Alloexidiopsis gen. nov., A Revision of Generic Delimitation in Auriculariales (Basidiomycota)

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Auriculariales is a fungal order with highly diverse morphological traits of basidiomes, which partially leads to a poor understanding of its taxonomic system at the generic level. To identify our recently collected specimens of Auriculariales to a species level, we perform a comprehensive phylogenetic analysis of the generic relationships in Auriculariales. In association with morphological characteristics, a new genus Alloexidiopsis belonging to Auriculariaceae is erected with two new species, namely, A. australiensis and A. schistacea. Moreover, Exidiopsis calcea separated from the generic type E. effusa and Heteroradulum niveum and H. yunnanense recently inaccurately described as members of Heteroradulum are recovered in the clade of Alloexidiopsis. These three species are thus transferred to this new genus. One collection of Exidiopsis grisea also falls in the clade of Alloexidiopsis, whereas another collection of this species is separated far from Alloexidiopsis and E. effusa. Since we have no collection to confirm the species identity of E. grisea, its generic position is uncertain. The main taxonomic morphological differences among Alloexidiopsis and related corticioid genera in Auriculariales are summarized. A key to all the five accepted species of Alloexidiopsis is provided. As two unnamed lineages exist in Alloexidiopsis besides the abovementioned five species, it is assumed that more new species will be revealed from this genus under its current circumscription.

Keywords: Agaricomycetes, Auriculariaceae, Exidiopsis, Heteroradulum, wood-inhabiting fungi, six new taxa

INTRODUCTION

Auriculariales is a fungal order being mainly composed of wood-inhabiting macrofungi in Agaricomycetes and Basidiomycota (Hibbett et al., 2007). The type genus of this order is Auricularia, which together with several other gelatinous genera, namely, Exidia, Guepinia, and Pseudohydnum, comprise important edible and medicinal fungi (Wu et al., 2019). Therefore, interest in species diversity in these gelatinous genera has grown significantly in recent years (Bandara et al., 2015; Chen et al., 2020; Shen and Fan, 2020; Ye et al., 2020; Wang and Thorn, 2021; Wu et al., 2021).

Contrary to the gelatinous genera, most species in Auriculariales bear tough, resupinate, and effused to reflexed basidiomes as corticioid and polyporoid fungi (Miettinen et al., 2012; Zhou and Dai, 2013; Malysheva and Spirin, 2017). With the aid of molecular phylogeny, the corticioid species traditionally placed in Eichleriella, Exidiopsis, and Heterochaete according to morphological characters have been rearranged to make genera monophyletic. After the erection of...
some new genera, e.g., *Adustochaete*, *Amphistereum*, *Crystallocladon*, *Proterochaete*, and *Sclerotrema* and reinstatement of several previously known genera, e.g., *Hirneolina*, *Heteroradulum*, and *Tremellochaete* (Malyshева and Spirin, 2017), *Eichleriella* is accepted to be a monophyletic genus, while *Exidiopsis* and *Heterochaete* seem to be synonymous with a priority of the latter genus (Malyshева and Spirin, 2017; Alvarenga et al., 2019; Alvarenga and Gibertoni, 2021). However, certain species of *Exidiopsis*, even sequenced ones such as *E. calcea* and *E. grisea*, still have no appropriate placement at the generic level (Malyshева and Spirin, 2017; Li et al., 2022b). In addition, the generic placement of certain recently described species of *Heteroradulum* is questionable as indicated in a study by Li et al. (2022b) and our understanding of the phylogenies in Guan et al. (2020) and Li et al. (2022a). This phenomenon indicates the generic delimitation in *Auriculariales* that should be further clarified.

When revisiting specimens collected in the last few years, some of them are identified to be previously known and new species in *Auriculariales*, but cannot be placed in any known genus. Therefore, a new genus is erected for these species and also for other related species.

**MATERIALS AND METHODS**

**Morphological Examination**

Sixteen studied specimens were sampled in northwestern and southwestern China, Vietnam, and Australia from May to November 2017–2020. These specimens were dried using a portable drying instrument at 35° C on the day of sampling and are preserved at the Fungram, Institute of Microbiology, Chinese Academy of Sciences (HMAS), Beijing, China and the National Herbarium of Victoria (MEL), Melbourne, Australia. Macromorphological characters of basidiomes were examined with the aid of a Leica M125 stereomicroscope (Wetzlar, Germany) at magnifications up to 100×. Color terms follow Petersen (1996). Microscopic examination was carried out with an Olympus BX43 light microscope (Tokyo, Japan) at magnifications up to 1,000× following a study by Liu et al. (2021). All the measurements were taken from the sections mounted in cotton blue. The following abbreviations are used: L = mean basidiospore length (arithmetic average of all the basidiospores), W = mean basidiospore width (arithmetic average of all the basidiospores), Q = variation in the L/W ratios between the specimens studied, and n = number of basidiospores measured from a given number of specimens.

**Deoxyribonucleic Acid Extraction and Sequencing**

The cetyltrimethylammonium bromide (CTAB) plant genome rapid extraction kit (Beijing Demeter Biotech Co., Ltd., Beijing, China) was employed for DNA extraction from dried specimens. The internal transcribed spacer (ITS) and nuclear large subunit (nLSU) gene regions were amplified with the primer pairs ITS5/ITS4 (White et al., 1990) and LR0R/LR7 (Vilgalys and Hester, 1990), respectively. The PCR procedure for ITS was initial denaturation at 95° C for 3 min, followed by 35 cycles at 94° C for 40 s, 54° C for 45 s, 72° C for 1 min, and a final extension of 72° C for 10 min, while that for nLSU was initial denaturation at 94° C for 1 min, followed by 34 cycles at 94° C for 30 s, 50° C for 1 min, 72° C for 1.5 min, and a final extension of 72° C for 10 min. The PCR products were purified and sequenced at the Beijing Genomics Institute (BGI), China. All the newly generated sequences were submitted to GenBank (https://www.ncbi.nlm.nih.gov/genbank/).

**Phylogenetic Analysis**

The current dataset for phylogenetic analysis included all the main lineages in *Auriculariales* as ingroup taxa, while *Sistotrema brinkmannii* was selected as an outgroup taxon following a study by Li et al. (2022b). The ITS and nLSU regions were separately aligned using MAFFT version 7.110 (Katoh and Standley, 2013) with the G-INS-i strategy (Katoh et al., 2005), and then the two resulting alignments were concatenated as a single alignment. The concatenated alignment was submitted to TreeBASE (http://www.treebase.org; accession number S29452). jModelTest 2.1.10 (Guindon and Gascuel, 2003; Darrasa et al., 2012) was used to determine the best-fit evolutionary model of the concatenated alignment based on the Akaike information criterion (AIC). Following the resulting model, maximum likelihood (ML) and Bayesian inference (BI) analyses were performed. For the ML analysis, raxmlGUI 2.0 (Stamatakis, 2014; Edler et al., 2021) was used with the calculation of bootstrap (BS) replicates under the auto fiber channel (FC) option (Pattengale et al., 2009). For the BI analysis, MrBayes 3.2 (Ronquist et al., 2012) was used with two independent runs of four chains, and trees were sampled every 1,000th generation. The first 25% of the resulting trees were discarded as burn-in, while the remaining 75% of the resulting trees were used for constructing a 50% majority consensus tree and calculating Bayesian posterior probabilities (BPPs). Chain convergence was determined using Tracer 1.7 (Rambaut et al., 2018). The trees were visualized in FigTree 1.4.4 (Rambaut, 2018) and edited in Adobe Illustrator cc 2020.

**RESULTS**

A total of 15 ITS and 15 nLSU sequences were newly generated from all the 16 studied specimens (*Table 1*). The concatenated alignment of ITS and nLSU regions has 117 collections and 1,675 characters. GTR + I + G was estimated as the best-fit evolutionary model for this alignment. The ML analysis ended after 200 BS replicates. The BI analysis converged after 20 million generations, which was indicated by the effective sample sizes of all the parameters above 5,000 and the potential scale reduction factors close to 1.00. The topology resulting from the ML analysis is shown along with BS values of more than 50% and BPPs of more than 0.8 at the nodes (*Figure 1*).

The *Auriculariaceae* is well recovered (BS = 96%, BPP = 1) by the current phylogeny (*Figure 1*). In *Auriculariaceae*, besides four sequences representing *Heteroradulum kmetii* (LWZ 20200813-6a, LWZ 20200813-7b, LWZ 20200813-23b, and LWZ 20200928-30c), additional newly sequenced specimens (*Table 1*) grouped with *Exidiopsis calcea*, one of the collections of “*E. grisea*” (TUFC 100049), *Heteroradulum niveum*, and *H.
| Species                  | Voucher number | GenBank accession number |
|-------------------------|----------------|-------------------------|
|                        |                | ITS                     | nLSU       |
| **Adustochaete rava**   | KHL15526       | MK391517                | MK391526   |
| **Adustochaete interrupta** | LR23435       | MK391518                | MK391527   |
| Alloexidiopsis australiensis | LWZ 20180513-22 | OM801933                | OM601918   |
| A. australiensis        | LWZ 20180514-18 | OM801934                | OM601919   |
| A. calcea               | MW 331         | AF291280                | AF291326   |
| A. calcea               | LWZ 20180904-14 | OM801935                | OM601920   |
| A. calcea               | LWZ 20180904-19 | OM801936                | OM601921   |
| A. calcea               | LWZ 20180904-22 | OM801937                | OM601922   |
| A. calcea               | LWZ 20180904-24| OM801938                | OM601923   |
| A. calcea               | LWZ 20191104-29 | OM801939                | OM601924   |
| A. nivea                | CLZhao 11204   | MZ352947                | MZ352932   |
| A. nivea                | CLZhao 11210   | MZ352948                | MZ352933   |
| A. nivea                | CLZhao 16260   | MZ352940                | MZ352934   |
| A. nivea                | CLZhao 16280   | MZ352941                | MZ352935   |
| A. nivea                | CLZhao 16398   | MZ352942                | MZ352936   |
| A. nivea                | CLZhao 16424   | MZ352943                | MZ352937   |
| A. nivea                | CLZhao 16432   | MZ352944                | MZ352938   |
| A. nivea                | CLZhao 16472   | MZ352945                | MZ352939   |
| A. nivea                | CLZhao 16483   | MZ352946                | MZ352939   |
| A. nivea                | LWZ 20171014-11| OM801941                | OM601926   |
| A. nivea                | TUF3C4333      | AB871764                | AB871745   |
| A. schistacea           | LWZ 20200819-21a| OM801939               | OM601932   |
| A. yunnanensis          | CLZhao 4023    | MT215568                | MT215564   |
| A. yunnanensis          | CLZhao 8136    | MT215569                | MT215566   |
| A. yunnanensis          | CLZhao 9132    | MT215570                | MT215566   |
| A. yunnanensis          | CLZhao 9200    | MT215571                | MT215567   |
| A. sp.                  | LWZ 20171014-1| OM801940                | OM601925   |
| A. sp.                  | LWZ 20180920-9| OM801943                | OM601928   |
| A. sp.                  | LWZ 20180920-16| OM801942                | OM601927   |
| Amphistereum levellaeum | FP-106715      | KX262119                | KX262168   |
| A. schrenki             | Burdssal 8476  | KX262130                | KX262178   |
| Aporpium canescens      | Miettinen 13532.2| JX044112               |            |
| A. cyanae               | Miettinen 14774| JX044145               |            |
| A. cyanae               | WD2207         | AB871751                | AB871730   |
| A. hexagonoides         | ML297          | AB871754                | AB871735   |
| A. stellatae            | FO 25132       | AF291271                | AF291292   |
| A. mesenterica          | TUF12805       | AB913519                | AB913519   |
| A. polychtra            | TUF12920       | AB871752                | AB871733   |
| Basidiobadenron eyrei   | VS 12000       | MT040880                | MT040854   |
| B. globosporus          | VS 12929       | MT040884                | MT040864   |
| B. lutriogriseum        | KHL 16022      | MT040881                | MT040861   |
| B. peluin               | KHL 16014      | MT040875                | MT040862   |
| Boudtoria galzini       | OM 15900.4     | MG757511                | MG757511   |
| Cryptocodon             | RC             | MN475888                | MN475884   |
| subgelatinosum          | 1609-URM93444  | MN475889                | MN475885   |
| C. subgelatinosum       | TSB 4b-URM93446| MN475890                | MN475886   |

(Continued)
MycoBank: MB 844125.

Etymology: *Alloexidiopsis* (Latin), refers to the segregation from *Exidiopsis*.

Diagnosis: It differs from *Exidiopsis* in the combination of resupinate, leathery basidiomes and the presence of cystidia and hyphidia.

Type species: *Alloexidiopsis schistacea* S.L. Liu, Z.Q. Shen & L.W. Zhou (described below).

Type specimen: China: Sichuan, Ping Shan County, Laojunshan National Nature Reserve, on the fallen angiosperm trunk, 19 August 2020, LW Zhou, LWZ 20200819-21a (holotype in HMAS).

Description: Basidiomes annual, resupinate, effused, thin, leathery, closely adnate. Hymenophore smooth or with sterile spines, greyish white to ochraceous, cracked or not. Hyphal system monomitic, generative hyphae with clamp connections, hyaline, thin-walled. Cystidia cylindrical to clavate, thin-walled. Hyphidia abundant, covering hymenium, hyaline, thin-walled, smooth, inamyloid, indextrinoid, acyanophilous. On wood.

Notes: *Alloexidiopsis* is characterized by grayish-white to ochraceous, corticioid basidiomes, a monomitic hyphal system, and the presence of cystidia and hyphidia. Besides *Exidiopsis* as indicated in diagnosis, this new genus is also close to *Crystallodon* and *Heteroradulum* in morphology. However, *Crystallodon* differs in the presence of hyphal pegs surrounded by crystals (Alvarenga and Gibertoni, 2021), while *Heteroradulum* has brightly colored (pinkish or reddish) basidiomes and a mono- or dimitic hyphal system with thick-walled generative hyphae (Malyshева and Spirin, 2017; Li et al., 2022b). The main taxonomic morphological differences among *Alloexidiopsis* and related corticioid genera in *Auriculariales* are summarized in Table 2.

### Taxonomy

#### *Alloexidiopsis*

**L.W. Zhou & S.L. Liu, gen. nov.**

*MycoBank: MB 844125.*

**Etymology:** *Alloexidiopsis* (Latin), refers to the segregation from *Exidiopsis*.

**Diagnosis:** It differs from *Exidiopsis* in the combination of resupinate, leathery basidiomes and the presence of cystidia and hyphidia. The other two lineages, represented by the specimens LWZ 20180904-14, LWZ 20180904-22, LWZ 20180904-24, and LWZ 20191104-29, one belongs to *H. niveum* (LWZ 20171014-11). The remaining sequences formed four new lineages. The two other lineages, represented by the specimens LWZ 20180920-9, and LWZ 20180920-16 are sterile and thus, the two lineages represented by them are not included in the subsequent taxonomic treatment. The main taxonomic morphological differences among *Alloexidiopsis* and related corticioid genera in *Auriculariales* are summarized in Table 2.

**Alloexidiopsis australiensis** S.L. Liu, Z.Q. Shen & L.W. Zhou, sp. nov. (Figures 2A,B, 3).

*MycoBank: MB 844126.*

**Etymology:** *australiensis* (Latin), refers to Australia.

**Diagnosis:** It is characterized by smooth, cream hymenophore.

**Type:** *Australia:* Tasmania, Hobart, and Mount Wellington, on the fallen angiosperm branch, 13 May 2018, LW Zhou, LWZ 20180513-22 (holotype in MEL, isotype in HMAS).

**Description:** Basidiomes annual, resupinate, membranaceous, becoming leathery upon drying, closely adnate, widely effused, up to 12 cm long, 2 cm wide, 100–200 μm thick. Hymenophore smooth, cream to pale orange when fresh, becoming white upon drying. Margin gradually thinning out, thin, concolorous with or slightly darker than subiculum.

**Hyphal system** monomitic; generative hyphae with clamp connections. Subiculum composed of crystal clusters and agglutinated hyphae; subicular hyphae hyaline, thin-walled, frequently branched, closely interwoven, 1–2 μm in...
FIGURE 1 | Phylogenetic position of Alloexidiopsis in Auriculariales inferred from the concatenated dataset of internal transcribed spacer (ITS) and nuclear large subunit (nLSU) regions. The topology generated from the maximum likelihood analysis is shown along with bootstrap values and Bayesian posterior probabilities of more than 50% and 0.8, respectively, at the nodes. The new genus Alloexidiopsis is highlighted with the bluish background color, while the specimens of the newly described species are in boldface.
TABLE 2 | Morphological comparison among Alloexidiopsis and related corticioid genera in Auriculariales.

| Genus             | Basidiomes               | Hymenophore                    | Hyphal system | Cystidia                                      | Hyphidia                             | Basidiospores                         |
|-------------------|--------------------------|--------------------------------|---------------|-----------------------------------------------|---------------------------------------|---------------------------------------|
| Adustochaete      | Annual, small-sized, orbicular, waxy | Spiny or tuberculate, grayish to brownish | Monomitic     | Clavate to fusiform, thin-walled              |variably branched                      | Cylindrical to broadly cylindrical, straight or curved |
| Alloexidiopsis    | Annual, effused, leathery | Smooth or with sterile spines, more or less grayish | Monomitic     | Cylindrical to clavate, thin-walled          | nodulose or richly branched           | Cylindrical to broadly cylindrical, slightly curved |
| Amphistereum      | Annual or perennial, cupulate-orbicular, hard leathery | Smooth, pale-colored | Dimitic | Rare, narrowly clavate, thin-walled          | richly branched                        | Cylindrical to broadly cylindrical, slightly curved |
| Crystallodon      | Annual, effused, gelatinous to crustaceous | Covered by sharp-pointed sterile spines, brownish | Monomitic     | Fusiform to cylindrical, often sinuous, thin-walled | branched                              | Cylindrical to broadly cylindrical, slightly curved |
| Exidiopsis        | Annual, effused or effused-reflexed, waxy gelatinous, arid waxy or coriaceous | Smooth or with sterile spines, gray, buff, ochraceous | Monomitic     | Present or absent, cylindrical, clavate or fusiform, thin-walled | simple or richly branched             | Subgibose, ellipsoid, cylindrical to allantoid |
| Heteroradulum     | Annual or perennial, effused-reflexed, leathery | Smooth, with sterile spines, pinkish or reddish | Mono- or dimitic | Clavate to fusiform, thin to thick-walled    | richly branched                        | Cylindrical to broadly cylindrical, sometimes curved |
| Metulochaete      | Effused, gelatinous to waxy-arid | Smooth or covered by sterile spines, pale-colored | Monomitic     | Metuloid, covering hymenial spines, thick-walled | richly branched                        | Allantoid, straight to slightly curved |
| Proterochaete     | Annual, orbicular, arid | Smooth or irregularly spiny, cream-colored to grayish or pale ochraceous | Monomitic     | Occasional, sinuous, accidentially dichotomously branched, thin-walled | richly or sparsely branched            | Cylindrical to broadly cylindrical, slightly curved |
| Sclerotrema       | Perennial, orbicular, leathery | Smooth, grayish brown | Monomitic | Hyphoid to fusiform, thick-walled              | richly branched                        | Allantoid, distinctly curved           |

Cystidia cylindrical with an obtuse apex, ventricose, 21.5–24.5 × 9.5–12 µm, with a clamp connection at base. Hyphidia arising from hyphae, nodulose or richly branched, hyaline, thin-walled, 22–33 × 1–2 µm. Basidia ellipsoid to ovoid, longitudinally septate, four-celled, embedded, 18–21 µ 13–18 µm, occasionally with a short base stalk, with a clamp connection at base. Basidiocarps cylindrical to broadly cylindrical, slightly curved (allantoid), hyaline, thin-walled, smooth, acyanophilous, inamyloid, indextrinoid, with oily inclusions, (12–13)25–(25.5) × (6.5–7)–11(–12) μm, L = 20.0 μm, W = 9.0 μm, Q = 2.3 (n = 60/2).

Other specimens (paratype) are also examined: Australia: Timbs Track, on dead standing angiosperm, 14 May 2018, LW Zhou, LWZ 20180514-18 (HMAS).

Notes: Alloexidiopsis australiensis resembles A. calcea and A. nivea (both transferred below) by smooth hymenophore in Alloexidiopsis. However, A. calcea differs in grayish-white to ochraceous hymenophore when fresh and has a distribution in the Northern Hemisphere (Wells, 1961), while A. nivea differs in smaller basidiospores (6.5–13.5 × 2.7–5.5 μm; Li et al., 2022a). Exidiopsis macropsora is similar to A. australiensis by the leathery basidiomes and the presence of cystidia and hyphidia; however, it differs in the reflexed basidiomes when dry and smaller basidiospores (10–15 μm × 5–7.5 μm; Wells, 1961).

Alloexidiopsis calcea (Pers.) L.W. Zhou & S.L. Liu, comb. nov. (Figures 2C,D).
FIGURE 2 | Basidiomes of Alloexidiopsis. (A,B) A. australiensis (LWZ 20180513-22, holotype). (C,D) A. calcea (LWZ 20180904-24). (E,F) A. schistacea (LWZ 20200819-21a, holotype). (G,H) A. sp. (LWZ 20180920-16). Scale bars: (A,C,E,G) = 1 cm, (B,D,F,H) = 2 mm.
FIGURE 3 | Microscopic structures of Alloexidiopsis australiensis (drawn from the holotype). (A) Basidiospores. (B) Basidia. (C) Basidioles. (D) Cystidia. (E) Hyphidia. (F) Hyphae from subiculum. Scale bars = 10 µm.
consistent with the description of *E. calcea* (Wells, 1961). Taking *E. calcea* falling within the clade of the newly erected genus into consideration together, this species is transferred to *Alloexidiopsis*. 

**Alloexidiopsis nivea** (J.J. Li & C.L. Zhao) L.W. Zhou & S.L. Liu, **comb. nov.**

MycoBank: MB 844129.

Basionym: *Heteroradulum niveum* J.J. Li & C.L. Zhao, in Li, Zhao, and Liu, Diversity 14 (1, no. 40):5 (2022).

Notes: *Alloexidiopsis nivea* was recently described as a member of *Heteroradulum* (Li et al., 2022a). When the independence of this species was phylogenetically supported, its relationship with additional species of *Heteroradulum*, however, failed to receive reliable statistical support in the original phylogeny with a sampling on *Auriculariaceae* (Figure 1 in Li et al., 2022a). Although the original phylogeny with a narrower sampling focusing mainly on *Heteroradulum* did not reject the close relationship of *H. niveum* with other species of *Heteroradulum*, the practice for this phylogenetic analysis (lack of additional in-group taxa for reference) cannot accurately determine the monophyly of *Heteroradulum* and, thus, the phylogenetic position of *H. niveum* (Figure 2 in Li et al., 2022a). Including a broader sampling of reference sequences, the current phylogeny unambiguously recovers this species in the newly erected genus *Alloexidiopsis* (Figure 1), so we formally propose the transfer here.

**Alloexidiopsis schistacea** L.W. Zhou & S.L. Liu, **sp. nov.** (Figures 2E,F, 4).

MycoBank: MB 844127.

Etymology: *schistacea* (Latin), refers to the slate-like color (grayish) of hymenophore.

Diagnosis: Characterized by grayish hymenophore with small tubercles.

Type: **China**: Sichuan, Pingshan County, Laojunshan National Nature Reserve, on the fallen angiosperum trunk, 19 Aug 2020, L.W Zhou, LWZ 20200819-21a (holotype in HMAS).

Description: Basidiomes annual, resupinate, membranaceous, becoming leathery upon drying, closely adnate, widely effused, up to 15 cm long, 2.5 cm wide, about 200 µm thick. Hymenophore smooth, covered by regularly arranged sterile spines, greyish when fresh. Margin gradually thinning out, thin, concolorous with or slightly darker than subiculum.

Hyphal system monomitic; generative hyphae with clamp connections. Subiculum composed of crystal clusters and agglutinated hyphae; subicular hyphae hyaline, thin-walled, frequently branched, closely interwoven, 2−3 µm in diam. Cystidia cylindrical with an obtuse apex, 25−50 × 4−6 µm, with a clamp connection at base. Hyphidia arising from hyphae, nodulose or branched, hyaline, thin-walled, 20−40 × 1−3 µm. Basidia ellipsoid to ovoid, longitudinally separte, four-celled, embedded, 15−20 × 7−10 µm. Basidiospores cylindrical to broadly cylindrical, slightly curved (allantoid), hyaline, thin-walled, smooth, acyanophilous, inamyloid, indextrinoid, with oily inclusions, (8.5−9.5)−11−(12.5) × (4.3−)14.5−5.5 µm, L = 10.4 µm, W = 5.0 µm, Q = 2.1 (n = 30/1).

Notes: *Alloexidiopsis schistacea* resembles *Alloexidiopsis yunnanensis* (transferred below) by grayish, grandinioid to odontoid hymenophore; however, the latter species differs in two- to three-celled basidia and larger basidiospores (17−24 µm × 5−8 µm; Guan et al., 2020). Micromorphologically, *Exidiopsis badia* and *E. umbrina* resemble *A. stichacea* by the presence of cystidia and hyphidia; however, these two species produce gelatinous, but not leathery basidiomes (Roberts, 2003). Moreover, *E. badia* has larger basidiospores than *A. stichacea* (13−15 µm × 5.5−6 µm; Roberts, 2003). Although only one collection is available for *A. stichacea*, its distinct morphological characters and phylogenetic position make the large enough basidiomes suitable to be described as a new species.

**Alloexidiopsis yunnanensis** (C.L. Zhao) L.W. Zhou & S.L. Liu, **comb. nov.**

MycoBank: MB 844130.

Basionym: *Heteroradulum yunnanense* C.L. Zhao (as “yunnanensis”), in Guan, Liu, Zhao and Zhao, Phytotaxa 437(2):57 (2020).

Notes: *Alloexidiopsis yunnanensis* was originally described in Yunnan, China as a member of *Heteroradulum* (Guan et al., 2020). However, the generic placement of this species is inaccurate as indicated in a study by Li et al. (2022b), who, thus, excluded it from *Heteroradulum* and left its generic position open. The current phylogeny recovers this species in the newly erected genus *Alloexidiopsis* (Figure 1), so we formally propose the taxonomic transfer here.

A Key to All the Five Species of *Alloexidiopsis*

1. Hymenophore smooth. .................................................. 2
2. Hymenophore grandinioid to odontoid. .......................... 4
3. Basidiomes less than 7 µm wide. .......................... *A. nivea*
4. Basidiomes more than 7 µm wide. .......................... 3
5. Hymenophore greyish white to ochraceous when fresh; in the Northern Hemisphere. .......................... *A. calcea*
6. Hymenophore cream to pale orange when fresh; in the Southern Hemisphere. .......................... *A. australiensis*
7. Basidiomes more than 14 µm long. .......................... *A. yunnanensis*
8. Basidiomes less than 14 µm long. .......................... *A. stichacea*

**DISCUSSION**

In this study, we further revise the generic delimitation of corticioid fungi in *Auriculariales* based on previous studies (Malysheva and Spirin, 2017; Li et al., 2022b). A new genus *Alloexidiopsis* is erected for two new species, namely, *A. australiensis* and *A. stichacea*, a new combination from *Exidiopsis* as *A. calcea* and two new combinations from *Heteroradulum* as *A. nivea* and *A. yunnanensis*. A key to all the five species currently accepted in *Alloexidiopsis* is provided.

Besides the five accepted species, two unnamed distinct lineages are recovered in *Alloexidiopsis* (Figures 1, 2G,H). The poor growth stage of these specimens restricts accurate morphological examinations, so no taxonomic treatment is proposed for them. However, this phylogeny indicates that the species diversity in *Alloexidiopsis* could be higher.
Systematic field trips for collections of Alloexidiopsis and comprehensive taxonomic studies will result in more new members of Alloexidiopsis.

After the transfer of Exidiopsis calcea to Alloexidiopsis, Exidiopsis is closer to being a monophyletic genus. A sample “E. grisea” (TUFC100049) also falls in the clade of Alloexidiopsis, whereas another collection of this species (RK 162) is separated far from Alloexidiopsis as a basal lineage of Auriculariaceae (Figure 1). We have neither collection for morphological examinations and, thus, cannot challenge the taxonomic determinations given. Moreover, the texture of E. grisea is waxy gelatinous (Wells, 1961), which makes this species distinguished from all the members of Alloexidiopsis. Consequently, it is premature to change the taxonomic position of E. grisea at this stage.

It is noteworthy that the same research group separately described two new species of Heteroradulum, viz., H. niveum and H. yunnanensis quite recently (Guan et al., 2020; Li et al., 2022a). However, the generic placement of these two species is inaccurate and thus, they are transferred to the new genus Alloexidiopsis. Even if the inaccurate placement has mainly resulted from the practice of phylogenetic analyses, this phenomenon also indicates that the taxonomic system of Auriculariales is poorly established. It has not been tried to do so since the publication of Weiß
and Oberwinkler (2001) 20 years ago, which even leaves the monophyly of *Auriculariales* unconfirmed. A multilocus-based phylogeny with a wider sampling of various morphological groups in *Auriculariales* is urgently needed to achieve a more natural classification of this order, as in other orders within *Agaricomycetes* (Wang et al., 2021).

**DATA AVAILABILITY STATEMENT**

The data presented in the study can be found in the GenBank (https://www.ncbi.nlm.nih.gov/GenBank; accession numbers: OM801918-OM801947) and TreeBASE (http://www.treebase.org; accession number: S29452) repositories.

**AUTHOR CONTRIBUTIONS**

S-LL, Z-QS, X-YL, and L-WZ made morphological examinations. S-LL and Q-ZL performed phylogenetic analyses. L-WZ conceived and supervised the study. S-LL, Z-QS, and L-WZ wrote the manuscript. All authors have approved the final version of the manuscript.

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