1 Introduction

Hebeloma collections are usually relatively straightforward to identify as *Hebeloma*, but they have been regarded as notoriously difficult to determine to species level. There are several possible reasons for this, for example: recent speciation, morphological stasis after speciation, morphological plasticity within species, reticulate evolution or incomplete lineage sorting. Whatever the reason, it is true that a number of species are macroscopically similar and even enjoy the same habitats. It is not unusual to find '*Hebeloma* hotspots' where several different species are growing together.

Until recently, a huge part of the problem has been the lack of definition of species limits, which has led to widely varying interpretations of species. As a result, different authors had different species concepts and, in consequence, contradictory species descriptions were published. Further, the molecular analyses that existed were confusing, as it appeared that every clade could contain every species and every species might come up in several different clades! So, the determination of *Hebeloma* spp. is difficult, not only morphologically, but also in many cases molecularly.

A number of years ago, two of us (H.J.B. and U.E.) began working with the late Jan Vesterholt to develop a methodology to resolve this problem, based on both morphological and molecular techniques. At that time, Vesterholt had already spent some fifteen years working on the genus *Hebeloma*. His book (Vesterholt, 2005) on the genus within Northern Europe was published soon after this collaboration began. At that time, it was well known that a number of issues existed with regard to species delimitation, but that it would take several years before all these issues could be resolved. Vesterholt (2005) provided a "state-of-the-art" view. In May 2016, a monograph on the genus *Hebeloma* in Europe was published, which brought together all the results to that point. Beker, Eberhardt and Vesterholt (2016) – from now on referred to as the Monograph – described 84 species of *Hebeloma* that are known to occur in Europe.

While the Monograph did cover all of Europe, the authors made clear in the manuscript that, despite many trips to 'fill the gaps', the collections they had studied were biased towards western and northern Europe, where they lived and had collected. This work goes some way towards remedying this bias, with a focus on *Hebeloma* collected in Italy.

The methodology developed for the Monograph was based on both morphological and molecular techniques and hinges on assembling a database of all collections and their associated data. This was achievable, thanks to the use of a sophisticated database (BioloMICS from Bioaware SA NV) – from now on referred to as the Database – within which the molecular and morphological analysis of every cited collection is stored as a series of parameters and statistics. This allows the species descriptions for any set of cited collections to be amalgamated and compiled into a single description based on that set of collections. To address the morphology, given the similarity of many species, a set of parameters was developed, to describe a *Hebeloma*, both macroscopically and microscopically. Every *Hebeloma* collection, found by us or sent to us, is registered on the Database (referred to as a *Hebeloma* collection). Each Database collection has a set of parameters attached that describe that collection, morphologically and molecularly, in addition to all the details of where and when it was found. This allows searches of all collections in the Database, based on these parameters. In this way, collections with similar properties may be clustered, parameters of collections that fall into the same phylogenetic clades may be compared and keys may be built on the Database, which are continually tested against all the Database collections. The parameters used have been refined from the character set that various authors (for example Bruchet, 1970, 1973; Romagnesi, 1965, 1983; Favre, 1955, 1960; Boekhout,

1982; Smith & al., 1983; Vesterholt, 1995), had developed over a period of years. To address the molecular analysis, several loci, both nuclear and mitochondrial (ITS, *RPB2*, *Tef1a*, V6 and V9 of the mitochondrial SSU, for more details see Eberhardt & al., (2013, 2015b), were studied to gain insight, search for consistency and eventually to improve the molecular support for species and infrageneric groups. Additionally, given the confusion that already existed with regard to species interpretation, all European types that could be located, were studied and added to the Database. This was also not straightforward! Many types had very brief diagnoses, often original material could not be found and at times type collections turned out to be mixed. At the time of publication of the Monograph, the Database contained some 4000 European collections, of which some 200 were from Italy; at the time of writing there are almost 10,000 collections in the Database and 526 are from Italy.

The species descriptions provided in the Monograph were assembled based on the actual collections analysed and cited for each species.

This technique has advantages and disadvantages. The greatest advantage, and the reason for this approach, is that the species description is a genuine description based on a given set of collections, without any subjectivity being introduced by the authors. As the number of collections included in the analysis increases, one can have confidence that much of the variation that naturally occurs (and for which the genus *Hebeloma* is renowned) will be captured in the overall species description. At this point, it should be emphasised that within the genus *Hebeloma,* not only is there sometimes considerable variation occurring between collections, but also within a collection or even a single basidiome. In analysing a collection, one cannot analyse, for example, the cystidia on every single lamella of every basidiome; the analyst hopes that as more and more collections are analysed so the natural variation that occurs will be incorporated into the species description.

However, this technique of amalgamating a set of species descriptions has the disadvantage that, for those species for which only a small number of collections exist, and hence a small set of cited collections, that the resulting description may be too narrow and not fully represent the variability that exists. Of course, nature being nature, even with a large set of cited collections, there will always be some unexpected variability that occurs, to confound us all! It is noted that within the species descriptions provided in the Monograph, standard deviations on all spore and cheilocystidium numeric statistics were provided.

The keys that were published in the Monograph were all tested on the Database and built as a set of queries. This was a 'snapshot in time', based on some 4000 collections. Species delimitation and the keys that are developed are based on hypotheses for which each new collection is a test. If the observational data on which they are grounded are sufficiently numerous, they will be corroborated in most cases. (Even then, unless the description is very broad, eventually one may run into a case that falsifies the hypotheses; to catch all possible natural variation is really not possible, or useful.) For the most part the feedback from users of the keys has been very good, however, there have occasionally been difficulties arising, particularly when dealing with species for which the description was based on few cited collections.

The keys suffer from the same limitations as the species descriptions and, so for species where the number of collections was low, the ranges quoted may be too narrow, i.e. fail to capture the full variability that exists in nature. When building keys, one is always faced with a dilemma: whether the goal is to have keys that never fail (but will produce a high number of collections without unique identification) or to provide keys that cover a high percentage of the collections, but that may lead to misidentification in the remaining cases. With dichotomous keys, the possibilities are severely limited.

Every addition of new data (i.e. new collections in the Database) will potentially affect the concept of a species and broaden its description. At the present time, work is ongoing to develop a synoptic key online, with free-access, which can be continually-updated as more collections are added to the Database and species concepts are refined. With such a key it will be possible to generate a probabilistic view of to which species any new collection should be referred.

As mentioned earlier, at the time of writing the Monograph, the authors had access to many collections from southern Europe, but in some cases, the number of collections of each species was relatively low. Since that time, the authors have examined many more collections from southern Europe. Importantly, a collaboration between the authors of the Monograph and the first author of this work, who has assembled a huge herbarium collection of *Hebeloma*, over many years, enabled a far more thorough examination of many species typical of southern Europe. Analysing the data from the Italian collections, meant, not surprisingly, being confronted with morphological variability occasionally lying outside the quantitative diagnostic values used in the species descriptions and keys published in the Monograph. This is the case especially for taxa with descriptions based on a relatively low number of collections, but less frequently also for other taxa. With *Hebeloma* one is often faced with sets of species that are morphologically (and indeed molecularly) very close, in which small differences can have crucial consequences for morphological species identification. As pointed out in the Observational protocol, it is essential to adopt a standardized approach and to be particularly meticulous in collecting observational data.

Nonetheless, given the narrow morphological gaps between species, problems do arise as occasionally experienced by us, when different analyses of the same sample result in differences in quantitative results, especially when measuring cystidia. This appears to be especially the case for the apex of cheilocystidia, which in *Hebeloma* is a taxonomically important character. It should also be noted that occasionally different sections of lamella edge, even of the same basidiome, might give different results. There seem to be rare cases in which a number of apexes tend to be abnormally swollen. Under these circumstances, measurements may be highly variable depending on the number of swollen apexes occurring in a given mount. The necessity must be stressed, especially when measuring cystidia, to measure a sufficient number. While ensuring, as far as possible, that the set to be measured is representative, it is imperative, not to be selective as to which cystidia to measure, i.e. to avoid over-representing the 'showy' or 'well-formed' examples.

As pointed out in various cases in the notes and comments on the species presented, the morphological variability shown by some of the Italian material will require us, eventually, to revisit the morphological delimitation of some species and, consequently, to propose amendments to the keys included in the Monograph and republished here. However, as discussed above, this will be better served by the development of an online synoptic key based on probabilities and statistics. Hence, for the time being, no amendments to the keys are proposed, but collections that 'challenge' the species descriptions given in the Monograph are highlighted and, "identification tips" for each species are included, where the main features, separating a given species from its closest allies or those species with which it is liable to be confused, are summarized.

Within the present work, the *Hebeloma* funga of Italy are reviewed and intraspecific variation, with a particular focus on species from southern Europe, is discussed. After a brief introduction, the 61 species for which there are confirmed Italian records in the Database, are presented. These 61 taxa include one taxon, *Hebeloma alpinicola*, which was not included in the 84 described in the Monograph. While *Hebeloma alpinicola* was originally described from

North America (Smith & al., 1983) and has recently been reported again (Cripps & al., 2019), in this work it is described for the first time from Europe. For all 61 species, an Italian collection is described, and a commentary and an illustration provided, as well as comments on intraspecific variation that has been observed in additional material from Italy. Finally, those European species, not as yet confirmed as present within Italy, but which might be expected to be present, are discussed.

Although mostly meant as a supplement to the Monograph, to give this book some autonomy, some general information is also provided. In the Monograph, for all taxa, information is given on the original diagnoses, types, etymology and the list of all the known synonyms, both homotypic and heterotypic. To avoid repetitions, here the reader is referred to the Monograph for information on the types, original diagnoses and etymologies, reported here are only the heterotypic synonyms that, having had some currency in the literature, may still be cause of doubts or confusion. The systematic framework followed is that of the Monograph, the infrageneric taxa are treated in the same order as in the Monograph, and, within each group, the species are presented in alphabetical order.

The first step to identify a *Hebeloma* is to determine the section to which it belongs. With a small amount of microscopy, and a certain amount of experience, this is relatively straightforward. Determination at this level depends on just a few characters: odour, number of full-length lamellae, habitat, whether there are remnants of a veil, the shape and dextrinoidity of the spores and the shape of the cheilocystidia. However, before presenting the keys for this process, it is necessary to establish some protocol and terminology.

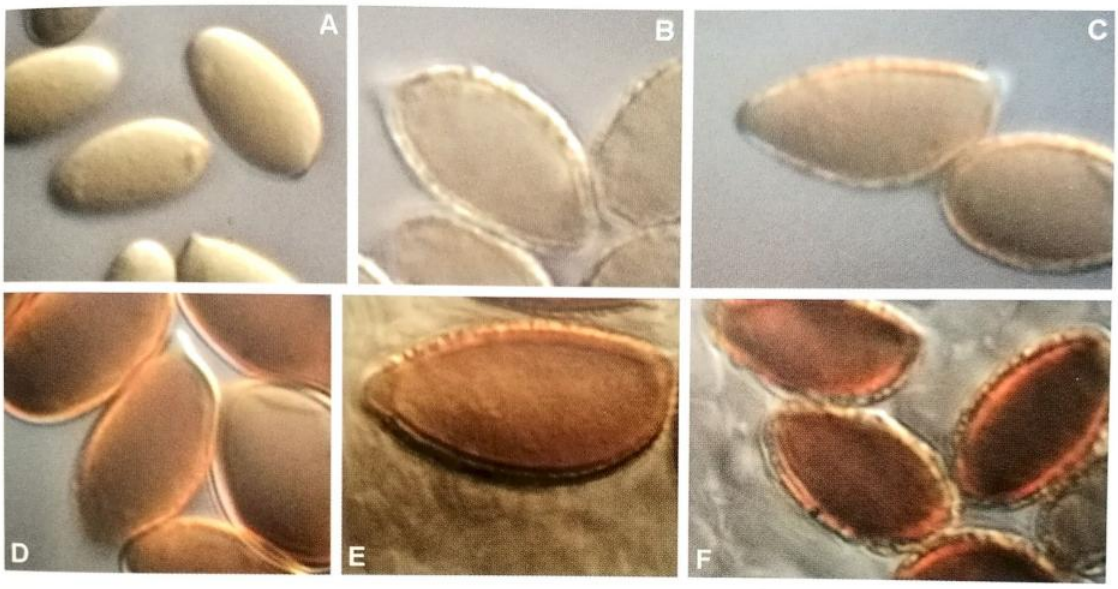

Plate 2 – Examples of spore dextrinoidity in *Hebeloma*. **A** – *H. mesophaeum* D0; **B** – *H. geminatum* D1; **C** – *H. fragilipes* D2; **D** – *H. velutipes* D3; **E** – *H. nauseosum* D3,D4; **F** – *H. birrus* D4.

Photographs H. J. Beker.

II Observational protocol, descriptive terminology and coding conventions

The Monograph provides all the necessary information on the genus *Hebeloma* and a detailed analysis of all the characters currently utilized in species delimitation. To avoid repetitions, such information is here limited to what is strictly necessary. We do expand our discussion of how the cystidia are measured, as it has become clear that the discussion in the Monograph was inadequate.

Regarding the collecting and processing of most of the collections specifically analysed and presented in this study, the approach followed was rather similar to that fully described in the Monograph. However, while the majority of collections were made by experienced mycologists, not all parameters, with regard to the fresh material, were noted in every case. Consequently, some of these characters and parameters had to be deduced from photographs and the exsiccata, which is often less accurate, and can be misleading. The following methodology for collecting is recommended.

In the field, after taking one or more photographs in situ, special attention should always be given to the observation of habitats and the careful recording of the possible mycorrhizal partners and all basidiome characters that may change in time or on handling, such as odour, lamellar beading, hygrophany, occurrence of veil remnants, stipe floccosity and discolouration processes. Since many species, especially the ones phylogenetically close, share much the same appearance, one should always be aware of the risk of making mixed collections. The risk is high in areas where the production of basidiomes is abundant, particularly when the growth habit is scattered. A way of minimizing the risk is erring on the side of caution by not combining collections that do not grow in the very same spot and storing separately the basidiomes which, one way or the other, look suspect.

At some point in the day, while daylight is still good, the pileus colours should be recorded, noting also whether the pileus is unicoloured or bicoloured. Pileal colours are generally described using basic colour names, their derivatives and combinations (e.g. "brown", "brownish", "yellowish-brown"); colour coding, when recorded, refers to Ridgeway (1912), Munsell Soil Color Chart (1975) or Kornerup & Wansher (1978), conventionally abbreviated as R, M and K&W respectively. Then, after cutting each basidiome lengthwise (excepting the immature ones), pileus width, stipe length, stipe width in the stipe median and stipe base width should be recorded, along with all the relevant basidiome macroscopic features. With regard to the pileus, of importance are the shape of the pileus, the possible occurrence of regular spotting, whether it is rugulose or pruinose, as well as any particular characters of the pileus margin. The attachment of lamellae does not appear to have a diagnostic importance, but it should be recorded all the same, along with lamellar breadth and the features of the edge. A very important character is the number of full-length lamellae (L), i.e. lamellae that stretch from the pileus edge to the stipe, which appears to be a consistent character within a species, largely independent of the basidiome size. Since the recording of lamellar spacing from fresh material was not available for all the collections presented, when the estimate of the number of full-length lamellae is approximate (based on exsiccates and photographs), the values are preceded by the abbreviation "*ca.*" (circa). The likelihood of error, when L is estimated in this way, should be emphasised and, so, where it is estimated, caution must be applied.

Regarding the stipe, the shape of the stipe base should be recorded, whether it is bulbous, subbulbous, clavate, cylindrical, tapering or rooting. The stipe surface is recorded as fibrillose, velutinous, pruinose, pruinose at apex, floccose, floccose at apex, while the inner part of the stipe is recorded as stuffed or fistulose, and in the latter case whether there occurs a basal and/or apical wick. Also recorded is whether the lower half of the stipe shows any discolouration process, and

whether there are hyphal cords attached to the base of the stipe.

For brevity's sake, the microscopic description given, is limited to the core characters of spores and cheilocystidia and, when present, pleurocystidia, i.e. only the characters providing diagnostic information that is used, here, for determination. In rare cases where it is relevant, basidium measurements are also provided. Moreover, since clamp connections are common in all *Hebeloma* species, their presence is taken for granted; they are only mentioned when they are present as an integral part of a cystidium. In most cases, one or, at most, two basidiomes per collection were analysed, unless quantitative data were exceptional as compared to the variability ranges recorded in the Monograph.

Spore measurements were taken in Melzer's reagent. They do not include the apiculum and, if it is the case, the expanding myxosporium (perispore). The estimate of spore characters (ornamentation, myxosporium (perispore) loosening and dextrinoidity) and the coding convention follow Vesterholt (2005). Given the importance of these spore characters, and the intention that this volume should stand alone, the method in which these values are assigned is reproduced here.

Ornamentation: The ornamentation is an important and relatively consistent character, with all mature spores exhibiting similar ornamentation. A scale to quantify this character is given below, ranging from 1–4. The value 0 is omitted as all *Hebeloma* species are believed to have ornamented spores:

O1: hypodistinct, "spores almost smooth, even under immersion"

O2: subdistinct, "spores very weakly ornamented, only visible under immersion"

O3: distinct, "spores distinctly ornamented, ornament visible without immersion but not conspicuous"

O4: coarse, "spores with fairly strong ornamentation, always easy to see without immersion"

Loosening of the myxosporium: In the light microscope, the loosening of the myxosporium is observed as a hyaline sack or blisters around the spores. The myxosporium is indextrinoid and usually clearly observable in Melzer's reagent. This character may appear to vary considerably between studied collections and even within a single preparation, but it is relatively consistent for mature spores. In an attempt to quantify this character, based only on mature spores, a scale from 0 to 3 has been constructed[1]:

P0: undilating, "myxosporium not loosening"

P1: rugulose, "myxosporium somewhat loosening (in few to all spores) – immersion often needed"

P2: vesiculate, "myxosporium distinctly loosening (in few to all spores) – also visible without immersion"

P3: calyptrate, "myxosporium strongly and consistently loosening"

Dextrinoid reaction: The dextrinoid reaction of the spores has been shown to be a very important character in the genus. The colour of the endosporium mounted in Melzer's reagent is

[1] The coding P4, occasionally used in the descriptions, refers to a situation here described, following Clemençon (1997), with the term "utriculate", when the loosened myxosporium is well visible also at the spore apex, as in some of the spores of *Hebeloma radicosum* (Fig. 37.1.1) or some species of *H.* sect. *Scabrispora* such as *H. anthracophilum* (Fig. 40.1.1) or *H. birrus* (Fig. 41.1.1).

observed in mature and undamaged spores flowing at a distance from the hymenium. Spores on or near the lamella tissue usually show a less distinct dextrinoid reaction or none at all. All mature and normally developed spores within a preparation show roughly the same colour in Melzer's reagent. The apex of the spores is typically almost indextrinoid, particularly noticeable when there is a well-developed papilla, and this often gives the dextrinoid spores a bicoloured appearance in Melzer's reagent. In some cases, the spores are completely indextrinoid, in other cases a deep red-brown colour develops. However, intermediate reactions are frequent and therefore, a scale from 0 to 4 has been used in order to quantify this character:

D0: nil, "spores completely indextrinoid"

D1: very weak, "spores with an indistinct brownish tint"

D2: weak, "spores weakly but distinctly dextrinoid, becoming pale brown or yellow brown"

D3: strong, "spores rather strongly dextrinoid, becoming medium brown"

D4: very strong, "spores strongly dextrinoid, immediately becoming deep and intensely red-brown"

Occasionally, to provide some objectivity (although it is difficult to be objective when assessing colour), dextrinoidity is coded also with reference to Kornerup & Wanscher (1978).

Average spore statistics were determined by measuring at least 50 spores from each analysed basidiome. Since a spore print was only rarely available, measures were often taken from a lamellar squash of exsiccata, considering only mature spores with well-developed ornamentation and with both ends in focus. The importance of including only mature spores cannot be overemphasised; experience shows that it is all too easy to be misled into low values by including immature spores. Extreme measurements (which may occur, for example, when there are some 1-, 2- or 3-spored basidia present within a hymenium that is dominated by 4-spored basidia) were excluded from the calculation of average measurements.

The Spore Code: **Ox; Py; Dz**, for a collection should represent mature spores. In any typical lamellar squash, there will be spores at all stages of maturity: only mature spores should be assessed. In this case, the highest values consistently seen in mature (undamaged) spores are those to record, not the whole range observed. If uncertain between values, e.g. D2 or D3, then both should be recorded. (So, if two values are recorded from a single squash, they will always be consecutive.) Where the Monograph gives a range of values, in a species description, this is with respect to a number of collections, and if a value is in brackets, then it has been recorded on just a few of the collections on which the description is based. So, for example, a species with the ornamentation code **(O1) O2 O3** means that for most collections O2 or O3 (or both) was recorded and, infrequently, O1 was recorded, possibly alongside O2.

When measuring cystidia, care is needed. The measurements, and the statistics derived, are important in species determination; they are designed to give a quantitative representation of the shape of the cystidia. Hence when selecting cystidia to be measured, first the dominant shape must be decided upon. For most species there is a single dominant shape, although there can be a great deal of variation and irregularity (more in some species than others); for a few species there is more than one shape, usually at most two, rarely more. The cheilocystidia, to be measured, should be chosen to provide a representation of the cheilocystidia observed (see Plate 1), emphasising the main shape(s), not to represent every shape and variation that exists. The four cheilocystidium measurements used are L length, A width of apex, M median width and B width of the base.

Given its diagnostic value, the average width of the apex (A) of cheilocystidia, particularly those swollen near the apex, should be assessed based on at least 100 cheilocystidia from a mount of lamellar section, unselectively measuring all apexes properly in focus within a field. When discussing the width of the apex, it is really the maximum width at the apex, or just below the apex, that is the value to be measured, from which an average may be calculated. From experience, beginners will tend to produce higher average values for A, resulting from a tendency to select the larger, more 'showy', apexes and ignore the small, less obvious cystidia.

For the average measures of the other cheilocystidium features (L length, M median width and B width of the base), a minimum of 20 entire cheilocystidia, from squashed mounts, is usually sufficient. As already emphasised the set selected should be representative, again avoiding selecting just larger 'showy' examples but ensuring, as far as possible, a cross section. The length (L) is usually measured from the apex to the first clamped septum, although sometimes when there are several clamped septa all the way down the cystidium, they are clearly an integral part of the cystidium and knowing where to stop can be difficult! Again, a common error is to overestimate this statistic, L, by selecting only the largest cystidia rather than ensuring a good cross section.

For the width of the base (B), this is usually straightforward and is the widest part of the lower half of the cystidium but avoiding the very base of the cystidium where it often widens just before the clamped septum at the base. Again, achieving a good statistic for the average is dependent on having chosen a representative sample.

With regards to the median width (M), this can cause problems. It is important to bear in mind that the intention is to provide a quantitative representation of the shape, but consistency is also paramount. Where this should be measured does, in practice, rather depend on the cystidial shape. Where there is a constriction below the apex, as often happens with species from *H.* sect. *Denudata*, for example, M should be measured at this constriction, thus giving a measure of the constriction. Where the top half of the cystidium is more or less cylindric (as often happens in *H.* sect. *Hebeloma*) or where the cystidium was more or less cylindric in its entire length (as often happens in *H.* sect. *Scabrispora*) or where the cystidium was more or less gently clavate from the base towards the apex (as often happens in *H.* sect. *Velutipes*), M should be measured about a third of the way down from the apex (not necessarily at the narrowest point, which might often be in the lower part of the cystidium). This description is not as precise as one might wish, but unfortunately the cystidia in *Hebeloma* are not as regular as one would hope. Most important to bear in mind, as stated above, is that the goal is to generate statistics that provide a reasonably consistent quantitative representation of the shape of the cystidia. Where one shape is dominant then, ideally, it is that dominant shape that is represented. Where there is more than one shape (often within *H.* sect. *Velutipes*, for example), then selecting a set of cystidia that represent the proportions of the different shapes that are present, can be challenging.

For each cystidium, once the three measures, A, M and B are obtained, the ratios A/M, A/B and B/M ratios are calculated. Finally, the seven measures (L, A, M, B, A/M, A/B, B/M) are all averaged across all cystidia measured. These statistics are useful in describing the overall cheilocystidium shape, and allowing comparisons.

Also noted within the specimen description, are special cystidium features that are observed on several occasions. Examples might include thickening of the walls, perhaps, in the median part or at the apex, a bifid apex, septa and so on. Such features are only noted if they occur several times, and, hence, give the impression they may be regular features for that species.

The presentation of quantitative data of spores and cheilocystidia follows Grilli & al. (2016). It has the form (a) b c d (e), in which the values between parentheses are the smallest and the highest values recorded (but excluding those that are clearly not representative, exceptionally large or small), b and d the 5% and 95% percentiles and c the average. For spores the format is length x width, followed by Q value; for cheilocystidia the format is L x A x M x B.

III Determining the correct section[1]

A few *Hebeloma* species can be recognised in the field with reasonable certainty; examples, which occur in Italy, include *Hebeloma bulbiferum, H. laterinum, H. porphyrosporum, H. pseudoamarescens, H. radicosum* and *H. sinapizans.* However, this is not the case for the majority of species, and, hence, a system of classification is helpful.

Thirteen sections of *Hebeloma* were recognised in the Monograph. In Italy, representatives of all 13 sections are present.

The '*Hebeloma sacchariolens* smell' is usually clearly identifiable and places the collection into *Hebeloma* sect. *Sacchariolentia*; a strong smell of marzipan places the collection into *Hebeloma* sect. *Myxocybe* (which in Europe has only the one species, *H. radicosum*). A raphanoid odour is common in *Hebeloma* and does rule out certain sections like *Hebeloma* sect. *Naviculospora* and, generally, *Hebeloma* sect. *Scabrispora*; a raphanoid odour plus the remains of a cortina do imply *Hebeloma* sect. *Hebeloma*. Similarly, the presence of a cortina and ventricose (lageniform) cheilocystidia also implies the collection belongs to *Hebeloma* sect. *Hebeloma.*

The number of full-length lamellae (lamellae reaching from the edge of the stipe to the edge of the pileus) is a very useful character. If the number of full-length lamellae is at least 80 and the spores are strongly dextrinoid then the species belongs to *H.* sect. *Sinapizantia*. The habitat can provide many clues. For example, if the collection is from burnt ground and the spores are strongly dextrinoid and very small (on average at most 10 x 6 µm) and most of the cheilocystidia are swollen at the base and the apex (clavate-ventricose), then the collection is from *H.* sect. *Pseudoamarescens* (which in Europe has only one species, *H. pseudoamarescens*).

If none of the above characters has led to a specific section, then it is time to look at the shape of the cheilocystidia (see Plate 1). If the cheilocystidia are small, versiform, subcylindraceous and often irregular in shape, then this belongs to one of *Hebeloma* sect. *Duracinus, H.* sect. *Naviculospora* or *H.* sect. *Scabrispora. Hebeloma* sect. *Duracinus* has only one known member in Europe, *H. duracinoides,* which is a very distinctive mushroom, reminiscent of a *Cortinarius.* Members of *H.* sect. *Scabrispora* have a tendency to have a rooting stipe and the cheilocystidia can be small and very rudimentary in shape. For *H.* sect. *Naviculospora*, the cheilocystidia have a more distinctive shape and can be rather irregular. If the spores are strongly dextrinoid and the cheilocystidia are rather large, either gently clavate at the apex and tapering towards the base or they are ventricose, then this belongs to *H.* sect. *Velutipes*. If the cheilocystidia are clavate-ventricose but very short (on average less than 40 µm) then the collection belongs to *H.* sect. *Theobromina*. Finally, if the cheilocystidia are not so short and are abruptly clavate, spathulate or capitate at the apex and usually constricted below the apex, either tapering towards the base (clavate-stipitate) or swollen towards the base (clavate-ventricose) then the collection belongs to *H.* sect. *Denudata*, which is the largest section of *Hebeloma* with, at least in Europe, one third of the species. This discourse is expressed more formally in the key below. While at first it may appear rather complex, with a little experience placing a collection in the correct section of the genus is not too difficult. When examining material identified by mycologists who have received some training within the genus, even if determination to species may not have been achieved, it is rare that the collection has been placed in the wrong section.

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[1]The keys to follow are republished without modifications from the Monograph.