Soc. South Australia* 42: 115 (1918); Cleland, *Toadstools and Mushrooms of South Australia*, p. 124 (1934–1935).

Illustration: Cleland & Cheel (1918) colour.

The species has been described fully by Grgurinovic (1997), who distinguished it from *Gymnopilus purpuratus* (Cooke & Massee) Singer by the presence of a supra-hilar plage on the spores and the absence of deep fulvous-brown, resinous encrustation on the cheilocystidia.

Gymnopilus mullaunius is not found frequently, but enjoys a wide area of distribution in coastal regions in the southern part of Australia including Western Australia. It can be quite variable in colour, ranging from uniform, dull vinaceous-purple to delicate salmon-pink with small patches of teal to aqua-blue colour in the pileus surface. Collections from South and Western Australia tend to be larger and more maroon-red in colour. Depending on age and degree of hydration, these colours can fade to light ochre, with or without purple lingering on in the tips of the scales. Although the type is described as having no velar remains, NSW collections have been seen with remnants of a white fibrillose, fugacious, annulus high up on the stipe in young specimens. Context may be yellow to purple. Although the size range of spores at 6.3–7.5 (–8.7) × 4.5–6.3 µm, (*E* = 1.47–1.56), is smaller than *Gymnopilus purpuratus* K type, the presence of a small plage is consistent with Kew and Chile collections of *G. purpuratus* described above (Figure 1 [7 & 8]). The spores are paler in colour than the type or Chile collections of *G. purpuratus* and have a prominent guttule. They are without bright rust ornamentation. The majority of *Cheilocystidia* are similar in shape to the Chilean material and lie intermediate in size between Northern and Southern Hemisphere collections of *G. purpuratus*. Only occasional pigmented structures are to be found on lamella margins or faces, and saccate to vescicular structures common to the Kew and Chile collections of *G. purpuratus* are rare. Both pleuro- and caulocystidia are absent. The pileipellis consists of radially parallel, lightly encrusted hyphae ranging from 5.3–18 µm wide. Taste varies from slightly to strongly bitter.

Habitat: Solitary to scattered on unidentified decaying logs in wet or dry sclerophyll or occasionally rainforest.

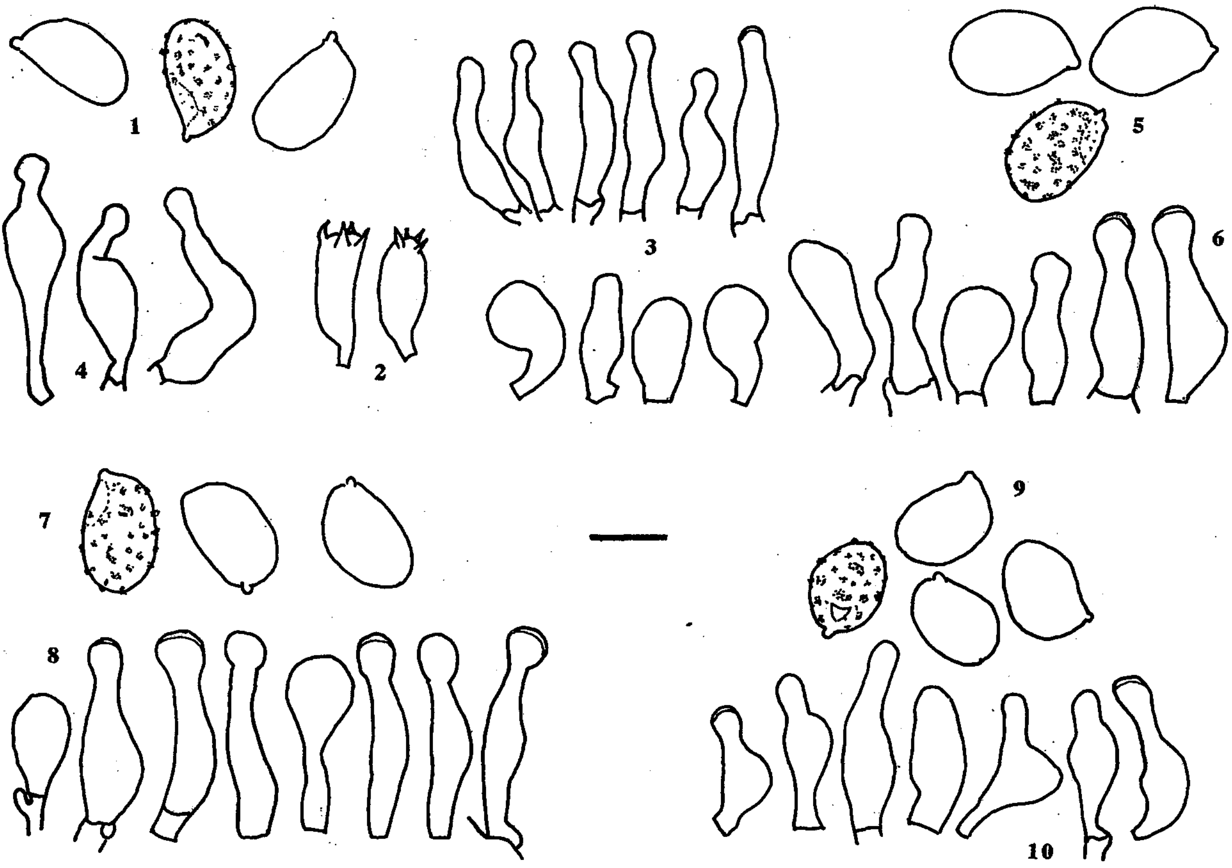

Fig. 1. Gymnopilus purpuratus (K) Type: 1. basidiospores, 2. basidia, 3. cheilocystidia, 4. caulocystidia. Chile collection (SGO) 7080: 5. basidiospores, 6. cheilocystidia. Australian collection (UNSW) 99/28: 7. basidiospores, 8. cheilocystidia. Switzerland (ZT) 684.85/245.86: 9. basidiospores, 10. cheilocystidia. Scale bar = 5 μm for basidiospores, 10 μm for other structures.

Material examined: **New South Wales**: Mosman, Atholl Gdns, 12.v.1918, *J.B. Cleland*, AD 4895; Sydney, Neutral Bay, 26.v.1918, *J.B. Cleland*, AD 4894 (holotype); Audley, Royal Natl Pk, *B.J. & N.W.Rees*, UNSW 99/35, UNSW 99/40. **South Australia**: Belair Natl Pk, 20.ii.2002, *D. Catcheside*, BRSA 02/01; Port Augusta, Mambrey Creek, *B.J. & N.W.Rees*, 24.vi.02, BRSA 02/11. **Western Australia**: Tunney, Old School Site, 16.vi.1999, *B.J. Rees*, BRWA 99/14.

Gymnopilus mullaunius is very similar to *Gymnopilus purpuratus* macro-and microscopically, (Figure 1 [7 & 8]), differing only in the almost total lack of pigmentation of basidia, basidioles and cystidia. Saccate forms are rare and unpigmented. Spores are also paler in colour and their ornamentation is not so rust-coloured, but a small plage is present as in *G. purpuratus* from Chile. South and Western Australian collections of the species tend to be larger and more maroon-red in colour. They also show a tendancy towards having larger basidia. The presence of pleuro- and caulocystidia do not seem to be good taxonomic characters for this species. The similarity of macro- and micro-morphological features between *Gymnopilus purpuratus* type collection from Kew, *G. purpuratus* from Chile and *G. mullaunius* from Australia points to the conclusion that *G. mullaunius* (including the type species) and *G. purpuratus* (Cooke & Massee) Singer are the same species. Although there is variation in pigmentation and the proportion of cystidial shapes present, fruit bodies from all three continents are remarkably similar in appearance, and both species possess spores and cystidia of the same overall size. The Chilean collections show a greater degree of pigmentation, but differences are not thought sufficient to warrant separate species status in the absence of morphological variation. *Gymnopilus mullaunius* Grgurinovic is therefore reduced to synonymy with *G. purpuratus* (Cooke & Massee) Singer.

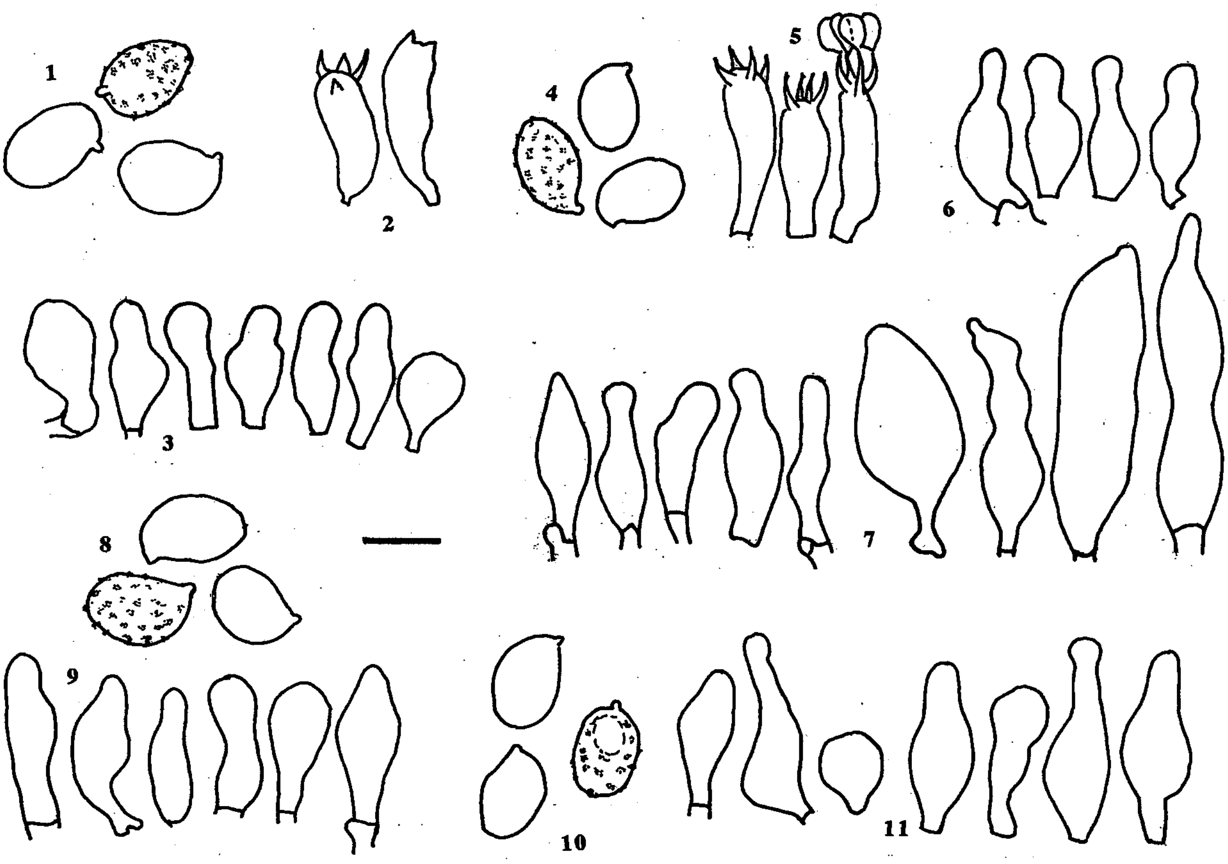

Fig. 2. Gymnopilus dilepis (K) Sri Lankan spirit collection Sivapalan (1984): 1. basidiospores, 2. basidia, 3. cheilocystidia. Gt. Britain Leech AR 982: 4. basidiospores, 5. basidia. 6. cheilocystidia (mature fruit body), 7. cheilocystidia (young fruit body). G. dilepis UNSW 89/12: 8. basidiospores, 9. cheilocystidia. **G. norfolkensis** CANB HL 1283: 10. basidiospores, 11. cheilocystidia. Scale as for Fig. 1.

Gymnopilus purpuratus **collection from Switzerland**

Gymnopilus purpuratus has also been described from a tropical glasshouse in Zurich Botanical Garden by Gsell (1995) and critical features are illustrated in Figure 1 (9 & 10). Two connate fruit bodies forwarded (14–20 mm) were small compared with sizes quoted by Gsell (60 mm), with squamules restricted to the disc of the pileus, and with spore laden, fibrillar, velar remains one fifth of the way down a very slender, elongated stipe (40–50 × 1–1.5 mm). Spores were smaller than the type or Chilean collections of *Gymnopilus purpuratus* (6.6–7.8 × 4.5–5.4 µm, E = 1.46) with a small plage, but still amygdaliform to broadly ellipsoid. Cystidia tended to be smaller overall (15–22 (–24) × 5–7 µm), more lecythiform than either the type or Chilean collections of the species, but were clearly capitate with a distinct neck section rather than cylindrocapitate or utriform. Basidioles were pigmented like the Chilean form of *G. purpuratus*. Pleuro- and caulocystidia were not observed. The suprapellis consists of radially parallel hyphae which do not inflate properly in 5% KOH, but which can occasionally be seen to be quite wide (4.8–14.4 µm). This collection is featured in *Fungi of Switzerland* (Breitenbach & Kränzlin 2000) and has been equated with *Gymnopilus luteofolius* Peck (Singer) by Bon & Roux (2002) in their key to European species. However, spores of the latter species are not as large and cystidia are more fusiform than the Zurich collection. We consider the species to be *G. purpuratus*.

Gymnopilus luteofolius (Peck) Murrill Figure 3 (1 & 2)

Queries have been received within Australia as to whether the identity of scaly, red to purple colored species of *Gymnopilus* occurring on *Pinus radiata* thinnings in plantations in Victoria could be the North American species *Gymnopilus luteofolius* (Peck) Murrill. Illustrations of the species indicate a pink to rose-red pileus and a fairly

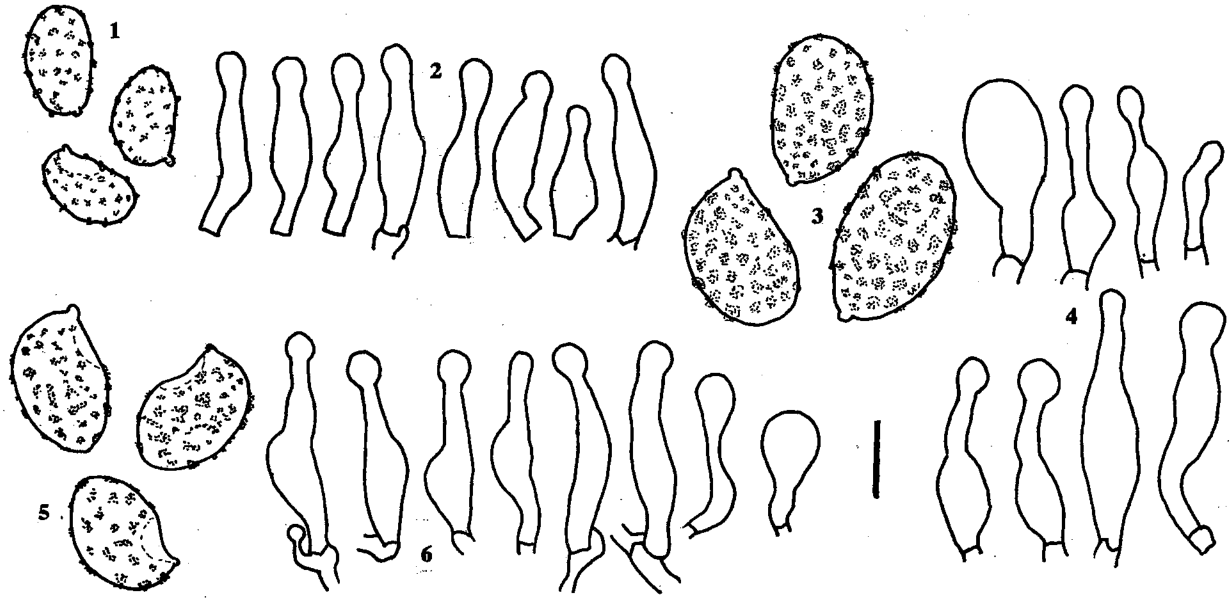

Fig. 3. Gymnopilus luteofolius Type (Forestburgh 1874): 1. basidiospores, 2. cheilocystidia. **G. megasporus** Type AD 4612: 3. basidiospores, 4. cheilocystidia. **G. moabus** UNSW 85/266: 5. basidiospores, 6. cheilocystidia. Scale as for Fig. 1.

stout stipe at maturity. Examination of the type and other collections of *G. luteofolius* indicated a much more robust species than the Victorian collection under study, with spores 6.9–7.8 × 4.0–4.5 µm, and narrowly cylindro-capitate to lecythiform cystidia. There was none of the large spathulate cystidia that are present in the Victorian material. Microcharacters of *Gymnopilus luteofolius* collections from N. America are clearly distinct from Australian collections of *G. dilepis* and despite their robust stature appear more closely related microscopically to the Zurich collection of *Gymnopilus purpuratus*. The fungus from the Victorian pine plantations is *Gymnopilus dilepis*.

Gymnopilus megasporus Grgurinovic Figure 3 (3 & 4)

A collection of this species, which has been comprehensively described by Grgurinovic (1997), was found in South Australia growing high up on the rough, dry trunk of a *Xanthorrhea* species (the grass tree) under its green skirts. The species has been recorded as having reddish brown colours, and has a minority of cystidia similar in shape to those found in *Gymnopilus purpuratus* [(Figure 3 (3 & 4)]. Although spore sizes are very large, four spored basidia predominate with occasional two-spored forms present.

Both *Gymnopilus luteofolius* and *Gymnopilus megasporus* appear to be good species separate from *Gymnopilus purpuratus*.

2. ***Gymnopilus dilepis*** (Berk. & Broome) Singer, *Lilloa* 22: 560 (1951)

Type: Sri Lanka. Kandy District, Peradeniya. Thwaites 878 (K).

Agaricus dilepis Berk. & Broome, *J. Linn. Soc. Bot.* 11: 542 (1871).
A. rhodomalus Berk. & Broome, *loc. cit.* 514.
Armillaria rhodomala (Berk. & Broome) Sacc., *Syll. Fung.* 5: 78 (1887).
Flammula dilepis (Berk. & Broome) Sacc., *Syll. Fung.* 5: 812 (1887).
F. rhodomala (Berk. & Broome) Petch, *Ann. Roy. Bot. Gard., Peradeniya* 9: 125 (1924).

Illustrations: Guzmán-Dávalos (2003), Leech (2002), Thomas *et al.* (2003), Thwaites type (K) cum icon., Treu (1998), Watling (1998).

This species has been comprehensively described (Guzmán-Dávalos 2003, Pegler 1986, Thomas *et al.* 2003). As type material was not available for loan, a spirit collection from Sri Lanka, Northern Province, Jaffna was examined and critical features are presented (Figure 2 [1–3]) Macroscopically both fruit bodies from the spirit collection agreed broadly with previous descriptions, although purple colours were not present. The pileus margins appeared to be striate (possibly an artefact of spirit preservation). Stipes were reasonably stout compared with the original description. Microscopic features were in agreement with Thomas *et al.* (2003), but none of the additional fusiform pseudocystidia illustrated by Guzmán-Dávalos (2003) were present. Cystidia were not as rostrate as indicated by Pegler (1986) for the type collection. No pleurocystidia were observed.

Habitat: The type collection was described as occurring on 'most likely conifer species' (Berkeley & Broome 1871). Modern descriptions indicate a broader substrate range.

Material examined: **Sri Lanka**: Northern Province, Jaffna, 1984, Sivapalan.

The spirit collection of *Gymnopilus dilepis* can be differentiated from *Gymnopilus purpuratus* by its generally smaller spores and utriform rather than ventricose-capitate cheilocystidia. Although pigmented basidia, basidioles, and cystidia are present in *G. dilepis*, no pigmented vesciculate to saccate structures common in *G. purpuratus* are present (Figure 2 [1–3]). Pleurocystidia are not recorded from the type (Thomas *et al.* 2003) or from the spirit collection. In a recent type study of *G. dilepis* Guzmán-Dávalos (2003) has indicated additional widely subfusiform, hyaline or pigmented pseudocystidia with a wide apex are present, but has not indicated whether they are present on the faces of the lamellae.

Gymnopilus dilepis **in Australia** Figure 2 (8 & 9), Plate 1 (B)

Apart from *Gymnopilus purpuratus*, a second, more coarsely scaly, wine-red to purple *Gymnopilus vinaceus nom. prov.* was recognised as being present on mainland Australia (Rees 1996) with smaller spores. These collections did not have cystidia similar to those described for *G. dilepis* by Pegler (1986), but had numerous, heavily pigmented spathulate cystidia at the lamella margin and faces. Now that these have been reported from the type by Guzman-Davalos (2003), the Australian mainland material has been equated with *G. dilepis*.

Australian mainland collections of *Gymnopilus dilepis* have occasional deep blue-green colours in the scales and a substantial fibrillose veil at first. They also have pigmented, spathulate cystidia on lamella margins and faces which may be difficult to detect at maturity. Pigmented basidia and basidioles initially described for *G. dilepis* from India (Thomas *et al.* 2003), did not include spathulate shapes. They have been included in a susequent description of the type collection by Guzmán-Dávalos (2003).

Material examined: **New South Wales**. Lismore, Bungabee State Forest, 23.iii.1984, *A.E. Wood & N. Gartrell*, UNSW 84/311a; Hunters Hill, suburban garden, 19.iii.1989, *B.J. Rees*, UNSW 89/12; Ourimbah, private property, *B.J. Rees* et al. UNSW 99/33; Chatswood West, 'Fairyland', after fire, 11.iii.1995, *N.W. Rees*, UNSW 95/2. **Queensland**. Banyo, in pot plant, date not recorded, O'Leary 5. **Victoria.** Nelson, Kentbruck Pine Plantation, 7.vi.1992, *B. Fuhrer*, BA5.

A collection comprising several fruit bodies was also examined from Christmas Island, another Australian Federal Territory, which lies west of the Wallace line and closer to Java than Australia. The pileus (–30 mm) was yellow with reddish brown scales and had appendiculate velar remains at the margin. The stipe was slender (40 × 4 mm) with longitudinal striations and purple colour. Spores were small 6.3–6.9 × 4.2–4.8 μm, and pale to mid-gold. Cheilocystidia were mostly utriform and hyaline, but some large sphaeropedunculate shapes were also present. They resemble Australian collections of *Gymnopilus dilepis*.

A similar species *Gymnopilus norfolkensis* was published from the Australian Federal Territory Norfolk Island (Rees & Lepp 2000) with spathulate, heavily pigmented cystidia (Figure 2 (10 & 11). *Gymnopilus norfolkensis* (Plate 1D) has many features in common with *Gymnopilus dilepis*. It has small scales which are erect at the disc, and more appressed at the margin. The underlying pileus surface colour is yellow-brown rather than the orange described for *G. dilepis*, and the context is yellow. The stipe width (40 × 10–26 mm), is rather variable within the same collection, but generally fairly stout and longitudinally striate, with less conspicuous purple striations than

G. dilepis Watling collection (1998). Mature spores are marginally smaller, with a more prominent plage. A high proportion of immature small spores 4.0–5.2 × 3.2–4.0 µm with poorly developed ornamentation are also present at all stages of maturity. Lamella margins are crowded with cystidia 15–30 × 6–8 µm, utriform to lecythiform with a pedicellate base and capitate apex 3–4 µm wide, accompanied by conspicuous spathulate to saccate forms, all filled with deep rust pigment (Figure 2 [10 & 11]). Pleurocystidia are abundant, similar to the cheilocystidia and also conspicuously filled with dark-rust pigment.

Although the two species are obviously closely related, *Gymnopilus norfolkensis* differs from *Gymnopilus dilepis* in having a percentage of smaller, poorly ornamented spores, and cheilocystidia which are more broadly lecythiform in shape. In addition, cystidia are heavily pigmented and are present at all stages of maturity on lamella margins and faces. *Gymnopilus norfolkensis* cannot be confused with *Gymnopilus purpuratus* which has smaller scales, larger spores, and in Australia is almost totally devoid of pigmentation, nor *Gymnopilus moabus*, which is a scaly, small-statured species without an annulus, with a persistent deep, wine-red colour. In addition *G. moabus* [Figure 3 (5 & 6)] has strongly verrucose spores and cylindrical to tibiiform cheilocystidia (Rees *et al.* 1999). *Gymnopilus norfolkensis* bears a close resemblance to photographic illustrations of *Gymnopilus luteofolius*, but has smaller spores, and spathulate, utriform to lecythiform, deeply pigmented cheilo- and pleurocystidia, rather than the more narrowly lecythiform cystidia of the latter species.

Recent collections of *Gymnopilus dilepis* from the United Kingdom

Two collections identified as *Gymnopilus dilepis* were found on woodchip piles produced from local timbers on site, in two successive years at two separate locations in Norfolk, England-Beeston Common near Sherringham, and Holt Lowes, 8 km away near Holt. Microscopic examination indicated initially that these collections were not the same species.

Material examined: **Great Britain**. Norfolk, Sherringham, Beeston Common, viii.2001, *F. Farrow*, LEECH 982; Holt, Holt Lowes, 10.viii. 2002, *A.R. Leech*, LEECH 406.

Habitat: On woodchips produced on site from local timbers and therefore not imported with the fungus.

The first, from Beeston Common, consisted of small (–25 mm), densely connate fruit bodies, deep golden-yellow in colour, covered with purple scales on the pileus, and purple fibrils on the stipe. A well-developed, densely fibrillose veil was intact in most fruit bodies between the pileus margin and the stipe. Size range of the moderately verrucose, ellipsoid to amygdaliform spores (6.3–7.2 × 4.5–5.1 µm, *E* = 1.42) and the presence of ventricose-rostrate and spathulate cheilo-and pleurocystidia closely resembled Australian collections identified as *Gymnopilus dilepis*. Cheilocystidia at the margin were extremely variable in shape and size, and were the most variable of any *Gymnopilus* species encountered [Figure 2 (6)].

The second collection from Holt-Lowes was of larger fruit bodies (–95 mm), more rust-coloured in the dry state, but with hints of purple in the minutely squamulose pileus. No velar remains were present. Spores were slightly larger, 6.9–7.8 × 4.8–5.1 µm, (*E* =1.48), and were ellipsoid to amygdaliform, and also moderately verrucose. Cheilocystidia were lecythifom to sub-lageniform with a sub-capitate apex. No utriform or spathulate shapes were present and all structures were hyaline at lamella margins and faces [Figure 2 (4 & 5, 7)].

The absence of heavily pigmented structures at the lamella margins at maturity was similar to that encountered in mature collections of *Gymnopilus dilepis* on the Australian mainland, especially in mid- to northern New South Wales.

Molecular results

The sequences analysed had an aligned length of 594 bases, including ITS1 (212 bases used—about 50 bases were truncated from upstream end, because of poor sequence quality); 5.8S (154 bases) and ITS2 (228 bases). Table 2 shows absolute numbers of base differences between pairs of accessions, according to this alignment. For the purposes of this table and the cladistic analysis, gaps were considered to be missing data. Figure 4 shows the relationships inferred by maximum parsimony analysis.

Table 2. Pairwise numbers of sequence differencecs in the ITS1, 5.8S, and ITS2 region of Gymnopilus accessions.

	ZT02.01	UNSW99.35	UNSW99.40	BRSA02.01	BRSA02.11	BRWA99.14	BRSA02.02	JFA12367	BA5	HL1283	Leech AR406	Leech AR982	UNSW89.12	UNSW99.3	UNSW95.2	HL70329	BRI O Leary5	UNSW89.311a	BRV99.1	BRSA99.29	AS25690	UNSW98.24	IB70.320	UNSW02.02	UNSW99.38	AS97.103
ZT02.01																										
UNSW99.35	2																									
UNSW99.40	3	1																								
BRSA02.01	2	0	1																							
BRSA02.11	3	1	2	1																						
BRWA99.14	2	0	1	0	1																					
BRSA02.02	15	6	14	10	13	13																				
JFA12367	14	6	13	9	11	12	8																			
BA5	20	13	19	16	18	18	18	17																		
HL1283	19	12	18	15	17	17	17	14	6																	
Leech AR406	18	11	17	14	16	16	14	15	4	4																
Leech AR982	17	11	16	13	15	15	15	14	3	3	1															
UNSW89.12	18	11	17	14	16	16	14	15	4	4	0	1														
UNSW99.3	17	11	16	13	15	15	15	14	3	3	1	0	1													
UNSW95.2	17	11	16	13	15	15	16	14	3	4	2	1	1	0												
HL70329	13	10	11	10	10	11	13	12	2	2	1	0	1	0	0											
BRI O Leary5	17	11	16	13	15	15	14	13	3	3	0	0	0	0	1	0										
UNSW89.311a	18	11	17	14	16	16	14	15	4	4	0	1	0	1	2	1	0									
BRV99.1	37	28	38	34	37	37	37	35	37	37	35	34	35	34	35	26	33	35								
BRSA99.29	36	27	37	33	36	36	36	34	36	36	34	33	34	33	34	25	32	34	1							
AS25690	36	27	37	33	36	36	36	34	37	36	35	34	35	34	35	26	33	35	2	1						
UNSW98.24	36	27	37	33	36	36	36	34	36	36	34	33	34	33	34	25	32	34	1	0	1					
IB70.320	19	10	19	17	18	19	18	17	18	18	17	16	17	16	17	11	15	17	0	0	1	0				
UNSW02.02	43	24	42	39	42	41	45	40	42	42	41	40	41	40	41	24	39	41	24	23	24	23	12			
UNSW99.38	27	18	26	21	25	25	24	23	27	29	25	26	25	26	26	19	25	25	32	32	33	32	19	39		
AS97.103	61	36	60	58	60	59	65	58	61	62	64	63	64	63	65	36	63	64	67	66	67	66	43	72	64	

Red- to purple-coloured *Gymnopilus* species with a fugacious, densely fibrillose annulus form a separate clade which is clearly separate from those with a persistent membranous annulus such as *Gymnopilus junonius*. *Gymnopilus moabus*, a dark, wine-red, scaly species with no evidence of a veil at any stage in its development, and with very different microcharacters, is well separated from the other red to purple species.

Within the red- to purple-coloured species with a fugacious annulus, two sister groups are apparent, one containing *Gymnopilus dilepis* and the other *Gymnopilus purpuratus*. *Gymnopilus megasporus* and *Gymnopilus luteofolius* are more closely related to *Gymnopilus purpuratus* than *G. dilepis* but are nevertheless distinct, sharing some common features despite the big difference in spore sizes. Character differences between the species (Table 2) indicate that within the clade containing *Gymnopilus dilepis*, collections from northern and southern hemispheres differ by four to six bases in the total ITS sequence, with geographically more remote Norfolk Island and Victorian collections exhibiting the greatest variation from the remainder of those from the Australian mainland, Christmas Island and Great Britain.

The sister clade containing *Gymnopilus purpuratus*, *Gymnopilus megasporus* and *Gymnopilus luteofolius* are separated from the *G. dilepis* group by up to 20 bases (Table 2), and within the clade, collections of *Gymnopilus purpuratus* from Europe and the southern parts of Australia differ by a maximum of only three bases. South and Western Australian collections of *G. purpuratus* with more maroon-red color and slightly larger basisidia, differ by only one base from east coast collections in ITS sequence. In Australia, this species has not been found north of the Sydney Basin so far. *Gymnopilus luteofolius* differs by 15 bases from *Gymnopilus purpuratus* from Zurich.

Plate 1: A. *Gymnopilus purpuratus* (UNSW 99/40) pink form with flecks of blue-green colour. B. *G. dilepis* (UNSW 89/12) from Australian mainland. C. *G. purpuratus* (UNSW 99/35) purple form. D. *G. dilepis* (CANB (HL) 70329) from Christmas Island. E. & F. *G. norfolkensis* (CANB (HL) 1283). Photography: A.E. Wood & H. Lepp.

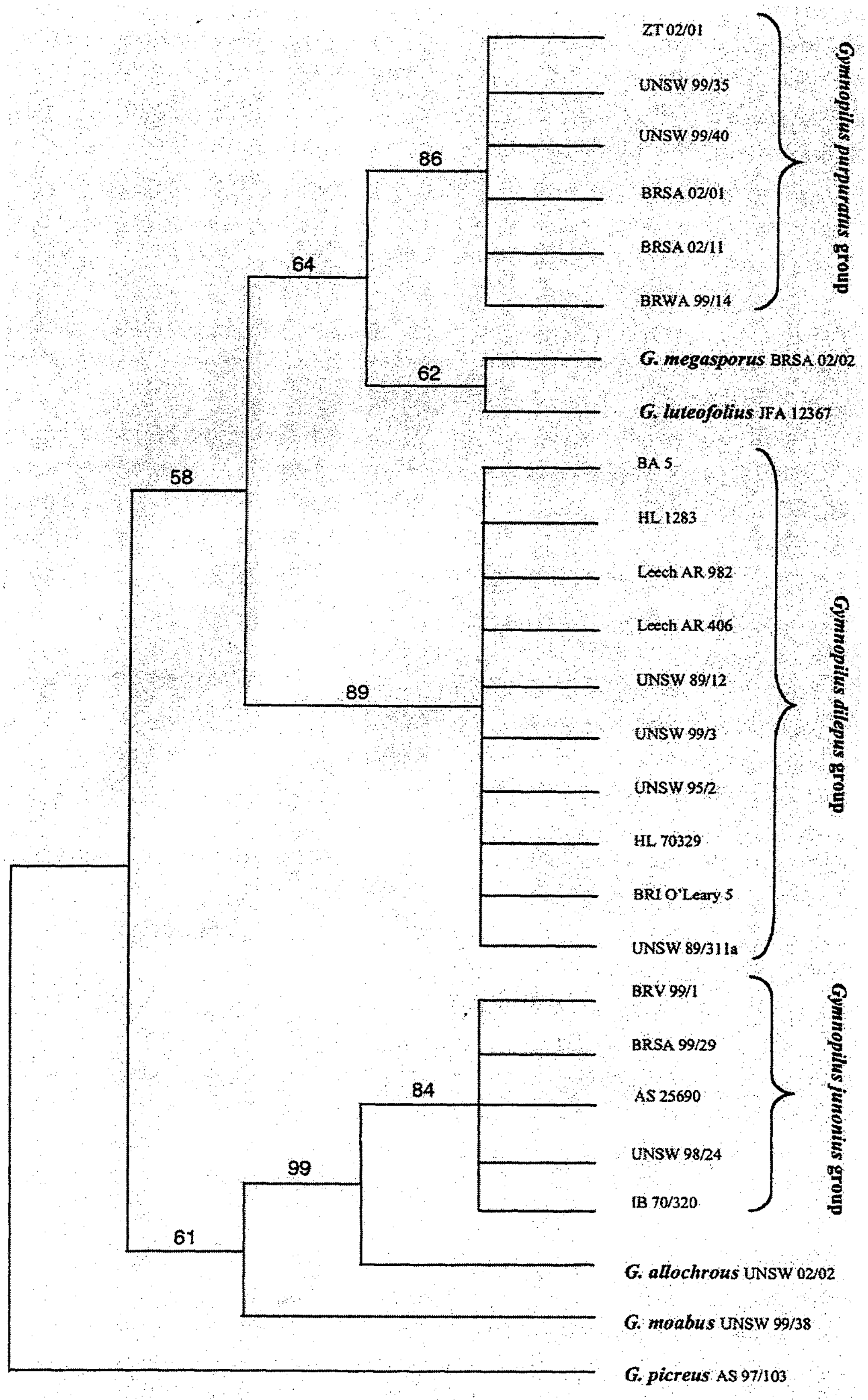

Figure 4. Consensus maximum parsimony tree, of 100 bootstrap replicates of ITS sequence data from *Gymnopilus* accessions. *G. picreus* was defined as the outgroup, with the ingroup constrained to be monophyletic. Consistency index = 0.8217; Retention index = 0.8935. Bootstrap consensus values are indicated.

DISCUSSION

Morphological and molecular results confirm that *Gymnopilus dilepis* and *Gymnopilus purpuratus* are closely related but distinct species, on the basis of spore size and cystidia shape and cladistic analysis of ITS region of ribosomal DNA. Both of these species are present in Australia. *Gymnopilus megasporus* and *Gymnopilus luteofolius* were more closely related to *Gymnopilus purpuratus* species, but were nevertheless distinct, and showed greater similarity with each other despite their obvious spore size differences.

Although recently collected material was not available for DNA extraction, morphological findings from the Kew type and Chilean collections of *Gymnopilus purpuratus* were substantially in agreement. The species is characterised morphologically by bright rust spores with rust-coloured ornamentation and a small plage, and cylindro-capitate cheilocystidia accompanied by pigmented saccate forms. No spathulate cystidia were present. The Australian collections of this species are similar microscopically but are noticeably devoid of pigment at all stages of maturity with a tendancy to develop larger basidia and more maroon-red colour in Western Australia. These similarities indicate that the species is most likely Gondwanan in distribution and that the Australian species has developed with little pigmentation. As a result the Australian species has been reduced to synonymy with *Gymnopilus purpuratus* (Cooke & Massee) Singer. The collection of *Gymnopilus purpuratus* from Switzerland, (Breitenbach & Kränzlin 2000), has smaller spores and somewhat differently shaped cystidia from Australian and Chilean material, but emerges with *Gymnopilus purpuratus* in bootstrap analysis of ITS sequence results. It is clearly distinct from *Gymnopilus luteofolius* from N. America.

Not all red-coloured, squamulose *Gymnopilus* species in Australia are closely related. Those with persistent, deep, wine-red colour which intensifies with age, and which have no annulus of any sort, such as *Gymnopilus moabus* are more closely related to *Gymnopilus sapineus* (Fr.) Maire (Rees *et al.* 2002). However, *G. megasporus* with transient purple colour is related to *Gymnopilus purpuratus* but is clearly separable on the basis of spore size (10.8–15.3 × 6.9–9.0 µm). These findings indicate that spore size may not be a reliable character for grouping species within the genus as proposed by Hesler (1969) and Guzmán-Dávalos (1995). Small-spored species of *Gymnopilus* have also been found not to be a natural group within Australia (Rees & Ye 1999).

Recent collections identified as *Gymnopilus dilepis* from Great Britain were examined in detail. The collections were made in different seasons at locations 8 km apart in Norfolk, and appeared initially to be different from each other morphologically. The woodchips from which they grew were produced on site and not imported with the fungus (Leech pers. comm). The first, from Beeston Common, was similar to Australian collections of *G. dilepis*, with spathulate pleuro- and cheilocystidia in abundance. Cheilocystidia from the second collection from Holt-Lowes in Norfolk lacked pigment and had more ventricose-rostrate to lecythiform cystidia with a terminal small capitellum rather than broadly utriform as in the type collection. No pigmented structures were present at the lamella margin and no spathulate cheilocystidia were apparent. This second collection differed in molecular analysis by one base only from the first, and had an identical ITS sequence to New South Wales collections of the same species.

These apparent differences in *G. dilepis* appear to be age related. As the species matures, pigment is rapidly lost from the heavily encrusted, extremely variable cystidia which must collapse or are masked by the heavy spore load, as they cannot be detected at maturity. Their disappearance is accompanied by a loss of purple colour in the whole fruit body, and although spore characters remain the same, only the utriform to ventricose-rostrate cheilocystidia remain visible. Examination of freshly expanded young, as well as mature fruitbodies is necessary for accurate identification of this species. It has smaller spores with less rust-colored ornamentation than *Gymnopilus purpuratus* and plentiful, extremely versiform, pigmented cheilo- and pleurocystidia in freshly expanded juvenile fruit bodies. *Gymnopilus dilepis* is widespread in South-East Asia according to Treu (1998) and Watling (1998).

Are these species native to Europe or have they been introduced from tropical or Southern Hemisphere warmer climates comparatively recently, surfacing only in the wild when suitable growth conditions are available? It is hard to account for the relative absence of reports of native red to purple-coloured *Gymnopilus* species in Europe since 1929. Although the species are not frequently encountered in other countries, they are by no means rare, and it would seem unlikely that the species has passed un-noticed for 60 years during which the mycota has been so actively documented. A source of inoculum must be present in the environment for colonisation of appropriate substrates. The sudden reappearance of *G. purpuratus* in Europe on woodchip and fibreboard (Kreisel &

Lindequist 1988), may mean the species has been imported recently into Europe on either seeds, woodchip or packaging and has escaped into the environment.

It is tempting to speculate that these species have evolved in warmer climates, and that *Gymnopilus purpuratus* Kew type occurred on a tree-fern brought to England from Chile in the late 19th century while *Gymnopilus dilepis* has been imported into Europe from Australia and has escaped into the environment in the last twenty to thirty years, finding suitable substrates with changing agricultural practices. The collections of *Gymnopilus purpuratus* from Zurich and *Gymnopilus igniculis* from coal slag heaps in Belgium may have similar origins.

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References

Berkeley, M.J. & Broome, C.E. (1871). The Fungi of Ceylon (Hymenomycetes, from *Agaricus* to *Cantharellus*). *Journal of the Linnean Society, Botany* **11**, 494–567.

Bon, M. & Roux, P. (2002). Le genre *Gymnopilus* P. Karst. en Europe. *Fungi non Delineati.* **17**, 1–52.

Breitenbach, J. & Kränzlin, F. (2000). *Fungi of Switzerland V. Agaricales 3. Cortinariaceae.* 340 pp. Mykologia, Lucerne.

Cooke, M.C. (1888). *Illustrations of British Fungi.* Vol. 8. Suppl. Williams & Norgate, London.

Cooke, M.C. & Massee, G. (1890). New British Fungi. *Grevillea* **18**, 73–74.

Deneyera, Y., Moreau, P.-A. & Wuilbaut, J.-J. (2002). *Gymnopilus igniculus sp. nov.*, nouvelle espèce muscicole des terrils de charbonnage. *Documents Mycologiques* **32**, 11–15.

Grgurinovic, C.A. (1997). *Larger Fungi of South Australia.* The Botanic Gardens of Adelaide and State Herbarium and the Flora and Fauna of South Australia Handbooks Committee, Adelaide.

Gsell, H. (1995). *Gymnopilus purpuratus*, ein Pilz-Exote. *Schweizerische Zeitschrift für Pilzkunde* **73**, 49–55.

Guzmán-Dávalos, L. (1995). Further investigations on *Gymnopilus* (Agaricales, Cortinariaceae). A new section and a new species from Mexico. *Mycotaxon* **54**, 117–124.

Guzmán-Dávalos, L. (2003). Type studies of *Gymnopilus* (Agaricales) I. *Mycotaxon* **86**, 395–423.

Henrici, A. (2002). Notes and records. *Field Mycology* **3**, 28–30.

Hesler, L.R. (1969). North American species of *Gymnopilus*. *Mycological Memoirs* **3**. Haffner, New York.

Høiland, K. (1990). The genus *Gymnopilus* in Norway. *Mycotaxon* **39**, 257–279.

Holmgren, P.K., Holmgren, N.H. & Barnett, L.C. (1990). *Index Herbariorum Part I. The Herbaria of the World.* 8th Edition. Botanical Gardens, New York.

Kreisel, H. & Lindequist, U. (1988) *Gymnopilus purpuratus*, ein psilocybinhaltiger Pilz adventif im Bezirk Rostock. *Zeitschrift fur Mykologie* **54**, 73–76.

Massee, G. (1893). *British Fungus Flora Vol II: A classified textbook of Mycology.* Bell & Sons, London.

Pegler, D.N. (1986). Agaric Flora of Sri Lanka. *Kew Bulletin.* Add. Ser. **XII**, 1–519. H.M.S.O., London.

Petch, T. (1907). Revisions of Ceylon Fungi. *Annales of the Royal Botanic Garden. Peradeniya* **4**, 21–68.

Rees, B.J. (1996). A taxonomic study of the genera *Gymnopilus, Pyrrhoglossum* and *Phaeocollybia* in Southern Australia. Ph D thesis. School of Biological Science, University of New South Wales.

Rees, B.J. & Lepp, H. (2000). A new species of *Gymnopilus* from Norfolk Island. *Australasian Mycologist* **19**, 36–40.

Rees, B.J. & Ye, J.L. (1999). *Pyrrhoglossum* and the small-spored species of *Gymnopilus* (Cortinariaceae) in Eastern Australia. *Australian Systematic Botany* **12**, 255–270.

Rees, B.J., Orlovich, D.A. & Marks, P.B.D. (1999). Treading the fine line between small-statured *Gymnopilus* and excentrically stipitate *Galerina* species in Australia. *Mycological Research* **103**, 427–442.

Rees, B.J., Zuccarello, G.C. & Orlovich, D.A. (2002). Relationships between Australian and Northern Hemisphere *Gymnopilus* species II. A preliminary phylogeny of Species of *Gymnopilus* and related genera based on Internal Transcribed Spacer (ITS) region of ribosomal DNA. *Mycotaxon* **84**, 93–110.

Rees, B.J., Marchant, A.D., Zuccarello, G.C., Heslewood, M.M. & Bartlett, J. (2003). A Southern Hemisphere contribution to the phylogenetic study of the Agarics. *Australasian Mycologist* **21**, 102–110.

Romagnesi, H. (1942). Quelque points de Taxonomie. *Bulletin de la* Société. *Mycologique de France* **58**, 88–89.

Singer, R. (1929). Pilz aus dem Kaukasus I. Ein Beitrag zur Flora des Südwestlichen Zentralkaukasus. Beihefte zum Botanische Centralblatt **46**, 71–113.

Singer, R. (1951). The Agaricales in Modern Taxonomy. *Lilloa* **22**, 5–832.

Singer R. (1969). Mycoflora Australis. *Beihefte Nova Hedwigia* **29**, 1–405. J. Cramer, Vaduz.

Swofford, D.L. (2001) 'PAUP': Phylogenetic Analysis Using Parsimony (*and other methods", version 4. Sinauer Associates, Sunderland.

Tantram, R. (1998). *Nature Line* (Hants WT), 20.

Thomas, A.T., Guzmán-Dávalos, L. & Manimohan, P. (2003). A new species and new records of *Gymnopilus* from India. *Mycotaxon* **85**, 297–305.

Thompson, J.D., Plewniak, F., Jeanmougin, F. & Higgins, D.J. (1997). The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **24**, 4876–4882.

Treu, R. (1998). Macrofungi in Oil Palm Plantations of South East Asia. *Mycologist* **12**, 10–14.

Vellinga, E.C. (1988). Glossary, *in* Bas, C., Kuyper, Th.W., Nordeloos, M.E. & Vellinga, E.C. (eds) *Flora Agaracina Neerlandica.* A.A. Balkema, Rotterdam.

Watling, R. (1998). Profiles of Fungi. *Mycologist* **12**, 60–61.