Squamanitaceae and three new species of Squamanita parasitic on Amanita basidiomes

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Abstract

The systematic position of the enigmatically mycoparasitic genus Squamanita (Agaricales, Basidiomycota) together with Cystoderma, Phaeolepiota, Floccularia, and Leucopholiota is largely unknown. Recently they were recognized as Squamanitaceae, but previous studies used few DNA markers from a restricted sample of taxa from the family and lacked a formal taxonomic treatment. In this study, with newly generated sequences of the type of the genus Squamanita, S. schreieri, and several additional species of the family, the phylogeny is reinvestigated with a concatenated (18S-5.8S-nrLSU-RPB2-TEF1-α) dataset. This study reveals that Cystoderma, Phaeolepiota, Squamanita, Floccularia, and Leucopholiota are a monophyletic clade with strong statistical support in Bayesian analysis and form Squamanitaceae. Phaeolepiota nested within Cystoderma; Squamanita, Leucopholiota, and Floccularia clustered together as two monophyletic subclades; and Squamanita was present as a monophyletic clade with strong statistical support in both Maximum Likelihood and Bayesian analyses. The family name Squamanitaceae is formally emended and a detailed taxonomic treatment is presented to accommodate the five genera. Meanwhile, another concatenated (18S-ITS-nrLSU-RPB2-TEF1-α) dataset is used to investigate phylogenetic relationships and species delimitation in Squamanita. Our data indicates that “S. umbonata” from the Northern hemisphere forms two species complexes, one complex includes six specimens from North America, Europe, and East Asia, the other includes two specimens from Central America and North America respectively. Furthermore, species of Squamanita can parasitize species of Amanita, besides other fungal species. Squamanita mira parasitizes A. kitamagotake (A. sect. Caesareae), while S. orientalis and S. sororcula are parasites of species belonging to the A. sepiacea complex (A. sect. Validae). “Squamanita umbonata” from Italy occurs on A. excelsa (A. sect. Valdinae). Three new species of Squamanita from East Asia, viz. S. mira, S. orientalis and S. sororcula are documented with morphological, multi-gene phylogenetic, and ecological data, along with line drawings and photographs, and compared with similar species. A key for identification of the global Squamanita species is provided.

Keywords: Amanita, Mycoparasitic fungi, Squamanita, Host preference, Three new taxa
INTRODUCTION

*Squamanita* is one of the most enigmatic genera of the Agaricales (Halama 2016; Mondiet et al. 2007; Redhead et al. 1994), and the members of this genus are extremely rare and sporadic all over the world (Griffith et al. 2019; Holden 2005; Matheny and Griffith 2010). *Squamanita* was originally described from riverine forest in Switzerland. After examining the type material, Horak (1968) presented a full re-description of the microscopic characters including features not reported in the protologue. Almost all the species of *Squamanita* are biotrophic parasites on other agaric species (Halama 2016; Harmaja 1987; Henrici 2013; Matheny and Griffith 2010; Nagasawa et al. 1990; Redhead et al. 1994; Reid 1983). The basidiomes of *Squamanita* grow from other agaric species and deform the host basidiomes so that they become incorporated into an enlarged base of the stipe of the *Squamanita*. Eventually, the host is completely deformed and more or less unrecognizable (Halama 2016; Matheny and Griffith 2010; Redhead et al. 1994). Parasitized host tissue has been formed and more or less unrecognizable (Halama 2016; Mondiet et al. 2007; Vizzini and Girlanda 1997), and sometimes multiple basidiomes come out from a “mycocecidium” (Bas 1965; Mondiet et al. 2007).

To date, 12 species of *Squamanita* have been accepted in the current literature ([http://www.indexfungorum.org/Names/names.asp](http://www.indexfungorum.org/Names/names.asp); Fraiture et al. 2019). It is reported that these species can parasite at least seven different genera of Agaricales, viz. *Amanita* (Bas 1965; Redhead et al. 1994), *Cystoderma* (Griffith et al. 2019; Harmaja 1987; Holden 2005; Matheny and Griffith 2010; Redhead et al. 1994; Reid 1983; Singer 1986), *Galerina* (Redhead et al. 1994), *Hebeloma* (Bas and Lessee 1999; Mondiet et al. 2007; Vesterholt 1991), *Inocybe* (Vizzini and Girlanda 1997), *Kuehneromyces* (Cervini 2008; Gülden et al. 1977), *Phaeolepiota* (Nagasawa et al. 1990; Redhead et al. 1994), and possibly also *Myccena* (Stridvall 1994). The total genomic DNA of all the materials of the parasitic species and the coexisting *Amanita* species was extracted by using the Extract-N-Amp kit (Sigma, USA). Universal primer pairs LR0R/LR5 (Vilgalys and Hester 1990), ITS1F/ITS4 (Gardes and Bruns 1993; White et al. 1990), NS1/NS41 (Bruns lab; Hibbett 1996) and NS51/NS8 (Bruns lab; White et al. 1990), and EF1-983F/EF1-1567R (Rehner and Buckley 2005), RPB2-6F/RPB2-7R (Hall lab), RPB1-Af/RPB1-Dr (Hall lab) were used for amplifying the large nuclear ribosomal RNA subunit (nLSU), the internal transcribed spacers 1 and 2 with the 5.8S rDNA (ITS), the small subunit (18S) region, translation elongation factor 1-α (TEF1-α), the RNA polymerase II second largest subunit (RPB2), and RNA polymerase II largest subunit (RPB1) respectively.

**MATERIAL AND METHODS**

**Morphology, sampling, DNA extraction, PCR amplification and sequencing**

Specimens studied are listed in Tables 1 and 2. For morphological study, we follow Cui et al. (2018) and the references therein. To verify the mycoperasitic features of the target species, routine samples (HKAS100826) for DNA extraction were separately taken both from the basidiome (five samples for basidiome labeled from C1 to C5) and the mycocecidium (six samples labeled from B1 to B6 as illustrated in Fig. 6). In addition, samples of other specimens were taken from different locations from their basidiomes and mycocecidia respectively, and then mixed for improving the success probability of DNA extraction in case of poor sample quality. Particularly, the volval remnant-like structure on the cap of the *Squamanita* specimen (HKAS74862A) was sampled. All Chinese collections are deposited in the Herbarium of Cryptogams of Kunming Institute of Botany, Chinese Academy of Sciences, China (HKAS).

The genus *Squamanita* was assigned on the basis of morphology to different families in the past, including *Squamanitaceae* and *Cystodermataceae*. Based on phylogenetic analysis of combined nuclear ribosomal RNA genes, Matheny and Griffith (2010) suggested that *Squamanita*, *Cystoderma*, and *Phaeolepiota* represent a monophyletic clade. In the subsequent molecular works by Matheny et al. (2015), Griffith et al. (2019) and Vizzini and et al. (2019), *Squamanita* and allied genera were referred as *Squamanitaceae*. Recently, *Squamanita*, *Cystoderma*, *Phaeolepiota*, *Floccularia*, and *Leucopholiota* were classified into *Squamanitaceae* ([http://www.agaric.us](http://www.agaric.us)) (Kalichman et al. 2020), but without a formal taxonomical treatment. In addition, the host species of *Squamanita* have been identified mainly based on morphological data and ecological evidence (Bas 1965; Mondiet et al. 2007), except for a few studies (Griffith et al. 2019; Matheny and Griffith 2010; Mondiet et al. 2007), which used molecular phylogenetic techniques to identify the hosts.

In the survey of macrofungi in China, we collected three species of *Squamanita* and two collections of *Amanita* sect. *Caesareae* and one collection of *A*. sect. *Validae* (Cui et al. 2018) with similar “mycoceidia” of two *Squamanita* species in the nearby localities respectively. To validate the taxonomical, phylogenetic and ecological traits, detailed morphological and anatomical studies and molecular phylogenetic analyses are carried out. To understand the species recorded in China, additional specimens collected in other parts of the world are examined and included in the present report.
| Taxon               | Specimen | Locality      | ITS       | LSU       | TEF1-α     | RPB2      | RPB1      | 18S       | PNS1/NS41 & NS51/NS8 |
|--------------------|----------|---------------|-----------|-----------|------------|-----------|-----------|-----------|----------------------|
| Agaricus bisporus  | H97      | –             | genome    | genome    | genome     | genome    | –         | genome    |                      |
| Agaricus campestris| LAPAG370 | Spain         | KM657927  | KP739803  | KR006636   | KT951556  | –         | –         |                      |
| Agrocybe praecox   | AFTOL-ID 728 | –         | AY818348  | AY646101  | DQ061276   | DQ385876  | –         | AY706956  |                      |
| Anícola luteolibrillosa | TU10320 | Estonia       | JN943976  | JN938776  | –          | –         | –         | JN939103  |                      |
| Amanita brunnescens| AFTOL-ID 673 | –         | AY780979  | AY631902  | AY881021   | AY780936  | –         | AY707096  |                      |
| Auritella foetida  | TENN: 063905 | India     | NR_119762 | GU062739  | MK426177   | GU062738  | –         | MK429332  |                      |
| Bolbitius vitellinus| AFTOL-ID 730 | –         | DQ200920  | AY691807  | DQ408148   | –         | –         | AY706955  |                      |
| Ceropemycetes crocodilinus | UTC258260 | USA     | JX409897  | JX968180  | JX968296   | JX968404  | –         | –         |                      |
| Chlorophyllum agaroides | AFTOL-ID 440 | –         | DQ200928  | AY700187  | DQ457631   | –         | –         | AY657010  |                      |
| Chlorophyllum molybdites | Z.W.Ge 3381 | USA     | MG741993  | MG742034  | MG742091   | MG742063  | –         | –         |                      |
| Oromyophylla muscicola | ARAN-Fungi 3210 | Spain     | MF623836  | MF623835  | MF948156   | MF623838  | –         | –         |                      |
| Conocybe lactea    | AFTOL-ID 1675 | –         | DQ486693  | DQ457660  | –         | –         | –         | DQ437683  |                      |
| Conocybe tenera    | NL-1615  | –             | JX968180  | JX968296  | JX968404   | –         | –         | –         |                      |
| Coprinellus micaceus| FP101781 | –             | genome    | genome    | genome     | genome    | –         | genome    |                      |
| Coprinus comatus   | AFTOL-ID 626 | –         | AY854066  | AY635772  | AY881026   | AY780934  | –         | AY665772  |                      |
| Cortinarius sodagnitus | AFTOL-ID 811 | –         | DQ083812  | AY684151  | DQ061275   | DQ083920  | –         | AY752975  |                      |
| Cortinarius violaceus | AFTOL-ID 814 | –         | DQ486695  | DQ457662  | –         | DQ470835  | –         | AY706950  |                      |
| Oreocephalidium cf. applanatus | AFTOL-ID 817 | –         | DQ202273  | AY380406  | DQ028581   | AY333311  | –         | AY706951  |                      |
| Cruentulum laeve   | AFTOL-ID 1334 | –         | DQ486696  | AF336246   | –         | DQ470836  | –         | AF026624  |                      |
| Cystoderma striatus | AFTOL-ID 1333 | –         | DQ486697  | AF336247   | GU187694   | DQ472711  | –         | AF026617  |                      |
| Cystoagaricus strobilomyces | E Nagasawa 9740 (TMI) | Japan   | AY176347  | AY176348   | –         | –         | –         | –         |                      |
| Cystoderma amianthinum | HKAS102638 | China   | MW258857  | MW258909   | –         | MW289802  | MW289812  | MW258936 & MW258887 |
| Cystoderma amianthinum | HKAS105568 | China   | MW258858  | MW258910   | –         | MW289813  | MW258917 & MW258888 |
| Cystoderma amianthinum | HKAS537757 | China   | MW258859  | MW258911   | MW324503   | MW289803  | MW289814  | MW258938 & MW258899 |
| Cystoderma amianthinum | HKAS107328 | China   | MW258860  | MW258912   | MW324504   | MW289805  | MW289815  | MW258939 & MW258890 |
| Cystoderma amianthinum | HKAS107326 | China   | MW258861  | MW258913   | –         | MW289804  | MW289816  | MW258940 & MW258891 |
| Cystoderma amianthinum | HKAS107327 | China   | MW258862  | MW258914   | MW324496   | MW289806  | MW289817  | MW258941 & MW258892 |
| Cystoderma amianthinum | TENN: 063549 | UK      | GU296098  | EF535265   | –         | –         | –         | GU296097  |                      |
| Cystoderma amianthinum | AFTOL-ID 1553 | –         | DQ192177  | DQ154108   | –         | –         | –         | DQ440632  |                      |
| Cystoderma superburn | HKAS107329 | China   | MW258863  | MW258915   | MW324497   | MW289818  | MW258942 & MW258893 |
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| Taxon                        | Specimen          | Locality       | ITS         | LSU          | TEF1-α       | RPB2        | RPB1        | 18S         |
|------------------------------|-------------------|----------------|-------------|--------------|--------------|-------------|-------------|-------------|
| **Cystoderma superbum**      | REG (Oct 1976)    | Germany        | AM946503    | AM946443     | –            | –           | –           | –           |
| **Cystodermella cinnabarina**| TAA147423         | Estonia        | AM946512    | AM946429     | –            | –           | –           | –           |
| **Cystodermella granulosa**  | TAA147491         | Estonia        | AM946518    | AM946431     | –            | –           | –           | –           |
| **Descolea tenuipes**        | TENNO63871        | Australia      | HQ832453    | HQ832466     | –            | –           | –HQ832443   | HQ832432    |
| **Descomyces sp. PDD 105133**| PDD 105133        | New Zealand    | KP191860    | KP191723     | MH594070     | –           | –           | –           |
| **Echinoderma asperum**      | HKAS 106783       | North Macedonia| MN810133    | MN810088     | MN820902     | MN820967    | –           | –           |
| **Flammula alnicola**        | AFTOL-ID 1501     | –              | DQ486703    | DQ457666     | GU187699     | DQ472714    | DQ113916    | –           |
| **Flammulaster sp. PBM 1871**| PBM 1871          | USA            | MG773817    | MT237465     | –            | –           | –           | –           |
| **Floccularia luteovirens**  | Y1                | China          | genome      | genome       | genome       | genome      | genome      | genome      |
| **Floccularia luteovirens**  | FLZJUC10          | China          | genome      | genome       | genome       | genome      | genome      | genome      |
| **Floccularia albolanaripes**| HKAS107739        | China          | MW258875    | MW258923     | MW324498     | MW289809    | MW258944    | MW258896    |
| **Floccularia albolanaripes**| HKAS107740        | China          | MW258876    | MW258924     | MW324499     | MW289810    | MW258945    | MW258897    |
| **Floccularia albolanaripes**| HKAS107741        | China          | MW258877    | MW258925     | MW324500     | MW289811    | MW258946    | MW258898    |
| **Galerina marginata**       | AFTOL-ID 465      | –              | DQ192182    | DQ457669     | –            | –           | –           | DQ440635    |
| **Galerina semilanceata**    | AFTOL-ID 1497     | –              | DQ486706    | AY038309     | AY337357     | –           | –           | DQ440639    |
| **Hebeloma mesophaeum**      | KRAMF57431        | Romania        | KT071038    | KT071100     | KT071077     | –           | –           | –           |
| **Hebeloma velutipes**       | AFTOL-ID 980      | –              | AY818351    | AY745703     | GU187707     | DQ472718    | –           | AY752972    |
| **Heinemannomyces splendidissimus** | E.C. Vellinga ecv3586 (UC) | Thailand | HM488760 | HM488769 | – | HM488793 | – | – |
| **Hypholoma fasciculare**    | AFTOL-ID 597      | –              | AY818349    | AY380409     | AY337413     | –           | –           | AY78215     |
| **Inocybe myriadophylla**    | AFTOL-ID 482      | –              | DQ221106    | DQ435791     | AY803751     | –           | –           | AY657016    |
| **Inocybe rimosoides**       | AFTOL-ID 520      | –              | DQ404391    | AY702014     | DQ435790     | DQ435884    | –           | AY752967    |
| **Inosperma calamistrata**   | PBMI105           | USA            | JQ801386    | JQ815409     | MK426203     | JQ464666    | –           | MK429958    |
| **Kuehneromyces rostratus**  | AFTOL-ID 1676     | –              | DQ400638    | DQ457684     | GU187712     | DQ472730    | –           | DQ457624    |
| **Laccaria laccata**         | GMM7605           | –              | JX504146    | KU685901     | KU686154     | KU686048    | –           | –           |
| **Laccaria ochropurpurea**   | AFTOL-ID 477      | –              | –           | AY700200     | DQ472731     | –           | –           | AY654886    |
| **Lacrymaria velutipes**     | AFTOL-ID 478      | –              | DQ400639    | AY700198     | DQ472733     | –           | –           | AY654885    |
| **Leptonia clypeolaria**     | HKAS87248         | China          | MN810123    | MN810080     | MN820932     | MN820941    | –           | –           |
| **Leucoagaricus rubrotinctus**| HKAS54317         | China          | JN944082    | JN940294     | JN93685     | JN94034    | –           | –           |
| **Leucoagaricus cepistipes** | xml2014128        | China          | LT716023    | KY418838     | KY419045     | KY418990    | –           | –           |
| **Leucocoprinus fragilissimus** | ZRL20151466      | China          | LT716029    | KY418844     | KY419049     | KY418994    | –           | KY418913    |
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| Taxon                     | Specimen     | Locality   | ITS     | LSU     | TEF1-α   | RPB2   | RPB1   | 18S     |
|---------------------------|--------------|------------|---------|---------|----------|--------|--------|---------|
| **Leucopholiota aff. decorosa** | AJ790        | USA        | –       | MK278297| –        | –      | –      | –       |
| **Leucopholiota decorosa**   | TENN068830   | USA        | KY777364| MF797662| –        | –      | –      | –       |
| Lycoperdon ericaeum     | ZRL20151498  | China      | LT716030| KY418845| KY418995 | –      | KY418914| –       |
| Lycoperdon perlatum      | KA13–0555    | China      | KP340193| KU764403| KU764393 | –      | –      | –       |
| Lycoperdon pyforme       | AFTOL-ID 480 | –          | –       | –       | –        | –      | –      | –       |
| Macropleiota dolichaula  | AFTOL-ID 481 | China      | DQ221111| DQ435785| DQ385886 | –      | –      | –       |
| Macropleiota procera     | HKAS8108     | China      | –       | JN940277| JN93697  | –      | –      | –       |
| Malloocybe terrigera     | JV 16431 (WTU)| –         | –       | –       | –        | –      | –      | –       |
| Micropsalliota globocystis| ZRL2013465   | –          | LT716024| KY418839| KY419046 | KY418991| –      | –       |
| Mycocalia denudata       | AFTOL-ID 2018| Canada     | DQ911596| DQ911597| –        | –      | –      | –       |
| Mythicomyces corneipes   | AFTOL-ID 972 | –          | DQ404393| AY745707| DQ409137 | DQ405110| –      | –       |
| Nematoloma longisporum   | AFTOL-ID 1893| –          | DQ40634 | DQ457681| –        | –      | –      | –       |
| Nidula niveotomentosa     | AFTOL-ID 1945| Canada     | DQ917654| DQ986295| –        | –      | –      | –       |
| Nidula sp.                | ZRL20151405  | China      | LT716028| KY418843| –        | –      | –      | –       |
| Nidularia falcata         | AFTOL-ID 1933| Sweden     | GU296100| EF535276| –        | –      | –      | –       |
| Nidularia falcata         | ZRL2015047   | –          | LT716025| KY418840| KY419047 | –      | –      | –       |
| Nidularia farcta          | ZT 9250      | India      | KX171343| EU604546| MK426212 | EU600094| –      | MK429965|
| Parasola conopila        | ZRL20151990  | China      | LT716064| KY418880| KY419025 | –      | –      | –       |
| Parasola conopilea       | TUB 011587   | –          | –       | DQ071706| –        | –      | –      | –       |
| Parasola plicatilis      | SZMC-NL-0295 | –          | FM163216| FM160693| FM897242 | –      | –      | –       |
| Phaeocollybia festiva    | AFTOL-ID 1489| –          | DQ494682| AY509119| AY509118 | –      | –      | –       |
| Phaeolepiota aurea        | HKAS93945    | China      | MW258864| MW258916| MW324501 | MW289807| –      | MW258943 & MW258894|
| Phaeolepiota aurea        | HKAS107738   | China      | MW258865| MW258917| MW324502 | MW289808| –      | – & MW258895|
| Phaeomarasmius proximans | AFTOL-ID 979 | –          | DQ404381| AY380410| DQ28592 | AY333314| –      | AY752970 |
| Phaeonematoloma myosotis  | SJ97002      | Sweden     | AF195599| AY586697| –        | –      | –      | –       |
| Pholiota lenta            | PB42333      | USA        | MN209743| MN251131| MN329707 | –      | –      | –       |
| Pholiota squarrosa        | AFTOL-ID 1627| –          | DQ494683| DQ470818| –        | –      | –      | –       |
| Pholiota sibirica         | AFTOL-ID 1488| –          | DQ494684| DQ470819| –        | –      | –      | –       |
| Phoathomyces leucocarpum  | PB40316      | New Zealand| HQ840659| HQ840660| HQ840662 | –      | –      | HQ840661|
| Phoathomyces luteolus     | ZRL20151400  | China      | LT716063| KY418879| KY419075 | KY419024| –      | KY418945|
| Phoathomyces panaeoloides | SZMC-NL-2537 | –          | FM87022 | FM876279| –        | –      | –      | –       |
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| Taxon                                      | Specimen Locality | ITS  | LSU  | TEF1-α | RPB2 | RPB1 |
|--------------------------------------------|-------------------|------|------|--------|------|------|
| Patrinella speciosa                        | EU-2180           | –    | –    | –      | –    | –    |
| Paripodium eurytrichum                     | –                 | –    | –    | –      | –    | –    |
| Psathyrella spadicea                       | AFTOL-ID 1628     | –    | DQ494690 | DQ470822 | –    | –    |
| Psathyrella spadicea                       | SZMC-NL-3996      | –    | FN396132 | FN396180 | FN396132 | –    |
| Pseudolepiota zangmui                      | Z.W.Ge 2175       | –    | –    | –      | –    | –    |
| Pseudosperma rimosum                      | PBM3901 USA       | –    | JQ495234 | JQ495283 | JQ495342 | –    |
| Psilocybe montana                          | AFTOL-ID 820      | –    | DQ494692 | DQ470823 | –    | –    |
| Psilocybe subaeruginosa                    | PBM3218 Australia | –    | –    | –      | –    | –    |
| Ripartitella brasiliensis                  | –                 | –    | –    | –      | –    | –    |
| Simocybe serrulata                         | –                 | –    | –    | –      | –    | –    |
| Squamanita fimbriata                       | –                 | –    | –    | –      | –    | –    |
| Squamanita mira                            | –                 | –    | –    | –      | –    | –    |
| Squamanita mira (holotype)                 | –                 | –    | –    | –      | –    | –    |
| Squamanita odorata                         | O-F-310485 Norway | –    | –    | –      | –    | –    |
| Squamanita odorata                         | O-F-146740 Norway | –    | –    | –      | –    | –    |
| Squamanita odorata                         | O-F-146740 Norway | –    | –    | –      | –    | –    |
| Squamanita odorata                         | E:204926 Scotland | –    | –    | –      | –    | –    |
| Squamanita odorata                         | E:282464p Wales   | –    | –    | –      | –    | –    |
| Squamanita odorata                         | R.E.Halling 7691 | –    | –    | –      | –    | –    |
| Squamanita paradoxa                        | –                 | –    | –    | –      | –    | –    |
| Squamanita paradoxa                        | –                 | –    | –    | –      | –    | –    |
| Squamanita pearsonii                       | –                 | –    | –    | –      | –    | –    |
| Squamanita pseudofimbriata                 | –                 | –    | –    | –      | –    | –    |
| Squamanita schreieri (epitype)             | ZT Myc 2158 North Carolina, USA | –    | –    | –      | –    | –    |
| Squamanita sororcula (holotype)            | –                 | –    | –    | –      | –    | –    |
| Squamanita umbonata                        | –                 | –    | –    | –      | –    | –    |
| Squamanita umbonata                        | –                 | –    | –    | –      | –    | –    |
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| Taxon                     | Specimen | Locality        | ITS     | LSU      | TEF1-α   | RPB2     | RPB1     | 18S       | PNS1/NS41 & NS51/NS8 |
|---------------------------|----------|-----------------|---------|----------|----------|----------|----------|----------|---------------------|
| "Squamanita umbonata"    | H.E.Bigelow17431(NY2776224) | Massachusetts, USA | MW258854 | MW258906 | –        | –        | –        | MW258933 & MW258884 |
| "Squamanita umbonata"    | CBAS3808 (NY1840398)       | Massachusetts, USA | MW258855 | MW258907 | –        | –        | –        | MW258934 & MW258885 |
| "Squamanita umbonata"    | HKAS107325A                | Liguria, Italy    | MW258856 | MW258908 | MW324508 | –        | –        | MW258935 & MW258886 |
| Stagnicola perplexa      | ALV17086                | Denmark           | MK351604 | MK353788 | –        | MK359087 | –        | MK353797 |
| Stropharia ambigua       | AFTOL-ID 726             | –                 | AY818350 | AY646102 | GU187756 | DQ484054 | –        | DQ092924 |
| Tubaria confragosa       | AFTOL-ID 498             | –                 | DQ267126 | AY700190 | –        | DQ408113 | –        | AY665776 |
| Tubaromyces sp.           | BB6018                 | Zambia             | MK421965 | EU600887 | MK426220 | EU600886 | –        | MK429974 |
| Tulostoma calcareum      | GB MJ6965               | Sweden             | NR_164015 | KUS19086 | KU843881 | –        | –        | –        |
| Verrucospora flavofusca   | AFTOL-ID 655            | China              | DQ241779 | DQ470825 | –        | –        | –        | AY66783  |
Table 2  Specimens used to identify the mycocecidia of new species of *Squamanita* in this study are listed with their Herbarium ID and accession numbers. Newly generated sequences are highlighted in boldface.

| Taxon                      | Specimen   | Locality | ITS       | LSU         | TEF1-α     |
|----------------------------|------------|----------|-----------|-------------|------------|
| *Amanita aff. excelsa*     | HKAS107325B | Italy    | MW258872  | MW258873    |            |
| *A. aff. hemibapha*        | TRTC161164  | Viet Nam | –         | KF877244    | KF877133   |
| *A. aff. hemibapha*        | TRTC161171  | Viet Nam | –         | KF877245    | KF877134   |
| *A. aff. hemibapha*        | BPI HPUB 560 | India    | –         | KF877234    | KF877125   |
| *A. aff. javanica*         | HKAS56957   | China    | JX998039  | JX998068    | JX998017   |
| *A. aff. javanica*         | HKAS56863   | China    | JX998040  | JX998071    | JX998014   |
| *A. aff. javanica*         | HKAS3281    | China    | JX998041  | JX998070    | JX998016   |
| *A. aff. sepiacea* sp. 1   | HKAS107306B | China    | MW258871  | –           | MW324505   |
| *A. aff. sepiacea* sp. 2   | HKAS74862   | China    | MW258869  | –           | –          |
| *A. aff. sepiacea* sp. 2   | HKAS74862B  | China    | MW258870  | –           | –          |
| *A. arkanseana*            | RET-354-9   | USA      | JX844674  | KF877197    | KP724414   |
| *A. brunneolimbuta*        | HKAS78459   | China    | MH508274  | –           | –          |
| *A. brunneolimbuta*        | HKAS101392  | China    | MH508272  | –           | –          |
| *A. brunneolimbuta*        | HKAS78460   | China    | MH508275  | –           | –          |
| *A. caesarea*              | RET-4271-1  | Italy    | JX844685  | KF877207    | KF877106   |
| *A. caesariae*             | RET-356-10  | China    | –         | KF877209    | KF877107   |
| *A. cinnamomescens* (isotype) | RET-290-5  | Pakistan | JX844699  | KF877221    | KF877114   |
| *A. citrina*               | HKAS53467   | Germany  | MH508312  | –           | –          |
| *A. cochiseana* nom. prov. | RET-498-1   | USA      | JX844705  | KF877226    | KP724516   |
| *A. fritillaria*           | HKAS100521  | China    | MH508360  | –           | –          |
| *A. fritillaria*           | HKAS100520  | China    | MH508359  | –           | –          |
| *A. garabitoana* (paratype) | RET-333-6   | Costa Rica | JX844711 | KF877231    | KF877122   |
| *A. hemibapha*             | RE-342-8    | India    | JX844716  | KF877233    | KF877124   |
| *A. jacksonii*             | RET-393-7   | USA      | JX844724  | KF877252    | KP724554   |
| *A. javanica*              | S-170       | Japan    | LC056770  | LC056748    | –          |
| *A. javanica*              | S-329       | Japan    | LC056772  | –           | LC164656   |
| *A. javanica*              | S-76        | Japan    | AB750726  | LC164662    | LC164654   |
| *A. kitamagotake*          | HKAS100824  | China    | MW258866  | MW258918    | MW324492   |
| *A. kitamagotake*          | HKAS100825  | China    | MW258867  | MW258919    | MW324493   |
| *A. kitamagotake*          | HKAS107309B | China    | MW258874  | MW258921    | MW324495   |
| *A. kitamagotake*          | HKAS100826B | China    | MW258868  | MW258920    | MW324494   |
| *A. kitamagotake* (ex-holotype) | EN-4       | Japan    | AB721450  | AB721450    | LC164658   |
| *A. porphyria*             | HKAS92088   | China    | MH508506  | –           | –          |
| *A. porphyria*             | MB-100156   | Germany  | MH508507  | –           | –          |
| *A. rubromarginata* (isotype) | RET-383-1   | Japan    | JX844739  | KF877229    | KF877164   |
| *A. sepiacea*              | HKAS80090    | China    | MH508589  | –           | –          |
| *A. sepiacea*              | HKAS79669   | China    | MH508588  | –           | –          |
| *A. sepiacea*              | HKAS74750   | China    | MH508587  | –           | –          |
| *A. sepiacea*              | HKAS70045   | China    | MH508586  | –           | –          |
| *A. sepiacea*              | HKAS68614   | China    | MH508585  | –           | –          |
| *A. sepiacea*              | HKAS56799   | China    | MH508584  | –           | –          |
| *A. sepiacea*              | HKAS100604  | China    | MH508582  | –           | –          |
| *A. sinocitrina*           | HKAS100530  | China    | MH508598  | –           | –          |
and then cloned using pClone007 simple vector kit (Tsingke, Beijing). For the recently collected specimen (HKAS100826) and the volval remnants like structure on the cap of a Squamanita specimen (HKAS74862A), 10 clones of each ITS and nrLSU PCR products of each sampling point were randomly selected from a 90 mm petri dish for sequencing with primer pair M13–47/M13–48 to investigate the mycelium distribution of hosts and parasitising fungi. The cloning, PCR amplification and sequencing followed the protocols described by Cai et al. (2016) and Cui et al. (2018).

Results of sequencing

For specimen of HKAS100826, the ITS and nrLSU sequences were successfully amplified from all eleven sampling points (C1–C5, B1–B6). Among them, there are two bands occurring in gel electrophoresis diagram of each of the PCR products of ITS from six sampling points of mycocecidium (B1, B2, B3, B4, B5, B6), see Fig. 1. By cloning and sequencing all of the purified PCR products of ITS and nrLSU, a total of 50 ITS and 50 nrLSU sequences were generated from all points (C1–C5). After alignment and comparison, all of them belong to the same species, namely the mycoparasitic species itself. For the mycocecidium, each band of PCR productions with two bands were excised from gel respectively, and then purified and sequenced, generating a total of 120 ITS and 60 nrLSU sequences from sampling points B1–B6. After analysis, two types of mushroom sequences were detected for each DNA locus. Statistically, 50% ITS, 90% nrLSU matched to the potential mycoparasitic species and 50% ITS, 10% nrLSU belong to the potential host species. For the volval remnants on the cap of the Squamanita specimen (HKAS74862A), 60% ITS, 90% nrLSU were the potential mycoparasitic species and 20% ITS, 0% nrLSU were assigned to the potential host species, others are Trichoderma hirsutum or vector sequences.

For the other specimens of Squamanita and nearby Amanita, all sequences were amplified then directly sequenced or obtained by cloning from PCR products. One hundred forty-five sequences have been submitted to GenBank and used for phylogenetic analyses (Tables 1 and 2). The sequences of the two potential species of hosts are the same as those of the coexisting Amanita species respectively, and were finally identified to belong to A. kitamagotake (Fig. 4) and the A. sepiacea complex (Fig. 5). The potential mycoparasitic species are clustered into the genus Squamanita (Figs. 2 and 3).

DNA sequence alignment

Sequences used in study are listed in Tables 1 and 2 with their Herbarium ID and accession numbers. Four

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**Table 2** Specimens used to identify the mycocecidia of new species of Squamanita in this study are listed with their Herbarium ID and accession numbers. Newly generated sequences are highlighted in boldface

| Taxon Specimen | Locality | ITS | LSU | TEF1-α |
|----------------|----------|-----|-----|--------|
| A. sinocitrina HKAS83445 | China | MH508601 | – | – |
| A. sinocitrina HKAS100531 | China | MH508599 | – | – |
| A. vernicoccora (paratype) 7020 | USA | GQ250401 | GQ250416 | – |

**Fig. 1** Gel electrophoresis diagram of the PCR products amplified from 11 sampling points on the basidiome (C1–C5) and mycocecidium (B1, B2, B3, B4, B5, B6) of Squamanita mira (HKAS100826, holotype), as indicated on Fig. 6. I and L indicate ITS and LSU (nrLSU), respectively.
datasets, namely 18S-5.8S-nrLSU-RPB2-TEF1-α, 18S-ITS-nrLSU-RPB2-TEF1-α, ITS-nrLSU-TEF1-α, and ITS were used in our study to reinvestigate the phylogeny of Squamanitaceae, identify the phylogenetic position of the basidiomes and mycocecidia of the mycoparasitic species. From the first dataset to the last, a total of 4100, 4743, 1878 and 693 characters were used in the phylogenetic analyses, respectively. Moreover, two phylogenetic trees which only use ITS and nrLSU sequences were used to investigate the phylogeny of Squamanitaceae are provided as additional files (Additional files 1 and 2), respectively. The final alignments have been submitted to
Fig. 3 Maximum-Likelihood (ML) phylogenetic tree of Squamanita inferred from the 18S-ITS-nrLSU-RPB2-TEF1-α dataset, with SH-aLRT (left), ultrafast bootstrap (UFB) (middle), and PPs values (right) near by the corresponding node. Only one of SH-aLRT > 80 or UFB > 95 for ML and PPs > 0.90 for BI are indicated along branches (SH-aLRT/UFB/PP). Cystidium present or absent, and the shape and taxon of mycocecidia of counterpart Squamanita species are shown. New species Squamanita mira, S. orientalis, S. sororcula are highlighted in boldface.

| Host | Cystidium | Mycocecidia | Shape | Taxon |
|------|-----------|------------|-------|-------|
| A. = Amanita | present | A. aff. excelsa | A. sect. Validae |
| C. = Cystoderma | present | A. aff. replecua sp. 2 | A. sect. Validae |
| H. = Hebeloma | present | A. strabiliomedor or A. echmochondra (A. sect. Echmochondra) | |
| K. = Kuehneromyces | present | A. kitamagotake (A. sect. Caisaerue) | |
| A. = Amanita | absent | A. kitamagotake (A. sect. Caisaerue) | |
| C. = Cystoderma | absent | A. aff. excelsa | A. sect. Validae |
| H. = Hebeloma | absent | A. strabiliomedor or A. echmochondra (A. sect. Echmochondra) | |
| K. = Kuehneromyces | absent | A. aff. replecua sp. 2 | A. sect. Validae |

For each dataset, the sequences were aligned using MAFFT v6.8 (Katoh et al. 2005), manually edited with BioEdit v7.0.9 (Hall 1999) and concatenated with Phyutility v2.2.1 (Smith and Dunn 2008). Unsampled gene regions were coded as missing data. In the concatenated datasets, all introns of RPB2 and TEF1-α were excluded because of the difficulty in alignment. Maximum likelihood (ML) analyses were performed using IQ-TREE 1.6 (Trifinopoulos et al. 2016). Bayesian Inference (BI) analyses were used to analyze the datasets with MrBayes v3.1.6 (Ronquist et al. 2012). The optimal substitution models for each dataset were determined by using the Akaike Information Criterion (AIC) implemented in MrModeltest v2.4 (Nylander 2004), with 18S, 5.8S/ITS and nrLSU treated as a single block. In ML analyses, the substitution model options for four datasets were auto evaluated after provided partition file by using IQ-TREE 1.6 (http://iqtree.cibiv.univie.ac.at/), clade support for the ML analyses was assessed using an SH-aLRT test with 1000 replicates (Guindon et al. 2010) and 100 replicates of the ultrafast bootstrap (UFB) (Hoang et al. 2018). In the ML analyses, nodes with support values of both SH-aLRT ≥80 and UFB ≥95 were considered well supported, nodes with one of SH-aLRT ≥80 or UFB ≥95 were weakly supported, and nodes with both SH-aLRT <80 and UFB <95 were unsupported, and the other parameters use the default settings. For BI analyses, the selected models for four datasets were 18S–5.8S-nrLSU(GTR + I + G)-RPB2(GTR + I + G)-TEF1-α(GTR + I + G), 18S-ITS-nrLSU(GTR + I + G)-RBP2(SYM + I)-TEF1-α(SYM + I + G), ITS(SYM + G)-nrLSU(HKY + I)-TEF1-α(SYM + G), and ITS (GTR + G) respectively. Bayesian analyses used the selected models and four chains were run simultaneously for 2 million generations with trees sampled every 100 generations. The sampling of the posterior distribution was considered to be adequate when the average standard deviation of split frequencies was lower than 0.01. Chain convergence was
determined by checking the effective sampling size (ESS > 200) in Tracer v. 1.5 (Rambaut and Drummond 2009). Nodes with Bayesian posterior probability (PP) > 0.90 were considered well supported. Subsequently, trees are summarized and posterior probabilities were obtained by using the sumt and sump command implemented in MrBayes by discarding the first 25% generations as burn-ins.

RESULTS
For the four datasets, topologies of the phylogenetic trees generated from ML and BI analyses are nearly identical with minimal variation in statistical support values, and thus only the trees inferred from the ML analyses are displayed. The tree generated from the 18S–5.8S-nrLSU-RPB2-TEF1-α dataset reveals that *Squamanita*, *Cystoderma*, *Phaeolepiota*, *Floccularia*, and *Leucopholiota* form a monophyletic clade with weakly statistical support in ML analysis but with strong statistical support in BI analysis (SH-aLRT/UFB/PP = 98.4/100/0.99), *Squamanita* and *Leucopholiota* are sister groups of *Floccularia* (SH-aLRT/UFB/PP = 99.9/100/0.99), *Phaeolepiota* nested within *Cystoderma* (SH-aLRT/UFB/PP = 99.9/100/0.99), and *Squamanita* is a monophyletic group with strong statistical support in both of ML and BI analyses (SH-aLRT/UFB/PP = 99.3/100/1) (Fig. 2). Taking the study of Matheny and Griffith (2010) and Kalichman et al. (2020) into consideration, the family *Squamanitaceae* is formally emended to accommodate the above-mentioned five genera. Besides, both trees generated from 18S–5.8S-nrLSU-RPB2-TEF1-α and 18S-ITS-nrLSU-RPB2-TEF1-α datasets reveal that the three potential *Squamanita* species from China are novel (Figs. 2 and 3). They are described below as *S. mira*, *S. orientalis* and *S. sororcula*, respectively. The tree generated from the 18S-ITS-nrLSU-RPB2-TEF1-α dataset also shows that several “*S. umbonata*” from North America, Europe and East Asia harbor a complex of species, with six subclades in the phylogenetic tree (Fig. 3), and one “*S. umbonata*” from Central America harbors a monophyletic clade with a sequence from North Carolina, USA (Fig. 3). The trees generated from ITS-nrLSU-TEF1-α and ITS datasets reveal that the host of *S. mira* is *A. kitamagotake* (Fig. 4), and those of *S. orientalis* and *S. sororcula* are species of the *A. sepiacea* complex (Fig. 5).

TAXONOMY

*Squamanitaceae* Jülich, *Bibliothca Mycol.* 85: 390 (1981).

Type: *Squamanita* Imbach, *Mitt. Naturf. Ges. Luzern* 15: 81 (1946).

Synonym: *Cystodermataceae* Locq., *Mycol. gén. struct.*: 108 (1984); nom. inval. (Art. 36.1, lacking a Latin diagnosis or reference to a previously published Latin diagnosis).

Emended description: Basidiome lepiotoid to tricholomatoid, small to medium-sized, with pileus and central stipe; lamellae adnexed to adnate, or with decurrent tooth, never free. *Stipe* with or without annulus. *Mycocecidia* subglobose or subcylindrical to clavate fusiform. *Stipe* and pileus often with a floccose layer composed of loose sphaerocysts. *Hyphal system* monomitic. *Hyphae* cylindrical or slightly inflated, thin-walled, smooth, with clamps. *Cystidia* absent or present; if present, thin- to slightly thick-walled, smooth. *Basidia* narrowly clavate, 4-spored. *Basidiospores* subglobose to ellipsoid or subreniform, rarely angular, thin- to slightly thick-walled, colorless, yellowish or brownish mostly smooth, in some taxa finely verrucose to finely echinulate, without germ pore, amyloid or inamyloid, not or slightly dextrinoid. *Conidia* present or absent, if present, globose, subglobose, ovoid, irregularly clavate, cylindrical, ellipsoid, broadly fusiform or fusiform, 7–16 (–19) × 4–7.5 (–12.5) μm, with clamps when young, later more or less bifid at base, colourless to pale brownish yellow, smooth or ornamented, with thickened wall, development of conidia basifugal. *Conidiospores* colourless, septate when young, thin walled, densely branching, 4–6 μm wide, with clamps, the older conidia-bearing branches non-septate, sickle-shaped. *Chlamydospores* present or absent, if present, obovoid, clavate, rarely ventricose-fusiform, rectangular to variously shaped, inamyloid, colorless to yellowish, thick-walled.

Substrate: On soil, wood or parasitizing agarics.

Genera included: *Squamanita*, *Cystoderma*, *Phaeolepiota*, *Leucopholiota*, and *Floccularia*.

Notes: Here we fix the application of the generic name *Squamanita* by lecto- and epitypifying the type species of the genus, *S. schreieri*, and describe the new species discovered in this study.

*Squamanita schreieri* Imbach, *Mitt. Naturf. Ges. Luzern* 15: 81 (1946).

Type: Imbach, *Mitt. Naturf. Ges. Luzern* 15: 80 [un-numbered plate] (1946) –lectotype designated here (MBT 394854). Germany: Baden-Württemberg, Tauber-giessen Nature Reserve, Alluvial forest, close to a *Populus* tree, 10 Oct 1991, Leg. M. Wilhelm (no. 295) ZT Myc 2158 – epitype designated here (MBT 394983).

Notes: The original description cited the following collections: “Schreier, 17 Jul. 1935; Schreier, 4 Aug. 1936; Schreier, 8 Aug. 1937; Arndt, 11 Jul. 1942; Haller, 17 Oct. 1943; Furrer, Schlaper & Imbach, 18 Jul. 1944; Rohl-Wütherich, Aarau & Imbach, 31 Jul. 1945”. None of these original collections could be located in G, and the only remaining original material is the illustration provided by Imbach which is therefore designated as lectotype here. As a specimen is essential to fix the application of the name, we designate as an epitype a modern collection in Eidgenössische Technische Hochschule Zürich which fits the original diagnosis and plate.
**Squamanita mira** J. W. Liu & Zhu L. Yang, sp. nov.  
— Fungal Names FN570781;  
MycoBank 836,584. (Figs. 6 and 7).

**Etymology:** — *mirus* (Lat.), wonderful or extraordinary, referring to the wonderful basidiome.

**Diagnosis:** *S. mira* differs from other species of the genus by the mycoecidia which have a limbate volva-like structure and the absence of cystidia.

**Type:** China: Yunnan Province: Ailaoshan Natural Reserve, Chuxiong, Nanhua, in the forests dominated by...
**Description:** Pileus ca. 40 mm diam, subconical to convex, distinctly umboate; surface dry, yellowish brown (6C6–7) or honey-yellow (6A8), or viscid if moist, covered with dark orange (6A8), yellow-tawny (6B7–8) or honey yellow (6C6–8), repent, fibrillose squamules; margin incurved, strongly appendiculate, irregularly and densely corniform and fibriiform squamules derived from breaking up of the veil, and slightly paler than the pileus surface. Lamellae adnexed to adnate, moderately crowded, narrow; edge irregularly serrate-dentate or subundulate. Stipe 43–46 × 12–24 mm, subcylindrical, densely covered with brown (6A7–8), tawny yellow (6B7–8) to yellowish brown (5A6–7), appressed or recurved fibrillose and villiform squamules, at the upper part of the stipe covered with fluffy and villose, brown (5A6–8), tawny yellow (6B7–8) to yellowish brown (6C6–7) appressed or erect, fibrillose or obliquely lacerate scales arranged in irregular rings, 4–6 mm from apex, extreme apex off-white (1A1–2) and subglabrous. Mycocecidia subglobose to napiform, 40–46 × 5–16 mm, nearly smooth, whitish (1A1) or locally yellow (6A4–5) on external surface; Volval limb arising from margin of mycocecidia, 6–20 mm tall; context of pileus and stipe

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![Maximum-Likelihood (ML) phylogenetic tree inferred from the ITS dataset for detecting the phylogenetic relationships of the mycocecidia (hosts) of Squamanita orientalis, S. sororcula and one specimen (HKAS74861) of Amanita sepiacea that was collected nearby S. orientalis (these three specimens are highlighted in boldface), with SH-aLRT (left), ultrafast bootstrap (UFB) (middle), and PPs values (right) near by the corresponding node. Only one of SH-aLRT > 80 or UFB > 95 for ML and PPs > 0.90 for BI are indicated along branches (SH-aLRT/UFB/PP).](image-url)
white (1A1), with a strong aromatic smell, like that of Tricholoma matsutake; context of mycocecidia white, unchanging on exposure, odour not distinctive.

**Basidiospores** [60/1/1] (5.5–7) × 4–5 (6) μm, (Q = (1.16) 1.33–1.75 (−1.8), Qm = 1.53 ± 0.13), ellipsoid or subreniform, colorless, hyaline, smooth, inamyloid.

**Basidia** 22–65 × 9–12 μm, fusiform to ventricose-fusiform, hyaline; sterigmata 4–5 μm long; **Cystidia** absent. **Subhymenium** 10–20 μm thick, composed of 4–7 μm wide filamentous hyphal segments. **Lamellar trama** regular, composed of colorless, thin-walled hyphae 4–17 μm diam, branching, sometimes anastomosing. **Pileipellis** a cutis with transition to a trichoderm at regular intervals, composed of loosely and more or less radially arranged, thin-walled hyphae 90–200 (−370) × 5–20 μm, and upper part of pileipellis often with fine brownish granular incrustations and yellowish to brownish filamentous hyphae, constricted at septa; **Mycocecidia** composed of abundant ovoid to subglobose inflated cells, and filamentous hyphae similar to those on the pileus, clamp connections present; chlamydospores not observed.

**Ecology:** Parasitic on *Amanita kitamagotake* (HKAS100826B, GenBank Acc. nos.: ITS = MW258868, nrLSU = MW258920, TEF1-α = MW324494; HKAS107309B, GenBank Acc. nos.: ITS = MW258874, nrLSU = MW258921, TEF1-α = MW324495) growing on soil under trees of Fagaceae and Pinaceae.

**Distribution:** Currently known from Jiangxi and Yunnan Province, central and Southwest China.

**Notes:** In this study, molecular evidence confirms that the hosts of *S. mira* as well as two collections of *Amanita* in the nearby area, within 2 km of *S. mira*, are *A. kitamagotake* (Figs. 4, 6).
Morphologically, *S. mira* highly resembles the informally published "*S. tropica*" (nom. Prov.) (Bas 1965), because both are parasitic on basidiomes of *Amanita* and form a volva-like structure at the base of the stipe. Furthermore, they share abundant tawny squamules on the pileus surface, serrate-dentate or subundulate lamellae edges, irregular ring analogues on the upper part of the stipe and ellipsoid to subreniform basidiospores. However, *S. mira* differs from *S. tropica* in its subconical to convex pileus with a distinct umbo. The material of *S. tropica* is lost (Bas 1965).

*Squamanita mira* is also more or less similar to *S. schreieri* and the specimens under the two species complexes of "*S. umbonata*" from all over the world in some morphological features. However, *S. mira* can be distinguished from the aforementioned taxa by its mycocecidia with a limbate volva-like structure and absence of cystidia. Phylogenetically, they are grouped, however, in different clades (Figs. 2 and 3).

Additional specimens examined: **China**: Jiangxi Province: Jian, Jinggangshan City, Jinggangshan scenic spots, 800–900 m elev. 19 July. 2019, Chunlei Pan JGS001 (HKAS107309A, GenBank Acc. nos.: 18S = MW258892 & MW258879, ITS = MW258848, nrLSU = MW258900, TEF1-α = MW324491, RPB2 = MW289799).

Fig. 8 **a–b** Basidiomes of *Squamanita orientalis* (HKAS74862A, holotype). Photos by Gang Wu. Bars: 10 mm. A lump of clay is attached on the center of pileus, and the apical part of volval remnants on mycocecidiium can be observed between clay and pileus under anatomical lens. **c** Basidiome of *Amanita sepiacea* (HKAS74861). Photos by Gang Wu. Bars: 50 mm

**Squamanita orientalis** J. W. Liu & Zhu L. Yang, sp. nov. — Fungal Names FN570782; MycoBank 836585. (Figs. 8, 9 and 10).

**Etymology:** — *orientalis* (Lat.): from the East.

**Diagnosis:** *S. orientalis* differs from other species by its irregular fibrillose annular zone on the upper part of the stipe and ciliate squamules on the pileal margin, and subglobose mycocecidia. Phylogenetically, they are grouped, however, in different clades (Figs. 2 and 3).

**Type:** China: Yunnan Province: Laowopo dunk, Chongren, Nujiang, 1700–1800 m elev., in forest dominated by *Fagaceae* and *Rhododendron*, 7 Aug. 2011, Gang Wu 548 (HKAS74862A – holotype; GenBank Acc. nos.: 18S = MW258890 & MW258881, ITS = MW258851, nrLSU = MW258903, TEF1-α = MW324509, RPB2 = MW289799).
extreme apex white (1A1) and nearly smooth, the part below the ring is covered with orange (6A6–7), tawny yellow (6C7) or yellowish brown (6D7–8) appressed or erect, obliquely lacerate scales. *Mycocecidium* subglobose 35 × 20–30 mm, nearly smooth, and whitish or grey spots on external surface. The transitional zone between stem and mycocecidium with some irregular rings of tawny-ochraceous (6B7–8) or dingy brown (6E5) color, fibrillose, appressed, or with erect, obliquely upward-pointing scales or lacerate scales.

**Basidiospores** [50/1/1] (5–) 5.5–6 (– 6.5) × 4–5 (– 6) μm [Q = (1.2–) 1.5–1.65, Q = 1.43 ± 0.10], broadly ellipsoid, ellipsoid to elongate, sometimes subreniform in side view. **Basidia** 20–35 × 5–10 μm, subclavate, 4-spored, fusiform to ventricose-fusiform, hyaline; sterigmata 3–4 μm long; basal septa often with clamps. **Cystidia** numerous, 90–105 × 17–27 μm, fusiform to ventricose-fusiform, with obtuse to acute apex, upper part slightly to moderately thick-walled (up to 1 μm diam.), sometimes with refractive incrustations, hyaline. **Lamellar trama** regular, composed of colorless, thin-walled hyphae 4–15 μm diam, branching, sometimes anastomosing; clamps present and common. **Subhymenium** 10–15 μm thick, composed of 4–6 μm wide filamentous hyphal segments; **volval remnants** of host on pileus composed of ± irregularly arranged elements: inflated cells very abundant (to locally dominant), subglobose (30–50 × 30–50 μm) or ovoid to broadly clavate (30–60 × 20–30 μm), solitary and terminal, or in chains of 2–3 and then terminal, inflated cells sometimes external upset (up to 1 μm thick), usually colorless and hyaline, occasionally with brownish vacular pigments, and the majority of hyphae without clamp connection; inner part of volval remnants near pileus surface composed of ± irregularly arranged elements: inflated cells usually brownish to fawn colored, two types of filamentous hyphae in the tissues: either with filamentous hyphae usually colorless and hyaline, 2–6 μm wide, without clamp connection; or with hyphae similar to lotus root, 60–150 × 4–15 μm, swollen in the middle but constricted at septa, with clamp connection. **Mycocecidium** composed of abundant ovoid to subglobose inflated cells (45–110 × 24–65 μm) and filamentous hyphae colorless and hyaline, 2–6 μm wide, with clamp connections similar to those on the pileus; chlamydospores not observed.

**Ecology:** Parasitic on *Amanita sepiacea* (HKAS74862B, GenBank Acc. nos.: ITS = MW258870) growing on soil under trees of *Fagaceae* and *Rhododendron*.

**Distribution:** Currently known from Yunnan Province, Southwest China.

**Notes:** Our morphological data and molecular phylogenetic evidences confirm that the host of *S. orientalis* and the collection of *Amanita* in the nearby area within two kilometers’ range of *S. orientalis* are *A. sepiacea* (Figs. 5, 8, 10). Interestingly, some volval remnants of *A. sepiacea* are found on the center of the pileal surface of...
Fig. 10 Microscopic features of volval remnants on the pileus of *Amanita sepiacea* (HKAS32519) and *Squamanita orientalis* (HKAS74862A, holotype). **a** the upper part of a volval remnant on the pileus of *A. sepiacea*. **b** the lower part of a volval remnant on the pileus of *A. sepiacea*. Drawings by Zhuliang Yang (2005). **c** Upper layer of a volval remnant on the pileus of *S. orientalis*. **d** Inner layer of a volval remnant on the pileus of *S. orientalis*. Drawings by Jianwei Liu. Bars = 20 μm. Cells with vacuolar pigment and vascular hyphae are dotted and shaded respectively. Hyphae with clamps belong to *S. orientalis*.

Fig. 11 **a-b** Basidiomes of *Squamanita sororcula* (HKAS107306A, holotype). Photos by Fa Li. Bars: 20 mm.
S. orientalis (Fig. 8), and its anatomical features are those of A. sepiacea (Yang 2005) (Fig. 10), and the filamentous hyphae with clamp connection belong to S. orientalis (Fig. 10).

Squamanita orientalis is similar to S. schreieri. However, the latter species has no cystidia. Furthermore, the former is a parasite on A. sepiacea, while S. schreieri is possibly associated with A. strobiliformis or A. echinocephala (Bas 1965).

Squamanita orientalis is also similar to S. sororcula and S. umbonata. However, S. orientalis differs from S. sororcula by its irregular fibrillose annular zone on the upper part of the stipe and ciliate squamules on the pileal margin, and larger cystidia (90–105 × 17–27 μm). In addition, there are ca. 50 and ca. 40 base differences in ITS and nrLSU regions between the two species respectively, and even though their hosts are identified as A. sepiacea for both species, there are ca. 25 different bases in the ITS region from host material. Squamanita umbonata differs from S. orientalis by its umbonate pileus, and narrower cystidia (60–95 × 9–20 μm), cylindrical to clavate fusiform mycrocecidia.

Squamanita sororcula J. W. Liu & Zhu L. Yang, sp. nov. — Fungal Names FN570782; MycoBank 836586. (Figs. 11 and 12).

Etymology: — sororcula (Lat.): little sister, indicating a close relation with S. orientalis.

Diagnosis: S. sororcula differs from other species by without irregular fibrillose annular zone on the upper part of the stipe, with subglobose mycrocecidia.

Type: China: Yunnan Province: Laojun Mountain, Jinchuan City, Dali, 26°38'51.792"N, 99°49'10.43E, 2756 m elev., in a forest dominated by plants of Pinus yunnanensis, 10 Aug. 2019, Fa Li 237 (HKAS107306A – holotype; GenBank Acc. nos.: 18S = MW258929, ITS = MW258850, nrLSU = MW258902, TEF1-α = MW324507).

Description: Pileus medium-sized, ca. 45 mm diam, at first globose, then hemispheric, plano-convex with slightly incurved margin, thick-fleshed; surface buff (6B7–8), viscid when wet, covered with buff (6B7–8) floccose-fibrillose or slightly fibrillose squamules; pileal margin strongly appendiculate, with irregularly and densely corniform and fibrillose squamules derived from breaking up of the veil. Lamellae white (1A1), adnexed to adnate, moderately crowded, denticulate, rather thin, 6–7 mm wide. Stipe 50 × 10–19 mm, nearly cylindrical, usually tapering upward; surface covered with buff (6B7–8) floccose-fibrillose or slightly fibrillose scaly zones, but not forming an irregular fibrillose annular zone at the upper part of the stipe, extreme apex white.

Fig. 12 Microscopic features of Squamanita sororcula (HKAS107306A, holotype). a Basidiospores. b Hymenium and subhymenium with one pleurocystidia covered with refractive incrustations. c Pleurocystidia, four of them covered with refractive incrustations. d Pileipellis section. Drawings by Jianwei Liu. Bars = 10 μm
and nearly smooth. *Mycocecidia* subglobose 35 × 25 mm, white (1A1) with brownish (6A4–5) to rusty (6B7–8) spots. The transitional zone between stem and mycocecidia with some irregular rings of tawny-ochraceous (6B7–8) or dingy brown (6E5), fibrillose, appressed, or erect, obliquely upward-pointing or lacerate scales. Context white (1A1), rather firm. Smell rather strongly musty when crushed.

*Basidiospores* [40/1/1] 5.5–7.5 (−9) × (3.5–) 4–5 (−5.5) μm [Q = (1.2–) 1.3–1.8 (−2), Q = 1.6 ± 0.8], broadly ellipsoid, ellipsoid to elongate, sometimes subreniform in side view. *Basidia* 20–35 × 8–10 μm, subclavate, 4-spored, fusiform to ventricose-fusiform, hyaline; sterigmata 4–9 μm long; basal septa often with clamps. *Pleurocystidia* and *cheilocystidia* numerous, 60–90 × 13–17 μm, fusiform to ventricose-fusiform, with obtuse to acute apex, nearly all upper part of cystidia are slightly thick-walled (up to 1.5 μm), sometimes with refractive incrustations, hyaline. *Lamellar trama* regular, composed of colorless, thin-walled hyphae 5–10 μm diam, branching, sometimes anastomosing; clamps present and common. *Subhymenium* consisting of 4–6 μm wide filamentous hyphal segments, narrow. *Pileipellis* a cutis with transition to a trichoderm at regular intervals, composed of loosely and more or less radially arranged, thin-walled hyphae 60–120 × 5–20 μm, and at the upper of the pileipellis often with fine brown granular incrustations, hyaline. *Mycocecidia* composed of abundant subglobose to broadly clavate inflated cells (20–55 × 20–40 μm), and colorless and hyaline clampless filamentous hyphae, 2–6 μm wide, elongate-fusiform hyphae nearly 5–15 μm wide similar to those on the pileus; chlamydospores not observed.

**Ecology:** Parastic on *Amanita sepiacea* (HKAS107306B, ITS = MW258871, TEF1-α = MW324505) growing on soil in forest dominated by *Pinus yunnanensis*.

**Distribution:** Currently known from Hunan and Yunnan Provinces, central and Southwest China.

**Notes:** *Squamanita sororcula* is similar to *S. mira*, *S. orientalis*, *S. schreieri*, *S. umbonata*, and other collections assigned to the “*S. umbonata*” complex. The differences between the first two and *S. sororcula* have been discussed above. Besides, *S. sororcula* differs from *S. schreieri* by the presence of cystidia and differs from *S. umbonata* by its subglobose mycocecidia.

Wang and Yang (2004) treated two collections (HKAS38127 and 38149) as “*S. umbonata*” collected from Hunan province, central China. Unfortunately, the collections have not been traced by us. However, the two collections are without an annular zone, and should be close to *S. sororcula* rather than *S. orientalis*.

### Key to *Squamanita* worldwide

| 1. Basidiomata aripiforme  | 1. Basidiomata teretiforme  |
| 2 (1) Basidiocarpus 5–4 × 4–1 mm (2A1), white (1A1), papillate | 2 (1) Basidiocarpus 5–4 × 4–1 mm (2A1), white (1A1), papillate |
| 3 (2) Basidiocarpus 5–4 × 4–1 mm (2A1), white (1A1), papillate | 3 (2) Basidiocarpus 5–4 × 4–1 mm (2A1), white (1A1), papillate |

Wang and Yang (2004) treated two collections (HKAS38127 and 38149) as “*S. umbonata*” collected from Hunan province, central China. Unfortunately, the collections have not been traced by us. However, the two collections are without an annular zone, and should be close to *S. sororcula* rather than *S. orientalis*. 
DISCUSSION
Systematic position of Cystodermateae
Singer (1986) included in Cystodermateae the following seven genera, viz. Cystoderma, Dissodera (current name Squamanta), Horakia (current name Verrucospora), Phaeolepiota, Pseudobaeaspora, Ripartitella, and Squamanita. Based on the phylogenetic analyses of Matheny and Griffith (2010), Matheny et al. (2015), Vizzini et al. (2019), Kalichman et al. (2020) and our present studies, three genera among Cystodermateae, viz. Cystoderma, Phaeolepiota, and Squamanita together with Leucopholiota and Floccularia can be assigned to the Squamantuaceae within Agaricineae (agaricoid clade). Pseudobaeaspora was recognized as a member of the Tricholomataceae s. str. within Tricholomatinae (tricholomatoid clade) in the multigene phylogenetic analyses of Sánchez-García and Matheny (2017) and He et al. (2019). Molecular data of two species of Verrucospora, V. flavofusca, confirm placement in Agaricineae s.lat. with strong consistent support (SH-aLRT/UFB/PP = 95.4/98/0.99) in our study (Fig. 2). Oberwinkler (1976) and Singer (1986) supposed that Horakia (now included in Verrucospora) belonged to Thelephorales or Cystodermatae of Agaricales, respectively, which are incorrect placements based on our molecular phylogenetic data. Phylogenetic placements of Ripartitella, and Cystodermella, which was separated from Cystoderma by Harmaja (2002), are unclear at present, although previous research based on the LSU, RPB1 and ITS molecular sequences indicated that Ripartitella and Cystodermella are near Cercopmyces (Baroni et al. 2014). Our study (Fig. 2) is consistent with Baroni et al. (2014), and these three genera are close to Hydnangiaceae in their phylogenetic tree (Fig. 2).

Saar et al. (2016) treated Phaeolepiota aurea as Cystoderma aureum because it was nested within Cystoderma. However, P. aurea, with large inamyloid fusoid and asperulate spores, differs from Cystoderma, species of which have amyloid, ellipsoid, oblong, or fusiform and smooth spores. In our multigene phylogenetic tree (Fig. 2), and the supplementary trees of Varga et al. (2019), P. aurea nested within Cystoderma, but clustered with Cystodermella superbum (Fig. 2), a unique species commonly reported to be amyloid but in only a small area of the basidiospore surface, which is a morphotaxonomic character that differs from other species of Cystoderma. In the study of Matheny and Griffith (2010), and supplementary trees of that study (Additional files 1 and 2), a close relationship among P. aurea, Cystoderma and C. superbum was not well supported. Therefore, for the moment, we continue to recognize Phaeolepiota for P. aurea. Further studies with more samples and using more DNA makers are necessary to clarify the position of P. aurea and C. superbum in relation to other species of Cystoderma.

Up to now, 12 described species of Squamanita have been accepted, although Matheny and Griffith (2010: Table 1) listed 15, including three not validly published designations: S. cottoiana (nom. inval.), S. phaeolepitiocola (nom. prov.), and S. tropica (nom. prov.).

Diversity of the “S. umbonata” species complex
Our study indicated that material of “Squamanita umbonata” from the Northern Hemisphere clustered into two species complexes each consisting of several different species (Figs. 2 and 3), including S. orientalis, S. sororcula, and several undefined specimens. Morphological characteristics of collection R. E. Halling 7691 (NY79971) (Fig. 13) from Costa Rica are mostly consistent with the descriptions of the type (NY27684) by Sumstine (1914) and Bas (1965), with an umbonate pileus, cylindrical to clavate fusiform mycocecidia, and thin-walled cystidia. However, considering that the type of S. umbonata was from Pennsylvania, USA, we are reluctant to identify R. E. Halling 7691 as S. umbonata until molecular data from the type are available.

The collection H. E. Bigelow 17431 (NY2776224) (Fig. 13) has a subglobose mycocecidium, slightly smaller basidiospores (5–7 μm × 3.5–5 μm) and cystidia (45–65 μm × 12–18 μm) in comparison with those of S. umbonata, and the mycocecidium is composed of abundant inflated cells, indicating the possibility of Amanita as host. C. Bas 3808 (NY1840398) (Fig. 13) was published as S. umbonata by Bas (1965). However, Cortés-Pérez et al. (2014) showed that the upper parts of the cystidia in this collection were slightly to moderately thick-walled, which is consistent with our observations of the collection. Phylogenetically C. Bas 3808 forms a monophyletic branch with DAOM 199323 [GenBank accession no.: AF261508], submitted by Moncalvo et al. (2002), and may well be conspecific with that (Fig. 3). A collection from Italy (HKAS107306A; Fig. 13) is sister to H. E. Bigelow 17, 431, C. Bas 3808, and DAOM 199323 (Fig. 3), and its hosts belong to the species complex of A. excelsa (GenBank accession no.: MW258872 and MW258873). Squamanita umbonata is also reported from Japan (Ikeda 1996), Italy (Vizzini and Girlanda 1997), and Mexico (Cortés-Pérez et al. 2014). Further efforts are necessary to reveal the species diversity of “S. umbonata” globally and delimit the constituent species, including a clear application of the name S. umbonata.

Host preference or specificity of Squamanita species
Our study reveals that the basidiomes of S. mira are composed of its own hyphae, while the mycocecidia also include hyphae of the host, which is consistent with the observations on S. paradoxa by Mondiet et al. (2007)
and Griffith et al. (2019). Interestingly, host hyphae are found in the volval remnants that are attached to the pileal surface of *S. orientalis* (Figs. 5, 8, 10). This character may provide additional help for the host identification of *Squamanita*. Although sometimes the basidiomes of *Squamanita* may macromorphologically deform the hosts, most of the time the shapes of infected hosts (mycocecidia) still largely maintain consistent morphological characteristics with nearby uninfected basidiomes of the same species. Our study showed that *S. orientalis*, *S. sororcula* and “*S. umbonata*” (HKAS107325A) from Italy, with subglobose mycocecidia, are parasitic on *A. sect.* *Validae*, while *S. mira*, with the sheathing volva arising from the margin of a bulb, is parasitic on *A. kitamagotake*. Therefore, the shape and the size of the mycocecidia could be a reliable morphological character at species level.

**CONCLUSION**

The monophyly of the family *Squamanitaceae* was confirmed by multi-gene Bayesian phylogenetic analysis, with five genera, namely *Cystoderma*, *Phaeolepiota*, *Squamanita*, *Floccularia* and *Leucopholiota* falling in the family. Three new species from China, parasitizing two different species from two sections of *Amanita*, were uncovered and described based on morphological and molecular evidence. Furthermore, a multi-gene phylogenetic analysis on “*Squamanita umbonata*” from North America, Central America, Europe, and East Asia showed that it represents two species complexes harboring eight subclades. Further morphological studies are needed to reveal the species diversity and distribution patterns of “*Squamanita umbonata*”.

**Abbreviations**

nrLSU: The large nuclear ribosomal RNA subunit; ITS: The internal transcribed spacers 1 and 2 with the 5.8S rDNA; 5.8S: 5.8S gene; 18S: The small subunit region; TEF1-α: Translation elongation factor 1-α; RPB1: RNA polymerase II largest subunit; RPB2: RNA polymerase II second largest subunit; CTAB: Cetyltrimethyl ammonium bromide; HKAS: Herbarium of Cryptogams, Kunming Institute of Botany of the Chinese Academy of Sciences; ML: Maximum likelihood; UFB: Ultrafast bootstrap support values of IQTREE; SH-aLRT: The Shimodaira–Hasegawa-like aLRT test support values; PP: Bayesian posterior probability; NY: The New York Botanical Garden

**Supplementary Information**

The online version contains supplementary material available at https://doi.org/10.1186/s43008-021-00057-z.
Additional file 1. Maximum-Likelihood (ML) phylogenetic tree of Squamanitaceae inferred from ITS sequences, with SH-ALRT (left), ultrafast bootstrap (UFB) (right), only one of SH-ALRT > 80 or UFB > 95 for ML are indicated along branches (SH-ALRT/UFB). New species Squamanita mira, S. orientalis, S. soroculata are highlighted in boldface.

Additional file 2. Maximum-Likelihood (ML) phylogenetic tree of Squamanitaceae inferred from LSU sequences, with SH-ALRT (left), ultrafast bootstrap (UFB) (right), only one of SH-ALRT > 80 or UFB > 95 for ML are indicated along branches (SH-ALRT/UFB). New species Squamanita mira, S. orientalis, S. soroculata are highlighted in boldface.

Acknowledgements
We are very grateful to the fungaria of New York Botanical Garden, Eidgenössische Technische Hochschule Zürich, and also Reinhard Berndt, Fabrizio Boccardo, Li-Hong Han, Fa Li, and Gang Wu for providing specimens and images for this study; Shannon Asencio for providing helpful locality information on DAOM 199323 and DAOM 225481; and Bang Feng, Xiao-Bin Liu, Yan-Liang Wang, and Gang Wu for revising early manuscript. Zhu L. Yang and Jian-Wei Liu designed the research. Jian-Wei Liu performed experiments, analyzed data and wrote the manuscript. Zhi L. Yang, Zai-Wei Ge, Egon Horak, Alfredo Vizzini, Roy. E. Halling revised the manuscript. Egon Horak, Alfredo Vizzini, Roy E. Halling and Chun-Lei Pan also provided some specimens. The authors read and approved the final manuscript.

Adherence to national and international regulations
Not applicable.

Authors’ contributions
Zhu L. Yang and Jian-Wei Liu designed the research. Jian-Wei Liu performed experiments, analyzed data and wrote the manuscript. Zhu L. Yang, Zai-Wei Ge, Egon Horak, Alfredo Vizzini, Roy E. Halling revised the manuscript. Egon Horak, Alfredo Vizzini, Roy E. Halling and Chun-Lei Pan also provided some specimens. The authors read and approved the final manuscript.

Funding
This work was supported by the Second Tibetan Plateau Scientific Expedition and Research Program (2019QZKK00503) and the Biodiversity Investigation, Observation and Assessment Program (2019–2023) of the Ministry of Ecology and Environment of China, and the International (Regional) Cooperation and Exchange Projects of the National Natural Science Foundation of China (No. 31961143010).

Availability of data and materials
The datasets generated for this study (Tables 1 and 2) can be accessed via GenBank: https://www.ncbi.nlm.nih.gov/genbank/. Alignments analysed during the current study are available at TreeBase: https://www.treebase.org/.

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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Received: 18 August 2020 Accepted: 16 February 2021

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