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OREONETIDES BEATTYI, A NEW TROGLOBITIC SPIDER (ARANEAE: LINYPHIIDAE) FROM EASTERN NORTH AMERICA, AND RE-DESCRIPTION OF *OREONETIDES FLAVUS*

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Abstract: A new troglobitic Linyphiidae, *Oreonetides beattyi* n.sp., is described from caves of eastern North America. The species is morphologically close to *Oreonetides flavus* Emerton and proposed as sister-species. Both species are described, illustrated and their distribution is documented. The intra-specific variation of *O. beattyi* is detailed: female genitalia display unusual variability, but males provided stable species level diagnosis. A male from Bull Cave (Tennessee) that shows significant genitalic variation is problematic, however. With limited sampling, the genetic bar-coding approach did not provide helpful insights to determine if this specimen belongs to a different species, is morphologically aberrant, or simply belongs to a population geographically distant enough to explain genetic variability. We propose the cryophilic affinities/relict population hypothesis to explain the ecological affinities of some Linyphiidae that are restricted to caves in most of their ranges, but occur on the surface at the northern edge of their distribution. We suggest an evolutionary scenario for the disjunct distribution of *Oreonetides beattyi* n.sp. in eastern caves and *O. flavus* in more northern latitudes on the west coast of North America.

Introduction

In taxonomy, species boundaries are determined by the examination of series of closely related species in order to identify distinctive characters or gaps in gradation of shapes, length, counts, etc. of variable morphological features. Characters retained to delimit species are detailed and used as diagnostic. Intra-specific variability is rarely reported and remains a neglected aspect of most taxonomic papers, and consequently, there is a widespread perception that variation within a species is highly unusual. In spider taxonomy, intra-specific variability has been documented for color patterns [e.g. *Araneus* (Levi, 1971; Court and Forster, 1988), *Theridion frondeum* Hentz, 1850 (Emerton, 1882, plate 3, fig. 1), *Latrodectus katipo* Powell, 1870 (Vink et al., 2008), *Sitticus fasciger* (Simon, 1880) (Proszynski, 1968)], but coloration is rather volatile, easily altered in preserved specimens, and rarely used to delimit species. Genitalic characters, however, are reputed to be stable within a species, while providing the needed information to distinguish species (Eberhard, 1986), which makes these features ideal for taxonomic purposes. Intra-specific variability of genitalia is therefore much more problematic. Nonetheless, several cases are known. For instance, Roberts (1987, p. 180), provided examples of intra-specific variability of the male palp of *Araneus diadematus* Clerck (1757) (Araneidae), Levi (1971) illustrated genitalic variation of male and female *Araneus*, Gertsch (1984) illustrated the variation he admitted for the male genitalia of *Eidmanella pallida* (Emerton, 1875) (Nesticidae) and Blest and Vink (2000) documented the variability of the retrolateral tibial apophysis (RTA) for a few species of Stiphidiidae. Important intra-specific variations of female genitalia have been shown for *Cicurina* (Dictynidae) (Paquin and Hedin, 2004; Paquin et al., 2008), and supported by genetic data (Paquin and Hedin, 2004, 2007). These examples are troubling as many species are based on the examination of few specimens, where species are differentiated only by minor genitalic details and are found in sympatry.

A sound evaluation of intra-specific variability is largely dependent on the number of specimens available, but in the case of rare species, often known only from one or two specimens, it is impossible to assess. Misevaluation of this variation can lead to the erroneous interpretation of species limits because characters that are randomly variable within a species must not be used to establish taxa. In such cases, a re-assessment of the taxonomy based on longer series of specimens results in synonymies. Synonyms usually have relatively minor significance because species names are scientific hypotheses to be refuted, modified, redefined, or improved. However, synonymies have deep impacts when involving species that are legally protected (threatened,

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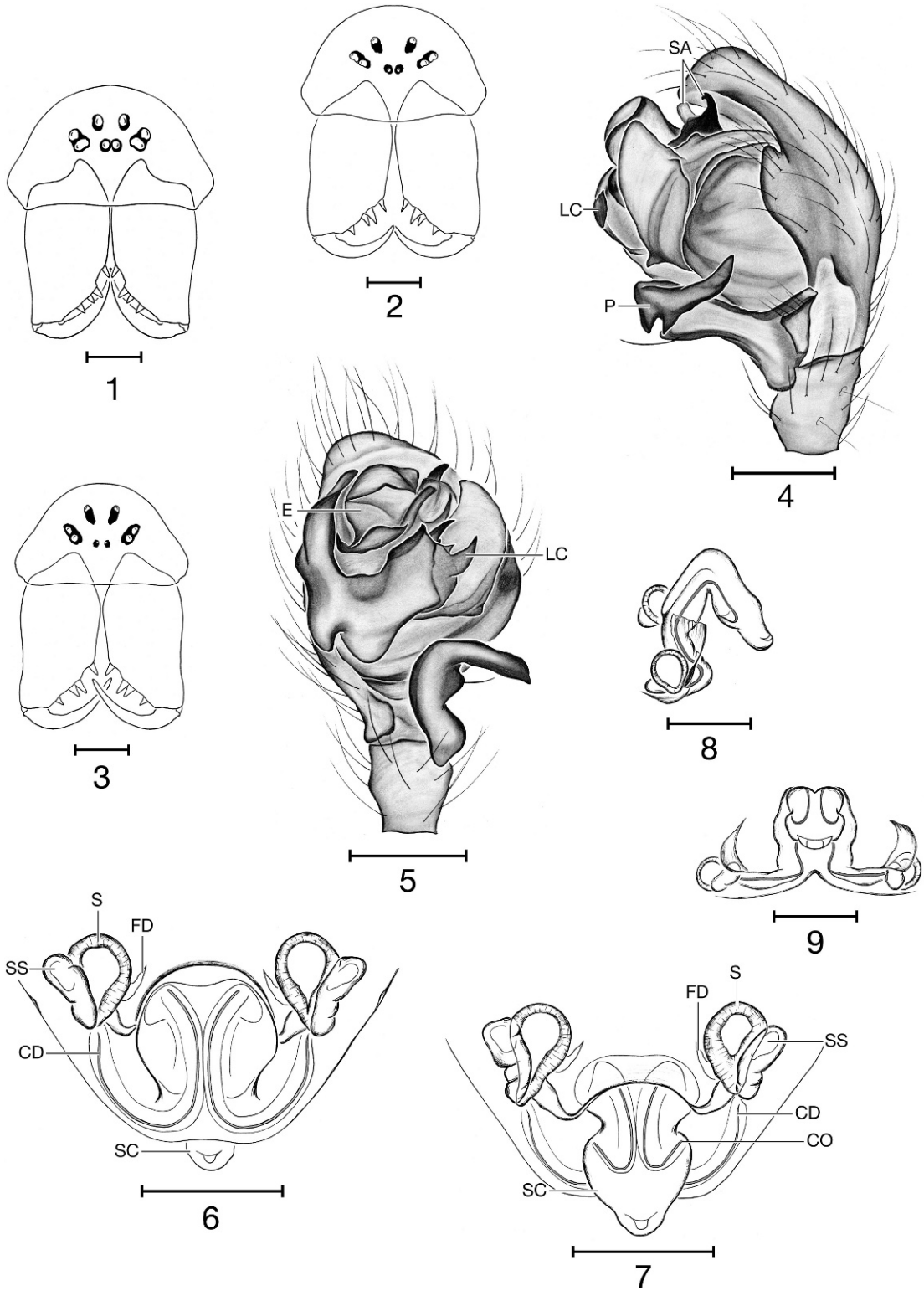


Figures 1–9. ***Oreonetides beattyi*** **n.sp. 1, face of male, frontal view (Calf Cave, Tennessee); 2, face of female, frontal view (Smith's Folly Cave, Indiana); 3, face of female, frontal view (JJ's Sister Cave, Indiana); 4, palpus of male, retrolateral view; 5, palpus of male, ventral view; 6, cleared epigynum, ventral view; 7, cleared epigynum, dorsal view, 8, cleared epigynum, lateral view; 9 cleared epigynum, posterior view. Abbreviations used: CD copulatory ducts, CO copulatory openings, E embolus, FD fertilization ducts, LC lamella characteristica, P paracymbium, SA suprategular apophysis, SC scape, S spermatheca, SS secondary spermatheca. Scale bars for Figures 1–3, 5–9 = 0.1 mm; Figure 4 = 0.05 mm.**

listed, or species considered for listing) (see Longacre, 2000; Bender et al., 2005). Legal protection is ultimately funneled into a species name, a system that does not harmonize well with a discipline that progresses by proposing revised hypotheses. For instance, Paquin et al. (2008) synonymized two names of eyeless troglobitic *Cicurina* that were the focal point of a legal debate around the taxonomic soundness of cave spiders that are species of concern in Texas (United States). This synonymy was a direct consequence of an initial misevaluation of intra-specific variability due to the rarity of identifiable material. Such synonymy suggests that caution should be used in the description of cave-restricted taxa, because the rarity, narrow distributions, and high dependence on sensitive habitats make troglobites ideal candidates for enhanced conservation measures.

Recent cave surveys carried out in Indiana (Lewis and Rafail, 2002; Lewis et al., 2004; Lewis and Lewis, 2008a, b) and Tennessee (Reeves, 2000; Lewis, 2005) revealed the existence of a new troglobitic spider belonging in *Oreonetides* Strand 1901. Further research led to the discovery of additional specimens from other eastern caves in museum collections. Based on this information, we conducted additional sampling in 2004 in order to increase the number of specimens available for study, particularly the males. The collection of fresh material allowed the use of a DNA bar-coding approach (Hebert et al., 2003) for an independent assessment of species limits and variability. In the present paper, we describe this new troglobitic spider and document its intra-specific variability. We re-describe the epigean species *Oreonetides flavus* (Emerton, 1915) which is hypothesized as sister-species. The distribution of the two species is discussed in the light of a possible evolutionary scenario behind the speciation of the troglobitic species. The limitation of the bar-coding approach is also briefly addressed.

Methods

Specimen Examination

Specimens were examined in 70% ethanol under a SMZ-U Nikon dissection microscope. A Nikon Coolpix 950 digital camera attached to the microscope was used to take a photograph of the structures to be illustrated. The digital photo was then used to trace proportions, the illustration was detailed and then shaded by referring to the structure under the microscope. Female genitalia were excised using a sharp entomological needle and transferred to lactic acid to clear non-chitinous tissues. A temporary lactic acid mount was used to examine the genitalia under an AmScope XSG Series T-500 compound microscope, where genitalia were photographed and illustrated as explained above. For the study of the embolic division, the male palps were placed for ~10 minutes in warm KOH and washed in 80% alcohol.

All measurements are in millimeters and were made using an optical micrometer on the microscope. When possible, five specimens of each sex were measured for the descriptions. Calculation for the location of Tm I follows Denis (1949). Palpal and epigynal terminology follows Saaristo (1972), van Heldsingen (1981) and Hormiga (1994). Color description was done under halogen lighting, using traditional color names. Subsequently, we matched the color of the specimen to a reference Pantone chart (Pantone Formula Guide, solid matte) and added the color code to the description. Latitude and longitude data are given in decimals and should be considered an approximation, and in the case of cave locations, they are not given in order to preserve the confidentiality of the information.

Molecular Analysis

Specimens recently collected were preserved in the field in 100% ethanol and preserved on ice to avoid DNA degradation (Vink et al., 2005). DNA extraction was done using a DNEasy® kit following the manufacturer's indications. Using PCR (polymerase chain reaction), we amplified a ~1 kb fragment of the Cytochrome Oxidase I (CO1) mtDNA gene using primers C1-J-1751-SPID, C1-J-2309, C1-N-2568, and C1-N-2776-SPID (Hedin and Maddison, 2001, Vink et al., 2005) and PCR protocols similar to those detailed in Paquin and Hedin (2004). PCR products were purified using the Wizard® SV Gel and PCR Clean-up System of Promega following the manufacturer's indications and sequenced at the core facilities (Portland State University and Berkeley University). Templates were sequenced in both directions for each fragment, using PCR primers and except for the shorter fragment, only sequenced from the 5-foot-end using C1-N-2776-SPID. The sequences read were assembled into sequence contigs and edited using Sequencer 4.5 and MacClade 4.0 (Maddison and Maddison, 2003). MrModeltest version 2.2 (Posada and Crandall, 1998; Nylander, 2004) and PAUP* 4.0b10 (Swofford, 2002) were used to select a best-fit model of molecular evolution using the Akaike Information Criterion (AIC) (see Posada and Buckley, 2004). Phylogenetic analyses were conducted using MrBayes version 3.1.2 (Ronquist and Huelsenbeck, 2003) software. We used a GTR+I+G model with fixed substitution and rate parameters (obtained in MrModeltest) to conduct an un-partitioned Bayesian analysis using this best-fit model of molecular evolution. All analyses were run for ten million generations, sampling every 1000th tree (all other parameters set to program defaults (Ronquist and Huelsenbeck, 2003)). Majority rule consensus trees were constructed, discarding the first 2000 trees as burn-in. The analysis includes two other surface *Oreonetides* species, *Pithyohyphantes* sp., a basal Linyphiidae and *Pimoa* sp. (Pimoidae), a sister group to Linyphiidae (Hormiga 1994, 2000) used as outgroup.

The bulk of specimens were collected by JJL, and by PP, ND and Jeremy Miller (curated in the Collection

Paquin-Dupérré; CPAD, Shefford, Québec). Voucher specimens are also deposited in the collection of Donald J. Buckle (DBC, Saskatoon, Saskatchewan, Canada). Specimens from the following collections were also examined: American Museum of Natural History (AMNH, New York, USA); Canadian National Collection (CNC, Ottawa, Ontario Canada), Museum of Comparative Zoology (MCZ, Harvard, Cambridge, Massachusetts, USA); Lyman Entomological Museum (LEM, McGill University, Ste-Anne-de-Bellevue, Canada) and the Burke Museum University of Washington (UWBM, Seattle, Washington, United States).

Taxonomy

Family: Linyphiidae Blackwall, 1859

Genus: *Oreonetides* Strand, 1901

Type Species: *Oreonetides vaginatus* (Thorell, 1872).

Diagnosis: See van Heldsingen (1981).

Composition: Includes 15 described species, 6 of which are found in North America. Several North American species remain undescribed.

Distribution: Russia, China, Mongolia, Europe, Japan and North America (Platnick, 2008).

New Species

Oreonetides beattyi (Figs. 1–19 and 27–28)

Oreonetides flavus (Emerton, 1915) (Reeves, 2000). Misidentification.

Oreonetides sp. (Peck, 1998; Gertsch, 1992).

Type Material: HOLOTYPE: United States: Lawrence Co., Smith's Folly Cave, Tincher Hollow Special Area, Hoosier National Forest, 26.viii.2004, in cave, 1♂, P. Paquin and J. Miller (AMNH).

Material Examined: United States: *Indiana*: Jefferson Co., Grays Cave, on Middle Fork Creek, Big Oaks National Wildlife Refuge, 03.ii.2001, in cave on rotting wood, hand collected, 1♀, J. Lewis, (CPAD); 25.viii.2004, in cave, hand collected, 2♀, P. Paquin, (CPAD); Lawrence Co., Sullivan Cave, 2 mi. W. Springville, 29.xii.2007 1♀, J. Lewis and S. Lewis (CPAD); JJ's Sister Cave, 1 mi. SW Bryantsville, 29.ix.2000, in cave, hand collected, 3♀, J. Lewis and R. Burns (CPAD); 29.ix.2000, in cave, hand collected, 1♀, J. Lewis and R. Burns (CPAD); 26.viii.2004, in cave, hand collected, 1♂, J. Miller (CPAD); Smith's Folly Cave, Tincher Hollow Special Area, Hoosier National Forest, 29.vii.2001, in cave, hand collected, 1♀, J. Lewis and S. Rafail (CPAD); 29.ix.2000, Berlese extraction of leaf litter from cave, 1♀, J. Lewis and R. Burns (CPAD); 25.vii.2002, 2♂ 1♀, J. Lewis (DBC); 26.viii.2004, in cave, 1♂ 8♀, P. Paquin and J. Miller (CPAD); 27.x.2001, in cave, 1♀, J. Lewis and R. Burns (CPAD); Ripley Co., Louis Neill Cave, Big Oaks National Wildlife Refuge, 16.iv.2001, in cave, hand collected, 1♀, J. Lewis, S. Miller and T. Vanosdol-Lewis (CPAD); *Maryland*: Washington Co., Snivley's Cave, near Keedysville, 12.ix.1968, 1♀ [no collector] (AMNH); Snivley's Cave No.2, near Eakles Mill, 04.viii.1973, between rocks and litter, 1♀, A. Norden and B. Ball (AMNH); 03.v.1969, 1♀ (AMNH); *Pennsylvania*: Armstrong Co., Hineman Cave, 2 mi. W. Buffalo Mills, 11.vii.1957, 1♂, C. Krekeler and J.R. Himann (AMNH); Dauphin Co., Indian Echo Cave, 16.i.1937, in cave, hand collected, 1♀, K. Dearwolf (AMNH); Brownstone Cave, 16.i.1937, in cave, hand collected, 6♀, K. Dearwolf (AMNH); *Tennessee*: Blount Co., Bull Cave, Great Smoky Mountains National Park, 02.viii.2000, in cave, hand collected, 1♀, M. Hedin (CPAD); Calf Cave #1, Great Smoky Mountains National Park, 28.vii.2004, in cave, hand collected, 1♂, P. Paquin (CPAD); Marion Co. Speegle Cove Cave, 7 mi. N.W. Jasper, 28.x.2004, inside cave, 1♀, J. Lewis and C. Holliday (CPAD); *Virginia*: Tazewell Co., Rosenbaum's Water Cave, 02.ix.1962, 1♀, J. Holsinger (AMNH); Montgomery Co., Vickers Road Cave, 16.x.1971, 1♀, L.M., T.B.L. Ferguson and J.R. Holsinger (AMNH).

Diagnosis: Males and females of *O. beattyi* n.sp. differ from all other members of the genus by the presence of noticeably reduced eyes which vary from approximately one third the size of the eyes of *O. flavus* to tiny, pale white spots. Males are diagnosed by the bidentate ridge of distal arm of paracymbium, their short terminal apophysis and lamella characteristica. Females are characterized by their oval spermathecae, and their elongated secondary spermathecae positioned ventrally.

Description: Male (n = 4): Total length: 1.54 ± 0.18; carapace length: 0.72 ± 0.04; carapace width: 0.56 ± 0.04; carapace off-white to light yellow-orange (142M), smooth, shiny, with 4–5 erect setae along midline. Eyes of irregular form, reduced in particular the anterior median (AME) and the posterior median eyes (PME) (Figs. 1–3), to almost completely absent, with presence of white pale spots. Chelicerae light yellow (134M) to yellow-orange (142M), promargin with 4 teeth, retromargin with 4–5 denticles (Figs. 1–3). Cheliceral stridulatory organ visible, with ~35–40 ridges. Abdomen off-white to light gray (Warm gray 1M), densely covered with long semi-erect setae, venter of abdomen with oval striated epigastric plates. Legs light yellow (134M) to light yellow-orange (142M); leg formula 4-1-2-3; tibia I-III with two long dorsal macrosetae, tibia IV with one such setae; metatarsus I with dorsal trichobothrium, TmI situated at 0.35-0.41; metatarsus IV lacking dorsal trichobothrium, coxa IV with small stridulatory pick. Total length leg I: 2.26 ± 0.4; leg II: 2.16 ± 0.12; leg III: 1.89 ± 0.08; leg IV: 2.40 ± 0.13. Palpal femur with small, basal stridulatory pick. Palpus length: 0.33 ± 0.05. Male palp: cymbium with lateral lobe (Fig. 4); paracymbium (P) with one basal protrusion cup-shaped, tip covered with minuscule papillae, second protuberance bearing 5 setae (Fig. 4), trunk of paracymbium bearing an isolated seta distally and a longitudinal ridge basally, distal arm of paracymbium with sclerotized bidentate ridge (Fig. 4); embolus (E) tri-partate, middle part bearing the

sperm duct (Figs. 10 and 11); radix (R) with a small pointed, mesal projection (Figs. 10 and 11); terminal apophysis (TA) short, basally enlarged and pointed apically (Figs. 10 and 11) lamella characteristica (LC), short, large, translucent and curved (Figs. 10 and 11), distal end slightly variable, either rounded and rugose (Figs. 10–12) or pointed and smooth (Figs. 11 and 13).

Female (n = 5): Total length: 1.85 ± 0.2; carapace length: 0.80 ± 0.04; carapace width: 0.58 ± 0.06; overall coloration as in male. Carapace smooth and shiny, with 4–5 erect setae along midline. Eyes as in male, with (AME) and (PME) reduced, to almost completely absent, with presence of white pale spots. Cheliceral promargin with 4 teeth, retromargin with 4–5 denticles. Cheliceral stridulatory organ with ~30 ridges. Abdomen densely covered with long semi-erect setae; venter with oval striated epigastric plates. Leg formula 4-1-2-3; tibia I-III with two dorsal macrosetae, and tibia IV with one such setae; metatarsus I with dorsal trichobothrium situated at 0.36–0.39; metatarsus IV lacking dorsal trichobothrium; coxa IV with small stridulatory pick. Total length leg I: 2.66 ± 0.4; leg II: 2.57 ± 0.24; leg III: 2.32 ± 0.23; leg IV: 2.86 ± 0.31. Palpal femur with small basal stridulatory pick; palpal tarsus without claws. Epigynum width 0.24 ± 0.03. Epigynum consists of a tightly folded scape (Fig. 8), distal part of scape protruding basally (Figs. 6 and 7), primary spermathecae ovale (S), secondary spermathecae (SS) elongated, situated either ventro-laterally, ventro-mesally, or ventro-internally in relation to primary spermathecae (Figs. 14–19), copulatory ducts (CD) long and sinuous (Figs. 14–19), copulatory openings (CO) located midway on ventral surface of scape (S) (Fig. 7), fertilization ducts (FD) rather short and straight (Figs. 6 and 7).

Distribution: Known only from caves from the Appalachian Valley in Virginia, the Appalachian Plateau from Pennsylvania south to Tennessee and west to the Interior Low Plateaus in Indiana (Figs. 27–28).

Habitat: All known specimens were collected in caves.

Etymology: Named in honor of Joseph A. Beatty, professor emeritus, Department of Zoology, Southern Illinois University-Carbondale.

Species

Oreonetides flavus (Emerton, 1915), (Figs. 20–25 and 28)

Microneta flava (Emerton, 1915, plate III, fig. 2).

Aigola flava (Crosby, 1937, plate I, figs. 5–6).

Oreonetides flavus (van Helsdingen, 1981, figs 7–12; Crawford, 1988; Buckle et al., 2001).

Type Material: *Microneta flava* Emerton, MCZ, EXAMINED.

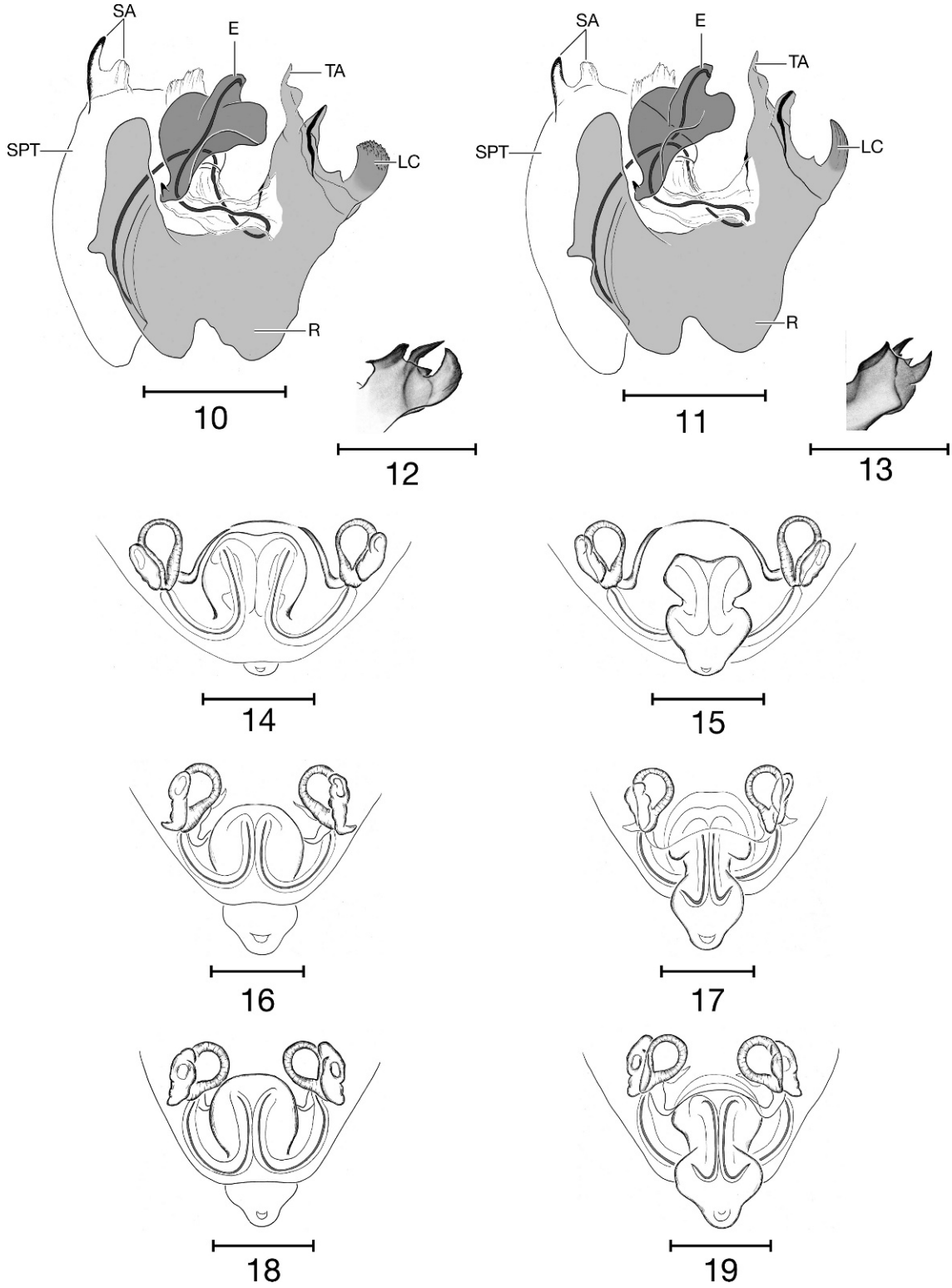
Label: "*Microneta flava* Emerton, Canada: Alberta: Louggan, Lake Louise, in moss, Aug. 10, 1905 J. H. Emerton Collection" [51.4252′N, 116.1805′W] MCZ #21313 holotype: male, syntype: female.

Material Examined: Canada: *Alberta*: 36 km NW Hinton, 3.75 W of Rock Lake Rd. [53.9333′N, 118.0833′W] 03.-17.vi.2004, 1♂, pitfall, H. Williams (LEM); Cameron Lake, Waterton Lakes National Park [49.0166′N, 114.0667′W] 04.vii.1980, interception trap, 1♀, H.J. Teskey (CNC); Bow Pass, 64 mi NW of Banff [53.7167′N, 116.5002′W] 12.x.1953, Berlese sample in spruce duff, 5♀, O. Peck (CNC). United States: *Washington*, Okanagan Co. Tiffany Sping Camp, 6700′ [2042 m] [48.699′N, 119.955′W], 31.vii.1985, 2♀, R. Crawford (UWBM).

Diagnosis: Males and females of *O. flavus* are distinguished from *O. beattyi* by the presence of well developed eyes. Males are further diagnosed by their long and spine-like terminal apophysis (TA) and their significantly longer lamella characteristica (LC). Females are diagnosed by their rounded spermathecae (S) and the dorso-mesally positioned secondary spermathecae (SS).

Description: Male (n = 2): Total length: 1.59 ± 0.11; carapace length: 0.75 ± 0.07; carapace width: 0.61 ± 0.01; carapace smooth, shiny, light orange (135M), 4–5 erect setae along midline. Eyes well-developed, rounded and ringed with black pigment (Fig. 20). Sternum light yellow-orange (134M). Chelicerae light orange (135M), promargin with 5–6 teeth (Fig. 20), retromargin with 5–6 denticles. Cheliceral stridulatory organ visible with ~30 striae. Abdomen light gray (warm gray 1M) densely covered with long semi-erect setae; venter of abdomen with oval striated epigastric plates. Legs light yellow (1205M) to light orange (134M), leg formula 4-1-2-3; tibia I-IV with two long dorsal macrosetae, metatarsus I with dorsal trichobothrium, TmI located at 0.33, metatarsus IV lacking dorsal trichobothrium, coxa IV with small stridulatory pick. Total length leg I: 2.15 ± 0.04; leg II: 2.00 ± 0.08; leg III: 1.79 ± 0.13; leg IV: 2.40 ± 0.02. Palpal femur of with small, basal stridulatory pick. Palpus length: 0.35 ± 0.02. Male palp: cymbium with lateral lobe (Fig. 21); paracymbium (P) with one basal cup-shape protrusion, covered with minuscule papillae, second basal protuberance bearing 4 setae (Fig. 21), trunk of paracymbium bearing an isolated seta distally and a longitudinal ridge basally, distal arm of paracymbium with sclerotized ridge (Fig. 21); embolus (E) tri-partate (Figs 22–23), middle part bearing the sperm duct; radix (R) with a small rounded, mesal projection (Fig. 23); terminal apophysis (TA) long, smoothly tapering apically (Fig. 23); lamella characteristica (LC) transparent, long, curved, with rugose tip (Figs 22–23).

Female (n = 6): Total length: 1.84 ± 0.16; carapace length: 0.80 ± 0.06, carapace width 0.61 ± 0.01; overall coloration as in male. Carapace smooth and shiny, with 4-5 erect setae along midline. Eyes normal, rounded, ringed with black pigment. Cheliceral promargin with 5–6 large teeth, retromargin margin with 5–6 small denticles. Cheliceral stridulatory organ with ~25 striae.



Figures 10–19. ***Oreonetides beattyi*** **n.sp. 10, embolic division of male palpus, schematic view (Calf Cave, Tennessee); 11, embolic division of male palpus, schematic view (Smith's Folly Cave, Indiana); 12, lamella characteristica of male palpus (Calf Cave, Tennessee); 13, lamella characteristica of male palpus (Smith's Folly Cave, Indiana); 14, cleared epigynum, ventral view (Bull Cave, Tennessee); 15, cleared epigynum, dorsal view (Bull Cave, Tennessee); 16, cleared epigynum, ventral view (Snivley's Cave, Maryland); 17, cleared epigynum, dorsal view (Snivley's Cave, Maryland); 18, cleared epigynum, ventral view (Rosenbaum's Cave, Virginia); 19, cleared epigynum, dorsal view (Rosenbaum's Cave, Virginia). Abbreviations used: E embolus, LC lamella characteristica, R radix, SA suprategular apophysis, SPT suprategulum, TA terminal apophysis. Scale bars for Figures 10–19 = 0.05 mm.**

Abdomen covered with long semi-erect setae; venter with oval striated epigastric plates. Leg formula 4-1-2-3; tibia I-IV with two long dorsal macrosetae, metatarsus I with dorsal trichobothrium, TmI located at 0.33–0.36, metatarsus IV lacking dorsal trichobothrium, coxa IV with small stridulatory pick. Total length leg I: 2.50 ± 0.11; leg II: 2.32 ± 0.12; leg III: 2.13 ± 0.09; leg IV: 2.81 ± 0.02. Palpal femur with small stridulatory pick set basally; palpal tarsus with no claws. Epigynum width: 0.29 ± 0.01. Epigynum consists of a tightly folded scape (S), distal part of scape protruding basally (Figs. 24–25); primary spermathecae rounded (S) (Figs. 24–25); secondary spermathecae (SS) elongated, situated dorso-mesally (Figs. 24–25); copulatory duct (CD) long and sinuous (Figs. 24–25); copulatory openings (CO) located midway on ventral surface of scape (S) (Figs. 24–25); fertilization ducts (FD) rather short and curved (Fig. 25).

Distribution: Canada: Alberta; United States: Washington (Fig. 28).

Habitat: Epigean species, apparently associated with forest litter.

Note: The specimen from Sea Cliff, New York, reported by van Helsdingen (1981) could not be located for examination despite numerous efforts at the Museum of Comparative Zoology (Harvard), and its identity remains uncertain. This surface record is indicated on the distribution map by a star (Fig. 28, see also discussion).

Results

Morphological Variability

The examination of available material clearly allows the distinction of *O. flavus* from *O. beattyi* n.sp. and shows similarities that suggest a close relationship between the two species. The amount of eye reduction observed in *O. beattyi* ranges from significantly reduced to almost completely absent with only pale spots remaining, which leaves no doubt about troglobitic adaptations. *Oreonetides flavus* displayed no variability of genitalic features. Examination of the epigynum of *O. beattyi*, however, showed surprising variability, particularly in the distance between the primary spermathecae and the position of the secondary spermathecae in relation to the primary spermathecae (Figs. 14–19). Such variation was observed between females collected in the same cave and sometimes within a single female as some epigynums were not symmetrical. Males of *O. beattyi* showed no variation in palpal morphology, except for the one collected from Bull Cave, Tennessee (Figs. 10 and 12), which differed in the shape and texture of the lamella characteristica and could not be comfortably assigned to the species.

Molecular Analysis

Seven individuals belonging to *O. beattyi* were sequenced in order to test if morphological variability could reveal multiple species. The phylogenetic tree (Fig. 26) shows a strongly supported tip clade (0.92) of five individuals from three caves in Indiana that display little genetic variability. As expected, specimens collected in the same cave share more similar haplotypes. However, the specimen from Calf Cave #1 in Tennessee (*Oreonetides*-7) is distinct from the tip clade with a strongly supported (value 1.00) relatively short branch length.

Distribution

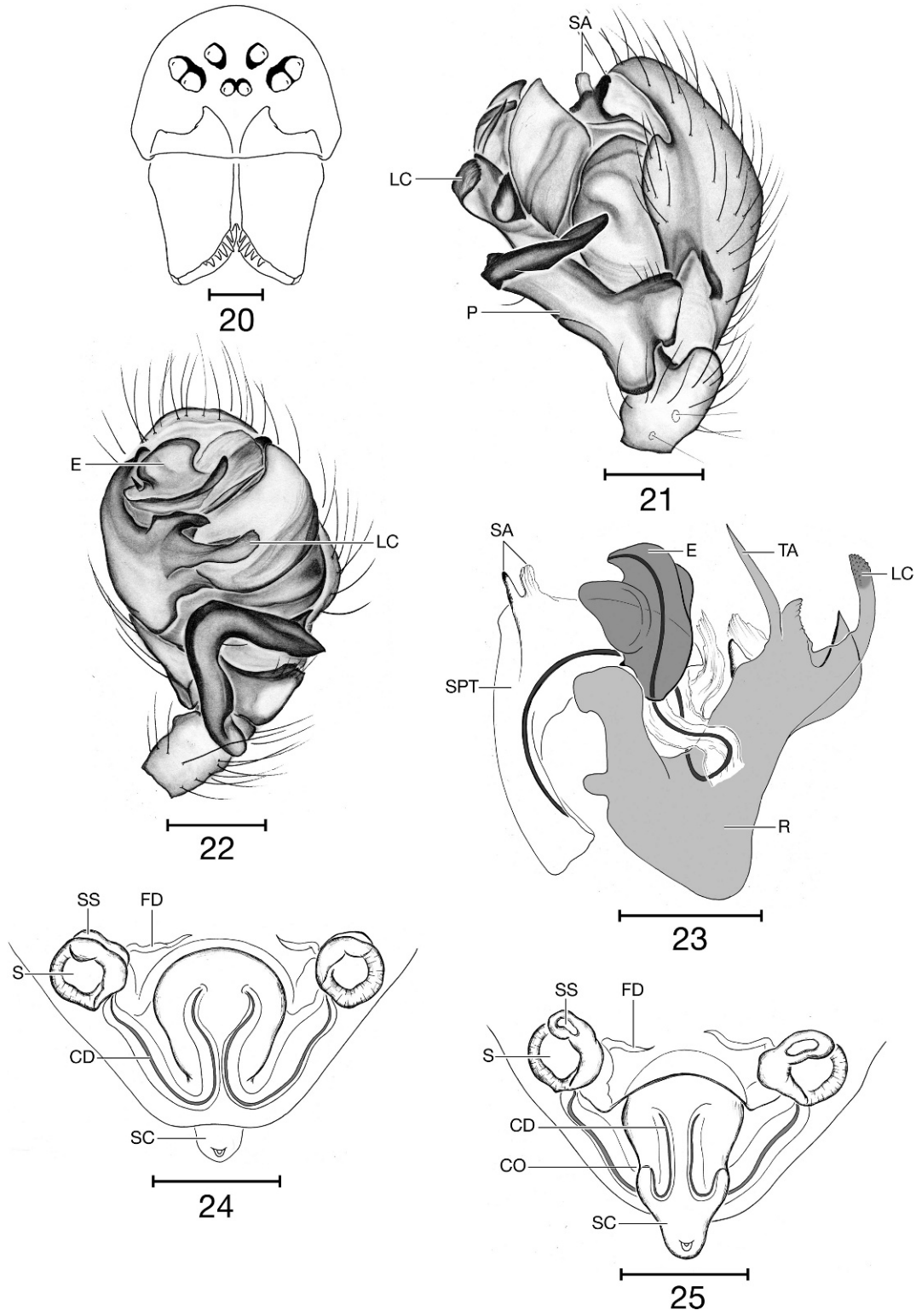
Given the proposed relationship as sister species, the disjunct distribution is remarkable with *O. flavus* occurring in the western part of the continent and comparatively more to the north. *O. beattyi* n.sp. is confined to the east and found exclusively in caves (Fig. 28).

Discussion

Species Variability of *Oreonetides beattyi* n.sp.

The series of specimens studied provides insights into the understanding of genitalic variability of the species, particularly for females. Variation of the spermathecae is rarely reported in Linyphiidae, a set of characters otherwise perceived as stable. However, based on a number of specimens that allowed a robust assessment of morphological variation, Schikora (1995) reported significant intraspecific variability of male and female genitalic structures. In a troglobitic linyphiid, comparable intra-specific variability has been reported for females of *Porrhomma cavernicola* (Keyserling, 1886) by Miller (2005). In the present case, the collection of several specimens of *O. beattyi* n.sp. from the same cave displaying variability of the epigynum is convincing evidence that the variation is intra-specific. There is no doubt that female characters cannot be used reliably to recognize more than one species. Comparatively, an important radiation of troglobitic spiders found in Texas (*Cicurina*, subgenus *Cicurella*) (see Gertsch, 1992; Cokendolpher, 2004; Paquin and Dupérré, 2009) did not benefit from a long series of specimens, and many species were described on the basis of a single female, which led to taxonomic confusion (Paquin et al., 2008).

The information provided by the males however, may suggest a different interpretation. The genitalia of all known males are similar, even between localities that are distant from each other, suggesting a single species. However, the male collected from Bull Cave (Tennessee) displayed noticeable variability, with a broader lamella characteristica and a different configuration of the rugose tip (Figs. 10 and 12). Considering the stability of this structure in all other known males, this could be interpreted as a species-level character, although slight variability of the lamella characteristica has been shown in genera such as *Agyneta* Hull, 1911 (Saaristo and Koponen, 1998; Dupérré and Paquin, 2007) and *Maro* O. Pickard-Cambridge, 1906 (Dondale and Buckle, 2001).



Figures 20–25. ***Oreonetides flavus*****. 20, face of male, frontal view; 21, palpus of male, retrolateral view; 22, palpus of male, ventral view; 23, embolic division of male palpus, schematic view; 24, cleared epigynum, ventral view; 25, cleared epigynum, dorsal view. Abbreviations used: CD copulatory ducts, CO copulatory openings, E embolus, FD fertilization ducts, LC lamella characteristica, P paracymbium, R radix, SA suprategular apophysis, SC scape, S spermatheca, SPT suprategulum, SS secondary spermatheca, TA terminal apophysis. Scale bars for Figures 20–25 = 0.1 mm.**

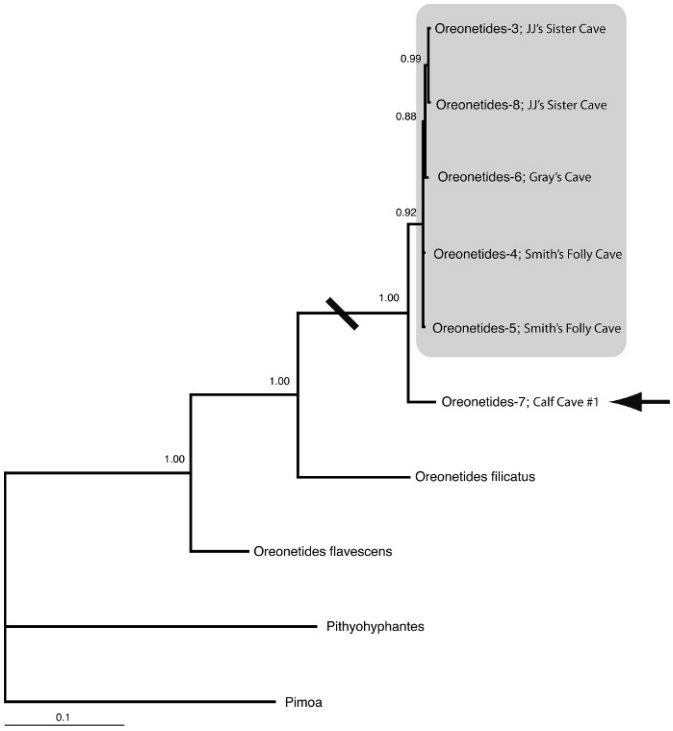


Figure 26. Bayesian consensus phylogram based on COI sequence data. Values above branches are posterior probabilities.

The molecular data provide support for the identification of the variability of female genitalia as intra-specific (grey box, Fig. 26). For the male from Bull Cave, the phylogenetic tree does not support or reject that the species found in that cave differs from *O. beattyi*. A female (*Oreonetides*-7, arrows in Fig. 26) from Calf Cave #1, which is located only a few meters from Bull Cave within the same sinkhole and likely harbors the same *Oreonetides* species, was included for DNA analysis. The genetic distinctiveness of *Oreonetides*-7 does not allow us to determine whether this is due to its being a different species, part of an isolated population, restricted gene flow as expected between cave populations, or geographic distance between Bull Cave and Calf Cave #1 and the cluster from Indiana (see Fig. 27). Such a result clearly exemplifies one of the numerous limitations in the application of the genetic bar-code approach for species level identification as advocated by Hebert et al. (2003). A tree with *Oreonetides*-7 nested within the tip clade, or *Oreonetides*-7 as distinct as *O. filicatus* or *O. flavescens* would have provided interpretable insights, but the tree obtained here is inconclusive in that regard. The physical barriers to dispersal and gene flow inherent to cave life result in additional difficulties for accurate interpretations, especially with a limited number of specimens, as is often the case for troglobites. Paquin and Hedin (2007) showed genetic divergences within a single troglobitic spider in an area of ~30 × 15 km, that are greater than for all North America for mobile species of Lepidoptera (Nice et al., 2005). Such discrepancies are still poorly understood and suggest the cautious use of the bar-code approach.

As with the morphological and molecular data, geography and distribution do not provide insights that favor either a distinct species or intra-specific variability. The cluster from Tennessee (that includes Bull Cave and Calf Cave #1) could either harbor a different species or a distinct population of the same species, and both scenarios would be geographically cohesive. Based on available data, it seems best to consider the male from Bull Cave to belong to *O. beattyi* n.sp. and represent variation within the same species. A single specimen does not provide enough certitude to discard the possibility of an aberrant specimen and propose a robust species hypothesis. However, this interpretation may be easily refuted by future collections of additional males displaying morphology similar to that specimen.

Troglobitic Linyphiidae and the Cryophilic Affinities/Relict Population Hypothesis

Affinities for caves have been previously reported in the genus: *Oreonetides shimizui* (Yaginuma, 1972) is found in Japanese caves, although the species does not display obvious morphological adaptations to cave life such as noticeable eye reduction (Yaniguma, 1972; Eskov, 1992). In eastern North America, several linyphiid species display different degrees of troglobitic adaptations. *Anthrobia mammouthia* Tellkampf, 1844 shows pronounced adaptations with leg elongation and a total lack of eyes, *Porrhomma cavernicola* (Keyserling, 1886) and *Islandiana* spp. still have eye remnants, while *Phanetta subterranea* (Emerton, 1875) known from at least eleven U.S. states and more than a thousand localities, does not show striking morphological adaptations to cave life such as pronounced eye reduction. None of these species are known from surface records, even *P. subterranea,* with its absence of pronounced troglomorphic characters. In other cases, however, the dependence to cave habitats is not as clear. *Bathyphantes weyeri* (Emerton, 1875), *Centromerus latidens* (Emerton, 1882), *Taranucnus ornithes* (Barrows, 1940) are widespread in caves of the eastern North America; almost all records are known from caves, but some specimens have been found on the surface at the northern edge of their distributions. A similar pattern is observed for *Oaphantes* n.sp. on the west coast. We propose the cryophilic affinities/relict population hypothesis to explain this troublesome restriction to caves in southern locations and surface records at the northern edge, within the same species. The implications of this hypothesis have been referred to, at least indirectly, by some authors (see Barr, 1967; Peck, 1973; Peck and Lewis, 1978; Barr and Holsinger, 1985), but not formally proposed as such. Affinity for colder conditions, or avoidance of warm climate, is a driving force behind the dynamic of distribution ranges (Parmesan and Yohe, 2003) and invasion of caves (Barr, 1967). Facing conditions tending

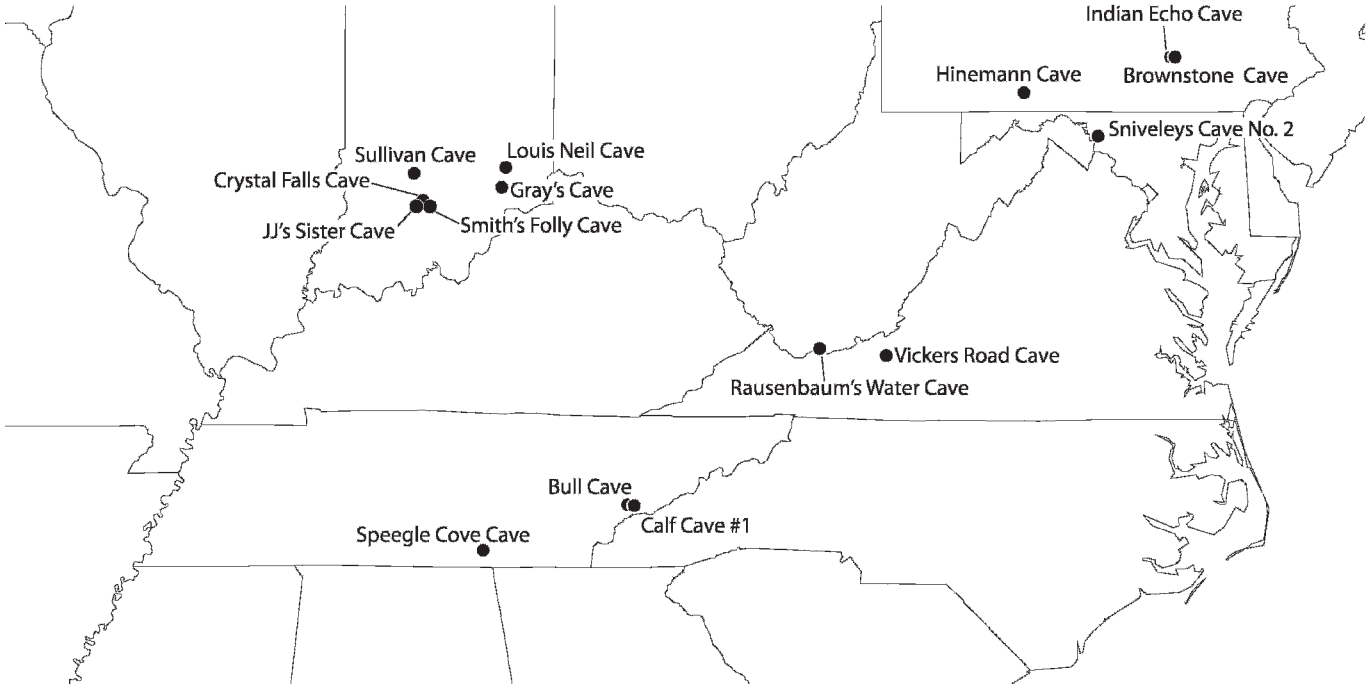


Figure 27. Distribution map of *Oreonetides beattyi* n.sp. in eastern North America.

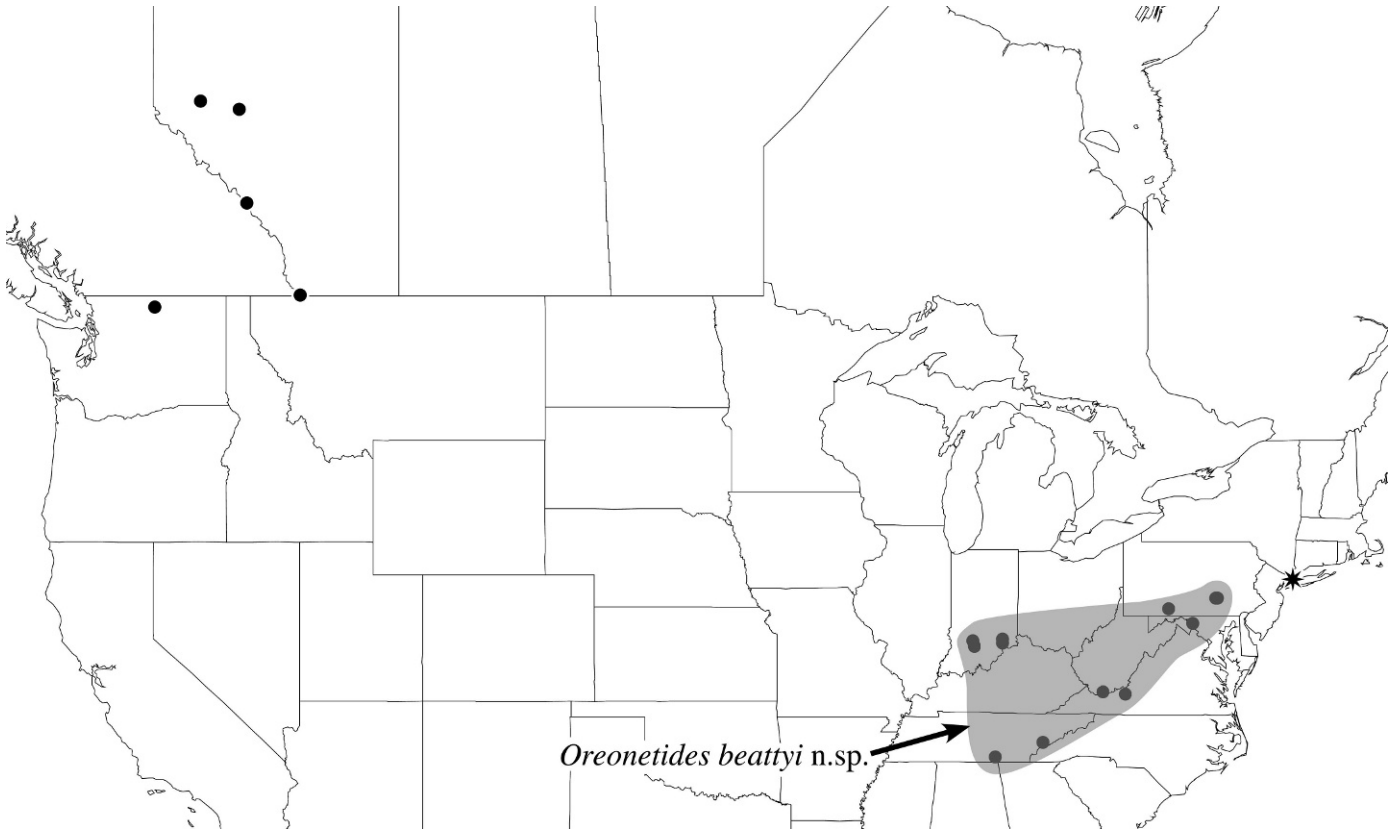


Figure 28. Distribution map *Oreonetides flavus* in North America. The star symbol represents an older record of *O. flavus* that could not be verified. The distribution of *O. beattyi* n.sp. is provided (shaded area) for comparative purposes.

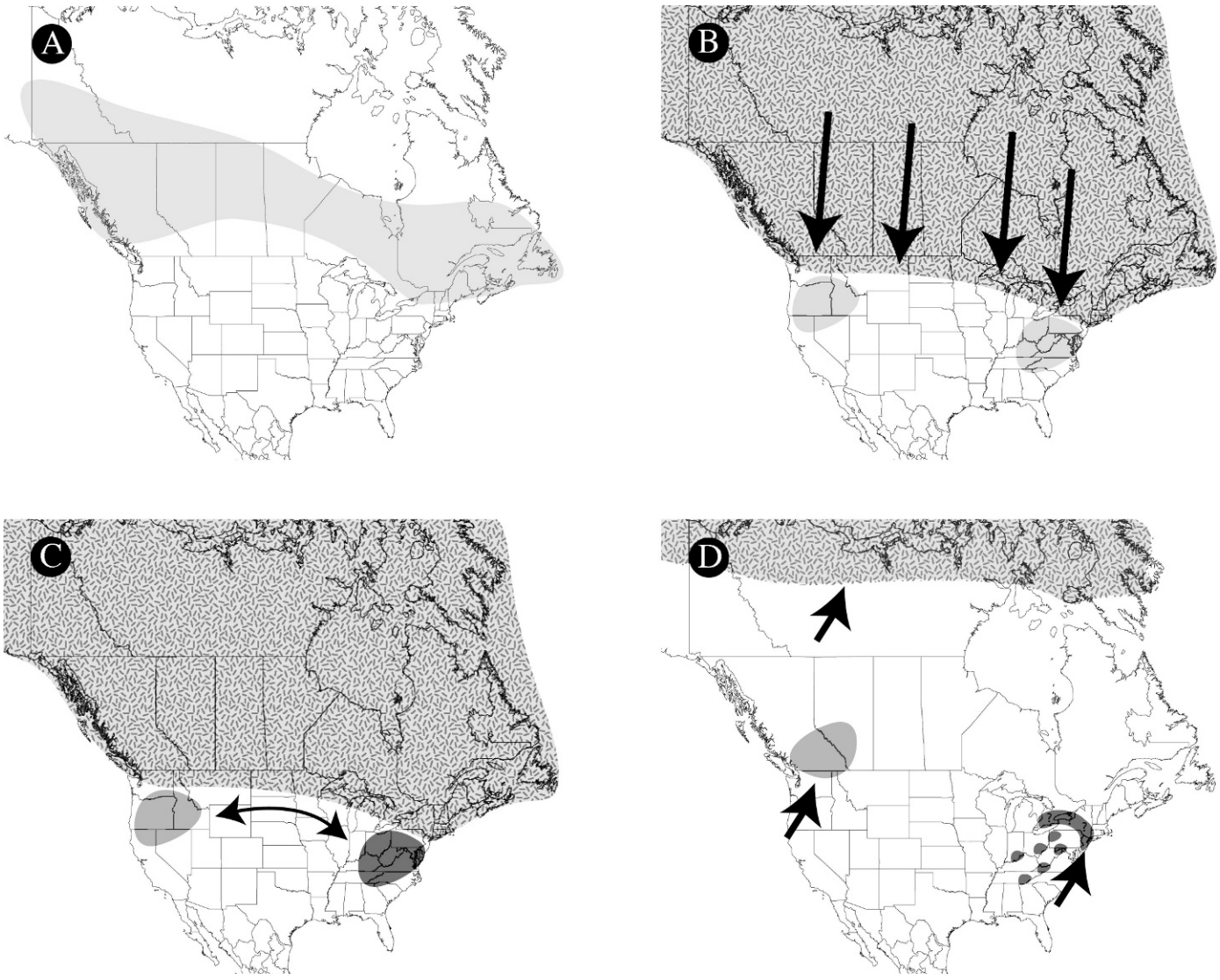


Figure 29. Evolutive hypothesis of *O. beattyi* n.sp. and *O. flavus* proposed as sister species. A) Boreal distribution of the hypothesised ancestor associated with cool and moist forest habitats. B) Glaciations are sweeping down the ancestor into two areas defined by forest components. C) Isolation and speciation. D) Following the retreat of the Wisconsin glacial ice sheet, species shift up north. In the case of *O. beattyi* n.sp., the populations found in the southern limits are restricted to caves and northernmost probable records are surface ones; *O. flavus* is now found in previously glaciated areas.

towards warmer and dryer climate, cryophilic species shifted their ranges northward, leaving behind pockets of populations in cool habitat such as bogs, mountain tops, scree slopes, or caves (Fig. 29). These areas are subsequently under warmer conditions, which lead to the extinction of epigean populations, and favor the survival in the subterranean habitat, or other suitable habitat. Such pressure differs or is absent at the northern edge, allowing species to survive on the surface.

Like many cave spiders from eastern North America, *Oreonetides beattyi* n.sp. has a broad distribution across multiple physiographic regions, including several karst areas of the Appalachians and Interior Low Plateaus (Hunt, 1974). The theoretical background for these broad distributions is unclear (but see Barr and Holsinger, 1985), particularly with such differences in the degree of cave adaptation for the different species. On one hand, this suggests that cave invasions by linyphiid species were not synchronized and are much more recent than cave formation, which would have limited and shaped the species distributions according to the physio-geographic evolution of these areas. For instance, a species restricted to a particular geological formation would suggest that the mechanisms driving such distribution are related to the evolution of the geological unit, but a distribution that encompasses several karst units suggests otherwise. On the other hand, the mechanisms behind the evolution and dispersal of troglobites are poorly understood and could

involve alternative scenarios. For instance, species may disperse by way of alternate hypogean habitats such as mammal burrows (Skelley and Kovarik, 2001), scree slopes (Ruszyka and Klimes, 2005), mesocavern or *espace sous-terrain superficiel* (subterranean underground compartments) (Juberthie et al., 1980), which provide a connection between apparently isolated cave systems. In addition, the perception of being isolated is often qualified by their actual state; apparently disconnected fragments may have been part of a complex network that evolved into a fragmented habitat, giving a biased impression of independence of its inherent units. Such fragmentation may not have been the physical conditions present when cave life evolved in these systems. Another possibility is that the distribution of these troglobites is the result of multiple cave colonizations by epigean ancestors. The intermediate stages of cave dependence suggested by the cryophilic affinities/relict population hypothesis provides a theoretical pathway for the evolution and distribution of troglobites that explains distributions by postulating surface connections between cave systems in colder times, followed by the isolation of disjunct cave populations as the climate warmed. Given the range of species mentioned above, it seems unlikely that a single scenario could explain their widespread distributions. The information presently available is not sufficient to conclusively favor any of these alternatives, but the widespread distribution and the different degrees of troglomorphism observed in eastern cave Linyphiidae likely represent different, and relatively early, stages in the evolution towards strict dependence on cave habitat when compared to the ~80 North American cave spiders that are totally eyeless, display highly fragmented distribution, or extremely narrow endemism (Gertsch, 1974; 1984; 1992).

The Problematic Record from Sea Cliff (New York)

In the light of actual data, the identity of the specimen reported by van Helsdingen (1981) from Sea Cliff (New York) remains problematic (see Fig. 28). Given the similarity of both species, it is possible that this record is a misidentification of *O. beattyi* n.sp., as suggested by its location on the eastern side of the continent. Such record would be the first surface mention of the species, otherwise restricted to caves. A surface record would indicate similar affinities to those displayed by to *B. weyeri* and *C. latidens,* which are found at the surface at the northern edge of their distribution. However, it is also possible that this record is indeed of *O. flavus*, and the apparent distribution gap due to incomplete sampling or to a disjunct distribution like that of *Poeciloneta aggressa* (Chamberlin and Ivie 1943) (Paquin et al., 2001). Location of the Sea Cliff specimen, or the collection of additional specimens, is necessary to clarify the situation.

Speciation Hypothesis

The study of *O. beattyi* n.sp. and *O. flavus* leaves no doubt about their close relatedness. Given the highly disjunct distribution of the two species and the clear affinities of *O. beattyi* n.sp. for cave habitat, we propose the following evolutionary scenario to explain their particular distribution. Like many Linyphiidae, and most North American *Oreonetides* species (van Helsdingen, 1981), the proto *beattyi/flavus* ancestor displayed affinities for cool and moist environments and had widespread boreal distribution (Fig. 29a). During the Wisconsinan age, most life forms occurring in northern latitudes were displaced southward by a glacier ice complex that covered nearly all of Canada (Prest et al., 1967; Matthews, 1979; Danks, 1993). In central North America, the ice-front habitat consisted of a thin band of mixed open conifer forest and tundra, with dry plains beyond. Some boreal species were able to live in this environment but many were not, and their populations were split into widely separated Cordilleran and eastern forest components (Scudder, 1979; Pielou, 1991) (Fig. 29b). Prolonged isolation led to speciation into western and eastern forms (*O. flavus* and *O. beattyi* n.sp.) (Fig. 29c). Such disjunct distribution of related species is similar to other pairs of taxa that display a similar eastern-western division (Scudder, 1979). For instance, the two North American species of *Cryphoeca* (Araneae, Hahniidae) are similarly distributed: *C. montana* Emerton 1909 is found in the East, while *C. exlineae* Roth 1988 is restricted to the West. Similar patterns also have been reported for several species of beetles such as Carabidae, Staphylinidae, Helodidae (Scudder, 1979). Such eastern-western distributions are well-known and used as broad categories in Danks (1994). The warming climate and retreat of the Wisconsin glacial ice sheet from 14 to 11 ka (Peck, 1988; Schwert, 1992) provided suitable habitat for rapid northward expansion for species with affinities for cold and moist conditions. The progressive northward movement of species with such requirements is well known (Schwert, 1992). Following the cryophilic affinities/relict population hypothesis proposed here, *O. beattyi* n.sp shifted northward in the east, leaving behind isolated populations in caves, while *O. flavus* reoccupied more northerly areas previously not available (Fig. 29d). This scenario is close to the speciation hypothesis proposed for the cave fauna of Illinois by Peck and Lewis (1978). It provides better theoretical support for the actual distribution of the species than treating *O. beattyi* n.sp. as a simple postglacial offshoot from *O. flavus*. Despite their clear phylogenetic affinities, the morphological differences observed between the two species are large enough to suggest a longer history than one originating only from the end of the last glaciation. The rarity of the species could result in incomplete sampling that may obscure an accurate assessment of their distributions, but the proposed hypothesis seems the most plausible one given available data. Hopefully, additional collections will either

confirm the proposed scenario by producing surface specimens of *O. beattyi* from northeastern North America or suggest a better one to explain the particular distributions and dynamics of these related species.

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