Zootaxa 1013: 1–18 (2005)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

1013

The crane flies (Diptera: Tipuloidea) of Great Smoky Mountains National Park

MATTHEW J. PETERSEN[1], CHARLES R. PARKER[2] & ERNEST BERNARD[3]

[1]*Iowa State University, Department of Entomology, 3211 Science II, Ames, IA, 50010; e-mail: mp13@iastate.edu*

[2]*United States Geological Survey, Biological Resources Discipline, Great Smokies Field Station, 1314 Cherokee Orchard Road, Gatlinburg, TN 37738; e-mail: Chuck_Parker@usgs.gov*

[3]*University of Tennessee, Department of Entomology and Plant Pathology, 205 Ellington Plant Science Building, Knoxville, TN, 37919; e- mail: ebernard@utk.edu*

Abstract

The list of crane flies (Diptera: Ptychopteridae, Tipuloidea, Trichoceridae) known from Great Smoky Mountains National Park is updated. Sampling in association with the All Taxa Biodiversity Inventory of Great Smoky Mountains National Park resulted in the addition of 107 new Park records, bringing the current list to 250 species. This species assemblage is much richer than those of surrounding areas, although similar in composition. Total richness is estimated to be between 450 and 500 species for Great Smoky Mountains National Park.

Key words: ATBI, Ptychopteridae, Tipuloidea, Trichoceridae, Great Smoky Mountains

Introduction

Crane flies (Diptera: Tipuloidea) are a diverse array of small (3 mm) to large (> 50 mm) delicate, long-legged flies of the families Cylindrotomidae, Limoniidae, Pediciidae, and Tipulidae. This exceedingly rich superfamily contains approximately 15,000 described species worldwide (Byers 1996, Oosterbroek 2005), with about 1,600 species known from the Nearctic Region (Borror et al. 1989, Oosterbroek 2005). Young and Gelhaus (2000) have documented that crane fly diversity may represent nearly 2% of the entire organismal diversity of an area. The ecological diversity of crane flies is seen in the range of habitats used by the various species of this group. Crane fly larvae occupy a wide range of aquatic, semi-aquatic, and terrestrial habitats, including streams and seeps, mosses and liverworts, burrows in the leaves of plants, thin films of water trickling over vertical rock faces, dry to soggy decaying wood, rich organic to dry sandy soils, fungi, accumulations of detritus,

Accepted by P. Adler: 8 Jun. 2005; published: 30 Jun. 2005

and even nests of birds and mammals (Alexander 1919, Alexander and Byers 1981, Gelhaus 2002). Adults can be found at all times of the year, with Nearctic activity concentrated in the late spring and early fall. Adult emergence may extend over two to six months, or an entire population may emerge during a period of two weeks or less (Pritchard 1983). Adult life span may last no more than a few weeks (Alexander 1919), with adults generally staying in close proximity to their larval habitat (Barnes 1925, Rogers 1933, Freeman 1968, Merritt and Lawson 1981).

The last large-scale effort to document the species of crane flies of Great Smoky Mountains National Park (GRSM) of western North Carolina and eastern Tennessee was conducted more than 60 years ago by Alexander (1940, 1941). At that time, much of the 210,000-ha park was in the early stages of re-growth, following extensive deforestation that had resulted from the logging and settlement of the area prior to the establishment of the National Park in 1934 (Pyle 1988, MacKenzie and White 1998). Alexander documented 165 species, including 26 newly described species. A subsequent listing of the known crane fly species of GRSM was compiled by Hynes (1996), who updated the taxonomy and added 14 species. The majority of species had been collected in late spring and early summer. Since attaining National Park status, regeneration in GRSM has continued unabated. Presently, 95% of the area is now covered by forest (Sharkey 2001). GRSM boasts a diverse array of forest communities (White et al. 2003), having 1,637 species of vascular plants including 130 native trees species (Sharkey 2001), and is recognized as possessing the greatest organismal diversity of any National Park in the United States (Boetsch et al. 1998).

The All Taxa Biodiversity Inventory (ATBI) of GRSM is an ambitious effort begun in 1997 with a goal of documenting the organismal diversity found within the boundaries of the Park (Sharkey 2001). The scientific program for the ATBI (White and Morse 2000) envisions parallel traditional and structured sampling approaches. Traditional sampling involves the activities of taxonomic authorities, students, and volunteers collecting by means of insect nets, light traps, searches of optimal habitats, “bioblitzes”, and other traditional techniques. Structured sampling, on the other hand, involves the use of identically configured plots set up with bulk samplers, such as Malaise traps, pitfall traps, and other devices. A pilot study to evaluate the structured sampling program began in October of 2000. The crane flies collected during this two-year study are presented here to update the previous species list.

Methods

Insects were collected between October 2000 and October 2002 with 22 Townes-style Malaise traps (Townes 1972) located on 11 1-ha ATBI reference plots (see “Site Descriptions”). The Malaise traps were placed within each plot in obvious flight corridors or in specific microhabitats. Specimens were collected into 70%-90% ethanol. Malaise

traps were operated year-round, with collected material retrieved approximately every two weeks by research staff, GRSM park staff, and numerous volunteers. Collected materials were taken to laboratories at Twin Creeks Natural Resource Center or to the University of Tennessee, where crane flies were separated from other arthropods. Flies were sorted and preserved in 95% ethanol. Specimens were identified to species, using standard taxonomic references (Alexander 1919, 1920, 1940 1941, 1942; Byers 1961, 1983; Tangelder 1983; Oosterbroek 1984; Young 1987). When necessary for the purpose of identification, male genital structures were cleared by immersing removed genitalia in a warm 5% potassium hydroxide solution for five minutes followed by rinsing in ethanol. Voucher specimens collected during this investigation are housed in the entomology collections of the University of Tennessee and the natural history collection of Great Smoky Mountains National Park.

Additional species records were obtained from the species list complied by Hynes (1996), GRSM crane fly species lists compiled by ATBI collaborators, and sampling conducted during the environmental impact assessment of Ravensford tract, GRSM (Morse et al. 2002).

Species collection curves were created for each Malaise trap and each plot by plotting the number of species collected at each site against specimens collected (Willott 2001). Potential species richness for GRSM was estimated using EstimateS Version 6 (Colwell 1997) for all traps combined. Distributions for each species were determined to be widespread (ranging from Florida to Canada and considerably westward), northern (appearance in TN/NC is southernmost extent of range), southern (range radiates from the southern US and typically extends into the tropics), or TN/NC (species is known only from the Tennessee/North Carolina area). Species were categorized as aquatic (lotic or lentic habit), semi-aquatic (seeps, springs, bogs, aquatic margins, or saturated earth or wood), or terrestrial (dry soils, wood, leaf litter, non-water saturated habitat).

Taxonomy and species range information is based on Oosterbroek (2005), where crane flies are recognized as Tipuloidea and comprised of the families Cylindrotomidae, Limoniidae, Pediciidae, and Tipulidae. The families Ptychopteridae, Tanyderidae, and Trichoceridae, referred to as primitive crane flies, phantom crane flies, and winter crane flies, respectively, have historically been included in crane fly studies and were additionally investigated here. Subspecies classifications were not included for discovered species due to questions of taxonomic validity.

Site descriptions

The eleven ATBI research plots used in this study were chosen to represent a cross-section of the habitat types found in GRSM. They are listed here with a short description of each habitat type based on the NatureServe International Classification of Ecological Communities applied to GRSM (White et al. 2003).

Albright Grove (35.7333 N–83.28056 W, 1034 m elevation) is located in the northeastern area of GRSM and situated in one of the largest tracts of remaining old-growth forest on the east coast of the United States. The forest is in the *Tsuga canadensis* Engelm – *Halesia tetraptera* Ellis – (*Magnolia fraseri* Walt – *Fagus grandifolia* Ehrh*) / Rhododendron maximum* Linnaeus / *Dryopteris intermedia* (Willdenow) alliance, with a Southern Appalachian Acid Cove forest (silverbell type) community type.

Andrews Bald (35.53889 N–3.49417 W, 1757 m elevation) is a Southern Appalachian Grassy Bald, *Danthonia compressa* Austin herbaceous vegetation alliance. The surrounding forest is a mixture of red spruce (*Picea rubra* Sarg.) and Fraser fir (*Abies fraseri* (Pursh).

Brushy Mountain (35.67667 N–83.43083 W, 1467 m elevation) is a Southern Appalachian Laurel Bald. This community type occurs along ridges and steep rocky slopes at mid-elevations (1219-1524 m) in the southern Blue Ridge. This community results from secondary succession following logging, fire, windfall, or landslide, and is naturally maintained through these same processes.

Cades Cove (35.59251 N–83.84376 W, 457 m elevation) is a large open field in the western end of GRSM that was originally cleared for agricultural use by early settlers, but now is an abandoned agricultural field dominated by *Fescue* species with sparse native grasses, woody shrubs, and trees, with a surrounding Cove Hardwood forest. The National Park Service now maintains this area as open grassland through periodic burning.

Cataloochee (35.58639 N–83.08167 W, 1382 m elevation) is a High-Elevation Red Oak Forest (deciduous type) in the *Quercus rubra* Linnaeus forest alliance. Red oak dominates the canopy, while the subcanopy is comprised of *Acer rubrum* Linnaeus, *Ilex montana* (Torr. and Grey) and *Hamamelis virginiana* Linnaeus.

Clingmans Dome (35.56028 N–83.49528 W, 1944 m elevation) is the highest point in Tennessee and the second highest point east of the Mississippi River. This high-elevation plot is a representative of the southern Appalachian fir forest (deciduous type), which is dominated by Fraser fir (*Abies fraseri* Pursh) and red spruce (*Picea rubens* Sarg.).

Goshen Prong (35.61056 WN–83.54278 W, 895 m elevation) was heavily deforested by logging and settlement. The re-grown forest in the large cove in which this plot is located represents a rich montane Southern Appalachian Cove Forest, *Liriodendron tulipifera* Linnaeus – *Tilia americana* var. *heterophylla* (Vent.) – *Aesculus flava* Ait. – *Acer saccharum* Linnaeus forest alliance.

Indian Gap (35.61083 N–83.44361 W, 1672 m elevation) is located in one of the least common forest communities in GRSM, the high-elevation Southern Appalachian Beech Gap Community in the *Betula alleghaniensis* Britton – *Fagus grandifolia* Ehrh. – *Aesculus flava* Ait. forest alliance. These stands are dominated by American beech (*Fagus grandifolia*) and are limited to areas over 1,370 m elevation. Beech gaps typically occur on north facing, steep slopes and on the north and northeast sides of gaps.

Purchase Knob (35.59194 N–83.06028 W, 1529 m elevation) is in the Northern Hardwood forest community, similar to that of forests in the northeastern United States. The forest canopy is comprised of yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), and yellow buckeye (*Aesculus flava*).

Snake Den Ridge (35.74333 N–83.22000 W, 993 m elevation) shares much in common with Albright Grove. Both are classified as Southern Appalachian Cove Forest (Silverbell type) and have been relatively undisturbed by settlement or logging. Snake Den Ridge differs from Albright Grove in being much more dominated by *Tsuga canadensis* Carr. (Linnaeus). Additionally, the topography of this plot is different, as it is located on a moderately steep talus slope.

Twin Creeks (35.68500 N–83.49900 W, 594 m elevation) is classified as Early Successional Appalachian Hardwood forest, *Liriodendron tulipifera* forest alliance. This community type is found at elevations below 914 m in areas that had been impacted by heavy settlement, farming, or logging. Forest canopy is dominated by *Liriodendron tulipifera* and *Acer rubrum* with understory vegetation variable in composition, but often comprised of various vining species.

Results

Two years of continuous sampling resulted in the collection of 9,319 crane fly specimens representing 176 species in 52 genera and 6 families (Table 1), bringing the total number of crane flies known from GRSM to 250 species. One-hundred thirteen species known to exist in GRSM were recollected during this study, while 72 species previously known to GRSM were not recollected. Site-specific collection results can be found in Petersen (2002). In all, traps were operated for a total of 15,626 trap days, with 0.011 new species collected per trap day. Seventy species were recorded from GRSM for the first time, including two species new to science (Petersen and Gelhaus 2004). Forty-two percent of the crane fly species collected in this study have unknown larval stages. Of those collected for which the larval stages are known, species previously known to occur in the Park were approximately equally distributed between aquatic, semi-aquatic, and terrestrial habitats, while species new to the Park were largely terrestrial.

Species accumulation curves at all traps, plots, and all traps combined did not reach an asymptote (Fig. 1), indicating incomplete species accumulation at all levels investigated. Species richness estimators for all traps combined showed a range of between 201 (Bootstrap) and 262 (Jacknife 2) species and averaged 228 species among all estimators. Combining all presently authenticated identifications brings the species list for GRSM to 250 species (Table 1). Regional records of crane flies from the Cumberland Plateau of Tennessee (Rogers 1930), the mountains of western North Carolina (Alexander 1941), and the vicinity of Mountain Lake, Virginia (Byers 2002), include more than 200 species not presently known from GRSM. Considering these species as potential Park inhabitants, the actual crane fly diversity of GRSM may be as high as 450-500 species.

TABLE 1. Crane flies of Great Smoky Mountains National Park. ATBI sampling conducted October 2000-2002 by site (AB=Andrews Bald, AG=Albright Grove, BM=Brushy Mountain, CA=Cataloochee, CC=Cades Cove, CD=Clingmans Dome, GP=Goshen Prone, IG=Indian Gap, PK=Purchase Knob, SR=Snake Den Ridge, and TC=Twin Creeks). Species indicated by *h* were on the Hynes (1996) list but not collected during the ATBI, and *o* indicates species collected during other sampling. Taxonomy is as presented by Oosterbroek (2005), with family names in bold.

	AB	AG	BM	CA	CC	CD	GP	IG	PK	SR	TC
Cylindrotomidae (1 species)											
Liogma nodicornis (Osten Sacken)	X				X					X	X
Limoniidae (149 species)											
Antocha (Antocha) biarmata Alexander *h*											
Antocha (Antocha) obtuse Alexander *o*											
Antocha (Antocha) opalizens Osten Sacken					X						
Antocha (Antocha) saxicola Osten Sacken					X						X
Atarba (Atarba) picticornis Osten Sacken		X	X	X			X		X		X
Austrolimnophila (Austrolimnophila) toxoneura (Osten Sacken)	X	X					X	X	X	X	X
Cheilotrichia (Empeda) stigmatica Osten Sacken									X		
Chionea (Chionea) scita Walker	X		X			X	X	X		X	X
Chionea (Chionea) valga Harris	X		X			X	X	X			
Chionea (Chionea) wilsoni Byers	X			X		X	X	X			
Cladura flavoferriugenia Osten Sacken	X	X	X	X		X	X	X	X	X	X
Dactylolabis (Dactylolabis) cubitalis (Osten Sacken) *h*											
Dactylolabis (Dactylolabis) hudsonica Alexander	X	X				X	X			X	X
Dactylolabis (Dactylolabis) montana Alexander	X										
Dactylolabis (Dactylolabis) pemetica Alexander									X		
Dicranomyia (Caenoglochina) apicata subapicata (Alexander) *h*											
Dicranomyia (Dicranomyia) adirondacensis Alexander	X										
Dicranomyia (Dicranomyia) brevivena Osten Sacken				X							X
Dicranomyia (Dicranomyia) distans Osten Sacken											X
Dicranomyia (Dicranomyia) distendens Lundstrom	X										
Dicranomyia (Dicranomyia) divisa (Alexander)	X	X	X	X	X		X	X		X	X
Dicranomyia (Dicranomyia) gladiator Osten Sacken		X						X		X	
Dicranomyia (Dicranomyia) humidicola (Osten Sacken) *h*											
Dicranomyia (Dicranomyia) immodesta Osten Sacken *h*											
Dicranomyia (Dicranomyia) pudicoides (Alexander) *h*											
Dicranomyia (Dicranomyia) stulta (Osten Sacken) *h*											
Dicranomyia (Erostrata) globithorax Osten Sacken						X	X	X			X
Dicranomyia (Glochina) liberta Osten Sacken	X		X	X	X	X	X	X			X
Dicranomyia (Melanolimonia) morioides Osten Sacken *h*											
Dicranomyia (Melanolimonia) spinifera Alexander	X					X					

..... continued on the next page

TABLE 1 (continued)

	AB	AG	BM	CA	CC	CD	GP	IG	PK	SR	TC
Dicranomyia (Numantia) fusca (Meigen)		X	X				X			X	
Dicranoptycha acanthophallus Alexander									X		X
Dicranoptycha elsa Alexander											X
Dicranoptycha germana Osten Sacken				X					X		
Dicranoptycha septemtrionis Alexander		X					X		X		X
Discobola annulata (Linnaeus)											
Discobola nigroclavata (Alexander)		X		X				X	X	X	X
Elephantomyia (Elephantomyia) westwoodi Osten Sacken								X			X
Eloeophila aprilina Osten Sacken *h*											
Eloeophila johnsoni (Alexander)											X
Eloeophila seticellula (Alexander) *h*											
Eloeophila solstitalis (Alexander)											X
Epiphragma (Epiphragma) fasciapenne (Say)	X	X	X	X		X	X	X	X	X	X
Epiphragma (Epiphragma) solatrix (Osten Sacken)					X						X
Erioptera (Erioptera) megophthalma Alexander *h*											
Erioptera (Erioptera) septemtrionalis Alexander *h*											
Erioptera (Erioptera) vespertina Osten Sacken h											
Erioptera (Mesocyphona) caliptera Say					X						
Erioptera (Mesocyphona) needhami Alexander *h*											
Erioptera (Mesocyphona) parva Osten Sacken *h*											
Eugnophomyia luctuosa (Osten Sacken)											X
Euphylidorea albipes (Leonard)	X					X				X	
Euphylidorea cherokeensis (Alexander) *h*											
Euphylidorea lutea (Doane)	X					X					
Euphylidorea niveitarsis (Osten Sacken)	X					X				X	
Geranomyia diversa (Osten Sacken) *h*											
Geranomyia rostrata (Say)					X						
Gnophomyia tristissima Osten Sacken				X			X		X	X	X
Gonempeda nyctops (Alexander) *h*											
Gonomyia (Gonomyia) bidentata Alexander					X						
Gonomyia (Gonomyia) subcinerea Osten Sacken *h*											
Gonomyia (Lipophleps) manca Osten Sacken									X		
Gonomyia (Lipophleps) sulphurella Osten Sacken *h*											
Helius (Helius) flavipes (Macquart) *h*											
Hexatoma (Eriocera) albitarsis (Osten Sacken)		X									X
Hexatoma (Eriocera) aurata (Doane) *h*											
Hexatoma (Eriocera) brachycera (Osten Sacken)	X										

..... *continued on the next page*

TABLE 1 (continued)

	AB	AG	BM	CA	CC	CD	GP	IG	PK	SR	TC
Hexatoma (Eriocera) brevioricornis Alexander	X	X			X				X	X	
Hexatoma (Eriocera) cinerea (Alexander) *h*											
Hexatoma (Eriocera) fuliginosa (Osten Sacken) *h*											
Hexatoma (Eriocera) tristis (Alexander) *h*											
Hoplolabis (Hoplolabis) armata Osten Sacken *h*											
Limnophila (Arctolimnophila) subcostata (Alexander)						X					
Limnophila (Dicranophragma) angustula Alexander *h*											
Limnophila (Dicranophragma) fuscavoria Osten Sacken	X	X							X	X	X
Limnophila (Idiolimnophila) emmelina Alexander							X		X		X
Limnophila (Lasiomastix) macrocera (Say)	X										
Limnophila (Lasiomastix) tenuicornis Osten Sacken											X
Limonia indigena (Osten Sacken)	X	X		X		X	X	X	X	X	X
Limonia macateei (Alexander)						X	X		X	X	
Limonia maculicosta (Coquillett)	X	X	X			X				X	
Limonia parietina (Osten Sacken)		X		X				X	X	X	X
Limonia tristigma (Osten Sacken)	X					X		X			
Lipsothrix sylva (Alexander)	X					X			X		X
Metalimnobia (Metalimnobia) cinctipes (Say)	X	X	X	X	X	X		X	X	X	X
Metalimnobia (Metalimnobia) fallax (Johnson)				X			X		X		X
Metalimnobia (Metalimnobia) immatura (Osten Sacken)	X	X	X	X	X		X	X	X	X	X
Metalimnobia (Metalimnobia) triocellata (Osten Sacken)	X	X		X		X	X	X	X	X	X
Molophilus (Molophilus) fultonensis Alexander	X					X			X	X	X
Molophilus (Molophilus) hirthipennis (Osten Sacken)	X					X			X	X	X
Molophilus (Molophilus) perflaveolus Alexander					X						
Molophilus (Molophilus) cramptoni Alexander *h*											
Molophilus (Molophilus) pubipennis (Osten Sacken) *h*											
Neocladura delicatula (Alexander)	X	X	X	X	X	X	X	X	X	X	X
Neolimnomyia (Brachylimnophila) brevifurca (Osten Sacken) *h*											
Neolimnophila appalachicola Alexander	X					X					
Neolimnophila ultima (Osten Sacken) *h*											
Neolimonia rara (Osten Sacken)					X	X	X				X
Ormosia (Oreophila) parviala Petersen and Gelhaus	X					X	X				
Ormosia (Ormosia) adirondacensis Alexander *h*											
Ormosia (Ormosia) arcuata (Doane) *h*											
Ormosia (Ormosia) bilineata Dietz						X					
Ormosia (Ormosia) carolinensis Alexander				X							X
Ormosia (Ormosia) harrisoniana Alexander	X										

..... continued on the next page

TABLE 1 (continued)

	AB	AG	BM	CA	CC	CD	GP	IG	PK	SR	TC
Ormosia (Ormosia) holotrichia (Osten Sacken)		X				X				X	
Ormosia (Ormosia) hubbelli Alexander									X		
Ormosia (Ormosia) lilliana Alexander	X					X		X			
Ormosia (Ormosia) monticola (Osten Sacken)	X										
Ormosia (Ormosia) romanovichiana Alexander	X	X	X	X		X	X	X	X	X	X
Ormosia (Ormosia) serridens Alexander *h*											
Ormosia (Ormosia) tennesseensis Alexander										X	
Ormosia (Ormosia) townesi Alexander						X	X	X			
Ormosia (Paraormosia) nigripila (Osten Sacken)			X								
Ormosia (Paraormosia) palpalis Dietz										X	
Ormosia (Paraormosia) pygmae (Alexander)									X		X
*Paradelphomyia (Oxyrhiza) ame*ricanus (Alexander) *h*											
Paradelphomyia (Oxyrhiza) minutes (Alexander) *h*											
Paradelphomyia (Oxyrhiza) pleuralis (Dietz) *h*											
Pilaria tenuipes (Say)					X						
Prionolabis munda (Osten Sacken)	X	X	X			X		X		X	
Prionolabis politissima (Alexander)	X	X				X	X	X		X	X
Prionolabis rudimentis (Alexander)						X					
Prionolabis rufibasis (Osten Sacken)	X	X		X		X	X	X	X	X	X
Prionolabis terebrans (Alexander)							X				
Prionolabis walleyi (Osten Sacken)	X					X				X	X
Prolimnophila areolata (Osten Sacken)	X						X	X		X	X
Pseudolimnophila (Pseudolimnophila) australina Alexander							X		X	X	X
Pseudolimnophila (Pseudolimnophila) contempta (Osten Sacken)	X								X		X
Pseudolimnophila (Pseudolimnophila) inornata (Osten Sacken)										X	X
Pseudolimnophila (Pseudolimnophila) luteipennis (Osten Sacken)					X						
Pseudolimnophila (Pseudolimnophila) noveboracensis (Alexander)					X					X	
Rhabdomastix (Sacandaga) flava (Alexander)			X								
Rhabdomastix (Sacandaga) bracyneura Alexander *h*											
Rhabdomastix (Sacandaga) hansoni Alexander *h*											
Rhabdomastix (Sacandaga) margarita Alexander *h*											
Rhipidia (Rhipidia) bryanti Johnson											X
Rhipidia (Rhipidia) domestica Osten Sacken	X	X	X		X	X	X		X		X
Rhipidia (Rhipidia) fidelis Osten Sacken	X	X	X				X	X	X	X	X
Rhipidia (Rhipidia) maculata Meigen	X	X	X	X	X	X	X	X	X	X	X
Rhipidia (Rhipidia) shannoni Alexander	X	X	X		X						X
Scleroprocta apicalis (Alexander)											X

..... continued on the next page

TABLE 1 (continued)

	AB	AG	BM	CA	CC	CD	GP	IG	PK	SR	TC
Scleroprocta innocens (Osten Sacken) *h*											
Shannonomyia lenta Alexander									X		
Symplecta (Symplecta) cana (Walker)	X	X	X	X	X	X	X	X	X	X	X
Tasiocera (Dasymolophilus) ursina (Osten Sacken) *h*											
Teucholabis(Teucholabis) immaculata Alexander *h*											
Trimicra pilipes (Fabricius)					X						
Ulomorpha pilosella (Osten Sacken)	X		X					X		X	X
Ulomorpha rogersella Alexander	X										
Pediciidae (19 species)											
Dicranota (Eudicranota) catawbiensis Alexander *h*											
Dicranota (Paradicranota) eucera Alexander					X						
Dicranota (Plectromyia) confusa (Alexander) *h*											
Dicranota (Rhaphidolabina) flaveola (Osten Sacken)						X					
Dicranota (Rhaphidolabis) hickmanae Alexander *h*											
Dicranota (Rhaphidolabis) persimilis (Alexander) *h*											
Dicranota (Rhaphidolabis) rubescens (Alexander) *h*											
Pedicia (Pedicia) albivitta Walker		X					X			X	X
Pedicia (Pedicia) margarita Alexander	X	X					X	X	X		
Tricyphona (Pentacyphona) autumnalis Alexander						X					
Tricyphona (Pentacyphona) huffae (Alexander)	X					X					
Tricyphona (Tricyphona) auripennis (Osten Sacken)						X					
Tricyphona (Tricyphona) gigantea (Alexander)	X	X					X				
Tricyphona (Tricyphona) inconstans (Osten Sacken)	X					X			X		X
Tricyphona (Tricyphona) katahdin Alexander							X				
Tricyphona (Tricyphona) vernalis (Osten Sacken)							X				X
Tricyphona (Tricyphona) calcar (Osten Sacken) *h*											
Ula (Ula) elegans Osten Sacken	X	X	X	X			X	X	X	X	X
Ula (Ula) paupera Osten Sacken	X	X	X	X		X	X	X	X	X	X
Ptychopteridae (3 species)											
Bittacomorpha clavipes Fabricius *h*											
Bittacomorpha jonesi (Johnson) *h*											
Ptychoptera rutocincta Meigen										X	
Tipulidae (73 species)											
Brachypremna dispellens (Walker)											X
Ctenophora (Ctenophora) apicata Osten Sacken		X							X		
Ctenophora (Ctenophora) nubecula Osten Sacken							X			X	
Dolichopeza (Dolichopeza) americana Needham						X		X			X

..... continued on the next page

TABLE 1 (continued)

	AB	AG	BM	CA	CC	CD	GP	IG	PK	SR	TC
Dolichopeza (Oropeza) carolus Alexander *h*											
Dolichopeza (Oropeza) johnsonella (Alexander)						X		X			
Dolichopeza (Oropeza) obscura (Johnson)						X					
Dolichopeza (Oropeza) sessilis Alexander *h*											
Dolichopeza (Oropeza) subalbipes (Johnson)											X
Dolichopeza (Oropeza) subvenosa Alexander *h*											
Dolichopeza (Oropeza) tridenticulata Alexander *h*											
Dolichopeza (Oropeza) walleyi (Alexander) *h*											
Leptotarsus (Longurio) minimus (Alexander)	X										
Leptotarsus (Longurio) testaceus Loew *h*											
Nephrotoma calinota (Dietz) *h*											
Nephrotoma cingulata (Dietz)		X			X					X	X
Nephrotoma eucera (Loew)											X
Nephrotoma ferruginea (Fabricius) *h*											
Nephrotoma gnata (Dietz)					X						X
Nephrotoma incurva (Loew) *h*											
Nephrotoma macrocera (Say)					X						
Nephrotoma subalterna Oosterbroek *h*											
Nephrotoma tenuis (Loew) *h*											
Nephrotoma virescens (Loew)		X	X	X			X				X
Tanyptera (Tanyptera) dorsalis (Walker)	X	X	X	X		X	X	X	X	X	X
Tipula (Arctotipula) williamsiana Alexander *h*											
Tipula (Lindnerina) illinoiensis Alexander				X			X	X	X		X
Tipula (Lindnerina) senega Alexander		X							X		
Tipula (Lunatipula) apicalis Loew		X									
Tipula (Lunatipula) atreia Petersen and Gelhaus					X						
Tipula (Lunatipula) duplex Walker		X		X			X	X	X		X
Tipula (Lunatipula) flavibasis Alexander							X		X		X
Tipula (Lunatipula) fuliginosa (Say)							X				
Tipula (Lunatipula) mallochi Alexander *h*											
Tipula (Lunatipula) monticola Alexander	X			X					X		
Tipula (Lunatipula) submaculata Loew		X									
Tipula (Lunatipula) translucida Doane *h*											
Tipula (Lunatipula) tuscarora Alexander *h*											
Tipula (Lunatipula) valida Alexander *h*											
Tipula (Nobilotipula) collaris Say	X	X									
Tipula (Nobilotipula) nobilis (Loew)	X						X		X		

..... continued on the next page

TABLE 1 (continued)

	AB	AG	BM	CA	CC	CD	GP	IG	PK	SR	TC
Tipula (Nippotipula) abdominalis (Say) *h*											
Tipula (Platytipula) cunctans Say *h*											
Tipula (Pterelachisus) angulata Loew				X							
Tipula (Pterelachisus) coleana Alexander						X					
Tipula (Pterelachisus) entomophthorae Alexander			X								
Tipula (Pterelachisus) margarita Alexander *h*											
Tipula (Pterelachisus) penobscot Alexander	X										
Tipula (Pterelachisus) trivitatta Say	X	X	X					X	X	X	X
Tipula (Savtshenkia) fragilis Loew						X					
Tipula (Savtshenkia) ignobilis Loew	X		X								
Tipula (Schummelia) friendi Alexander		X				X				X	
Tipula (Schummelia) hermannia Alexander										X	X
Tipula (Schummelia) stenorhabda Alexander								X			
Tipula (Trichotipula) algonquin Alexander											X
Tipula (Trichotipula) oropezoides Johnson	X										
Tipula (Trichotipula) stonei Alexander								X			X
Tipula (Trichotipula) unimaculata (Loew)									X		
Tipula (Triplicitipula) integra Alexander			X								
Tipula (Triplicitipula) triplex Walker	X	X			X						X
Tipula (Triplicitipula) umbrosa Loew					X					X	
Tipula (Vestiplex) loniventris Loew	X		X					X			X
Tipula (Yamatotipula) aprilina Alexander					X						
Tipula (Yamatotipula) brevifurcata Alexander *h*											
Tipula (Yamatotipula) calopteroides Alexander *h*											
Tipula (Yamatotipula) catawbiana Alexander *h*											
Tipula (Yamatotipula) cayuga Alexander *h*											
Tipula (Yamatotipula) furca Walker					X						
Tipula (Yamatotipula) iroquois Alexander	X										
Tipula (Yamatotipula) nephophila Alexander *h*											
Tipula (Yamatotipula) noveboracensis Alexander *h*											
Tipula (Yamatotipula) tephrocephala Loew	X										
Tipula (Yamatotipula) tricolor Fabricius					X						
Trichoceridae (5 species)											
Trichocera bimaculata Walker	X		X	X	X	X	X	X			X
Trichocera brevicornis Alexander	X	X	X	X		X	X	X	X	X	X
Trichocera fattigiana Alexander					X						
Trichocera garretti Alexander				X			X				X
Trichocera heimalis (De Greer)	X	X	X	X	X	X	X	X	X	X	X

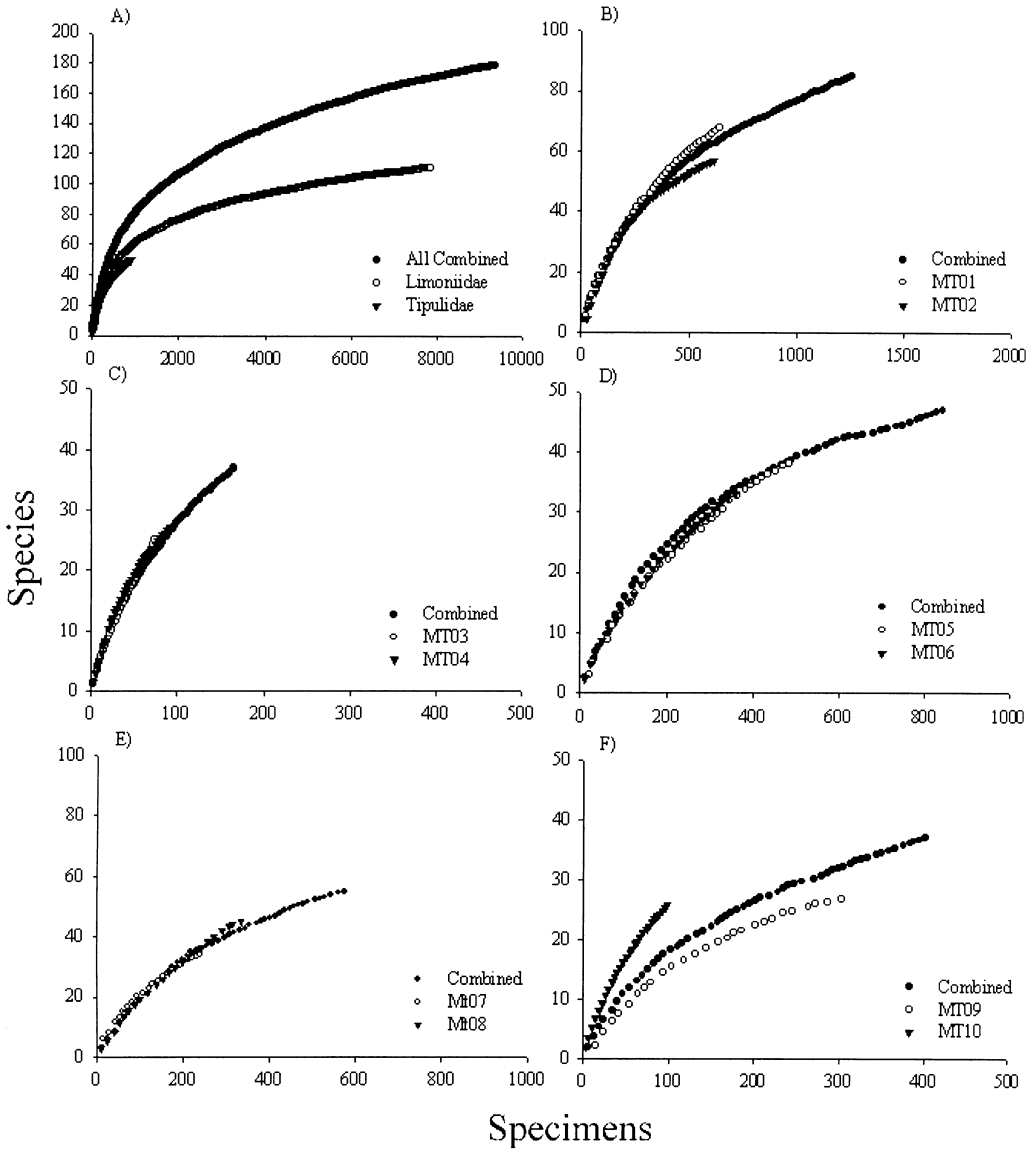

FIGURE 1. Species accumulation curves. **A**) All traps; Limoniidae, Tipulidae. **B**) Twin Creeks. **C**) Cades Cove. **D**) Indian Gap. **E**) Purchase Knob. **F**) Cataloochee. Plots in Figs. 1B-F are presented as specimens collected in each Malaise trap and for traps at each plot combined.

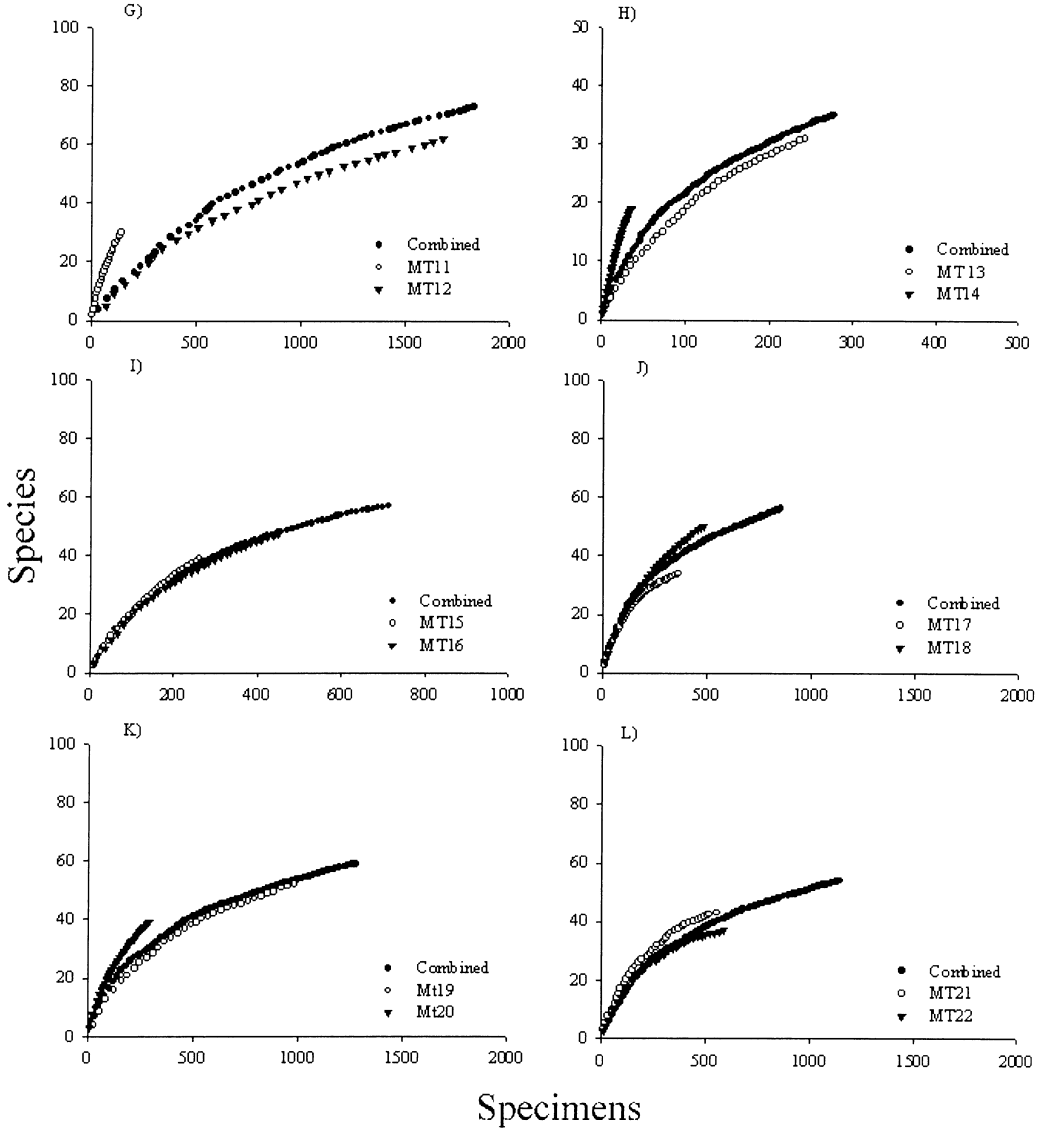

FIGURE 1. Continued. **G**) Andrews Bald. **H**) Brushy Mountain. **I**) Clingmans Dome. **J**) Albright Grove. **K**) Snake Den Ridge. **L**) Goshen Prong. Plots 1G-L are presented as specimens collected in each Malaise trap and for traps at each plot combined.

The GRSM crane fly fauna is strongly influenced by the presence of species that have widespread distributions that were found across the elevation gradient of the Park (Table 2). Species that radiate from a southeastern distribution comprised a much smaller proportion of the total species encountered, and are more commonly encountered at lower elevations. The higher elevations have a greater percentage of species with northern distributions and species endemic to the mountains of Tennessee and North Carolina.

TABLE 2. Range distributions of species collected during ATBI sampling. Information is listed for all species collected, those found only at upper elevations (>1500 m), and those from only lower elevations (< 1000 m), and is shown as percentages with actual numbers in parentheses. Range distributions are based on Oosterbroek (2005).

Range	All Species	Upper Elevations	Lower Elevations
Widespread	41% (72)	37% (11)	47% (18)
Northern	40% (71)	40% (12)	24% (9)
Southern	12% (20)	3% (1)	26% (10)
TN/NC	7% (13)	20% (6)	3% (1)

TABLE 3. Larval condition of species found in Great Smoky Mountains National Park. Percent of species representing each state are listed for species collected during the ATBI, those collected during the ATBI and new to the Park, and those from Hynes (1996).

Larval state	ATBI	ATBI new	Hynes
Aquatic	18%	14%	23%
Semi-aquatic	16%	8%	21%
Terrestrial	25%	36%	17%
Unknown	41%	42%	39%

Collections of adult crane flies (Tipuloidea) indicated two major periods of species emergence during the year: a spring emergence from April to June and a fall emergence from July to October. Species collected across the elevation gradient typically showed up in trapping earlier at lower elevations than at higher elevations. Trichoceridae adults were collected from October through April with greater numbers collected at middle and lower elevations. Phenology diagrams depicting species-specific emergence patterns for all crane flies collected during the ATBI can be found in Petersen (2002) or at www.ent.iastate.edu/dept/research/systematics/tipulidae/.

Discussion

A major goal of the ATBI is to identify all forms of life within the borders of Great Smoky Mountains National Park. Towards this end, this sampling has nearly doubled previous knowledge of crane fly species richness in the Park. The documented crane fly community of GRSM now stands as the richest fauna in the southeastern United States. The lack of sampling completeness at individual traps, as well as all traps combined, indicates that the species richness documented here is an underestimate. The estimate provided by the species-collection curves is seen as an underestimate due to the observation that numerous

microhabitat types such as seeps, springs, stream margins, and bogs were under sampled using this protocol and the avoidance of traps by larger flies (Petersen, personal observation). Direct comparisons cannot be made between the previous sampling conducted by Alexander (1941, 1942) because of differences in sampling protocols; however, the large number of species not recollected during this work indicated either a possible shift in the species assemblage found here or an indication that additional habitats will be needed to be sampled to ascertain the true assemblage of GRSM.

The observed crane fly fauna of the surrounding areas and the inability to saturate a collection curve after this intensive sampling lends support to our conjecture that the actual richness of GRSM may be as much as doubled when it is more fully known. While an estimate of between 450 and 500 species is likely, continued sampling in those as-yet uninvestigated areas, such as the southeastern region of GRSM, may result in an even greater richness than is proposed here. Additional sampling within GRSM should concentrate on the spring and fall seasonal peaks in emergence, the surprisingly rich summer fauna in the higher elevations (>1,500 m), and in under-collected areas such as the southwestern region of the Park, and in microhabitats such as seeps, springs, and bogs.

A paucity of information on the larval habitats of many crane fly species hinders our ability to explain why this area achieves such high species richness. However, both the diversity of habitat types known to be used by the crane fly fauna and the diversity of habitats offered in this sanctuary are extensive. Distributional ranges of collected species indicate that the elevation gradient of the mountains contributes to the observed richness. The Park's location in the southeastern United States gives it a generally mild climate with abundant moisture and a long warm season. The elevation gradient and topographic complexity of the Park have resulted in the development of a myriad of microclimatic and habitat types that span almost the entire range of climatic and habitat types found in the entire Appalachian Mountain range. The resulting fauna is one comprised of a mixture of species, with a high proportion of species with southern Nearctic distributions at lower elevations and an increase in species with a northern Nearctic distribution in the upper elevations.

Acknowledgements

This research was supported by a United States Geological Survey grant titled "How to conduct an all taxa biodiversity inventory of Great Smoky Mountains National Park" awarded to C. R. Parker and E. C. Bernard; by the Tennessee Agricultural Experiment Station; and by a Jessup Fellowship awarded to Matt Petersen from the Academy of Natural Sciences, Pennsylvania.

We thank the staff of the National Park Service and Great Smoky Mountains National Park for the opportunity to collect and document the vast number of species found there. Along with numerous other volunteers, Ian Stocks was responsible for plot collection and

maintenance as well as specimen sorting. We thank Jon Gelhaus, The Academy of Natural Sciences, for aid in identification of crane fly specimens.

This paper is a portion of a thesis presented by the first author in partial fulfillment of the M.S. degree.

References

Alexander, C.P. (1919) The crane-flies of New York. Part I. Distribution and taxonomy of the adult flies. *Cornell University Agricultural Station Memoir*, 25, 766–933.

Alexander, C.P. (1920) The crane-flies of New York. Part II. Biology and phylogeny. *Cornell University Agricultural Station Memoir*, 38: 695–1133.

Alexander, C.P. (1940) Records and descriptions of North American crane-flies (Diptera). Part I. Tipulomorpha of the Great Smoky Mountains National Park, Tennessee. *American Midland Naturalist*, 24, 602–644.

Alexander, C.P. (1941) Records and descriptions of North American crane-flies (Diptera). Part II. Tipulomorpha of mountainous western North Carolina. *American Midland Naturalist*, 26, 281–319.

Alexander, C.P. (1942) Family Tipulidae. *Bulletin of the Connecticut State Geological and Natural History Survey*, 64, 196–509.

Alexander, C.P. & Byers, G.W. (1981) Tipulidae. *In*: McAlpine, J.F. et al., (Eds.). *Manual of Nearctic Diptera*, Vol. 1, Agriculture Canada Research Branch Monograph 27, pp. 153–190.

Barnes, H.F. (1925) The ecological distribution of adult crane flies in Carnarvonshire. *Journal of Ecology*, 13, 138–148.

Boetsch, J., Defoe, D., Dellinger, R., Langdon, K. & Rock, J. (1998) *Vascular Plants of Great Smoky Mountains National Park: A Checklist for the Vascular Plants of Great Smoky Mountains National Park*. Great Smoky Mountains Natural History Association.

Borror, D.J., Triplehorn, C.A. & Johnson, N.F. (1989) *An Introduction to the Study of Insects*, Harcourt Brace College Publishers, Philadelphia, 875 pp.

Byers, G.W. (1961) The crane fly genus *Dolichopeza* in North America. *University of Kansas Science Bulletin*, 42 (6), 665–924.

Byers, G.W. (1983) The crane fly genus *Chionea* in North America. *University of Kansas Science Bulletin*, 52 (6), 59–195.

Byers, G.W. (1996) Tipulidae. *In*: Merritt, R.W. & Cummins, K.W. (Eds.), *An Introduction to the Aquatic Insects of North America*, 3rd ed. Kendall/Hunt Publishing Company, Dubuque, Iowa, pp. 549–570.

Byers, G.W. (2002) Summer crane flies (Tipulidae) of the Mountain Lake Vicinity, Virginia. *Banisteria*, 20, 3–30.

Colwell, R.K. (1997) EstimateS: Statistical estimation of species richness and shared species from samples. Version 6. Available from http://viceroy.eeb.uconn.edu/estimates (accessed 13 June 2001).

Freeman, B.E. (1968) Studies on the ecology of adult Tipulidae (Diptera) in southern England. *Journal of Animal Ecology*, 37, 339–362.

Gelhaus, J.K. (2002) *Manual for the Identification of Aquatic Crane Fly Larvae for Southeastern United States*. Carolina Area Benthological Workshop, Durham, N.C., USA, 205 pp.

Hynes, C.D. (1996) *Tipulomorpha of the Great Smokey Mountains National Park*. (unpublished report).

MacKenzie, M.D. & White, J.S. (1998) Vegetation of Great Smoky Mountains National Park, 1935-1938. *Castanea*, 63, 323–336.

Merritt, R.W. & Lawson, D.L. (1981) Adult emergence patterns and species distribution and abundance of Tipulidae in three woodland floodplains. *Environmental Entomology*, 10, 915-921.

Morse, J.C., Harrington, R.C., & Jones, D.R. (2002) *Aquatic Insects of Raven Fork, Great Smoky Mountains National Park, Swain County, North Carolina, USA*. Prepared for Wetland Natural Resource Consultants, Inc, Waynesville, NC, 22 pp.

Oosterbroek, P. (1984) A revision of the crane fly genus *Nephrotoma* Meigen 1803 in North America (Diptera, Tipulidae). Part II: The non-Dorsalis Species-Groups. *Beaufortia*, 34 (5), 117–180.

Oosterbroek, P. (2005) Catalogue of the Craneflies of the World. Available from http://ip30.eti.uva.nl/ccw/ (accessed 11March 2005).

Petersen, M.J. (2002) *Crane Flies (Tipulomorpha; Diptera) Collected During the All-Taxa Biodiversity Inventory of Great Smoky Mountains National Park, Tennessee and North Carolina: An Ecological Study.* Masters Thesis. University of Tennessee, Knoxville, TN, 140 pp.

Petersen, M.J. & Gelhaus, J.K. (2004) New species and records of crane flies (Tipuloidea, Diptera) from Great Smoky Mountains National Park, Tennessee and North Carolina, U. S. A. *Transactions of the American Entomological Society*, 130, 439–455.

Pritchard, G. (1983) Biology of Tipulidae. *Annual Review of Entomology*, 28, 1–22.

Pyle, C. (1988) The type and extent of anthropogenic vegetation disturbance in the Great Smoky Mountains before National Park Service acquisition. *Castanea*, 53, 183–196.

Rogers, J.S. (1930) The summer crane-fly fauna of the Cumberland Plateau in Tennessee. *Occasional Papers of the Museum of Zoology, University of Michigan*, 215, 1–50.

Sharkey, M.J. (2001) The all taxa biological inventory of Great Smoky Mountains National Park. *Florida Entomologist*, 84, 556–564.

Tangelder, I.R.M. (1983) A revision of the crane fly genus *Nephrotoma* Meigen 1803 in North America (Diptera, Tipulidae). Part I: The Dorsalis Species-Group. *Beaufortia*, 33 (8), 111–205.

Townes, H. (1972) A lightweight Malaise trap. *Entomological News*, 18, 239–247.

White, P. & Morse, J. (2000) The science plan for the All Taxa Biodiversity Inventory in Great Smoky Mountains National Park, North Carolina and Tennessee. Available from http://dlia.org/atbi/Science Plan.pdf (accessed 5 January 2005).

White, R.D., Patterson, K.D., Weakley, A., Ulrey, C.J. & Drake, J. (2003) *Vegetation Classification of Great Smoky Mountains National Park*. Unpublished report submitted to BRD-NPS Vegetation Mapping Program. NatureServe: Durham, NC.

Willott, S.J. (2001) Species accumulation curves and the measure of sampling effort. *Journal of Applied Ecology*, 38, 484–486.

Young, C.W. (1987) A revision of the crane fly genus *Dicranoptycha* in North America. *University of Kansas Science Bulletin*, 53 (5), 215–274.

Young, C.W. & Gelhaus, J.K. (2000) *Crane flies of Pennsylvania: Preliminary Checklist and Database Development with emphasis on Aquatic Species*. Report submitted to The Wild Resource Conservation Fund (Harrisburg, PA) and PA Fish & Boat Commission (Bellefonte, PA).

