

## Natural history and distribution of the enigmatic southern Appalachian opilionid, *Fumontana deprehendor* Shear (Laniatores: Triaenonychidae), with an assessment of morphological variation

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### Abstract

The opilionid species *Fumontana deprehendor* Shear, 1977 (Laniatores: Triaenonychidae) represents a monotypic genus, previously known from only four specimens collected at two published localities, both old-growth forest sites in the southern Appalachian mountains. In an effort to increase the biogeographic and taxonomic information available for this phylogenetically and morphologically unique opilionid, we undertook a focused sampling effort throughout the southern Appalachians. These field efforts uncovered both more individuals (n = 141) and a broader distributional range (22 newly-discovered populations) for this monotypic genus. Examination of both somatic and penis morphology reveals little geographic variation across spatially disjunct populations. Our results provide a new perspective on conservation priorities for *F. deprehendor*. Rather than representing a single, hyper-rare taxon of limited distribution, our data suggest a broader distribution across the uplands of the southern Appalachians. We recommend that conservation attention be focused on learning more about the distribution, biology and relative rarity of *F. deprehendor* in the smaller, geographically isolated units.

**Key words:** Appalachian mountains, Opiliones, cryophilic arthropod, cryptic species

### Introduction

The opilionid species *Fumontana deprehendor* (Laniatores: Triaenonychidae) was once believed to be one of the rarest opilionids in North America (Shear 1977, 1978). The monotypic genus *Fumontana* was originally described from single adult male (holotype) and female (paratype) specimens, collected in Greenbrier Cove, Great Smoky Mountains

National Park, Sevier County, Tennessee (Shear 1977). Later, two additional specimens (male and female) were collected from a second locality (Joyce Kilmer Memorial Forest, Graham Co., NC), about 55 km southeast of the type locality in a different mountain system (Shear 1978). These two sites, and the four specimens discovered at these sites, remained the only published records of *F. deprehendor* until present.

*Fumontana deprehendor* is not only apparently extremely rare and habitat-limited, but also phylogenetically and morphologically unique. The genus is currently placed in the subfamily Triaenonychinae, within the family Triaenonychidae, due to the presence of two short branches on the posterior claws, the narrow sternum and genitalic morphology (Shear 1977; Kury 2003). Tarsal claw morphology is a well-established character for higher-level classification in opilionids and the presence of a three pronged, forked claw has traditionally been used to identify triaenonychids (Briggs 1967). This taxonomic placement makes *F. deprehendor* the sole triaenonychid in the eastern United States, as other nearctic triaenonychids are known only from western/northwestern portions of the United States and Canada (Briggs 1971). *Fumontana deprehendor* is also morphologically distinct from all other known North American laniatorean genera, most noticeably in their characteristic, long spined tubercles of legs one and two (Figs. 6–9; see also Shear 1977, figs. 13–14). Although formal phylogenetic analyses have not yet been conducted, the presence of tuberculate legs, the position and form of the eye tubercle, and the presence of anteriolateral spines on the scute suggest affinity to triaenonychids from southern temperate regions such as South America, South Africa, New Zealand, Madagascar and Australia (Shear 1977). As such, *F. deprehendor* may represent a very old, relictual lineage with Gondwanan affinities. The Appalachian millipede genus *Choctella* shows similar patterns of relationship to taxa from the southern hemisphere (Hoffman 1965).

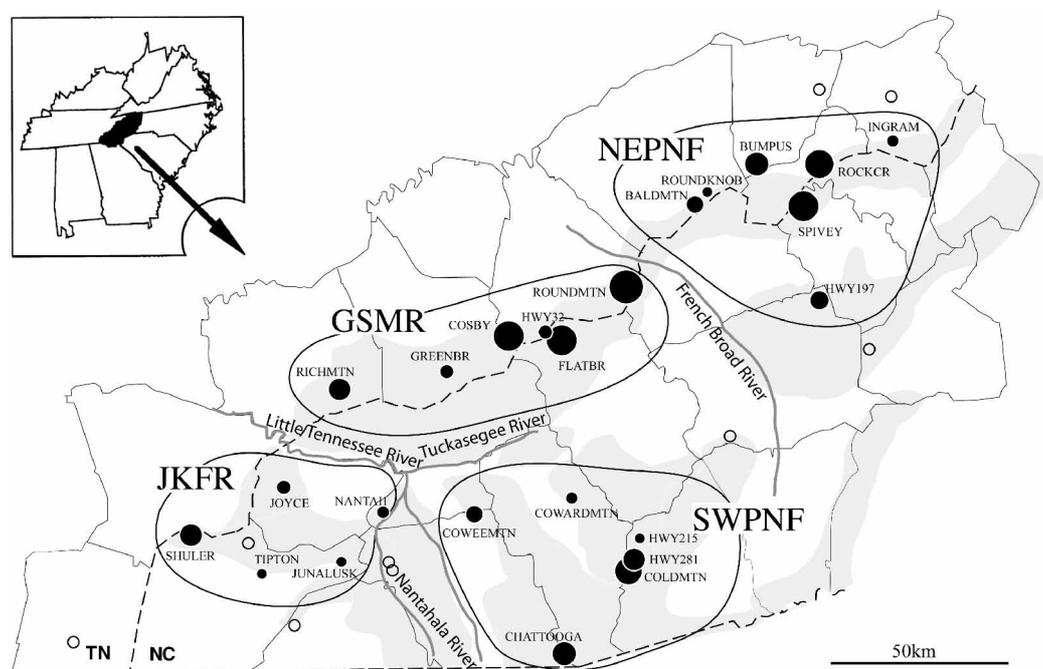
At the time of description, specific habitat preference could not be established due to the extreme rarity of collected specimens. However, both published localities represent rich, old growth hardwood forest habitats, suggesting that *F. deprehendor* may be a habitat specialist. Scattered opportunistic collections over the past few years indicate that this taxon is both found in more places and in more ecological situations than published records indicate. To further document the natural history, abundance, and full distribution of *F. deprehendor*, we undertook a focused sampling effort spanning the southern Appalachian mountains. After discovering a greater abundance and broader distribution than previously realized, we conducted an analysis of morphological variation for this new population sample.

## Material and methods

### *Field Methods*

*Fumontana deprehendor* specimens were collected from August 6–23, 2004, adding to smaller collections from previous years, with two additional sites collected in August

2005. Our sampling effort spanned most of the southern Appalachian mountains, including habitats in southwestern Virginia, eastern Tennessee, western North Carolina, and northern Georgia (Table 1, Fig. 1). Based on previous publications and experience, we searched in fallen and decayed hemlock logs in hemlock-dominated mid-elevation forests. After finding a sufficiently decayed log, we searched through the log by hand. Although often difficult to locate, once found, *F. deprehendor* individuals are unmistakable due to their distinctive morphology (unique orange-yellow coloration, long leg tubercles). We limited ourselves to about 1–2 hours per site; however, there were instances where we were able to collect a large series of specimens relatively quickly (see Results). Specimens were collected into vials using an aspirator. Collected specimens were transferred to either 100% or 80% ethanol in the field (for DNA and morphological work, respectively), or kept alive in a cooler and transported back to San Diego State University.

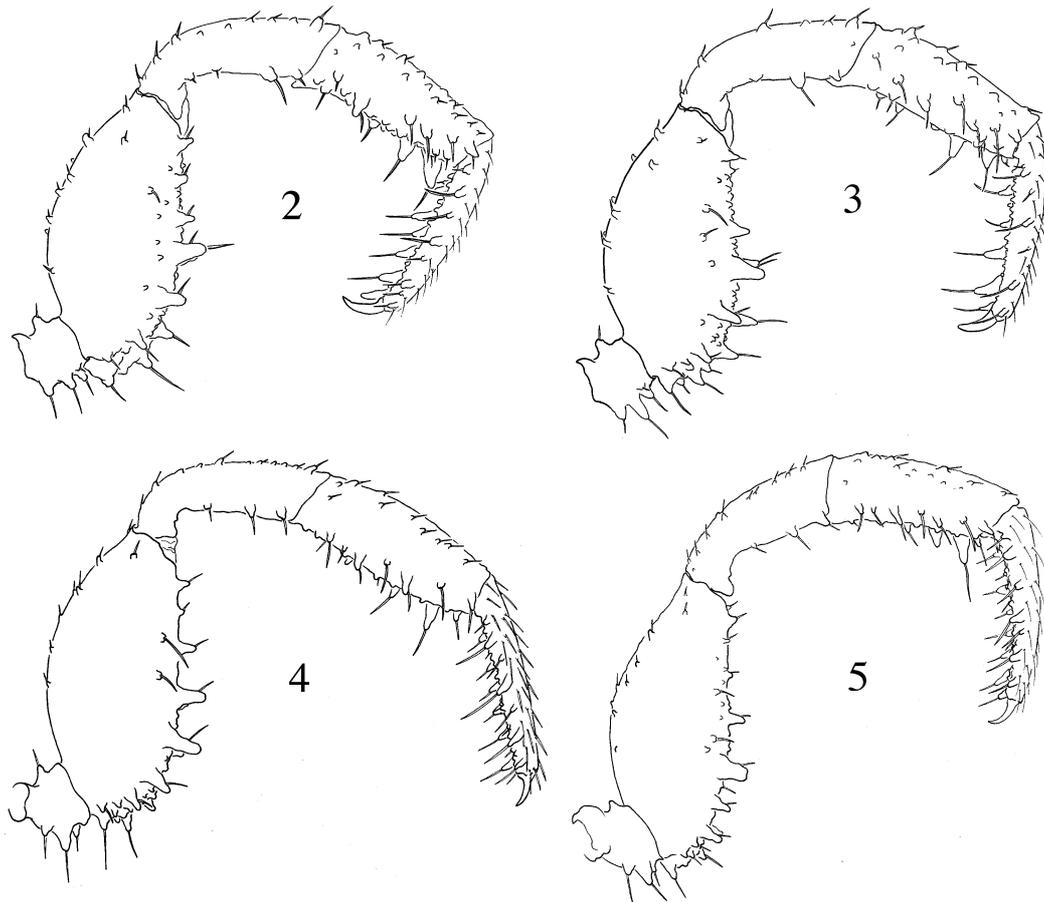


**FIGURE 1.** Distribution of sampled *Fumontana deprehendor* in the southern Appalachian mountains. A total of 24 localities were sampled, including both previously published localities (Shear 1977, 1978), labeled here as GREENBR and JOYCE. Dark circles represent sampled localities, with the size of circles proportional to the number of specimens collected. Open circles represent unsuccessful collecting attempts. Dark lines represent the four regions of “predicted endemism” (defined in the text) used as grouping variables in morphological analyses. These areas are regional highlands separated by major lowland riverine barriers. Stippled areas indicate elevations above 1000 meters.

### Morphology

*Illustrations.* We initially included four specimens spanning the full distributional

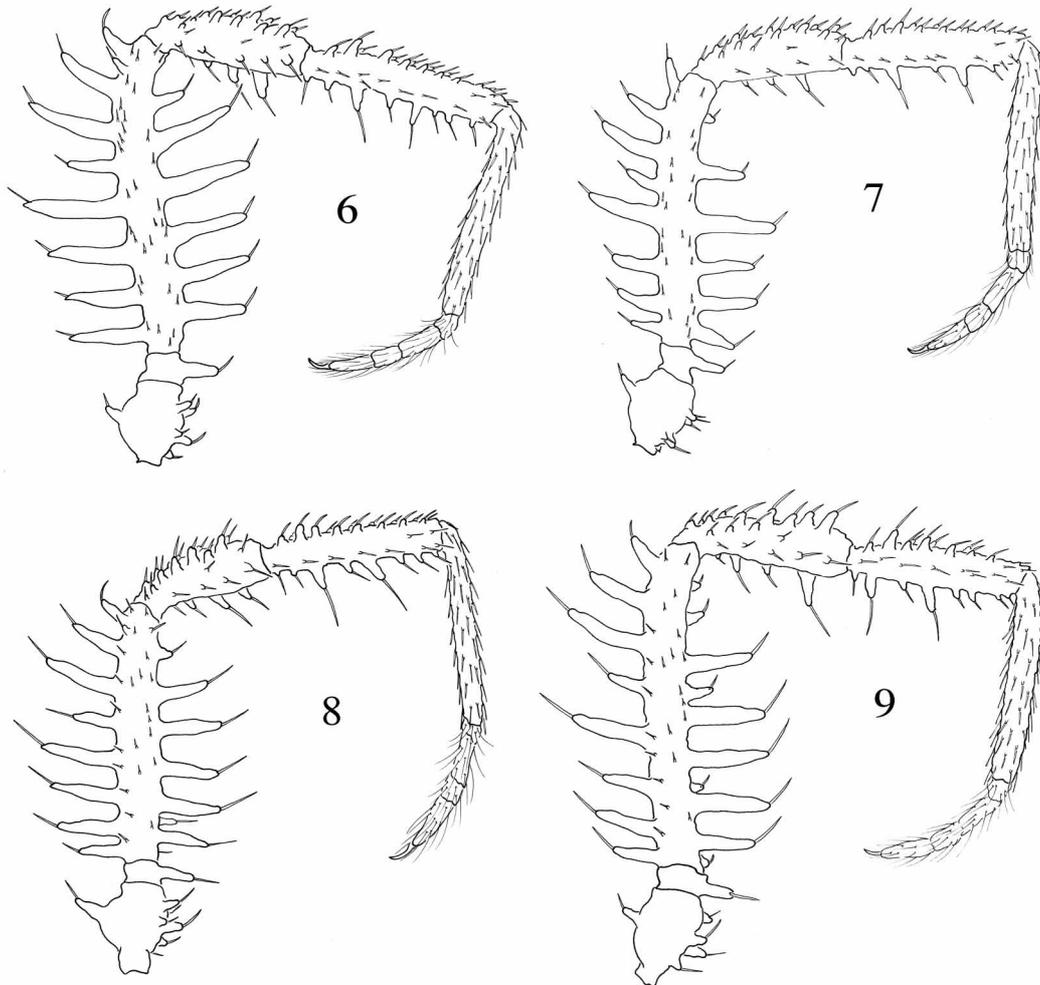
range in an attempt to assess gross morphological variation in the shape of left palp and first leg of representative male specimens. A digital camera attached to a stereomicroscope was used to capture images, which were then enlarged and printed. A tracing of this printed image was then detailed and shadowed, with repeated reference to the specimen under the microscope.



**FIGURES 2–5.** Illustrations of pedipalps of representative males from the four regions of “predicted endemism” (prolateral view). Corresponding localities indicated on Figure 1 by the following abbreviations: 2, BUMPUS; 3, FLATBR; 4, SHULER; 5, COLDMTN.

*Penis morphology.* Penis variation is typically analyzed when assessing divergence in closely related laniatorean taxa (e.g., Ubick & Briggs 1989). We assessed variation in *F. deprehendor* penis morphology via SEM imaging. At least two specimens from each geographic region (see below) were imaged (n=10). Male specimens were manually manipulated such that their penis was extended. This procedure involved removing the genital operculum and gently applying pressure to the penis through a small incision made near the anal operculum. Specimens were dehydrated using a Samdri-790 Critical Point

Dryer, metal coated using a Hummer VI Sputter Coater, and imaged using a Hitachi S-2700 Scanning Electron Microscope. An accelerating voltage of 15kV was used with the working distance varying from 25–30 mm. All SEM materials and equipment used are part of the Electron Microscope Facility at San Diego State University.



**FIGURES 6–9.** Illustrations of the first legs of representative males from the four regions of “predicted endemism” (prolateral view). Corresponding localities indicated on Figure 1 by the following abbreviations: 6, BUMPUS; 7, FLATBR; 8, SHULER; 9, COLDMTN.

*Measurements.* Measurements were taken from every male specimen that was preserved for morphological work (n=16), including at least two representatives from all major geographic regions (see below). Measurements were taken using an ocular micrometer housed in an Olympus SZX12 dissecting microscope. A total of 25 variables were assessed, including linear measurements of the scute, eye tubercle, palps, and anterior legs (see Appendix). Because of difficulties in taking measurements of leg tarsi,

these were not included as a variable. Body length was measured dorsally at the midline. Scute width and eye tubercle width were measured dorsally at the widest distance. Length and width of cheliceral segments were measured along the dorsal surface. Length and depth of most palp segments were measured along the retrolateral surface; with the exception of length and width of the tarsus, which were measured along the dorsal surface. Length of leg segments was measured along the retrolateral surface. All length measurements were taken from the most distal articulation point on either side of the segment, whereas width and depth were measured at the widest/deepest point on the segment.

### *Biogeography*

Population groups were defined using geographic criteria, following “predicted areas of endemism” as recognized in other arthropod taxa of the region [e.g., *Trechus* beetles (Kane *et al.* 1990), *Nesticus* spiders (Hedin 1997) and *Hypochilus* spiders (Catley 1994, Hedin 2001)]. Four groupings were defined for this analysis, including those localities that are (1) south and west of the Little Tennessee River (Joyce Kilmer Forest Region, JKFR), (2) the Great Smoky Mountains north of the Little Tennessee and Tuckasegee Rivers, and immediately eastern neighboring mountains west of the French Broad River (Great Smoky Mountain Region, GSMR), (3) south of the Tuckasegee River and east of the Little Tennessee River (South-West Pisgah National Forest, SWPNF), and (4) east of the French Broad River and Asheville Basin (North-East Pisgah National Forest, NEPNF). These areas of endemism are regional highlands separated by major lowland riverine barriers (see Fig. 1). A one-way ANOVA was used to assess significance of variation between population groups, conducted using the statistics software package SPSS v.11.0.2. Principal Component Analysis (PCA) of morphometric data (see appendix) was also used to visualize multivariate divergence within and between these predicted population groupings.

## **Results**

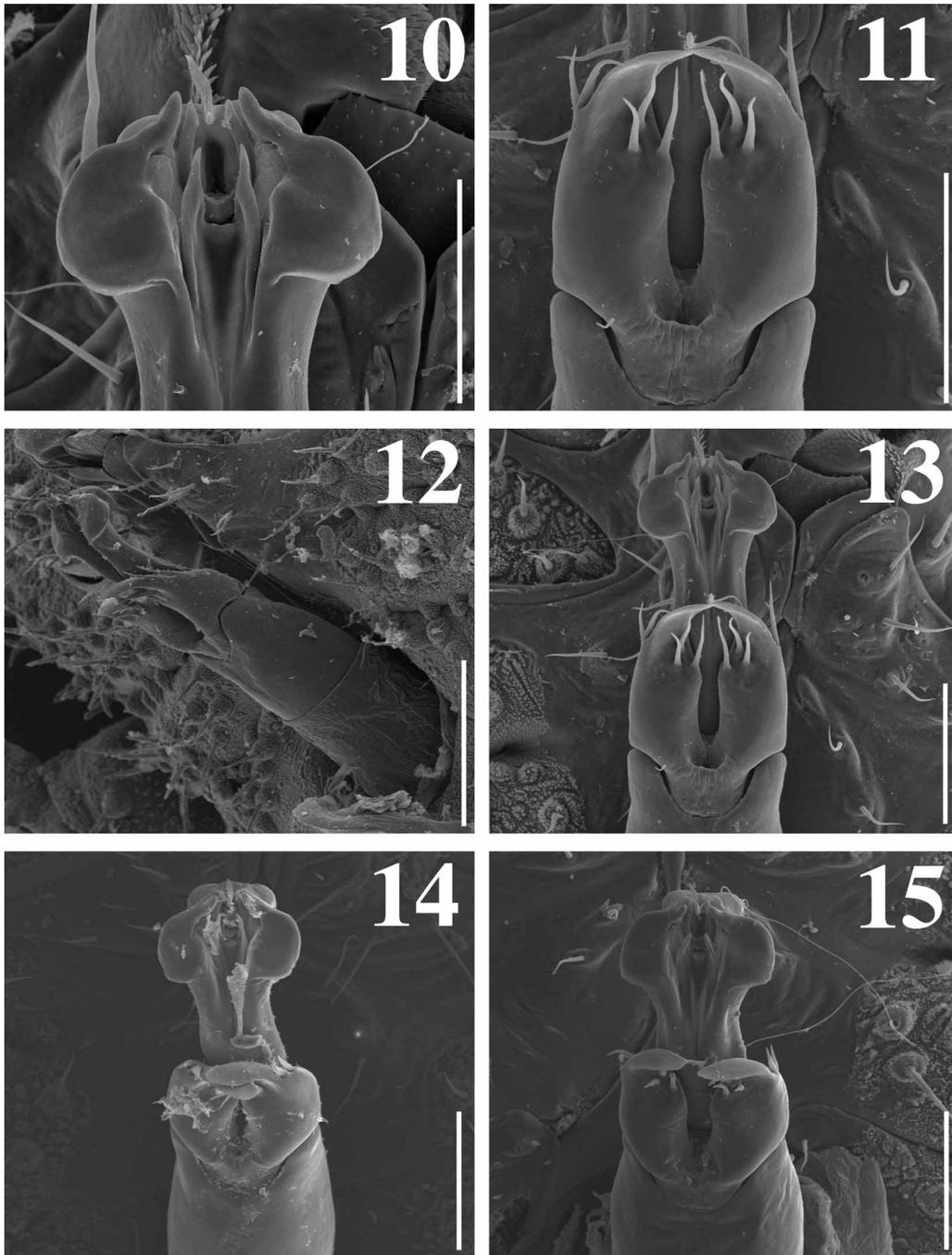
### *Distribution, natural history and abundance*

We collected 141 *F. deprehendor* specimens from 24 different sites in the southern Appalachian mountain region (Table 1, Fig. 1). Sites at which these opilionids were found varied in elevation from approximately 425 to 1035 meters, although the majority of specimens were collected above 750 meters. *Fumontana deprehendor* was most consistently found in well-decayed hemlock logs on moderate slopes, and seemed most abundant in logs that are decayed to the point that the soil/log boundary becomes indefinite. An optimal moisture level most likely explains the observed trend towards moderate slopes. Despite this apparent habitat preference, we were also able to collect *F. deprehendor* in a variety of other microhabitats (e.g., under rocks, in leaf litter, etc.),

TABLE 1. Locality, abundance, and habitat association data for sampled *Fumontana deprehendor* populations.

Locality information	Locality abbreviation	Latitude/ longitude	Sex distribution	Habitat association	Geographic region
TN: Blount Co., Rich Mtn Rd	RICHMTN	N 35.6508°/W 083.7979°	2 ♂, 3 ♀, 2 imm.	Rotting logs	GSMR
TN: Sevier Co., GSMNP, Greenprier Cove	GREENBR	N 35.7082°/W 083.3847°	2 ♀, 1 imm.	Rotting logs	GSMR
NC: Haywood Co., Flat Branch Rd	FLATBR	N 35.7526°/W 083.0895°	5 ♂, 4 ♀, 3 imm.	Rotting logs	GSMR
TN: Cocke Co., GSMNP, Cosby Campground	COSBY	N 35.7633°/W 083.2115°	7 ♂, 4 ♀, 2 imm.	Under rocks	GSMR
TN: Cocke Co., Hwy 32 @ Stateline	HWY32	N 35.7703°/W 083.1128°	1 ♂, 2 ♀	Rotting logs	GSMR
TN: Cherokee Co., S of Round Mtn	ROUNDMTN	N 35.8350°/W 082.9519°	5 ♂, 7 ♀, 2 imm.	Rotting logs and rocks (1)	GSMR
NC: Cherokee Co., along Tipton Creek	TIPTON	N 35.2503°/W 084.0724°	1 ♀	Under rocks	JKFR
NC: Cherokee Co., Nantahala River	NANTAH	N 35.3305°/W 083.5921°	1 ♂	Non-hemlock rotting log	JKFR
NC: Swain Co., Joyce Kilmer Memorial For.	JOYCE	N 35.3585°/W 083.9291°	1 ♂, 2 ♀	Rotting logs	JKFR
NC: Graham Co., Junaluska Rd	JUNALUSK	N 35.1760°/W 083.7680°	1 ♂	Under rock	JKFR
NC: Cherokee Co., Shuler Creek	SHULER	N 35.2424°/W 084.2227°	2 ♂, 5 ♀	Rotting logs	JKFR
NC: Buncombe Co., Hwy 197	HWY197	N 35.8036°/W 082.3536°	1 ♂, 4 ♀	Rotting logs	NEPNF
TN: Greene Co., Bald Mtn Rd	BALDMTN	N 36.0284°/W 082.7253°	3 ♂, 1 imm.	Rotting logs	NEPNF
NC: Yancey Co., E Spivey Gap	SPIVEY	N 36.0342°/W 082.4043°	5 ♂, 5 ♀, 2 imm.	Under rocks	NEPNF
TN: Greene Co., Bald Mtns, Round Knob Rd	ROUNDKNOB	N 36.0799°/W 082.6859°	1 ♂	Under rock	NEPNF
TN: Unicoi Co., Rook Creek Rec. Area	ROCKCR	N 36.1379°/W 082.3482°	3 ♂, 7 ♀, 1 imm.	Rotting logs	NEPNF
TN: Washington Co., Bumpus Cove	BUMPUIS	N 36.1424°/W 082.5079°	4 ♂, 4 ♀	Rotting logs	NEPNF
TN: Carter Co., Ingram Branch Rd	INGRAM	N 36.2140°/W 082.1456°	2 ♂	Rotting logs	NEPNF
NC: Macon/Jackson Co. line, Chattooga River	CHATTOOGA	N 35.0172°/W 083.1262°	2 ♂, 6 ♀, 1 imm.	Rotting logs	SWPNF
NC: Transylvania Co., Cold Mtn Rd	COLDMTN	N 35.1611°/W 082.9791°	2 ♂, 5 ♀, 3 imm.	Rotting logs	SWPNF
NC: Transylvania Co., Hwy 281	HWY281	N 35.1957°/W 082.9608°	1 ♂, 6 ♀	Under rocks	SWPNF
NC: Transylvania Co., Hwy 215	HWY215	N 35.2575°/W 082.9204°	1 ♀	Under rock	SWPNF
NC: Macon Co., S of Cowee Mtns Lookout	COWEEMTN	N 35.3168°/W 083.3735°	1 ♂, 2 ♀, 1 imm.	Rotting logs	SWPNF
NC: Jackson Co., Coward Mountain	COWARDMTN	N 35.3606°/W 083.1037°	2 imm.	Under rocks	SWPNF

Notes: Geographic coordinates are given in decimal degrees. "Rotting logs" refers to rotting hemlock logs, unless otherwise noted. Geographic regions are defined as in text and Figure 1.



**FIGURES 10–15.** SEM of *F. deprehendor* penes in ventral view (10–11, 13–15) and in ventrolateral view (12). Figures 10–11 shown to demonstrate typical morphology under optimal imaging conditions: 10, glans (FLATBR population); 11, setose lobes (FLATBR population). Figures 12–15 shown for the purpose of comparison across geographic regions: 12, NWPNF (BUMPUS population); 13, GSMR (FLATBR population); 14, JKFR (JOYCE population); 15, SWPNF (COWEEMTN population). Scale bars: 70  $\mu\text{m}$  (10), 100  $\mu\text{m}$  (11, 13–15), 200  $\mu\text{m}$  (12).

sometimes finding specimens coincidentally while searching for other cryophilic arthropods. It must be emphasized, however, that based on our experience this result appears to be an exception. When uncovered, specimens generally remained motionless, or moved very slowly.

There were several sites where we failed to find specimens in apparently favorable habitats. These sites are mostly at the southwestern border of the sampled area (see Fig. 1) and might correspond to the distributional limits of *F. deprehendor*. However, there were also occasions where we failed to find specimens, despite the presence of apparently good habitat, within what seems to be the range of the species. This could be due to a lack of adequate collecting effort, as *F. deprehendor* can be sometimes very difficult to locate.

We also discovered a greater abundance of individuals than previous records indicate. In some instances, we were able to collect 10 adult specimens in less than 20 minutes at a single site. Most specimens collected were adults. Immature specimens are much smaller, without significant pigmentation, and likely go undetected. Our records indicate no apparent bias in the sex ratio of collected adult specimens (see Table 1). It was generally the case that multiple specimens could be found in individual logs. However, when found under rocks, it was usually the case that only individual specimens would be found. One particularly interesting exception was the COSBY locality in the Great Smoky Mountains, where multiple specimens (i.e., 2–4) were found under individual rocks.

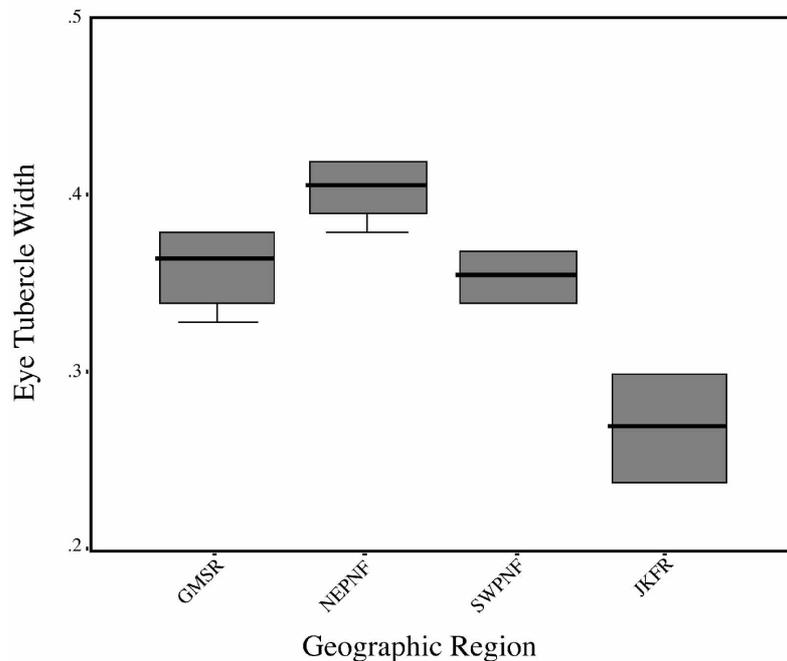
#### *Morphological variation*

*Somatic morphology.* Comparison of the palps and first legs of four males representing populations in major biogeographic regions do not indicate obvious qualitative morphological differences (see Figs. 2–5 and 6–9, respectively). Further qualitative comparisons were not attempted due to this observed lack of relevant variation.

*Penis morphology.* Close examination of penis morphology revealed no obvious differences between populations from different geographic regions (Figs. 10–15), aside from artifactual differences resulting from inconsistencies in specimen positioning. All penes examined are consistent with that of the holotype described by Shear (1977, figs. 5–6), who described the penis as having a “glans with two flanking setose lobes” and a seminal canal ending in a “spine-like projection”. More detailed study as provided by SEM showed penis morphology to include a complement of five pairs (three ventral, two dorsal) of hairlike processes associated with the flanking lobes; these processes appear integral with the lobes, rather than arising from a point of articulation. The “spine-like projection” consists of seven distally oriented structures: two from up-turned portions of the lobe-like tip of the penis, two pairs of projections flanking the end of the seminal canal, and an unpaired projection arising dorso-distally from the penis (see Figs. 10–15). All specimens examined (n=10) share this penis morphology.

*Measurements.* A one-way ANOVA identified sixteen characters exhibiting significant variation between populations in different regions ( $p < 0.05$ ). These characters include

scute width, eye tubercle width, first and second cheliceral segment length, palpal femur length and depth, palpal patella length and depth, palpal tibia length, palpal tarsus length, first leg femur, patella and metatarsus length, and second leg femur, tibia and metatarsus length. Many of these length measurements are likely correlated with one another. Figure 16 illustrates the differences observed between geographic regions for eye tubercle width, showing a general trend (seen in most characters) where specimens from populations in the JKFR region are slightly smaller than average, and those from the NEPNF region are slightly larger than average. A Principal Component Analysis (PCA) illustrates multivariate differentiation between regions (Fig. 17), again indicating a general trend of size differentiation across regions. However, there is also considerable variation within regions, such that regional divergence is not strictly non-overlapping.



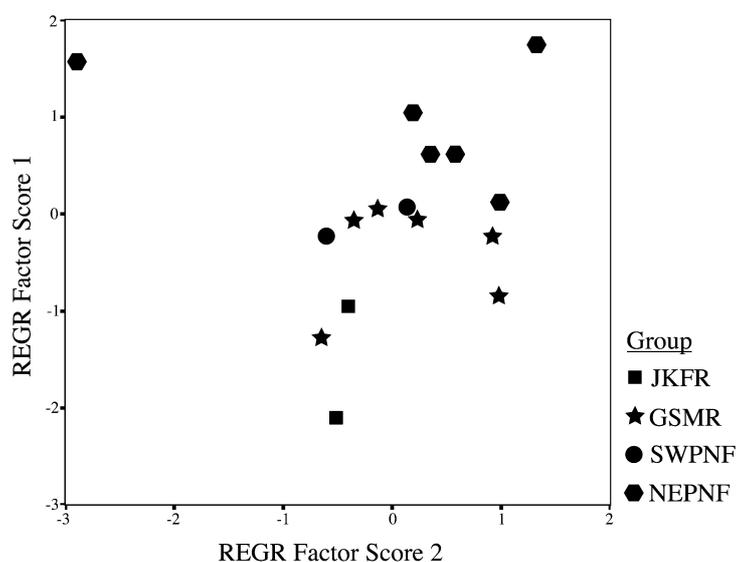
**FIGURE 16.** Boxplot demonstrating the range of eye tubercle width for the different geographic regions of “predicted endemism”.

## Discussion

### *Natural history, distribution and morphological divergence*

Prior to this study, *F. deprehendor* was thought to be exceedingly rare. Published records (Shear 1977, 1978) included only four animals from two locations, with subsequent opportunistic collecting throughout the southern Appalachians having turned up few additional specimens. Our work indicates that *F. deprehendor* is found in greater

abundance across a broader distributional range than was originally believed. Although additional systematic sampling in the southern Appalachians will almost certainly add to our knowledge of the distribution, at this time we feel reasonably confident in defining the distributional limits of the species. Unsuitable low-elevation habitats found to the west, north, and southeast of the inferred range likely preclude occurrence in these areas. Suitable habitat is found in the mountains of northern Georgia, and we expect *F. deprehendor* to be ultimately found there. Likewise, suitable habitats are found in the mountains to the northeast (i.e., southwest Virginia), although reasonable search efforts in this region have failed to turn up specimens.



**FIGURE 17.** Results of the PCA of morphometric data taken from 25 characters (see appendix), with the two principal components explaining the greatest percentage of variation plotted against one another.

Our perception is that *F. deprehendor* has limited powers of dispersal and may therefore be particularly susceptible to divergence via geographic isolation. However, aside from minor size differences, we were unable to find obvious morphological evidence for such divergence. This result is somewhat surprising, as many other arthropod taxa with similar Appalachian distributions show clear evidence for fine scale divergence and speciation. Examples include *Trechus* beetles (Kane *et al.* 1990), *Nesticus* spiders (Hedin 1997), *Hypochilus* spiders (Catley 1994) and xystodesmid millipedes (Hoffman 1999). *Fumontana deprehendor* either has greater dispersal abilities than would seem apparent, or alternatively, its populations may be susceptible to cryptic divergence, that is, genetic divergence with little or no morphological change. Cryptic divergence and speciation (as elucidated by molecular data) has been demonstrated many times in habitat-specialist

arthropod taxa (e.g., Bond *et al.* 2001; Bond & Sierwald 2002; Bond 2004; Wilcox *et al.* 1997) and is being investigated in *F. deprehendor* in an on-going study.

#### *Conservation implications*

We have shown that the perceived rarity of *F. deprehendor* is likely an artifact of lack of knowledge with regards to their natural history (in the past, specimens had only been collected based on chance encounters), rather than reflecting an actual biotic property. Alternatively, while *F. deprehendor* is clearly more abundant than previous records would indicate, these opilionids are still relatively rare animals, and in our experience, are generally more rare than other southern Appalachian laniatorean opilionids. We believe that this cryophilic opilionid deserves regional conservation attention for several reasons. *Fumontana deprehendor* clearly holds a unique position geographically and taxonomically within the Triaenonychidae. Management decisions should consider not only species richness, but also phylogenetic uniqueness (Polasky *et al.* 2001, Rodrigues & Gaston 2002). The family distribution also allows for useful comparative studies with other taxa exhibiting similar predominately Gondwanan distributions. Furthermore, observed habitat specificity would imply that *F. deprehendor* might act as an indicator of forest health. Indeed, previous studies suggest that habitat-limited triaenonychids from the Pacific Northwest forests have great difficulty in adapting to habitat change (e.g., lumbering) (Briggs 1971). Personal observations have shown that locations in the southern Appalachians that had been lumbered consistently failed to turn up *F. deprehendor* specimens, suggesting an inability to cope with such changes.

Our results provide new perspective for regional biogeography and redefine the conservation priorities for *F. deprehendor*. Given this new distributional and abundance data, we recommend that conservation attention be focused on learning more about the distribution, biology, and relative rarity of this species within major continuous mountain ranges. An on-going study examining phylogeographic divergence in this taxon will assist in this endeavor.

#### **Acknowledgements**

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## References

- Bond, J.E., Hedin, M.C., Ramirez, M.G. & Opell, B.D. (2001) Deep molecular divergence in the absence of morphological and ecological change in the Californian coastal dune endemic trap-door spider *Aptostichus simus*. *Molecular Ecology*, 10, 899–910.
- Bond, J.E. & Sierwald, P. (2002) Cryptic speciation in the *Anadenobolus excisus* millipede species complex on the island of Jamaica. *Evolution*, 56, 1123–1355.
- Bond, J.E. (2004) Systematics of the Californian euctenizine spider genus *Apomastus* (Araneae: Mygalomorphae: Cyrtachaeniidae): the relationship between molecular and morphological taxonomy. *Invertebrate Systematics*, 18, 361–376.
- Briggs, T.S. (1967) An emendation for *Zuma acuta* Goodnight & Goodnight (Opiliones). *Pan-Pacific Entomologist*, 43, 89.
- Briggs, T.S. (1971) The harvestmen of family Triaenonychidae in North America (Opiliones). *Occasional Papers of the California Academy of Sciences*, 90, 1–43.
- Catley, K.M. (1994) Descriptions of new *Hypochilus* species from New Mexico and California with a cladistic analysis of the Hypochilidae (Araneae). *American Museum Novitates*, 3088, 1–27.
- Hedin, M.C. (1997) Speciation history in a diverse clade of habitat-specialized spiders (Araneae: Nesticidae: *Nesticus*): Inferences from geographic-based sampling. *Evolution*, 51, 1929–1945.
- Hedin, M.C. (2001) Molecular insights into species phylogeny, biogeography, and morphological stasis in the ancient spider genus *Hypochilus* (Araneae: Hypochilidae). *Molecular Phylogenetics and Evolution*, 18, 238–251.
- Hoffman, R.L. (1965) A second species in the diplopod genus *Choctella* (Spirostreptida: Choctellidae). *Proceedings of the Biological Society of Washington*, 78, 55–58.
- Hoffman, R.L. (1999) Checklist of the millipedes of North and Middle America. *Virginia Museum of Natural History Special Publication*, 8, 1–581.
- Kane, T.C., Barr, T.C. & Stratton, G.E. (1990) Genetic patterns and population structure in Appalachian *Trechus* of the *vandykei* group. *Brimleyana*, 16, 133–150.
- Kury, A.B. (2003) Annotated catalogue of the Laniatores of the New World (Arachnida, Opiliones). *Revista Ibérica de Aracnología*, 1, 5–337.
- Polasky, S., Csuti, B., Vossler, C.A. & Meyers, S.M. (2001) A comparison of taxonomic distinctness versus richness as criteria for setting conservation priorities for North American birds. *Biological Conservation*, 97, 99–105.
- Rodrigues, A.S.L. & Gaston, K.J. (2002) Maximising phylogenetic diversity in the selection of networks of conservation areas. *Biological Conservation*, 105, 103–111.
- Shear, W.A. (1977) *Fumontana deprehendor*, n. gen., n. sp., the first triaenonychid opilionid from eastern North America (Opiliones: Laniatores: Triaenonychidae). *Journal of Arachnology*, 3, 177–183.
- Shear, W.A. (1978) A new record for the rare opilionid *Fumontana deprehendor* (Opiliones, Triaenonychidae). *Journal of Arachnology*, 6, 79.
- Ubick, D. & Briggs, T.S. (1989) The harvestman family Phalangodidae. 1. The new genus *Calicina*, with notes on *Sitalcina* (Opiliones: Laniatores). *Proceedings of the California Academy of Sci-*

*ences*, 46, 95–136.

- Wilcox, T.P., Hugg, L., Zeh, J.A. & Zeh, D.W. (1997) Mitochondrial DNA sequencing reveals extreme genetic differentiation in a cryptic species complex of neotropical pseudoscorpions. *Molecular Phylogenetics and Evolution*, 7, 208–216.

APPENDIX

Measurements of morphological characters used in statistical analyses. Locality abbreviations are given in Table 1. All measurements are in millimeters. Abbreviations used: **BodyL** = body length; **ScW** = scute width; **EyTubW** = eye tubercle width; **Ch1stL**, **Ch2ndL** = first and second cheliceral segment length; **Ch1stW**, **Ch2ndW** = first and second cheliceral segment width; **PalpFemL**, **PalpPatL**, **PalpTibL**, **PalpTarl** = palpal femur, patella, tibia and tarsus length; **PalpFemD**, **PalpPatD**, **PalpTibD**, **PalpTarW** = palpal femur, patella, tibia and metatarsus width; **Leg1Tro**, **Leg1Fem**, **Leg1Pat**, **Leg1Tib**, **Leg1Met** = first leg trochanter, femur, patella, tibia and metatarsus length; **Leg2Tro**, **Leg2Fem**, **Leg2Pat**, **Leg2Tib**, **Leg2Met** = second leg trochanter, femur, patella, tibia and metatarsus length.

Locality	BodyL	ScW	EyTubW	Ch1stL	Ch1stW	Ch2ndL	Ch2ndW	PalpFemL	PalpFemD	PalpPatL	PalpPatD	PalpTibL	PalpTibD
FLATBR.1	1.76	1.28	0.38	0.29	0.16	0.59	0.17	1.24	0.53	0.80	0.24	0.78	0.29
FLATBR.2	1.74	1.19	0.37	0.30	0.17	0.56	0.17	1.19	0.51	0.78	0.22	0.77	0.28
FLATBR.3	1.52	1.16	0.34	0.26	0.14	0.56	0.17	1.08	0.44	0.68	0.21	0.67	0.27
RICHMTN	1.70	1.22	0.33	0.32	0.16	0.61	0.17	1.27	0.50	0.76	0.23	0.72	0.27
BALDMTN	1.85	1.35	0.42	0.34	0.12	0.72	0.17	1.35	0.56	0.89	0.27	0.83	0.25
ROCKCR	1.90	1.33	0.42	0.38	0.16	0.59	0.17	1.29	0.57	0.84	0.26	0.83	0.31
SPIVEY.1	1.72	1.30	0.39	0.33	0.18	0.61	0.18	1.27	0.54	0.79	0.26	0.80	0.24
SPIVEY.2	1.77	1.43	0.42	0.38	0.18	0.66	0.18	1.35	0.58	0.91	0.29	0.83	0.33
SPIVEY.3	1.74	1.31	0.38	0.32	0.17	0.60	0.17	1.24	0.53	0.79	0.26	0.79	0.33
SPIVEY.4	1.56	1.16	0.39	0.34	0.17	0.57	0.17	1.21	0.79	0.73	0.24	0.76	0.28
COWEE	1.76	1.19	0.34	0.26	0.16	0.58	0.17	1.16	0.47	0.71	0.24	0.70	0.26
COLDMTN	1.72	1.28	0.37	0.31	0.16	0.62	0.18	1.21	0.50	0.81	0.26	0.76	0.28
SHULER	1.52	1.08	0.30	0.26	0.14	0.54	0.15	0.98	0.38	0.61	0.21	0.57	0.23
JOYCE	1.67	1.06	0.24	0.24	0.16	0.58	0.16	1.08	0.48	0.69	0.23	0.70	0.28
ROUND.1	1.52	1.21	0.36	0.33	0.16	0.58	0.17	1.07	0.47	0.69	0.24	0.67	0.27
ROUND.2	1.62	1.27	0.38	0.29	0.16	0.58	0.18	1.13	0.51	0.69	0.26	0.73	0.30

## APPENDIX CONTINUED.

Locality	PalpTarL	PalpTarW	Leg1Tro	Leg1Fem	Leg1Pat	Leg1Tib	Leg1Met	Leg2Tro	Leg2Fem	Leg2Pat	Leg2Tib	Leg2Met
FLATBR.1	0.81	0.18	0.16	0.94	0.43	0.6	0.67	0.23	1.11	0.56	0.90	0.86
FLATBR.2	0.83	0.17	0.23	0.94	0.46	0.58	0.73	0.26	1.13	0.49	0.96	0.89
FLATBR.3	0.70	0.16	0.21	0.84	0.39	0.57	0.62	0.22	0.72	0.33	0.90	0.82
RICHMTN	0.77	0.16	0.24	0.89	0.43	1.06	0.66	0.19	1.10	0.52	0.90	0.93
BALDMTN	0.97	0.18	0.28	1.10	0.48	0.70	0.78	0.28	1.27	0.62	1.14	1.03
ROCKCR	0.95	0.17	0.22	1.00	0.44	0.64	0.76	0.22	1.24	0.58	1.10	0.97
SPIVEY.1	0.86	0.16	0.22	0.97	0.46	0.67	0.72	0.26	1.16	0.60	0.99	0.91
SPIVEY.2	0.91	0.12	0.26	1.02	0.5	0.72	0.79	0.27	1.30	0.65	1.13	1.00
SPIVEY.3	0.89	0.17	0.23	0.92	0.47	0.64	0.72	0.24	1.17	0.57	1.02	0.96
SPIVEY.4	0.80	0.17	0.22	0.93	0.46	0.62	0.68	0.24	1.10	0.56	0.97	0.88
COWEE	0.78	0.16	0.22	0.93	0.44	0.61	0.66	0.26	1.13	0.54	0.92	0.93
COLDMTN	0.81	0.18	0.21	0.94	0.43	0.59	0.62	0.19	1.13	0.47	0.94	0.86
SHULER	0.66	0.14	0.16	0.72	0.36	0.51	0.56	0.21	0.87	0.47	0.77	0.71
JOYCE	0.69	0.17	0.18	0.91	0.44	0.56	0.64	0.22	0.95	0.56	0.92	0.83
ROUND.1	0.72	0.16	0.13	0.84	0.4	0.61	0.62	0.22	1.03	0.56	0.91	0.77
ROUND.2	0.78	0.17	0.20	0.91	0.41	0.57	0.65	0.21	1.06	0.56	0.92	0.85