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Lecanora inaurata, a new member of the *L. subfusca* group from central North America

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Abstract: *Lecanora inaurata*, a corticolous member of the *L. subfusca* group, is described as new to science. This species is characterized by typically epruinose, reddish brown apothecial discs, a *chlarotera*-type epihymenium, *pulicaris*-type amphithecium, and chloroatranorin and zeorin as major constituents, often with accessory calycin in the thalline margins of the apothecia, imparting a distinctive yellow halo appearance when present in sufficient concentrations. *Lecanora inaurata* occurs in open hardwood-dominated woodlands of the Edwards Plateau and grasslands of the southern Great Plains in Oklahoma and Texas.

Key words: Cross Timbers, crustose lichens, *Lecanoraceae*, lichen chemistry, lichenized Ascomycota

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Introduction

The *Lecanora subfusca* group (*Lecanora* s. str.) includes members of the genus related to *L. allophana* (Ach.) Nyl (Brodo 1984). The group is characterized by having continuous to areolate, crustose thalli, lecanorine apothecia with corticate margins, calcium oxalate crystals in the amphithecium, medium-sized, ellipsoid ascospores, and filiform conidia (Brodo 1984; Lumbsch 1994*b*). Members of the group produce atranorin or related substances, as well as a variety of other secondary metabolites including orcinol depsides, depsidones, and their derivatives, pulvinic acid derivatives, triterpenoids, xanthones, fatty acids, and occasionally usnic acid and related compounds (Brodo 1984; Miyawaki 1988; Lumbsch 1994*b*; Guderley 1999). The *L. subfusca* group is well known, at least when compared with other species groups in *Lecanora* s. lat., with modern revisions for Australasia (Lumbsch 1994*b*), North America (Brodo 1984) including the Sonoran region (Ryan *et al.* 2004), and South America (Guderley 1999), as well as full or partial treatments for India (Upreti 1997, 1998; Upreti & Chatterjee 1997), Japan (Miyawaki 1988) and several European countries (Ibáñez & Burgaz 1998; Edwards *et al.* 2009; Malíček 2014), and smaller treatments of morphologically similar species (Brodo *et al.* 1994; Lumbsch *et al.* 1995, 1996, 1997). The results of several recent phylogenetic studies (e.g., Rodrigues *et al.* 2011; Kondratyuk *et al.* 2014; Miądlikowska *et al.* 2014; Lendemer 2015) suggest that the *L. subfusca* group as traditionally circumscribed is not monophyletic. To date, however, sequence data have not been generated for the greater part of this large and taxonomically complicated group, and the disposition of included species with respect to *Lecanora* s. lat. remains uncertain, as do the utility of anatomical and chemical characters in circumscribing monophyletic species groups.

During recent fieldwork in woodlands of the Edwards Plateau and southern Great Plains of central North America, the authors discovered a corticolous member of the *Lecanora subfusca* group which frequently produced yellowish apothecial margins, creating a distinctive and attractive halo effect. The yellowish pigmentation of the apothecial margins is sporadic, sometimes

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even within a single thallus. The species is described here as new to science.

Materials and Methods

Specimens were studied dry using dissecting microscopes and subjected to chemical analysis using standard spot tests (reagents are abbreviated following Brodo *et al.* 2001) and thin-layer chromatography (TLC). TLC was carried out at KANU using solvent systems A, B′, C, and E following the methods of Orange *et al.* (2001). Water mounts were hand sectioned with a razor blade. Microscopic characters were observed in water and images were captured and measured to the nearest 0.1μm. Measurements are presented as a simple range or, where sufficient material allowed, as the average ($\bar{x}$) ± one standard deviation (SD), bounded by the smallest and largest observed values, and followed by the sample size (*n*) (i.e. (smallest observed–) $\bar{x}$ − 1SD −$\bar{x}$ − $\bar{x}$ +1SD (–largest observed) (*n*)).

Taxonomy

Lecanora inaurata C. A. Morse & Ladd sp. nov.

MycoBank No.: MB 816296

A corticolous member of the *Lecanora subfusca* group with an esorediate, continuous, verruculose, pale grey to glaucous blue thallus; apothecial margins entire to flexuose, often crenulate, concolorous with the thallus or pale to bright yellow; apothecial discs reddish brown, typically epruinose or sometimes finely whitish grey pruinose; amphithecium with large crystals persisting in K (*pulicaris*-type); epihymenium of coarse, hyaline to brown crystals (*chlarotera*-type), sometimes sparse or rarely absent; ascospores ellipsoid to broadly ellipsoid, (7·3–)9·5–*10·8*–12·1(–14·0) × (4·9–)5·5–*6·4*–7·3(–8·7) μm; and secondary metabolites chloroatranorin and zeorin (major), with or without atranorin, and frequently with calycin in yellow portions of the apothecial margins.

Type: USA, Oklahoma, Comanche Co., *c.* 8 mi N, 3 mi E of Cache, Wichita Mountains Wildlife Refuge, vicinity of western terminus of Mt. Hood Bike and Foot Trail, 34·75075°–34·75517°N, 98·58026°–98·57452°W, elevation *c.* 1530–1600 ft, complex of woodlands and scrubby forest dominated by *Juniperus virginiana*, *Quercus marilandica* and *Q. stellata* and extensive glade-like areas of surfacing pink granite bedrock and boulders with little woody vegetation on gentle to moderate, primarily NW-facing slopes on NW end of Mt. Wall, and brushy riparian forest along Cedar Creek dominated by *Fraxinus pennsylvanica, Juglans nigra*, *Q. marilandica*, *Q. stellata*, and *Ulmus* with *Smilax bona-nox* abundant in understorey, on *Q. stellata*, 16 April 2011, *C. A. Morse* 22298a *& K. J. Logan* (KANU—holotype; CANL—isotype).

(Fig. 1)

Thallus to 5 cm diam., crustose, continuous, verruculose; prothallus scant to well developed, white, fibrous; verrucae ± evenly rounded, *c.* 0·2 mm broad; upper cortex smooth, lustrous, pale grey to frequently rough, ± glaucous blue (greenish blue to bluish grey), epruinose, esorediate; older specimens frequently covered with terpenoid crystals.

Apothecia sessile to constricted at base when mature, solitary and ± evenly scattered over the thallus to aggregated, (0·4–)0·6–*0·95*–1·3(–1·7) mm diam. (*n* = 54); *disc* plane, tan, yellowish brown, or more commonly medium brown or reddish brown, occasionally dark reddish brown, typically epruinose, but occasionally sparsely whitish pruinose, especially in smaller apothecia; margins *c.* 0·1 mm thick, entire to verruculose or crenulate, concolorous with thallus or with distinct, pale to bright yellow tones due to the presence of calycin, without a parathecial crown; *amphithecium* with numerous algal cells, with abundant fine crystals (POL+, dissolving in K) and large crystals (*pulicaris*-type; POL+, persisting in K, dissolving in concentrated HNO_3), corticate; cortex hyaline, poorly developed and frequently eroded in older apothecia, *c.* 17 μm thick at top to *c.* 42 μm thick basally, abundantly inspersed with small crystals (POL+, dissolving in K); parathecium hyaline, to 30 μm thick, lacking POL+ crystals or with crystals limited to the uppermost regions; *epihymenium* of coarse, hyaline to brown crystals (*chlarotera*-type; POL+, persisting in K, slowly dissolving in concentrated HNO_3), although sometimes sparsely granular (thus resembling *glabrata*-type); *hymenium* hyaline, 70–80 μm high; *paraphyses* slender, coherent, sometimes slightly expanded at the brown to reddish brown (K+ dull brown) tips, to *c.* 2·5 μm wide; *subhymenium* hyaline, *c.* 25 μm high; *hypothecium* hyaline. *Asci Lecanora*-type, 8-spored, narrowly clavate, 43–58 × 12–13 μm. *Ascospores* colourless, ellipsoid to broadly ellipsoid, (7·3–)9·5–*10·8*–12·1(–14·0) × (4·9–)5·5–*6·4*–7·3(–8·7) μm, l/w ratio = (1·2–)1·5–*1·7*–1·9(–2·3) (*n* = 75), wall 0·50–0·75 μm thick.

Pycnidia common, half-immersed, oblong, 0·12–0·20 μm wide, 0·18–0·30 μm high, apices black, lustrous, the walls appearing

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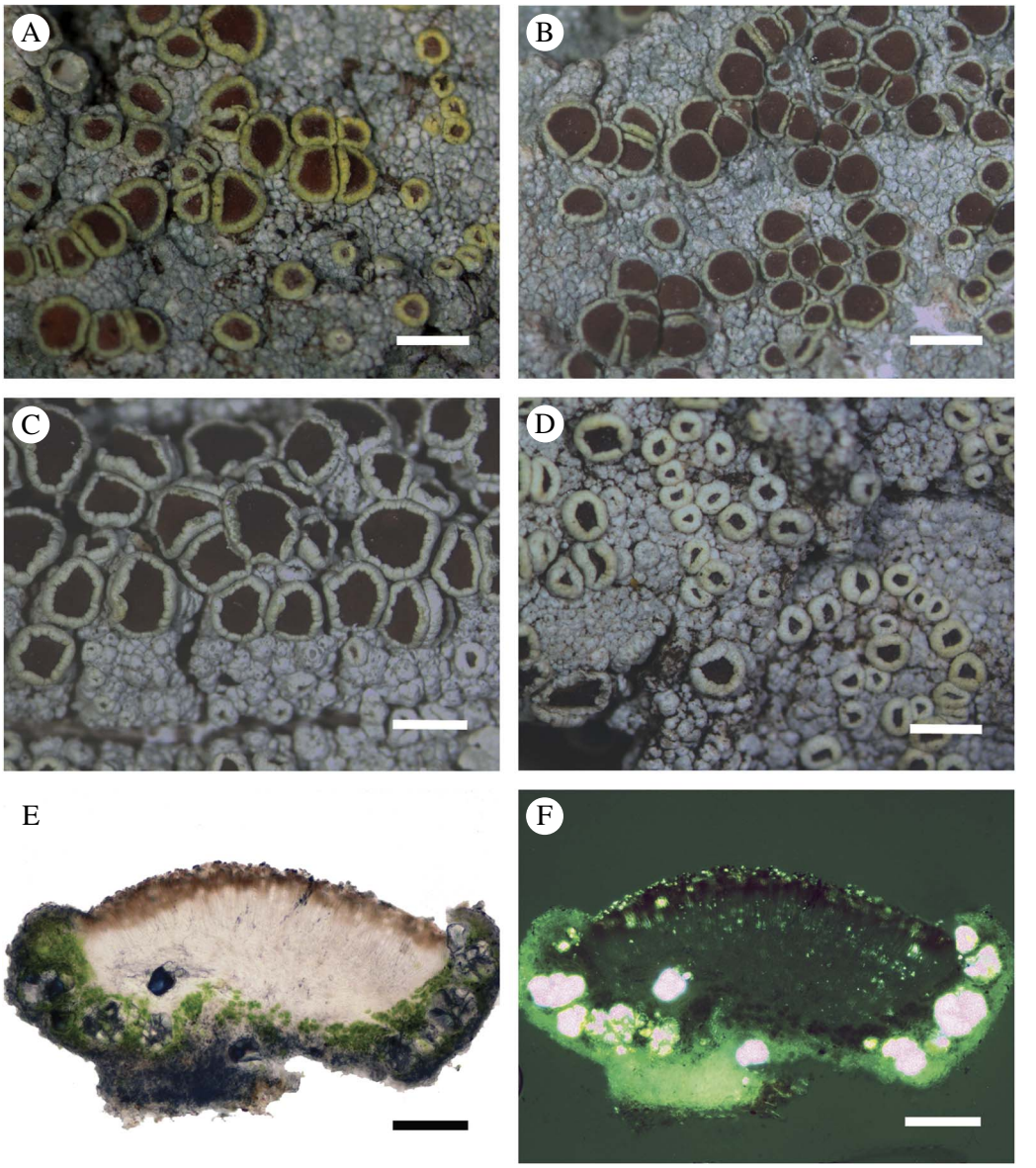

FIG. 1. *Lecanora inaurata*, showing variability in gross morphology. A, apothecia with bright yellow thalline margins (*Morse* 22298a—holotype); B, apothecia with pale yellow margins (*Morse* 22298a—isotype, KANU); C, apothecia with grey margins and reddish brown discs (*Morse* 18509); D, developing apothecia with grey margins and reddish brown discs (*Morse* 23467). E & F, section of apothecium; E, in bright field illumination; F, polarized light (*Morse* 22298a—isotype, KANU). Scales: A–D = 1 mm; E & F = 100 µm.

brown in section; *conidia* colourless, filiform, arcuate, *c.* 19–33 × 1 µm.

Chemistry. TLC (all specimens analyzed): ±atranorin (minor or trace), chloroatranorin (major), zeorin (major), calycin present in yellow portions of apothecial margins, although often not detectable with TLC, several unknown triterpenoids and other unidentified substances variably present.

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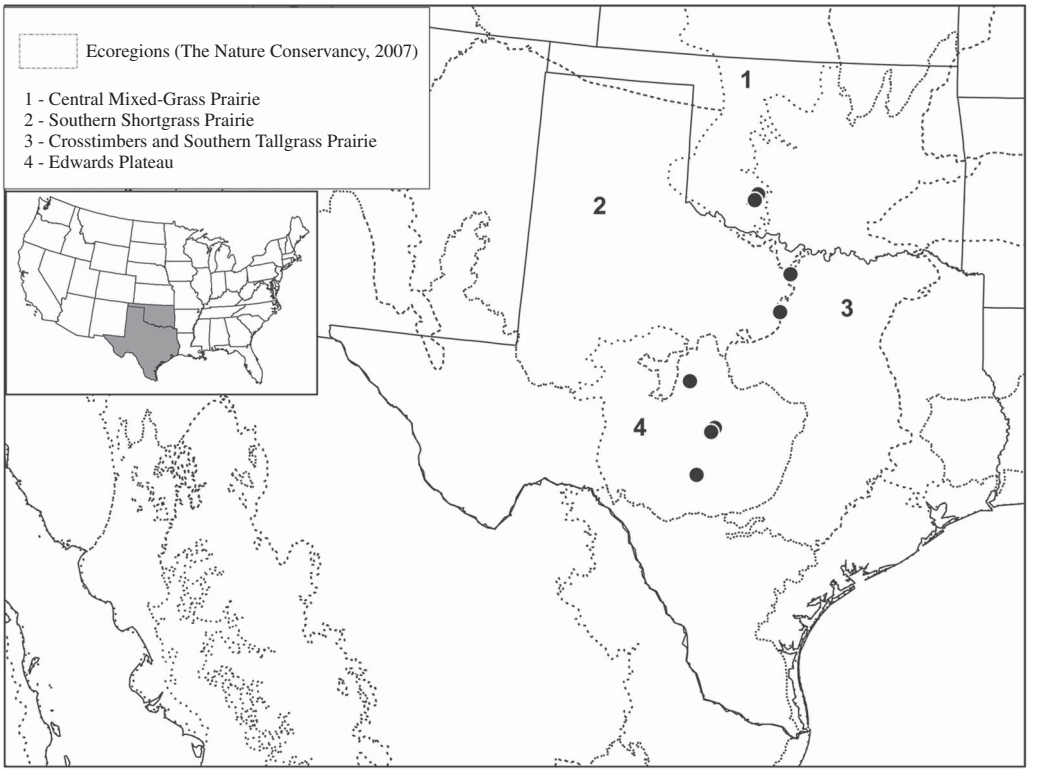

FIG. 2. Distribution of *Lecanora inaurata* in north-central Texas and south-central Oklahoma in central North America together with the ecoregions within which it occurs.

Spot tests of thallus K+ yellow, C−, KC−, P+ yellow, UV−.

Etymology. The common meaning of the Latin adjective *inauratus* is 'overlaid with gold', but it may occasionally mean the opposite, 'not gilded'. We take it up as an apt epithet to describe the thalline margins of *Lecanora inaurata*, only some of which are pale to bright yellow.

Distribution and ecology. Lecanora inaurata is known from open woodlands in north-central Texas and south-central Oklahoma in central North America, where it occurs in the Edwards Plateau ecoregion, and along the eastern edges of grasslands bordering the Cross Timbers ecoregion, at elevations of 275–652 m above sea level (Fig. 2). It grows in moderately shaded to exposed habitats, and has been documented on branches and boles of *Quercus buckleyi*, *Q. fusiformis*, *Q. marilandica*, *Q. stellata*, *Fraxinus pennsylvanica*, *Juniperus ashei*, *J. virginiana*, and *Ulmus crassifolia*. Frequent associates include *Caloplaca camptidia* (Tuck.) Zahlbr., *C. chrysophthalma* Degel., *C. microphyllina* (Tuck.) Hasse, *C. pollinii* (A. Massal.) Jatta, *Haematomma persoonii* (Fée) A. Massal., *Lecanora horiza* (Ach.) Linds., *Parmotrema reticulatum* (Taylor) M. Choisy, *Pertusaria propinqua* Müll. Arg., *Phaeophyscia hirsuta* (Mereschk.) Essl., *Physcia aipolia* (Ehrh. ex Humb.) Fürnr., *Physcia stellaris* (L.) Nyl., *Punctelia bolliana* (Müll. Arg.) Krog, *P. graminicola* (B. de Lesd.) Egan, *Rinodina papillata* H. Magn., and *Xanthomendoza weberi* (S. Kondr. & Kärnefelt) L. Lindblom. The discovery of another new lichen taxon from the Great Plains of central North America adds to a growing body of interesting lichen records from the area (e.g. Sheard *et al.* 2011;

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Westberg *et al*. 2011; Ladd & Morse 2012; Morse & Ladd 2013) and further reinforces both the biological significance of the region and the continuing need for fieldwork in North America.

Discussion. The presence of chloroatranorin in North American members of the *Lecanora subfusca* group is largely unstudied and its taxonomic significance as a major constituent in *L. inaurata* is unclear. Brodo (1984) did not separate atranorin from chloroatranorin, indicating instead the ubiquity of "atranorin *s.l.*" in members of the group. However, Lumbsch (1994*b*), Guderley (1999), Lumbsch *et al.* (2003), and Ryan *et al.* (2004) reported seven tropical and subtropical members of the *L. subfusca* group in which chloroatranorin and zeorin are major constituents and atranorin is minor. Aptroot & van Herk (1999) described *L. barkmaniana* Aptroot & van Herk, a species with this chemistry, from central Europe. Differences between *L. inaurata* and these species (*L. barkmaniana*, *L. casuarinophila* Lumbsch, *L. flavidomarginata* B. de Lesd., *L. fulvastra* Krempelh., *L. glaucodea* Nyl., *L. orizabana* Vain., *L. subalbellina* Vain. (= *L. caesiorugosa* B. de Lesd.; see Guderley 1999), and *L. subumbrina* Müll. Arg.) are summarized in Table 1. None of these taxa appear to have distributions that overlap with that of *L. inaurata*, although *L. casuarinophila*, *L. flavidomarginata*, and *L. orizabana* were documented from the Sonoran region (Lumbsch *et al.* 2003; Ryan *et al.* 2004). Several species listed in Table 1, however, differ only subtly from *L. inaurata* in their morphology, and may be closely related to the new species. In addition to containing usnic acid, *L. flavidomarginata* has densely pruinose apothecia and is occasionally sorediate (*fide* Guderley 1999). *Lecanora fulvastra* has a yellowish white to whitish grey thallus and produces smaller, sessile apothecia with orange to yellow-orange discs, and calycin on the discs rather than the margins (Lumbsch 1994*a*). *Lecanora orizabana* similarly produces a yellowish thallus, typically has entire thalline margins, and the amphithecial cortex is basally thickened to (75–)120(–150) µm (Lumbsch *et al.* 2003). The thallus of *L. subalbellina* is whitish grey or yellowish grey and the apothecial discs are orange to brown and densely pruinose (Lumbsch *et al.* 1997; Guderley 1999).

Thin-layer chromatography performed in conjunction with this study demonstrated that *Lecanora miculata* Ach. also has a chemistry similar to that of *L. inaurata*, with atranorin (minor or absent), chloroatranorin (major), and zeorin (major), but that species also produces lichexanthone in the pruina of the apothecial discs. In addition to its chemistry, *L. miculata* differs from *L. inaurata* in its paler, consistently pruinose apothecial discs (Table 1). *Lecanora miculata* appears to be mostly subtropical, restricted to the south-eastern coastal plain of North America and adjacent regions (Brodo 1984). Its range does not appear to overlap with that of *L. inaurata*.

Lumbsch *et al.* (1995) and Guderley (1999) noted morphological similarities between *Lecanora flavidomarginata* and *L. subalbinella*, even suggesting that broader taxonomic concepts for these entities would lead to them being placed in synonymy. We have considered whether *L. inaurata* could be included in an expanded concept of *L. fulvastra*. Excepting the presence of calycin, however, *L. inaurata* does not appear to be more similar to *L. fulvastra* than it does to most of the species included in Table 1. Indeed, while most of these taxa may occasionally be difficult to distinguish from one another (sharing similar epihymenial and amphithecial characters, as well as a tendency to produce pruinose apothecia, broadly elliptical spores, and secondary chemistry) there is no reason to expect that they are particularly closely related to one another. Papong *et al.* (2012) found some support for utilizing anatomical characters in circumscribing phylogenetic relationships within the *L. subfusca* group. Notably, however, those authors found little support for secondary chemistry as a predictor of relationships. To date, none of the species in Table 1 has been the subject of a molecular phylogenetic study. Members of the *L. subfusca* group sharing these anatomical characters are not limited to the species

TABLE 1. *Members of the* Lecanora subfusca *group reported to produce chloroatranorin + zeorin as major constituents.*

Taxon (references)	Thallus colour	Apothecial diam. (mm)	Apothecial discs	Thalline margin	Epihymenial pigment	Ascospores (µm)	Other features
L. inaurata	pale grey, green-blue to blue-grey	0·4–1·3(–1·7)	tan, medium brown, or red-brown, ±pale grey pruina	concolorous or yellow, thick, entire to verruculose or crenulate	red-brown, dissolving in K	9·5–12·1 × 5·5–7·3	calycin on margins
L. barkmaniana (4)	white-grey to brown-grey	0·4–0·7	pale brown to buff, epruinose	pale grey, crenulate, often sorediate	pale brown, dissolving in K?	7–10 × 3–4	soredia
L. flavidomarginata (3,5,7)	yellow-white to yellow-grey or white-grey to grey	0·4–1·5	bright red-brown to orange-brown or grey-brown, +white to blue-grey pruina	concolorous, thin to thick, not flexuose, entire, verrucose, verruculose, or crenulate	colourless to yellow-brown, dissolving in K	11–15 × 5–8	±soredia; usnic acid
L. fulvastra (2,5)	yellow-white to white-grey, or green-grey	0·3–1·0	red-brown, orange-brown, or yellow-orange, ±yellow or white pruina	concolorous or slightly brighter, thin, entire to verruculose	yellowish, yellow-brown, or orange-brown, dissolving in K	12–15 × 5·0–7·5	calycin in pruina of discs, unidentified triterpenoids
L. glaucodea (5)	white-grey, yellow-grey, or brown-grey	0·4–0·8	orange-brown to brown, +white to blue-grey pruina	concolorous or brighter, verrucose or verruculose	light to dark brown, persistent in K	10·5–13·5 × 6·0–8·5	saxicolous; ±soredia; *pulicaris*-type epihymenium; usnic acid + 2,7-dichloro-3-*O*-methylnorlichexanthone
L. miculata (1)	pale yellow-grey to yellow-white	0·5–0·8(–1·3)	dark to greyish yellow-pink or pale purple-blue, +white pruina	concolorous, thick	yellow-brown, dissolving in K	11–13 × 6–8	lichexanthone in pruina of discs
L. orizabana (6,7)	yellow-grey to yellow-white	0·6–1·6	waxy red to waxy rose or dark red-brown +white to blue-grey pruina	concolorous, thick, entire	dark red-brown to dark brown, dissolving in K	9·5–15·5 × 6·5–9·0	cortex of thalline margin to 75 (120)150 µm thick at base
L. subalbellina (5)	white-grey, seldom yellowish brown-grey	0·4–1·2	orange, orange-brown, or brown, +pale grey pruina	concolorous, brighter, or seldom yellow-white, entire to verruculose	light brown, dissolving in K	11·5–14·0 × 5·5–8·5	atranorin occasionally major, chloroatranorin occasionally minor
L. subumbrina (3)	yellow-white to white-grey	0·2–0·7(–1)	light brown to orange-brown, +pale grey pruina	concolorous, entire to verruculose	red-brown, dissolving in K	14·5–20·5 × 4·5–6·5	2,4-dichloronorlichexanthone, 2,5-dichloronorlichexanthone, thiophanic acid

References: 1, Brodo (1984); 2, Lumbsch (1994*a*); 3, Lumbsch (1994*b*); 4, Aptroot & van Herk (1999); 5, Guderley (1999); 6, Lumbsch *et al.* (2003); 7, Ryan *et al.* (2004).

discussed here, and it is not unreasonable to expect that a study including a broader taxonomic sample will show that the replacement of atranorin with chloroatranorin as a major constituent has occurred more than once within the group, or that species containing chloroatranorin and zeorin as major constituents are closely related to species with a different chemistry.

The majority of the *Lecanora* species described by Bouly de Lesdain (1914) from Mexico have been treated by other authors (Lumbsch 1994*b*; Printzen 2001; Ryan *et al.* 2004). The species *L. azulensis* B. de Lesd., however, has not been the subject of modern revision. Syntypes (México: *Michoacán*: Morelia, Cerro Azul, *Arsène* 3776, 3777) apparently were not discovered during exhaustive searches by Lumbsch (1994*b*) or Guderley (1999), and were not located by us. *Lecanora azulensis* was described by Bouly de Lesdain (1914) as having a finely granulose-rugose thallus, sessile, epruinose apothecia, 1·0–1·5 mm diam., with pale red discs and a flexuose margin, a yellow, granulose epithecium, and slightly larger spores, 13–15 (–17) × 7–9 µm. The correct application of this name remains uncertain.

With the exception of *Lecanora miculata*, the species with a *chlarotera*-type epihymenium treated by Brodo (1984) lack zeorin and typically contain other secondary metabolites. However, specimens of *L. inaurata* examined for this study demonstrated some variability in the presence and abundance of epihymenial granules. For instance, crystals were abundant in *Morse* 23455, sparse in *Morse* 23467, and essentially absent in *Morse* 23570. Brodo (1984) commented on a similar pattern of variability in *L. pseudargentata* Lumbsch (= *L. sp. 2* of Brodo 1984). Specimens of *L. inaurata* with grey apothecial margins and sparse epihymenial crystals might be confused with *L. pseudargentata* or with a species with a *glabrata*-type epihymenium, such as *L. argentata* (Ach.) Malme, *L. perplexa* Brodo, or *L. subrugosa* Nyl. *Lecanora argentata*, *L. pseudoargentata*, and *L. subrugosa* all lack zeorin and produce other secondary metabolites, and their ranges do not overlap with *L. inaurata* (Brodo 1984). *Lecanora perplexa* differs from *L. inaurata* in having a white to yellowish grey or greenish grey, often distinctly granular thallus, in having slightly larger spores ((10·5–)12·0–15·5(–16·5) × (6·0–)7·0–8·5(–9·5) µm *fide* Brodo 1984), and in its chemistry. Examination by TLC of *L. perplexa* revealed atranorin, zeorin, and an unidentified triterpenoid below zeorin in solvent system A; calycin and chloroatranorin were absent. *Lecanora perplexa* is known from eastern North America and South America (Argentina) (Brodo 1984; Guderley 1999).

In the field, *Lecanora inaurata* may be confused with several other corticolous members of the *L. subfusca* group known from the region. The most common of these are *L. chlarotera* Nyl., *L. meridionalis* H. Magn., and *L. horiza*, which occur in association with the new species. Even when the distinctive yellow apothecial margins are lacking, *L. inaurata* can be distinguished from *L. chlarotera* and *L. meridionalis* by its larger, reddish brown apothecia with verruculose thalline margins and blue-grey thallus, as opposed to the smaller, sessile, greyish brown (in *L. chlarotera*) or black (in *L. meridionalis*) apothecia with entire thalline margins and white to pale grey thalli. *Lecanora inaurata* can be distinguished in the field from *L. horiza* by its blue-grey, verruculose thallus and yellow or concolorous margins, as opposed to the pale grey to greenish grey, typically smooth, rimose thallus with brighter, whitish apothecial margins of *L. horiza*; in some cases, however, identification may require confirmation of anatomical differences in the apothecia. All of these species produce atranorin as a major constituent and lack zeorin.

In Kerr County, Texas, *Lecanora inaurata* occurred in close proximity to a morphologically similar species, which contained atranorin and usnic acid (*Morse* 23590). This taxon was strikingly similar to forms of *L. inaurata* with pale yellow apothecial margins, also producing yellowish margins, and differed primarily in having a paler grey thallus and yellowish brown apothecial discs. However, confirmation of the presence of atranorin and usnic acid in *Morse* 23590, and absence of zeorin, was required to separate

the two species with certainty. The identity of this taxon is uncertain. It is similar both to *L. achroa* Nyl., differing from that species primarily in producing larger apothecia (to 1·3 mm diam.) with constricted bases and in lacking xanthones and 2′-*O*-methylperlatolic acid (Guderley 1999; Ryan *et al.* 2004), and to *L. demosthenesii* Lumbsch *et al.*, differing from that species in having apothecia with constricted (not stipitate) bases, a thinner amphithecial cortex (*c.* 20 µm), broadly ellipsoid spores (8·2–12·6 ×4·9–8·4 µm) and in producing only atranorin and usnic acid (both major) (Lumbsch *et al.* 2003).

The presence of calycin is unusual in *Lecanora*, but has been reported from the thallus and pruina of apothecial discs of the Himalayan *L. somervellii* Paulson, the thallus of the Macaronesian *L. sulphurella* Hepp, and in *L. fulvastra* (Lumbsch 1994*a* and references therein), of which only the last is similar to *L. inaurata*. In this study, calycin was confirmed by TLC only in a population producing particularly bright yellow margins (*Morse* 22298a). The substance appears to be present in varying amounts in *L. inaurata*, and thalli with concolorous margins occurred adjacent to thalli with distinctly (albeit often pale) yellow apothecial margins in all populations studied. We presume the latter thalli also contained calycin, although our attempts to isolate the substance by TLC were mostly unsuccessful. Śliwa *et al.* (2014) reported similar difficulty in identifying calycin in *L. fulvastra* by TLC, attributing this to the small amount of material analyzed for their study.

Specimens examined. **USA:** *Oklahoma*: Comanche Co., *c.* 4·25 mi N, 2·0–2·5 mi W of Cache, Wichita Mountains Wildlife Refuge, N side of Eagle Mountain and vicinity of The Narrows, 34·70°N, 98·67°W, 2010, *Morse* 20565 (KANU). *Texas*: Coleman Co., *c.* 9–10 mi S, 9–10 mi W of Valera, Jane Padgitt Ranch, 31·61°N, 99·71°W, 2012, *Morse* 23406 *& Freeman* (KANU); Kerr Co., *c.* 4·5 mi S, 7·75 mi W of Mountain Home, Kerr Wildlife Management Area, 30·11°N, 99·50°W, 2012, *Morse* 23625 *& Freeman* (KANU); Mason Co., *c.* 6·5 mi N, 2 mi E of jct of Ranch Rd 386 & US Hwy 87/377 in Mason, Mason Mountain Wildlife Management Area, 30·84°N, 99·20°W, 2012, *Morse* 23455 *& Freeman, Morse* 23467 *& Freeman* (both KANU); *c.* 5 mi N of jct of Ranch Rd 386 & US Hwy 87/377 in Mason, Mason Mountain Wildlife Management Area, 30·83°N, 99·22°W, 2012, *Morse* 23555 *& Freeman*, *Morse* 23570 *& Freeman* (both KANU); Montague Co., *c.* 0·5 mi N, 6·25 mi W of Sunset, property of Wayne and Jeanne Erickson, E-W-trending ridge above Lake Amon G. Carter, 33·46°N, 97·87°W, 2009, *Morse* 18672 *& Ladd* (KANU); Parker Co., *c.* 2 mi N, 4·5 mi E jct of US Hwys 180W and 281 in Mineral Wells, Lake Mineral Wells State Park, NW side of lake, just N and E of Cross Timbers Camping Area, 32·83°N, 98·04°W, 2009, *Morse* 18509 *& Ladd*, *Morse* 18527 *& Ladd* (both KANU).

Other specimens examined. Lecanora aff. achroa: **USA:** *Texas*: Kerr Co., *c.* 4·5 mi S, 7·75 mi W of Mountain Home, Kerr Wildlife Management Area, 30·11°N, 99·50°W, 2012, *Morse* 23590 *& Freeman* (KANU).

Lecanora miculata: **USA:** *Arkansas*: Franklin Co., Ozark National Forest, *c.* 1·5 mi E of Shores Lake, along FS 1501 at bridge over Spirits Creek, near junction with FS 1515, 35°37′58″N, 93°58′29″W, 2005, *Ladd* 27601 (hb. Ladd); Howard Co., Stone Road Glade, *c.* 1·7 mi W of Hwy 369, E of Dawson Creek, *c.* 7 mi ESE of Dierks, 1996, *Ladd* 19681 (hb. Ladd); Stone Co., *c.* 0·1 mi N, 2·4 mi E of Fifty-Six, Ozark National Forest, Blanchard Springs Recreation Area, near Blanchard Spring and circle parking area for spring, 35·96°N, 92·17°W, 410–500 ft, 2014, *Morse* 24273 *et al.* (KANU).

Lecanora perplexa: **Canada:** *Ontario*: Navan, 1902, *collector unknown* s.n. (CANL); Thunder Bay District, SE of Marathon, S of Heron Bay, 1962, *Henssen* 14276p *& Cain* (CANL); Thunder Bay District, Ouimet, at Ouimet Canyon, 48°45′N, 88°35′W, 1954, *Brodo* 6070 *et al.* (CANL). *Quebec*: Ottawa Region, 3·5 mi N of Mayo, along the Rivière Blanche, 45°42′N, 75°21′W, 800–900 ft, 1980, *Brodo* 23585 *et al.* (CANL).

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References

Aptroot, A. & van Herk, C. M. (1999) *Lecanora barkmaneana*, a new nitrophilous sorediate corticolous lichen from the Netherlands. *Lichenologist* **31:** 3–8.

Bouly de Lesdain, M. (1914) *Lichens du Mexique (états de Puebla et Michoacán) Recueillis par le Frère G. Arsène Brouard*. Mexico: Imprenta I. Escalante.

Brodo, I. M. (1984) The North American species of the *Lecanora subfusca* group. *Beihefte zur Nova Hedwigia* **79:** 63–185.

Brodo, I. M., Owe-Larsson, B. & Lumbsch, H. T. (1994) The sorediate, saxicolous species of the *Lecanora subfusca* group in Europe. *Nordic Journal of Botany* **14:** 451–461.

Brodo, I. M., Sharnoff, S. D. & Sharnoff, S. (2001) *Lichens of North America*. New Haven, London: Yale University Press.

Edwards, B., Aptroot, A., Hawksworth, D. L. & James, P. W. (2009) *Lecanora* Ach. in Luyken (1809). In *The Lichens of Great Britain and Ireland* (C. W. Smith, A. Aptroot, B. J. Coppins, A. Fletcher, O. L. Gilbert, P. W. James & P. A. Wolseley, eds): 465–502. London: British Lichen Society.

Guderley, R. (1999) Die *Lecanora subfusca*-Gruppe in Süd- und Mittelamerika. *Journal of the Hattori Botanical Laboratory* **87:** 131–257.

Ibáñez, I. & Burgaz, A. R. (1998) Epiphytic species of the *Lecanora subfusca* group (*Lecanoraceae*) in Spain. *Nova Hedwigia* **67:** 45–58.

Kondratyuk, S. Y., Kim, J., Kondratyuk, A. S., Jeong, M.-H., Jang, S.-H., Pirogov, M. V. & Hur, J.-S. (2014) First data on molecular phylogeny of the genus *Protoparmeliopsis* M. Choisy (*Lecanoraceae*, Ascomycota). *Modern Phytomorphology* **5:** 63–68.

Ladd, D. & Morse, C. A. (2012) Endemism lost: *Lecanora pallidochlorina* (*Lecanorales*, lichenized Ascomycotina) in the Great Plains, U.S.A. *Opuscula Philolichenum* **11:** 60–63.

Lendemer, J. C. (2015) *Lecanora layana* (*Lecanoraceae*), a new sorediate species widespread in temperate eastern North America. *Bryologist* **118:** 145–153.

Lumbsch, H. T. (1994*a*) Calycin in *Lecanora fulvastra*. *Lichenologist* **26:** 94–96.

Lumbsch, H. T. (1994*b*) Die *Lecanora subfusca*-Gruppe in Australasien. *Journal of the Hattori Botanical Laboratory* **77:** 1–175.

Lumbsch, H. T., Feige, G. B. & Elix, J. A. (1995) A revision of the usnic acid containing taxa belonging to *Lecanora sensu stricto* (*Lecanorales*: lichenized Ascomycota). *Bryologist* **98:** 561–577.

Lumbsch, H. T., Guderley, R. & Elix, J. A. (1996) A revision of some species of *Lecanora sensu stricto* with a dark hypothecium (*Lecanorales*, Ascomycotina). *Bryologist* **99:** 269–291.

Lumbsch, H. T., Plümper, M., Guderley, R. & Feige, G. B. (1997) The corticolous species of *Lecanora sensu stricto* with pruinose apothecial discs. *Symbolae Botanicae Upsalienses* **32(1):**131–162.

Lumbsch, H. T., Messuti, M. I. & Nash, T. H., III. (2003) New or overlooked species in the *Lecanora subfusca* group from southwestern North America (*Lecanorales*, Ascomycotina). *Bryologist* **106:** 552–559.

Malíček, J. (2014) A revision of the epiphytic species of the *Lecanora subfusca* group (*Lecanoraceae*, Ascomycota) in the Czech Republic. *Lichenologist* **46:** 489–513.

Miądlikowska, J., Kauff, F., Högnabba, F., Oliver, J. C., Molnár, K., Fraker, E., Gaya, E., Hafellner, J., Hofstetter, V., Gueidan, C., *et al.* (2014) A multigene phylogenetic synthesis for the class Lecanoromycetes (Ascomycota): 1307 fungi representing 1139 infrageneric taxa, 317 genera and 66 families. *Molecular Phylogenetics and Evolution* **79:** 132–168.

Miyawaki, H. (1988) Studies on the *Lecanora subfusca* group in Japan. *Journal of the Hattori Botanical Laboratory* **64:** 271–326.

Morse, C. A. & Ladd, D. (2013) A new species of *Fellhanera* (lichenized Ascomycota: *Pilocarpaceae*) from central North America. *Lichenologist* **45:** 341–346.

Orange, A., James, P. W. & White, F. J. (2001) *Microchemical Methods for the Identification of Lichens*. London: British Lichen Society.

Papong, K., Boonpragob, K., Parnmen, S. & Lumbsch, H. T. (2012) Molecular phylogenetic studies on tropical species of *Lecanora sensu stricto* (*Lecanoraceae*, Ascomycota). *Nova Hedwigia* **96:** 1–13.

Printzen, C. (2001) Corticolous and lignicolous species of *Lecanora* (*Lecanoraceae*, *Lecanorales*) with usnic or isousnic acid in the Sonoran Desert region. *Bryologist* **104:** 382–409.

Rodrigues, S. A., Terrón-Alfonso, A., Elix, J. A., Pérez-Ortega, S., Tønsberg, T., Fernández-Salegui, A. B. & Soares, A. M. V. M. (2011) *Lecanora sorediomarginata*, a new epiphytic lichen species discovered along the Portuguese coast. *Lichenologist* **43:** 99–111.

Ryan, B. D., Lumbsch, H. T., Messuti, M. I., Printzen, C., Śliwa, L. & Nash, T. H., III (2004) *Lecanora*. In *Lichen Flora of the Greater Sonoran Desert Region, Vol. 2.* T. H. Nash III, B. D., Ryan, P. Diederich, C. Gries & F. Bungartz, eds): 176–286. Tempe, Arizona: Lichens Unlimited, Arizona State University.

Sheard, J. W., Knudsen, K., Mayrhofer, H. & Morse, C. A. (2011) Three new species of *Rinodina* (*Physciaceae*) and a new record from North America. *Bryologist* **114:** 453–465.

Śliwa, L., Flakus, P. R., Wilk, K. & Flakus, A. (2014) New records of *Lecanora* for Bolivia. II. *Polish Botanical Journal* **59:** 97–103.

The Nature Conservancy (2007) *TNC Terrestrial Ecoregions* (vector digital data). Arlington, Virginia: The Nature Conservancy.

Upreti, D. K. (1997) Notes on corticolous, K+ yellow species of *Lecanora* in India. *Feddes Reportorium* **108:** 185–203.

Upreti, D. K. (1998) Notes on saxicolous species of the *Lecanora subfusca* group in India. *Bryologist* **101:** 256–262.

Upreti, D. K. & Chatterjee, S. (1997) Notes on some Indian species of *Lecanora* s. str. with a dark hypothecium. *Feddes Repertorium* **108:** 575–582.

Westberg, M., Morse, C. A. & Wedin, M. (2011) Two new species of *Candelariella* and a key to the *Candelariales* (lichenized Ascomycetes) in North America. *Bryologist* **114:** 325–334.