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A COMPARISON OF THE APPLICATION OF A BIOLOGICAL AND PHENETIC SPECIES CONCEPT IN THE HEBELOMA CRUSTULINIFORME COMPLEX WITHIN A PHYLOGENETIC FRAMEWORK

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A method is presented to derive an operational phenetic species concept for the *Hebeloma crustuliniforme* complex in northwestern Europe. The complex was found to consist of at least 22 biological species (intercompatibility groups; ICGs). Almost none of these biological species could be recognised unambiguously by morphological criteria. It is therefore necessary to base a phenetic species concept on combinations of biological species. However, such species delimitation must be performed within an explicitly phylogenetic context. It is crucial therefore to have a reliable estimate of the phylogeny of 22 biological species in that complex. Based on two nuclear sequences, we present a best estimate of the phylogeny of biological species within the complex. Using this phylogeny, on the basis of strict monophyly only two species can be morphologically recognised among 22 biological species. Relaxing the criterion of monophyly and allowing paraphyletic groupings of biological species as phenetic species would result in the recognition of three phenetic species. A tree, with the five ICGs of the previously defined morphospecies *H. crustuliniforme* (1, 2, 3, 4 and 5) constrained as a monophyletic group, can not be rejected. This constrained tree, together with the relaxed criterioon that allows for paraphyletic groupings of biological species, leads to the recognition of four phenetic species, viz. *H. crustuliniforme*, *H. helodes*, *H. incarnatulum* and *H. velutipes*. These phenetic species are described and a key is provided. Other taxon names are briefly discussed. The very limited ability to translate a biological species concept into an operational phenetic species concept is explained by the lack of qualitative characters and the plasticity of quantitative characters. Recency of common evolutionary history is also a major factor. Intercompatibility tests and DNA based phylogenies indicate that most biological species are very closely related and hence provide support for the claim that correspondence between a biological species concept and a phenetic species concept in the *H. crustuliniforme* complex is not likely to be forthcoming. In an Appendix morphological descriptions are provided of the 22 ICGs.

Among the various genera of the Agaricales the genus *Hebeloma* (Fr.) Kumm. has often been regarded as taxonomically difficult. The status of a number of described species is uncertain, and taxonomic controversies abound. This somewhat frustrating situation has been eloquently described by Favre (1960): "Il n'est pas de genre où la taxonomie des espèces soit plus embrouillée. C'est un véritable chaos. Même pour les espèces les plus répandues le désaccord règne entre les mycologues. Placé dans la nécessité de

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parler des hébélomes (...), je me trouve dans le plus grand embarras." Within the genus the complex of taxa around *H. crustuliniforme* (Bull.) Quél. has been particularly problematic. For the purpose of this paper that species complex is operationally described as follows: Very small to large mushrooms. Pileus viscid, ranging from white to dark reddish brown, but often with a paler margin. Cortina absent. Lamellae clay-brown, often exuding drops of water ('lamellae weeping'). Stipe shorter to (much) longer than pileus diameter, white fibrillose, with a pruinose to flocculose apex. Spore print clay-brown. Spores ornamented. Cheilocystidia cylindrical to clavate to (sub)capitate, thin-walled, but sometimes with thickened wall in the median or upper part, hyaline. Pleurocystidia absent. Ectomycorrhizal with a very wide range of trees, under a large range of ecological conditions.

In the framework of a study on species and speciation in the *H. crustuliniforme* complex (Aanen & Kuyper, 1999; Aanen et al., 2000a, 2001) the question about an optimal taxonomy was also addressed. However, an optimal taxonomy can only be defined in relation to species concepts (Levin, 2000). Discussions on species concepts are as old as the taxonomic practice. Even a classification of the various kinds of species concepts is liable to heated debate, because the terms for the various concepts have as much an ideological as an explanatory function. For the purpose of this paper we recognise two classes of species concepts, viz. the mechanistic and non-mechanistic or historical species concepts. Mechanistic species concepts, often taken together under the denominator biological species concept, are based on the various processes and mechanisms by which species originate (speciate) or by which they cohere. Mechanisms of speciation relate to the origin of reproductive isolation related to the origin of genetic divergence (incompatibility first or divergence first; Aanen et al., 2000b), and mechanisms of cohesion refer to genetic and ecological mechanisms that allow interbreeding within that species and simultaneously prevent breeding with members of different species. Among the non-mechanistic species concepts, which consider pattern instead of process, two concepts have attracted much attention, viz. a phylogenetic concept, which emphasises monophyly of all the members of the species, and a phenetic concept, which emphasises morphology.

Each of the three species concepts has been applied to the *H. crustuliniforme* complex. Aanen & Kuyper (1999) studied intercompatibility groups (ICGs) and arrived at the conclusion that at least 20 different ICGs ('biological species') could be recognised. However, a subsequent analysis of a subset of these isolates showed that intercompatibility was not a qualitative character ('all or nothing'), but that degrees of compatibility could be recognised. One isolate turned even out to be fully compatible with members of 2 ICGs, which were otherwise incompatible (Aanen et al., 2000b). Apparently, intercompatibility may be a plesiomorphous character and the mechanistic species concept does not always allow to determine unambiguously to which species a certain fungus belongs. The ICGs were subsequently subjected to a phylogenetic analysis, based on sequence data of the internal transcribed spacers (Aanen et al., 2000a). This phylogenetic analysis also showed that ICGs did not always meet the criterion of monophyly. The phenetic species concept ('morphological species concept') has been applied by different authors (e.g. Bruchet, 1970; Vesterholt, 1995) but, as Favre's words testify, consensus was hardly reached.

In this paper we attempt to reconcile the various species concepts, or, if the concepts are fundamentally incompatible, at least to arrive at an operational taxonomy that is consistent with genetics, morphology and phylogeny. We compare a mechanistic ('biological') and phenetic ('morphological') species concept within an explicit phylogenetic framework. Our ultimate aim is the phenetic species concept as this is the only concept useful for the general user of a Flora (Kuyper, 1988). The criterion for consistency is intended to put constraints on the phenetic species concept. First, no intercompatible collections should be classified as different species. Second, interincompatible collections should be regarded as belonging to the same phenetic species, if there are no morphological criteria by which these biological species can be separated. Third, combinations of biological species as phenetic species should only be accepted if the group of biological species forms a monophyletic entity. However, even these conditions can conflict. For example, if one non-basal ICG can be morphologically separated from a monophyletic group of ICGs, the remainder of that group automatically turns into a paraphyletic group.

The strict criterion of monophyly of species has therefore been challenged. We recognise that biological species can form paraphyletic groups. De Queiroz & Donoghue (1988, 1990) have stressed that interbreeding units need not necessarily be monophyletic. As speciation often involves the splitting off of marginal and/or local populations (Levin, 1993; Rieseberg & Brouillet, 1994), a consequence is that after such a speciation event the parent species has become paraphyletic. If the rules of the cladistic game prevent recognition of such paraphyletic groupings as species, we must accept a new mechanism of speciation, described by Templeton (1998) as speciation by remote control. Aanen et al. (2001) noted that ICG 17 (*H. velutipes*) was paraphyletic, as it contained two ITS types that belonged to different clades. Paraphyly of biological species has also been observed in the genus *Pleurotus* (Vilgalys & Sun, 1994). In that genus biological species were monophyletic within a continent, but paraphyletic when investigated over various continents. The same pattern likely has occurred in ICG 17. The ITS polymorphism occurred in Europe and in North America. A plausible scenario for this polymorphism in the face of concerted evolution is divergence in allopatry, followed by bilateral migration to both continents. This could have occurred with the introduction of plantation forest trees, such as *Pseudotsuga menziesii* in Europe, where the phenetic species *H. velutipes* is regularly found (Aanen et al., 2001).

If, however, one accepts paraphyletic taxa at the level of biological species, one may wonder why combinations of biological species, forming phenetic species, could not also form paraphyletic entities. We therefore also considered the consequences of relaxing the criterion of strict monophyly and decided to recognise paraphyletic phenetic species as well. Alternatively, we could accept such paraphyletic taxa on infraspecific level. However, we considered polyphyletic entities unacceptable as phenetic species. To test for monophyly of groups of ICGs, which have formerly been recognised as morphospecies, the most parsimonious tree(s) were compared with constrained trees in which such morphospecies (*H. crustuliniforme*, *H. lutense*, *H. pusillum*) were monophyletic.

A crucial step in our approach is to have a reliable estimate of the phylogeny of the biological species. For the *H. crustuliniforme* complex as a whole, we have estimated phylogenetic relationships based on ITS sequences (Aanen et al., 2000a). Taxonomic

resolution based on ITS sequences turned out to be insufficient for a group of nine ICGs belonging to different morphospecies such as *H. crustuliniforme*, *H. leucosarx* and *H. pusillum*). For that group the Intergenic Spacer (IGS) was also studied (Aanen et al., 2000b).

Different data sets that have the same evolutionary history are expected to converge onto the true species phylogeny of the group under study, if analysed using appropriate phylogenetic methods (Mes, 1995). In principle, such data sets can be combined. Kluge (1989) proposed that phylogenetic analysis should always be performed using all the available evidence (the 'total evidence' approach). In this approach, all of the independent characters available to the systematist should be combined and then analysed using parsimony. However, others have argued against this approach (e.g. Lutzoni & Vilgalys, 1995). Miyamoto & Fitch (1995) argued that phylogenetic trees should be estimated separately from each data set and the different estimates should be compared using taxonomic congruence. Under this separate analysis approach, each partition represents an independent estimate of the tree, and these different estimates can be judged for congruence. It is often argued that congruence among different data partitions provides some of the strongest evidence that a particular phylogenetic estimate is accurate (Hillis et al., 1996). A compromise between the 'total evidence' approach and the 'separate analysis' approach is the 'conditional combination' approach (Huelsenbeck et al., 1996a) as advocated by Bull et al. (1993) and De Queiroz (1993). Under this approach, data sets are statistically tested for homogeneity. Heterogeneous data sets are those that result in significantly different estimates of phylogeny when analysed separately and these data sets can not be combined. If the test result is non-significant, i.e. the data sets do not result in significantly different estimates of the phylogeny, then these data sets should be combined (Huelsenbeck et al., 1996a). As an alternative to combining the data sets, the resulting trees can be combined (Mes, 1995; Sanderson et al., 1998). A 'supertree' is an estimate of a phylogeny assembled from sets of smaller estimates (source trees) sharing at least some taxa (Sanderson et al., 1998).

To the morphological characters studied belong those traditionally used in *Hebeloma* taxonomy (Bruchet, 1970; Vesterholt, 1995). Since many of the characters used are quantitative, we did not reconstruct phylogenies based on these characters. Instead, we i) reconstructed organismal phylogenies based on molecular data; and ii) tried to define morphologically recognisable monophyletic entities. Using the best estimate of the phylogenetic relationships of ICGs within the *H. crustuliniforme* complex, we addressed the following questions:

1. How many morphological taxa, consisting of (strictly) monophyletic groups of ICGs (biological species) can be recognised in this complex?
2. How would relaxing the criterion of monophyly and allowing paraphyletic groupings of ICGs affect the number of phenetic species that can be recognised?
3. How would relaxing the criterion of monophyly and allowing groupings of ICGs in previously recognised morphospecies that can not statistically be rejected against the most parsimonious tree(s), affect the number of phenetic species that can be recognised?
4. What is the phylogenetic quality of some previously recognised morphospecies such as *H. alpinum*, *H. lutense* or *H. pusillum*?

MATERIALS AND METHODS

MATERIAL

Sexual intercompatibility was tested for 110 collections (Aanen & Kuyper, 1999). This analysis led to the recognition of at least 20 intercompatibility groups (ICGs). Two collections (isolates 9692 and 9694) were not compatible with any of the other collections. However, since these collections have neither shown compatibility in intracollection pairings nor in intercollection pairings, the possibility that these two collections were 'incompetent' could not be excluded (R. Petersen, pers. comm.). Therefore, it was not warranted to give a formal status as ICG to these two collections. However, assuming that the two collections are competent, they represent two other ICGs. We therefore consider them as representants of two further biological species: ICG 13 and ICG 22. The macroscopical characters were determined for all 110 collections, the microscopy for 78 collections.

MORPHOLOGICAL DESCRIPTIONS OF ICGS AND MORPHOLOGICAL CHARACTERS USED

Each ICG was described morphologically and the range of character states was described for each ICG. The morphological characters used are listed in Table I. Many of these characters are quantitative. Full descriptions of the ICGs are given in the Appendix.

PHYLOGENETIC ANALYSIS AND COMBINING DATA SETS

For clade I (the *H. velutipes* clade), we had only the ITS data to reconstruct an organismal phylogeny. For clade IIa, we had different data sets. The first estimate of the phylogeny was based on ITS sequences (Aanen et al., 2000a). Clade IIa, except for the two ICGs of *H. pusillum*, was studied in detail using different sequences: the nuclear IGS and a mitochondrial intron (Aanen et al., 2000b). Here we include IGS sequences of the two ICGs of the morphospecies *H. pusillum*, ICG 7 and 9. We performed a new parsimony analysis with the inclusion of those two additional taxa. For the details of the parsimony analysis we refer to Aanen et al. (2000a). Gaps were coded according to Hibbett et al. (1995) for all data sets. The reason that we used gap coding for the ITS data here but not in Aanen et al. (2000a) is that the analysis here was limited to a group of closely related taxa, the alignment of which was straightforward, whereas the alignment with the extended data set was more ambiguous.

Sixteen collections were common for the two nuclear data sets, the ITS and IGS sequences (ICG 1: 9503, 9618, 9621, 9673; ICG 2: 9570, 9627; ICG 3: 9680; ICG 4: 9602; ICG 5: 9581; ICG 7: 9654; ICG 8: 9538; ICG 9: 9509; ICG 14: 9566; ICG 15: 9624; ICG 20: 9688; ICG 21: 9650). Eleven collections were common for all data sets (ICG 1: 9503, 9618, 9621, 9673; ICG 2: 9570, 9627; ICG 3: 9680; ICG 4: 9602; ICG 14: 9566; ICG 20: 9688; ICG 8: 9538). The Partition Homogeneity Test (Farris et al., 1995; Huelsenbeck et al., 1996b; implemented in PAUP*) was used (with 1000 replicates) to determine whether the different data sets were in conflict. In this test, the observed sites from all genes for each individual are pooled and resampled without replacement to give an artificial data set in which sites have been swapped randomly among loci. Many

Table I. Morphological characters used to describe ICGs.

Macroscopical:	pileus:	diameter
		colour
		shape
		presence of hygrophanous spots
	lamellae:	number
		shape
		weeping
	stipe:	length
		width
		presence of bulb
		presence of pendent marrow strand
		covering
	general habit	
	smell	
Microscopical:	spores:	length
		width
		Q (ratio l/w)
		dextrinoidy (scale D0–D4, see Vesterholt, 1995)
		shape
		perispore loosening (scale P0–P3, see Vesterholt, 1995)
		ornamentation (scale O0–O4, see Vesterholt, 1995)
	cheilocystidia:	length
		width at median part
		width at apex
		Q (width apex/width median part)
		shape
		wall thickness
		presence of apical bifurcations
Host tree genera		

such artificial data sets are produced. MP trees are then made for each newly sampled partition in each artificial data set. If the data sets have the same evolutionary history, the sums of the lengths of the gene trees for the observed and resampled data should be similar, but if they have different evolutionary histories, the sums of the tree lengths should be longer than that for the actual data, because of extra homoplasy in the data (Geiser et al., 1998).

Furthermore, some alternative topologies were tested. Three species traditionally considered to be 'good' morphospecies are *H. crustuliniforme* sensu stricto, *H. pusillum* and *H. lutense*. We first did a parsimony analysis with the constraint that the biological species of which the morphospecies *H. crustuliniforme* consisted (ICGs 1, 2, 3, 4 and 5) formed a monophyletic group. Secondly, an analysis was performed with the morphospecies *H. pusillum* as a monophyletic group (ICGs 6, 7, 8 and 12). Thirdly, a constrained analysis was performed with the morphospecies *H. leucosarx* as a monophyletic group (ICG 14 and 15). The constrained trees found were compared with the unconstrained trees using the Kishino-Hasegawa (1989) test and Templeton's (1983) nonparametric test as implemented in PAUP*.

STRATEGY TO ARRIVE AT AN OPERATIONAL TAXONOMY

The first species concept that was tested as an operational species concept was the biological species concept. We considered the morphology of biological species and tested if different biological species could be recognised by morphological criteria. We recognised the possibility that biological species could represent paraphyletic taxa. For eight ICGs we have included more than one strain in the phylogenetic analysis: ICGs 1, 2, 3, 4, 9, 11, 17 and 21. For those ICGs we tested the hypothesis that strains of a single ICG form a monophyletic group.

The second species concept that was tested as an operational species concept was based on combinations of biological species within a phylogenetic framework. On the basis of an estimate of the phylogenetic relationships within *Hebeloma*, we tested for every sister group whether both sister taxa could be morphologically separated. The morphological descriptions of the ICGs were used to do this. As an initial help, we used a set of 13 morphological characters, divided into discrete classes (Table II). Sister taxa were separated if they showed no overlap in at least one of these characters. If both of them could indeed be unambiguously demarcated, they were (at least provisionally) accepted as valid phenetic species. The process was then repeated at the next higher level till all sister group relations had been dealt with. If sister taxa could not be recognised separately as phenetic species, both sister taxa were lumped and the morphological variability for the composite species was assessed. Again the process was repeated till all sister group relations had been dealt with. We introduced an additional criterion for recognition, viz. that morphological relationships between such provisional morphotaxa could be upheld across hierarchical levels. Essentially, in this approach the two sister groups A and B, even when sufficiently different to be kept apart by standard taxonomic practice, were lumped when clade C, the sister group of AB, could not be treated as separate from either group A or B.

In cases where the consensus cladogram did not yield sister group relationships but showed unresolved polytomies, each taxon in a polytomy was compared with every other taxon. Inevitably, this could result in a complex pattern of relationships within the polytomy where some taxa could be unambiguously separated from each other whereas some other ones could not. Again, the criterion of consistency across levels was used.

A more relaxed version of this procedure was tested as well. In this version, paraphyletic taxa were recognised, viz. when the sister groups A and B could be separated, but clade C could only be separated from A, but not from B, we recognised the monophyletic A, and the paraphyletic (B, C).

RESULTS

PHYLOGENY OF ICGs

For the 16 collections for which both ITS and IGS sequences were determined, we determined whether these data sets were in conflict using the partition homogeneity test. The actual summed tree length of 171 was equal to or longer than 65.6% of the artificial data sets, indicating that the gene trees did not have significantly different topologies (Fig. 1a). Therefore, we combined the ITS and IGS data sets to reconstruct a nuclear

phylogeny. The sister taxon of clade II, *H. sarcophyllum* was used as the outgroup. Doing a parsimony analysis with gaps coded according to Hibbett et al. (1995), four trees were found of length 237 (c.i. = 0.86; excluding uninformative characters, 1 = 113, c.i. = 0.69), the strict consensus of which is depicted in Fig. 2. For the 11 collections for which all three sequences were determined, we also did the partition homogeneity test. The actual summed tree length of 134 was smaller than 99.9% of the artificial data sets, indicating that the gene trees did have significantly different topologies (Fig. 1b). Therefore, we conclude that the mitochondrial and nuclear phylogenies can not be combined. Aanen et al. (2000b) showed that the incongruence between the nuclear and mitochondrial tree was mainly due to ICG 1, which had a different position in both phylogenies. As a possible cause we proposed a hybridisation with different mitochondrial and nuclear contributions. Here we use the nuclear phylogeny, but we consider the consequences of other positions of ICG 1.

RECOGNIZABILITY AND MONOPHYLY OF ICGS

In the appendix morphological descriptions are given of 20 ICGs and two putative ICGs (ICGs 13 and 22). *Hebeloma incarnatulum* is the single ICG that can be separated from all the other taxa of the *H. crustuliniforme* complex by the shape of its cylindrical to very narrowly clavate cheilocystidia. All other species of this complex have clavate to (sub)capitate cheilocystidia. Of the ICGs represented by more than one collection, ICGs 1, 2, 9 and 21 were monophyletic, and the two strains of ICG 11 had identical ITS sequences but did not form a monophyletic group. The partially compatible ICGs 3 and 4 did not form monophyletic groups, together they constituted a monophyletic group, however. Strains of ICG 17 did not form a monophyletic group. Two ITS types were found within this ICG that belonged to two different clades.

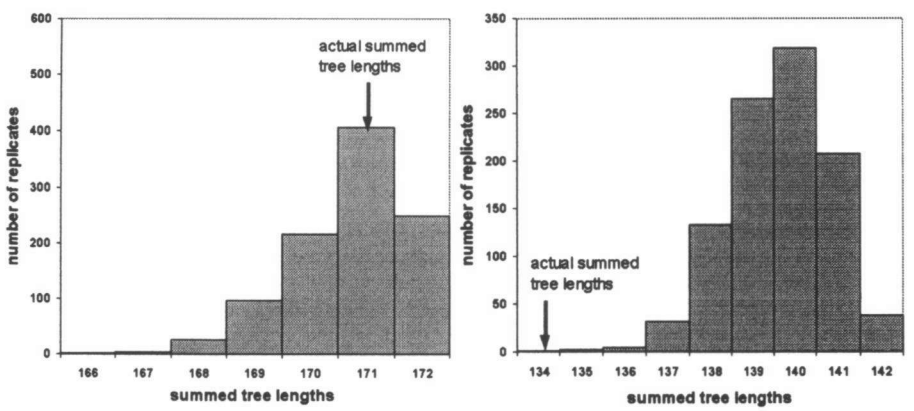

Fig. 1. Partition homogeneity test results.

MONOPHYLETIC RECOGNISABLE ENTITIES

Since most of the ICGs could not be uniquely characterised, we tested if we could recognise monophyletic combinations of ICGs. For every sister group we tested whether both sister taxa could be morphologically separated. The consecutive steps for combining ICGs into monophyletic units are illustrated in Fig. 3 and described in Table III. Some of the characters of the morphological descriptions of the ICGs and of combinations of sister groups are presented in Table II.

To illustrate the procedure, we discuss some examples. At the lowest taxonomic level some sister groups could not be separated and were combined and others could be separated and were, at least provisionally, maintained (Fig. 3 and Table III). ICG 1 and 14 could be separated on the basis of general habit and pileus colour and were therefore maintained at this point. The same was the case for ICG 5 and 7 (stipe-pileus ratio and pileus colour). However, in subsequent steps, those taxa could not be maintained any longer, because ICG 1 could not be separated from 5. ICGs 10 and 15 could be separated on the basis of pileus colour, spore form, and general habit (stipe-pileus ratio). These taxa were therefore maintained at this point. However, the sister group of the pair [10, 15], ICG 20, could not be separated from 10, although it could be separated from 15. Therefore, these three taxa were lumped to g.

This analysis ultimately led to the recognition of 2 morphologically recognisable monophyletic groups, one consisting of three ICGs (clade I), and one consisting of 19 ICGs (clade II). If paraphyletic species would be recognised, ICG 18 (*H. incarnatulum*) could be recognised as an additional monophyletic morphospecies, with the two ICGs of *H. velutipes* forming a paraphyletic phenetic species. The acceptance of paraphyletic taxa (e.g. the pair [1, 5] or [10, 20]) did not have any influence on the final number of species recognised in clade II. Only the moment of combining ICGs was postponed in some cases if paraphyletic entities were (temporarily) accepted.

CONSTRAINED ANALYSIS

The main difference between the nuclear and mitochondrial phylogenies was the position of ICG 1. In the mitochondrial tree, ICG 1 belonged to a clade together with ICG 2, 3 and 4 (and probably 5, see hypothesised gain and loss of different introns in Aanen et al., 2000b). To test the hypothesis that ICG 1, 2, 3, 4 and 5 formed a monophyletic group in the nuclear tree as well, we did a parsimony analysis on the nuclear data set with the constraint that *H. crustuliniforme* was monophyletic. A total of 16 trees were found of length = 241, which could not be rejected in favour of the unconstrained trees (Kishino-Hasegawa test: $p \geq 0.10$, Templeton's test: $p \geq 0.22$). Performing the sister group analysis on the strict consensus tree of those 16 constrained trees did not give other conclusions than the analysis of the unconstrained trees. However, under the relaxed version of the sister group analysis, viz. if we recognised paraphyletic taxa as well, the 5 ICGs of *H. crustuliniforme* could now be recognised as a monophyletic group versus the paraphyletic rest of clade II.

A parsimony analysis on this data set with the constraint that the four ICGs of *H. pusillum* formed a monophyletic group (ICGs 6, 7, 8 and 12) gave 583 trees of length

(text continued on p. 298)

Taxon	Pileus[a] diameter[a]	pileus colour[b]	stipe width[c]	stipe Q[d]	stipe covering[e]	spore length[f]	spore Q[g]	spore dextrinoidy[h]	Perispore loosening[i]	spore smoothness[j]	cheilo-cystidia width[k]	cheilo-cystidia Q_{av}[l]	optional characters[m]
ICG 1	2–3	1	2–3	1	1	1–2	2–3	0–1	0–1	1–2	1–2	4	0
ICG 2	2–3	1–2	3	1–2(–3)	1	1–2	2–3	0–1	0	1–3	1–2	3–4	0
ICG 3	2–3	1	3	1–2	1	2–3	1–3	0–1	0–1	1–3	2	3–4	0
ICG 4	2–3	1	2–3	1	1	2–3	2–3	0–1	0	1–2	2	3–4	0
ICG 5	2–3	1	3	1–2(–3)	1	2	3	0–2	0	1–3	1–2	3–4	0
ICG 6	1	3	1	3	2	3	3	0–1	0	2	1	4	0
ICG 7	1	3	1	3	2	1–2	2–3	0–2	0	2–3	1–2	4	0
ICG 8	1	3	1	3	2	2–3	3	0–2	0–1	1–3	1–2	4	0
ICG 9	1–3	2–3	1–2	2–3	2	1–2	2–3	0–1	0–1	2–3	1	3–4	0
ICG 10	2–3	1–2	2	2	2	1–2	2–3	0–1	0	1–3	1	2	0
ICG 11	2–3	1–2	2–3	1–2	2	1–2	2–3	0–1	0	2–3	1–2	2–4	0
ICG 12	1–2	2–3	1–2	2–3	2	1–2	2–3	0–2	0	2–3	1–2	4	0
ICG 13	2	1–2	2	2	2	1	2	0–1	0	2–3	1	2–3	0
ICG 14	1–2	3	1–2	1–2	2	2–3	2–3	0–1	0–1	2–3	1–3	4	0
ICG 15	1–2	3	1–3	1–2	2	3	3	0–2	0–1	1–3	1–3	3–4	0
ICG 16	2–3	(1–)2	2–3	1–3	2	1–2	1–2	2–4	0–1	2–3	3	2–3	1
ICG 17	2–3	(1–)2	2–3	1–3	2	1–2	1	2–4	0–1	1–3	2–3	2–3	1
ICG 18	3	(1–)2	2	3	3	1	1	3–4	0	2–3	3	1	1
ICG 19	2	2	1–2	3	2	1	2	0–1	0–1	2–3	2	2	0
ICG 20	2–3	2	3	1–2	2	2	2	0–2	0	1–3	1–2	3	0
ICG 21	2–3	2	2–3	2–3	2	1–2	2–3	0–1	0	2–3	1–2	2–4	0
ICG 22	2–3	2	2–3	1–2	2	1–2	2–3	0–1	0	1–2	1	3	0
A (1,5)	2–3	1	2–3	1–2	1	1–2	2–3	0–2	0–1	1–3	1–2	3–4	0
B (3,4)	2–3	1	2–3	1–2	1	2–3	1–3	0–1	0–1	1–3	2	3–4	0
C (8,9)	1–3	2–3	1–2	2–3	2	1–3	2–3	0–2	0–1	1–3	1–2	3–4	0
D (13,22)	2–3	1–2	2–3	1–2	2	1–2	2–3	0–1	0	1–3	1	2–3	0
E (16,17,18)	2–3	2	2–3	1–3	2–3	1–2	1–2	2–4	0–1	1–3	2–3	1–3	1
F (1,5,7,14)	1–3	1–3	1–3	1–3	1–2	1–3	2–3	0–2	0–1	1–3	1–3	3–4	0
G (2,a)	2–3	1–2	2–3	1–2	1	1–3	1–3	0–1	0–1	1–3	1–2	3–4	0
H (10,15,20)	1–3	1–3	1–3	1–2	2	1–3	2–3	0–2	0–1	1–3	1–3	2–4	0
I (e,f)	1–3	1–3	1–3	1–3	1–2	1–3	1–3	0–2	0–1	1–3	1–3	2–4	0
J (c,g,11,19)	1–3	1–3	1–3	1–3	2	1–3	2–3	0–2	0–1	1–3	1–3	2–4	0
K (h,b)	1–3	1–3	1–3	1–3	1–2	1–3	1–3	0–2	0–1	1–3	1–3	2–4	0
L (i,12)	1–3	1–3	1–3	1–3	2	1–3	2–3	0–2	0–1	1–3	1–3	2–4	0
M (k,j)	1–3	1–3	1–3	1–3	1–2	1–3	1–3	0–2	0–1	1–3	1–3	2–4	0
N (6,l)	1–3	1–3	1–3	1–3	1–2	1–3	1–3	0–2	0–1	1–3	1–3	2–4	0
O (m,21)	1–3	1–3	1–3	1–3	1–2	1–3	1–3	0–2	0–1	1–3	1–3	2–4	0

Table III. Consecutive steps for combining ICGs into monophyletic units.

1st level	
– compare 1, 14	– can be separated (general habit, stipe-pileus ratio, pileus colour) – maintain 1 and 14.
– compare 5, 7	– can be separated (general habit, stipe-pileus ratio) – maintain 5 and 7.
– compare 3, 4	– can not be separated – combine to a.
– compare 8, 9	– can not be separated – combine to b.
– compare 10, 15	– can be separated (general habit, stipe-pileus ratio) – maintain 10 and 15.
– compare 13, 22	– can not be separated – combine to c.
– compare 16, 17, 18 in all combinations	– 16 and 17 can not be separated – combine to d.*
2nd level	
– compare 1, 14, 5 and 7 in all combinations	– 1 and 5 can not be separated – combine to e.
– compare a, 2	– can not be separated – combine to f.
– compare 10, 20 and 15, 20	– 10, 20 can not be separated – combine 10, 15 and 20 to g.
3rd level	
– compare e and f	– can not be separated – combine to h.
– compare g, 19, 11 and c in all combinations	– none of them can be separated – combine to i
4th level	
– compare h, b	– can not be separated – combine to j.
– compare i, 12	– can not be separated – combine to k.
5th level	
– compare j, k	– can not be separated – combine to l.
6th level	
– compare l, 6	– can not be separated – combine to m.
7th level	
– compare m, 21	– can not be separated – combine to n.
8th level	
– compare d, n	– can be separated – maintain d and n.

* ICG 18 can be separated from all ICGs because of the shape of its cheilocystidia. However, under the constraint of strict monophyly of recognisable groups, ICG 18 can not be maintained, since 16 and 17 can not be separated. Moreover, strains of ICG 17 itself form a paraphyletic group.

←

Table II. Summary of 13 morphological characters for 22 ICGs and combinations of ICGs. — a = Maximum for a collection – 1: ≤ 30, 2: 30–50, 3: ≥ 50 (in mm); b = 1: pale, 2: pale with dark centre, 3: dark; c = maximum for a collection – 1: ≤ 4, 2: 4–8, 3: ≥ 8 (in mm); d = 1: ≤ 7, 2: 7–10, 3: ≥ 10; e = 1: coarsely floccose, 2: floccose, 3: flocculose; f = 1: ≤ 11, 2: 11–12, 3: ≥ 12 (in µm); g = 1: < 1.7, 2: 1.7–1.8, ≥ 1.8; h = grouped 0–4 (Vesterholt, 1995); i = grouped 0–3 (Vesterholt, 1995); j = grouped 0–4 (Vesterholt, 1995); k = just below the apex – 1: < 4.5, 2: 4.5–4.8, 3: > 4.8 (in µm); l = 1: < 1.2, 2: 1.2–1.7, 3: 1.7–2, 4: ≥ 2; m = 0: less than four of the following six (optional) character states: bulbous stipe, pendant marrow strand, forked apex of cheilocystidia, hygrophanous spots on pileus, dextrinoid spores (≥ 3), Q spores ≤ 1.7; 1: at least four of these six (optional) character states.

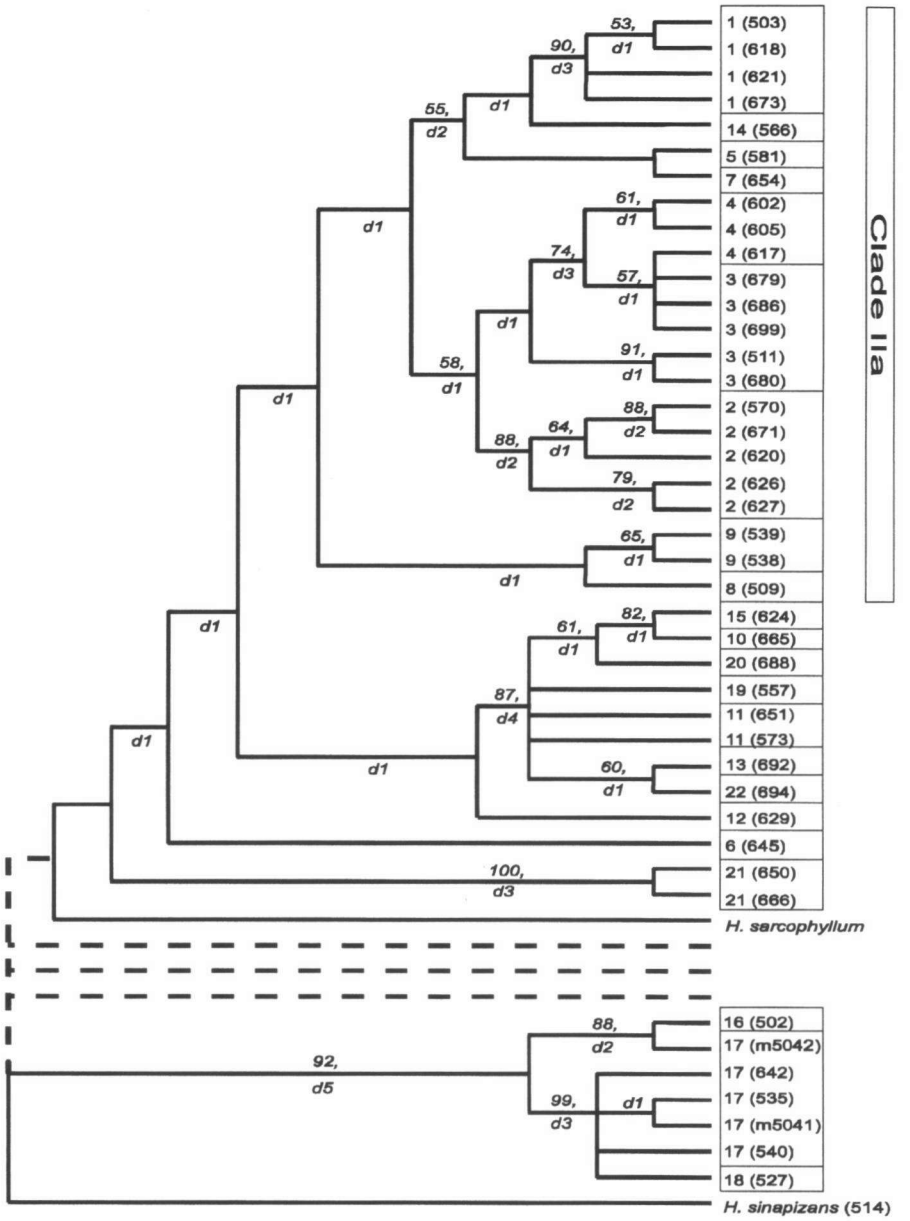

Fig. 2. Phylogenetic relationships in the *Hebeloma crustuliniforme* complex based on nuclear ribosomal ITS sequences. For clade IIa and strains 9624, 9688 and 9650 IGS sequences were determined as well and these sequences were also used in this phylogenetic analysis. The two clades I and II were analysed separately, but are placed in the same figure. Indicated are bootstrap values and decay indices (preceded by d).

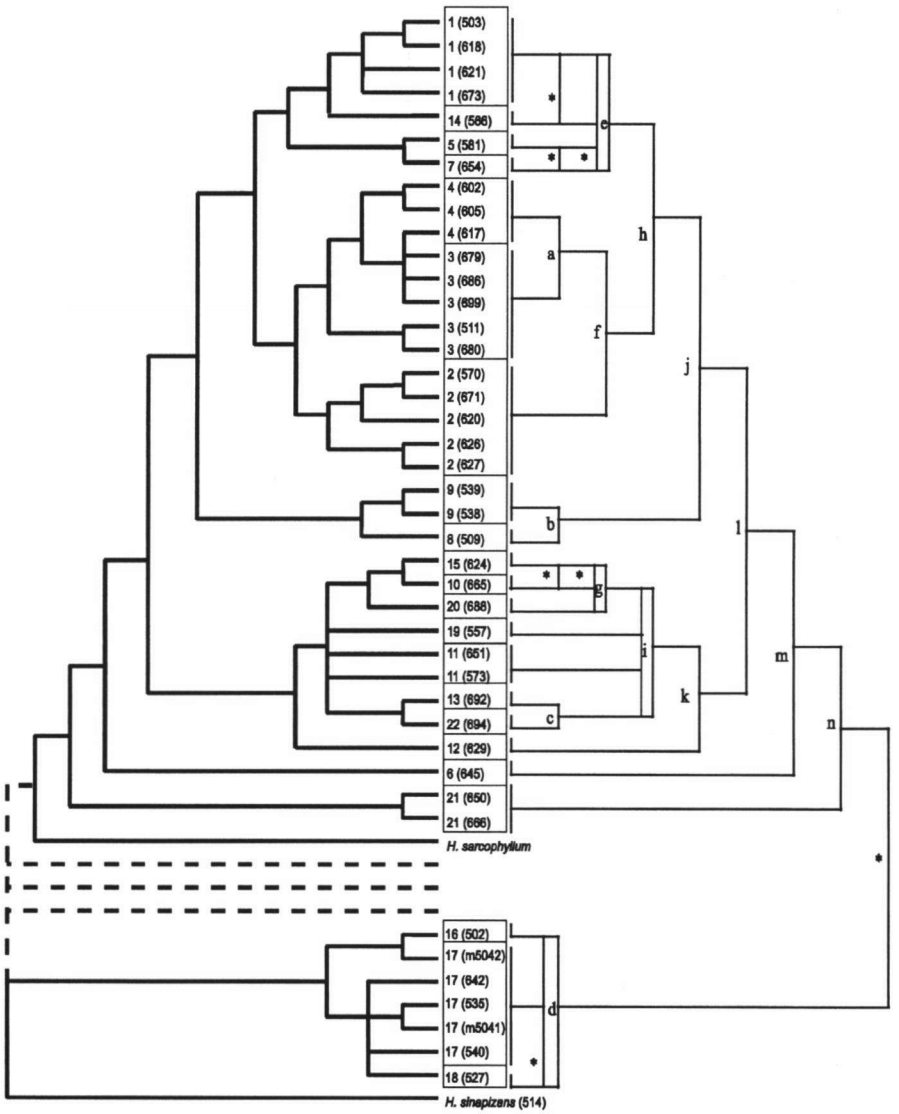

Fig. 3. Consecutive steps for combining ICGs into monophyletic units. If two sister groups can not be separated, this is indicated with *, if two sister groups can be separated, they are combined and a letter is given to the provisional taxon. These steps are repeated at the next level. This analysis ultimately leads to the separation of two morphologically recognisable monophyletic groups, one consisting of three ICGs (clade I), and one consisting of 19 ICGs (clade II).

= 245, that could be rejected in favour of the unconstrained trees (Kishino-Hasegawa test: $p < 0.05$, Templeton's non parametric test: $p < 0.1$). We conclude that the ICGs of the morphospecies *H. pusillum* do not form a monophyletic group and that *H. pusillum* can not be maintained as a valid phenetic species. A parsimony analysis on the data set with the constraint that the two ICGs of *H. lutense* formed a monophyletic group (ICG 14 and 15) gave 60 trees of length = 255. These trees could be rejected in favour of the unconstrained trees (Kishino-Hasegawa test and Templeton's non parametric test: $p < 0.01$ in both cases). We conclude that the ICGs of the morphospecies *H. lutense* do not form a monophyletic group and that *H. lutense* can not be maintained as a valid species.

DISCUSSION

Most biological species could not be recognized using morphological characters. Only ICG 18 could be separated unambiguously from the remaining taxa. ICG 18 is accepted as the phenetic species *H. incarnatulum* (Smith, 1984). The remaining ICGs could not be uniquely characterised, implying that cryptic biological species are the rule within the *H. crustuliniforme* complex. Similar observations have been made in other species groups such as the Corticiaceae (Hallenberg, 1991) and the genera *Paxillus* (Fries, 1985) and *Laccaria* (Mueller, 1991; Mueller & Gardes, 1991), although in some cases morphological differences could be found between ICGs. The biological species of the *H. crustuliniforme* complex are also not meaningful ecological entities. Most collections (70%) of *H. crustuliniforme* and *H. helodes* were made with members of the Salicaceae as the ectomycorrhizal host tree while most collections of *H. velutipes* (93%) were made with other trees as ectomycorrhizal hosts. As the first group consisted of 19 biological species, with very short branch length in the molecular phylogeny, we conclude that extensive speciation took place after a host switch. Extensive speciation after host switches is apparently not uncommon. The same phenomenon has been reported for *Suillus* (Kretzer et al., 1996) and *Leccinum* (H. den Bakker, pers. comm.). It is also known to occur in several species complexes in the genus *Lactarius* (three spp. of the *L. obscuratus* complex associated with *Alnus*; four spp. of the *L. torminosus* complex associated with *Betula* (Molina et al., 1992)). Interestingly, extensive speciation after host switches to the Salicaceae has occurred at least in three clades in *Hebeloma*, viz. the *H. crustuliniforme*/*H. helodes* clade, the *H. mesophaeum* complex (Vesterholt, 1989) and the *H. sacchariolens* complex (Gröger & Zschieschang, 1981). One would be tempted to speculate whether there is a causal relationship between the host switch to Salicaceae and fungal speciation. Salicaceae belong to the monophyletic order Malphigiales. All families in this order form arbuscular mycorrhiza, except Salicaceae that form predominantly ectomycorrhiza. The most parsimonious explanation for this pattern of host tree colonisation is that Salicaceae have been colonised by ectomycorrhizal fungi separately and probably relatively recently. The colonisation of this new and empty niche may have been the factor that favoured rapid speciation. Rapid speciation in the genus *Hebeloma* may also be related to a recent ecological switch from saprotrophy to the mycorrhizal symbiosis. Both the genus *Hebeloma* and its sister group *Alnicola* (Aanen et al., 2000a; Peintner et al., 2001) contain species that live as ectomycorrhizal symbionts and species that have (maintain) a saprotrophic life style, e.g. on old fire places. The sister group of that clade may be the saprotrophic genus *Agrocybe* (Aanen et al., 2000a; Moncalvo et al., 2000).

Since most of the biological species in this species complex could not be recognized, we tested if monophyletic (or paraphyletic, but not polyphyletic) combinations of biological species could be recognized by morphological criteria. Crucial in this approach was to have a reliable estimate of the phylogeny of the biological species. The two nuclear data sets were shown to be not significantly different and were therefore combined. The mitochondrial based phylogeny, however, was shown to be significantly different. We used the nuclear phylogeny as our best guess for the phylogeny of the ICGs, but we considered the mitochondrial based tree as well. If paraphyletic taxa are recognised, three taxa can be recognised. Under the constraint that the five ICGs of *H. crustuliniforme* (ICGs 1, 2, 3, 4 and 5) form a monophyletic group, trees are found that can not be rejected against the most parsimonious tree. The idea that the five ICGs of *H. crustuliniforme* form a monophyletic group is in agreement with the mitochondrial tree.

After evaluating the pros and cons of a phenetic species concept that allows inclusion of paraphyletic groupings of biological species and groupings of biological species that can not be rejected as belonging to a monophyletic group, we decided to accept four phenetic species in the *H. crustuliniforme* complex. They are keyed out as follows.

KEY TO FOUR RECOGNISED SPECIES OF THE H. CRUSTULINIFORME COMPLEX

1a. Spores distinctly, often rather strongly dextrinoid (D2–D4), ellipsoid to oblong ($Q_{av} \leq 1.7$); cheilocystidia cylindrical to cylindrico-clavate, but sometimes with bifid apex; stipe usually distinctly bulbous, flocculose; generally associated with Pinaceae, Betulaceae, Carpinaceae and Fagaceae 2

b. Spores not to weakly dextrinoid (D0–D1(–D2)), oblong to fusiform ($Q_{av} \geq 1.7$); cheilocystidia clavate to subcapitate, never with bifid apex; stipe usually cylindrical to clavate to subbulbous, often (coarsely) floccose; generally associated with Salicaceae 3

2a. Cheilocystidia cylindrico-clavate, in upper part on average more than 6.0 μm broad (6.2–10.2 μm), and $Q_{av} = 1.2–2.0$ ..... 1. *H. velutipes*

b. Cheilocystidia cylindrical, in upper part on average less than 6.0 μm broad (5.6 μm), and $Q_{av} = 1.1$ ..... 2. *H. incarnatulum*

3a. Stipe 2–10.5 mm broad, minutely flocculose to (sub)floccose, distinctly darkening from base upwards; pileus 13–75 mm, usually with straight margin when young, yellowish to red-brown, often distinctly paler towards margin and then ± bicolorous; cheilocystidia usually (sub)capitate ..... 3. *H. helodes*

b. Stipe 6–14 mm broad, coarsely floccose, white, not or hardly darkening from base upwards; pileus 35–170 mm, with involute margin when young, whitish to yellowish, ± unicolorous, cheilocystidia clavate to slightly subcapitate
4. *H. crustuliniforme*

General note

This paper does not (and could not) aim at a full taxonomic revision of all taxa in this complex. It could not do so, because the biological species concept can not be applied to type collections (unless there exist ex-type cultures). Therefore our nomenclator will inevitably be incomplete. We only list major names that have been used recently and

comment upon the biological (what is the relationship between biological species and morphological taxa?), phylogenetic (are morphospecies that are commonly mentioned, mono-, para- of polyphyletic?) and morphological (how well are different morphospecies in common use separated from each other?) quality of species names in common use.

Hebeloma velutipes Bruchet

Hebeloma velutipes Bruchet, Bull. mens. Soc. linn. Lyon (Suppl.) 39 (1970) 127.

Hebeloma bulbiferum Maire, Publ. Inst. bot. Barcelona 10 (3) (1937) 108. — *Hebeloma crustuliniforme* var. *bulbiferum* (Maire) J. Favre, Ergebn. wiss. Unters. schweiz. NatParks, NF 6 (1960) 488 (invalid, basionym not cited).

Hebeloma bulbosum Romagn., Sydowia 36 (1983) 263, non *H. bulbosum* Fayod 1893. — *Hebeloma favrei* Romagn. & Quadr., Doc. Mycol. 14 (56) (1985, '1984') 31.

Misapplied. Hebeloma crustuliniforme sensu auct.; *Hebeloma longicaudum* sensu J.E. Lange, Fl. agar. dan. 3 (1938) 95; sensu P.J. Keizer & Arnolds, Persoonia 16 (1995) 92; sensu Bruchet, Bull. mens. Soc. linn. Lyon (Suppl.) (1970) 77 (see notes); *Hebeloma leucosarx* sensu Vesterh., Svampe 25 (1992) 16; Symb. bot. Upsal. 30 (3) (1995) 136 (see notes).

Pileus to 32–78 mm, convex to applanate, without umbo to rather distinctly umbonate, dry, slightly to distinctly viscid, sometimes seemingly hygrophanous with irregular spots, in centre red-brown, (pale) yellow-brown to pale ochraceous yellow (Mu. 5 YR 4–5/3, 10 YR 4–6/4, 5–6/6, 2.5 Y 7–8/2–4, 10 YR 7–8/4–6), uniformly coloured (especially in paler specimens) to ± distinctly paler outwards and at margin sometimes even whitish. Lamellae, L = 40–70, l = 3–7, thin, (very) crowded, rather broadly to narrowly adnate, to 8 mm, not ventricose to subventricose, ochraceous buff to brownish ochraceous (Mu. 10 YR 7/2–3 to 6/3–4); edge fimbriate, whitish; weeping (but sometimes not distinctly so). Stipe to 34–120 × 5–10 mm, Q = 5.3–12, shorter to longer than diameter of pileus, usually ± distinctly bulbous (to 20 mm), sometimes (sub)clavate or even equal, fistulose, with pendent narrow strand, sometimes solid, whitish, discolouring to brownish on damage from base upwards, (sub)flocculose to subflocculose, especially in upper part. Context thick, firm, white. Smell raphanoid.

Spores (9.5–)10.0–13.0 × 6.0–7.5 µm, on average 10.4–11.9 × 6.3–7.2 µm, Q = 1.5–1.8(–1.9), Q_{av} = 1.57–1.80, weakly to distinctly dextrinoid (D2–D4), regular to subamygdaliform, exceptionally sublimoniform; perispore not or very slightly loosening (P0–P1); almost smooth or slightly to rather distinctly verruculose (O1–O3). Cheilocystidia (36–)40–87(–106) × 4–7(–8) × 6–13 µm, on average 45.5–72.2 × 4.5–6.3 × 6.2–10.2 µm, Q = (1.0–)1.2–2.2(–2.8), Q_{av} = 1.2–2.0, straight to flexuose, subcylindrical to subclavate, usually not distinctly enlarged apically, but exceptionally tending to subspathuliform or subcapitate, exceptionally also subcylindrical and not swollen towards apex, sometimes slightly swollen in basal part and then slenderly subutriform, thin-walled to slightly thick-walled, sometimes bifid in apical part in varying frequency (absent to fairly common, and then apex to 19 µm broad).

Habitat — Associated with various deciduous and coniferous trees (*Betula*, *Fagus*, *Quercus*, *Carpinus*, *Corylus*, *Picea*, *Pinus*), only very exceptionally in the vicinity of *Salix*.

Notes — 1. *Hebeloma velutipes* is well recognized by relatively broad, dextrinoid spores and clavate, non-capitate cheilocystidia. Many collections also show a number of the following characters: pileus with hygrophanous spots; stipe distinctly bulbous (*H. bulbiferum* Maire); stipe hollow with pendent marrow strand; part of the cheilocystidia with bifid apex. The taxon is accepted as a paraphyletic phenetic species, consisting of ICG 16 and 17. *Hebeloma leucosarx* sensu Vesterholt and *H. longicaudum* sensu Keizer & Arnolds are identical (ITS-RFLP patterns of both taxa studied, D.K. Aanen, unpubl. obs.).

2. In the literature on ectomycorrhizal fungi the name *H. crustuliniforme* is very repeatedly encountered. It is likely that many, if not most, of these cultures actually refer to *H. velutipes*.

3. *Hebeloma longicaudum* has originally been characterised by a pale pileus and a long stipe. However, the case of *H. pusillum* serves as a warning with regard to the taxonomic value of habit characters. Descriptions of several pale-coloured ICGs also indicate that habit can be very variable. The name is therefore considered a *nomen ambiguum*.

4. *Hebeloma leucosarx* was described by Orton (1960) as a species with relatively slender spores, distinctly capitate cheilocystidia and associated with *Salix*. On the basis of that description it has been considered a member of the *H. helodes* complex by Dutch mycologists. Vesterholt (1995), however, noted that the holotype had distinctly dextrinoid spores and non-capitate cheilocystidia, which makes this collection a member of the *H. velutipes* clade. Vesterholt also suggested that *H. velutipes* might be identical. We have not studied the type. Considering the divergent interpretations of the name *H. leucosarx*, the name is not accepted in our paper; instead we continue to use the name *H. velutipes*. *Hebeloma leucosarx* sensu auct. neerl. belongs to *H. helodes* (q.v.).

5. *Hebeloma fragilipes* Romagn. was defined on the basis of the shape and median wall thickening of the cheilocystidia. The microscopical characters mentioned by Vesterholt (1992, 1995) on the basis of a large number of collections from a number of European countries, suggest both elements of *H. velutipes* (spores distinctly dextrinoid, cheilocystidia that are not much swollen apically) and *H. helodes* (spores indextrinoid, oblong to fusiform). Slightly thick-walled cheilocystidia have been observed in both ICG 16 and 17 (*H. velutipes*) and in various ICGs of the *H. helodes* complex (also mentioned by Vesterholt); our collections with a somewhat thickened cheilocystidial wall (in median or apical part) were completely interfertile with specimens with thin-walled cystidia, so we think that at least some doubt exists whether this morphospecies could be maintained. No collections have been made by us that exactly fit Vesterholt's descriptions, so we refrain from a conclusion about its taxonomic status.

Hebeloma incarnatulum A.H. Sm.

Hebeloma incarnatulum A.H. Sm., Sydowia 37 (1984) 280.
Hebeloma bryogenes Vesterholt, Windahlia 20 (1993) 55.

Pileus to 60 mm, convex to almost applanate, with a low broad umbo, very viscid, uniformly yellow-brown (Mu. 10 YR 7–8/4–6). Lamellae, L = 55, l = 1–3, thin, normally crowded, to 5 mm, not ventricose, broadly adnate, ochraceous (10 YR 7/2–3); edge fimbriate, whitish; weeping. Stipe to 110 × 7 mm, Q = 15.7, longer than diameter of pileus, bulbous (to 20 mm), fistulose with pendent marrow strand, white, finely flocculose. Context thin, firm, white. Smell raphanoid.

Spores (10.0–)10.5–11.5(–12.0) × (6.0–)6.5–7.0 µm, on average 10.9 × 6.5 µm, Q = 1.6–1.7(–1.8), Q_{av} = 1.67, distinctly dextrinoid (D3–D4), regular to subamygdaliform, not sublimoniform; perispore not loosening (P0); distinctly verruculose (O2–O3). Cheilocystidia (45–)46–59(–72) × (4–)5–6 × 5–6(–7) µm, on average 54.5 × 5.0 × 5.6 µm, Q = 1.0–1.2(–1.3), Q_{av} = 1.1, cylindrical, partly somewhat inflated in basal part and then subventricose-slenderly utriform, near apex not or hardly inflated, not clavate, thin-walled.

Habitat — Associated with *Pinus* among living *Sphagnum*.

Note — Only a single collection was studied of ICG 18. The differences with *H. velutipes* are rather subtle (narrower cheilocystidia). Possibly *H. incarnatulum* has also a slightly different ecology (natural moist forests with *Sphagnum*).

Hebeloma helodes J. Favre

Hebeloma helodes J. Favre, Beitr. Krypt.-fl. Schweiz 10 (3) (1948) 214.
Hebeloma hiemale Bres., Fung. trident. 2 (1892) 52.
Hebeloma pusillum J.E. Lange, Fl. agar. dan. 5 (1940) iv.
Hebeloma cavipes Huijsman, Persoonia 2 (1961) 97.
Hebeloma lutense Romagn., Bull. trimest. Soc. mycol. Fr. 81 (1965) 342.
Hebeloma oculatum Bruchet, Bull. mens. Soc. linn. Lyon 39 (Suppl.) (1970) 126.
Hebeloma pusillum var. *longisporum* Bruchet, Bull. mens. Soc. linn. Lyon 39 (Suppl.) (1970) 126.
Misapplied. Hebeloma leucosarx sensu auct. Neerl. (see notes).
Excluded. Hebeloma helodes sensu Keizer & Arnolds, Persoonia 16 (1995) 88 (= *H. velutipes*).

Pileus 13–75 mm, plano-convex to applanate, finally even slightly depressed, with or without umbo, margin sometimes subinvolute, viscid to rather dry, subshiny, two-coloured and in centre reddish ochraceous to (dark) reddish brown (Mu. 2.5–5 YR 3/2, 5 YR 3–4/4, 5/6, 7.5 YR 4/2–4, 5/4, 5/6, 10 YR 6–7/6, 5/4–6, 3–4/3), outwards slightly to distinctly paler, at margin slightly paler to whitish or rather uniformly coloured and paler, pale yellow-brown or pale yellow (10 YR 7–8/3, 2.5 Y 8/2–4, 2.5 Y 7/8). Lamellae, L = 25–70, l = 1–5(–7), thin, normally crowded, sometimes very crowded, to 6 mm broad, rather narrow to subventricose, broadly to narrowly adnate or emarginate, pale brown to (greyish) ochraceous brown (10 YR 4/4, 5/4, 6/3–4, 7/2–3) edge fimbriate, whitish; weeping, sometimes only indistinctly. Stipe 18–90 × 2–10.5 mm, Q = 2.4–25, shorter to (much) longer than diameter of pileus, equal to slightly swollen, sometimes clavate to subbulbous (to 10 mm), solid, with age fistulose, whitish above, somewhat to distinctly darkening from base upwards, yellow-brown to brown in lower part, especially with age, (minutely) flocculose or even (sub)floccose, especially in upper part, in lower part more fibrillose, sometimes flocculose over whole length. Context thin to thick in larger specimens, whitish to (pale) brownish buff. Smell raphanoid, sometimes weakly so.

Spores 8.5–17.0 × 5.0–8.0(–9.0) µm, on average 9.0–14.9 × 5.0–7.2 µm, Q = (1.5–)1.6–2.1(–2.2), Q_{av} = 1.64–2.03, not to weakly dextrinoid (D0–D2), subamygdaliform, a few tending to sublimoniform; perispore not or slightly loosening (P0–P1); almost smooth, weakly ornamented to distinctly verruculose (O1–O3(–O4)). Cheilocystidia (34–)36–78(–80) × 3–6 × (5–)6–16(–17) µm, on average 41.0–64.0 × 3.7–5.1 × 5.9–13.3 µm, Q = 1.2–3.8(–4.0), Q_{av} = 1.4–3.0, straight, but in some collections flexuose, (sub)cylindrico-(sub)clavate to cylindrico-subspathuliform or cylindrico-subcapitate, sometimes rather conspicuously so, but sometimes only hardly swollen apically, thin-walled or with slightly to distinctly thickened yellowish or brownish wall in upper part, especially in subcapitate cheilocystidia, exceptionally slightly thick-walled in median part or throughout.

Habitat — Usually associated with *Salix*, sometimes with other deciduous trees (*Populus*, *Quercus*, *Betula*, *Fagus*, *Tilia*), exceptionally with conifers (*Picea*, *Pinus*).

Notes — 1. *Hebeloma helodes* was originally described as a taxon very close to *H. pusillum* (same habit, same size, and same colour). Subsequent authors have gradually enlarged this circumscription (*H. helodes* sensu Vesterholt, 1995, is paler) or misinterpreted the name (*H. helodes* sensu Keizer & Arnolds). Bruchet (1970) did not treat *H. helodes*. On the basis of our cladogram *H. helodes* is accepted as the name for a paraphyletic grouping, as a sister group to *H. crustuliniforme*, which is considered a separate phenetic species. Species circumscription of *H. helodes* is still quite broad, which is consistent with the relatively high amount of molecular variation (compared to *H. crustuliniforme*). Intermediates between *H. helodes* and *H. crustuliniforme* could possibly occur (cf. *H. cavipes*, note 3). Considering the wide circumscription of *H. helodes*, it becomes inevitable that *H. pusillum* and *H. lutense* have to be included; this conclusion is not surprising, considering the enlarged description of *H. helodes* by Vesterholt. As a consequence, variation in morphology and microscopical characters is substantial. The phenetic species is comprised of ICGs 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 19, 20, 21, 22.

2. The name *H. helodes* is not the oldest name available. We decided to use it as a name that is less liable to confusion over its application and circumscription than e.g. *H. pusillum* or *H. hiemale*.

3. *Hebeloma cavipes* was accepted by Vesterholt (1995) as a valid species, only known from the type collection in an open vegetation under *Cistus*. Vesterholt noted that in its microscopical characters it was very similar to both *H. crustuliniforme* and *H. helodes*, and these three taxa could only be kept apart on the basis of size, hollow stipe (also a supposed characteristic of *H. alpinum*, see under *H. crustuliniforme*), and cheilocystidia that are often widened in the basal part. As the species is known from one collection only, it is likely therefore that finding additional collections of *H. cavipes* could either collapse the distinction with *H. crustuliniforme* (if somewhat larger specimens were found) or with *H. helodes* (if smaller specimens were found). Vesterholt further suggested that *H. cavipes* could be conspecific with *H. lutense* (note 6), a species that is usually regarded as having a darker pileus and for that reason was not treated in Vesterholt (1995). A culture collection of *H. cavipes* had the same ITS sequence as collections of *H. hiemale*, *H. lutense* (ICG 15), and *H. helodes* (ICG 10). The taxon is therefore accepted as a synonym of *H. helodes*.

4. *Hebeloma hiemale* was not treated by Vesterholt. According to Bruchet (1970) it is a xerophilous species, usually associated with *Cistus* in the Mediterranean region, although he also cited a note from Huijsman that the species is common in the Dutch dunes (which raises suspicion that it is very close to *H. lutense*, see note 6). On the basis of the species description, it seems to come very close to *H. helodes*. The ITS sequence of a culture collection of *H. hiemale* was identical to those of *H. cavipes*, *H. lutense* (ICG 15) and *H. helodes* (ICG 10). The taxon is therefore accepted as a synonym of *H. helodes*.

5. *Hebeloma leucosarx* was described by Orton (1960) as a species with relatively slender spores, distinctly capitate cheilocystidia and associated with *Salix*. On the basis of that description it has been considered a member of the *H. helodes* complex by Dutch mycologists. Vesterholt (1995), however, noted that the holotype had distinctly dextrinoid spores and non-capitate cheilocystidia, which makes this collection a member of the *H. velutipes* clade. Vesterholt also suggested that *H. velutipes* might be identical. We have not studied the type. Considering the divergent interpretations of the name *H. leucosarx*, the name is not accepted.

6. In the Netherlands *H. lutense* (= *H. leucosarx* sensu auct. neerl.) is recognized mainly by habit (relatively stout specimens, compared to *H. pusillum*) and habitat (usually associated with *Salix repens* often in early successional, relatively open sites). The first character may reflect an adaptation to the relatively open structure (and hence drier microclimate) of *S. repens* vegetation. The species also differs from several interpretations of *H. helodes* by darker colours. Collections that fit the description of *H. lutense* belong to two different ICGs. ITS sequence of ICG 15 is similar to that of *H. cavipes*, *H. hiemale*, and *H. helodes* (ICG 10). A constrained tree in which both ICGs with the characteristics of *H. lutense* were combined, had to be rejected. Morphological variability within some of the ICGs also suggests that *H. lutense* can neither be separated from *H. helodes* nor from *H. pusillum*. Vesterholt (1995) suggested that *H. lutense* could be a synonym of *H. cavipes* (note 2).

7. The name *H. pusillum* is used for small and slender specimens with a dark pileus, associated with *Salix*. The species is somewhat variable in spore size. This species also got a slightly enlarged circumscription, e. g. by Bruchet (1970; where it almost certainly includes *H. helodes*) and Phillips (1981; which also seems to fit better into the concept of *H. helodes*). *H. pusillum* consists of four different ICGs. A tree, constrained to make *Hebeloma pusillum* a monophyletic entity, must statistically be rejected against the most parsimonious trees, indicating that the defining characters of *H. pusillum* (slender habit with small basidiocarps) have likely arisen repeatedly.

8. *Hebeloma fragilipes* Romagn. was defined on the basis of the shape and median wall thickening of the cheilocystidia. The microscopical characters mentioned by Vesterholt (1992, 1995) on the basis of a large number of collections from a number of European countries, suggest both elements of *H. velutipes* (spores distinctly dextrinoid, cheilocystidia that are not much swollen apically) and *H. helodes* (spores indextrinoid, oblong to fusiform). Slightly thick-walled cheilocystidia have been observed in both ICG 16 and 17 (*H. velutipes*) and in various ICGs of the *H. helodes* clade (also mentioned by Vesterholt); our collections with a somewhat thickened cheilocystidial wall (in median or apical part) were completely interfertile with specimens with thin-walled cystidia, so we think that at least some doubt exists whether this morphospecies could

be maintained. No collections have been made by us that exactly fit Vesterholt's descriptions, so we refrain from a conclusion about its taxonomic status.

Hebeloma crustuliniforme (Bull.) Quél.

Agaricus crustuliniformis Bull., Herb. Fr. (1787) pl. 308; *Hebeloma crustuliniforme* (Bull.) Quél. in Mém. Soc. Emul. Montbéliard, sér. II, 5 (1872) 128.

Hebeloma populinum Romagn., Bull. trimest. Soc. mycol. Fr. 81 (1965) 326.

Hebeloma crustuliniforme var. *alpinum* J. Favre, Ergebn. wiss. Unters. schweiz. NatParks, NF 5 (1955) 121; *Hebeloma alpinum* (J. Favre) Bruchet, Bull. mens. Soc. linn. Lyon 39 (Suppl.) (1970) 68.

Hebeloma ochroalbidum Bohus, Annls hist.-nat. Mus. nat. hung. 64 (1972) 71.

Hebeloma crustuliniforme var. *tiliae* Bresinsky, Z. Mykol. 53 (1987) 294.

Excluded. Hebeloma crustuliniforme sensu auct. (= *H. velutipes*).

Pileus 35–170 mm, convex to applanate, without umbo or with indistinct umbo, margin (sub)involute, (slightly) viscid when moist, rather pale, in centre pale yellow to pale yellow-brown (Mu. 10 YR 7–8/3; 2.5 Y 6–7–8/2–4–6), but sometimes more brownish (10 YR 5–6/4–6 to 4/4), paler towards outer part or rather uniformly pale ochraceous yellow, at margin whitish or white. Lamellae, L = 45–100, l = 1–3–5, thin, (very) crowded, to 8 mm, subventricose, narrowly adnate to emarginate, ochraceous to pale grey-brown (10 YR 7/3–6/3–4); edge fimbriate, whitish; weeping. Stipe 23–115 × 6–14 mm, Q = 2.1–11.5, usually shorter to longer than diameter of pileus, at base somewhat clavate (to 16 mm) to (almost) equal, solid, fistulose with age, white, coarsely floccose, especially in upper part. Context thick in pileus, firm, white. Smell raphanoid, sometimes mixed with a sweetish component.

Spores (9.5–)10.0–13.0(–14.0) × (5.0–)5.5–7.5 µm, on average 10.3–12.5 × 5.8–7.1 µm, Q = 1.6–2.1, Q_{av} = 1.68–1.92, not dextrinoid, sometimes indistinctly dextrinoid (D0–D1(–D2)), regular to subamygdaliform, not or exceptionally tending to sublimoniform; perispore not (or very slightly) loosening (P0–P1); almost smooth to distinctly verruculose (O1–O2(–O3)). Cheilocystidia (36–)43–77(–90) × (3–)4–6 × (6–)7–12(–14) µm, on average 49.8–66.4 × 3.8–4.8 × 7.6–10.3 µm, Q = (1.2–)1.4–2.8(–3.0), Q_{av} = 1.7–2.2, (slenderly) (sub)cylindrico-(sub)clavate, exceptionally cylindrical, gradually broadened towards apex, but only a (small) minority tending to subcapitate and then apical part more distinctly enlarged, thin-walled, exceptionally slightly thick-walled in upper part and slightly refringent.

Habitat — Mainly associated with *Salix* and *Populus*, but also with *Tilia*, *Betula*, *Corylus*, *Quercus*, or *Dryas* and *Helianthemum*. Occurring from the lowland to the alpine region.

Notes — 1. *Hebeloma crustuliniforme* as presently conceived by Vesterholt (1995) is maintained as an autonomous species, after the criteria of monophyly and parsimony are relaxed to include paraphyletic groupings of ICGs and less parsimonious trees that cannot be rejected against the most parsimonious trees. Moreover, the mitochondrial tree supported the monophyly of ICGs 1, 2, 3 and 4 of *H. crustuliniforme* and did not exclude the possibility that ICG 5 belonged to it as well. It consists of ICG 1, 2, 3, 4 and 5.

2. In the literature on ectomycorrhizal fungi the name *H. crustuliniforme* is very repeatedly encountered. It is likely that many, if not most, of these cultures actually refer to *H. velutipes*.

3. The application of the name *Agaricus fastibilis* Pers. :Fr. was extensively discussed by Kuyper & Vesterholt (1990). They concluded that the name, as originally conceived, referred to a taxon very close to *H. crustuliniforme*. However, another interpretation has been widespread in which *H. fastibile* is a cortinate species, also recently known as *H. mesophaeum* var. *crassipes* (Vesterholt, 1989).

4. *Hebeloma alpinum* was originally described by Favre (1960) as a variety of *H. crustuliniforme*. Favre invoked a number of morphological characters to delimit this taxon (small habit, broader lamellae, hollow stipe) but wondered whether these characters might just reflect adaptations to the microclimatic conditions in the alpine zone. However, as Favre did not observe specimens that were transitional between the alpine variant and the typical *H. crustuliniforme* (actually, he did not even observe typical *H. crustuliniforme* in the upper subalpine zone), he considered these differences to be genetically fixed and hence worthy of recognition on varietal status. Bruchet (1970) elevated the taxon to species rank and gave an enlarged description of it (much larger size than Favre's taxon, taste less bitter), whereas Vesterholt (1995), who also accepted species status, used a partly different set of characters than Favre to keep this taxon apart (spores weakly dextrinoid, in *H. crustuliniforme* indextrinoid or nearly so). Our alpine collections from this group showed substantial variation in size. They belong to three different ICGs, two of which contained both alpine and lowland collections (ICGs 1 and 2), and one of which (ICG 4) was partially compatible with a lowland ICG (ICG 3). Partial intercompatibility between these four ICGs furthermore strongly suggest that *H. alpinum* can not be maintained any longer. Moreover, in a phylogeny between populations of these ICGs, the alpine populations did not form a distinct monophyletic group (Aanen et al., 2000b).

A CONSENSUS TAXONOMY FOR THE H. CRUSTULINIFORME COMPLEX?

Most of the characters used, traditionally and also in this study, in *Hebeloma* taxonomy, are quantitative. Different types of characters can be recognised. First, there are characters that are absolutely discriminating between taxa, one taxon always has state A, whereas the other taxon always has state B. Such characters are rare in this group of ICGs. In fact the only character of this type is the shape of the cheilocystidia, with a unique state for *H. incarnatulum*. A second type of characters are characters that have a rare unique state. The presence of such a state is informative and can be decisive to place a specimen in a certain taxon, whereas its absence is uninformative. Examples of such a character are cheilocystidia with a bifid apex, or the presence of hygrophanous spots on the pileus. Both characters have only been found in *H. velutipes* and never in *H. helodes* or *H. crustuliniforme*. However, in *H. velutipes* these character states do not occur constantly. Therefore, only the presence of this state is informative, whereas its absence is not. Some combinations of characters are unique for certain species groups and can be used as well. The combination of characters, coded in Table III, is such a set. This combination of characters, of which none is necessary, is jointly sufficient to assign a collection to the phenetic species *H. velutipes*. The individual characters that comprise a set, however, do not necessarily uniquely characterise phenetic species. Relatively broad spores, or slender, non-capitate cheilocystidia occur in *H. helodes* and *H. crustuliniforme*, but the combination of these

characters has never been encountered in this clade. The last type of characters we recognise are statistical characters. For example, 74% of the collections of *H. helodes* and *H. crustuliniforme* have been found with Salicaceae, whereas only 7% of the collections of *H. velutipes*. The latter species usually occurs in association with members of Pinaceae, Fagaceae and Betulaceae. Such characters can never be decisive themselves but can give additional support for doubtful collections.

The lack of reliable qualitative characters may seem surprising, considering the number of species described in that group. The almost complete similarity in microscopical characters between the different intercompatibility groups is consistent with a scenario of a slow evolution (or even stasis) of morphological characters. However, as the molecular data show a high sequence similarity and consequently short branch length between biological species, especially in the *H. crustuliniforme*/*H. helodes* clade, it is more likely that the members of the group diverged only recently, with ITS sequences evolving at slower rates than compatibility characteristics and micro-morphological characteristics evolving at an even lower rate, while some macroscopical characters are highly plastic.

A scenario of rapid speciation would at first sight contradict the existence of well recognised morphospecies such as *H. alpinum*, *H. pusillum* or *H. lutense*. However, both latter taxa had to be rejected because phylogenetic trees, in which these taxa were constrained to form a monophyletic group, performed significantly worse. It is more likely, that these morphospecies are recognised on the basis of plastic characters such as habit (length/width ratio of stipe; ratio of pileus diameter and stipe length) and that these characters reflect more habitat conditions than genetically fixed characters. A similar explanation may be true for *H. alpinum*, where again differences in habit (small pileus, short and thick stipe) could be more plastic than normally assumed. The high plasticity and variability in macroscopical characters and the relative uniformity in microscopical characteristics may ultimately be the explanation for our failure to recognise more than four phenetic species with a minimal phylogenetic quality in this taxon complex.

The comparison of a biological and morphological species concept within a phylogenetic framework indicated that these various concepts can not be reconciled to produce an unambiguous, unique solution to the species problem in the *H. crustuliniforme* complex. Even under the assumptions (which not all mycologists would accept!) that i) the phylogeny estimate is sufficiently accurate and ii) the value of morphological characters has been exhaustively studied, the number of species ultimately depends on the rules of the game (acceptability of paraphyletic groupings, acceptability of less parsimonious trees that can not be rejected in favour of the most parsimonious tree). It would therefore be necessary to seek consensus about these rules, so that these incompatible demands on taxonomy (species should really exist, be recognisable and have minimal phylogenetic quality) can be sorted out and an acceptable solution can be found for this complex. Between the Scylla of morphology (which would have forced us to accept taxa that must statistically be rejected because of lack of phylogenetic quality) and the Charybdis of the biological species concept (which would have forced us to produce a taxonomy that can not be applied in daily practice), the recognition of four species seems a workable alternative.

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APPENDIX

ICG 1

Pileus to 40–85 mm, convex to plano-convex, without umbo, margin involute, (slightly) viscid when moist, rather pale, in centre pale yellow to pale yellow-brown (Mu. 10 YR 7–8/3, 2.5 Y 6–7/4), paler towards outer part, at margin whitish or white. Lamellae, L = 55–60, l = 1–3(–5), thin, crowded, to 6.5 mm, subventricose, narrowly adnate to emarginate, ochraceous (10 YR 7/3); edge fimbriate, whitish; weeping. Stipe 35–50 × 7–14 mm, Q = 2.6–5.7 usually shorter than diameter of pileus, but sometimes equal to or slightly longer than diameter of pileus, at base somewhat clavate (to 16 mm) to almost equal, solid, but sometimes fistulose with age, white, coarsely floccose, especially in upper part. Context thick in pileus, firm, white. Smell raphanoid.

Spores (9.5–)10.0–13.0(–14.0) × (5.5–)6.0–7.0 µm, on average 10.5–11.6 × 6.0–6.4 µm, Q = 1.7–2.1, Q_{av} = 1.74–1.92, not dextrinoid (D0–D1), regular to subamygdaliform, not or exceptionally tending to sublimoniform; perispore not (or very slightly) loosening (P0–P1); almost smooth to indistinctly verruculose (O1–O2(–O3)). Cheilocystidia (41–)44–70(–80) × 4–6 × (7–)8–12(–13) µm, on average 56.1–61.3 × 4.3–4.7 × 8.9–10.3 µm, Q = (1.4–)1.8–2.8(–3.0), Q_{av} = 2.0–2.2, (sub)cylindrico–(sub)clavate, gradually broadened towards apex, but only a (small) minority tending to subcapitate and then apical part more distinctly enlarged, thin-walled.

Associated with *Salix* (4 ×), *Betula* (1 ×) or *Dryas* (1 ×).

ICG 2

Pileus to 36–170 mm, convex to applanate, without umbo or with indistinct umbo, margin (sub)involute, slightly viscid when moist, in centre yellowish (Mu. 10 YR 7/3, 10 YR–2.5 Y 7–8/4–6), but sometimes more brownish (10 YR 5/6–4/4), paler outwards, at margin whitish. Lamellae, L = 55–70, l = 3–5, thin, crowded, to 7 mm, subventricose, (very) narrowly adnate to emarginate, ochraceous brown (10 YR 6/4); edge fimbriate, whitish; weeping. Stipe to 25–100 × 8–13 mm, Q = 2.1–11.1 shorter to longer than diameter of pileus, slightly swollen to clavate (to 16 mm), but sometimes equal, solid or fistulose, white, coarsely floccose in upper part. Context thick, firm, white. Smell raphanoid.

Spores (9.5–)10.0–12.0(–12.5) × (5.0–)5.5–6.5 µm, on average 10.3–11.2 × 5.8–6.1 µm, Q = 1.6–1.9(–2.0), Q_{av} = 1.76–1.87, not dextrinoid (D0–D1(–D2)), regular to subamygdaliform, not or very exceptionally tending to sublimoniform; perispore not loosening (P0); finely to distinctly verruculose (O1–O3). Cheilocystidia (36–)45–77(–83) × (3–)4–5(–6) × 7–10(–14) µm, on average 50.3–66.4 × 3.8–4.5 × 7.6–8.6 µm, Q = (1.5–)1.6–2.3(–2.8), Q_{av} = 1.7–2.0, (slenderly) cylindrico-(sub)clavate, very exceptionally tending to clavate-subcapitate with enlarged apical part, thin-walled, exceptionally slightly thick-walled in upper part, colourless.

Associated with *Salix* (8 ×), *Dryas* & *Helianthemum* (1 ×) or *Corylus* (1 ×).

ICG 3

Pileus to 45–58 mm, plano-convex to applanate, without umbo to indistinctly umbonate, margin involute when young, slightly viscid when moist, pale ochraceous yellow (Mu. 2.5 Y 7–8/2–4), uniformly coloured or paler outwards and at margin whitish. Lamellae, L = 55–65, l = 3–5, thin, crowded, to 8 mm, subventricose, narrowly adnate to emarginate, pale ochraceous (10 YR 7/3); edge fimbriate, whitish; weeping. Stipe to 45–60 × 8–11 mm, Q = 4.4–9.8, usually longer than diameter of pileus, equal to subclavate (13 mm), solid, with age becoming fistulose, white, coarsely floccose, especially in upper part. Context thick in pileus, firm, white. Smell raphanoid.

Spores (10.5–)11.0–13.0 × 6.0–7.5 µm, on average 11.3–12.5 × 6.3–7.1 µm, Q = 1.6–1.9, Q_{av} = 1.68–1.81, not dextrinoid (D0–D1), regular to (sub)amygdaliform, not to partly tending to sublimoniform, perispore not to slightly loosening (P0–P1); finely to distinctly verruculose. Cheilocystidia (40–)43–74(–90) × 4–6 × 7–11 µm, on average 49.8–60.6 × 4.5–4.8 × 8.3–9.4 µm, Q = (1.3–)1.5–2.5, Q_{av} = 1.8–2.0, (sub)cylindrico-(sub)clavate to (sub)clavate, broadened towards apex, exceptionally to partly subclavate-subcapitate with enlarged apex, thin-walled or slightly thick-walled in upper part, colourless.

Associated with *Populus* (4 ×), *Salix* (2 ×) and *Tilia* (1 ×).

ICG 4

Pileus to 42–70 mm plano-convex to applanate, without umbo, margin involute, slightly viscid when moist, pale yellow in centre (Mu. 2.5 Y 7–8/2–4), but sometimes darker, to ochraceous or brownish ochraceous (10 YR 5–6/4–6, 10 YR 6/4), outwards paler and at margin whitish. Lamellae, L = 45–70, l = 3–5, thin, crowded, narrowly adnate; ochraceous; edge fimbriate, whitish; weeping. Stipe to 23–35 × 6–12 mm, Q = 2.3–4.2 shorter than diameter of pileus, clavate (to 14 mm), white, coarsely floccose. Context thick, firm, white. Smell raphanoid, sometimes mixed with sweetish component.

Spores (10.5–)11.0–13.0(–13.5) × 6.0–7.0(–7.5) μm, on average 11.3–12.4 × 6.4–7.0 μm, Q = (1.6–)1.7–1.9, Q_{av} = 1.72–1.83, not dextrinoid (D0–D1), regular to subamygdaliform, not to partly tending to sublimoniform; perispore not loosening (P0); slightly verruculose to almost smooth (O1–O2(–O3)). Cheilocystidia (49–)50–70(–75) × 4–5 × (7–)8–11 μm, on average 56.4–65.3 × 4.5–4.6 × 8.0–9.6 μm, Q = 1.6–2.5, Q_{av} = 1.8–2.1, (sub)cylindrico-(sub)clavate, somewhat broadened towards apex, not or exceptionally tending to (sub)capitate, thin-walled.

Associated with *Salix* (8 ×) and *Dryas* (3 ×).

ICG 5

Pileus to 45–60 mm, convex to applanate, without umbo or with an indistinct umbo, margin sometimes involute, viscid when moist, in centre pale yellowish (Mu. 2.5 Y 7–8/2–4) to ochraceous (10 YR 5/4–6), outwards paler and at margin whitish to white. Lamellae, L = 80–100, thin, (very) crowded, to 6 mm broad, sometimes subventricose, narrowly adnate to slightly emarginate, ochraceous to pale grey-brown (10 YR 6/3); edge fimbriate, whitish; weeping. Stipe to 40–115 × 10–11.5 mm, Q = 3.6–11.5 shorter to longer than diameter of pileus, equal to subclavate (16 mm), solid to fistulose, white, coarsely floccose, especially in upper part. Context firm, white. Smell raphanoid.

Spores (10.5–)11.0–12.5 × 6.0–7.0 μm, on average 11.5–11.9 × 6.1–6.4 μm, Q = 1.7–2.0, Q_{av} = 1.81–1.90, not to indistinctly dextrinoid (D0–D2), subamygdaliform, not tending to sublimoniform; perispore not loosening (P0), rather weakly to ± distinctly verruculose (O1–O3). Cheilocystidia 40–71(–89) × (3–)4–5 × (6–)7–10(–11) μm, on average 58.7–62.5 × 4.1–4.6 × 7.9–8.5 μm, Q = (1.2–)1.4–2.3(–2.5), Q_{av} = 1.7–2.1, cylindrico-clavate to subclavate, but sometimes almost cylindrical, a minority tending to clavate-subcapitate, but in one collection not swollen at apex at all, thin-walled, colourless or with slightly refringent wall.

Associated with *Tilia* (2 ×) or *Quercus* (2 ×), sometimes mixed with *Corylus*.

ICG 6

Pileus to 13–23 mm, plano-convex to applanate, with or without umbo, margin sometimes subinvolute, viscid, subshiny, in centre reddish ochraceous to red-brown (Mu. 5 YR 5/6, 7.5 YR 5/4), outwards slightly to distinctly paler, at margin slightly paler to whitish. Lamellae, L = 25–35, l = 1–3(–5), thin, normally crowded, to 2 mm broad, narrowly adnate, ochraceous brown; edge fimbriate, whitish; weeping. Stipe to 30–33 × 2.5–3 mm, Q = 11–12 longer than diameter of pileus, equal, whitish above, somewhat darkening downwards, especially with age, slightly flocculose, especially in upper part. Context thin. Smell weak, raphanoid.

Spores 12.0–14.5(–15.0) × 6.0–7.5 μm, on average 12.6–13.5 × 6.5–7.0 μm, Q = (1.7–)1.8–2.0(–2.1), Q_{av} = 1.92–1.93, not dextrinoid (D0–D1), subamygdaliform, not tending to sublimoniform; perispore not loosening (P0); moderately weakly ornamented (O2). Cheilocystidia (50–)53–74(–75) × 4–5 × (8–)9–16(–17) μm, on average 60.2–64.0 × 4.1–4.4 × 9.3–13.3 μm, Q = 2.0–3.8(–4.0), Q_{av} = 2.3–3.0, cylindrico-subclavate to cylindrico-subspathuliform or cylindrico-subcapitate, sometimes rather conspicuously so, thin-walled or with slightly thickened yellowish wall in upper part, especially in subcapitate cheilocystidia.

Associated with *Salix* (2 ×).

ICG 7

Pileus to 21–31 mm, plano-convex to applanate, with or without umbo, viscid, in centre (dark) brown (Mu. 7.5 YR 4/4–5/6), towards margin paler. Lamellae, L = 30–40, l = 3, thin, normally crowded, emarginate, pale brown; edge fimbriate, whitish; weeping. Stipe to 35–40 × 3.5–4 mm, Q = 10 equal to longer than diameter of pileus, equal to slightly swollen, fistulose, ochraceous, flocculose. Context thin. Smell raphanoid.

Spores 10.0–12.0(–12.5) × (5.5–)6.0–7.0 μm, on average 10.9–11.3 × 6.1–6.3 μm, Q = 1.6–1.9(–2.1), Q_{av} = 1.72–1.84, not to weakly dextrinoid (D0–D2), subamygdaliform, exceptionally tending to sublimoniform, perispore not or very slightly loosening (P0(–P1)); (sub)distinctly verruculose (O2–O3). Cheilocystidia 48–79 × 4–5 × (6–)7–12(–13) μm, on average 58.0–59.9 × 4.2–4.8 × 8.3–10.3 μm, Q = (1.4–)1.5–2.5(–2.6), Q_{av} = 2.0–2.1, subcylindrico-(sub)clavate, partly more tending to (sub)capitate, thin-walled or very slightly thick-walled in upper part.

Associated with *Salix* (2 ×).

ICG 8

Pileus to 18–25 mm, plano-convex, usually (sub)umbonate, but sometimes without umbo, viscid, two-coloured, in centre red–brown (Mu. 5 YR 3–4/4), outwards paler, at margin pale yellow-brown (Mu. 10 YR 7–8/4) to whitish. Lamellae, L = 25–35, l = 1–3, thin, normally crowded, to 3 mm broad, rather narrow, narrowly adnate to emarginate, brownish ochraceous (10 YR 7/3); edge fimbriate, whitish; weeping. Stipe to 25–58 × 2–3 mm, Q = 10–25, equal to much longer than diameter of pileus, equal to subclavate, soon fistulose, initially whitish, on damage discolouring to (yellow-)brown from base upwards, at apex (minutely) flocculose, downwards slightly fibrillose. Context thin, firm, whitish to pale brownish buff. Smell raphanoid.

Spores (10.5–)11.0–14.0(–15.0) × 5.5–7.0(–7.5) μm, on average 11.8–13.3 × 5.9–6.8 μm, Q = (1.8–)1.9–2.0(–2.1), Q_{av} = 1.93–1.99, not to weakly dextrinoid (D0–D2), subamygdaliform, none to a few tending to sublimoniform; perispore not or slightly loosening (P0–P1); weakly to distinctly verruculose (O1–O3). Cheilocystidia (36–)39–73(–80) × 4–5(–6) × (7–)8–15 μm, on average 44.1–60.9 × 4.2–4.5 × 9.3–12.2 μm, Q = (1.6–)2.0–3.5(–3.8), Q_{av} = 2.1–2.9, cylindrico-(sub)clavate, partly tending to subspathuliform or subcapitate, thin-walled or with slightly thickened yellowish wall in apical part.

Associated with *Salix* (6 ×).

ICG 9

Pileus to 20–66 mm, plano-convex to applanate, usually not or hardly umbonate but sometimes more distinctly umbonate, viscid, sometimes only slightly so, in centre orange ochraceous to reddish brown (Mu. 10 YR 6–7/6, 5/4–6), outwards paler, sometimes rather contrasting with centre of pileus and then ± bicoloured, at margin whitish to white. Lamellae, L = 30–45, thin, normally crowded, broadly to narrowly adnate or emarginate, to 6 mm, subventricose, ochraceous (10 YR 6/3); edge fimbriate, whitish; (distinctly) weeping. Stipe to 26–90 × 3–7.5 mm, Q = 6.4–14, longer than diameter of pileus, equal, not clavate or bulbous, solid but sometimes becoming fistulose, white, flocculose over whole length. Context thick, firm, white to brownish. Smell raphanoid.

Spores (9.0–)10.0–12.0(–12.5) × 5.0–6.5 μm, on average 10.2–11.4 × 5.5–6.1 μm, Q = 1.7–2.0, Q_{av} = 1.79–1.88, not dextrinoid (D0–D1(–D2)), regular to subamygdaliform, a few tending to sublimoniform; peri-spore not or very slightly loosening (P0–P1), (moderately) distinctly verruculose ((O1–)O2–O3). Cheilocystidia (39–)40–74 × 3–5 × 6–12 μm, on average 50.5–58.6 × 3.7–4.1 × 6.7–9.1 μm, Q = 1.5–2.5(–3.0), Q_{av} = 1.8–2.2, often (conspicuously) flexuose but sometimes straight, cylindrico-subclavate, towards apex partly more (sub)spathuliform or subcapitate, but sometimes not or hardly broadened towards apex, thin-walled.

Associated with *Salix* (5 ×).

ICG 10

Pileus to 50 mm, applanate to slightly depressed, without umbo, viscid, pale yellow (Mu. 2.5 Y 8/2–4), outwards slightly paler. Lamellae, L = 63, l = 3, thin, (very) crowded, emarginate, ochraceous; edge fimbriate, whitish; weeping. Stipe to 75 × 8 mm, Q = 9.3, longer than diameter of pileus, equal, fistulose, whitish, indistinctly flocculose. Context white. Smell raphanoid.

Spores (10.0–)10.5–12.5(–14.5) × (5.5–)6.0–6.5(–7.0) μm, on average 10.9–12.0 × 6.2–6.4 μm, Q = 1.6–2.0(–2.1), Q_{av} = 1.72–1.94, not dextrinoid (D0–D1), subamygdaliform, not to partly tending to sublimoniform; perispore not loosening (P0); almost smooth, slightly to moderately verruculose (O1–O3). Cheilocystidia 36–50(–52) × 4–5 × (5–)6–7(–8) μm, on average 41.0–46.3 × 4.0–4.2 × 6.4–6.6 μm,

Q = (1.3–)1.4–1.8, Q_{av} = 1.5–1.7, cylindrico-subclavate, only slightly swollen towards apex, not tending to subcapitate or subspathuliform, in general rather small and narrow, thin-walled.

Associated with *Salix* (1 ×) and *Betula* (1 ×).

ICG 11

Pileus to 37–75 mm, plano-convex to applanate, without or with low broad umbo, (slightly) viscid when moist, in centre yellowish to pale yellow-brown (Mu. 10 YR 7–8/3, 6–7/4), outwards paler, at margin whitish to white. Lamellae, L = 50–60, l = 3, thin, normally crowded, to 4 mm, not or hardly ventricose, narrowly adnate or emarginate, greyish ochraceous (10 YR 7/2); edge fimbriate, whitish; weeping. Stipe to 50–53 × 5–10 mm, Q = 5–10, shorter to longer than diameter of pileus, clavate to ± bulbous (10 mm), solid to subfistulose, white, flocculose. Context thick, firm, white to brownish. Smell raphanoid.

Spores (9.5–)10.0–12.0(–12.5) × 5.5–7.0 μm, on average 10.7–11.1 × 5.9–6.4 μm, Q = (1.6–)1.7–1.9, Q_{av} = 1.74–1.82, not dextrinoid (D0–D1), subamygdaliform, not to exceptionally tending to sublimoniform; perispore not loosening (P0); rather distinctly verruculose (O2–O3). Cheilocystidia (39–)41–63(–76) × 4–5 × (5–)6–12 μm, on average 52.3–53.7 × 4.2–4.5 × 6.1–9.7 μm, Q = 1.2–2.5, Q_{av} = 1.4–2.2, cylindrical to (sub)clavate, not or only a minority tending to subspathuliform or subcapitate, thin-walled.

Associated with *Salix* (2 ×) or at forest edge with various trees (*Fagus*, *Picea*).

ICG 12

Pileus to 25–38 mm, convex to applanate, without or with low umbo, margin sometimes involute, distinctly viscid, in centre pale yellow, ochraceous, (dark) yellow-brown to red-brown (Mu. 10 YR 7/4–6, 5–6/6, 4–5/4, 7.5 YR 4/4), outwards paler, at margin whitish. Lamellae, L = 40–50, l = 3–5, thin, crowded, narrowly adnate to emarginate, pale ochraceous; edge fimbriate, whitish; weeping. Stipe to 53–65 × 3–7 mm, Q = 9.3–17.7, shorter to longer than diameter of pileus, equal to slightly clavate, fistulose or solid, white, flocculose. Context white. Smell raphanoid.

Spores 8.5–12.0 × 5.0–6.5(–7.0) μm, on average 9.0–11.2 × 5.0–5.8 μm, Q = (1.5–)1.6–2.0, Q_{av} = 1.74–1.96, not to weakly dextrinoid (D0–D2), regular to subamygdaliform; not to partly tending to sublimoniform; perispore not loosening (P0); verruculose, sometimes rather coarsely so (O2–O3(–O4)). Cheilocystidia (37–)40–63(–68) × 4–5 × (7–)8–13 μm, on average 44.9–55.5 × 4.2–4.5 × 9.4–10.8 μm, Q = (1.4–)1.8–3.0(–3.3), Q_{av} = 2.1–2.6, (sub)clavate, usually (distinctly) swollen towards apex and sometimes tending to subcapitate, a minority remaining subcylindrico-subclavate, thin-walled or very slightly thick-walled, especially in apical part in ± subcapitate cheilocystidia, exceptionally slightly thick-walled throughout.

Associated with *Salix* (5 ×) or *Populus* (1 ×).

ICG 13

Pileus to 25–37 mm, plano-convex to applanate, slightly umbonate, viscid, in centre pale yellow (Mu. 2.5 Y 6–7/4), paler outwards, at margin white. Lamellae, L = 55, l = 3–5, thin, crowded, emarginate, pale ochraceous; edge fimbriate, whitish; weeping. Stipe to 45 × 6 mm, Q = 7.5, slightly longer than diameter of pileus, subclavate, solid, white, (sub)floccose. Context white. Smell raphanoid.

Spores (9.0–)9.5–10.0(–11.0) × (5.0–)5.5–6.0(–6.5) μm, on average 9.9 × 5.7 μm, Q = (1.6–)1.7–1.8(–1.9), Q_{av} = 1.74, not dextrinoid (D0–D1(–D2)), regular to subamygdaliform, not tending to sublimoniform; perispore not loosening (P0); verruculose (O2–O3). Cheilocystidia 38–56 × 4–5 × (5–)6(–7) μm, on average 45.0 × 4.3 × 5.9 μm, Q = 1.2–1.5(–1.8), Q_{av} = 1.4, cylindrical to somewhat subclavate, only slightly broadened apically, not tending to subspathuliform or subcapitate, sometimes even more subutriform and slightly broadened in lower part, thin-walled.

Associated with *Populus* (1 ×).

ICG 14

Pileus to 22–35 mm, plano-convex to applanate, without umbo, not or hardly viscid, usually bicoloured, in centre (dark) red-brown to ochraceous brown (Mu. 7.5 YR 4/2, 4–5/4, 10 YR 5–6/4), at margin paler, pale brown to whitish (10 YR 6–7/4, 8/3 or paler). Lamellae, L = 30–40, l = 1–3, thin, normally

crowded, to 4 mm, subventricose, almost free to narrowly adnate or emarginate, ochraceous brown (10 YR 5/4); edge fimbriate, whitish; not distinctly weeping. Stipe to 18–32 × 4–7.5 mm, Q = 2.6–8, usually shorter than but sometimes equal to diameter of pileus, equal or slightly bulbillose, solid to fistulose, white, discolouring to brown with age or on damage from base upwards, flocculose to subfloccose. Context thick, firm, white to brownish. Smell raphanoid.

Spores (11.0–)11.5–14.0(–15.0) × 6.5–8.0(–8.5) µm, on average 12.0–13.1 × 6.9–7.2 µm, Q = 1.6–1.9(–2.0), Q_{av} = 1.72–1.84, not dextrinoid (D0–D1(–D2)), regular to subamygdaliform, not to partly tending to sublimoniform; perispore not to very indistinctly loosening (P0(–P1)); moderately weakly to distinctly verruculose ((O1–)O2–O3). Cheilocystidia 39–75 × (3–)4–6 × (7–)8–12(–14) µm, on average 49.9–62.7 × 4.1–5.1 × 9.3–11.2 µm, Q = (1.3–)1.6–3.5(–3.7), Q_{av} = 2.1–2.6, usually clavate to (indistinctly) (sub)capitate or more (sub)spathuliform, a minority more cylindrico-(sub)clavate and hardly broadened towards apex, sometimes somewhat broadened in middle part and then cylindrico-subutriform, thin-walled or slightly thick-walled with brownish wall in apical part in subcapitate cheilocystidia.

Associated with *Salix* (4 ×).

ICG 15

Pileus to 19–45 mm, plano-convex to applanate, without or with rather indistinct umbo, dry to slightly viscid, in centre dark red-brown to orange brown (Mu. 2.5–5 YR 3/2, 5–7.5 YR 4–5/4–6, 10 YR 3–4/3), outwards almost concolorous to paler. Lamellae, L = 35–55, l = 1–3, thin, crowded, to 4.5 mm, subventricose, narrowly adnate to emarginate, brown, ochraceous brown to greyish brown (10 YR 4/4, 5–6/4, 6–7/3–4); edge fimbriate, whitish; weeping, but sometimes not (distinctly) weeping. Stipe to 23–45 × 3–10.5 mm, Q = 2.4–9, shorter than to equal to diameter of pileus (exceptionally somewhat longer than diameter of pileus), equal, solid to fistulose, white, discolouring to yellow-brown on ageing or damage from base upwards, at apex flocculose. Context thick, firm, white. Smell raphanoid.

Spores 12.5–17.0 × (6.5–)7.0–8.0(–9.0), on average 13.7–14.9 × 6.9–7.6 µm, Q = (1.7–)1.8–2.1(–2.2), Q_{av} = 1.83–2.03, not to weakly dextrinoid (D0–D2), (sub)amygdaliform, partly tending to sublimoniform; perispore not or slightly loosening (P0–P1); slightly to distinctly verruculose (O1–O3). Cheilocystidia (34–)41–63(–65) × 4–6 × (6–)7–13(–14) µm, on average 50.4–52.0 × 4.4–4.9 × 8.3–10.7 µm, Q = 1.3–2.8(–3.0), Q_{av} = 1.9–2.3, subcylindrical to clavate, partly more tending to subcapitate, partly somewhat swollen in middle part and subcylindrical-subutriform, thin-walled or with a slightly thickened yellowish wall in apical part, especially in subcapitate cheilocystidia, in one collection with slightly thickened wall halfway.

Associated with *Salix* (4 ×), *Populus* (1 ×) or *Pinus* (1 ×).

ICG 16

Pileus to 34–65 mm, convex to applanate, without or with rather distinct umbo, slightly viscid, in centre red-brown, yellow-brown to ochraceous (Mu. 5 YR 4–5/3, 10 YR 4–6/4, 5–6/6), uniformly coloured (especially in paler specimens) to ± distinctly paler outwards and at margin sometimes even whitish. Lamellae, L = 40–65, l = 3–7, thin, (very) crowded, rather broadly to narrowly adnate, to 6 mm, not ventricose to subventricose, ochraceous buff to brownish ochraceous (10 YR 7/2–3 to 6/3–4); edge fimbriate, whitish; weeping (but sometimes not distinctly so). Stipe to 34–60 × 5–9 mm, Q = 6.7–10.5, usually ± distinctly bulbous, sometimes (sub)clavate, fistulose, with pendent marrow strand, whitish, (sub)flocculose to subfloccose. Context thick, firm, white. Smell raphanoid.

Spores (9.5–)10.0–12.5(–13.0) × 6.0–7.0 µm, on average 10.5–11.8 × 6.4–6.6 µm, Q = 1.5–1.8(–1.9), Q_{av} = 1.62–1.80, weakly to distinctly dextrinoid (D2–D4), regular to subamygdaliform, exceptionally sublimoniform; perispore not or very slightly loosening (P0–P1); slightly to rather distinctly verruculose (O2–O3). Cheilocystidia (40–)47–87(–106) × (4–)5–6(–8) × 6–9(–12) µm, on average 55.2–72.2 × 4.9–5.7 × 6.7–10.2 µm, Q = 1.2–1.8(–2.4), Q_{av} = 1.3–2.0, subcylindrical to subclavate, usually not distinctly enlarged apically, but exceptionally tending to subspathuliform, sometimes slightly swollen in basal part and then slenderly subutriform, thin-walled to very slightly thick-walled.

Associated with various deciduous trees in mixed forest (*Betula*, *Fagus*, *Quercus*, *Carpinus*, *Corylus*).

ICG 17

Pileus to 32–78 mm, convex to applanate, without umbo to ± distinctly umbonate, very viscid to almost dry, sometimes seemingly hygrophanous with irregular spots, in centre usually varying between pale ochraceous yellow to pale yellow-brown (Mu. 2.5 Y 7–8/2–4, 10 YR 7–8/4–6), sometimes more ochraceous brown (7.5–10 YR 5–6/4), uniformly coloured (especially in paler specimens) to distinctly paler outwards and then whitish at margin. Lamellae, L = 45–70, l = 1–3–7, thin, (very) crowded, to 8 mm, subventricose, rather broadly to narrowly adnate, ochraceous brownish (10 YR 6–7/3–4); edge fimbriate, whitish; weeping. Stipe to 40–120 × 5–10 mm, Q = 5.3–12, shorter to longer than diameter of pileus, usually distinctly bulbous (to 20 mm), but sometimes only subclavate or even equal, usually fistulose with pendent marrow strand but sometimes solid, white, discolouring to brownish on damage from base upwards, minutely flocculose to subfloccose, especially in upper part. Context thin, firm, white. Smell raphanoid.

Spores (9.5–)10.0–13.0 × 6.0–7.5 μm, on average 10.4–11.9 × 6.3–7.2 μm, Q = 1.5–1.7(–1.8), Q_{av} = 1.57–1.69, weakly to distinctly dextrinoid (D2–D4), regular to subamygdaliform, sometimes tending to sublimoniform; perispore not loosening (P0(–P1)); almost smooth to distinctly verruculose (O1–O3). Cheilocystidia (36–)40–81(–83) × 4–7(–8) × 6–13 μm, on average 45.5–66.0 × 4.5–6.3 × 6.2–9.3 μm, Q = (1.0–)1.2–2.2(–2.8), Q_{av} = 1.2–2.0, straight to flexuose, usually subcylindrico-subclavate, only slightly broadened towards apex (but in two collections more distinctly broadened and even tending to subspathuliform or subcapitate), a few more subcylindrical and hardly swollen towards apex, sometimes slightly swollen in basal part and then slenderly subutriform, thin-walled to slightly thick-walled, sometimes bifid in apical part in varying frequency (absent to fairly common, and then apex to 19 μm broad).

Associated with various conifers (*Pinus*, 6 ×; *Picea*, 4 ×) and deciduous trees (*Betula*, 5 ×, *Quercus*, 2 ×, *Fagus*, 1 ×, *Carpinus*, 2 ×); in two collections vicinity of *Salix* also noted.

ICG 18

Pileus to 60 mm, convex to almost applanate, with a low broad umbo, very viscid, uniformly yellow-brown (Mu. 10 YR 7–8/4–6). Lamellae, L = 55, l = 1–3, thin, normally crowded, to 5 mm, not ventricose, broadly adnate, ochraceous (10 YR 7/2–3); edge fimbriate, whitish; weeping. Stipe to 110 × 7 mm, Q = 15.7, longer than diameter of pileus, bulbous (to 20 mm), fistulose with pendent marrow strand, white, finely flocculose. Context thin, firm, white. Smell raphanoid.

Spores (10.0–)10.5–11.5(–12.0) × (6.0–)6.5–7.0 μm, on average 10.9 × 6.5 μm, Q = 1.6–1.7(–1.8), Q_{av} = 1.67, distinctly dextrinoid (D3–D4), regular to subamygdaliform, not sublimoniform; perispore not loosening (P0); distinctly verruculose (O2–O3). Cheilocystidia (45–)46–59(–72) × (4–)5–6 × 5–6(–7) μm, on average 54.5 × 5.0 × 5.6 μm, Q = 1.0–1.2(–1.3), Q_{av} = 1.1, cylindrical, partly somewhat inflated in basal part and then subventricose-slenderly utriform, near apex not or hardly inflated, not clavate, thin-walled.

Associated with *Pinus* among living *Sphagnum*.

ICG 19

Pileus to 35–49 mm, applanate, only indistinctly umbonate, viscid, ochraceous yellow-brown (Mu. 10 YR 6/6) in centre, outwards paler. Lamellae, L = 55, l = 3, thin, normally crowded, to 5.5 mm, subventricose, narrowly adnate, ochraceous brown (10 YR 6/4); edge fimbriate, whitish; weeping. Stipe 42–75 × 4–7 mm, Q = 10–12.5, longer than diameter of pileus, equal, not bulbous, white, flocculose in upper part. Context thick, firm, white. Smell raphanoid.

Spores 10.5–11.0 × 6.0–6.5 μm, on average 10.7 × 6.2 μm, Q = (1.6–)1.7–1.8, Q_{av} = 1.74, not dextrinoid (D0–D1), subamygdaliform, not tending to sublimoniform; perispore not or hardly loosening (P0(–P1)); moderately coarsely verruculose (O2–O3). Cheilocystidia (38–)39–55(–57) × 4–5 × (5–)6–7(–8) μm, on average 46.2 × 4.6 × 6.4 μm, Q = (1.2–)1.6(–1.8), Q_{av} = 1.4, subcylindrical-subclavate, exceptionally more distinctly clavate, partly somewhat swollen below middle part and then tending to slenderly subutriform, thin-walled.

Associated with *Quercus* (1 ×).

ICG 20

Pileus to 48–60 mm, plano-convex to applanate, with or without umbo, viscid, pale brownish yellow (Mu. 10 YR–2.5Y 6–8/4), outwards paler, at margin whitish. Lamellae, L = 60–70, l = 1–7, thin, normally crowded, to 5 mm, not ventricose, narrowly adnate to emarginate, pale ochraceous grey; edge fimbriate, whitish; probably weeping. Stipe to 60–62 × 8–9 mm, Q = 6.7–7.8, equal to diameter of pileus, equal to slightly clavate, whitish, solid, flocculose in upper part. Context thick, firm, white. Smell raphanoid.

Spores (10.5–)11.0–12.0(–12.5) × 6.0–7.0(–7.5) μm, on average 11.3–11.4 × 6.5–6.8 μm, Q = 1.6–1.8, Q_{av} = 1.64–1.76, not to weakly dextrinoid (D0–D2), subamygdaliform, not sublimoniform; perispore not loosening (P0); very slightly to distinctly verruculose (O1–O3). Cheilocystidia (44–)45–72(–74) × 4–5 × (6–)7–9 μm, on average 55.0–59.7 × 4.3–4.5 × 7.4–7.5 μm, Q = 1.4–2.0(–2.3), Q_{av} = 1.7, subcylindrico-subclavate to somewhat more distinctly clavate, partly even tending to somewhat subcapitate, but partly somewhat swollen in lower part and then tending to slenderly utriform, thin-walled or sometimes distinctly thick-walled in upper part, especially in subcapitate cheilocystidia.

Associated with *Quercus* (2 ×).

ICG 21

Pileus to 46–50 mm, plano-convex to applanate, slightly umbonate, slightly viscid, in centre brownish yellow (Mu. 10 YR 6–7/4–6), outwards paler, at margin whitish. Lamellae, L = 40–50, l = 3, thin, normally crowded, not ventricose, emarginate, ochraceous; edge fimbriate, whitish; weeping. Stipe to 70–75 × 6.5–9 mm, Q = 8.3–10.8, longer than diameter of pileus, equal to slightly swollen, fistulose, whitish, flocculose. Context thick, firm, white. Smell raphanoid.

Spores 9.5–12.5 × 5.5–6.5(–7.0) μm, on average 10.4–11.6 × 5.8–6.3 μm, Q = 1.7–2.0, Q_{av} = 1.75–1.88, not dextrinoid (D0–D1), subamygdaliform, not to weakly sublimoniform; perispore not loosening (P0); verruculose (O2–O3). Cheilocystidia (42–)45–68(–73) × 4–5 × 6–11(–15) μm, on average 48.9–57.3 × 4.3–4.6 × 7.3–9.8 μm, Q = (1.2–)1.4–2.5(–3.0), Q_{av} = 1.6–2.3, cylindrico-subclavate, usually only slightly broadened apically to more distinctly subspathuliform or subcapitate, a minority tending to subcylindrical-subclavate, thin-walled, but sometimes with slightly thickened wall in middle part.

Associated with *Betula* (1 ×) and *Tilia* (1 ×).

ICG 22

Pileus to 35–70 mm, convex, without umbo, viscid, pale ochraceous yellow(Mu. 2.5 Y 7/8), more or less uniformly coloured, only at margin somewhat paler. Lamellae, L = 55, l = 3–7, thin, normally crowded, emarginate, ochraceous; edge fimbriate, whitish; weeping. Stipe 20–45 × 3.5–10 mm, Q = 4.5–7.5, shorter than diameter of pileus, at base slightly swollen, white, subflocculose. Context thick, firm, white. Smell raphanoid.

Spores (11.0–)11.5–12.0(–12.5) × 6.0–6.5 μm, on average 11.7 × 6.2 μm, Q = 1.8–2.0, Q_{av} = 1.88, not dextrinoid (D0–D1), (sub)amygdaliform, partly tending to sublimoniform; perispore not or very slightly loosening (P0); almost smooth to slightly verruculose (O1–02). Cheilocystidia (43–)47–67(–70) × (3–)4(–5) × 6–8(–9) μm, on average 57.5 × 3.9 × 7.2 μm, Q = (1.5–)1.6–2.0(–2.3), Q_{av} = 1.8, cylindrico-(sub)clavate, at apex slightly to distinctly broadened but not or hardly tending to (sub)capitate or (sub)spathuliform, thin-walled, colourless.

Associated with *Betula* (1 ×).