

# Notes on *Amanita* section *Caesareae*, *Torrendia*, and *Amarrendia* (*Agaricales*, *Amanitaceae*) with provisional division into stirpes and annotated world key to species of the section

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This web publication is dedicated to Dr. Cornelis Bas on the occasion of his eightieth birthday.

## Summary

Sectional rank for the *Caesareae* is accepted. The genera *Amarrendia* and *Torrendia* (generally recognized as polyphyletic and accepted as such) are proposed as synonyms of *Amanita* sect. *Caesareae*. Provisional (phylogenetically “flat”) subdivision of the section is provided by definition of ten stirpes: *Caesarea*, *Calyptroderma*, *Calyptroderma*, *Chambersiana*, *Grandis*, *Hemibapha*, *Oleosa*, *Pachysperma*, *Pulchella*, and *Ristichii*. An annotated list of excluded species is provided as is a similar list of taxa probably assignable to the *Caesareae*, but for which data is presently insufficient to make a definitive placement to stirpes. Keys to the provisionally defined stirpes of the *Caesareae* and to the accepted species of the section are provided. The number of taxa believed to belong to stirpes *Hemibapha* is now between 45 and 50. (The key to the stirpes provided in this article has 47 termini.) The number of taxa here assigned to stirpes *Caesarea* is six; to stirpes *Calyptroderma*, at least four; to stirpes *Calyptroderma*, *Chambersiana*, *Pulchella*, and *Ristichii*, one each; to stirpes *Grandis* and *Oleosa*, two each; and to stirpes *Pachysperma*, three. The number of taxa proposed for the *Caesareae* is now in the range of 65 to 75.

## Introduction

Since the publication of (Tulloss, 1986) and its second version (Tulloss, 1998), a number of new species have been described in stirpes *Hemibapha*; and it is past time for an update on this fascinating and colorful group of taxa that play roles as valued comestibles in diverse cultures—especially in eastern and southern Asia, in Mexico and parts of Central America, and in Africa. In developing the revised key, it became apparent that, having collected data for more than 20 years, it was not a very complicated task to consider a provisional subdivision of *Amanita* sect. *Caesareae* Singer (1951) into phenetically meaningful supraspecific taxa and a key to most of its taxa excluded (at least for the moment) from stirpes *Hemibapha*.

My past concerns that sectional level treatment might not be justified because of some unknown divergence of morphology within the *Caesareae* does not now seem justified. The influx of new taxa in recent years (on average, about one per year since 1961) has produced no surprises. Molecular studies have been more or less supportive of the *Caesareae* as a monophyletic unit (Weiss et al., 1998; Drehmel et al., 1999; Moncalvo et al., 2002; Hallen et al., 2004). The number of relevant taxa sampled for, and reported from, such studies is still small; and it is limited to *A. caesarea*, the taxa of *Amarrendia* and *Torrendia* and a few taxa in stirpes *Hemibapha*. However, work on multi-locus studies is underway (Moncalvo, pers. comm.). These studies will significantly expand the number of taxa for which phylogenetic data from well-determined collections are available. My scepticism concerning the recognition of the *Caesareae* at sectional rank has had to give way. I follow the taxonomic subdivision of *Amanita* Pers. of Yang (1997), which emends the taxonomy of Corner and Bas (1962) and Bas (1969).

This article provides a key to division of the section into ten proposed stirpes and to the known taxa comprising these stirpes. In addition, the key takes into account several probably distinct taxa known under misapplied names, by provisional names, or by temporary alphanumeric codes. The total number of terminal nodes in the current stirpes *Hemibapha* key is 47. A survey of the dates of original publication (provided in the key) demonstrates that a large majority of these taxa (38) have been discovered and reported in, or since publication of, the seminal paper of Corner and Bas (1962), which marks the beginning of the modern study of *Amanita* taxonomy.

The first key presented is one that determines many taxa not absolutely clearly assignable to *Amanita* stirpes *Hemibapha* (Tulloss, 1998). Following the primary key, a key to stirpes *Hemibapha* is provided. All known taxa not in the keys are treated in annotated lists.

Some species of the genera *Amarrendia* Bougher & Lebel (2002) and *Torrendia* Bres. (1902) are included within *Amanita* sect. *Caesarea*.

### Methods and materials

In the sets of spore data, bold face **Q** is the average of the length/width ratios (**Q** values) of all measured spores for a single specimen. (Some authors do not provide this data, but simply give a value I call **Q'**—the average of length/width of all spores measured from all specimens.) Some authors have not provided any data on spore shape other than in qualitative terms. In such cases, I have estimated the value(s) of **Q** or **Q'** from available data. When more than one specimen has been examined by me, a range of values of **Q** is presented.

The range of values of **Q** (length/width ratio for a single spore) gives a feeling for the shape of the spores as Bas (1969) observed: 1.0 - 1.05, globose; 1.05 - 1.15, subglobose; 1.15 - 1.30, broadly ellipsoid; 1.30 - 1.60, ellipsoid; 1.60 - 2.0, elongate; 2.0 - 3.0, cylindrical; > 3.0, bacilliform. Bas' quantitative definitions of these terms are used in this paper except where we quote the undefined use of shape terminology by previous workers or workers that clearly are not following Bas.

Other terminology, notation, and methodology follow Tulloss (2000) and Tulloss and Lindgren (2005).

Herbarium codes used are those of Holmgren et al. (1990). Authorial citation abbreviations follow Kirk and Ansell (1992). All taxa that appear in one of the keys have their author citation given in that key.

### *Torrendia*, *Amarrendia*, and *Amanita* sect. *Caesareae*

Hallen et al. (2004) provide a preliminary phylogenetic study of *Torrendia*, *Amarrendia*, and *Amanita*. Moncalvo et al. (2002) had previously reported that the type of *Torrendia* was apparently assignable to *Amanita* sect. *Caesareae*. Hallen et al. report that a.) the taxa of *Torrendia* all are descendant from ancestors that also have descendants universally agreed to be assignable to *Amanita* and b.) the taxa of *Amarrendia* have ancestry spread over a number of different genera including *Amanita*. For our purposes, we exclude from further discussion all *Amarrendia* species found to be descendant from ancestors other than ancestors of taxa of *Amanita*. In the cases of both *Torrendia* and *Amarrendia*, the type species (*T. pulchella* and *A. oleosa*) have proven to be amanitas. The morphological argument for *Torrendia* was made in a landmark paper of Bas (1975). The argument for *Amarrendia* is made in its protologue (Bougher & Lebel, 2002). The molecular phylogenetic demonstration is provided by Hallen et al.

The type species of both genera have inamyloid spores, which places their ancestry in subgenus *Amanita*. Moreover, the types of the two sequestrate genera share three morphological character states that can be seen as limiting the potential sources for their respective genomes within the genus *Amanita*: a.) inamyloid spores (limiting ancestry to subgenus *Amanita*), b.) common to plentiful clamp connections in the basidiomes, and c.) pseudoparenchymatous (cellular) subhymenia. Character states b and c limit possible ancestry to either the muscarioid taxa of sect. *Amanita* or to sect. *Caesareae* or to a common ancestor of the two sections. For our discussion, we further exclude taxa placed in *Torrendia* by recent authors if the spores of those taxa are amyloid, the subhymenium is not cellular, or clamps are not common or plentiful at bases of basidia. The latter phrase is chosen because Bas (1969) concluded from his experience in observation of clamps that, if these structures were present anywhere in an *Amanita* basidiome, they were present on the bases of basidia.

Hallen et al. present two trees one comprising a set of taxa based on sequencing an ITS locus and the other based on a 28S locus. The two trees differ extensively in terms of the species included and the phylogenetic relationships computed. In the ITS tree, our species of interest are shown arising from an ancestor in common with such taxa as *A. muscaria* (L. : Fr.) Lam. (type species of *Amanita*, subg. *Amanita*, sect. *Amanita*, etc.). In the 28S tree, the taxa of interest are shown to share a common ancestor with taxa belonging to sect. *Caesareae*. [At this point it must be stated that (while it is beside the point in our search for proper placement of "muscarioid/caesareoid" taxa of the sequestrate genera), morphological and molecular phylogenetic evidence make it very clear that application of the names *Amarrendia* and *Torrendia* have resulted in polyphyletic assemblages in both cases. This appears to be the case even if the genera are emended to contain only those taxa that are amanitas.]

We can make another observation that limits further the ancestral origin of the type of *Torrendia* (*T. pulchella*). The species is notable for its having a fleshy universal veil that remains in part as a saccate volva at the stipe base. Moreover, this volva is attached to the stipe only at the latter's bottom and is comprised of filamentous hyphae and, at least locally plentiful to dominant inflated cells. These characters are not shared with species of sect. *Amanita*, but are shared with species of sect. *Caesareae*. The stipe in *T. pulchella* satisfies Bas' definition (1969) of "totally elongating," a character limited to sections *Caesareae* and *Vaginatae* in subg. *Amanita*. Moreover, the developing basidiome of *T. pulchella* appears to be centrally located in the primordium, a character that is similarly limited. Hence, in the case of *Torrendia*, its type can be argued to have an ancestor within the circumscription of *Amanita* sect. *Caesareae*. Indeed, in the following section of this paper, a proposal is made for a definition of the section that will apply to both sequestrate and epigeous-agaricoid taxa. In the 28S tree of Hallen et al., *T. pulchella* appears in a moderately well-supported clade including as its other leaf taxa only European, Asian, and North American members of sect. *Caesareae*, including the section's type, *A. caesarea*, and diverse members of what is called herein stirps *Hemibapha*. Taking all evidence together, the type of *Torrendia* appears to have originated from within *Amanita* sect. *Caesareae*.

Molecular phylogenetic support for placement of the species *T. inculta*, *T. grandis*, *Amarrendia oleosa*, and *A. grandispora* is not so unambiguous. The 28S results of Hallen et al. do not contravene the evidence of relation of the *Torrendia* taxa to sect. *Caesareae*; however, the taxa in question are placed in the 28S tree (with little support) as a sister clade to the clade including *T. pulchella*. At this point, it appears that sequencing additional loci may be needed



Observation 3: In a large majority of the section's epigeous-agaric taxa (at least, in all known taxa of stirpes *Caesarea*, *Calyptroderma*, and *Hemibapha*) the usually fleshy limbus internus of the universal veil has a felted extension that encircles the stipe between the upper edge of the limbus internus and approximately the point at which the partial veil joins the stipe.<sup>1</sup> This felted extension may be seen on mature stipes as felted-fibrillose squamules (sometimes in a color contrasting to that of the stipe surface).

Observation 4: In a large majority of the species in this section, independent of the form of the basidiome, the subhymenium is pseudoparenchymatous. Known exceptions occur only in the epigeous-agaricoid taxa of stirpes *Calyptroderma* and *Calytratoides*.

Observation 5: Many of the epigeous-agaricoid taxa of the section are valued in their region of occurrence as desirable foods and are collected for personal ingestion or to be sold in markets.

Observation 6: In the sequestrate taxa of the section, basidia are arranged on, and attached (at their bases) to, the surfaces of locules. With one possible exception, these locules are filled with liquid in fresh material. The locules of *Torrendia* have been reported (Bas, 1975) not to be altered interlamellate spaces, but to be hollows provided by migration and transformation of primordial inflated cells that pre-empt the development of the acrophysalides of the basidiome context. [check references in Bas (1975)]

Observation 7: The description of the context of *Amarrendia* (Bougher & Lebel, 2002) as derived from the universal veil of an amanitoid ancestor is worth questioning. The context of *Torrendia*, which is composed of very similar hyphae and inflated cells is simply acrophysalidic tissue (Bas, 1975) directly analogous to that found in the pilei of the hundreds of epigeous-agaricoid species of *Amanita*. *Amarrendia* apparently comprises a "reduction" to epigeous form of taxa that are phylogenetically related to Australian taxa of *Torrendia* [exactly how is not clear, see Hallen et al. (2004)] and, in the type species, retains the liquid filled locules of the secotioid genus. If a context is already available in a secotioid ancestor and the locules within the context are retained unchanged, why would "reinvention" of context development be necessary?

Observation 8: The peridium of *Amarrendia* seems very similar to either a sparse remnant of *Amanita* pileipellis tissue or a sparse remnant of a thin layer of hyphae-dominated tissue from the exterior layer or the inner surface layer of the *Amanita* universal veil.

### **Taxa omitted from the keys for lack of information**

a.) *Amanita annulatovaginata* Beeli (1927) [described from Republic of Congo, with four varieties distinguished by Beeli (1927, 1931), but not all accepted by later authors] cannot be dealt with in the key because nothing is known of its microscopic anatomy. Spores from the type were apparently not measured correctly by Beeli. Drawings of nine spores from the type (Gilbert, 1940) yield these dimensions: 11.1 - 14.9 × 6.5 - 10.5 μm, with  $Q = 1.38 - 1.76$  and  $Q' = 1.56$ . The spore drawings for the types of Beeli's varieties differ considerably as to spore size; and, unfortunately,

<sup>1</sup>. Many taxa of sect. *Caesareae* share a morphological feature that is often not appreciated or even mentioned in the literature. All species of stirpes *Caesarea*, *Calyptroderma*, and *Hemibapha* that have been examined for the character by Tulloss have a felted extension of the limbus internus of the universal veil.

The fleshy [or fleshy portion of the] limbus internus of the universal veil is often detectable in sections *Caesareae* and *Vaginatae* as a small limb encircling the interior surface of the main limb of the saccate part of the universal veil. Good illustrations of this feature have been provided by Bas (1969: 312, fig. 8g-h), Neville and Poumarat (2004: 40-41, figs. 17-19), and others. The limbus internus may be found at the point at which the main limb is appressed to the stipe surface or may be placed higher than that point of juncture. The vertical cross section of the limbus internus is wedge-shaped. This part of the volva originates as tissue separating the stipe from the underside of the annulus in annulate species or separating the stipe from the marginal cells of the lamellae in exannulate species. A membranous limbus internus in sect. *Vaginatae* can be fleshy to very thin and nearly diaphanous, elongate or very short. In taxa such as *A. ceciliae* it may be friable and deposited on the lower stipe as a (often darkening) ring. Even in some material with a nonfriable universal veil, the limbus internus can be extremely difficult to locate if a basidiome is senile, very small, etc. The limbus internus in sect. *Caesareae* is often rather robust.

In the three stirpes mentioned above, the felted extension of the limbus internus encircles the developing stipe below the partial veil. It is almost always bonded to the stipe and never bonded extensively to the partial veil at the time when stipe elongation and pileus expansion begin. As a consequence, fragments of this felted extension are usually shredded and become fibrillose-felted decorations on the (often contrastingly colored) stipe surface. In a single taxon (so far as is known), there is a strong tendency for the felted extension to be firmly bonded to the stipe at about the mid-point between the partial veil and the top of the saccate volva. The expansion of the pileus apparently breaks the connection between the felted extension and the fleshy part of the limbus internus; and, as a result, the felted extension projects roughly perpendicular to the stipe surface as a ragged-edged "second annulus." The taxon in question is as yet unnamed; it is commonly called "*Amanita caesarea*" in southeastern Arizona. It is called species AZ6 in the primary key. The mechanism by which the cap expansion could create this "second annulus" is demonstrated on occasion in *Amanita jacksonii*. The incurved pileus margin in the expanding "button" of this species may be aligned with not only the outer edge of the partial veil, but also with the point of fracture of the fleshy component of the limbus internus and its felted extension. Hence, in *A. jacksonii*, the felted extension is occasionally seen to be peeled off the stipe by expansion of the pileus. It is presumed that the creation of the "second annulus" in *A. sp. AZ6* originates because of a similar (but common) alignment of (and firmer connection between) pileus margin and two parts of the limbus internus.

the sample size is small. Any drawing not showing a spore in lateral view is just about useless and was ignored when Gilbert's drawings were measured. This comment applies to all the Gilbert drawings of Beeli spores mentioned below.

b.) *Amanita bresadolana* Neville and Poumarat (2004) ( $\equiv$  *A. cinerea* Bres. nom. illeg., described in a minimal protologue from Mediterranean Europe) cannot be dealt with in the key because nothing is known of its microscopic anatomy.

c.) *Amanita cinereoannulosa* Cleland (1933) (described from South Australia) is accepted in sect. *Caesareae*, but insufficiently known to place it in the key. It has common clamps at the bases of its basidia and otherwise satisfies the emended definition of sect. *Caesareae*; however, when the six specimens of the lectotype were examined, they had largely unrehydratable subhymenia; although inflated cells were present, it could not be discerned whether or not the subhymenia were truly pseudoparenchymatous. Spores of this species measure (9.3-) 9.9 - 14.7 (-20.3)  $\times$  (5.6-) 6.4 - 8.6 (-10.2)  $\mu\text{m}$ , with  $Q = 1.58 - 1.66$  (-1.83). A type study of *A. cinereoannulosa* will be included with these keys in a future journal publication.

d.) *A. cokeriana* Singer (1948, described from the southeastern USA) cannot be dealt with in the key because little is certain with regard to its microscopic anatomy. I have not seen a holotype of this species. However, the fact that some material that Murrill determined as his *Venenarius gemmatus* var. *volvatus* ( $\equiv$  *A. murrilliana*) appears to conform to the protologue of *A. cokeriana* suggests that the two taxa may be similar. The just cited material comprises a non-conforming paratype of *V. gemmatus* var. *volvatus*. The nonconforming paratype had a volval sac connected along the side of the stipe base as in typical *A. murrilliana*. Five specimens from Murrill's cited paratype (FLAS) may be assignable to *A. cokeriana*. These have spore length = (10.5-) 11.5 - 14.7 (-19.0)  $\mu\text{m}$ , with  $Q = 1.86 - 1.97$ . It is important to segregate *A. cokeriana* from *A. recutita* sensu Coker. Despite his claim of synonymy, Singer did not include in his protologue of *A. cokeriana* the well-documented material from Chapel Hill, North Carolina (USA) or the plates of it that Coker (1917) published. The material Singer ignored was the basis for Coker's concept of *A. recutita* sensu Coker (see key, below). Hence, the latter is still in need of a name and awaits a new collection of sufficient quality on which to base that name.

e.) *Amanita elegans* Beeli (1935) (described from Republic of Congo) is almost certainly a species of stirps *Hemibapha*. Unfortunately, a recent description of the species by Pegler and Shah-Smith (1997) based on material from Zambia and Malawi has created uncertainty because they report that the species lacks clamps at the bases of basidia. If this is correct, the species (despite an annulate stipe and pseudoparenchymatous subhymenium) cannot be placed in sect. *Caesareae*.

f.) *Amanita illudens* Sacc. (1891) (described from the Harkaway Ranges, Victoria, Australia) is known only from a lectotype (a type study has been completed and will be published). This collection is not sufficiently well-preserved to permit rehydration of key tissues. In addition, the basidia and spores are not all hyaline and colorless. Whether this is an artifact of preservation or not is unknown. As best as could be told from the lectotype, the subhymenium may not be pseudoparenchymatous. The stipe tissue of the single surviving specimen of this species is longitudinally acrophysalidic; and I do not doubt that the species belongs in *Amanita*. The above characters suggest that *A. illudens* may not belong in any of the stirpes herein described.

g.) *Amanita luteoflava* Beeli (1931) (described from Republic of Congo) cannot be dealt with in the key because nothing is known of its microscopic anatomy. A watercolor of the species was painted by Mme. Goossens (the collector of Beeli's specimens), but it has never been published. As is often the case, Beeli's spore measurements do not match the few scale drawings of spores made by Gilbert (1940) from the type collection. Gilbert's (1940) spore drawings yield the following dimensions: 10.6 - 13.6  $\times$  9.7 - 12.9  $\mu\text{m}$ . The spores in the drawing are globose to subglobose—with  $Q$  values less than or equal to 1.15. If the species were assignable to stirps *Hemibapha*, it would represent a unique combination of globose to subglobose, large spores and a bright colored pileus (varying from orange over the disc to yellow at the margin). Hopefully, if it is collected again, it will be rather easy to recognize.

h.) *Amanita robusta* (1931) (described from Republic of Congo) cannot be dealt with in the key because nothing is known of its microscopic anatomy. The spore drawings of Gilbert (1940) include only two usefully oriented spores; they (in addition to data in Gilbert's text) yield the following measurements: 8.7 - 9.6 (-10.4)  $\times$  6.5 - 7.3 (-8.8)  $\mu\text{m}$ , with est.  $Q' = 1.33$ .

i.) *Amanita strobilaceovolvata* Beeli (1935) (described from Republic of Congo) cannot be dealt with in the key because nothing is known of its microscopic anatomy. The spore drawings of Gilbert (1940) yield the following: 9.3 - 11.3  $\times$  8.1 - 9.5 (-9.9)  $\mu\text{m}$ . The spores in the drawings are subglobose to broadly ellipsoid (roughly, with  $Q$  between 1.05 and 1.30). The species has an annulate stipe and a saccate volva connected only to the very bottom of the stipe (collector's watercolor includes cross-section). Its habit suggests a species of sect. *Hemibapha*.

### Taxa excluded

Two taxa are excluded from section *Caesareae* [despite their inclusion by Singer (1986)] because they do not satisfy neither Singer's revised definition of the section nor the emended definition (above). They are as follows: a.) *Amanita lactea* Malençon et al. (1968) is excluded because it has basidia that do not (or very rarely) bear clamp connections at their bases (Tulloss, 1994; Tulloss and Gminder, 2000). b.) *Amanita gayana* (Mont.) Mont. in Gay (1853, 1854) nom. dub. (described from Chile) could be in either sect. *Caesareae* or sect. *Phalloideae* due to lack of information in the protologue's figure and text. Apparently no exsiccatum exists. For the present the taxon should be considered a nomen dubium (Simmons et al., 2002).

**Primary key for *Amanita* sect. *Caesareae***

The fact that there are several taxa that are the sole members of their stirpes and that their segregation is not based on characters of the subhymenium indicates that there is still insufficient available knowledge about the more unusual or lesser known taxa in sect. *Caesareae*. For example, it seems quite plausible that stirps *Pachysperma* could be absorbed into stirps *Hemibapha* in some future revision of this work. Stirps *Pulchella* is likely to be merged with stirps *Caesarea* or stirps *Hemibapha* (see comment in key, below). Dealing with unauthored stirpes for the moment forestalls the further cluttering of *Amanita* literature with supraspecific names that have often been ill-considered and based on limited knowledge (e.g., restricted to taxa of an author's home region).

**1. Basidiomes sequestrate.****2. Basidiomes secotiid. [*Torrendia* p.p.]**

- 3. Species known from the western Mediterranean region, in coastal habitat (probably including *Pinus*); spores "13.5 - 18 × 5 - 7"  $\mu\text{m}$ , with "Q = 2.4 - 3.2" and est. Q' = 2.7 $\pm$  (Bas, 1975).....**

1. *Torrendia pulchella* Bres. (1902).

See also (Malençon, 1955) and, especially, (Bas, 1975) [Sole member of stirps *Pulchella*.

Based on sequencing of the 28S locus (Hallen et al., 2004), this stirps might be merged, in the future, with either stirps *Caesarea* or stirps *Hemibapha*.]

- 3. Species known from Western Australia, in semiarid habitat. [Stirps *Grandis*. Note: Unlike other taxa reported in this paper spore measurements of the Bougher & Lebel taxa include the apiculus, probably somewhat elevating the spores' Q values. On the other hand, there is no indication that the spores were measured consistently in lateral view or even if the spores of *Torrendia* have a distinctive "lateral view."]**

- 4. Pileus 18 - 40 mm broad, remaining entire during basidiome expansion; "in remnant eucalypt woodland of the Western Australian wheatbelt"; spores "12 - 14.5 × 8.5 - 9.5 (-10)"  $\mu\text{m}$ , with Q' = "1.48" .....**

2. *Torrendia grandis* Bougher (1999).

- 4. Pileus 8 - 15 mm broad, dividing into rings each overlying ring-like fragments of the gleba and with such (combined) structures distributed along much of the stipe during expansion; "in remnant eucalypt woodlands of the Western Australian wheatbelt, although not always in the immediate vicinity of eucalypts (e.g. in *Allocasuarina* and *Acacia* thickets)"; spores "(9[typo?]-) 9 - 14 (-14.5) × (5.5-) 6 - 7  $\mu\text{m}$ , with Q' = "1.84"**

3. *Torrendia inculta* Bougher (1999).

- 2. Basidiomes hypogeous, known only from Western Australia in semiarid habitat. [Stirps *Oleosa*—*Amarrendia* p.p. Note: Unlike other taxa reported in this paper spore measurements of the Bougher & Lebel taxa include the apiculus, probably somewhat elevating the spores' Q values. On the other hand, there is no indication that the spores were measured consistently in lateral view or even if the spores of *Amarrendia* have a distinctive "lateral view."]**

- 5. Basidiome 12 - 35 × 9 - 30 mm, lacking notable sterile region; gleba white, becoming cream; locules of gleba containing a clear liquid; in young *Eucalyptus* forest on former bauxite mines and under *Cassia*, *Gastrolobium*, and *Eucalyptus* in sandy or gravelly soil; spores "12.5 - 15 (-16) × (8.5-) 9 - 11 (-11.5)"  $\mu\text{m}$ , with Q' = "1.39" .....**

4. *Amarrendia oleosa* Bougher & Lebel (2002).

- 5. Basidiome 10 - 20 × 16 - 18 mm, occasionally having a basal pad of sterile tissue; gleba white, becoming pale pinkish brown; locules of gleba empty; in young *Eucalyptus* plantations in Tasmania and in eucalypt forest in Victoria; spores "(12-) 13 - 17 (-18) × (8-) 9.5 - 11.5 (-12)"  $\mu\text{m}$ , with Q' = "1.43" .....**

5. *Amarrendia grandispora* (Beaton et al.) Bougher & Lebel (2002)

≡ *Alpova grandispora* Beaton et al. (1985).

**1. Basidiomes epigeous-agaricoid.**

- 6. Species small and having over 30% of basidia bisterigmate or species with stipe taking on the appearance of a tallow candle or species with very hard stipe (cutting like a soft wood).**

7. Species with very hard stipe (cutting like a soft wood); pileus grayish, fading with age, with short marginal striations; partial veil proportionately small; known only from USA (central Atlantic seaboard states, Connecticut to North Carolina); spore length (9.0-) 10.0 - 13.5 (-14.5)  $\mu\text{m}$ ;  $Q = 1.73 - 1.89$ .....  
 6. *Amanita recutita* sensu Coker (1917).  
 [Sole taxon of stirps *Chambersiana*, proposed English classification "Coker's False Caesars."]
7. Species small and having over 30% of basidia bisterigmate or species with stipe taking on the appearance of a tallow candle.
8. Pileus grayish brown; stipe taking on the appearance of a tallow candle due to water saturating the outer portion of the stipe context, with partial veil appearing to slowly "dissolve into" stipe surface; described from California (USA); recorded from central California with *Quercus* to neovolcanic region of central Mexico in mixed *Pinus-Quercus-Abies* forest; spore length (8.5-) 9.8 - 14.0 (-17.0)  $\mu\text{m}$ ;  $Q = (1.40-) 1.44 - 1.70$  .....  
 7. *Amanita calyptratoides* Peck (1909).  
 [Sole taxon of stirps *Calyptratoides*, proposed English classification, "Candlestick False Caesars."]
8. Species frequently having small basidiome; usually having at least 30% of basidia bisterigmate.
9. Pileus white with proportionately short marginal striations; lamellae often orangish white or pinkish; described from New Hampshire (USA); reported from Prov. Quebec, Canada, and the northern New England states (USA); spore length (9.2-) 10.2 - 13.9 (-17.0)  $\mu\text{m}$ , with  $Q = 1.42 - 1.57$ .....  
 8. *Amanita ristichii* Tulloss (1989).  
 [See also (Tulloss, 1993).]  
 [Sole taxon of stirps *Ristichii*, proposed English classification, "Ristich's Little Caesars."]
9. Pileus with proportionately long marginal striations, gray with darker disc or avellaneous to brownish and then paler (to white) near pileus margin; lamellae without orange or pink tint. [*Amanita* stirps *Pachysperma*, proposed English classification "Little Caesars."]
10. Pileus gray, with disc darker to nearly black; described from North Carolina, USA, in mixed deciduous and coniferous forest; reported from middle Atlantic seaboard states (Massachusetts to North Carolina) of USA, often associated with mature or old *Quercus*, otherwise with *Quercus* or *Pinus*; spore length (9.5-) 10.5 - 16.2 (-20), with  $Q = (1.30-) 1.31 - 1.64$  .....  
 9. *Amanita pachysperma* G. F. Atk. (1918)  
 [See also (Tulloss, 1993).]
10. Pileus avellaneous to brownish, with pallid to white margin.
11. Pileus rather deep brown or grayish brown over disc; originally described from Virginia, USA, with *Quercus*; recorded from the eastern USA (Tennessee northward to Massachusetts and westward to southern Illinois), with *Aesculus*, *Fagus*, *Pinus*, *Quercus*, and *Tsuga*; spore length (9.1-) 11.5 - 15.0 (-21);  $Q = (1.16-) 1.21 - 1.42 (-1.55)$ .....  
 10. *Amanita virginiana* (Murrill) Murrill (1914a, 1914b).  
 [See also (Tulloss, 1993).]
11. Pileus avellaneous over disc; originally described from Florida, USA, in specialized habitat known as "hummock" (a locally elevated, mesic area dominated by hardwoods such as *Quercus* and *Magnolia*); also recorded from Florida in mixed *Pinus*-hardwood forest; spore length (9.0-) 10.5 - 13.8 (-15.5)  $\mu\text{m}$ ;  $Q = 1.33 - 1.37$ .....  
 11. *Amanita subvirginiana* (Murrill) Murrill (1941a).  
 [See also (Tulloss, 1993).]
6. Basidia 4-sterigmate in mature basidiomes; stipe not having the appearance of a tallow candle, not hard—not cutting like soft wood.
12. Subhymenium an obviously branching network of relatively short hyphal segments that are uninflated or only partially inflated—not pseudoparenchymatous; known from western temperate North America and

largely montane regions of Mexico. [*Amanita* stirps *Calyptroderma*, proposed English classification “[American] False Caesars.”]

13. Pileus orange-brown to yellow-orange, yellower at the margin, rather rapidly fading in sunlight; stipe yellow or somewhat orangish yellow with approximately concolorous felted-decoration much of which forms a ragged-edged “second annulus” below the partial veil; recorded from southeastern Arizona (USA) in Pinus forests or forests of Pinus combined with any of the following: Abies, Pseudotsuga, and Quercus. Spore length (8.2-) 9.0 - 11.9 (-13.6)  $\mu\text{m}$ ; **Q** = (1.29-) 1.34 - 1.49.....

12. *Amanita* sp. AZ6 [Tulloss].

[Basidiomes of this general form with different colored pilei are reported from the middle to southern Rocky Mountains. More than one taxon may be involved.]

13. Stipe decorated with fibrillose-felted material, but never having a “secondary annulus.”

14. Pileus orange to orange-brown to brown, often with darkest pigmentation over disc; entire basidiome sometimes described as having a green tint (e.g., in the type of *A. calyprata*); described from California (USA) where it occurs in the autumn and early winter; reported from the Pacific coastal states (USA) south and probably extending into Baja California (Mexico) with Abies, Pseudotsuga, and Quercus; spore length (8.6-) 9.0 - 12.0 (-24)  $\mu\text{m}$ ; **Q** = 1.55 - 1.68 (-1.69).....

13. *Amanita calyptroderma* G. F. Atk. & Ballen (1909)

=*A. calyprata* Peck (1900a) non Lam.<sup>2</sup>

=*A. lanei* (Murrill) Sacc. & Trotter (1925).

14. Pileus white to shades of yellow.

15. Pileus white to pale yellowish white, usually with no yellow tint at maturity according to protologue; partial veil always membranous; no odor reported; recorded from Mexico in forests including Abies, Pinus, and Quercus; spore length (8.4-) 10.3 - 15.4 (-25)  $\times$  (6.3-) 7.5 - 10.0 (-14.0)  $\mu\text{m}$ ; **Q** = 1.25 - 1.37 (-1.40).....

14. *Amanita tuza* Guzmán (1975).

15. Pileus yellow to pale yellow to yellowish white; with odor fish-like for some people; recorded from the Pacific coastal states (USA), where it occurs in late winter and spring, south possibly as far as the neovolcanic region of central Mexico with Quercus and Abies, Arbutus, Picea, Pinus, Pseudotsuga, and Quercus; spore length (9.0-) 9.5 - 12.4 (-17.2)  $\mu\text{m}$ ; **Q** = 1.53 - 1.67.....

15. “*Amanita calyptroderma* yellow spring variant.”

[This taxon includes some unusual variation that suggests more than one taxon may be involved. In some basidiomes, the partial veil is not strictly membranous, but forms a thick layer appressed to the upper stipe. This form of partial veil has been observed both in California and in Tlaxcala edo., Mexico. The taxonomic significance, if any, is not known.]

12. Subhymenium pseudoparenchymatous (comprising inflated cells, often with branching relationship not immediately apparent).

16. Subhymenium comprising 1 - 2 (-3) layers of such inflated cells; often (not always) with a proportionately thin-fleshed pileus, resulting in the presence of an umbo and proportionally long marginal striations; known from central Africa, eastern and southern Asia including insular southeast Asia (Pakistan to Japan, southern India and Sri Lanka to the Russian Far East), northeastern Australia, eastern North America (southward

2. The taxon *A. calyprata* var. *albescens* Peck (1900b) is poorly understood. It was described as a white species with saccate volva and annulate stipe from New York (USA), not in the western part of the country. Jenkins (1978) study of Peck’s type confirms that it has inamyloid spores and is assignable to sect. *Caesareae*. Jenkins found the length range of spores of the type to be “12.5 - 13” and **Q** to be “1.31” In recent years some material (*Amanita* sp. QUE1) that might be referred to this taxon has been found. It does not appear to be assignable to stirps *Calyptroderma*. It seems more likely to belong in stirps *Hemibapha*. If the recent material is being interpreted correctly, then Peck’s taxon is distributed as far north as Prov. Quebec, Canada, where the collection of QUE1 was made in association with *Fagus*, *Ostrya*, and *Tilia*. The spore length in sp. QUE1 is 10.8 - 13.0 (-14.2)  $\mu\text{m}$ , and **Q** = 1.30. The reader may wish to compare this information with the data presented for *A. murrilliana* in the key for stirps *Hemibapha*, below.

from Prov. Quebec, Canada), and montane Central America (northward from Costa Rica). [Amanita stirps Hemibapha, proposed English classification "Slender Caesars." See separate key, below.]

16. Subhymenium comprising 3 - 5 layers of such inflated cells; usually with pileus proportionately thick-fleshed resulting in lack of a central umbo and proportionately short (or very short) marginal striations; known from regions surrounding the Mediterranean Sea and North America (apparently concentrated in Mexico). [Amanita stirps Caesarea, proposed English name "[true] Caesars."]

17. Species of Eurasian and north African distribution; described from Mediterranean Europe; pileus commonly orange to red-orange, also occasionally yellow, red-brown, or white; stipe yellow above, pallid below, decorated with orangish fibrillose-felted material; recorded from southern Europe and forested regions near the Mediterranean in Africa and Asia Minor; associated with Castanea and Quercus or with Pinus and Arbutus or with Pinus and Cistus or with Quercus and Cistus; spore length (8.0-) 8.9 - 12.9 (-17.8)  $\mu\text{m}$ , with **Q** = (1.40-) 1.47 - 1.59 .....

16. Amanita caesarea (Scop. : Fr.) Pers. (1801)  
See also (Neville and Poumarat, 2004).

17. Species of North [and Central?] American distribution.

18. Pileus ranging from sordid cream to gray-brown to brown, often pallid at first, then developing pigment, with pigmentation often creating a virgate pattern; persistent partial veil white at first, becoming gray with age; saccate remnant of universal veil at stipe base often proportionately short; described from New York (USA); recorded from eastern USA southward to the coast of the Gulf of Mexico in association with Betula, Carya, Fagus, Ostrya, Quercus, and (probably) Pinus; spore length (7.7-) 9.4 - 13.1 (-15.5)  $\mu\text{m}$ ; **Q** = 1.60 - 1.81 .....

17. Amanita spreata (Peck) Sacc. (1887).

18. Pileus white to cream or some shade of red, orange, or yellow; described/recorded from Mexico.

19. Pileus white to cream; stipe whitish, with pale yellow partial veil; lamellae pale yellow; recorded from the vicinity of Nabogame, Chihuahua edo., Mexico, in *Pinus-Quercus* forest; spore length (7.5-) 9.2 - 12.8 (-15.0)  $\mu\text{m}$ ; **Q** = 1.43 - 1.47 .....

18. Amanita sp. Laferrière 927  
See (Laferrière, 1991; Laferrière and Gilbertson, 1992).

19. Pileus some shade of red, orange, or yellow. [According to photographs I have seen, there may be a lemon yellow member of this group in Mexico.]

20. Pileus orange to reddish orange from the outset; stipe orange-yellow or yellow orange above, becoming pallid toward base, with fibrillose-felted decoration concolorous or more intensely orange (becoming brownish orange with age or bruising), with partial veil orange to orange-yellow; lamellae various shades of yellow or orange-yellow in side view; described from Mexico without notes on habitat; recorded in montane forest associated with *Pinus* or in *Pinus-Alnus* forest or in *Abies-Pinus* forest or in forest dominated by *Quercus*, *Pinus*, *Abies*, *Baccharis*, and *Arbutus*; spore length (8.0-) 9.0 - 11.8 (-18.0)  $\mu\text{m}$ ; **Q** = (1.45-) 1.51 - 1.64 .....

19. Amanita basii Guzmán & Ramírez-Guillén (2001).

20. Pileus blood red, dark red, or red at first. Known only from the original descriptions. [The original descriptions and their illustrations seem to be confused and overly reliant on characters (such as spore size and shape) that vary a great deal between freshly collected material and material purchased in a market. These taxa have to be considered poorly understood at the moment.]

21. Pileus becoming entirely yellow or orange yellow or brownish orange-yellow, often with a browner disc at maturity; stipe with ground color originally pallid (according to photographs) but described as varying from yellow to a shade of red [possibly due to confusion with bruising of fibrillose felted squamules], with partial veil yellow to orange; lamellae yellowish to yellow; described from Mexico, in montane forest associated with *Pinus* and *Quercus*; spore length "(8-) 9 - 11 (-12)(-13)(-14)"  $\mu\text{m}$ ; **Q**'[?] = "1.38" .....

20. Amanita laurae Guzmán & Ramírez-Guillén (2001).

21. Pileus becoming yellow to yellow from the margin inward with age and exposure, but with a large central red area persisting for some time (remaining distinct in market photographs); stipe whitish to yellow sometimes more orange toward base, with fibrillose-felted decoration concolorous [with lower stipe?] and darkening from handling/bruising, with partial veil yellow to orange-yellow to pink-yellow; lamellae whitish to yellow; described from Mexico in montane forest associated with *Pinus* and/or *Quercus*; spore length “(9-) 10-13 (-14)(-15)” or “(8-)(9-) 10 - 11 (-12)”  $\mu\text{m}$ ;  $\mathbf{Q}[\text{?}] = “1.55”$  or [est.]  $\mathbf{Q}' = 1.53$  .....

21. *Amanita yema* Guzmán & Ramírez-Guillén (2001)  
= *Amanita tecomate* Guzmán & Ramírez-Guillén (2001).

### Key to stirps *Hemibapha*

There are two groups of names or provisional names that may actually represent a single taxon each. These are to be found in key couplets 6 and 32. Hence, between 45 and 47 taxa are represented in this key. Additional material from India and southeast Asia (representing as many as 5 additional taxa) has been seen by me, but not reviewed microscopically. In addition, there is work underway in several quarters that will undoubtedly clarify species concepts involved and the relations among the taxa. For example, Zhu L. Yang (1997) produced a very detailed account of the amanitas of southwestern China in his Ph.D. thesis (Tübingen University) and continues to publish new taxa from Asia frequently. Other authors have also recently published taxa in the present stirps.

Morphological taxonomy of the taxa of stirps *Hemibapha* is very reliant on a set of characters that is unfortunately rather limited. The segregation into stirpes is greatly facilitated once the value of the subhymenial anatomy is realized. However, the next most useful characters have the problem of varying with age or other factors. This limitation must be taken into account. Thorough annotation of fresh collections (including color photographs) and careful drying and attentive preservation are required in order to expand our knowledge base.

The characters that have been used in developing the key to stirps *Hemibapha* are a.) pigmentation of pileus, stipe, felted extension of limb internus, lamellae, and partial veil; b.) color change of these elements with age or handling/bruising; c.) ratio of length of marginal striations to pileus radius; d.) presence or absence of an umbo on the pileus, e.) spore length; and f.) spore shape. Alternatively spore width could have been used instead of spore shape [for a fixed spore length, width and shape (interpreted as the length/width ratio of a spore) vary inversely]. Shape was selected because proportion can be perceived approximately without exact measurement. Perhaps as the knowledge of the anatomy of these taxa expands, more characters will be recognized as of taxonomic value.

Accurate knowledge of geographic ranges of the included taxa is not always available; I have listed what information on ranges is known to me.

It seems plausible that stirps *Pachysperma* eventually may be found to be embedded in stirps *Hemibapha* through molecular phylogenetic studies.

For a discussion of *A. calyprata* var. *albescens*, which is probably referable to stirps *Hemibapha*, see the footnote associated with *A. calyptroderma* in the primary key (above). The reader may wish to compare the limited information on *A. calyprata* var. *albescens* to the data on *A. murrilliana*, below.

1. Taxa having 95% of spores  $\leq 10 \mu\text{m}$  long.

2. Taxa having  $\mathbf{Q} < 1.4$ .

3. Pileus dominated by brownish olive, isabelline, fuscous, fuliginous, umbrinous, or black tones.

4. Pileus between isabelline and light brownish olive, gradually changing to honey yellow to chamois near its margin: described from Java; recorded from Malaya, Singapore, and Borneo, at least sometimes with *Quercus*;  $\mathbf{Q} = 1.15 - 1.2$ ; spore length  $7.0 - 9.9 \mu\text{m}$ .....

1. *Amanita similis* Boedijn (1951)

= *Amanita hemibapha* subsp. *similis* (Boedijn) Corner & Bas (1962).

4. Pileus dark umbrinous brown, coal-black over disc; described from Republic of Congo; known with certainty only from the type locality;  $\mathbf{Q} \mathbf{d} 1.4$ ; spore length  $9.1 - 10.0 \mu\text{m}$ .....

2. *Amanita infusca* E.-J. Gilbert ex Singer (1951)

= *A. umbrina* Beeli (1931) non *A. umbrina* Pers.

3. Pileus with red, orange, orange-brown, yellow, yellow-brown, or grayish yellow tones dominating.
5. Pileus orange-brown to yellow-brown at first, then yellow-tan to grayish yellow; lamellae margin red; described from Ishigaki Isl., Okinawa, Japan, in mixed deciduous forest of *Quercus* and *Castanopsis*;  $Q = 1.34$ ; spore length 7.5 - 9.5 (-10.5)  $\mu\text{m}$ .....  
3. *Amanita rubromarginata* Har. Takahashi (2004).
5. Pileus red to orangish red from center to margin, or pileus orange or red over disc and otherwise yellow.
6. Pileus red to orangish red from center to margin
7. Described from far eastern Russian (Kamchatka Peninsula) in *Quercus* forest, also known from south-western China (in markets), Korea, Japan (in forest dominated by, for example, *Abies* and *Castanopsis*), and northern India (with *Pinus*, *Quercus*, and *Rhododendron*);  $Q = 1.17 - 1.33$ ; spore length (7.0-) 7.5 - 9.5 (-12.0)  $\mu\text{m}$ .....  
4. *Amanita caesareoides* Lyu. N. Vassiliyeva (1950)  
= *Amanita hemibapha* subsp. *hemibapha* sensu auct. japon.  
= *Amanita hemibapha* subsp. *hemibapha* sensu R. P. Bhatt.  
= *A. caesarea* sensu A. Kumar et al. (1990) p.p.
7. Pileus entirely red or orangish red at least at first, fading throughout with age; described from Prov. Québec, Canada, recorded from throughout SE Canada and NE USA (with range extending southward in Appalachian Mountains) in deciduous forest including *Quercus* or in mixed forest (most often then with *Pinus*), and also known in montane eastern Mexico in association with *Pinus*;  $Q = 1.25 - 1.40$  (-1.42); spore length (7.0-) 7.8 - 10.0 (-12.1)  $\mu\text{m}$ .....  
5. *Amanita jacksonii* Pomerleau (1984)  
= *Amanita umbonata* Pomerleau (1980) non (Sumst.) Sartory & L. Maire  
= *Amanita tullossii* Guzmán & Ramírez-Guillén (2001).
6. Pileus orange or red over disc, otherwise yellow. [Possibly a single taxon.]
8. Recorded from SW China, in forest dominated by *Quercus* and *Rhododendron*;  $Q = 1.20$ ; spore length (6.0-) 7.0 - 9.0 (-9.5)  $\mu\text{m}$ .....  
6. *Amanita hemibapha* sensu Zhu L. Yang (1997).
8. Recorded from Himachal Pradesh, India, in mixed forest with *Quercus* and, sometimes, *Rhododendron* and *Pinus*;  $Q = 1.14 - 1.25$ ; spore length (7.2-) 8.0 - 9.5 (-11.5)  $\mu\text{m}$ .....  
7. *Amanita* sp. IHJ6 [Tulloss].
2. Taxa having  $Q \geq 1.4$ . [See also *A. jacksonii*, above.]
9. Pileus nearly uniformly orange-tan to brownish orange, lacking red areas; known from NE Queensland, Australia, habitat not recorded; spores with  $Q = 1.53 - 1.54$ ; spore length 8.5 - 10.2  $\mu\text{m}$ .....  
8. *Amanita* sp. AUS3 [Tulloss].
9. Pileus yellow for outer half of radius, “beautiful scarlet” for inner half, often (not always) lacking umbo; described from Sri Lanka, with unrecorded symbionts; recorded from southern India (Kerala) in association with tree genera such as *Myristica* (nutmeg) and the dipterocarpaceous *Hopea* and *Vateria*;  $Q = 1.4^{\pm} - 1.54$ ; spore length (7.5-) 7.9 - 10.1 (-10.2)  $\mu\text{m}$ .....  
9. *Amanita hemibapha* (Berk. & Broome) Sacc. (1887) subsp. *hemibapha*  
= *Agaricus hemibaphus* Berk. & Broome (1871),  
see also (Vrinda et al., 2005).
1. Taxa *not* having 95% of spores  $\leq 10 \mu\text{m}$  long.
10. Taxa having 95% of spores  $\leq 12 \mu\text{m}$  long.

11. Taxa having  $Q < 1.3$  with one exception and, then, having  $Q \leq 1.33$  in more than 90% of collections.
12. Pileus dominated by white or shades of brown or gray, not dominated by shades of yellow, orange or red.
13. Pileus brown to grayish brown;  $Q' = 1.04 \pm 0.04$ ; spore length (8.0-) 8.8 - 10.8 (-12.0)  $\mu\text{m}$ ; described from Japan, in forests with *Quercus* and members of the Pinaceae .....  
10. *Amanita imazekii* T. Oda et al. (2001)<sup>3</sup>
13. Pileus white or largely white or whitish with disc taking on brown tones at maturity or with brown or yellow-brown disc and pallid margin from the first.
14. Pileus white at first, with disc taking on brown tones at maturity, with marginal striations  $< 0.2R$ ; described from Queensland, Australia, in open eucalypt forest;  $Q = 1.14 - 1.17$ ; spore length (7.0-) 9.1 - 11.2 (-13.0)  $\mu\text{m}$ . .....  
11. *Amanita egregia* D. A. Reid (1978, 1980)  
= *A. egregia*<sup>4</sup> A. E. Wood (1997)  
non *A. egregia* sensu A. E. Wood.
14. Pileus with brown to yellow-brown disc from the outset.
15. Pileus yellowish brown to ochraceous over disc, paler toward margin, with marginal striations 0.25-0.4R; universal veil with surface cracking (reminiscent of *A. zambiana*); described from Singapore with symbionts unrecorded (“in deep forest”); also reported from China in undetailed forest habitat;  $Q = 1.09 \pm 0.04$ ; spore length (8.5-) 9.0 - 11.5 (-12.0) (Yang *et al.*, 2001)) .....  
12. *Amanita princeps* Corner & Bas (1962).
15. Pileus brown over disc, virgate between disc and very pallid to white region over striations, with marginal striations rather short; recorded from Thailand, in mixed dipterocarp forest;  $Q = 1.11 - 1.17$ ; spore length (8.2-) 9.2 - 11.0 (-13.0)  $\mu\text{m}$  .....  
13. *Amanita* sp. Thai 3 [Tulloss].
12. Pileus dominated by shades of yellow, orange, or red.
16. Pileus with brownish and/or olivaceous tones.
17. Pileus brownish yellow to brownish orange, darkest over disc; stipe pale yellow to nearly white, with patches concolorous at first, becoming deeper yellow or orange when handled; described from Arkansas, USA, recorded throughout SE USA, in frondose woods;  $Q = 1.22 - 1.38$  (-1.50); spore length (7.0-) 7.7 - 11.4 (-15.0)  $\mu\text{m}$  .....  
14. *Amanita arkansana* Rosen (1926).
17. Pileus with olivaceous tones at least at first, with umbo reddish brown and margin brownish yellow; stipe yellow, having sordid yellow patches at first; recorded from Honduras and Costa Rica in association with *Quercus*;  $Q = (1.22-) 1.24 - 1.37$  (-1.40); spore length (7.5-) 8.0 - 11.0 (-13.6)  $\mu\text{m}$ . .....  
15. *Amanita garabitoana* Tulloss et al. nom. prov.
16. Pileus with strong red and yellow tones, lacking brown tones.
18. Pileus reddish with orange disc; described from Himachal Pradesh, India, in association with *Cedrus*;  $Q = 1.25$ ; spore length 7.0 - 11.5  $\mu\text{m}$  .....  
16. *Amanita simlensis* R. P. Bhatt et al. in A. Kumar et al. (1990)

3. The drawing of the subhymenium in the protologue appears to depict an immature condition. Since the pictures of basidiomes also appear immature, I assume that the subhymenium is not fully inflated as depicted and would have a typical stirps *Hemibapha* subhymenium in mature material.

4. Spelling correction. In the protologue, the spelling was “*egreginus*.” The descriptions of taxa in (Wood, 1997) are, unfortunately, plagued with vague or contradictory descriptions and the presence of illustrations that contradict the text. One or two of the taxa described for *Amanita* sect. *Caesareae* by Wood seem to be assignable to *Amanita* sect. *Amanita*, instead. Certainly a basal bulb on a stipe should exclude a species from sect. *Caesareae*—as Wood states. Nevertheless, he describes such a taxon under the name *A. egregia* [sensu Wood].

18. Pileus yellow with brilliant reddish orange disc; recorded from Florida, USA, in Pinus-Quercus forest;  $Q = 1.26$ ; spore length 9.1 - 10.8 (-12.6)  $\mu\text{m}$ .....  
 17. *Amanita* sp. F10 [Tulloss].

11. Taxa often having  $Q > 1.3$ . (See also, *A. arkansana*, above.)

19. Pileus gray to grayish brown to sepia to fuliginous to umbraceous to fuscous.
20. Pileus gray, grayish brown to sepia, with plentiful, roughly evenly distributed, pallid, broadly subfusiform spots in the pileipellis; described from southwestern China, with Pinus and/or Quercus;  $Q' = 1.45 \pm 0.09$ ; spore length (8.5-) 9.5 - 12.0 (-13.0)  $\mu\text{m}$  (Yang, 1997) .....  
 18. *Amanita yuani* Zhu L. Yang (1994)
20. Pileus fuliginous to umbraceous to fuscous, completely lacking pallid spots in the pileipellis; recorded from Japan, with symbiont(s) unknown; est.  $Q' = 1.4$ ; spore length "7.5 - 10.5"  $\mu\text{m}$  (Imazeki et al., 1988)  
 19. *Amanita hemibapha* subsp. *similis* sensu auct. japon.
19. Pileus red-brown to red (fading to peach from margin inward), yellow (with red or orange disc in one species), yellow-orange, orange, yellow-brown, or orange-brown, or warm brown.
21. Pileus red-brown at least over disc at first; lacking an umbo (at least at first).
22. Pileus red-brown over disc, between Xanthine Orange and Orange toward margin; stipe white, decorated with yellowish fibrils; partial veil having cream-colored upper surface; recorded from Texas, USA, associated with Pinus;  $Q = 1.46 - 1.54$ ; spore length (7.3-) 7.6 - 10.6 (-14.1)  $\mu\text{m}$ .....  
 20. *Amanita* sp. T31 [Tulloss].
22. Pileus red-brown to red (fading to peach from margin inward); stipe peach with orange subfelted decoration; partial veil having ??color?? upper surface; recorded from Arkansas, USA, in open Quercus-Juniperus forest;  $Q = 1.44 - 1.48$ ; spore length (8.0-) 8.6 - 11.0 (-19.2)  $\mu\text{m}$  .....  
 21. *Amanita* sp. AR1 [Tulloss].
21. Pileus yellow (red or orange disc in one species), yellow-orange, orange, yellow-brown, or orange-brown, or warm brown.
23. Pileus yellow to yellow-orange, with color more saturated and redder over disc; described from Tanzania, from miombo woodland, holotype collected in association with *Brachystegia*, *Uapaca*, and in plantations of *Anacardium*;  $Q = 1.47 - 1.56$ ; spore length (8.5-) 8.6 - 10.8 (-12.1)  $\mu\text{m}$ .....  
 22. *Amanita masasiensis* Härk. & Saarim. in Härk., et al. (1994).
23. Pileus yellow to yellow-orange or orange-yellow or ocher yellow to yellow developing brown tinted disc or orange-brown at first becoming yellow-brown to orangish tan with age.
24. Pileus evenly yellow-orange or yellow at first and becoming yellow-brown to orange-brown at least in part or warm brown at first and becoming paler orangish brown at maturity.
25. Pileus evenly yellow-orange, lacking an umbo; described from Tanzania, in miombo woodland—dominated by *Brachystegia*;  $Q = 1.72$ ; spore length (8.5-) 9.0 - 11.4 (-12.6)  $\mu\text{m}$ .....  
 23. *Amanita tanzanica* Härk. & Saarim. in Härk. et al. (1994).
25. Pileus yellow at first and becoming yellow-brown to orange-brown at least in part or warm brown at first and becoming paler orangish brown at maturity; known from Asia or North America.
26. Pileus yellow and or orange-brown at first, soon (usually) dominantly yellow outside the disc, becoming yellow-brown to orange-brown over disc; stipe decoration persistently concolorous with pale yellow stipe; recorded from E USA, in forests dominated by *Fagus*, *Quercus*, and *Carya* or by *Pinus* and *Quercus*;  $Q = 1.39 - 1.60$  (-1.69); spore length (7.5-) 8.4 - 11.9 (-15.0)  $\mu\text{m}$  .....  
 24. *Amanita banningiana* Tulloss nom. prov.
26. Pileus orange-brown at first, becoming paler orangish brown overall at maturity; stipe decoration concolorous with pale yellow stipe at first, becoming orange-brown with age or handling; recorded

from NW Pakistan in mixed forest with *Abies* and *Taxus*;  $Q = 1.34 - 1.41$  (-1.47); spore length (7.8-) 8.5 - 11.8 (-18.0)  $\mu\text{m}$  .....

25. *Amanita cinnamomescens* Tulloss et al. nom. prov.

24. Pileus not entirely yellow to yellow-orange at first.

27. Pileus with red disc, otherwise yellow; recorded from Nepal, in *Shorea* forest (also, apparently in Himachal Pradesh and Uttarakhand states, India, with *Pinus*);  $Q = 1.53$ ; spore length (7.8-) 8.0 - 10.8  $\mu\text{m}$  .....

26. *Amanita* sp. IHJ4 [Tulloss].

27. Pileus lacking red disc.

28. Pileus with brownish orange disc and yellow margin, sometimes with other tints.

29. Pileus with brownish orange disc and yellow margin; known from NE Queensland, Australia, habitat not recorded; spores with  $Q = 1.44 - 1.49$ ; spore length 8.6 - 11.2  $\mu\text{m}$  .....

27. *Amanita* sp. AUS2 [Tulloss].

29. Pileus with orange-brown disc and yellow margin, often with reddish or olivaceous tints; known from Chiapas, Mexico; associated with *Quercus* forest; spores with  $Q = 1.50$  (est.); spore length (8.6-) 9.3 - 11.7 (-14.0)  $\mu\text{m}$  .....

28. *Amanita hyalyuy* Arora & G. H. Shepard (Shepard et al. 2008).

28. Pileus lacking brownish orange disc.

30. Pileus orange-yellow to ocher yellow, with yellow margin; described from Java, with symbiont(s) unknown;  $Q = 1.45$ ; spore length 8 - 12  $\mu\text{m}$  .....

29. *Amanita javanica* (Corner & Bas) Oda et al. (1999)

= *A. hemibapha* subsp. *javanica* Corner & Bas (1962).

30. Pileus light cadmium to lemon chrome; recorded from China and Tibet, with symbiont(s) unknown;  $Q = 1.6$  (est.); spore length 10 - 12  $\mu\text{m}$  .....

30. *Amanita caesarea* sensu Teng (1936).

10. Taxa *not* having 95% of spores  $\square$  12  $\mu\text{m}$  long.

31. Pileus entirely white (even at maturity) or with yellowish disc at maturity, described from Nepal in association with *Shorea*, recorded from SW China with unrecorded symbiont(s) and from Thailand in forest of Dipterocarpaceae and Fagaceae (Sanmee et al., 2008);  $Q = 1.14 - 1.15$ ; spore length (6.5-) 9.2 - 12.5 (-14.8)  $\mu\text{m}$

31. *Amanita chepangiana* Tulloss & Bhandary (1992), see also (Yang, 1997) for corrections to protologue.

31. Taxa usually having  $Q \geq 1.2$ .

32. Pileus brown with white or pallid (not yellow) region over marginal striations or white to cream, sometimes with olivaceous brown to tan to buff to straw-colored disc.

33. Pileus brown with paler region over marginal striations (0.3-0.5R); lamellae with pink tint, subdistant; described from Japan, with symbiont(s) unknown to me;  $Q' = 1.22 \pm 0.06$ ; spore length (9.5-) 10.0 - 12.5 (-13.5)  $\mu\text{m}$  (Yang, 1997) .....

32. *Amanita longistriata* S. Imai (1938).

33. Pileus white to cream, sometimes with olivaceous brown or tan to buff disc; with spores having  $Q$  in the range 1.24 - 1.41.

34. African taxa; fruiting body robust; universal veil attached only at very base of stipe (like all other taxa treated in this key with the exceptions noted in *the second half of this couplet*). [Possibly a single taxon.]

35. Pileus entirely white to pallid at first, soon olivaceous brown over disc and progressively paler toward margin; universal veil with surface cracking and darkening; described from Zambia, recorded

- from Zimbabwe and Tanzania, in miombo woodland—dominated by *Brachystegia*; **Q** = 1.24 - 1.41; spore length (10.0-) 10.5 - 13.8 (-21)  $\mu\text{m}$  .....  
 33. *Amanita zambiana* Pegler & Pearce (1980).
35. Pileus bright white to cream, sometimes with fawn colored disc; **Q** = 1.3; spore length 13 - 14  $\mu\text{m}$ ; described from Republic of Congo, known from central Africa, with symbiont(s) unknown .....  
 34. *Amanita loosii* Beeli (1936).
34. Taxa of eastern North America and Asia; fruiting body rather gracile; pileus never developing olivaceous brown tint; universal veil attached 5 - 10 mm up the sides of the stipe, not only at very base of stipe.
36. Asian taxon; pileus brown over disc, not virgate between disc and margin, gradually shading through pale tan to nearly white or cream at margin, with marginal striations 0.15-0.2R; recorded from Pakistan, associated with *Abies*; **Q** = 1.29 - 1.48; spore length (10.0-) 10.1 - 12.2 (-12.8)  $\mu\text{m}$ .....  
 35. *Amanita pakistanica* Tulloss, et al. (2001).
36. North American taxon; pileus with disc watery tan to straw color to pinkish buff to brown, with remainder cream to whitish or pale pinkish buff; described from Florida, USA, with *Quercus*; also recorded from Prov. Québec, Canada, and the U.S. states of Maine, Michigan, New Jersey, and North Carolina with *Fagus* and *Quercus* or isolated *Quercus* or with *Tsuga*, *Betula*, and *Rhododendron*; **Q** = 1.43 - 1.58; spore length (8.5-) 9.5 - 12.6 (-13.6)  $\mu\text{m}$  .....  
 36. *Amanita murrilliana* Singer (1951)<sup>5</sup>  
 =*Venenarius gemmatus* var. *volvatus* Murrill (1941b)  
 =*Amanita spreata* sensu McIlvaine (1902).
32. Pileus orange-brown to red-brown or evenly yellow-orange or gray-brown or fuliginous to umbrinous or brown and (often) yellow toward margin. See also *Amanita zambiana*, above.
37. Pileus fuliginous to umbrinous or gray-brown or brown and (often) yellow toward margin.
38. Pileus brown over disc and brown to yellow toward margin; recorded from China and Tibet, with *Abies*, *Picea*, *Pinus*, and *Quercus*; **Q** = 1.36 $\pm$ 0.10; spore length (8.0-) 9.0 - 12.5 (-17.0)  $\mu\text{m}$  .....  
 37. *Amanita hemibapha* var. *ochracea* Zhu L. Yang (1997).
38. Pileus fuliginous to umbrinous to gray to gray-brown to brown.
39. Pileus fuliginous to umbrinous; described from Japan, in *Pinus* forest; **Q** = 1.6; spore length 10.5 - 14  $\mu\text{m}$  .....  
 38. *Amanita esculenta* Hongo & I. Matsuda (Matsuda and Hongo, 1955).
39. Pileus gray to mouse gray to gray-brown to brown.
40. Pileus dark gray-brown, paler toward margin, with pigment distributed in distinctive concentric small patches, disc apparently not depressed; lamellae not pinkish; described from Hunan, China, in *Pinus* forest; **Q'** = 1.47 $\pm$ 0.10; spore length (8.0-) 9.5 - 12.5 (-15.5)  $\mu\text{m}$  (Yang and Zhang, 2002)....  
 39. *Amanita hunanensis* Y. B. Peng & L. H. Liu (1981).
40. Pileus pallid gray to gray to mouse gray to gray-brown to brown, with pigmentation continuous (not distributed in distinct patches), lamellae pale pink or shell pink or orangish white.
41. Pileus gray to gray-brown to brown, with center depressed; lamellae pale pink; described from Sichuan and Yunnan provinces, China, in *Pinus* forest; **Q'** = 1.38 $\pm$ 0.09; spore length (8.5-) 9.5 - 13.5 (-17.0)  $\mu\text{m}$ .....  
 40. *Amanita incarnatifolia* Zhu L. Yang (1997).
41. Differing in geographic distribution; to a lesser degree, differing in pileus color, spore size, or spore shape.

<sup>5</sup>. See the discussion of *A. cokeriana*, above, in the list of taxa excluded from this paper for lack of sufficient data. From available evidence, it seems likely that *A. cokeriana* would key out near *A. murrilliana* in this key.

42. Pileus brown, with center not depressed; lamellae orangish white; known from Long Island, New York, USA, in deciduous forest with *Cornus*, *Juglans*, and *Quercus*;  $Q = 1.45 - 1.47$ ; spore length (10.5-) 10.8 - 12.5 (-14.0)  $\mu\text{m}$ . .....  
41. *Amanita* sp. 53 [Tulloss].
42. Pileus pallid gray to mouse gray, convex to planar; lamellae pale pink to shell pink; described from New South Wales, Australia;  $Q = 1.49 - 1.56 (-1.71)$ ; spore length (9.6-) 9.9 - 12.6  $\mu\text{m}$ . ..  
42. *Amanita roseolamellata* A. E. Wood (1997).<sup>6</sup>
37. Pileus orange-brown to red-brown, yellow with red disc, or evenly yellow-orange.
43. Pileus orange-brown to red-brown, often with darker ring over inner ends of striations; described from Tanzania, in miombo woodland—dominated by *Brachystegia*;  $Q = 1.49$ ; spore length 10.5 - 12.7 (-15.8)  $\mu\text{m}$  .....  
43. *Amanita mafingensis* Härk. & Saarim. in Härk. et al. (1994).
43. Pileus yellow with red disc or evenly yellow-orange.
44. Pileus yellow with red disc; known from South Carolina, USA, with *Pinus* or *Castanea*;  $Q = 1.57$ ; spore length (8.4-) 8.6 - 14.3 (-15.5)  $\mu\text{m}$  .....  
44. *Amanita* sp. S10 [Tulloss].
44. Pileus evenly yellow-orange; recorded from Japan, in forest with *Pinus* and *Quercus*;  $Q = 1.38 - 1.47$ ; spore length (8.5-) 9.0 - 12.5 (-16.0)  $\mu\text{m}$  .....  
45. *Amanita hemibapha* subsp. *javanica* sensu auct. japon.

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<sup>6</sup> Spore size and shape in text conflicts notably with illustration of spores.

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