Chiang Mai J. Sci. 2014; 41(4) : 771-780
http://epg.science.cmu.ac.th/ejournal/
Contributed Paper

Two New Species in *Agaricus* Tropical Clade I

Samantha C. Karunarathna [a,b,c,d], Jacques Guinberteau [g], Jie Chen [b,c,d], Else C. Vellinga [e], Rui-Lin Zhao [f], Ekachai Chukeatirote [b,c], Jiye Yan*[a,b], Kevin D. Hyde [a,b,c,d] and Philippe Callac [g]

[a] Institute of Plant and Environment Protection, Key Laboratory of Urban Agriculture (North), Ministry of Agriculture, Beijing Academy of Agriculture and Forestry Sciences, Beijing 100097, P.R. China.

[b] Institute of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand.

[c] School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand.

[d] Mushroom Research Foundation, 128 M.3 Ban Pa Deng T. Pa Pae, A. Mae Taeng, Chiang Mai 50150, Thailand.

[e] Department of Plant and Microbial Biology, University of California, Berkeley CA 94720-3102, U.S.A.

[f] Key Laboratory of Forest Disaster Warning and Control in Yunnan Province, Faculty of Biology Conservation, Southwest Forestry University, Kunming, 650224 China.

[g] INRA, UR1264, MYCSA (Mycologie et sécurité des aliments) CS 20032, 33883 Villenave d'Ornon Cedex, France.

*Author for correspondence; e-mail:jiyeyan@gmail.com

Received: 19 November 2013
Accepted: 10 January 2014

ABSTRACT

As part of our efforts to study the saprobic mushrooms in Asia we have collected numerous taxa of the genus *Agaricus* in northern Thailand. It is likely that more than 40 new species occur in this region and many are potentially edible or medicinal. A recent phylogenetic study revealed that most species of this region belong to exclusively tropical clades of which the largest one, TR I, was suspected to represent section *Brunneopicti.* In this paper we introduce two new species as *Agaricus chiangmaiensis* and *A. megacystidiatus* based on fresh collections in addition to collections previously classified in two putative species of clade TR I. The new species are described and illustrated with line drawings and photographs and compared with similar taxa. *Agaricus chiangmaiensis* shows affinities with *A. brunneopictus.* However, taxonomical investigation on more species will be necessary to characterize the clade TRI and to clarify to what extend it would represent the section *Brunneopicti.*

Keywords: biodiversity, edible, taxonomy, tropics

1. INTRODUCTION

Agaricus (= *Psalliota*) is a large and well-known genus of edible mushrooms. Zhao *et al.* [1] hypothesized that the number of tropical species should be greater than the number of temperate species and that the existing number of species should be much higher than 400. Even though species in the genus are well-known as important edible and cultivated mushrooms, the characterization and delimitation of species in the genus is complex. The current concept of the genus *Agaricus* was derived from the Friesian subgenus *Psalliota* [2]. *Agaricus* is generally described as having a white, pink or brown

pileus, free lamellae with a regular trama when young, later becoming irregular, and a dark, chocolate brown, spore print. Basidiospores of *Agaricus* are smooth with a compound wall and not visibly pseudoamyloid. Most of taxonomic systems use three main characters for infrageneric classifications of the genus [3,4]: 1) Macrochemical reactions: Schäffer's cross-reaction – a chemical test with aniline and concentrated Nitric acid; the alkali test (application of strong alkali, either NaOH or KOH); 2) basidiome color change when bruised or broken; 3) the odor which is a subjective character, and that the mycologist's smelling aptitude needs to be trained beforehand. The most frequently referenced monographs on tropical *Agaricus* are those by Heinemann [3, 5-23], especially [17] and [21]. Heinemann's [17] and [21] treatments of *Agaricus* ranked species in subgenera and sections. With DNA sequencing and the rapidly expanding databases, researchers are developing new, more efficient tools for species classification, and the use of ribosomal DNA sequences to infer phylogenetic relationships among agaric fungi is now widely exploited [24, 1], but also disputed [25].

The first molecular phylogeny of *Agaricus* was carried out by Mitchell and Bresinsky [26] when 16 species from a selected range of sections were sequenced. In *Agaricus*, two sections are well-supported by molecular phylogeny, viz. sections *Bivelares* and *Xanthodermatei* [27-29]. Section *Bivelares* comprises a group of species allied with *A. bisporus* and *A. bitorquis* [27]. So far, most reports concerning the classification and phylogeny of *Agaricus* species are based on European and American taxa, but for the first time in history we published phylogenetic work for tropical *Agaricus* based in part on research in northern Thailand [1]. In that study, ITS 1+2 sequence data of 124 *Agaricus* species were phylogenetically analysed to identify the major clades in the genus and the distribution of the tropical species. Zhao *et al.* [1] identified eleven tropical clades and seven of these were well-supported. Tropical clade I (/TR I) which is the largest of the tropical clades and which was supported by 90% SH-like branch support and 82% Bayesian posterior probability, contains a collection of which the identification as *A. brunneopictus* Heinem. & Gooss.-Font., (no 16 of the phylogenetic tree of Zhao *et al.* [1]), the type species of *Agaricus* section *Brunneopicti* was not confirmed because the two examined specimens were immature [1]; on the other hand sequencing of the type specimen of this species several times failed [6, 7, O. Raspé, personal communication].

Section *Brunneopicti* Heinem. is characterized by small brown scales on the pileus and lower part of the stipe surface, formed by the general veil; medium to large basidiomes; whitish or yellowish brown pileus; solid or fistulose long stipes with rounded bulb at base; large lamellae with sharpened ends; almond odor; pleasant flavor; short pileipellis hyphae; and weak or no Schäffer's test results [6, 7].

The objective of the present study is to describe two new species of *Agaricus* belonging to tropical clade I and to compare them with putatively related taxa of section *Brunneopicti* that TR I could represent. *Agaricus chiangmaiensis* and *A. megacystidiatus* are described on the basis of specimens collected in northern Thailand and their ITS-1-5.8S-ITS2 rDNA sequences previously [30] or newly obtained.

This area, in particular around the Mushroom Research Centre, Chiang Mai is presently well-studied, resulting in many new fungal species and new records, documenting an amazing biodiversity [1, 30-45].

2. MATERIALS AND METHODS

2.1. Studied Collections and ITS-1-5.8S-ITS2 rDNA Sequences

Samples of *Agaricus* were collected in northern Thailand between June 2010 and October 2012. NTS116 and NTS115 (classified in species 13 in Zhao *et al.* [30]) and NTS113 (classified in species 15 in Zhao *et al.* [30]) have been previously sequenced but only sequences of NTS116 and NTS113 have been previously deposited (JF514532 and JF514531 respectively in Zhao *et al.* [30]).

The newly collected samples SCK-053, LD2012179 and LD2012168 were sequenced in the present study following the method of Zhao *et al.* [30]. Their ITS-1-5.8S-ITS2 rDNA sequences and that of NTS115 were deposited in GenBank under the accession numbers KC971099, KF305946, KF305947 and KC971098 respectively.

2.2 Morphological Character Examination

Macro-morphological characters were described based on fresh material, and documented by photographs. Colour designations (e.g., 4B5) are from Kornerup & Wanscher [46]. Specimens were dried and placed in plastic bags separately, and then deposited in the Herbarium of Mae Fah Luang University (MFLU). For micro-morphological examination, sections were cut with a razor blade from dried specimens and mounted on slides in 5% KOH and Congo red, and then observed, measured and illustrated using a compound microscope (Zeiss Axioskop 40). In the description of the basidiospores, "n" indicates the number of basidiospores (20 basidiospores per one collection) which were measured; L_m = mean basidiospore length over a population of basidiospores; W_m = mean basidiospore width over a population of basidiospores; Q = "length/width ratio" (L/W) of a basidiospore in side view; Q_m = average Q of all basidiospores measured. The phylogenetic relationships of the two species included herein are published in Zhao et al. [1].

3. RESULTS

The ITS1+2 sequences of the two novel species differ at 43 positions. There are not any significant differences between *A. chiangmaiensis* ITS 1+2 sequences (JF514531 & KC971098), whereas the polymorphic positions of four *A. megacystidiatus* ITS 1+2 sequences (JF514532, KC971098, KF305946 and KF305947) are shown in Table 1. Heteromorphism and homomorphisms at position 169 reflect the presence of two alleles at this locus and indicate that this species should not be homothallic since homothallic species are generally homokaryotic in Basidiomycota. This genotypic variation agrees with the belonging of the four samples to the same species.

Table 1. Variable positions within ITS 1+2 sequences of *A. megacystidiatus*. Used code at heteromorphic positions: R = A + G; S = G + C.

Sequence ID	ITS 1+2 polymorphic positions		
	160	169	597
KF305946	R	S	G
KF305947	A	G	G
JF514532	A	C	R
KC971098	A	C	R

3.1 Taxonomy

Agaricus chiangmaiensis Karunarathna, Guinb. & K.D. Hyde, sp. nov. (Figures 1 A-E; Figures 3A-D)

MycoBank: 800272

Pileus 100-170 mm in diameter when mature; lamellae free, crowded with 4 tiers of lamellulae; annulus well-developed, double; stipe 55-100×30 mm at the base, 55-100×15 mm at the middle, 55-100×15 mm at the top,

fistulose; basidiospores 7.0-8.5×3.0-4.0 µm, mostly oblong but rarely ellipsoid; basidia 20-25×6-8.5 (-9) µm, clavate, 4-spored; cheilocystidia 15-18×8-10 µm, broadly clavate; no discoloration observed in the pileus or stipe context on touching or cutting; no reaction with 5% KOH on pileus and stipe surface; Schäffer's reaction negative; benzene like odor.

Holotype: MFLU12-0136

Etymology: *chiangmaiensis*, in reference to the type location of the species.

Description: Pileus 100-170 mm in diameter when mature, circular in top view, hemispherical when young, convex when old; surface dry, smooth, with small flakes on the centre, yellowish white (2A2) at the center with light brown dots (5D4) composed of brownish appressed triangular-shaped scales, white (5A1) towards the margin when young and old; no color changes on cutting or bruising. Context in pileus 5-8 mm thick at the disc, fragile, white, soft. Lamellae free, crowded with 4 tiers of lamellulae, 3-4 mm wide with homomorph edge, light grey at first, then dark brown to chocolate brown (6F) at maturity, with concolorous even edge. Annulus is prominent, double, upper one membraneous, 20 mm in diameter, superior and pendent, stretched, white, lower side floccose; lower one the lower split into white to slight yellowish white (3A2) coarse scales that can form a cogwheel like in *Agaricus arvensis*. Stipe 55-100×30 mm at the base, 55-100×15 mm at the middle, 55-100×15 mm at the top, tapering upwards, centrally attached to pileus, buried, fistulose; context white, cottony; surface smooth and powdery granular in the lower third, slight yellowish white (2A2) at the top and yellowish white (3A2) at bottom; rhizomorphs absent at base. Spore print chocolate-brown (6F4). Unpleasant benzene like odor. No discoloration at the beginning then faint rufescent discoloration observed in the pileus or stipe context on touching or cutting.

Macrochemical reaction: no reaction with 5% KOH on fresh pileus surface and stipe surface (negative). Negative results obtained for the Schäffer's reaction on fresh context of pileus and stipe base.

Basidiospores 7.0-7.6 (8.5)×3.0-4.0 µm [n=40, L^m=7.20 µm, W^m=3.60 µm, Q=1.75-2.12, Q^m =2.00], mostly oblong but rarely ellipsoid, without germ pore, smooth, chocolate-brown in mass, thick-walled. Basidia 20-25×6-8.5 (-9) µm, clavate, 4-spored. Cheilocystidia 15-18×8-10 µm, pyriform with shortly cylindrical base, single, hyaline, smooth. Pleurocystidia absent. Pileipellis a cutis; hyphae 7.5-14 µm diam., inflated, hyaline, unbranched. Stipitipellis hyphae similar to pileipellis hyphae 12.5-15 µm diameter. Clamp connections absent.

Habitat: as a group on grassland with humus-rich, organic matter rich soil.

Fruiting during the middle of the rainy season, found in open grassland with a lot of organic litter mixed in the soil.

Edibility: unknown.

Distribution: Only known from Thailand (type distribution).

Material examined: Thailand, Chiang Mai Province, Mueang Chiang Mai District, Chiang Mai University Park, 18°48′22″N 98°57′10″E, 345m, 27 July 2010, S.C. Karunarathna & J. Guinberteau NTS113, herbarium (MFLU12-0136, **holotype**); ITS 1+2 GenBank accession number: JF514531); Thailand, Chiang Mai Province, Mueang Chiang Mai District, Chiang Mai University park, 2m away from the holotype, 18°48′22″N 98°57′10″E, 345m, 27 July 2010, S.C. Karunarathna & J. Guinberteau (SCK-052, herbarium MFLU12-0135); Thailand, Chiang Mai Province, Mueang Chiang Mai District, Chiang Mai University park, 18°48′22″N 98°57′10″E, 345m, 22 April 2011, S.C. Karunarathna (SCK-053, herbarium:

MFLU12-0140, ITS1+2 GenBank accession number: KC971098); Thailand, Chiang Rai Province, Mueang Chiang Rai District, Training centre, 19°54′25.80″N 99°49′51.44″E, 700 m, 10 July 2013, S.C. Karunarathna (TRSCK-015, herbarium: MFLU12-0140).

Notes: This new species is distinguished by its relatively moderate to large basidiomes with a soft, hemispherical and yellowish-white center and with a light brown dotted pileus; stipe with powdery granular surface in the lower third; 7-8.5×3-4 µm oblong, thick-walled basidiospores; well visible lower flocculose double annulus and relatively large, 15-18 ×8-10 µm, pyriform to broadly clavate cheilocystidia.

Agaricus megacystidiatus Karunarathna, Guinb. & K.D. Hyde, sp. nov. (Figures 2A-E; 3E-F)

MycoBank: 800273

Pileus 40-50 mm in diameter; lamellae free, crowded with 4 tiers of lamellulae; annulus double; stipe 55-70 ×20 mm at base, 55-70×12 mm at middle, 55-70×8 mm at top, tapering upwards, fistulose; basidiospores 8.0-9.5×4.0-5.0 µm, mostly oblong but rarely ellipsoid; cheilocystidia 30-39 (-45)× 8-25 µm, broadly clavate; red discoloration observed in the pileus or stipe context on touching and cutting; yellow with 5% KOH on pileus and stipe surface. Schäffer's reaction negative. Odor complex, mild and aniseed to stronger and unpleasant depending of the sample and the collector.

Holotype: MFLU12-0137

Etymology: *megacystidiatus*, in reference to the very large cheilocystidia of the taxon.

Description: Pileus 40-50 mm in diameter, circular in top view, obtusely conical when it is young and old; surface dry, smooth, with yellowish-brown (5D4) small scales on the top of pileus, with brownish appressed triangular scales, yellowish brown at the center (5D4), slightly orange white (6A2) towards margin when young and old; color change to red on cutting or bruising. Context in pileus 5-6 mm thick at the disc, chalky, white. Lamellae free, crowded with 4 tiers of lamellulae, 4-5 mm wide with homomorph edge, white to light brown (6D4) at first, then dark brown to chocolate brown (7F4) at maturity, with concolorous even edge. Annulus well visible superior but not pendent after cap opening, double, yellowish white (3A2), cottony, lower part thin and floccose. Stipe 55-70×20 mm at base, 55-70×12 mm at centre, 55-70×8 mm at top, tapering upwards, centrally attached to pileus, buried, fistulose, context white, color change to red by bruising, cottony, surface dry, smooth, slightly yellowish-white (4A1) at top, yellowish-white (3A2) at bottom; rhizomorphs absent at base, color change to red by bruising on the surface of stipe. Spore print chocolate-brown (6F4). Odor complex, mild and aniseed to stronger and unpleasant depending of the sample and the collector. This could reflect the presence of benzaldehyde mixed with other aromatic compounds exhibiting unpleasant odor.

Macrochemical reaction: 5% KOH on base of stipe and pileus surface, strong yellow. Negative results obtained for the Schäffer's reaction on fresh context of pileus and stipe base.

Basidiospores 8.0-9.5×4.0-5.0 µm [n=40, L^m=8.55 µm, W^m=4.72 µm, Q=1.60-2.00, Q^m=1.78], mostly oblong but rarely ellipsoid, without germ pore, smooth, chocolate-brown in mass, thick-walled. Basidia 18-23 ×5-6.5 (-8) µm, clavate, 4-spored. Cheilocystidia 30-39 (-45)×8-25 µm, pyriform with shortly cylindrical base, single, hyaline, smooth. Pleurocystidia absent. Pileipellis a cutis; hyphae 16-21 µm diam., inflated, hyaline, unbranched. Stipitipellis hyphae similar to pileipellis hyphae 11-14 µm diameter. Clamp connections absent.

Habitat: solitary in grassland with humus-

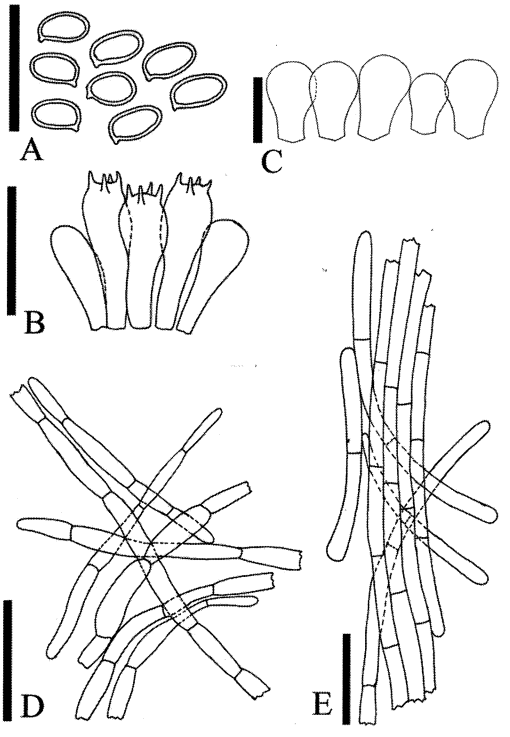

Figure 1. *Agaricus chiangmaiensis* sp. nov. A: Basidiospores; B: Basidia C: Cheilocystidia; D: Hyphae of stipitipellis; E: Hyphae of pileipellis. Scale bars: A, B = 20 μm; C = 10 μm; D, E = 50 μm.

rich, organic matter rich soil.

Fruiting during the middle of the rainy season, found in open grassland with lot of organic litter mixed soil.

Edibility: unknown.

Distribution: Only known from Thailand (type distribution).

Material examined: Thailand, Chiang Mai Province, Mueang Chiang Mai District, Chiang Mai University park, 18°48′22″N 98°57′10″E, 345m, 27 July 2010, S.C. Karunarathna & J. Guinberteau, NTS116, herbarium (MFLU12-0137, **holotype**); S1+2 GenBank accession number: JF514532); Thailand, Chiang Mai Province, Muang Chiang Mai District, Chiang Mai University park, 4 m away from the holotype, 18°48′22″N 98°57′10″E, 345m, 27 July 2010, S.C. Karunarathna (NTS115, herbarium MFLU12-0133, ITS-1-5.8S-ITS2 rDNA GenBank accession number KC 971098); Thailand, Phitsanulok province, Sakunothayan Waterfall 16°51′9.99″N 100°37′19.85″E, 185 m, 28 Aug. 2012, Asanka Ranjana Bandara (LD2012179, herbarium MFLU12-1004, ITS-1-5.8S-ITS2 rDNA GenBank accession number KF305946); Thailand, Chiang Mai Province, Muang Chiang Mai District, Chiang Mai University park, 18°48′22″N 98°57′10″E, 345m, 5 Aug. 2012, Jie Chen (LD2012168, herbarium MFLU12-0996, ITS-1-5.8S-ITS2 rDNA GenBank accession number KF305947).

Notes: This new species is distinguished by its small basidiomes, yellowish-brown center, orange white margine, yellowish-brown, scaled pileus; 8-9.5×4-5 μm oblong, thick-walled, smooth basidiospores and relatively large sized pyriform to broadly clavate cheilocystidia.

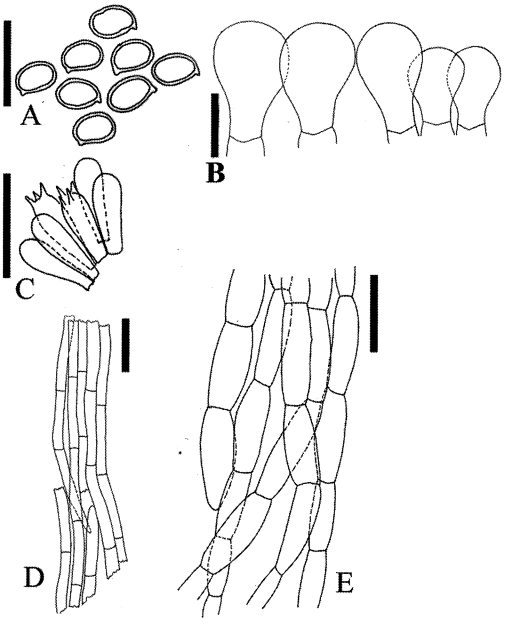

Figure 2. *Agaricus megacystidiatus* sp. nov. A: Basidiospores; B: Cheilocystidia, C: Basidia; D: Hyphae of stipitipellis; E: Hyphae of pileipellis. Scale bars: A, C = 20 μm; B = 20 μm; D, E = 50 μm

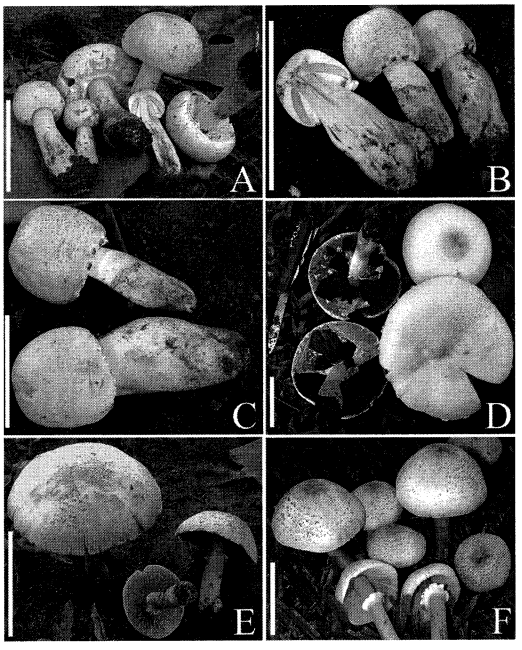

Figure 3. A-C. Basidiomes of *Agaricus chiangmaiensis* sp. nov. in the field (NTS113, MFLU12-0136), D. Basidiomes of *Agaricus chiangmaiensis* sp. nov. in the field (SCK053, MFLU12-0140), E. Basidiomes of *Agaricus megacystidiatus* sp. nov. in the field (NTS116, MFLU12-0137), F. Basidiomes of *Agaricus megacystidiatus* sp. nov. in the field (NTS115, MFLU12-0133). Scale bars: A, B = 100 mm; C, D, E, F = 50 mm.

4. DISCUSSION

We collected 150 *Agaricus* specimens in a small part of northern Thailand from May 2010 to July 2013 that most likely represents more than 40 novel species. This diversity indicates that *Agaricus* is a species-rich genus not only in temperate regions but also in the tropics.

The two new species, *A. chiangmaiensis* and *A. megacystidiatus* are members of Tropical Clade I [1]. For *A. chiangmaiensis*, the dot-like scales on the cap and the granular scales on the stipe could represent pieces of universal veil similarly described by Heimemann in *A. brunneopictus* Heinem. & Goos -Font. and *A. bingensis* Heinem. & Goos. In contrast, these traits were not observed in *A. megacystidiatus*. Further studies will be necessary to clarify what clade represents this section and how this section is morphologically characterized. Heinemann [20] acknowledged that section *Brunneopicti* was not well characterized. The shape of the annulus, the odor, reactions with KOH and the color reactions differ between the two new species and are not shared among the species of clade TRI which shows how diverse these species are, though they all share some characteristics like pyriform to broadly clavate basidia and cheilocystidia.

Major variations were not detected between samples of each species in terms of morphological traits, and in terms of molecular traits, only few polymorphisms were observed in the sequences of *A. megacystidiatus* (Table 1). Such a intraspecific variability remains moderate since the number of differences between the ITS sequences taken in all pairewise combination does not exceed one (heteromorphisms are not considered) as this is frequently the case in species of genus *Agaricus*.

It is acceptable to consider that *A. chiangmaiensis* is morphologically related to *A. brunneopictus*, but the available information is not sufficient to consider that the entire clade TR I represent the section *Brunneopicti* since many other species of this clade TR I have not yet been studied in detail. Conversely, samples of the species of the section *Brunneopicti* should have to be re-examined for the light of the large species diversity in clade TR I.

ACKNOWLEDGEMENTS

We are grateful to Phongeun Sysouphanthong, Komsit Wisitrassameewong, Nalin Wijayawardane, Rungtiva Pookamsak, Bencharong Thongbai, Pheng Phengsintham,

Kobeke Van de Putte, Putarak Chomnunti, Jian Kui-Liu, Asanka Ranjana Bandara and Thida Win Ko Ko for their valuable help in collecting. Putarak Chomnuti (MFLU) is thanked for her assistance in the herbarium. This study was financially supported by the French Ministry of Foreign Affairs and INRA (Project AGASIA of the regional program Bio-Asie), the project Value added products from basidiomycetes: Putting Thailand's biodiversity to use (BRN049/2553), the National Research Council of Thailand (NRCT), projects - Taxonomy, Phylogeny and cultivation of *Lentinus* species in northern Thailand (NRCT/ 55201020007), Mae Fah Luang University research division, the project – Taxonomy, Phylogeny and cultivation of *Lentinus* species in northern Thailand (MFU/54 1 01 02 00 48), and Thailand Research Fund grant - Taxonomy, Phylogeny and biochemistry of Thai Basidiomycetes (BRG 5580009).

REFERENCES

[1] Zhao R.L., Karunarathna S., Raspe O., Parra L.A., Guinberteau J., Moinard M., De Kesel A., Barroso G., Courtecuisse R., Hyde K.D., Guelly A.K., Desjardin D.E. and Callac P., Major clades in tropical *Agaricus*, *Fungal Divers*, 2011; **51**: 279-296.

[2] Cappelli A., *Agaricus L.: Fr. Libreria editrice Biella Giovanna*, I - 21047, Saronno, Italy, 1984.

[3] Heinemann P., Clave para la determinación *de* las especies *de Agaricus* (Agaricales) *de la* Patagonia y Tierra del Fuego, *Darwiniana*, 1987; **28**: 283-291.

[4] Parra L.A., *Agaricus L. Allopsalliota Nauta and Bas*, Edizioni Candusso, Alassio, 2008.

[5] Heinemann P., État actuel de la systématique de genre *Agaricus*, *Mushroom Science*, 1953; **2**: 8-11.

[6] Heinemann P., Champignons récoltés au Congo belge par Mme M. Goossens-Fontana, II. *Agaricus* Fr. s.s. *Bull Jard Bot l'État Bruxelles*, 1956a; **26**: 1-127.

[7] Heinemann P., Champignons récoltés au Congo belge par Mme M. Goossens-Fontana, II. *Agaricus*. Note complémentaire, *Bull Jard Bot l'État Bruxelles*, 1956b; **26**: 325-333.

[8] Heinemann P., *Agaricus* (suite) et *Pilosace*, *Flore Iconographique des Champignons du Congo*, 1957a; **6**: 121-130.

[9] Heinemann P., *Agaricus robynsianus* sp. nov. *Bull Jard Bot l'État Bruxelles*, 1957b; **27**: 449-452.

[10] Heinemann P., Agarici Austroamericani I. *Agarics* of Trinidad, *Kew Bull*, 1961; **15**: 231-248.

[11] Heinemann P., Agarici Austroamericani IV. Quatre *Agaricus* du Venezuela, *Bull Jard Bot l'État Bruxelles*, 1962a; **32**: 155-161.

[12] Heinemann P., Agarici Austroamericani II. *Agaricus* de Bolivie, *Bull Jard Bot l'État Bruxelles*, 1962b; **32**: 1-21.

[13] Heinemann P., Agarici Austroamericani III. Trois *Agaricus* de la Jamaïque, *Bull Jard Bot l'État Bruxelles*, 1962c; **32**: 23-29.

[14] Heinemann P., Agarici Austroamericani, V. Étude des types de C. Spegazzini, *Bulletin de l'Institut Agronomique et des Stations de Recherches de Gembloux*, 1962d; **30**: 273-282.

[15] Heinemann P., Quelques Psalliotes du Congo-Brazzaville, Cahier Makobe, 1971; **9**: 5-10.

[16] Heinemann P., *Agaricus kuehnerianus* sp. nov., la Psalliote géante des Alpes de Haute Provence, *Bulletin Mensuel de la Société Linnéenne de Lyon*, 1974; **43**: 181-187.

[17] Heinemann P., Essai d'une clé de determination des genres *Agaricus* et *Micropsalliota*, *Sydowia*, 1978; **30**: 6-37.

[18] Heinemann P., Les genres *Agaricus* et *Micropsalliota* en Malaisie et en Indonésie, *Bulletin du Jardin Botanique National de Belgique*, 1980; **50**: 3-68.

[19] Heinemann P., Quelques Psalliotes de Nouvelle Guinée (Papua New Guinea), *Bulletin du Jardin Botanique National de Belgique*, 1982; **52**: 405-413.

[20] Heinemann P., Agarici Austro-Americani VII. Agariceae des zones tempérées de l'Argentine et du Chili, *Bulletin du Jardin Botanique National de Belgique*, 1984; **60**: 331-370.

[21] Heinemann P., Agarici Austroamericani VI. Apercu sur les *Agaricus* de Patagonie et de la Terre de Feu, *Bulletin du Jardin Botanique National de Belgique*, 1986; **56**: 417-446.

[22] Heinemann P., *Agaricus singaporensis* sp. nov., *Bulletin du Jardin Botanique National de Belgique*, 1990; **60**: 417- 419.

[23] Heinemann P., Agarici Austroamericani VIII. Agariceae des régions Intertropicales d'Amérique du Sud., *Bulletin du Jardin Botanique National de Belgique*, 1993; **62**: 355-384.

[24] Geml J., Geiser D.M. and Royse D.J., Molecular evolution of *Agaricus* species based on ITS and LSU rDNA sequences, *Mycol Prog*, 2004; **3**: 157-176.

[25] Bruns T.D., ITS reality, *Inoculum*, 2001; **52**: 2-3.

[26] Mitchell D.A. and Bresinsky A., Phylogenetic relationships of *Agaricus* species based on ITS-2 and 28S ribosomal DNA sequences", *Mycologia*, 1999; **91**: 811-819.

[27] Challen M.P., Kerrigan R.W. and Callac P., A phylogenetic reconstruction and emendation of *Agaricus* section *Duploannulatae*, *Mycologia*, 2003; **95**: 61-73.

[28] Kerrigan R.W., Callac P., Guinberteau J., Challen M.P. and Parra L.A., *Agaricus* section *Xanthodermatei:* a phylogenetic reconstruction with commentary on taxa, *Mycologia*, 2006; **97**: 1292-1315.

[29] Kerrigan R.W., Callac P. and Parra L.A., New and rare taxa in *Agaricus* section *Bivelares* (Duploannulati), *Mycologia*, 2008; **100**: 876-892.

[30] Zhao R.L., Hyde K.D., Desjardin D.E., Raspé O., Soytong K., Guinberteau K.J., Karunarathna S.C. and Callac P., *Agaricus flocculosipes* sp. nov., a new potentially cultivatable species from the palaeotropics, *Mycoscience*, 2012; **53**; 300-311.

[31] Le T.H., Nuytinck J., Verbeken A., Lumyong S. and Desjardin E.D., *Lactarius* in northern Thailand: 1. *Lactarius* subgenus *Piperites*, *Fungal Divers*, 2007a; **24**: 173-224.

[32] Le T.H., Nuytinck J., Stubbe D., Verbeken A., Lumyong S. and Desjardin E.D., *Lactarius* in northern Thailand: 2. *Lactarius* subgenus *Plinthogali*, *Fungal Divers*, 2007b; **27**: 61-94.

[33] Sanmee R., Tulloss R.E., Lumyong P., Dell B. and Lumyong S., Studies on *Amanita* (Basidiomycetes: Amanitaceae) in northern Thailand, *Fungal Divers*, 2008; **32**: 97-123.

[34] Kerekes J. and Desjardin D.E., A monograph of the genera *Crinipellis* and *Moniliophthora* from Southeast Asia including a molecular phylogeny of the nrITS region, *Fungal Divers*, 2009; **37**: 101-152.

[35] Wannathes N., Desjardin D.E. and Lumyong S., Four new species of *Marasmius* section *Globulares* from northern Thailand, *Fungal Divers*, 2009a; **36**: 155-163.

[36] Wannathes N., Desjardin D.E., Hyde K.D., Perry B.A. and Lumyong S., A monograph of *Marasmius* (Basidiomycota) from northern Thailand based on morphological and molecular (ITS sequences), *Fungal Divers*, 2009b; **37**: 209-306.

[37] Zhao R.L., Desjardin D.E., Soytong K., Perry B.A. and Hyde K.D., A monograph of *Micropsalliota* in northern Thailand based on morphological and molecular data. *Fungal Divers*, 2010; **45**: 33-79.

[38] Karunarathna S.C., Callac P., Yang Z.L., Raspe O., KoKo T.W., Zhao R.L., Vellinga E.C., Bahkali A.H., Degreef G., Chukeatirote E. and Hyde K.D., *Lentinus giganteus* revisited following new collections in Sri Lanka and Thailand, *Mycotaxon*, 2012; **118**: 57-71.

[39] Karunarathna S.C., Yang Z.L., Zhao R.L., Vellinga E.C., Bahkali A.H., Chukeatirote E. and Hyde K.D., Three new species of *Lentinus* from northern Thailand, *Mycol Prog*, 2011; **10**: 389-398.

[40] Sysouphanthong P., Hyde K.D., Chukeatirote E., Bahkali A.H. and Vellinga E.C., *Lepiota* (*Agaricales*) in northern Thailand – 1. *L.* section *Stenosporae*, *Mycotaxon*, 2011; **117**: 55-85.

[41] Sysouphanhong P., Hyde K.D., Chukeatirote E., Bahkali A.H. and Vellinga E.C., *Lepiota* (Agaricales) in northern Thailand –2. *Lepiota* section *Lepiota*, *Cryptogam Mycol*, 2012; **33**: 25-42.

[42] Wisitrassameewong K., Karunarathna S.C., Thongklang N., Zhao R.L., Callac P., Chukeatirote E., Bahkali A.H. and Hyde K.D., *Agaricus subrufescens*: new records to Thailand, *CMJ Sci*, 2011; **39**: 281-291.

[43] Chen J., Zhao R.L., Karunarathna S.C., Callac P., Raspé O., Bahkali A.H. and Hyde K.D., *Agaricus megalosporus*: A new species in section *Minores*, *Cryptog Mycol*, 2012; **33**: 145-155.

[44] Van de Putte K., Nuytinck J., Stubbe D., Thanh., Le H. and Verbeken A., *Lactarius volemus* sensu lato (Russulales) from northern Thailand: morphological and phylogenetic species concepts explored, *Fungal Divers*, 2010; **45**: 99-130.

[45] Vellinga E.C., Sysouphanthong P. and Hyde K.D., The family Agaricaceae: phylogenies and two new white-spored genera, *Mycologia*, 2011; **103**: 494-509.

[46] Kornerp A. and Wanscher J.H., *Methuen handbook of colour*, 3rd ed. London, Eyre Methuen, 1978.