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Fishes of the Greenbrier river, West Virginia, with drainage history of the Central Appalachians

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ABSTRACT. The Mississippi river valley was the origin of dispersal of the majority of freshwater fishes east of the Rocky Mountains. The Pliocene Teays river was the major drainage from the east-central United States to the ancestral Mississippi. In the north, the Pittsburgh river flowed northward to join the Pliocene Laurentian river. The advance of Pleistocene glaciation brought about profound drainage reorganization and influenced faunal extinctions through ecological changes. Headwater tributaries, remote from the ice fronts, were less severely affected by these changes and served as refugia. The Allegheny–Ohio river eventually succeeded the Teays river as the major eastern drainage to the Mississippi. The New (upper Kanawha) river basin is a remnant of the ancient Teays system.

The Greenbrier river, a tributary to New river in West Virginia, was a subsequent centre of dispersal of fishes as the Pleistocene ice front receded. Major captures occurred with the Monongahela river to enhance dispersal, but were not limited to that drainage. A total of fifty-three fish species is presently known from the Greenbrier river, with eighteen others listed as expected. The depauperate fauna is influenced by limiting factors associated with the New river system.

Introduction

The Greenbrier river is located in eastern West Virginia and flows 274.7 km from northern Pocahontas County to enter the New river at Hinton, W.Va., just below Bluestone Dam (Fig. 1). It drains over 4000 km^2 and is associated with several sink areas, including the karst region of Greenbrier County (Jones, 1973). Reed (1974) reports widths of from 15 to 61 m and depths to 4.5 m; however, in general it is not a particularly deep river. The less resistant and younger Monongahela, Kanawha and Mississippi sandstones and shales to the west are drained by the Elk and Gauley rivers. The area to the east is drained by the Potomac and James rivers, while tributaries of the Monongahela and Potomac rivers drain the headwater areas to the north. Further information relative to these areas is presented in Campbell (1896a), Wright (1934), Addair (1944), Schwartz (1965) and Reed (1974).

In ichthyological literature, the New river system is synonymous with the upper Kanawha river system, i.e. that portion above Kanawha Falls (Denoncourt *et al.*, 1975). The New River drainage is an area with a high degree of endemism. The U.S. Department of Interior has identified twenty-three species of plants and animals as being endemic to this area (J.D. Williams, personal communication). Included are four fish species, three of which are known from the Greenbrier

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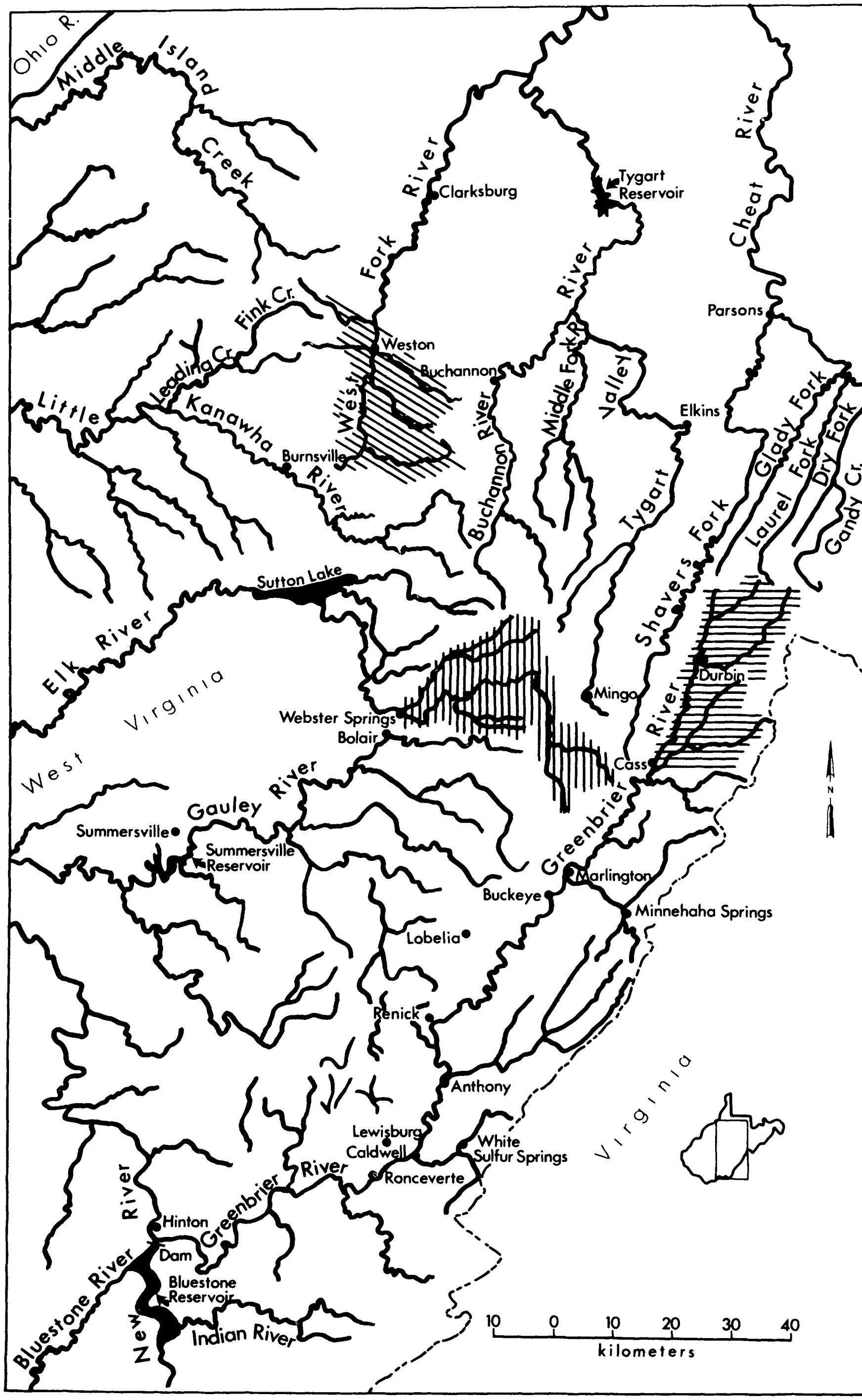

FIG. 1. Present drainage of Greenbrier river, West Virginia, and adjacent areas of stream capture as discussed in this manuscript (horizontal lines = Greenbrier river/Shavers Fork; vertical lines = Elk river/Gauley river; and diagonal lines = West Fork/Little Kanawha river.

drainage: *Nocomis platyrhynchus, Notropis scabriceps* and *Phenacobius teretulus. Etheostoma kanawhae* is endemic to the New system, but not known from the Greenbrier river. *Etheostoma osburni* is endemic to the Kanawha system and known from above and below Kanawha Falls (Jenkins, Lachner & Schwartz, 1972), including the Greenbrier river. Several invertebrates, including the Greenbrier crayfish (*Cambarus nerterius*), spiny cave scud (*Stygonectes spinatus*), other amphipods (*Crangonyx* sp. and *Apocrangonyx* sp.) and freshwater snails (*Fontigens*), are endemic to the Greenbrier valley. Holsinger, Baroody & Culver (1976) list seventeen troglobitic invertebrate species endemic to the Greenbrier valley, and note that a troglobitic salamander of the genus *Gyrinophilus* is presently being described. Approximately 90% of West Virginia's freshwater mussels have been extirpated, and several species known only from New river are facing extinction. Portions of the New–Greenbrier system are presently being considered for designation in the National Wild and Scenic Rivers system (J.D. Williams, personal communication).

Historically, fishes have been collected in the Greenbrier by E.L. Goldsborough and H. W. Clark, W.P. Hay, A.H. Wright, C.L. Hubbs, M.B. Trautman, J. Addair, E.C. Raney, R.H. Gibbs, F.J. Schwartz, R.D. Ross, J.D. Williams and the West Virginia Department of Natural Resources (W.Va. DNR). Many authors have mentioned the Greenbrier, but only the following have published records of species collected: Goldsborough & Clark (1908) reported on three collections and twelve species, Addair (1944) on fourteen collections and thirty species, and Reed (1974) on twenty-three collections with twenty-six species. Schwartz (1967) has published information relative to the Greenbrier and stream capture. Hubbs (1931) has published locations for *Exoglossum laurae*; Hambrick, Jenkins & Wilson (1975) for *Phenacobius teretulus*; Gilbert (1964) for *Notropis* (*Luxilus*); Schwartz (1965) and Miller (1968) for *Etheostoma blennioides*; Lachner & Jenkins (1971) for *Nocomis platyrhynchus*; Jenkins *et al.* (1972) for *Phoxinus oreas*; Gibbs (1957) for *Notropis spilopterus*; and Denoncourt, Hocutt & Stauffer (1977) for *Percina oxyrhyncha.*

The ancient Teays river, the precursor of the New–Kanawha system, was reportedly a major route of fish dispersal during and after Pleistocene glaciation (Ross, 1969; Jenkins *et al.*, 1972). Likewise, the Greenbrier river, a major tributary of the New (upper Kanawha) river system, has been proposed as a possible route of fish dispersal from the upper Kanawha (New) river to adjacent drainages. The purposes of this manuscript are to discuss the ichthyofauna of the Greenbrier river and to synthesize related information on drainage history in the central Appalachians.

Materials and methods

Thirty-two collections of fishes were made from thirty localities in the Greenbrier river drainage during the summers of 1972 and 1974. Collections were made with 1.3 × 3.3 m, 3.6 mm mesh nylon seines and an AC/DC electroshocking unit composed of a Coffelt Model WP-2C pulsator and 1500-watt generator. An effort was made to collect a representative qualitative sample at each location. All specimens were preserved in 10% formalin, stored in 40% isopropanol, and catalogued into the Fish Museum, Appalachian Enviromental Laboratory, University of Maryland, Frostburg, Maryland (AEL 86-107). Nomenclature followed Bailey *et al.* (1970), except for *Percina crassa roanaka*, which was discussed by Hocutt & Hambrick (1973) and Page (1974).

The localities collected (Fig. 2) and their respective numbers are: (Station 1) West Fork of Greenbrier river, Rt. 250 bridge, Durbin (two collections); (2) East Fork of Greenbrier river at confluence of Poca and Long Runs; (3) East Fork of Greenbrier river, Pocahontas County Road bridge, Thornwood; (4) Greenbrier river, Cass (two collections); (5) Greenbrier river, Renick; (6) Greenbrier river, Rt. 3 bridge, Alderson; (7) Greenbrier river, Bargers Springs; (8) Greenbrier river, just above mouth of Wolf Creek, Summers County; (9) Greenbrier river, *c.* 9.6 km upstream of confluence with New river; (10) Confluence of Greenbrier and New rivers, Hinton; (11) Rosen Run, *c* 1.2 km upstream of confluence with Deer Creek; (12) Deer Creek, Pocahontas County Road 718 bridge;

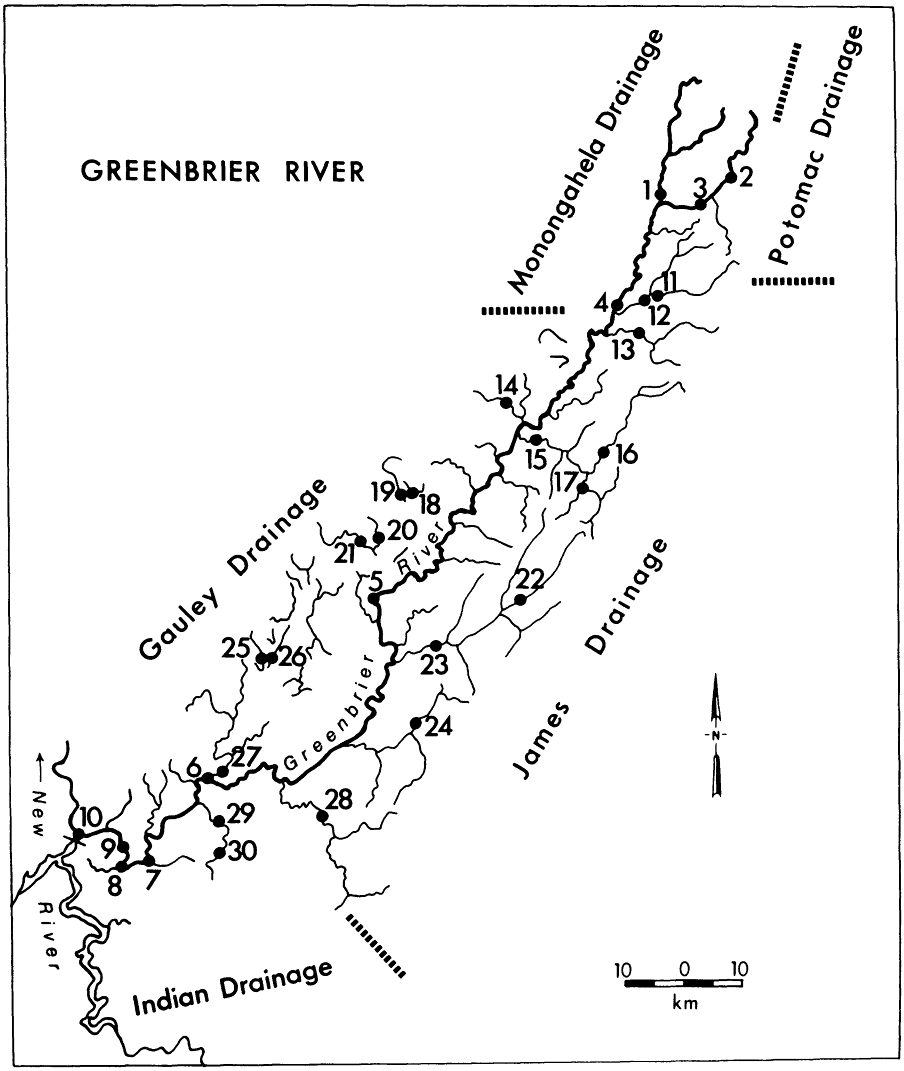

FIG. 2. Greenbrier river, West Virginia, with fish sampling localities noted.

(13) Sitlington Creek, Rt. 28 bridge, Dunmore; (14) Stony Creek, Pocahontas County Road bridge, 2.6 km NW. of Rt. 219; (15) Knapp Creek, 5.3 km E. of Marlington on Rt. 39; (16) Knapp Creek, S. of Westminster Church on Rt. 28, (17) Douthat Creek, Rt. 39 bridge, Minnehaha Springs; (18) Confluence of Cave Run and Bruffey Creek, Greenbrier County Road 29, near Lobelia, (19) Hills Creek, along Greenbrier County Road 29, Lobelia; (20) Robbins Run, *c.* 3.2 km upstream with confluence of Spring Creek; (21) Spring Creek, 0.46 km upstream of Oscar, Greenbrier County; (22) Anthony Creek, Rt. 92 bridge, Neola; (23) Anthony Creek, Anthony; (24) Jerico Draft, White Sulphur Springs; (25) Hughart Creek, Greenbrier County Road bridge, Hughart; (26) Sinking Creek, Greenbrier County Road bridge, Hughart; (27) Muddy Creek, Rt. 3 bridge, Palestine; (28) Second Creek, County Road bridge (Monroe) *c.* 0.3 km upstream of Rt. 219; (29) Wolf Creek, 1.6 km E. of Trinity Church on Rt. 3, Monroe County; and (30) Spring source of Wolf Creek, along Monroe County Road, Big Cove School.

TABLE 1. Fishes collected from the main-channel of the Greenbrier river 1972–1974

Species	Station number									
	1	2	3	4	5	6	7	8	9	10
Salvelinus fontinalis		1	1							
Campostoma anomalum	22	1	20	19		6		2	6	4
Exoglossum laurae	1	1								
Nocomis platyrhynchus	11			13	2	66	14	21	46	
Notropis chrysocephalus	11			17	9	40	11	7	38	5
N. photogenis	3		108	8		3	1	1		
N. rubellus			12	5	21		8	65	75	4
N. scabriceps	3		30							
N. spilopterus					1	15	6	45	37	26
N. telescopus								17	13	3
N. volucellus							17	22	27	8
Phenacobius teretulus	2		1							
Phoxinus oreas		10	18							
Pimephales notatus	3		8	5	1	5		13	7	6
Rhinichthys atratulus	1	37	26							
R. cataractae	5		1	1		3		2	1	1
Semotilus atromaculatus		6								
Catostomus commersoni		2								
Hypentelium nigricans	6		8	1		28		1	1	
Pylodictus olivaris							1	3		
Ambloplites rupestris				13	6	44	1	13	2	1
Lepomis cyanellus	2			1						
L. macrochirus										2
Micropterus dolomieui				8	10	59	16	21	21	
M. punctulatus										1
Etheostoma blennioides	19		3		7	4	1	12	10	1
E. flabellare	74	13	136	15	41			4		
E. osburni	9	2	11		2	1				
Percina maculata		1	6							
P. oxyrhyncha					1	10		3	2	
Cottus bairdi	13									
C. carolinae	27	4	18	3						

Fish survey: results

This survey of fishes in the Greenbrier river yielded 5076 specimens, these being representative of thirty-five species (Tables 1 and 2), including six species not previously reported from the drainage: *Ericymba buccata, Notropis telescopus, Pimephales promelas, Percina maculata, Percina oxyrhyncha* and *Cottus carolinae*. A brief discussion of these six species follows.

Ericymba buccata Cope. One specimen (35 mm SL) of the silverjaw minnow was collected at station 22 on Anthony Creek. Wallace (1973, p. 147) included most drainage systems of West Virginia as being in its distribution area, but did not report it from the Greenbrier. Addair (1944) noted that its limited distribution in the upper Kanawha, especially in the Greenbrier, was probably related to the absence of a preferred sandy substrate. Ross (1973) and Hocutt (1974) did not report it in their surveys of New river, Va.; however, Stauffer (1975) collected it near Glen Lyn, Va.

Notropis telescopus (Cope). Gilbert (1969) gave locations for *N. telescopus* in the upper New river of Virginia and suggested that it was introduced to the system. Hambrick *et al.* (1973) added this species to the known ichthyofauna of West Virginia, but did not record it from the Greenbrier. Its occurrence at three localities in the lower Greenbrier in this survey suggests that it has expanded its range into the system. Jenkins *et al.* (1972) considered *N. telescopus* as being possibly introduced to the upper Kanawha (New) system. Diagnostic features of our specimens compared favourably with those of Gilbert (1969): a prominent predorsal stripe,

TABLE 2. Fishes collected from the tributaries of the Greenbrier river 1972–1974

Species	Station number																			
	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Salvelinus fontinalis									1											
Campostoma anomalum	13	7	10		1	16	5	2	29	4	6	30	8	29			10	9	11	
Clinostomus funduloides												23		45			1			
Ericymba buccata												1								
Exoglossum laurae		1	5													1				
Nocomis platyrhynchus		6	2			6												2		
Notropis chrysocephalus	8	38	49		5	39	24					3	24	16			16	92	2	
N. photogenis	119	60	145		16	1	6						9					25	29	
N. rubellus		2	15		38	4						1					107	95		
N. scabriceps	88	5	18			126						50								
N. spilopterus						1											53		5	
N. telescopus																	2			
N. volucellus							12										7		2	
Pimephales notatus		4	8			50	166					90		1		34	9	1	24	
P. promelas																42				
Rhinichthys atratulus	49	6	27	15				11	29	5	5			52	18		1			
R. cataractae																	2	2		
Semotilus atromaculatus	1	3	22			3	8	70	3			10		3	17	56	1	3	11	
Catostomus commersoni		1		1								3			7	8				
Hypentelium nigricans	1	3	1															1	5	
Ambloplites rupestris							4	2								9	6		2	
Lepomis cyanellus							1	1												
L. macrochirus						1									1					
Micropterus dolomieui							2										1	3	2	
Etheostoma blennioides	2	6	2		3		5										8			
E. flabellare	53	82	37	5	11	4	5		114		30	24	13	55				4		
E. osburni	7	11	21		5								10							
Cottus bairdi				14	2		1						3	5						1
C. carolinae	6	11	16	5									1	20			3	18	3	7

pigment spots above and below the lateral line pores, and longitudinal stripes along the dorsolateral area. One specimen from Muddy Creek (AEL 115) had nine anal rays, as compared to the eight which are normally found.

Pimephales promelas Rafinesque. The fathead minnow has a curious distribution in the New river system. Hocutt (1974) and Stauffer (1975) reported it in small numbers from New river near the Virginia–West Virginia state line. Addair (1944) found it at two localities in the lower Kanawha drainage. We found it at only one locality, Sinking Creek of the karst formation west of Lewisburg, W.Va., where we collected forty-two specimens. More recently, we have collected it from the Gauley river drainage.

Percina maculata (Girard). Our collections yielded the first records of this species in the Greenbrier system. One specimen (50 mm SL) was collected from Station 2, and six specimens (51–57 mm SL) from Station 3. These stations are located close together on the East Fork, a stream of excellent water quality. Our experience shows that it is widely distributed in the New drainage, but nowhere is it abundant.

Percina oxyrhyncha (Hubbs and Raney). Sixteen specimens of the sharpnose darter, the first to be reported from the Greenbrier drainage, were taken from four localities during this study (Denoncourt *et al.*, 1977), thus supporting the hypothesis of stream capture between the New and Monongahela systems. Schwartz (1967) has noted *P. oxyrhyncha* from Shavers Fork and mentioned its presence in the Greenbrier, but gave no details. Hocutt & Hambrick (1973) have discussed the distribution of the sharpnose darter in New river. *P oxyrhyncha* was originally considered for posting by the Department of the Interior, Office of Endangered Species (Anon., 1973), but has been omitted from recent lists (J.D. Williams, personal communication).

Cottus carolinae ssp. (Gill). We collected *C. carolinae* at 14 stations, the first specimens reported from the system. Its distribution suggests that it is a headwater inhabitant confined to springs, and small-to-moderate sized streams. It is likely that this form was misidentified as *C. bairdi* in the past. Robins (1954) has recognized *C. carolinae* ssp. as being endemic to the New river drainage. J.D. Williams (personal communication) has collected an albino *Cottus* sp. from Buckeye Creek Cave, which may prove to be *C. carolinae* or a new species, pending further examination.

Twenty-nine other species collected in this survey (Tables 1 and 2) were similarly reported from the Greenbrier drainage by Goldsborough & Clark (1908), Hubbs (1931), Addair (1944), Jenkins *et al.* (1972), Reed (1974) and Hambrick *et al.* (1975). Additionally, verified literature and museum records of eighteen species increased the total known forms in Greenbrier drainage to fifty-three (Table 3). Seventeen species have been commonly collected in New river and its tributaries downstream from Claytor Lake Dam, Va., to Kanawha Fall, W.Va., but were not encountered in this survey. These species could be expected to occur in the Greenbrier river either rarely or seasonally, particularly near its mouth. These species are listed in Table 4 by scientific name, distributional proximity to the Greenbrier river, and source of information.

Hybridization

Three cyprinid hybrid combinations were collected from Greenbriers river: *Nocomis platyrhynchus* x *Notropis chrysocephalus*; *Notropis chrysocephalus* x *Notropis rubellus*; and *Notropis chrysocephalus* x *Notropis photogenis.* The intergeneric hybrid, *N. platyrhynchus* x *N. chrysocephalus*, is new to the literature (Stauffer, Hocutt & Denoncourt, 1977). The latter two hybrids are being compared by Denoncourt *et al.* (in press). Schwartz (1972) has noted records of *N. chrysocephalus* x *N. rubellus* from other drainage systems, and gave one reference (Raney, 1938) to *N. chrysocephalus* x *N. photogenis.* We also collected a hybrid *Lepomis* from Knapp Creek, but parental species could not be ascertained (AEL 93).

Other hybrids also are known from the Greenbrier drainage. Jordan (1888) has described *Notropis kanawha* as a new species, but it was later identified as an interspecific hybrid, *Notropis rubellus* x *Notropis volucellus*, by Bailey & Gilbert (1960), who noted one specimen (UMMZ 118854, 41.5 mm) from

TABLE 3. Species known from the Greenbrier river, but not collected in this survey. Locality information and source are noted.

Species	Locality	Source
Anguilla rostrata (Lesueur)	Greenbrier; near Alderson	Addair (1944)
Esox masquinongy (Mitchill)	Stocked in Sherwood Lake, Anthony Creek drainage	J.E. Reed (personal communication)
Salmo gairdneri Richardson	Stocked throughout drainage	Reed (1974)
Salmo trutta Linnaeus	Stocked throughout drainage	Reed (1974)
Cyprinus carpio Linnaeus	Second Creek; main channel Greenbrier	Addair (1944); Reed (1974)
Notropis albeolus Jordan	Greenbrier R., near Caldwell; 14 km S. of Hinton	Gilbert (1964); R.D. Ross (personal communication)
Notropis stramineus (Cope)	Second Creek and Greenbrier R. near mouth of Muddy Creek	Addair (1944)
Moxostoma rhothoecum (Thoburn)	Collected in 1871 near White Sulphur Springs; 1931, confluence of Second Creek and Greenbrier R.	Harvard University (MCZ 35704); Cornell University (CU 4957)
Ictalurus melas (Rafinesque)	Stocked in Sherwood Lake	J.E. Reed (personal communication)
Ictalurus p. punctatus (Rafinesque)	Greenbrier river	Goldsborough & Clark (1908); Addair (1944); Reed (1974)
Morone chrysops (Rafinesque)	Greenbrier R., 14 km S. of Hinton; confluence with New river	Virginia Polytechnic Institute and State University (VPISU 2429); (VPISU 2435)
Lepomis auritus (Linnaeus)	Confluence of Greenbrier & New rivers	(VPISU 2435)
Lepomis gibbosus (Linneaus)	Mouth of Greenbrier R.	(VPISU 2435)
Micropterus salmoides (Lacepede)	Greenbrier R. & stocked in farm ponds	J.E. Reed (personal communication)
Pomoxis annularis Rafinesque	Mouth of Greenbrier R.	(VPISU 2435)
Perca flavescens (Mitchill)	Mouth of Greenbrier R.	(VPISU 2435)
Percina crassa roanoka (Jordan & Jenkins)	Mouth of Greenbrier R.	(VPISU 2435)
Stizostedion v. vitreum (Mitchill)	Lower Second Creek; common in long deep pools of Greenbrier R.	Addair (1944); Reed (1974)

Second Creek. Furthermore, a specimen of *Nocomis platyrhynchus* x *Rhinichthys cataractae* (Male; 60 mm SL; USNM 108215) is known from the system; however, this specimen may prove to be '*Rhinichthys bowersi*' (Goldsborough & Clark, 1908), which was transferred from the Monongahela system to the Greenbrier via stream piracy. This problem is presently being studied by Stauffer & Hocutt (1976) and Denoncourt, who have records of over forty specimens from Shavers Fork, W. Va., from 1899 to 1976. J.D. Williams has collected a *Nocomis* x *Notropis* (University of Alabama Ichthyology Collection 3903) from the Greenbrier river at Ronceverte, W.Va., but the specimen was too small (35 mm SL) to make a positive identification.

Water quality

Water quality in the Greenbrier drainage is generally good (Jones, 1973; Reed, 1974; Clark, Chisholm & Frye, 1976). The upper Greenbrier downstream to Marlington (close to locality 15, Fig. 2) is of high quality, chiefly due to restricted land use and low population density: conductance usually ranges near 70 micromhos, dissolved solids at less than 100 mg/l, pH between 7.5 and 8.3, and BOD at less than 0.5 mg/l. From Marlington downstream to its mouth, there is a progressive increase in dissolved solids in the Greenbrier due to increases in hardness and sulphates: conductance may range to 200 micromhos, dissolved solids from 100 to 200 mg/l, pH up

TABLE 4. Species expected to potentially occur in Greenbrier River; their proximity in the New river drainage and authority are listed

Species	Known locality of occurrence	Authority
Alosa pseudoharengus (Wilson)	New River, Va., Pearisburg to Glen Lyn	Hocutt (1974), Stauffer (1975)
Dorosoma petenense (Gunther)	Claytor Lake, Va., and Bluestone Reservoir. W. Va.	Schwartz (1958)
Exoglossum maxillingua (Lesueur)	East river;	Hambrick *et al.* (1973), Stauffer *et al.* (1975);
	New river	Jenkins *et al.* (1972), Hocutt (1974), Stauffer (1975)
Hybopsis dissimilis (Kirtland)	Laurel Creek, W.Va.; New river drainage	Addair (1944); Jenkins *et al.* (1972)
Nocomis leptocephalus (Girard)	East river;	Hambrick *et al.* (1973), Stauffer *et al.* (1975);
	New river, Va., Pearisburg to Glen Lyn; Indian Creek, W. Va.	Hocutt (1974), Stauffer (1975); Our collections
Notemigonus c. crysoleucas (Mitchill)	New river, W. Va., below Bluestone dam and at Hinton;	R.D. Ross (personal communication);
	East river	Stauffer *et al.* (1975)
Notropis ardens (Cope)	East river;	Hambrick *et al.* (1973), Stauffer *et al.* (1975);
	Indian Creek;	Our collections;
	New river	Ross & Perkins (1959), Hocutt (1974), Stauffer (1975)
Notropis galacturus (Cope)	New river;	Ross & Perkins (1959), Hocutt (1974) Stauffer (1975);
	East river	Hambrick *et al.* (1973), Stauffer *et al.* (1975)
Notropis hudsonius (Clinton)	New R., Va., Radford to Glen Lyn	Ross (1973), Hambrick *et al.* (1973), Stauffer (1975)
Notropis procne (Cope)	New River, Va., Radford to Glen Lyn;	Ross (1973), Hocutt, Hambrick & Masnik (1973), Hocutt *et al.* (1974), Stauffer (1975);
	East river	Stauffer *et al.* (1975)
Ictalurus furcatus (Lesueur)	Indian Creek; New river	Addair (1944); Anglers (personal communication)*
Noturus insignis (Richardson)	New river, Va., at Lurick; East river;	Hocutt *et al.* (1973), Hocutt *et al.* (1974); Stauffer *et al.* (1975);
	Big Walker Creek, Va. (abundant)	Our collections
Labidesthes sicculus (Cope)	Vicinity of Bluestone reservoir	J.E. Reed (personal communication)
Morone saxatilus (Walbaum)	New river, W. Va., below Bluestone dam	R. Miles (personal communication)
Lepomis megalotis (Rafinesque)	East river	Stauffer *et al.* (1975)
Pomoxis nigromaculatus (Lesueur)	Bluestone reservoir	Addair (1944), J.E. Reed (personal communication);
	New river, Va., at Narrows	Hocutt (1974)
Etheostoma caeruleum Storer	New river, Va., at Glen Lyn;	Hocutt *et al.* (1973);
	East river	Hambrick *et al.* (1973), Stauffer (1975)
Etheostoma nigrum Rafinesque	New river, W. Va., above Gauley Bridge and Glade Creek;	Addair (1944);
	Gauley river (abundant)	Our collections

* Often confused with *Ictalurus punctatus*.

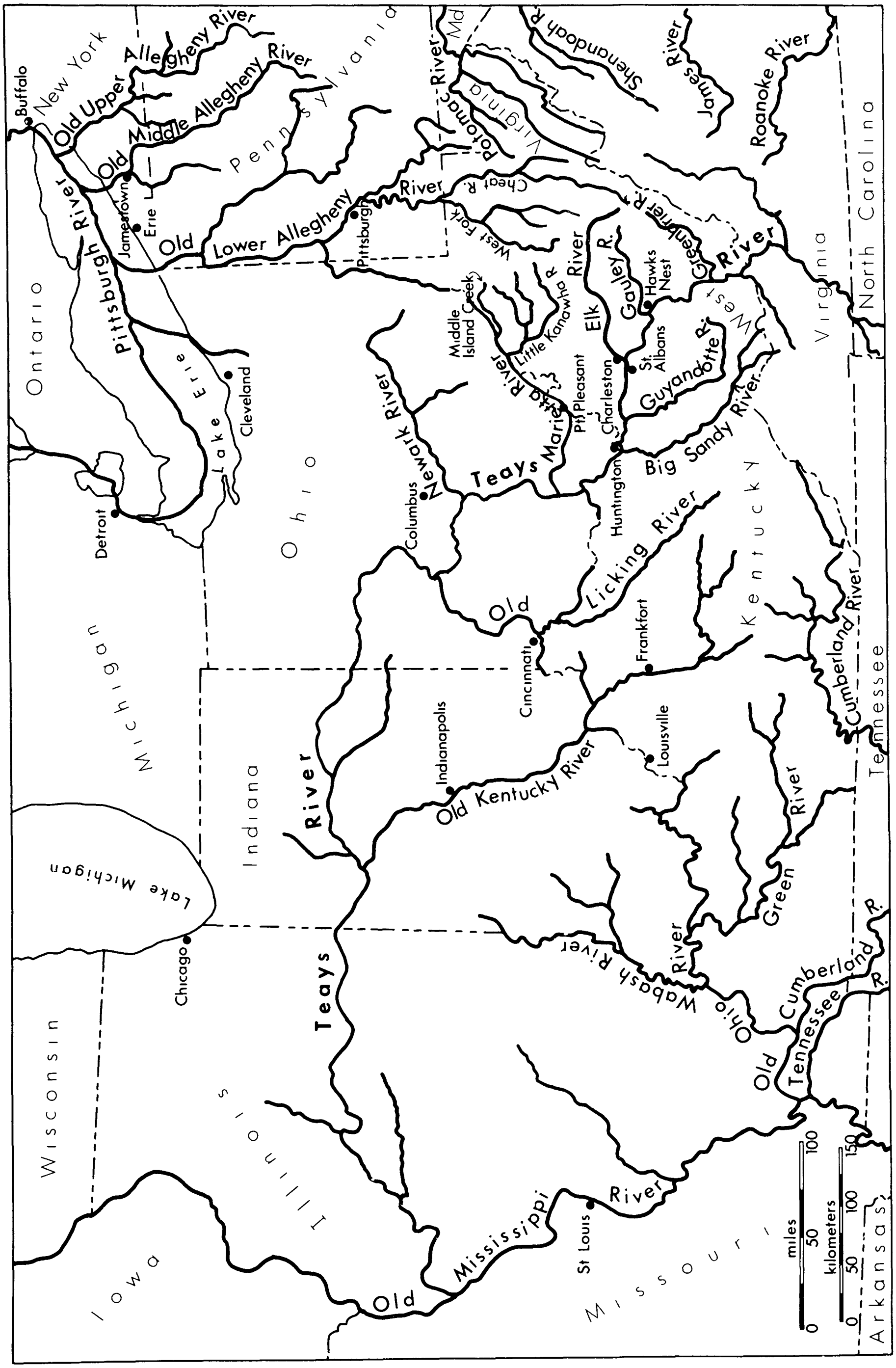

FIG. 3. The presumptive Pliocene drainage in northeastern U.S.A.: the Teays river and the Pittsburgh river drainages.

to 7.8, and BOD is usually less than 2.0 mg/l. Nutrient concentrations are low.

The subsurface drainages of the karst area west of Lewisburg are readily polluted by surface sources; the town has regularly injected sewage into the nearby sinks. Davis Spring discharges into the Greenbrier river near Lewisburg, and is characterized by particularly high BOD and nitrate concentrations (Clark, Chisholm & Frye, 1976).

Drainage history of the central Appalachians

Pliocene

Thornbury (1965, pp. 82–86) has reviewed several theories of pre-Pliocene drainage in the Appalachian Highlands of the eastern U.S.A. (Davis, 1889; Hobbs, 1904; Johnson, 1931; Meyerhoff & Olmsted, 1936; Thompson, 1939, 1949). These theories, or modifications proposed by others, are not without their weaknesses and they are of doubtful value to zoogeographers. A more realistic view of the presumptive Pliocene drainage of this region is that presented by Lachner & Jenkins (1971, their Fig. 30), which suggests that the Great Lakes and the Allegheny and Ohio rivers were not then in existence, and that instead (Fig. 3) there was a broad valley in the Lake Erie to Lake Huron and St Lawrence river areas, which was occupied by the Pliocene Laurentian river (Spencer, 1907; Flint, 1947; Fridley, 1950) and its southern tributary, Pittsburgh river (Tight, 1903, p. 18). Fairchild (1925, pp. 31–32) has described portions of this drainage as the Ontarian and Erigean rivers. Radforth (1944), Ross (1952), 1958) and Schwartz & Meredith (1962) have shown how this old drainage may have influenced fish distributions.

The Pittsburgh river apparently had three southeastern tributaries in western Pennsylvania: the Old Upper, the Old Middle and the Old Lower Allegheny rivers (Tight, 1903, p. 18). The divide between these and the Pliocene Susquehanna river was probably southeast of the present West Branch of the Susquehanna (Davis, 1954, p. 479). At that time, Sinnemahoning Creek may have formed the headwaters of the Old Upper Allegheny river (R.D. Ross, personal communication), while the West Branch of the Susquehanna south of McGee's Mills, Clearfield County, probably was one of the headwater tributaries of the Old Allegheny river via Mahoning Creek, Pa. (Thompson, 1949). Old Middle Allegheny river, if it actually existed, may have been principally composed of a Clarion river–Conewango Creek (reversed) component, to which Anderson Creek (Susquehanna drainage) was a headwater tributary (Thompson, 1939). Other tributaries to the Pittsburgh river were the ancestral Monongahela and Beaver rivers and the Old Upper Ohio river (the Steubenville river of Stout, Ver Steeg & Lamb, 1943) north of New Martinsville, W.Va.

The ancestral Potomac river shared a divide with the Old Lower Allegheny river which was probably more or less where the present divide between the Allegheny and the Potomac system lies today. The Potomac, Monongahela, James and Greenbrier rivers all rise from an up-warped domed structure in southwestern Pendleton and northern Pocahontas counties, West Virginia, and Highland County, Virginia (Price, 1927, p. 280). South of these drainages, the Pliocene Teays river was a great master stream flowing west to the ancestral Mississippi (Tight, 1903, Plate I). Its northeastern tributaries were the Vernon, Newark and Marietta rivers of Ohio (Tight, 1903). Little Kanawha river and Middle Island Creek represent remnants of the headwaters of the Pliocene Marietta river.

The Atlantic divide shared by the Teays river with the youthful James and Roanoke rivers of the Atlantic slope probably once stood at or near the Fall Line (Thornbury, 1965, pp. 106, 141), although opinions differ. Whatever the case, this divide has migrated northwestward during the Tertiary and Quarternary, due to the competitive erosional advantages of the coastal streams; it is now remarkably uneven, cutting across three physiographic provinces (Thornbury, 1965, p. 82; Dietrich, 1954, 1959; Spencer, 1964). Today it remains in the Blue Ridge province southwest of Roanoke, Va; the Roanoke and James rivers have caused a northwest migration of the divide by 64 to 120 km; the Potomac–Monongahela divide is now 130–160 km northwest of its original assumed position (Thompson, 1939; Thornbury, 1965); and the divide between the Susquehanna and greater Ohio (Allegheny and Monongahela) rivers has migrated even further to the west (Denoncourt, Potter & Stauffer, 1977). Ross (1952, 1969) has outlined a hypothetical history of the James, New and Roanoke rivers in Virginia, showing presumed changes in the divide during Pliocene and Pleistocene times.

The major southern tributaries of the Teays river in the Pliocene were the Old Kentucky and the Old Licking rivers, whose histories were revised recently by Teller (1973). Old Kentucky and Old Licking were once joined, and drainage then was north to the main channel of Teays river somewhere in western Ohio or eastern Indiana. Further to the east, on the Kentucky–West Virginia divide and in western West Virginia, the Big Sandy and Guyandotte rivers also were southern tributaries to Teays river. Their Pliocene courses seem to have been much as they are today (Tight, 1903, p. 15). The ichthyofaunas of the latter two streams are by no means unequally developed as reported in Jenkins *et al.* (1972), and our collections in the Guyandotte river in 1975 yielded seventeen species not recorded from the drainage by these authors, so increasing the number of known forms from forty-five to sixty-two. Evenhuis (1973) has recently completed an inventory and classification of streams in the Big Sandy drainage, Kentucky.

The Green and Cumberland rivers do not seem to have been a part of the Teays river system. Apparently, they flowed independently to the ancestral Mississippi river, or were tributaries to the pre-glacial Lower Ohio river (Galloway, 1919, p. 20; Flint, 1947, p. 165; Thornbury, 1965, p. 208). The lower Ohio river roughly corresponded to the present course of the Ohio river below Louisville, Kentucky.

To the south, the Teays river headed against the upper Tennessee river perhaps near the present divide. Ross (1972) has summarized the history of the Tennessee river, while Cooper (1944) and Ross & Carico (1963) have discussed some related drainage interchanges. Masnik (1973, 1974) has related fish distribution problems of the divide between the Clinch and Powell rivers of the upper Tennessee system, and the New river in western Virginia.

The course of the main channel of the Teays river has been discussed by many authors, notably Stout *et al.* (1943), Horberg (1945), Ver Steeg (1946), Fidlar (1948), and Fridley (1950). Janssen (1952) has summarized these and other works. Since then, Rhodehamel & Carlston (1963), Thornbury (1965, pp. 139–141), Barlow (1971) and Teller (1973) either have followed Janssen closely or have introduced minor modifications of his interpretation. There is general agreement that the course of the main channel was westwards towards the ancestral Mississippi river in western Illinois. Although Coffey (1961) and Durrell (1961) have suggested that the Teays river flowed to the north towards the Great Lakes region, Teller (1973, pp. 3677–3678) found no evidence for a 'Great Lakes' outlet during either the Pliocene or the Pleistocene. An alternative view is that the Teays river may have taken a southwesterly course through the present Wabash river valley on the Ohio–Indiana line (Fidlar, 1948). Most authorities, however, favour the idea that the Teays river passed through the pre-glacial 'Mahomet Valley' to the ancestral Mississippi (Fig. 3, based on Horberg, 1945; and Teller, 1973). Wayne (1952) believed that the ancestral course through 'Mahomet Valley' was blocked by an early ice advance, after which the Teays river found an outlet through the Wabash Valley; however, this needs further study. The Wabash river valley itself was overridden by ice in Illinoian time (Gerking, 1945), after which the Teays river drained westward by the Old Lower Ohio River.

Pleistocene

The advance of Pleistocene ice sheets brought about faunal extinctions, ecological changes and a profound reorganization of drainage. These events probably began in Kansan time (Ray, 1957, p. 545; Thornbury, 1965, p. 210; Neff *et al.*, 1970), perhaps in Nebraskan time (Flint, 1947, p. 166), or even earlier in the late Tertiary (Carlston, 1962). But regardless of the actual time of onset, the drainage was repeatedly modified thereafter.

Although the Lauretian–Pittsburgh drainage was virtually obliterated by the ice sheets, open-water refugia remained in the upper Genesee River, New York (Ross, 1952), in the Old Upper, Middle and Lower Allegheny rivers of Pennsylvania, and in the headwater tributaries of the Monongahela river in West Virginia, including the West Fork (Hennen, 1912, p. 35).

The Pleistocene ice advance eventually blocked the lower Pittsburgh river drainage, and diverted the Old Upper, Middle and Lower Allegheny rivers southwestward into the Monongahela (Carlston, 1962; Thornbury, 1965). The proglacial Lake Monongahela thus was formed (White, 1878), which is marked today by high-level terraces in the northern Monongahela valley. Clendening, Renton & Parsons (1967) have dated its sediments as ± 22 000 years BP. The former upper Ohio river still flowed north, however, to join the Monongahela in the vicinity of the present city of Pittsburgh.

In time, Lake Monongahela waters spilled over through West Fork (reversed) into Middle Island Creek (Hennen, 1912) and Little Kanawha river (White, 1896) (Fig. 1). Taff & Brooks (1896), Hennen (1912), Hennen & Reger (1913, pp. 47, 67), Reger (1916, p. 22) and Reger & Teets (1918), have described a number of piracies between the Monongahela and Middle Island Creek and Little Kanawha river, which relate to this or an earlier drainage phase. After the final retreat of the ice from this area, the Allegheny–Ohio river in its present form came into being.

Somewhat similar changes occurred in the Teays river system. Advances of the ice sheets in Illinois, Indiana and Ohio obliterated the main channel of this river, and blocked its northern and eastern tributaries. These found new outlets to the southwest, eventually joining to form the Lower Ohio river. The Old Kentucky and Old Licking rivers also were blocked from their northern outlets and diverted to the southwest, where they joined the pre-glacial (Lower) Ohio river. The Lower Ohio river thus became the master stream for the Green, Kentucky and Licking rivers; however, the Cumberland river was probably not a part of this drainage system.

The main valley waters of the Teays river were impounded at least once by Teays Lake (White, 1884; Wright 1884; Janssen, 1959). Krebs & Teets (1915, p. 35) believed that some of the terraces along the New–Kanawha river were of lacustrine origin from such a lake. Neff *et al.* (1970, pp. 233–234) found two sediment deposits from Teays Lake, the lower indicating stream deposition and the upper apparently being of lacustrine origin; they also traced the head of Teays Lake to the vicinity of Hawk's Nest, some 5 km southeast of Gauley Bridge, Fayette County, W.Va. They thought that Teays Lake had formed during the Kansan Stage, and had lasted for 25 000 to 30 000 years. Campbell (1900, pp. 1–3 and 1901, pp. 1–2) and Petty (1931), thought that this lake (or a later impoundment) diverted the Teays river from its former channel into its present course from St Albans to Point Pleasant, W.Va. (see below).

Furthermore, it is quite likely that several lakes were impounded in the lower Kanawha valley as the Kansan, Illinoian and Wisconsin Stages waxed and waned (Rhodehamel & Carlston, 1963, p. 251). Teays Lake received the outflow from Little Kanawha river, which also was impounded (Hennen, 1912), and whose lower course changed more than once during the Pleistocene (Grimsley, 1907, 1910; Hennen, 1912; Reger, 1916; Reger & Teets, 1918; Alexander, 1938). Outflow was to the southwest to join the Guyandotte and Big Sandy rivers, and the expanding Ohio river drainage system (Fenneman, 1916; Fowke, 1925, 1933; McFarlan, 1943; Flint, 1947; Thornbury, 1965; Frey, 1965).

Towards the end of Wisconsin time, fluviatile conditions returned to the Kanawha valley for the last time as the Pleistocene ice receded. Several minor drainage changes perhaps occurred at this time involving Coonskin, Coal and Pocatalico rivers in the St Albans–Charleston, W.Va. area (Campbell, 1900, 1901; Krebs & Teets, 1914, 1915), none of which had much biogeographical significance. A major drainage change occurred when the former channel through the Teays Valley west of St Albans was abandoned and the present course of the Kanawha River developed north of St Albans to Point Pleasant, West Virginia (Fig. 1). This drainage shift may have been due to ice damming (Campbell, 1900, 1901; Krebs & Teets, 1913, 1914, 1915). Rhodehamel & Carlston (1963, p. 251) thought that stream capture may have caused the diversion, but Thornbury (1965, p. 141) considered this explanation unconvincing.

Teays Lake may have been among the first of several partially-isolating biogeographical barriers to appear in the New–Kanawha river gorge. Addair (1944) and Ross & Perkins (1959) have discussed Kanawha Falls and other isolating factors. None of these in itself is a formidable obstacle, but together they may have interacted to contribute to the formation of the peculiar endemic and semi-endemic upper New River fish fauna (Hubbs, 1931; Hubbs & Trautmann, 1932; Hubbs & Raney, 1939, 1944; Raney, 1941; Jenkins *et al.*, 1972). The fishes of Greenbrier river are a part of that fauna.

Zoogeography

Greenbrier river

The upper Greenbrier river in Pocahontas County, West Virginia, is bounded on the east and west by long ridges. On the east, Allegheny Mountain forms the divide between the Greenbrier and the Potomac and James rivers of the Atlantic Coast drainage. To the west, Shavers Mountain separates Shavers Fork of Cheat river from the Greenbrier (Fig. 1). Leatherbark Run (in the Greenbrier system) is about to behead the Shavers Fork headwaters along this ridge (Wright, 1925, p. 55; Price, 1929; Fridley, 1933). Lynn Divide, on the northeastern part of the Randolph–Pocahontas County line, separates the southflowing Greenbrier headwaters from the north-flowing tributaries of the Monongahela–Cheat river system. This divide has shifted towards the northeast, due to the steep gradients and softness of substrate of the Greenbrier river headwater streams, which give them a competitive advantage over the Monongahela drainage.

The Greenbrier became a major centre of dispersal of New river fishes as the Pleistocene ice receded. Several stream captures then took place through which the Greenbrier expanded its drainage basin northwards at the expense of some of the southern headwater tributaries of the Monongahela system. Multiple piracies beheaded the Glady, Laurel, Dry and Gandy forks of Shavers Fork, along Lynn Divide. Fridley (1933) and Wright (1934) believed that the entire upper Greenbrier basin north of Cass (collection locality No. 4, Fig. 2) had once drained northwestward into Shavers Fork. Hennen & Reger (1913) also found evidence of drainage reversals in this region, but were uncertain as to whether these were due to structural control or to stream capture. Further to this, Reger (1913), found stream cobbles on the divide between Glady Fork and the West Fork of the Greenbrier. Also Blister Swamp, from which the East Fork of the Greenbrier rises, apparently once drained northward into the Laurel Fork of Shavers Fork. Active underground drainage could have contributed to these diversions. Indeed piracies have been common throughout the area and were not confined to the Monongahela–Greenbrier divide alone (Campbell, 1869a, b; Taff & Brooks, 1896; Hennen & Reger, 1913, 1914; Reger, 1923, 1931; Wright, 1925; Price, 1929; Nolting, 1931; Fridley, 1934a, b, 1939; Maxwell, 1935; Duncan *et al.*, 1967; Jones, 1973).

Biological evidence supports the thesis of piracy of Monongahela headwaters by the Greenbrier. Two fishes, *Exoglossum laurae* and *Percina oxyrhyncha*, have long been identified with the fauna of New river (Hubbs, 1931; Hubbs & Raney, 1939). More recently, *P. oxyrhyncha* has been collected from major Ohio drainages in West Virginia (our observations), Pennsylvania (B.A. Thompson, personal communication) and eastern Kentucky (Jenkins *et al.*, 1972). Schwartz (1967) also collected this species from the headwaters of the Monongahela system, into which it has presumably dispersed during capture by the Greenbrier. *E. laurae* is known from the Monongahela system, and Jenkins *et al.* (1972) hypothesized that its confinement to the upper drainage was related to a transfer from the Greenbrier. It was also noted that relict populations of *E. laurae* occur in Ohio, and that it is widespread in the Allegheny and Genesee rivers. *Clinostomus f. funduloides* is another species of the Monongahlea river system, whose presence is restricted to its headwaters and may be related to former piracy by the Greenbrier (Jenkins *et al.*, 1972).

Strong evidence of the Greenbrier serving as an avenue for the northern dispersal of fishes from the Teays system was related by

Lachner & Jenkins (1971). They suggested that *Nocomis micropogon* apparently evolved from a *N. platyrhynchus*-like stock, which is more primitive in character and endemic to the upper Kanawha system. Also, meristic and morphometric data for upper Monongahela chub populations indicate evidence of introgressive hybridization, which is carried over into *N. micropogon* populations of the upper Potomac river.

Wallace (1973) has hypothesized that *Ericymba buccata* either was established in the Teays system prior to the inception of Kanawha Falls, or that it used Teays Lake as a mode of upstream dispersal. Whichever is the case, its presence in the upper Monongahela system could feasibly be related to a Monongahela–Greenbrier theatre of piracy. Only one specimen of *E. buccata* was collected in this survey. Stauffer (1975) reported two specimens from New river Glen Lyn, Va., but neither Ross (1973) nor Hocutt (1974) collected it in their surveys. This species is widely distributed in the Gauley river, where it is locally abundant (our observations), and thus it is not unreasonable to assume that it was at one time more prevalent in the Greenbrier than at present. Further to this Schwartz (1965) felt that *Etheostoma blennioides* could have entered the Cheat drainage from the East Fork of Greenbrier river via a Blister Swamp–Laurel Creek route.

It seems probable that the northward emigration of fishes into the Monongahela drainage was followed by their eastward dispersal to the Potomac river, principally by two routes: the upper Cheat system (Schwartz, 1965; Lachner & Jenkins, 1971) and the Casselman river of the Youghiogheny drainage (Abbe, 1902; Thompson, 1939; Ross, 1952). Some species which have presumably crossed into the Atlantic slope by either of these routes, include: *Campostoma a. anomalum* (Ross, 1952), *Ericymba buccata* (Wallace, 1973), *Notropis s. spilopterus* (Gibbs, 1957), *Rhinichthys atratulus* (Hubbs & Lagler, 1958), *Carpiodes cyprinus* (Schwartz, 1965), *Etheostoma b. blennioides* (Schwartz, 1965) and *Percina c. caprodes* (Jenkins *et al.*, 1972).

An eastern route of dispersal also may have developed through piracies involving Greenbrier river with the James river system. Thompson (1939) gave evidence that Warwick Run of the James system had probably beheaded Knapp Creek, and is now undercutting Shock Run of the Greenbrier. Further, it appears that Back Creek has beheaded Little Devil Creek into the James, and Hughes Creek has probably captured a tributary to Meadow Creek at Ruckers Gap.

There is little doubt that the James river has derived part of its fauna from the Teays system either directly via the Greenbrier (Thompson, 1939), or indirectly through the Roanoke river (Ross, 1969). James river fauna of an apparent Teays origin includes: *Campostoma anomalum michauxi* (Ross, 1952), *Nocomis* spp. (Lachner & Jenkins, 1971), *Notropis ardens* (Jenkins *et al.*, 1972), *Notropis cerasinus* (Gilbert, 1964), *Notropis v. volucellus* (Jenkins *et al.*, 1972), *Notropis semperasper* (Gilbert, 1961), *Moxostoma* spp. (Jenkins, 1970), *Noturus* spp. (Taylor, 1969), *Etheostoma nigrum* ssp. (Cole, 1972), and *Stizostedion vitreum* (Jenkins *et al.*, 1972), among others. Dispersal to the James and Rappahannock also may have occurred during the development of the Shenandoah river, which also obtained its drainage by means of a series of piracies (Watson & Cline, 1913; Stose, 1922).

Gilbert (1964) has reviewed the status of the subgenus *Luxilus* in the New river system. Prior to this investigation, *Notropis chrysocephalus* was known from only one collection in the Greenbrier drainage, which Gilbert surmised was probably representative of an introduced population. We found it at twenty localities, which suggests that Gilbert's (1964) presumption was the result of a lack of available material. *N. albeolus* is rarely encountered in the Greenbrier.

Phenacobius teretulus, a New river endemic, is rare in the Greenbrier as well as most of West Virginia. Hambrick *et al.* (1975) documented it from the East Fork of the Greenbrier river, Indian Creek and Gauley river. Until more is learned about the ecology, distribution and abundance of this species in West Virginia, it should be posted by the State Department of Natural Resources as a rare and endangered species. *Notropis scabriceps*, another New river endemic, is locally common in the Greenbrier drainage, but rare elsewhere in West Virginia. *Phoxinus* *erythrogaster* is recorded from Howards Creek (Addair, 1944); however this collection probably represents *P. oreas.*

Moxostoma rhothoecum is known from the New drainage by one specimen collected from the Greenbrier system by A.R. Crandall in 1871 near White Sulphur Springs, and deposited at Harvard Univeristy (MCZ 35704). It was also collected in 1931 by A.H. Wright of Cornell University at the confluence of Second Creek and Greenbrier river (CU 4957). *M. rhothoecum* may have been extirpated from the New system at this time. Until our recent records of *M. erythrurum* from the Gauley river drainage (Hocutt, Denoncourt & Stauffer, in press), *M. rhothoecum* was the only reported *Moxostoma* sp. from the upper Kanawha system.

R.D. Ross has collected a single specimen of *Percina crassa roanoka* from the mouth of the Greenbrier river in 1970. Hocutt & Hambrick (1973) reported this species as being introduced to the New drainage below Claytor Lake Dam, Radford, Va. It has subsequently undergone a population explosion and rapidly extended its range; over 1000 specimens have been collected from New river, Va. by Ross (1973), Hocutt (1974) and Stauffer (1975).

Karst region

The Greenbrier Valley, particularly north and west of Lewisburg, W.Va., is underlain with the porous Greenbrier Limestone, and is well known for its extensive cave systems (Davies, 1965). Jones (1973) has studied the subsurface drainages of this karst area by dye-tracing techniques. The topography is characterized by sinking streams, caves, sinkholes, large springs and an almost complete lack of surface drainage. Subsurface drainage directions do not correspond to surface topography, although most did discharge into the Greenbrier or its tributaries.

It is not known to what extent interrupted stream flow has influenced fish distribution in the Greenbrier drainage. However, some authors have suggested subterranean drainage as a mode of dispersal for fish (Herald, 1957; Masnik, 1973; Nelson & Paetz, 1974). Holsinger (1969) and Steeves (1969) considered interstitial distribution patterns as being important in the dispersal of amphipods and asellids, respectively. Moreover Kuehne (1966) regarded *Chologaster agassizi* as a fish species which inhabited and survived in areas transitional between surface and subterranean drainages. Thus, it does not seem improbable that subsurface drainages might be an avenue of dispersal for fish species. Our study has shown that native fish fauna occur in the various interrupted streams; however, we did not collect these systems extensively since we believed that this unique area merited a thorough investigation of its own. Kuehne's (1966) investigation of a karst region near Mammoth Cave, Ky., noted a depauperate fauna related to various ecological conditions. No troglobitic ichthyofauna are known from West Virginia (Denoncourt *et al.*, 1975), but an albino *Cottus* sp. was taken from Buckeye Creek Cave (J.D. Williams, personal communication). We suspect that the karst near Lewisburg may yield true cave forms of fish, and are presently investigating this possibility. The practice of sewage injection and surface seepage into these aquifers has probably influenced subterranean fish distribution in recent years.

New river

Many authorities have acknowledged the depauperate fauna of the New river system (Addair, 1944; Ross & Perkins, 1959; Jenkins, 1970; Jenkins *et al.*, 1972; Lachner & Jenkins, 1971). Montane conditions which doubtlessly influenced the distribution and abundance of fauna are the bedrock-boulder-large rubble substrate, the high annual discharge (Hocutt, Hambrick & Masnick, 1973), the gradient (Stauffer, 1975), scouring effects and the general absence of plant life (Addair, 1944), and the prevailing falls, cataracts and rapids (Hubbs, 1931; Hubbs & Raney, 1939; Jenkins *et al.*, 1972). These factors, as well as the poor development of flood plains, the relative absence of lowland habitats, and the lack of a soft bottom substrate, have probably influenced the low numbers of catostomid species in the drainage (Jenkins, 1970; Jenkins *et al.*, 1972). Ross & Perkins (1959) have suggested that fish distribution in the New river also may be affected by high sulphate concentrations, and did not exclude the possibility of montane glaciation during the Pleistocene Faunal saturation and interspecific competition may have contributed further to the extirpation of many forms (Jenkins *et al.*, 1972).

Extensive water loss may have occurred by stream capture in this drainage. Certainly, the porous limestone features and solution of the lower New river contribute to periodic water loss. For instance, Clark *et al.* (1976) have stated that in October, 1971, New river had a flow loss of $22\,m^3/sec$ between the gauges at Glen Lyn, Va., and Hinton, W. Va., this being over 10% of the normal flow. Further studies have indicated that water loss to subterranean drainage is more pronounced in low-flow seasons and that the loss may return to the channel above Kanawha Falls.

The Kanawha Falls (Jenkins *et al.*, 1972), which are 7.3 m in height, were recognized by Hubbs & Raney (1939) and others (see previous section) as playing a distinctive role in limiting the dispersal of fishes into the upper Kanawha (New) river system. But Lachner & Jenkins (1971) have noted the period of inception of Kanawha Falls is unknown. Miller (1968) believed it was probably cut during the first major glacial recession, but lacked data to support this conclusion. Three other cataracts above Kanawha Falls are Wylie Falls at the Virginia–West Virginia line; Bull Falls at Warford, Summers County; and the previously-mentioned Sandstone Falls at Sandstone, Summers County. Lachner & Jenkins (1971) have suggested that the series of rapids, cascades and low falls of the New river gorge may have hindered upstream and downstream dispersal further. They mention that the conditions of stress common to the system may have initiated a speciation response. This was based on the fishes commonly identified as originating from and/or being endemic to the drainage, namely *E. laurae*, *N. platyrhynchus*, *N. scabriceps*, *P. teretulus*, *E. kanawhae*, *E. osburni*, *P. oxyrhyncha* and *C. carolinae* ssp.

The Pleistocene, no doubt, had direct and indirect effects on the New river fauna through climatic changes and temperature fluctuations, while dispersal may have been enhanced by the use of shore areas of Pleistocene lakes (Deevey, 1949; Rubec, 1975). More recently, it should not be forgotten that Goldsborough & Clark's (1908) survey of the fishes of West Virginia was prompted by the decrease in fish stocks attributed to lumbering and mining operations. These authors noted that many fishes had probably been killed by man's activities, including dynamiting, and that clear cutting had probably resulted in less ground water, higher temperatures, more surface runoff and, subsequently, more settleable solids which blanketed the substrate and destroyed the preferred habitat of many fish and food organisms. Addair (1944) further stressed the influence of industrial discharges in the lower Kanawha, and of tanneries on the Greenbrier at Durbin and Marlington, W.Va. Subsequently J.E. Reed (personal communication) has related that a tannery on the Greenbrier was responsible for an extensive fish kill in 1970. Thus, the present depauperate fauna may be not only the consequence of Pleistocene events, but also the result of recent human activity.

Conclusions

The Mississippi river valley was the origin of dispersal of the majority of freshwater fishes east of the Rocky Mountains. The Pliocene Teays river, a tributary to the ancestral Mississippi, drained an area in the east-central U.S.A. from the Appalachian Mountains to western Illinois. In the Pleistocene, glaciation blocked the northwest course of the Teays resulting in the inundation of the channel at least once to form Teays Lake; subsequently, Teays Lake found an outlet to the southwest similar in direction to that of the present day Ohio river.

Simultaneously, faunal exchanges between the Teays river and adjacent drainages facilitated the dispersal of Mississippi basin derived fish stock. Due to the competitive advantages of Atlantic slope streams, the Mississippi river/Atlantic slope divide migrated westward via stream captures. Some of the Teays river drainage was captured by the evolving Roanoke/James river systems. Fauna dispersed northward from this theatre by means of stream piracies between the James and Rappahannock/Potomac rivers and by coastal migration along the greater Susquehanna river. Piracies and interdrainage connections between the Roanoke river and the Tar/Neuse rivers to the south enhanced dispersal. Biological and geological evidence supports the contention that the Greenbrier river played an important role in faunal dispersion from the Pleistocene Teays system to the Monongahela river system to the north, and from there to the Potomac drainage to the east. Minor captures and dispersals may have occurred between Greenbrier and James rivers.

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