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.

Abstract—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 11 (eleven) stirpes: *Caesarea, Calyptratoides, Calyptroderma, Chambersiana, Cinderellae, 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 stirps. Keys to the provisionally defined stirpes of the *Caesareae* and to the accepted species of those stirpes are provided. The number of taxa belonging in stirps *Hemibapha* is now believed to exceed 46. The keys to world taxa provided in this article have 73 termini. The number of taxa here assigned to stirps *Caesareae* is six; to stirps *Calyptroderma*, at least five; to stirpes *Calyptratoides, Chambersiana, Pulchella*, and *Ristichii*, one each; to stirpes *Grandis* and *Oleosa*, two each; to stirps *Cinderellae*, at least one; and to stirps *Pachysperma*, three. The number of world taxa assignable to the *Caesareae* is now conservatively estimated to be in the range of 75 to 85.

Key words-

Introduction

Since the publication of (Tulloss 1986) and its second version (Tulloss 1998), a number of new species have been described in stirps *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 species and infraspecific taxa.

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 discrepancies [new secotioid taxa are not considered unusual because of the pre-existence of *Torrendia* Bres. (1902)]. 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* Bougher & Lebel (2002) and *Torrendia* and a few taxa in stirps *Hemibapha*. However, work on multilocus 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 stirps *Hemibapha* key is 48. A survey of the dates of original publication (provided in the key) demonstrates that a large majority of these taxa (44) 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 total termini of the combined keys is presently 73, and the conservatively estimated number of probable taxa worldwide is 75-85.

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

Some species of the genera Amarrendia and Torrendia are included within Amanita sect. Caesarea.

Methods and materials

In the sets of spore data, bold face \mathbf{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 \mathbf{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 \mathbf{Q} or \mathbf{Q}' from available data. When more than one specimen has been examined by me, a range of values of \mathbf{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, cylindric; > 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, 2009). Authorial citation abbreviations follow Kirk and Ansell (1992, 2009). All taxa that appear in one of the keys have their author citation given in that key rather than in the remainder of the text.

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 protolog (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. More-

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over, 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*. *ae*, 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 in order to gain further understanding. Among other things, it seems odd that *Amarrendia* taxa (which frequently lack any remnant of the stipe that is characteristic of *Amanita* and *Torrendia* species) would be basal to a clade that includes a *Torrendia* species in a position far from basal. The 28S tree makes it appear that combination of both European and Australian taxa in *Torrendia* may prove to create a polyphyletic assemblage, which is not surprising. One then can hypothesize that sect. *Caesareae* has for some time included taxa with certain built-in "genetic options" for adaptation to semi-arid habitat and that at least three or four independent mutations have taken similar adaptive routes on different occasions in the section's history.

Amendment of Amanita sect. Caesareae

Singer (1951) defines the *Caesareae* as follows: "Annulus and volva both constantly well developed; volva basal, membranous, with a wide saccate limb, not breaking into small vertucose fragments on the surface of the pileus; not containing any toxins." Since Singer does not define the subgenus to which sect. *Caesareae* is assigned as comprising species with inamyloid spores, the protolog could apply to an annulate species of section *Amidella* such as *A. peckiana* Kauffman in Peck (1913).



Figure 10. *Amanita garabitoana* Tulloss *nom. prov.* Photo by R. E. Tulloss

By the last edition of "Agaricales," Singer (1986) had corrected this omission. In the fourth edition, Singer's statement of the definition of the *Caesareae* was reworded: "Annulus and volva well developed; stipe not or slightly bulbous; volva saccate, neither friable (or rarely so) nor limbate; spores elongate (short ellipsoid, oblong or cylindric) [Note: Bas' definitions of these terms can't possibly apply here.]; as far as known, no poisonous matter present."

Singer (1986) was willing to consider the flocculent sheath or deciduous partial veil of *A. lactea* (see "Taxa excluded" below) as satisfying his criterion for "well developed." However, *A. lactea* differs from all other taxa that have been accepted in sect. *Caesareae* in that it lacks clamp connections at the bases of its basidia. Singer's mention of a bulb is misleading—if only because people have little or no guidance as to how to determine what a bulb is. For example, there is a small bulb at the base of the stipe of *A. farinosa* Schwein. (1822) (sect. *Amanita*), but there is a small volval cup at the base of *A. ceciliae* (Berk. & Broome) Bas (1984) (sect. *Vaginatae*). Bas' distinction between sections *Amanita* and *Vaginatae* sensu Corner and Bas (1962)—the latter then including sect. *Caesareae*—is not based on the absence of a bulb, but on the position of the developing basidiome in the primordium. This position is central in the *Vaginatae* and the *Caesareae*. The central position and the fact that the taxa of the *Vaginatae* sensu Corner and Bas have what

Bas (1969) called a totally elongating stipe eliminates the possibility of a real bulb, which is a consequence of eccentric (above center) placement of a developing basidiome in its primordium. In this latter case, the region of the primordium

below the developing stipe may grow in size but does not participate appreciably in stipe elongation—becoming a bulb of undifferentiated or only slightly differentiated primordial tissue (even if it is a very small bulb) at the stipe's base. Such a bulb may be obscured by further changes as the fruiting body matures. So the differences between the *Vaginatae* and *Caesareae* on the one hand and sect. *Amanita* on the other has to do with the development of the basidiome, which may or may not be detectable by presence or absence of a bulb in a basidiome's mature state.

Here is a draft of a proposed amendment of *Amanita* sect. *Caesareae* that can include the types of *Torrendia* and *Amarrendia*:

Amanita sect. *Caesareae* comprises those taxa (whether sequestrate or epigeous-agaricoid) of *Amanita* [defined by a.) acrophysalidic context and b.) hyaline, colorless, smooth (undecorated), and dominantly thin-walled spores] that are assignable to *Amanita* subg. *Amanita* [c.) defined by inamyloid spores] and that have d.) a basidiome developing centrally in the primordium (epigeous taxa represent a special case in which the entire primordium apparently develops into the basidiome), e.) a stipe (if present) that is totally elongating, and f.) clamps commonly born at the bases of basidia.

Not required in the emended definition, but also characteristic of the section are the following:

Observation 1: All taxa of this section that are secotioid or epigeous-agaricoid have a membranous to fleshy universal that, in whole or part, forms a saccate volva at the base of the stipe and is attached to the stipe only at the very bottom of the stipe (or in a small number of cases, for a short distance above the very base as well).

Observation 2: All epigeous-agaricoid taxa of this section bear a persistent, membranous partial veil on their stipes.

Observation 3: In a large majority of the section's epigeous-agaric taxa (nearly 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.¹ 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 *Calyptratoides*.

^{1.} 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 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.

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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-exist 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: $11.1-14.9 \times 6.5-10.5 \mu m$, 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, 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) (=*A. cinerea* Bres. nom. illeg., described in a minimal protolog 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) × (5.6–) 6.4– 8.6 (–10.2) µm, 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 U.S.A.) 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* (=*A. murrilliana*) appears to conform
- to the protolog of *A. cokeriana* suggests that the two taxa may be similar. The just cited material comprises a nonconforming 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 as-
- signable to *A. cokeriana*. These have spore length = (10.5-) 11.5–14.7 (–19.0) µm, 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
- protolog of *A. cokeriana* the well-documented material from Chapel Hill, North Carolina (U.S.A.) 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 *Hemiba-pha*. 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 Beeli (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: $8.7-9.6 (-10.4) \times 6.5-7.3 (-8.8) \mu m$, 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) µm. 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 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 protolog'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 *Caesareae* 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 secotioid. [*Torrendia* p.p.²]

². The taxa described and assigned to Torrendia by Miller and Horak (1992) had inamyloid spores and, thus, cannot be included in section Caesareae.

3. Species known from the western Mediterranean region, in coastal habitat (probably including *Pinus*); spores "13.5–18 × 5–7" μ m, with "Q = 2.4–3.2" and est. **Q**' = 2.7[±] (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)" μ 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 wood-lands 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 µm, 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 $12-35 \times 9-30$ 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)" µm, with $\mathbf{Q}' =$ "1.39"....

4. Amarrendia oleosa Bougher & Lebel (2002).

5. Basidiome $10-20 \times 16-18$ 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)" µm, with **Q'** = "1.43" 5. *Amarrendia grandispora* (Beaton et al.) Bougher & Lebel (2002)

 \equiv *Alpova grandispora* Beaton et al. (1985).

1. Basidiomes epigeous-agaricoid.

- **6**. Species having submembranous universal veil (apparently known only from eastern North America). [Stirps *Cinderellae.* The following two entries may be contaxic.]
 - 7. Pileus pale brownish gray, virgate, with margin striate (0.3–0.45R); stipe pale gray, becoming grayer with maturity, decorated below partial veil with gray-brown fibrils darker than ground color, with partial veil sub-felted-submembranous to subfelted-fibrillose, at first white above and gray below, becoming entirely gray, faintly striate (10× lens) above, deciduous, universal veil saccate and white at first, then graying and breaking into plaques or warts, 1.5–4.5 mm thick; known from Connecticut and New Jersey, U.S.A.; apparently associated with *Quercus*; spores [60/3/3] (8.0–) 8.7–11.5 (–12.9) × (6.3–) 6.6–8.0 (–8.5) µm, (L = 9.4–10.4 µm; L' = 9.9 µm; W = 7.1–7.5 µm; W' = 7.3 µm; Q = (1.22–) 1.25–1.50 (–1.58); Q = 1.33–1.39; Q' = 1.36)...... 6. *Amanita* species N4.
 - 7. Pileus "gray-brown to dark gray-brown," with margin "plicate-striate, sometimes tuberculate"; stipe ??, with partial veil; stipe "white to light grayish brown," with partial veil "superior, sometimes near median, "white to grayish, upper surface striate," "usually thin and collapsing on stipe," with universal veil "relatively thick,", saccate at first then breaking up into patches, white at first then gray; known from Jackson Co., Illinois,

U.S.A. (deposited in SIU); associated with mixed hardwoods including *Quercus*; spores "[74 spores] 8.5–15 \times 6–10.5 µm, (Q = 1.17–1.63; Q = 1.28–1.45)" (Began 1988), with est. Q' = 1.47. *Amanita* species Began 395.

- 6. Species having a membranous universal veil.
 - **8**. 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).
 - **9**. 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 U.S.A. (central Atlantic seaboard states, Connecticut to North Carolina); spores [77/4/2] (9.0–) 10.0–13.5 (–14.5) × (5.6–) 5.8–7.2 (–9.5) µm, (L = 10.9–12.9 µm; L' = 11.8 µm; W = 6.1–6.8 µm; W' = 6.5 µm; Q = (1.56–) 1.62–2.0 (–2.57); Q = 1.73–1.89; Q' = 1.80).

8. Amanita recutita sensu Coker (1917).

[Sole taxon of stirps *Chambersiana*, proposed English classification "Coker's False Caesars."]

9. Species small and having over 30% of basidia bisterigmate or species with stipe taking on the appearance of a tallow candle.

10. 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 (U.S.A.); recorded from central California with *Quercus* to neovolcanic region of central Mexico in mixed *Pinus-Quercus-Abies* forest; spores [260/12/11] (8.5–) 9.8–14.0 (–17.0) × (5.5–) 6.5– 8.9 (–11.8) μ m, (L = (11.2–) 11.6–13.0 μ m; L' = 12.0 μ m; W = (7.3–) 7.6–8.0 μ m; W' = 7.8 μ m; Q = (1.26–) 1.36–1.81 (–1.99); Q = (1.40–) 1.44–1.70; Q' = 1.55)....

9. Amanita calyptratoides Peck (1909). [Sole taxon of stirps Calyptratoides, proposed English classification, "Candlestick False Caesars."]

10. Species frequently having small basidiome; usually having at least 30% of basidia bisterigmate.

11. Pileus white with proportionately short marginal striations; lamellae often orangish white or pinkish; described from New Hampshire (U.S.A.); reported from Prov. Quebec, Canada, and the northern New England states (U.S.A.); spores [185/7/7] (9.2–) 10.2–13.9 (–17.0) × (6.6–) 7.0–9.0 (–12.8) μ m, (**L** = 11.5–12.4 μ m; **L'** = 12.1 μ m; **W** = 7.7–8.5 μ m; **W'** = 8.0 μ m; **Q** = (1.22–) 1.32–1.72 (–1.84); **Q** = 1.42–1.57; **Q'** = 1.50).

10. Amanita ristichii Tulloss (1989).

[See also (Tulloss, 1993).]

[Sole taxon of stirps Ristichii, proposed English classification, "Ristich's Little Caesars."]

- 11. 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."]
 - 12. Pileus gray, with disc darker to nearly black; described from North Carolina, U.S.A., in mixed deciduous and coniferous forest; reported from middle Atlantic seaboard states (Massachusetts to North Carolina) of U.S.A., often associated with mature or old *Quercus*, otherwise with *Quercus* or *Pinus*; spores [204/10/5] (9.5–) 10.5–16.2 (–20.0) × (6.0–) 7.5–10.5 (–12.5) µm, (L = (11.3–) 11.7–14.5 µm; L' = 13.1 µm; W = (8.1–) 8.6–9.7 µm; W' = 9.0 µm; Q = (1.12–) 1.26–1.75 (–2.10); Q = (1.30–) 1.31–1.64; Q' = 1.48)

11. Amanita pachysperma G. F. Atk. (1918) [See also (Tulloss, 1993).]

12. Pileus avellaneous to brownish, with pallid to white margin.

13. Pileus rather deep brown or grayish brown over disc; originally described from Virginia, U.S.A., with *Quercus*; recorded from the eastern U.S.A. (Tennessee northward to Massachusetts and westward to southern Illinois), with *Aesculus*, *Fagus*, *Pinus*, *Quercus*, and *Tsuga*; spores [960/48/19]

(9.1-) 11.5-15.0 $(-20.5) \times (6.5-)$ 8.5-11.2 $(-15.5) \mu m$, ($\mathbf{L} = (11.7-)$ 11.9-14.0 $(-14.1) \mu m$; $\mathbf{L'} = 13.1 \mu m$; $\mathbf{W} = (9.1-)$ 91-10.6 $(-10.9) \mu m$; $\mathbf{W'} = 9.9 \mu m$; $\mathbf{Q} = (1.07-)$ 1.16-1.52 (-1.89); $\mathbf{Q} = (1.16-)$ 1.21-1.42 (-1.55); $\mathbf{Q'} = 1.33$)....

12. Amanita virginiana (Murrill) Murrill (1914a, 1914b). [See also (Tulloss, 1993).]

13. Pileus avellaneous over disc; originally described from Florida, U.S.A., 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; spores [80/3/2] (9.0–) 10.5– 13.8 (–15.5) × (6.2–) 7.8–10.0 (-11.8) µm, ($\mathbf{L} = 11.6–11.9 µm$; $\mathbf{L}' = 11.7 µm$; $\mathbf{W} = 8.7–8.8 µm$; $\mathbf{W}' = 8.7 µm$; $\mathbf{Q} = (1.20–) 1.23–1.51 (–1.92)$; $\mathbf{Q} = 1.33–1.37$; $\mathbf{Q}' = 1.35$)

13. Amanita subvirginiana (Murrill) Murrill (1941a).

[See also (Tulloss 1993).]

- **8.** Basidia 4-sterigmate in mature basidiomes; stipe not having the appearance of a tallow candle, not hard—not cutting like soft wood.
 - 14. 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."]
 - 15. Pileus pale beige-brown (pinkish brown) over disc, paler at margin, pigment not evenly distributed (pileus subvirgate or appearing densely freckled), with margin short striate; stipe pale beige-brown (pinkish brown) over disc, paler at margin, pigment not evenly distributed (subvirgate or appearing densely freckled); found in *Pinus caribaea* var. *hondurensis* woodland; known from Belize; spores: [41/2/1] (10.0–) 10.2–13.2 (–13.8) × (5.8–) 6.5–7.8 (–8.2) µm, (L = 11.6–12.5 µm; L' = 12.0 µm; W = 7.2–7.3 µm; W' = 7.2 µm; Q = (1.47–) 1.50–1.81 (–1.83); Q = 1.62–1.72; Q' = 1.67)...

14. Amanita species BEL1.

- 15. Pileus not subvirgate or appearing freckled; species not known south of Mexico.
 - 16. Stipe often decorated with fibrillose-felted material, and at least sometimes bear a ragged "secondary annulus" of such material (actually derived from the *limbus internus* of the universal veil). [Note: Basidiomes of this general form with differently colored pilei are reported from the middle to southern Rocky Mountains, as well as from the segregated "mountain islands" to the south of the Rockies. More than one taxon may be involved.]
 - 17. 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 "secondary annulus" below the partial veil; recorded from southeastern Arizona (U.S.A.) in *Pinus* forests or forests of *Pinus* combined with any of the following: *Abies, Pseudotsuga*, and *Quercus*; spores [200/10/6] (8.2–) 9.0–11.9 (–13.6) × (6.0–) 6.8–8.1 (-9.4) µm, (L = (9.5–) 9.7–10.8 µm; L' = 10.2 µm; W = 6.9–7.5 (–7.8) µm; W' = 7.3 µm; Q = (1.09–) 1.25–1.57 (–1.63); Q = (1.29–) 1.34–1.49; Q' = 1.40

15. Amanita sp. AZ6 [Tulloss].

16. Stipe decorated with fibrillose-felted material, but never having a "secondary annulus."

18. 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. calyptrata*); described from California (U.S.A.) where it occurs in the autumn and early winter; reported from the Pacific coastal states (U.S.A.) south and probably extending into Baja California (Mexico) with *Abies*, *Pseudotsuga*, and *Quercus*;

spores [160/8/6] (8.6–) 9.0–12.0 (–24) × (5.5–) 5.8–7.0 (–8.5) μ m, (**L** = 9.9–10.9 (–11.1) μ m; **L'** = 10.4 μ m; **W** = (6.1–) 6.3–6.6 μ m; **W'** = 6.4 μ m; **Q** = (1.29–) 1.43–1.81 (–3.0); **Q** = 1.55–1.68 (–1.69); **Q'** = 1.62)

17. Amanita calyptroderma G. F. Atk. & Ballen (1909)
 =A. calyptrata Peck (1900a) non Lam.³
 <u>=</u>A. lanei (Murrill) Sacc. & Trotter (1925).

18. Pileus white to shades of yellow.

19. Pileus white to pale yellowish white, usually with no yellow tint at maturity according to protolog; partial veil always membranous; no odor reported; recorded from Mexico in forests including *Abies*, *Pinus*, and *Quercus*; spores [71/3/1] (10.0–) 10.8–13.7 (–15.4) × (7.1–) 7.8–10.1 (–11.5) μ m, (**L** = 11.6–12.4 μ m; **L'** = 12.0 μ m; **W** = 8.3–9.4 μ m; **W'** = 8.7 μ m; **Q**= (1.14–) 1.20–1.60 (–1.74); **Q** = 1.32–1.44; **Q'** = 1.39) ...

18. Amanita tuza Guzmán (1975).

19. Pileus yellow to pale yellow to yellowish white; with odor fish-like for some people; recorded from the Pacific coastal states (U.S.A.), 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*; spores [138/7/6] (9.0–) 9.5–12.4 (–17.2) × (5.5–) 6.0–7.8 (–9.8) µm; (L = 10.6–11.2 µm; L' = 10.9 µm; W = 6.6–7.3 µm; W' = 6.9 µm; Q = (1.35–) 1.40–1.77 (–2.18); Q = 1.53–1.67; Q' = 1.57)

19. "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 yet known.]

- 14. Subhymenium pseudoparenchymatous (comprising inflated cells, often with branching relationship not immediately apparent).
 - 20. Subhymenium comprising 1–2 (–3) layers of such inflated cells; often (not always) with a proportion-ately 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 from Prov. Quebec, Canada), and montane Central America (northward from Costa Rica). [Amanita stirps Hemibapha, proposed English classification "Slender Caesars." See separate key, below.]
- **20**. Subhymenium comprising 3–5 layers of such inflated cells; usually with pileus proportionately thickfleshed 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."]
 - **21**. 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*; spores [120/6/5] (8.0–)

³. The taxon *A. calyptrata* var. *albescens* Peck (1900b) is poorly understood. It was described as a white species with saccate volva and annulate stipe from New York (U.S.A.), 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. Quebee, 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) µm, 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.

8.9–12.9 (-17.8) × (5.3–) 6.0–8.5 (–14.3) μ m, (**L** = 9.7–11.0 (–11.4) μ m; **L**' = 10.6 μ m; **W** = (6.3–) 6.7– 7.6 μ m; **W**' = 7.1 μ m; **Q** = (1.21–) 1.30–1.70 (–2.0); **Q** = (1.40–) 1.47–1.59; **Q**' = 1.50) 20. *Amanita caesarea* (Scop. : Fr.) Pers. (1801) See also (Neville and Poumarat, 2004).

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

- 22. Pileus white to cream or some shade of red, orange, or yellow; described/recorded from Mexico.
 - **23**. 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; spores [60/2/1] (7.5–) 9.2–12.8 (–15.0) × (5.8–) 6.5–8.2 (–9.0) μ m, (**L** = 10.4–11.2 μ m; **L**' = 10.7 μ m; **W** = 7.3–7.6 μ m; **W**' = 7.4 μ m; **Q** = (1.10–) 1.27–1.67 (–2.16); **Q** = 1.43–1.47; **Q**' = 1.45)

22. Amanita sp. Laferrière 927

See (Laferrière 1991, Laferrière and Gilbertson1992).

- **23**. 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.]
 - 24. 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*; spores [121/6/6] (8.0–) 9.0–11.8 (–18.0) × (5.5–) 6.1–7.5 (–9.0) μm, (L = 9.7–11.3 μm; L' = 10.5 μm; W = 6.6–7.1 (–7.2) μm; W' = 6.8 μm; Q = (1.28–) 1.36–1.75 (–2.04); Q = (1.45–) 1.51–1.64; Q' = 1.54).

23. Amanita basii Guzmán & Ram.-Guill. (2001).

- 24. 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.]
 - **25**. 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*; spore⁴ "(8–) 9–11 (-12)(-13)(-14)" µm; **Q**'[?] = "1.38"....

24. Amanita laurae Guzmán & Ram.-Guill. (2001).

25. Pileus becoming yellower 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

⁴ Interpretation of the authors' nonstandard notation is problematic.

forest associated with *Pinus* and/or *Quercus*; spore⁵ "(9–) 10-13 (–14)(–15)" or "(8–)(9–) 10–11 (–12)" μ m; **Q'**[?] = "1.55" or [est.] **Q'** = 1.53...

25. Amanita yema Guzmán & Ram.-Guill. (2001)

=Amanita tecomate Guzmán & Ram.-Guill. (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 39. Hence, between 46 and 48 (the number of key termini) 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 the 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 limbus 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. calyptrata* 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. calyptrata* var. *albescens* to the data on *A. murrilliana*, below.

- **1**. Taxa having 95% of spores $\leq 10.0 \ \mu m \ long$.
 - **2**. Taxa having **Q** < 1.4.

I

- 3. Pileus dominated by brownish olive, isabelline, fuscous, fuligineous, 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*; spores [from dried material] "7–9.9 × (5.4–) 6.1–8.6 μ m," (**Q** = 1.15–1.2) (Corner & Bas 1962)

1. Amanita similis Boedijn (1951)

EAmanita 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; spores measured from scale drawings in (Gilbert 1940: tab. VII, fig. 6) $9.1-10.0 \times 6.5-7.5 \ \mu\text{m}$, ($\mathbf{L} = 9.6 \ \mu\text{m}$; $\mathbf{W} = 6.9 \ \mu\text{m}$; $\mathbf{Q} = 1.30-1.54$; $\mathbf{Q} = 1.41$).....

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

<u>=</u>*A. umbrina* Beeli (1931) non *A. umbrina* Pers.

⁵ Interpretation of the authors' nonstandard notation is problematic.

- **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*; spores [20/1/1] 7.5–9.5 (–10.5) × (5.8–) 5.9–6.9 (–7.6) µm, (L = 8.5 µm; W = 6.3 µm; Q = (1.21–) 1.22–1.43 (–1.69); Q = 1.34)....

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*); spores [90/4/4] (7.0–) 7.5–9.5 (–12.0) × (6.2–) 6.4–7.7 (–8.5) μ m, (L = 8.2–9.2 μ m; L' = 8.5 μ m; W = 6.9–7.2 μ m; W' = 7.0 μ m; Q = (1.01–) 1.11–1.39 (–1.52); Q = 1.17–1.33; Q' = 1.22)
 - 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 northeastern U.S.A. (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*; spores [297/14/10] (7.0–) 7.8–10.0 (–12.1) × (5.2–) 6.0–7.5 (–8.7) µm, (L = (8.1–) 8.4–9.5 µm; L' = 8.9 µm; W = (6.0–) 6.3–7.3 µm; W' = 6.7 µm; Q = (1.11–) 1.21–1.53 (–1.63); Q = 1.25–1.40 (–1.42); Q' = 1.33) 5. *Amanita jacksonii* Pomerleau (1984)

=Amanita umbonata Pomerleau (1980) non (Sumst.) Sartory & L. Maire

=Amanita tullossii Guzmán & Ram.-Guill. (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*; spores "[40/1/1] (6.5-) 8.0-9.5 (-10.0) × (5.5-) 6.5-8.0 (-8.5) μ m, (Q = (1.09-) 1.12-1.29 (-1.33); Q' = 1.20\pm0.05)"... 6. *Amanita hemibapha* sensu Zhu L. Yang (1997).
- 8. Recorded from Himachal Pradesh, India, in mixed forest with *Quercus* and, sometimes, *Rhododendron* and *Pinus*; spores [60/3/3] (7.2–) 7.8–9.5 (–11.5) × (6.0–) 6.5–8.0 (–9.0) μ m, (**L** = 8.4–8.9 μ m; **L'** = 8.6 μ m; **W** = 6.8–7.8 μ m; **W'** = 7.2 μ m; **Q** = (1.05–) 1.09–1.35 (–1.42); **Q** = 1.14–1.25; **Q'** = 1.20)..... 7. *Amanita* sp. IHJ6 [Tulloss].

2. Taxa having $\mathbf{Q} \ge 1.4$. [See also *A. jacksonii*, above.]

9. Pileus nearly uniformly orange-tan to brownish orange, lacking red areas; known from northeastern Queensland, Australia, habitat not recorded; spores with $\mathbf{Q} = 1.53-1.54$; spore length 8.5–10.2 µm (??up-grade??).

8. Amanita sp. AUS3 [Tulloss].

9. Pileus having yellow margin with disc orange to deep orange to scarlet.

10. Pileus yellow for outer half of radius, "beautiful scarlet" for inner half; stipe; described from Sri Lanka, with unrecorded symbionts; recorded from southern India (Kerala) in association with tree genera such as *Myristica* (nutmeg) and the dipterocarpous *Hopea* and *Vateria*; spores [20/1/1] (7.5–) 7.9–10.1 (–10.2) × (5.4–) 5.5–6.3 (–6.5) µm, (**L** = 9.1 µm; **W** = 5.9 µm; **Q** = (1.36–) 1.43–1.67 (–1.68); **Q** = 1.54) 9. *Amanita hemibapha* (Berk. & Broome) Sacc. (1887) subsp.*hemibapha*

see also (Vrinda et al. 2005).

[≡]Agaricus hemibaphus Berk. & Broome (1871),

10. Pileus deep yellow at margin with orange to deep orange disc, with margin striate (0.4R), at least sometimes slightly depressed in disc; annulus yellow and striate above; associated with ??; known from northern India; spores: $[20/1/1] 8.0-9.5 (-10.2) \times (5.8-) 6.0-6.5 \mu m$, (**L** = 8.8 μ m; **W** = 6.2 μ m; **Q** = (1.29-) 1.31-1.64 (-1.65); **Q** = 1.42).

10. Amanita species IHJ5 [Tulloss].

- 1. Taxa *not* having 95% of spores $\leq 10.0 \,\mu\text{m}$ long. (See also, *Amanita hemibapha* subsp. *hemibapha* and *Amanita* species AUS3, above.)
 - **11**. Taxa having 95% of spores $\leq 12 \ \mu m \log$.

12. Taxa having $\mathbf{Q} < 1.3$ with one exception and, then, having $\mathbf{Q} \le 1.33$ in more than 90% of collections. (See also, *Amanita* species IHJ7, below.)

13. Pileus dominated by white or shades of brown or gray, not dominated by shades of yellow, orange or red.

14. Pileus brown to grayish brown; in forests with *Quercus* and members of the *Pinaceae*; described from Japan; spores "[160/8/8] (8.0–) 8.8–10.8 (–12.0) × (7.6–) 8.4–10.4 (–10.8) μ m, (Q = 1.0–1.12 (–1.15); Q' = 1.04±0.04)"....

11. Amanita imazekii T. Oda et al. (2001)6

- 14. 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.
 - **15**. 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; spores [120/5/4] (7.0–) 9.1–11.2 (–13.0) × (6.5–) 7.7–9.5 (–11.6) µm, (**L** = 9.6–10.6 µm; **L'** = 10.1 µm; **W** = 8.2–9.1 µm; **W'** = 8.9 µm; **Q** = (1.05–) 1.09–1.24 (–1.55); **Q** = 1.14–1.17; **Q'** = 1.16)....

12. Amanita egregia D. A. Reid (1978, 1980)
=A. egregina⁷ A. E. Wood (1997)
non A. egregia sensu A. E. Wood.

15. Pileus with brown to yellow-brown disc from the outset.

- **16**. 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 unrecorded forest habitat; spores "[130/8/7] (8.5–) 9.0–11.5 (–12.0) × (7.5–) 8.5–10.5 (–11.0) µm," (est. L' = 10.2 µm; est. W' = 9.5 µm; "Q = (1.0–) 1.05–1.16 (–1.21); Q' = 1.09±0.04") (Yang et al. 2001)..... 13. *Amanita princeps* Corner & Bas (1962).
- 16. 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; spores [60/3/1] (8.2–) 9.2–11.0 (–13.0) × (7.8–) 8.2–9.8 (–11.0) μ m, (**L** = 10.0–10.6 μ m; **L'** = 10.2 μ m; **W** = 8.6–9.1 μ m; **W**' = 8.9 μ m; **Q** = (1.05–) 1.08–1.24 (–1.25); **Q** = 1.11–1.17; **Q'** = 1.15).....14. *Amanita* sp. Thai 3 [Tulloss].
- 13. Pileus dominated by shades of yellow, orange, or red.
 - 17. Pileus with brownish and/or olivaceous tones. See Amanita arkansana and A. garabitoana, below.

17. 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*; spores "7.0–11.5 × 6.0–9.0 μ m"; est. **Q**' = 1.25....

15. Amanita simlensis R. P. Bhatt et al. in A. Kumar et al. (1990)

⁶. The drawing of the subhymenium in the protolog 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.

^{7.} Spelling correction. In the protolog, 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 seems 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 suggesting that of *A. spreta*; stipe pallid, decorated with gray fibrils; recorded from Florida, U.S.A., in *Pinus-Quercus* forest; spores [20/1/1] 9.1–10.8 (–12.6) × (7.3–) 7.7–8.7 (–9.8) µm, (L = 10.2; W = 8.1; Q = 1.14–1.31 (–1.36); Q = 1.26).

16. Amanita sp. F10 [Tulloss].

11. Taxa often having Q > 1.3.

19. Pileus gray to grayish brown to sepia to fuligineous to umbraceous to fuscous.

20. Eastern Asian taxa; spores having $\mathbf{Q} < 1.55$.

- 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*; spores [90/3/2] (8.0–) 9.0–11.0 (–12.5) × (6.0–) 7.0–8.0 (–8.7) µm, (L = 10.1–10.3 µm; L' = 10.2 µm; W = 7.3–7.5 µm; W = 7.4 µm; Q = (1.15–) 1.33–1.46 (–1.57); Q = 1.36–1.38; Q' = 1.37).....
 18. *Amanita yuaniana* Zhu L. Yang (1994) [See also (Yang 1997).]
- **21**. Pileus fuligineous to umbraceous to fuscous, completely lacking pallid spots in the pileipellis; recorded from Japan, with symbiont(s) unknown; spores " $7.5-10.5 \times 5.5-7.5 \mu m$ " (Imazeki et al., 1988); est. **Q**' = 1.4

19. Amanita hemibapha subsp. similis sensu auct. japon.

- 19. Pileus red-brown (at least over disc at first), yellow (sometimes with red to red-orange disc), yellow-orange, orange, yellow-brown, orange-brown, or warm brown.
- **22**. Spores with $\mathbf{Q} = 1.20 1.50$ and $\mathbf{Q'} < 1.35$.
 - **23**. Pileus bright lemon yellow, lacking distinct umbo; stipe white with yellow sub-felted squamules; habitat unrecorded; known from northeastern India; spores: [40/2/1] (7.5–) 8.3–10.6 (–11.3) × (6.0–) 6.1–7.8 (–8.3) µm, (L = 9.2–9.3 µm; L' = 9.2 µm; W = 6.9 -7.0 µm; W' = 6.9 µm; Q = (1.19–) 1.22–1.47 (–1.58); Q = 1.30–1.35; Q' = 1.32)

20. Amanita species IHJ7.

- 23. Pileus not lemon yellow; North and Central American taxa.
 - 24. 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, U.S.A., recorded throughout southeastern U.S.A., in frondose woods; spores [260/12/7] (7.0–) 7.7–11.4 (–15.0) × (5.6–) 6.0–8.0 (–10.2) μ m, (**L** = 8.0–9.9 (–11.1) μ m; **L**' = 9.1 μ m; **W** = (6.3–) 6.5 –7.4 μ m; **W**' = 6.9 μ m; **Q** = (1.10–) 1.18–1.53 (–1.69); **Q** = 1.22–1.38 (–1.50); **Q**' = 1.31) 21. *Amanita arkansana* Rosen (1926).
 - 24. 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*; spores [293/15/10] (7.5–) 8.0–11.0 (–13.6) × (5.7–) 6.4–8.1 (–9.9) μ m, (L = (8.3–) 8.7–9.9 μ m; L' = 9.3 μ m; W = (6.6–) 6.9–7.6 μ m; W' = 7.2 μ m; Q = (1.06–) 1.14–1.43 (–1.73); Q = 1.22–1.37 (–1.40); Q' = 1.29)....

22. Amanita garabitoana Tulloss et al. nom. prov. (Tulloss 2009b).

22. Spores with $\mathbf{Q} \ge 1.35$ and $\mathbf{Q}' > 1.35$.

24. Spores with $\mathbf{Q'} \ge 1.60$.

- **25**. Pileus evenly yellow-orange, lacking an umbo; in miombo woodland dominated by *Brachystegia*; described from Tanzania; spores $[40/1/1](8.5-)9.0-11.4(-12.6) \times (5.0-)5.5-6.7(-7.8) \mu m$, (L = 10.4 μm ; W = 6.0 μm ; Q = (1.42-) 1.50-1.93 (-2.02); Q = 1.72) 23. *Amanita tanzanica* Härk. & Saarim. *in* Härk. *et al.* (1994).
- **24**. Spore with **Q'** < 1.55 in at least 90% of specimens reviewed. (See also *Amanita caesarea* sensu Teng, above)
- **26**. Spores with $\mathbf{Q}' > 1.41$; no parts of basidiome bruising cinnamon.
 - **27**. Pileus entirely a shade of red or with disc red, brownish red, or red-orange. (Also see *A. hyalyuy*, below.)
 - 28. Pileus brownish red at least over disc; eastern North American species.
 - **29**. 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; associated with *Pinus*; recorded from Texas, U.S.A.; spores [100/5/2] (7.3–) 7.6–10.6 (–14.1) × (5.0–) 5.3–6.8 (–8.5) μ m, (L = 8.3–9.5 μ m; L' = 9.0 μ m; W = 5.6–6.5 μ m; W' = 6.0 μ m; Q = (1.30–) 1.33–1.67 (–1.92); Q = 1.46–1.54; Q' = 1.49)....

26. Amanita sp. T31 [Tulloss].

29. Pileus red-brown to red (fading to peach from margin inward); stipe peach with orange subfelted decoration; partial veil having ??color?? upper surface; in open *Quercus-Juniperus* forest; recorded from Arkansas, U.S.A.; spores [60/3/1] (8.0–) 8.6–11.0 (–19.2) × (5.7–) 6.0–7.4 (–8.0) μ m, (L = 9.4 –9.7 μ m; L' = 9.6 μ m; W = 6.5–6.7 μ m; W' = 6.6 μ m; Q = (1.31–) 1.36–1.58 (–2.40); Q = 1.44–1.48; Q' = 1.45)....

27. Amanita sp. AR1 [Tulloss].

- 28. Pileus having a red or orange-red disc; African or south Asian species.

 - **30**. Pileus with red disc, otherwise yellow; recorded from Nepal, in *Shorea* forest (also, apparently in Himachal Pradesh and Uttarakhand states, India, with *Pinus*); spores Spores: [20/1/1] (7.8–) 8.0–10.8 × (5.2–) 5.5–7.2 (–7.8) µm, (L = 9.3 µm; W = 6.1 µm; Q = (1.33–) 1.36–1.69 (–1.74); Q = 1.53)....

29. Amanita sp. IHJ4 [Tulloss].

- 27. Pileus lacking tints dominated by red, dominated by shades of yellow, yellow-orange, yellowbrown, orange-brown, or warm brown.
 - **31**. 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; in forests dominated by *Fagus*, *Quercus*, and *Carya* or by *Pinus* and *Quercus*;

recorded from eastern U.S.A.; spores [274/14/11] (7.5–) 8.4–11.9 (–18.0) × (5.2–) 5.9–7.8 (–9.8) μ m, (**L** = 8.9–10.6 (–11.5) μ m; **L'** = 10.0 μ m; **W** = 6.3–7.0 (–7.3) μ m; **W'** = 6.7 μ m; **Q** = (1.14–) 1.33–1.71 (–2.14); **Q** = 1.39–1.61 (–1.69); **Q'** = 1.49)....

30. Amanita banningiana Tulloss nom. prov. (Tulloss 2009a).

31. **Q'** < 1.45.

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

- **33**. Pileus with brownish orange disc and yellow margin; known from northeast Queensland, Australia, habitat not recorded; spores [20/1/1] (8.5–) 8.6–10.2 (–11.3) × (5.9–) 6.0–7.4 µm, (L = 9.3 µm; W = 6.5 µm; Q = (1.31–) 1.34–1.55 (–1.59); Q = 1.44) 31. Amanita sp. AUS2 [Tulloss].
- **32**. Pileus orange-yellow to ocher yellow, with yellow margin; with symbiont(s) unknown; described from Java; spores⁸ $8-12 \times 6-8 \mu m$; est. **Q**' = 1.4...
 - 33. Amanita javanica (Corner & Bas) Oda et al. (1999)
 - \equiv *A. hemibapha* subsp. *javanica* Corner & Bas (1962).
 - [See also A. hemibapha subsp. javanica sensu auct. japon., below]
- **10**. Taxa *not* having 95% of spores $\leq 12 \mu m \log$.
 - **34**. 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); spores [150/4/4] (6.5–) 9.2–12.5 (–16.8) × (5.8–) 8.0–10.8 (–12.3) μ m, (L = 10.1–11.0 μ m; L' = 10.5 μ m; W = 8.7–9.4 μ m; W' = 9.1 μ m; Q = (1.02–) 1.06–1.26 (–1.39); Q = 1.14–1.17; Q' = 1.16)...

34. Amanita chepangiana Tulloss & Bhandary (1992).

[See also (Yang 1997) for corrections to protolog.]

- **34**. Taxa in which specimens frequently yield $\mathbf{Q} > 1.2$.
 - **35**. 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.
 - **36**. 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; spores of the type "[100/1/1] (9.5–) 10.0–13.0 (-14.0) × (7.5–) 8.0–11.0 (-12.0), (Q = (1.03–) 1.11–1.35 (-1.56); **Q'** = 1.22±0.08)" (Yang 1997); spores of other Japanese material: "[178/8/5] (8.0–) 9.0–12.0 (-13.5) × ((7.5–) 8.0–10.0 μm, (Q = (1.02–) 1.06–1.33 (-1.53); **Q'** = 1.19±0.08)" (Yang & Doi 1999)....

35. Amanita longistriata S. Imai (1938).

- **36**. Pileus white to cream, sometimes with olivaceous brown or tan to buff disc; with spores having **Q** in the range 1.24–1.41.
 - **37**. 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.]

38. Pileus entirely white to pallid at first, very soon (before pileus is entirely exposed) olivaceous brown over disc and progressively paler toward margin; universal veil with surface cracking and darkening;

⁸ It is not entirely clear to the present author whether the material attributed to this species in China and Japan is taxonomically identical to the material seen by Boedijn. From one Japanese collection (in NY), the author has the following data: [20/1/1] (9.2–) 10.0–13.0 (–16.0) × (6.5–) 7.2–8.2 (–10.0) µm, (L = 11.3 µm; W = 7.7 µm; Q = (1.39–) 1.40–1.55 (–1.62); Q = 1.47). Based on data including some kindly supplied by Dr. Zhu L. Yang, the following data was derived from Chinese collections attributed to *A. javanica*: [60/2/2] (8.5–) 9.0–12.0 (–12.5) × (6.3–) 6.6–8.5 (–9.0) µm, (L = 9.8–10.8 µm; L' = 10.3 µm; W = 7.1–7.6 µm; W' = 7.4 µm; Q = (1.28–) 1.32– 1.50 (–1.54); Q = 1.38–1.42; Q' = 1.40). Note that all sample sizes are small.

recorded from Zimbabwe and Tanzania, in miombo woodland—dominated by *Brachystegia*; described from Zambia; spores [140/6/3] (9.9–) 10.0–13.5 (–21.0) × (7.0–) 7.8–10.8 (–12.5) μ m, (**L** = 10.8–12.3 (–13.0) μ m; **L'** = 11.6 μ m; **W** = 8.2–9.5 (–10.5) μ m; **W'** = 9.1 μ m; **Q** = (1.09–) 1.13–1.53 (–1.91); **Q** = 1.19–1.30 (–1.41); **Q'** = 1.29)...

36. Amanita zambiana Pegler & Piearce (1980).

38. Pileus bright white to cream, sometimes with fawn colored disc; with symbiont(s) unknown; described from Republic of Congo, known from central Africa; spores $13-14 \times 9-12 \mu m$; est. **Q**' = 1.3. ??citation??

37. Amanita loosii Beeli (1936).

- **37**. 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.
 - **39**. 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; associated with *Abies*; described from Pakistan; spores [80/4/2] (10.0–) 10.1–12.2 (–12.8) × (6.5–) 7.0–8.8 (–9.2) µm, (L = 10.5–11.6 µm; L' = 11.0 µm; W = 7.8-8.1 µm; W' = 8.0 µm; Q = (1.17–) 1.23–1.64 (–1.97); Q = 1.29–1.48; Q' = 1.39)....

38. Amanita pakistanica Tulloss, et al. (2001).

39. Pileus with disc watery tan to straw color to pinkish buff to brown, with remainder cream to whitish or pale pinkish buff; with *Fagus* and *Quercus* or isolated *Quercus* or with *Tsuga*, *Betula*, and *Rho-dodenron*; described from Florida, U.S.A., with *Quercus*; also recorded from Prov. Québec, Canada, and the U.S. states of Maine, Michigan, New Jersey, and North Carolina⁹; spores [204/9/7] (8.5–) 9.5–12.6 (–13.6) × (5.6–) 6.4–8.4 (–9.2) µm, (L = 10.4–11.8 µm; L' = 11.2 µm; W = 6.6–7.9 µm; W' = 7.4 µm; Q = (1.23–) 1.32–1.74 (–1.88); Q = 1.43–1.58; Q' = 1.51)

39. Amanita murrilliana Singer (1951)¹⁰

EVenenarius gemmatus var. *volvatus* Murrill (1941b)

=Amanita spreta sensu McIlvaine and Macadam (1902).

- **35**. Pileus orange-brown to red-brown or evenly yellow-orange or gray-brown or fuligineous to umbrinous or brown and (often) yellow toward margin. See also *Amanita zambiana*, above.
 - 40. Pileus fuligineous to umbrinous or gray-brown or brown and (often) yellow toward margin.
 - **41**. Pileus brown over disc and brown to yellow toward margin; with *Abies*, *Picea*, *Pinus*, and *Quercus*; recorded from China and Tibet; with *Abies*, *Picea*, *Pinus*, and *Quercus*; spores "[190/9/6] (8.0–) 9.0– 12.5 (–17.0) × (6.0–) 7.0–9.0 (–10.0) μ m, (Q = (1.13–) 1.20–1.50 (–1.89); Q' = 1.36±0.10)"..... 40. *Amanita hemibapha* var. *ochracea* Zhu L. Yang (1997).
 - 41. Pileus fuligineous to umbrinous to gray to gray-brown to brown.
 - **42**. Pileus fuligineous to umbrinous; in *Pinus* forest; described from Japan; spores "10.5–14 × 7–8.5 μ m"; est. **Q**' = 1.6....

41. Amanita esculenta Hongo & I. Matsuda (Matsuda and Hongo, 1955).

42. Pileus gray to mouse gray to gray-brown to brown.

43. Pileus dark gray-brown, paler toward margin, with pigment distributed in distinctive concentric small patches, disc apparently not depressed; lamellae not pinkish; in *Pinus* forest; described from Hunan, China; spores from type study (??citation??) "[50/1/1] (8.0–) 9.5–12.0 (–15.5) × 6.5–8.5 (–10.0) µm, (Q = (1.23–) 1.33–1.62 (–1.71); Q = 1.49±0.11)"; spores from (Yang and Zhang 2002) "[140/6/4] (8.0–) 9.5–12.5 (–15.5) × 6.5–8.5 (–10.0) µm, (Q = (1.22–) 1.29–1.62 (–1.71); Q' = 1.47±0.10)".

42. Amanita hunanensis Y. B. Peng & L. H. Liu (1981).

^{9.} The Texas material listed on the *Amanita* Studies web site as "*Amanita* species T41" is probably assignable to *A. murrilliana* ¹⁰. 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.

- **43**. 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.
 - 44. Pileus gray to gray-brown to brown, with center depressed; lamellae pale pink; in *Pinus* forest; described from Sichuan and Yunnan provinces, China; spores "[240/9/4] (8.5-) 9.5-13.5 (-17.0) × (6.5–) 7.0–9.5 (–12.0) μ m, (**Q**' = 1.38±0.09)"....

43. Amanita incarnatifolia Zhu L. Yang (1997).

- 44. Differing in geographic distribution; to a lesser degree, differing in pileus color, spore size, or spore shape.
 - 45. Pileus brown, with center not depressed; lamellae orangish white; in deciduous forest with Cornus, Juglans, and Quercus; known from Long Island, New York, U.S.A.; spores [40/2/1] (10.5-) 10.8–12.5 $(-14.0) \times (7.4-)$ 7.5–8.7 $(-11.0) \mu m$, (L = 11.5–11.8 μm ; L' = 11.7 μm ; W = 8.0 μ m; **W**' = 8.0 μ m; **Q** = (1.31–) 1.35–1.56 (–1.67); **Q** = 1.45–1.47; **Q**' = 1.46) 44. Amanita sp. 53 [Tulloss].
 - 45. Pileus pallid gray to mouse gray, convex to planar; lamellae pale pink to shell pink; in sclerophyll forest; described from New South Wales, Australia; spores "(9.6-) 9.9–12.6 × 6.3–9.0 µm; Q = 1.49 - 1.56 (-1.71)," est. Q' = 1.47.....

45. Amanita roseolamellata A. E. Wood (1997).11

40. Pileus orange-brown to red-brown, yellow with red disc, or evenly yellow-orange.

46. Pileus orange-brown to red-brown, often with darker ring over inner ends of striations; in miombo woodland—dominated by *Brachystegia*; described from Tanzania; spores from isotype [20/1/1] 10.5– $12.7 (-15.8) \times (6.8-) 7.1-8.9 (-10.5) \mu m$, (L = 11.6 μm ; W = 7.8 μm ; Q = (1.34-) 1.35-1.61 (-1.64); Q = 1.49)

46. Amanita mafingensis Härk. & Saarim. in Härk. et al. (1994).

46. Pileus yellow with red disc or evenly yellow-orange.

47. Pileus yellow with red disc; with *Pinus* or *Castanea*; known from South Carolina, U.S.A.; spores [30/1/1] (8.4–) 8.6–14.3 (–15.5) × 5.5–8.0 (–8.3) µm, (L = 10.3 µm; W = 6.6 µm; Q = (1.38–) 1.41– 1.77 (-1.94); **Q** = 1.57)....

47. Amanita sp. S10 [Tulloss].

47. Pileus evenly yellow-orange; recorded from Japan, in forest with *Pinus* and *Ouercus*; spores from Japanese material (NY) [20/1/1] (9.2-) 10.0-13.0 (-16.0) × (6.5-) 7.2-8.2 (-10.0) µm, (L = 11.3 µm; $W = 7.7 \ \mu m; Q = (1.39-) \ 1.40-1.55 \ (-1.62); Q = 1.47);$ spores from Chinese material 48. Amanita hemibapha subsp. javanica sensu auct. japon. [See also, *Amanita javanica*, above.]

Material examined

In this section will be placed the information on all material examined in the presentation of this paper.

MATERIAL EXAMINED (Amanita ?): MATERIAL EXAMINED (Amanita ?): MATERIAL EXAMINED (Amanita ?): MATERIAL EXAMINED (Amanita ?): MATERIAL EXAMINED (Amanita sp. N4): U.S.A.: CONNECTICUT-Fairfield Co. - Stamford, S. S. Ristich 9-20-84-SSR-A (RET), 9-22-84-SSR-A (RET). ? Co. - ?, ?.ix.1993 participant in COMA Foray s.n. (RET) NEW JERSEY-Mercer Co. - Washington Crossing St. Pk., arboretum area, D. C. Tulloss 6-23-85-D (RET), R. E. Tulloss 7-5-92-G (RET), 7.vii.1992 Bruce E. Vansant s.n. [Tulloss 7-7-92-BEV2A] (RET).

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¹¹. Spore size and shape in text conflicts notably with illustrations of spores.

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