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Staurothele nemorum sp. nov. (Ascomycota: *Verrucariaceae*), with a revised key to North American *Staurothele* s. lat.

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Abstract: *Staurothele nemorum* is described as new to science from the southern Great Plains of central North America. The species is characterized by a thin, areolate, epilithic thallus, sessile perithecia, globose to oblong hymenial algal cells and 8-spored asci. *Staurothele hymenogonia* is restored to the North American flora, based on material from the south-western Great Plains. An updated key to North American members of *Staurothele* s. lat. is provided.

Key words: *Endocarpon*, glade, grassland, lichens, taxonomy, *Willeya*

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Introduction

Staurothele Norman s. lat. comprises *c.* 70 species of crustose *Verrucariaceae* with (1)2 or (4)8 muriform ascospores per ascus. Members of the genus contain a stichococcoid alga in their hymenia, a character shared with *Endocarpon* Hedw. Although not particularly closely related, *Endocarpon* species are similar to members of the core of *Staurothele* (including the type, *S. clopima* (Wahlenb.) Th. Fr.) in producing 2(–4) brown ascospores per ascus, but they differ in their squamulose habit and in having a eucorticate upper cortex, while *Staurothele* species are crustose and produce a pseudocortex; the two genera may also differ in their pycnidium types (Gueidan *et al.* 2007, 2009). Recent studies by Gueidan and colleagues have shown that members of *Staurothele* s. lat. with pseudocorticate, epilithic thalli with immersed perithecia and (6–)8, colourless ascospores per ascus belong to *Willeya* Müll. Arg.; members of *Willeya* may also share a common pycnidium type with *Endocarpon* (Gueidan *et al.* 2014). Two other species, *S. immersa* Dalla Torre & Sarnth. and *S. rupifraga* (A. Massal.) Arnold, with perithecia immersed in the substratum and (2–)4–8 red to brown ascospores per ascus, belong to a poorly resolved group that includes species currently assigned to *Polyblastia* A. Massal., *Thelidium* A. Massal. and *Verrucaria* Scop. (Gueidan *et al.* 2009). However, to date, only a handful of taxa have been studied (Gueidan *et al.* 2009) and the disposition of several 8-spored, European taxa remains uncertain. *Staurothele* s. lat. has been well documented in North America (Thomson 1991, 2002; Lendemer 2008; Gueidan & Lendemer 2015; McCune 2017); 19 species of *Staurothele* and one species of *Willeya* are currently reported (Esslinger 2018). Here we describe a new species of *Staurothele* s. lat. from the southern Great Plains of central North America.

Materials and Methods

Specimens were studied dry using dissecting microscopes. Microscopic characters were observed on material mounted in water, 10% KOH (K), Lugol's iodine (I), or K followed by I (KI). Measurements were made in water to the nearest 0·1 μm and 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)). Correlation coefficients (r) were calculated for the relationship between length and width of hymenial algal cells observed in two species

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examined for this study and are reported in the caption for Fig. 4. Associated taxa are provided below without taxonomic authorities. Concepts follow Esslinger (2018), where readers may find full author citations.

Taxonomy

Staurothele nemorum C. A. Morse & Ladd sp. nov.

MycoBank No.: MB 832393

A member of *Staurothele* s. lat. with a thin, areolate, epilithic thallus; sessile perithecia 0·2–0·3(–0·4) mm wide; hymenial algal cells globose to oblong or cuboid, (2·6–)3·3–*4·0*–4·7(–6·25) × (1·6–)2·7–*3·2*–3·7(–5·3) µm, l/w ratio = (0·9–)1·1–*1·3*–1·4(–2·1); and asci producing 8 hyaline or pale-coloured ascospores, (17·3–)23·8–*27·6*–31·4(–38·6) × (9·05–)11·5–*13·0*–14·4(–16·4) µm, l/w ratio = (1·3–)1·8–*2·1*–2·5(–2·9).

Type: USA, Kansas, Douglas Co., 1·75 mi N, 0·5 mi W of junction of US Highway 56 & Douglas County Road 1055 in Baldwin City, University of Kansas Ecological Reserves, north-west corner of Breidenthal Biological Reserve and south-east corner of Forest Legacy Tract, near 38·80845°N, 95·19566°W, 18 September 2018, *Morse et al.* 26478 (KANU 411414—holotype, isotype; hb. Ladd—isotype).

(Fig. 1)

Thallus visible at least near perithecial bases, thin, pale tan or grey to typically greyish green, granular or more commonly roughened-verrucate and ±continuous to weakly rimose or of flattened areoles, irregular in shape or occasionally incised, dispersed to crowded, occasionally subsquamulose when crowded, with margins ascending, *c.* 0·1–0·3 mm diam., to *c.* 0·3 mm thick; *cortex* poorly developed, 6·3–18·9 µm high, pale brown in section, of rounded cells *c.* 4·4–6·3 diam., these often crushed; *thalline algal layer* to *c.* 90 µm thick, cells spherical to slightly oblong, 6·5–12·2 µm long.

Perithecia dispersed or weakly aggregated in small groups, black, rough, 0·2–0·3(–0·4) mm wide, typically sessile to barely immersed in thallus (not in pits in rock) or occasionally with small amounts of attached thallus, rarely more or less covered with thallus and appearing verrucose (*Morse* 14795b); *ostiole* apical, slightly depressed, typically pale; *involucrellum* extending to base of exciple, indistinguishable from exciple laterally but often separating slightly at base, dark brown (black in K) except near ostiole, where cells thick-walled, angular, *c.* 5·0–7·5 × 2·5–3·5 µm, *c.* 50–80(–93) µm thick laterally; *exciple* medium brown to dark brown below hymenium, *c.* 20–45 µm thick; *centrum c.* 200–245 µm high × 230–325 µm wide; *hymenial gel* I+ red, KI+ blue; *periphyses* ± simple, slender, distal cells often curved or uncinate, 22–34 × 2·0–3·6 µm; *hymenial algal cells* globose to oblong or cuboid, (2·6–)3·3–*4·0*–4·7(–6·25) × (1·6–)2·7–*3·2*–3·7(–5·3) µm, l/w ratio = (0·9–)1·1–*1·3*–1·4(–2·1) ($n = 233$); *asci* KI–, broadly clavate, (6?) 8-spored, 87–115 × 25–51 µm; *ascospores* ellipsoid to broadly clavate, colourless to very pale yellowish brown, muriform, with 5–8(–9) longitudinal septa and (1–)2–3(–4) transverse septa, (17·3–)23·8–*27·6*–31·4(–38·6) × (9·05–)11·5–*13·0*–14·4(–16·4) µm, l/w ratio = (1·3–)1·8–*2·1*–2·5(–2·9) ($n = 128$).

Pycnidia rare (only one observed), black, minute, *c.* 0·06 mm diam.; *conidia* broadly bacilliform, 3·0–3·2 × 1·0–1·2 µm.

Etymology. The specific epithet (Latin, genitive plural from *nemus, -oris*, wood with open glades) refers to the occurrence of the new species in glades and glade-like openings, and in woodlands of the southern Great Plains.

Distribution and ecology. Staurothele nemorum is known from the southern Great Plains in central North America, occurring in the Central Tallgrass Prairie, Osage Plains/Flint Hills Tallgrass Prairie, Central Mixed-Grass Prairie, Cross Timbers and Southern Tallgrass Prairie, Edwards Plateau and Tamaulipan Thorn Scrub ecoregions (The Nature Conservancy 2007) (Fig. 3). Specimens were collected on pebbles and cobbles of limestone and calcareous sandstone at elevations of 237–420 m above sea level. In eastern Kansas and Missouri, the species occurred in rocky tallgrass prairies and overgrown limestone glade or glade-like communities, in moderately to highly disturbed sites, while a specimen from south-central Kansas (*Morse* 17442b) occurred on calcareous sandstone outcrops along a north-facing road cut in a highly agricultural

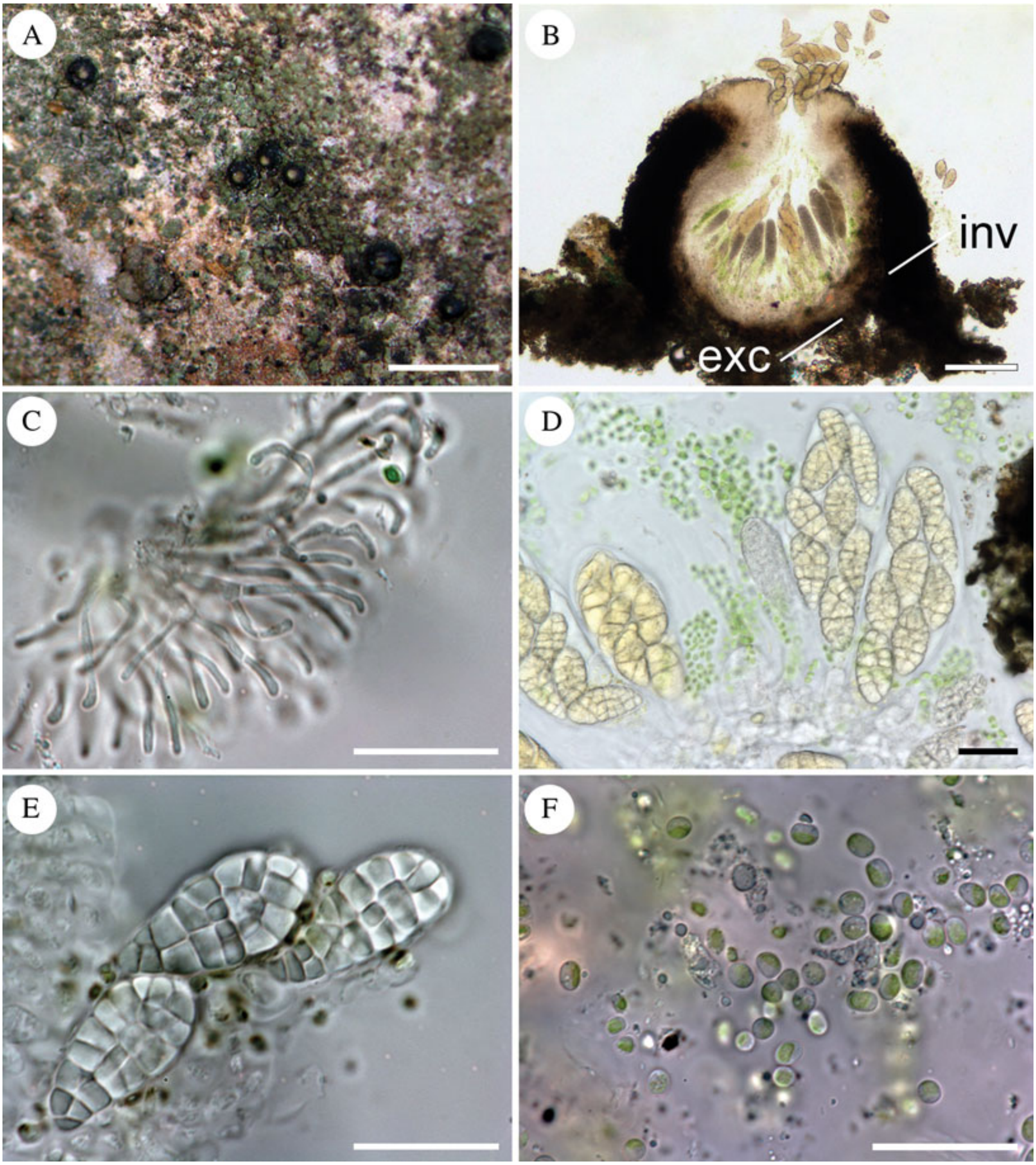

FIG. 1. *Staurothele nemorum*. A, habitus (*Morse* 26478); B, sectioned perithecium showing separation of involucrellum (inv) and exciple (exc) near base of exciple (*Morse* 26478); C, periphyses in 10% KOH (*Morse* 26478); D, ascospores in perithecial section (*Morse* 26478); E, ascospores (*Morse* 14795b); F, hymenial algal cells (*Morse* 26835). Scales: A = 1·0 mm; B = 100 μm; C–F = 20 μm. In colour online.

landscape. Material from Oklahoma was collected from calcareous sandstone fragments (*Morse* 14795b *&* *Ladd*) and cobbles (*Morse* 18788b *&* *Ladd*) in Cross Timbers woodland; specimens from Texas were collected on limestone pebbles in a juniper-oak woodland (*Tucker & Lievens* 30933) and *Acacia*-dominated Tamaulipan thorn scrub (*Morse* 23712b *et al.*). The species appears to be restricted to xeric sites, often on south or

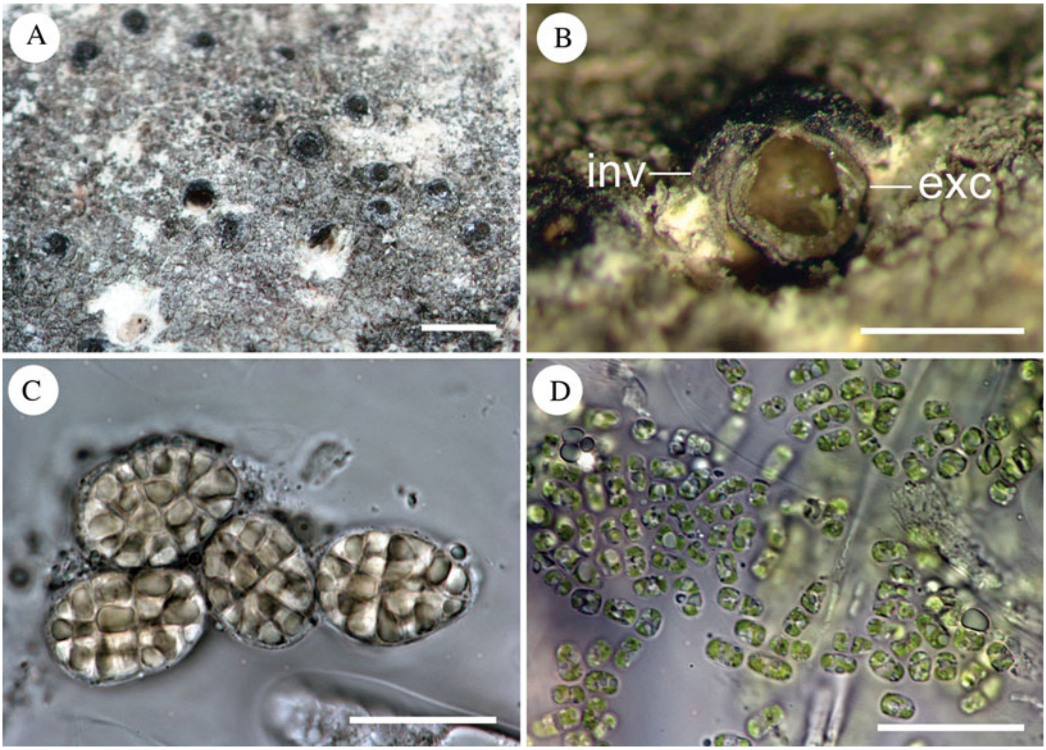

FIG. 2. *Staurothele hymenogonia* (*Morse* 17994). A, habitus; B, sectioned perithecium showing spreading involucrellum (inv) and exciple (exc); C, ascospores; D, hymenial algal cells. Scales: A = 1·0 mm; B = 0·5 mm; C & D = 20 µm. In colour online.

west-facing exposures, and well removed from permanent streams, although some sites may be subject to precipitation-associated run-off. Associated taxa on limestone included *Endocarpon pallidulum*, *E. petrolepidium*, *Monoblastiopsis konzana*, *Peltula obscurans* var. *deserticola*, *Sarcogyne regularis*, *Thelidium zwackhii*, *Verrucaria calkinsiana* and other unidentified species of *Verrucaria*. Associates on sandstone included *Anisomeridium distans*, *Thelidium minutulum*, *T. zwackhii* and an unidentified species of *Verrucaria*.

Discussion. The new species is similar to several other members of *Staurothele* s. lat. that produce (4)8-spored asci. *Staurothele nemorum* differs from *S. succedens* (Rehm. ex Arnold) Arnold in its thallus (areolate vs. lobed or branched, goniocyst-like elements), globose to broadly oblong hymenial algal cells (l/w ratio = 1·1–1·4(–2·1) vs. 1·3–4·5), narrower ascospores (11·5–14·4(–16·4) µm vs. (15–)17·0–21·5(–23) µm), and habitat. While *S. nemorum* occurs in exposed sites, away from areas of regular water flow, *S. succedens* occurs on damp substrata in humid sites or on regularly wetted rocks, for instance in splash zones along water courses or near waterfalls (Orange *et al.* 2009; Thüs & Schultz 2009). *Staurothele succedens* is known from Great Britain and Scandinavia, as well as mountainous areas of central and southern Europe, and western Asia (Breuss & John 2004; Orange *et al.* 2009; Thüs & Schultz 2009; Valadbeigi & Sipman 2010). McCarthy *et al.* (2017) reported *S. succedens* from sheltered, alpine limestone in Tasmania, albeit somewhat tentatively due to differences in the dimensions of hymenial algal cells in their material. The new species may be

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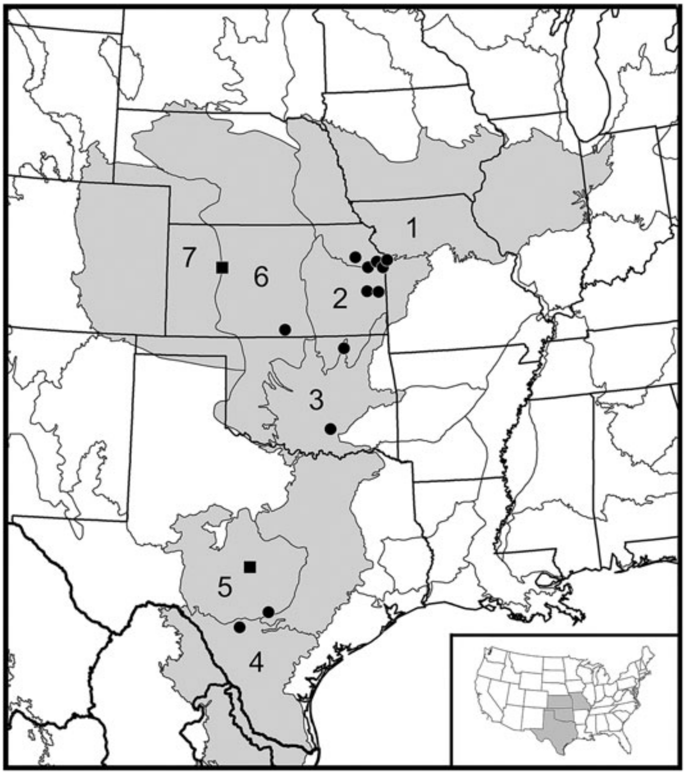

FIG. 3. Distribution of *Staurothele nemorum* (circles) and *S. hymenogonia* (squares) in North America, with the ecoregions within which the species have been documented. Ecoregions: 1 = Central Tallgrass Prairie; 2 = Osage Plains/Flint Hills; 3 = Cross Timbers and Southern Tallgrass Prairie; 4 = Tamaulipan Thorn Scrub; 5 = Edwards Plateau; 6 = Central Mixed-Grass Prairie; 7 = Central Shortgrass Prairie. Inset map of continental USA showing the states from which the species are known.

distinguished from *S. rugulosa* (A. Massal.) Arnold by its poorly developed thallus with flat areoles (to *c.* 200 µm high vs. well developed, 400–600 µm high, *fide* Swinscow (1963)), sessile perithecia (vs. half to fully immersed in the thallus) which are slightly smaller (to 0·3 mm in diam. vs. to 0·5 mm in diam.), and its slightly narrower ascospores (11·5–14·4(–16.4) µm vs. 12–20 µm, *fide* Wirth *et al.* (2013); 18·0–20·5 µm, *fide* Orange *et al.* (2009)). In addition, while the ascospores of *S. nemorum* are frequently pale yellowish brown, those of *S. rugulosa* are reported to be colourless throughout development (Orange *et al.* 2009). Differences between *S. nemorum* and *S. rugulosa* are largely a matter of degree, however, and the two species may be closely related. *Staurothele rugulosa* has been reported from Great Britain and central and southern Europe (Orange *et al.* 2009), and Asia (Oran & Öztürk 2007; Sinha *et al.* 2015). However, the characterization of material of *S. rugulosa* from India that forms the basis of a recent report (Sinha *et al.* 2015) differs from descriptions of European material (principally, in producing a rimose-areolate thallus with flat to slightly concave areoles and asci with 4 ascospores) and perhaps represents a distinct species. *Staurothele nemorum* differs from *S. hymenogonia* (Nyl.) Th. Fr. in its epilithic thallus and perithecia that are not immersed in its rock substratum and are smaller (to 0·3(–0·4) mm vs. to 0·6 mm in diam., *fide* Orange *et al.* (2009); 0·5–1·0 mm in diam., *fide* Wirth *et al.* (2013)). In *S. nemorum*, the involucrellum is mostly indistinguishable from the exciple laterally (Fig. 1B), while in specimens of *S. hymenogonia* examined for this study the involucrellum was found to be spreading and distinct except in the upper 1/3 to 1/4 of the exciple (Fig. 2B). In addition, hymenial algal cells are more regularly isodiametric in *S. nemorum* than in *S. hymenogonia* (l/w ratio = 1·1–1·4(–2·1) vs. 1·1–2·2(–3·3); l/w ratio = 1·3–2·5 times in *S. hymenogonia*, *fide* Orange *et al.* (2009)). *Staurothele hymenogonia* was removed from the North American checklist by Thomson (1991) but is restored here based on recently collected specimens, as described and discussed below.

Among 8-spored taxa previously documented for North America, *S. nemorum* may be distinguished from the south-western *S. verruculosa* Thomson by its thallus (areolate vs. 'subisidiose' and verruculose), thinner involucrellum (50–80(–93) µm vs. 125–150 µm), typically 8-spored (vs. 4(–8)-spored) asci, and ascospores that are 5–8(–9) × 2–3 septate (vs. 5–7 × 1–2 septate; Thomson 1991). In addition, while Thomson (1991) reported the ascospores of *S. verruculosa* to be 12–25 µm wide, ascospores of *S. nemorum* examined during this study did not exceed 16·4 µm in width. Thomson (1991) did not include descriptions of hymenial algal cells in his revision of North American *Staurothele*. However, examination of the holotype of *S. verruculosa* (*Nash* 8397; ASU 69276) shows them to be bacilliform. *Willeya diffractella* (Nyl.) Müll. Arg. (including *Staurothele tenuissima* Degel.; see Gueidan & Lendemer 2015), which is common throughout eastern North America, including the south-eastern Great Plains, produces a well-developed, rimose-areolate thallus with immersed perithecia. In localities where it occurs with *S. nemorum*, *W. diffractella* appears to have different ecological preferences, occurring on larger substrata of mesic, shaded outcrops and boulders rather than pebbles and cobbles in grassland openings. Finally, *S. elenkinii* Oxner, which is common on calcareous substrata throughout the western Great Plains, produces superficially similar perithecia but differs in its endolithic thallus, 2-spored asci and dark brown ascospores, which are longer than those of *S. nemorum* (27–62 µm, *fide* Thomson (1991)).

In the field, *Staurothele nemorum* is most likely to be confused with species of *Thelidium* A. Massal., *Verrucaria* Schrad. or *Anisomeridium distans*, with which it may co-occur. Members of these genera can easily be separated from *Staurothele* by examination of their ascospores, which are simple or transversely septate, as well as by the absence of algal cells in their hymenia. *Anisomeridium distans* may also be distinguished by its persistent interascal filaments and trentepohlioid photobiont.

Thomson (1991) followed the admonition of Ahmadjian & Heikkilä (1970) in rejecting the use of hymenial algal cells as a taxonomic character on the grounds that as such they were unreliable. However, subsequent publications on members of the genus (e.g. Harada 1992; Breuss & Etayo 1995; McCarthy 1995; Orange *et al.* 2009; McCune 2017; see also Swinscow 1963) have used this character to separate similar species. The results of this study support the use of hymenial algal cells in characterizing the new species, in which length-to-width ratios were 1·1–1·4(–2·1) and tended to remain consistent as cell size increased; cell length did not exceed 6·25 µm (Fig. 4A). In contrast, measurements of the hymenial algal cells of *S. hymenogonia* examined for this study showed more variable length-to-width ratios, 1·1–2·2(–3·3), with cells tending to become proportionately longer as size increased; individual cells were as long as 10·4 µm (Fig. 4B). The broad overlap of cell sizes in the two taxa shown in Fig. 4 is attributable to the inclusion of algal cells in *S. hymenogonia* that were immature, and therefore globose or cuboid.

Specimens examined. **USA:** *Kansas*: Anderson Co., 1 mi N, 2 mi E of Welda, University of Kansas Ecological Reserves, Welda Prairie Area Unit 3, 38·17°N, 95·25°W, 2015, *Morse* 24927b (KANU); Harper Co., 3 mi N, 0·6 mi W of jct. of KS Hwys 44 & 179 in Anthony, 37·20° N, 98·04°W, 2008, *Morse* 17442b (KANU); Johnson Co., 1·5 mi N of Aubry, Overland Park Arboretum and Botanical Garden, 38·80°N, 94·69°W, 2007, *Morse*

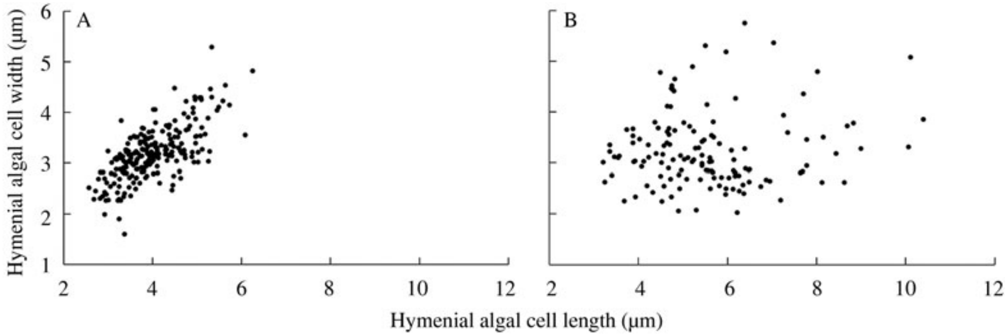

FIG. 4. Relationship between length and width of hymenial algal cells in *Staurothele nemorum* (bivariate Pearson correlation coefficient $r = 0{\cdot}6951$, $n = 233$, $P = 0{\cdot}0001$) (A), and *Staurothele hymenogonia* (including both European and North American specimens; $r = 0{\cdot}1152$, $n = 135$, $P = 0{\cdot}1833$) (B).

et al. 15322b (KANU); 2019, *Morse* 26835 & *Morse* (KANU); *c.* 1·5 mi S, 5 mi E of De Soto, Johnson County Park & Recreation District property along N side of Cedar Creek Pkwy N of KS Hwy 10, 38·95°N, 94·88°W, 2012, *Morse* 23840c & *Morse* (KANU); Linn Co., 3 mi W of jct. of KS Hwys 7 & 52 in Mound City, Dingus Natural Area, 38·13–38·14°N, 94·88–94·87°W, 2018, *Morse* 26531 & *Freeman* (KANU); Shawnee Co., just NE of Topeka city limits, Calhoun Bluff, along N side of NE Calhoun Bluff Rd, just W of KS Hwy 4 overpass, 39·09°N, 95·61°W, 2018, *Morse* 26592 *et al.* (KANU). *Missouri*: Jackson Co., Kansas City, Blue River Glades Natural Area, along E side of Blue River Rd, *c.* 0·75 road miles N of intersection of Blue River Rd and E 87th St, 38·98°N, 94·53°W, 2019, *Morse* 26833 & *Morse* (KANU). *Oklahoma*: Pontotoc Co., *c.* 4·75–5·25 mi N, 1·5 mi E of Connerville, TNC Pontotoc Ridge Preserve, Curlew Trail and Coal Creek Cave area, 34·51–34·52°N, 96·61°W, 2009, *Morse* 18788b & *Ladd* (KANU); Osage Co., 7·5 mi N, 3·75 mi E of Barnsdall, Woolaroc Wildlife Preserve, just W of Little Rock Creek, N of outlet of Clyde Lake, 36·67°N, 96·10°W, 2007, *Morse* 14795b & *Ladd* (KANU). *Texas*: Bexar Co., NW of San Antonio, Friederich Park (Friedrich Wilderness Park, 29·64°N, 98·63°W), 1991, *Tucker* 30933 & *Lievens* (LSU); Uvalde Co., 5·75 mi S, 3 mi W of jct. of US Hwy 90 and Ranch Rd 187 in Sabinal, Winston Ranch ('Guajillo Ridge'), 29·23°N, 99·51°W, 2012, *Morse* 23712b *et al.* (KANU).

Staurothele hymenogonia (Nyl.) Th. Fr.

Bot. Not. **1865**: 40 (1865).

(Fig. 2)

Staurothele hymenogonia was excluded from North America by Thomson (1991), since the original report of this species from the Mackenzie River region was based on a specimen of *S. discedens* (Nyl.) Zahlbr. The species is restored here to the North American list, based on recent collections described below.

Thallus immersed, visible as a scurfy or discoloured, brownish grey area in the substratum; *medulla* densely inspersed with small, angular, POL+ granules (bright under polarized light), these partially dissolving in 10% KOH; *thalline algal cells* oval to slightly oblong, 6·6–13·3 µm long.

Perithecia dispersed or occasionally paired, black, hemispherical to ±conical (*Morse* 23478d), rough, 0·3–0·5 mm wide, sessile to *c.* 1/2-immersed in thallus or in shallow pits in rock (*Morse* 23478d), often whitened due to the presence of rock dust adhering to surface (except for area immediately adjacent to ostiole); *ostiole* depressed, typically pale; *involucrellum* spreading, indistinguishable only along upper 1/3 to 1/4 of exciple, blackish brown (black in K), *c.* 75–105 µm thick laterally; *exciple* pale brown below hymenium; *centrum* *c.* 308 µm high × 309 µm wide; *hymenial gel* I+ red, KI+ blue; *periphyses* ± simple, slender, 21–30 µm long × 2·3–3·3 µm wide; *hymenial algal cells* initially globose to cuboid, typically oblong at maturity, (3·2–)3·8–*5·5*–7·1(–10·4) × (2·1–)2·5–*3·4*–4·2(–5·8) µm, l/w ratio = (0·9–)1·1–*1·7*–2·2 (–3·3) ($n = 98$); *asci* KI–, 8-spored, *c.* 75 × 27 µm; *ascospores* ellipsoid, colourless to pale brown, muriform, with (4–)5–7 longitudinal septa and (1–)2–3 transverse septa, (18·3–)

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20·0–*23·7*–27·5(–32·2) × (10·2–)11·6–*13·2*–14·8(–17·1) µm, l/w ratio = (1·3–)1·4–*1·8*–2·2(–3·1) (n = 38).

Pycnidia not observed.

Distribution and ecology. *Staurothele hymenogonia* has been well documented on calcareous substrata in Europe and western Asia (Orange *et al.* 2009; Shivarov & Stoykov 2012 and references therein). New North American records are from western Kansas and central Texas, along the contact of the Central Mixed-Grass Prairie and Central Shortgrass Prairie ecoregions and within the Edwards Plateau ecoregion (The Nature Conservancy 2007) (Fig. 3). Kansas specimens occurred on chalk pebbles in a disturbed upland mixed grass prairie at 777 m above sea level. The Texas specimen was collected from a limestone outcrop in a scrubby *Quercus buckleyi*-*Quercus fusiformis* woodland on N and W-facing slopes at 609 m above sea level. Associates included *Xanthocarpia crenulatella* on chalk and *Athallia holocarpa*, *Bagliettoa calciseda*, *B. marmorea*, *Caloplaca eugyra*, *Circinaria contorta*, *Diplotomma venustum*, *Endocarpon pallidulum*, *Lecania turicensis*, *Lichinella nigritella*, *Monoblastiopsis konzana*, *Pachyphysis ozarkana*, *Peltula obscurans* var. *deserticola*, *Placynthium nigrum*, *Psora pseudorussellii*, *Pyrenodesmia variabilis*, *Rinodina bischoffii*, *Sarcogyne regularis*, *Squamulea galactophylla*, *S. squamosa*, *Verrucaria calkinsiana* and several unidentified taxa of *Verrucaria* and *Lichinaceae* on limestone.

Discussion. Among species presently known from the Great Plains, *Staurothele hymenogonia* is most likely to be confused with *S. elenkinii*, which produces a similar endolithic thallus and roughened perithecia. However, *S. elenkinii* produces 2-spored asci with dark brown ascospores, which are longer (27–62 µm, *fide* Thomson (1991)) than those of *S. hymenogonia*. For differences with *S. nemorum*, see above.

Specimens examined. **Poland:** *Podkarpackie*: Sanok Co., Beskid Niski Mountains, Besko near Rymanów (Krosno District), 38·86°N, 21·96°E, 1976, *Nowak* s. n. (*Lichenes Poloniae Meridionalis* 239; ASU).—**USA:** *Kansas*: Gove Co., 14 mi S, 3 mi E of Quinter, Castle Rock area, 38·86°N, 100·17°W, 2005, *Morse* 12479 *&* *Freeman* (KANU); *c.* 14 mi S, 4 mi E of Quinter, Castle Rock area, 38·85°N, 100·18°W, 2008, *Morse* 17994 *&* *Logan* (KANU). *Texas*: 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* 23478d *&* *Freeman* (KANU).

Key to North American *Staurothele* s. lat.

Characters are drawn from Lendemer (2008), McCune (2017), Orange *et al.* (2009), Poelt (1969) and Thomson (1991, 2002). North American distributional information is drawn from Thomson (1991, 2002), except where noted.

1 Perithecia fully immersed in pits of rock substratum; involucrellum absent; thallus endolithic 2

Perithecia not fully immersed in pits of rock substratum (although sometimes partially immersed; in some species perithecia immersed in epilithic thallus); involucrellum present; thallus endolithic or epilithic 4

2(1) Ascospores dark brown at maturity, (2?)4(–5) per ascus; hymenial algal cells globose to oblong, 3–4 × 3 µm .... **S. rupifraga** (A. Massal.) Arnold

(Canada: British Columbia, Northwest Territories; USA: Utah)

Ascospores colourless at maturity, 2 or 8 per ascus; hymenial algal cells various ... 3

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3(2) Ascospores 8 per ascus, (30–) 32·0–37·5 × 14·0–16·5 (–17) µm; hymenial algal cells cylindrical, 3–10 × 1–3 µm .... **S. bacilligera** (Arnold) Arnold
(Canada: Newfoundland (Lendemer 2008))
Ascospores 2 per ascus, (33–) 41–49 (–50·5) × (17–) 19–23 (–25·5) µm; hymenial algal cells globose to oblong, 3–6 × 3–5 µm .... **S. guestphalica** (Lahm ex Körb.) Arnold
(Canada: Newfoundland (Lendemer 2008))

4(1) Ascospores 4–8 per ascus (*Staurothele* s. lat., *Willeya*) 5
Ascospores (1–)2 per ascus (*Staurothele* s. str.) 9

5(4) Perithecia immersed in greyish, *Pertusaria*-like globular verrucae; ascospores 37–45 µm long; hymenial algal cells globose to cuboid, 3–6 × 3 µm .... **S. discedens** (Nyl.) Zahlbr.
(Canada: Northwest Territories; USA: Alaska)
Perithecia not immersed in verrucae, although sometimes partially immersed in pits of substratum; ascospores ≤33(–39) µm long 6

6(5) Thallus well developed, rimose or verruculose; perithecia immersed in thallus 7
Thallus endolithic or poorly developed, scurfy or of scattered areoles; perithecia not immersed in thallus 8

7(6) Thallus verruculose, subisidose; ascospores 4(–8) per ascus, 12–25 µm wide .... **S. verruculosa** J. W. Thomson
(USA: Arizona)
Thallus rimose-areolate, upper surface smooth; ascospores (6–)8 per ascus, 9–15 µm wide .... **Willeya diffractella** (Nyl.) Müll. Arg.
(= *S. diffractella* (Nyl.) Tuck. including *S. tenuissima* Degel. (= *Endocarpon tenuissimum* (Degel.) Lendemer & E. A. Tripp)
(Canada: Ontario; USA: widespread throughout the eastern states)

8(6) Thallus endolithic or a scurfy brownish discoloration of substratum; perithecia 0·3–0·5 mm diam., sessile to 1/2-immersed in substratum; hymenial algal cells 4–7 (–10·5) × 2·5–4·0(–6) µm, l/w = 1·1–2·2(–3·3) ... **S. hymenogonia** (Nyl.) Th. Fr.
(USA: Kansas, Texas)
Thallus epilithic, of scattered, tan, grey or greenish grey areoles, at least proximal to perithecial bases, *c.* 0·1–0·3 mm diam.; perithecia 0·2–0·3(–0·4) diam., sessile; hymenial algal cells 3–5(–6) × 2·5–4·0(–5) µm, l/w = 1·1–1·4(–2·1) ....**S. nemorum** C. A. Morse & Ladd
(USA: Kansas, Oklahoma, Texas)

9(4) Perithecia ±sessile on rock substratum, without thalline covering; thallus endolithic or indistinct 10
Perithecia immersed in thallus, or at least with base covered with thalline tissue; thallus epilithic 12

10(9) Thallus grey-brown; hymenial algal cells oblong, 5–8(–12) × 4 µm; ascospores 32–48 (–65) × 12–18 µm .... **S. arctica** Lynge
(Canada: Northwest Territories)
Thallus pale; hymenial algal cells globose to broadly ellipsoid; ascospores various..11

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11(10) Perithecia hemispherical with constricted base, constricted involucrellum, to 0·7 mm diam.; ascospores 33–62 × 18–33 µm; hymenial algal cells 3·5–7·0 µm diam .... **S. elenkinii** Oksner

(*Staurothele sessilis* H. Magn., considered a synonym of *S. elekinii* by Thomson (1991), was described as producing ascospores 45–50 × 25–30(–35) µm and subcylindric hymenial algal cells 8–10 × 3·0–3·5 µm (Magnusson 1952))

(widespread in Canada and western USA)

Perithecia conical, with spreading involucrellum, to 0·5 mm diam.; ascospores 34·5–42 × 11·5–18(–20) µm; hymenial algal cells 2·5–3·7 × 2·5 µm ....**S. rufa** (A. Massal.) Zschacke

(USA: Oregon (McCune 2017))

12(9) Thallus with lobate marginal areoles 13
Thallus with elobate marginal areoles 14

13(12) Thallus brown to blackish brown; marginal areoles convex; on calcareous rocks..... .... **S. drummondii** (Tuck.) Tuck.

(widespread in Canada and western and north-eastern USA)

Thallus grey; marginal areoles flattened; on non-calcareous rocks .... **S. effigurata** J. W. Thomson

(México: Sonora; USA: Arizona, New Mexico, Utah)

14(12) Thallus with a continuous zone at periphery, areolate or not centrally; (semi-)aquatic or adjacent to water features 15
Thallus without a continuous zone at periphery, areolate marginally and centrally; terrestrial species 17

15(14) Perithecia immersed within thallus, ostioles not notably raised above thallus .... **S. clopimoides** (Anzi) J. Steiner

(widespread in Canada and (at high elevations?) western and north-eastern USA)

Perithecia covered by thallus in lower half and projecting above thallus 16

16(15) Hymenial algal cells subglobose to oblong-ellipsoid, 3·3–6·5(–12) × 3–5 µm, l/w = 1·0–1·6 .... **S. fissa** (Taylor) Zwackh

(widespread in Canada and western and north-eastern USA)

Hymenial algal cells bacilliform, 5–15 × 3–4 µm; l/w = 1·30–3·75 .... **S. clopima** (Wahlenb.) Th. Fr.

(USA: Alaska (McCune 2017))

17(14) Areoles subspherical, conspicuously constricted at base 18
Areoles flattened, not conspicuously constricted at base 20

18(17) Perithecia buried in thallus with only pruinose tip exposed ....**S. orispruinosa** J. W. Thomson

(USA: widespread throughout western states)

Perithecia with black involucrellum exposed around ostiole, epruinose 19

19(18) Ascospores 43·0–63·5 µm long; hymenial algal cells oblong to narrowly oblong, 5·7–8·0 × 2·5–3·0 µm, l/w = 2·0–4·3 .... **S. areolata** (Ach.) Lettau

(widespread in Canada, México, and western and north-eastern USA)

Ascospores (29–)33·5–48 µm long; hymenial algal cells globose to oblong-elliptic, 3·7–5·7 × 3·3–4·5 µm, l/w = 1·0–1·4 .... **S. frustulenta** Vainio

(Canada: British Columbia; USA: Montana (McCune *et al.* 2014))

20(17) Thallus grey or blue-grey, without brown or yellow tones; areoles pruinose or mealy 21
Thallus dark brown or greenish yellow, olive-grey; areoles epruinose (but sometimes with surfaces minutely roughened) 22

21(20) Ascospores brown, >50 µm long; areoles with very rough, pruinose surface; on calcareous rocks .... **S. rugosa** J. W. Thomson
(USA: Colorado, Utah)
Ascospores colourless, <40 µm long; areoles with mealy surface, but not distinctly roughened or pruinose (except over surface of perithecia); on non-calcareous rocks .... **S. lecideoides** B. de Lesd.
(México: Sonora; USA: Arizona, New Mexico)

22(20) Thallus dark brown, with minutely roughened surfaces; perithecium immersed in thallus with only apex of involucrellum visible; ascospores 23–39 × 10–18 µm; on non-calcareous rocks .... **S. polygonia** B. de Lesd.
(USA: Arizona, California, New Mexico, Texas, Utah)
Thallus greenish yellow to grey or olive-grey, with smooth surfaces; perithecia partially immersed in thallus, with involucrellum projecting distinctly above thallus; ascospores 26–60 × 10–26 µm; on calcareous rocks .... **S. monicae** (Zahlbr.) Wetmore
(USA: widespread throughout central and western states)

Notes. Thomson (1991) noted that *S. drummondii* may be difficult to separate from *S. areolata* when occurring on rough substrata. Indeed, marginal lobes are frequently poorly and erratically developed even on good specimens of *S. drummondii*. In these cases, Thomson (1991) recommended examining marginal areoles since *S. drummondii* tends to produce smaller sterile areoles towards the periphery of the thallus, while the sterile, marginal areoles of *S. areolata* are similar in size to fertile areoles of the central thallus. We have referred specimens with effigurate margins to *S. drummondii*, although these often produce perithecia in verrucules *c.* 0·2–0·3 mm in diam., smaller than those described in Thomson (1991).

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