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ABSTRACT. The caddisfly faunas of Stillfork Swamp, an unglaciated Carroll County site, and Watercress Marsh, a glaciated Columbiana County site, were evaluated in light of differences in physiography and past glacial history. The large and diverse fauna of Stillfork Swamp suggests that caddisflies, including numerous species of the predominantly northern Limnephilidae, survived the Pleistocene close to the southern extent of glaciation in eastern Ohio. The fauna of these periglacial wetlands suggests that physiography is a major factor in the distribution of Ohio Trichoptera.

INTRODUCTION

The order Trichoptera, one of the largest groups of aquatic insects, includes an estimated 1,200 North American species (Wiggins 1984) and a world-wide total exceeding 50,000 species (Schmid 1984). Trichoptera exhibit remarkable diversity of form, behavior, and habitat adaptations. Caddisfly larvae occupy most types of freshwater habitats from cold water springs to rivers, marshes, lakes, and temporary pools (Wiggins 1977). The greatest number of species of Ohio caddisflies is recorded from the Glaciated Appalachian Plateau (Huryn and Foote 1983; see Fig. 1, p. 785.). No doubt many additional species will be recorded from the Unglaciated Appalachian Plateau and other little studied physiographic regions of Ohio. Huryn (1982) conservatively estimated that a total of nearly 250 caddisfly species will be recorded from Ohio.

The purpose of the present study was to evaluate the effects of past geologic events on the caddisfly fauna of two isolated wetlands situated close to the Wisconsin Glacial boundary in eastern Ohio. Stillfork Swamp is located 5 km west of the Flushing Escarpment, a dissecting Lexington Penneplain ridge of the Unglaciated Appalachian Plateau physiographic province (Stout and Lamb 1938). Most of the valleys of northern Carroll and Jefferson Counties are underlain by Paleozoic shale, sandstones, limestones, and sedimentary rocks of the Pottsville and Allegheny Groups of the Pennsylvanian Age (White 1951). The Flushing Escarpment, extending north and south through eastern Carroll County, is a major drainage divide of preglacial origin (Stout and Lamb 1938). The surface immediately west of the Flushing Escarpment in northern Carroll County has low, narrow ridges and relatively broad shallow, and poorly drained valleys. During the pre-glacial Teays Stage, the area now occupied by Stillfork Swamp was a deep, V-shaped valley drained by tributaries of the Dover River that flowed north eventually joining the pre-glacial St. Lawrence River in the Lake Erie Basin (Stout and Lamb 1938).

As the great Pleistocene glaciers advanced from the north, they dammed this north-flowing river system causing the formation of glacial-edged finger lakes. Eventually, entirely new drainage patterns were created forming the large Muskingum River system of southeastern Ohio. Stillfork Swamp is located in one of the valleys that became a finger lake during glacial time (Stein 1974). The ice sheet advanced to within 9 km of the site before climatic changes caused the glaciers to retreat.

The base level of the headwaters flowing westward off the Flushing Escarpment essentially became elevated due to the deposition of sediments eroded from the nearby hills. When the last glacier retreated, the lake waters drained out of the Still Fork Valley and joined Sandy Creek, a tributary of the Tuscarawas River. The former V-shaped valley became a flat lake bed filled with Pleistocene sediments across which Still Fork Creek slowly meanders. Marshes and swamps developed along the poorly drained stream bed and valley floor. Many of the cold-climate wetland plants and animals became established in this and similar areas along the glacial border and persisted until disturbed by recent agricultural practices (Stein 1974).

Stillfork Swamp has existed as a large unglaciated aquatic habitat for an extensive period of time (Buchanan 1980) and supports a large and diverse caddisfly fauna (Usis and MacLean 1986). Watercress Marsh, a 50-ha fen, located 9 km south of Salem, Ohio, occupies a site of the Grand River Lobe of the Wisconsin Glacier near the southernmost extent of glaciation in Columbiana County. This site exhibits many characteristics typical of northeastern Ohio fens (Andreas 1980) with numerous springs, wet sedge meadows, open marsh, and swamp forest. MacLean and MacLean (1984) reported a total of 69 species of caddisflies from this site including 10 families and 32 genera. The close proximity (25 km) of these two sites made possible a comparison of the caddisfly faunas of two different Ohio physiographic regions (Usis and MacLean 1986; see Fig. 1, p.33).

COMPARISON OF THE CADDISFLY FAUNA OF STILLFORK SWAMP AND WATERCRESS MARSH

A primary objective of this study was to compare and contrast the caddisfly fauna of Stillfork Swamp with that of Watercress Marsh. Durrell and Durrell (1979) divided the Appalachian Plateau Province of Ohio into a glaciated section (location of Watercress Marsh) and an un glaciated section (location of Stillfork Swamp). Lafferty (1979) contrasted the two sections describing the unglaciated region as rugged hill country and the glaciated as rolling topography dotted with numerous lakes, marshes, and
occasional bogs and fens. Huryn (1982) stated that physiographic and historic differences are reflected in the Trichoptera inhabiting the two regions. His comparison of the Trichoptera of the Little Muskingum watershed in southeastern Ohio and the West Branch of the Mahoning River (McElravy 1976) revealed an increased faunal diversity in the glaciated region due to a greater number of lentic species.

In absolute terms, the Stillfork Swamp fauna was more diverse, with 104 species, whereas the Watercress Marsh fauna consisted of 69 species. While diversity and evenness values calculated from light trap data must be viewed with caution, weekly values of Brillouin’s diversity index (MacLean and MacLean 1984, Usis and MacLean 1986) were significantly different (t = 2.415, P < 0.05). However, evenness values showed no significant difference in relative species abundance. Potamyenia flava (Hagen), a species characteristic of large, slow-flowing streams (Ross 1944), was the most abundant species at both sites. Both areas possessed lotic habitats (e.g., Still Fork Creek) sufficient to support large populations of P. flava and other Hydropsychidae.

The largest number of caddisfly species at both sites belonged to the family Leptoceridae, all of which construct cases and many inhabit both lotic and lentic environments. Leptocerus americanus (Banks) and Ceraclea maculata (Vorhies) were frequently collected from May through mid-August in Watercress Marsh, whereas both species were poorly represented in collections from Stillfork Swamp. Oecetis inconspicua (Walker) was very abundant at both sites. Triaecnodes marginatus Sibley was dominant in Stillfork Swamp while T. tarsus Milne dominated at Watercress Marsh.

Similarities between the sites were reflected in a "shared species" total of 51 (Sorensen’s Coefficient of Similarity = 0.590; Brower and Zar 1977). The "shared species" assemblage represented species that are widespread throughout Ohio and the Northeast or have transcontinental distributions. Both sites were dominated by the shredder trophic category (Usis and MacLean 1986).

Although many temporary pond species were present at both sites, their populations were larger at Stillfork Swamp. The largest number of caddisfly species at both sites belonged to the family Leptoceridae, all of which construct cases and many inhabit both lotic and lentic environments. Leptocerus americanus (Banks) and Ceraclea maculata (Vorhies) were frequently collected from May through mid-August in Watercress Marsh, whereas both species were poorly represented in collections from Stillfork Swamp. Oecetis inconspicua (Walker) was very abundant at both sites. Triaecnodes marginatus Sibley was dominant in Stillfork Swamp while T. tarsus Milne dominated at Watercress Marsh.

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Although Watercress Marsh was overrun by the Grand River Lobe of the Wisconsin Glacier during its final advance approximately 13,000 B.P. (Matsch 1976), both sites support relic caddisfly species and are relatively remote from major drainage systems. Watercress Marsh is a headwater source of the Mahoning River whereas Stillfork Swamp’s headwaters are tributaries of the westward flowing Tuscarawas River. Historically, the St. Lawrence River drainage system may have had a greater influence on the composition of the caddisfly fauna of these two sites than did the pre-Ohio River drainage.

Differences between the caddisfly fauna of these two sites are best understood by the dissimilarities in physiography created by past geologic events. The valley of Stillfork Swamp is a sediment filled lake bottom through which meanders a slow-flowing stream. Watercress Marsh is fed by numerous underground springs and seeps that originate from the surrounding terminal moraines created by the Grand River Lobe of the Wisconsin Glacier. Differences in glacial history have greatly influenced the nature of aquatic habitats at these sites and account for much of the dissimilarity in their caddisfly faunas.

**DISCUSSION**

The influence of the Pleistocene on the distribution of Ohio Trichoptera was greatly affected by changes in the Teays River drainage pattern caused by glaciation. Stout, VerSteeg, and Lamb (1943) described the Teays River as the major pre-glacial drainage system of south central and western Ohio. The pre-glacial Marietta and Groveport Rivers drained southwestern and central Ohio, respectively, and were major tributaries of the Teays River. By the mid-Pleistocene (ca. 1 million B.P.), the Teays-age drainage pattern was affected by the advancing glaciers. Eventually, the Kansan Glacier completely buried the Teays River Valley and established a new major drainage pattern, the Ohio River.

Whereas Hobbs (1983) proposed that the Teays River system served as a corridor for dispersal of aquatic fauna into western Ohio during pre-glacial times, relatively little is known about the origins and post-glacial movements of Trichoptera in Ohio. Post-glacial lakes and drainage patterns have been altered greatly since the early
Pleistocene. Many watershed areas were completely rearranged due to glaciation. Nevertheless, a network of freshwater lakes and streams was present after the glacial retreat that provided a variety of aquatic habitats. Nimmo (1971) assumed that the area just south of the Wisconsin Glacier was occupied by lakes, creeks, and rivers that were sustained by glacial meltwater that provided suitable habitats for Trichoptera. It is evident from the abundance of Trichoptera throughout formerly glaciated regions of North America that a diverse fauna persisted for long periods in unglaciated regions. Refugia south of the ice have been known for a long time (Adams 1902, 1905) and include the Appalachian region, considered by Ross (1965) to be an important area for Trichoptera. The family Limnephilidae constitutes a dominant group at higher latitudes throughout much of North America (Wiggins 1977) and survived the Pleistocene south of the glacial ice and perhaps in the Beringian refugium.

Ross (1958) proposed that Eastern boreal populations of Trichoptera have spread chiefly northeast, whereas isolated Western populations spread westward and northward. However, Nimmo (1971) proposed that many eastern species dispersed to the West and reoccupied much of central and western Canada. Species of Cerclea, Triaenodes, and Bankstola, that are common in Stillfork Swamp and Watercress Marsh, spread from eastern North America into the western mountains (Ross 1958). For some cool-adapted species, the Pleistocene ice sheets created conditions along their southern edges that were suitable for both eastward and westward migration, resulting in transcontinental distributions (Ross 1956). As the ice receded, cool-adapted species became more restricted in their ranges as a result of intervening gaps of inhospitable terrain (Ross 1965). Nimmo (1971) stated that Holarctic species in Limnephilidae dispersed east and south from Alaska and other northern refugia, while Nearctic limnephilids appear to have dispersed northward (post-glacially) from south of the ice.

The predominantly lentic Holarctic genus Limnephilus contains approximately 95 North American species including many with boreal distributions. Presence of the Holarctic species L. moestus Banks, L. ornatus Banks, and L. rhombicus L. in Watercress Marsh but not in Stillfork Swamp, suggests that Limnephilus diversity is greater at sites with permanent bodies of water (MacLean and MacLean 1984). L. indivisus Walker, a northern transcontinental species, and L. submolitor Walker, which extends its range into the southern Appalachians (Erniér 1973), are both common inhabitants of temporary and intermittent lentic habitats in Stillfork Swamp and Watercress Marsh.

The genus Psychotryche Banks, comprised of 16 Neartic species (Wiggins 1977), was represented at Stillfork Swamp by five species. P. aglona Ross, a new state record collected from Stillfork Swamp, was previously reported from Wisconsin, Massachusetts, and Maine. Watercress Marsh was inhabited by four species, two of which [P. antica (Walker) and P. scabripennis Rambur] were absent in collections from Stillfork Swamp.

The genus Anabolia Stephens is widely distributed throughout the Holarctic with four North American species (Schmid 1955). A. consocia (Walker), reported from Stillfork Swamp and Watercress Marsh, has a transcontinental distribution (Nimmo 1971) and inhabits marshes, slow streams, and temporary pools (Flint 1960, Wiggins 1973).

Ironoquia punctatissima (Walker) and I. parvula (Banks) were present at both sites. Larvae inhabit temporary pools and streams (Flint 1960, Ross 1944, Wiggins 1973) and avoid drought conditions by aestivating in leaf litter around receding pond margins. Relative abundance of Ironoquia was greater at Stillfork Swamp and illustrates the extent of temporary aquatic habitats of this site.

The Holarctic genus Frenesia contains two species, F. difficilis (Walker) and F. missa (Milne) both of which were collected only in Stillfork Swamp. Adults emerge in November and larvae develop in small streams and spring-fed pools (Flint 1956).

Wiggins (1977) reported that Platycnemis species are tolerant of warm quiet waters but are not known to inhabit temporary vernal pools. P. radiatus (Say) was a prominent member of the trichopteran community at Watercress Marsh, yet was represented by only two individuals collected in Stillfork Swamp.

In summary, the above faunistic differences illustrate the influence of physiographic factors on the types of microhabitats present at these periglacial sites. Many of the differences seem to reflect the nature and permanence of lentic habitats that characterize Stillfork Swamp and Watercress Marsh.

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