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Northern Redistribution of Freshwater Pearly Mussels (Bivalvia: Unionoidea) During Wisconsin Deglaciation in tl Southern Glacial Lake Agassiz Region: A Review

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ABSTRACT.—The chronology of the reinvasion of freshwater pearly mussels (Bivalvia: Unionoidea) into the southern Glacial Lake Agassiz region is reconstructed from the published record of the latest Pleistocene (Wisconsin) deglaciation of the region and known spatial and temporal distributions. The earliest invading unionoidean fauna entered the region above the driftless area of southeastern Minnesota and western Wisconsin between 14,000 and 11,000 years before present; the remaining species colonized the region postglacially. The formation of St. Anthony Falls is correlated with the drainage of Lake Agassiz from the Herman to the Campbell Beach level as an estimate of its date of formation, and a new chronology and mechanism of mussel dispersal into the Red River of the North basin is proposed.

INTRODUCTION

Malacologists, working in the southern Glacial Lake Agassiz region (*e.g.*, Wilson Danglade, 1914; Dawley, 1947; Cvancara and Cvancara *et al.*, *see* below; Clarke, 1973, 1 and elsewhere (*e.g.*, Simpson, 1896; Ortmann, 1924; Johnson, 1970, 1980), recognized effect of the latest Pleistocene (Wisconsin) deglaciation on the distribution of freshw pearly mussels (Bivalvia: Unionoidea) in the Canadian Interior and Great Lakes basins. meltwater connections produced by wasting glaciers allowed the migration of mussels stream from southern refugia (Johnson, 1980). Once water levels fell after glaciers rece the basins took on their present configurations, limiting the dispersal of aquatic organ such as fish-dispersed unionoideans across the divides.

The dispersal chronology of mussels into the region's now disjunct watersheds ca determined by analyzing their past and present distributions in the light of the kn sequence of interbasin connections. Dawley (1944, 1947) recognized these aquatic con tions, but limited geological information prohibited her from proposing a mechanis chronology of dispersal. Cvancara (1966, 1967, 1970, 1975, 1976, 1983; Cvancara *et al.*, 1 1972; 1976, 1979; Ashworth and Cvancara, 1983) contributed a wealth of informatio the Recent and fossil Unionoidea of the southern Lake Agassiz basin but speculated on the origin of the region's mussel community. Underhill (1989) has previously prop a dispersal chronology for the reinvasion of the Minnesota's ichthyofauna; this is discu below.

Present hydrology.—The southern Glacial Lake Agassiz region is composed of the h waters of three major continental drainage basins (the Great Lakes, Hudson Bay and sissippi River basins), and was formerly occupied by the early stages of the Glacial L Agassiz watershed. It is here divided into five drainage systems: the Lake Superior, Lak the Woods, Red River, and Upper and Lower Mississippi River systems (Fig. 1).

The Lake Superior System, that portion of the Great Lakes basin within the reg includes Lake Superior and its tributaries in Ontario, Minnesota and Wisconsin. The I son Bay basin in the region includes only those tributaries of the Nelson River above l

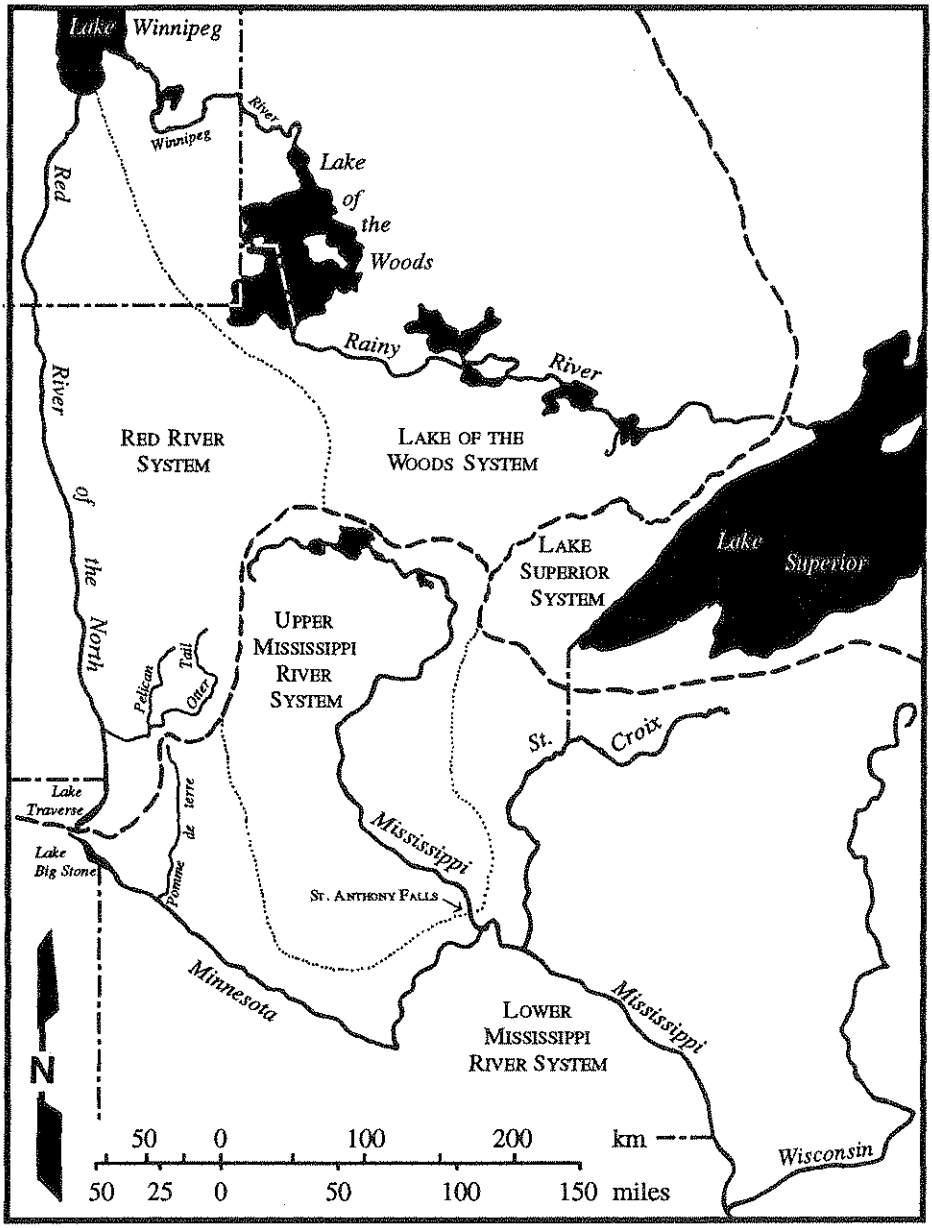

FIG. 1.—Diagram of the Southern Glacial Lake Agassiz Region. Drainage systems are defined in the text

Winnipeg. For the purposes of this paper, the Nelson River watershed is subdivided two drainage systems: the Red River System (the Red River of the North and all o tributaries) and the Lake of the Woods System (the Winnipeg River with its tributaries

The remainder of the study area drains to the Gulf of Mexico. This basin is subdivi into the Upper and Lower Mississippi River systems (following Underhill, 1989; also C 1997) based on their divergent histories and disparate mussel communities. The form that portion of the Mississippi River and all of its tributaries above St. Anthony Fall Minneapolis, Hennepin County, Minnesota. The Lower Mississippi River System is the r and all of its tributaries between St. Anthony Falls and the mouth of the Wisconsin R (an arbitrary southern limit).

These five drainages were in place by the beginning of the Holocene, but they have always been isolated. The enormous volume of meltwater left in the wake of wasting glac overran many of the region's present drainage divides and connected now separate ba until water levels receded.

UNIONOIDEAN DISTRIBUTIONS

Forty-six species of Unionoidea occur within the southern Glacial Lake Agassiz reg They were determined by examination of the holdings of the James Ford Bell Museur Natural History, University of Minnesota, St. Paul, and a review of the relevant litera (Baker, 1928; Goodrich and van der Schalie, 1932; Cvancara, 1970, 1983; Clarke, 1 Mathiak, 1979; Cummings and Mayer, 1992; Graf, 1997). The taxonomy follows Willian *al.* (1993) and figures of these mollusks can be found in Cummings and Mayer (1992) Clarke (1973).

Based on their distributions (Table 1), each species is placed into one of four unic idean faunas associated with the five drainage systems of the southern Glacial Lake Ag region. Unionoideans of the same fauna are assumed to have had similar modes and ten of dispersal via aquatic connections during the history of the study area.

Most species belong to the Lower Mississippi River Fauna (Table 1); these are the un oideans limited to the Lower Mississippi River System. The Upper Mississippi River Fa is composed of those unionoideans present in the Upper Mississippi River System and, the exceptions of *Strophitus undulatus* and *Utterbackia imbecillis,* the four other drair systems of the region. Five mussel species found only in the Lower Mississippi and Red R systems have been united as the Red River Fauna. *Elliptio complanata,* the lone unionoic of the Lake Superior Fauna, is found only in the Lake Superior System.

The fossil record.—Unlike the fish (Underhill, 1989), there is a fossil record, albeit limi of the Unionoidea of the region. The Quaternary unionoidean paleofauna of the south Lake Agassiz basin was reviewed by Ashworth and Cvancara (1983), the territory imm ately to the W by Cvancara (1976), and that of eastern North America in general by Bo and Grady (1991).

The available literature provides an adequate record of the temporal distribution unionoideans in the region and establishes that freshwater mussels inhabited environm in contact with glaciers (Clayton, 1961; Tuthill, 1961; Tuthill *et al.,* 1964a). Accordin the dated or correlatable Lake Agassiz fossil material reported by Ashworth and Cvan (1983) and Cvancara (1976), only *Lampsilis siliquoidea* is present in sediments older t 12,000 yr before present (ybp) (Moran *et al.,* 1973). *Anodontoides ferussacianus, Lasmi complanata, Lampsilis cardium* and *Pyganodon grandis* appeared between 12,000 and 8 ybp (Moran *et al.,* 1971). Although no Lake Agassiz unionoidean material is known for interval from 8000 to 4000 ybp, in sediments dated between 4000 ybp and the pre horizon, all the species of the Upper Mississippi River and Red River North faunas o

TABLE 1.—The distribution of the Unionoidea in the Southern Glacial Lake Agassiz Region. *See* text for definitions of each unionoidean fauna. LMRS = Lower Mississippi River System; UMRS = Upper Mississippi River System; RRS = Red River System; LWS = Lake of the Woods System; LSS = Lake Superior System; X = present

Species	LMRS	UMRS	RRS	LWS	LSS
Upper Mississippi River Fauna					
Lampsilis cardium Rafinesque	X	X	X	X	X
Lasmigona complanata (Barnes)	X	X	X	X	X
L. compressa (Lea)	X	X	X	X	X
Anodontoides ferussacianus (Lea)	X	X	X	X	X
Pyganodon grandis (Say)	X	X	X	X	X
Ligumia recta (Lamarck)	X	X	X	X	X
Lampsilis siliquoidea (Barnes)	X	X	X	X	X
Stophitus undulatus (Say)	X	X	X	X	
Utterbackia imbecillis (Say)	X	X			
Red River Fauna					
Potamilus alatus (Say)	X		X		
Lasmigona costata (Rafinesque)	X		X		
Fusconaia flava (Rafinesque)	X		X		
Amblema plicata (Say)	X		X		
Quadrula quadrula (Rafinesque)	X		X		
Lake Superior Fauna					
Elliptio complanata (Lightfoot)					X
Lower Mississippi River Fauna					
Mussels of the Lower Mississippi River Fauna	X				

[The Lower Mississippi River Fauna consists of: *Actinonaias ligamentina* (Lamarck), *Alasmidonta marginata* Say, *Anodonta suborbiculata* Say, *Arcidens confragosus* (Say), *Cumberlandia monodonta* (Say), *Cyclonaias tuberculata* (Rafinesque), *Ellipsaria lineolata* (Rafinesque), *Elliptio crassidens* (Lamarck), *Elliptio dilatata* (Rafinesque), *Epioblasma triquetra* (Rafinesque), *Fusconaia ebena* (Rafinesque), *Lampsilis higginsi* (Lea), *Lampsilis teres* (Rafinesque), *Leptodea fragilis* (Rafinesque), *Megalonaias nervosa* (Rafinesque), *Obliquaria reflexa* Rafinesque, *Obovaria olivaria* (Rafinesque), *Plethobasus cyphyus* (Rafinesque) *Pleurobema coccineum* (Conrad), *Potamilus capax* (Green), *Potamilus ohiensis* (Rafinesque), *Quadrula fragosa* (Conrad), *Quadrula metanevra* (Rafinesque), *Quadrula nodulata* (Rafinesque), *Quadrula pustulosa* (Rafinesque), *Simpsonaias ambigua* (Say), *Toxolasma parvus* (Barnes), *Tritogonia verrucosa* (Rafinesque), *Truncilla donaciformis* (Lea), *Truncilla truncata* (Rafinesque) and *Venustaconcha ellipsiformis* (Conrad).]

except *Lasmigona costata, Potamilus alatus* and *Utterbackia imbecillis* (Tuthill, 1964; Cvancara and Harrison, 1966; Cvancara, 1967; Cvancara *et al.*, 1972, 1976). Tuthill (1963b), Tuthill *et al.*, (1964b), and Zoltai (1969) reported only unidentifiable unionoidean fragments. The current Red River basin fauna is listed in Table 1.

Tuthill (1962, 1963a, 1967) erroneously noted numerous species from Pleistocene and Holocene Red River basin collections. These reports are based largely on Tuthill's own records, and they have not been replicated or substantiated by later collectors (*i.e.*, Cvancara, 1970; Clarke, 1973). By excluding these studies (and the works cited within them) no species other than those of the present mussel community have ever been identified from Lake Agassiz sediments. I have dealt with erroneous, nonfossil records from the Lake Agassiz basin of Minnesota elsewhere (Graf, 1997).

Little fossil material exists for the portion of the study region to the E of the Lake Aga basin. Cvancara *et al.* (1979) recorded *Pyganodon grandis* from Glacial Lake Aitkin s ments dated at 11,500 ybp. Zoltai and Herrington (1966) reported *Lampsilis siliquoidea Obovaria olivaria* from Canadian Lake Superior sediments older than 6000 ybp. Altho I haven't examined voucher material, the occurrence of the latter in the Lake Supe basin is considered erroneous unless further evidence for its presence becomes availab

RECONSTRUCTION OF MUSSEL INVASIONS

In order to reconstruct the migration of pearly mussels into the southern Glacial L Agassiz region based on their distributions and the accepted chronology of interbasin c nections, it is necessary to assume that they require aquatic connections for dispersal. Ne all unionoideans are dispersed by fish (except for *Simpsonaias ambigua* which parasit the mud puppy, *Necturus maculatus*), and mussels have very specific geographic distr tions limited to one or more drainage basins (van der Schalie, 1939). Terrestrial migra has never been proposed for the Unionoidea.

Some earlier authors (*e.g.*, Call, 1878; Kew, 1893; Simpson, 1893) believed it possible aquatic birds to disperse mussels. According to van der Schalie (1939), "no one has e established that freshwater mussels have actually been transported from one stream to other in this manner." Even if a bird did carry a unionoidean to a new watershed, it wo have to be a gravid female and an appropriate host would need to be present for the spe to become established (discussed by Johnson, 1970). Further, high glochidial and juve mortality (McMahon, 1991) surely prohibits this. Dawley (1944) noted that it was conc able that mussels may be distributed via transplanted fish; however, no evidence exists this has occurred within the study area.

Another necessary assumption is that the drainage systems have remained isolated wit the study area (except the Red River and Lake of the Woods systems, which are conflu at Lake Winnipeg) since their establishment at the close of the Pleistocene. Dawley (19 noted, however, that Lakes Big Stone and Traverse, on the Minnesota-Dakota border, be connected during times of high water, as they were in 1915. Cvancara (1970, p comm.) believed that the proximity of these two lakes probably still allows the transfe mussels today between the Red and the Lower Mississippi river systems. If such dispe occurred frequently, however, there would likely be a smaller difference between the n ber of species in the Red River System (13) and the species found in the Minnesota R basin (39) (Graf, 1997).

The following discussion outlines a proposed chronology for the invasion of each un oidean fauna into the southern Lake Agassiz region. The proposed chronology in e section is based on Underhill's (1989) hypotheses of the distribution of Minnesota's thyofauna, with exceptions as noted. All absolute dates are from Clayton and Moran (19 unless otherwise cited.

The late glacial invasion of the Upper Mississippi River Fauna.—St. Anthony Falls, beca it prevents the upstream migration of fish, is a barrier to unionoidean dispersal. Wil and Danglade (1914) believed that mussels above the Falls were carried by their fish h which were " . . . able to ascend the falls while [other glochidial hosts] could not accomp it." Underhill (1989), however, concluded that "St. Anthony Falls has been a barrier to migrants since the late Pleistocene." Any mussels found in the Upper Mississippi R System either (1) migrated into the basin previous to the formation of the Falls or (2) some postglacial dispersal route that bypassed the Falls.

St. Anthony Falls was formed by the rapid downcutting in the Minnesota River va associated with the initial flooding (Glacial River Warren) through the southern outle

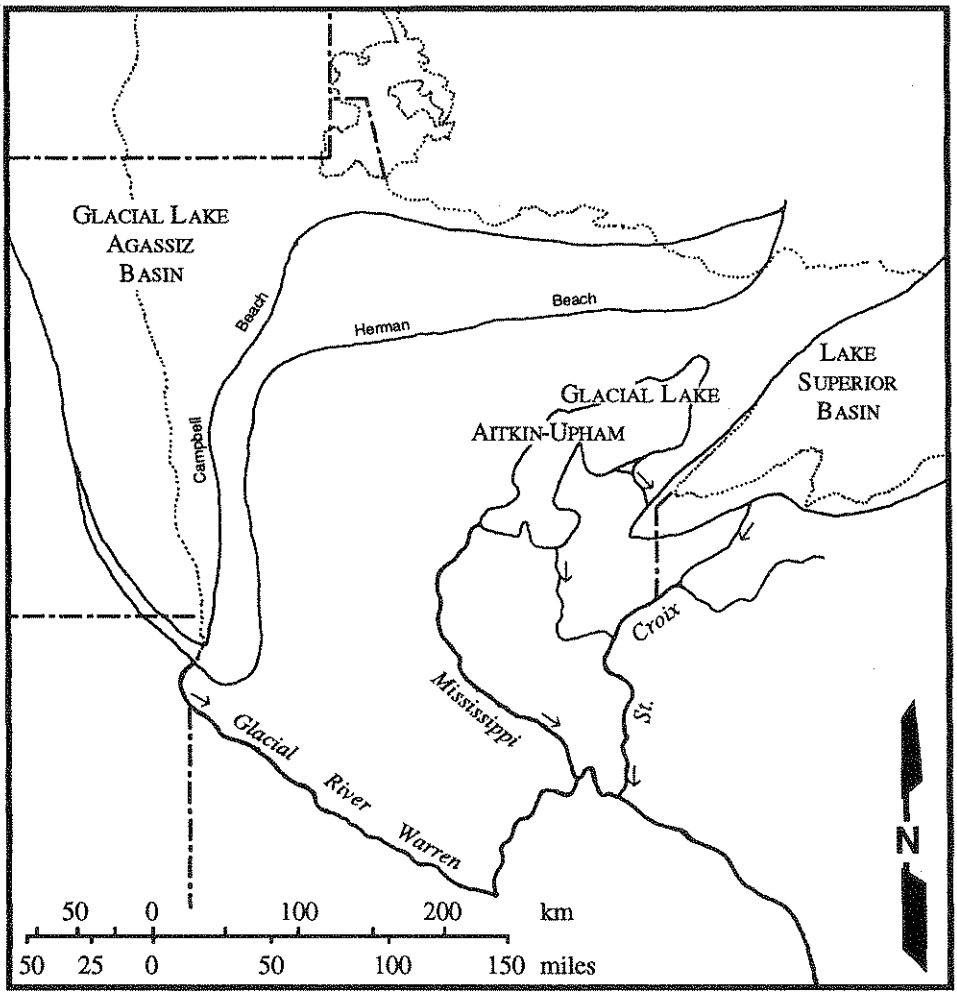

FIG. 2.—Diagram showing the extent of glacial lakes in the Southern Glacial Lake Agassiz Region. Arrows indicate the direction of drainage.

Glacial Lake Agassiz (Fig. 2) (Ojakangas and Matsch, 1982) but not with the flooding that occurred immediately before the final abandonment of that outlet. The latter flooding was not catastrophic and did not result in the lowering of the southern outlet (Fenton *et al.*, 1983). Thus, the formation of the Falls occurred sometime before 11,000 ybp (the end of the first round of drainage through the southern outlet) but well after 11,700 ybp (the beginning of the formation of a lake in the southern Lake Agassiz basin). This correlates with the drainage of Lake Agassiz from the Herman to the Campbell Beach level (Fig. 2).

Since the Upper Mississippi River System's aquatic connections to other drainages within the region depended on a Lake Agassiz level above that of the Herman Beach (Hobbs, 1983), such connections must have been severed by the time the Falls formed. Thus, the hypothesis that the mussels somehow postglacially skirted the barrier can be rejected.

The Upper Mississippi River Fauna populated the Hudson Bay and Lake Superior d ages via the impounded water that breached drainage divides during the highest v stages of Glacial Lake Agassiz (including Glacial Lakes Aitkin and Upham; Fig. 2). (those connections were severed with the drop in level of Lake Agassiz (Hobbs, 1983) Lake of the Woods and Lake Superior systems remained confluent with the Lower M sippi River System off and on for hundreds of years (Clayton and Moran, 1982). If u oidean species other than those of the Upper Mississippi River Fauna had been prese the region during this period, it is assumed that they would have colonized the forme basins. Because the mussels of the Upper Mississippi River are the only species abov Anthony Falls, they were the only unionoideans that migrated into the region befo formation.

The Upper Mississippi River Fauna first migrated from the Lower Mississippi River Sy into central Minnesota sometime after 14,000 ybp with the wastage of the stagnant Sup Lobe ice in the Twin Cities lowland and dispersed widely throughout the region b around 11,000 ybp (the latest time for the formation of the Falls of St. Anthony).

The postglacial invasion of the Red River Fauna.—The ice lobe that held Lake Agas a level high enough to drain through its southern outlet also forced the overflow of v in the Lake Superior basin to the Lower Mississippi River System via the St. Croix (Clayton, 1983) (Fig. 2). Retreat of this ice not only exposed lower outlets for Lake Ag to the Great Lakes but allowed the Lake Superior basin to drain to Lake Michigan as Thus, concurrent with a connection between Lake Agassiz and the Mississippi River, a Superior–Mississippi connection also existed.

If the unionoideans were carried along the path proposed previously for both the mu and fish (Dawley, 1944, 1947; Cvancara, 1970; Clarke, 1973; Underhill, 1989), the Red Fauna migrated up the Minnesota River valley to invade Lake Agassiz through its sout outlet. This hypothesis, however, fails to explain the absence of the Red River Fauna the Lake Superior System, even though there would have been access via the St. C River.

The Red River Fauna is also absent from the Lake of the Woods System, further lenging this hypothesis. While Lake Agassiz drained through its southern outlet, the River and Lake of the Woods systems would have been confluent over a large area. Inc they have been confluent for at least the last 9500 yr when Glacial Lake Agassiz perman abandoned its outlet to the Minnesota River, yet only two members of the Red River F (*Lasmigona costata* and *Potamilus alatus*) have reached the Winnipeg River below Lak the Woods (Clarke, 1973). The Winnipeg River appears to be the site of current mixin the Red and Upper Mississippi River faunas. However, the numerous waterfalls along river have surely arrested upstream dispersal since the withdrawal of Lake Agassiz fron region.

An alternative hypothesis is that the Red River Fauna entered the Lake Agassiz postglacially via stream capture. Radke's (1992) statistical comparison of the fish and m communities of Red and Minnesota River tributaries indicates the possibility of a postglacial riverine connection between the Otter Tail River [a tributary of the Red R and the Minnesota River. There are six species of fishes . . . which inhabit (or have in ited) the Otter Tail River and no other waters within the Red River System. [*Amia* and *Notropis anogenus*] do inhabit lakes, and could have migrated through Galcial Lake Agassiz to the Otter Tail, but there are four species of fishes [*Notropis texanus, pentelium nigricans, Etheostoma caeruleum* and *Percina phoxocephala*] which live only in r and streams . . . " However, according to Underhill (pers. comm.), this single record *phoxocephala* was based on a misidentified *P. maculata*. Radke's conclusions were also b

on two collections of mussels from the Otter Tail River: a single, dead *Actinonaias ligamentina* and a pair of *Elliptio dilatata,* later reidentified as *Lampsilis siliquoidea* and *Ligumia recta,* respectively (Graf, 1997).

The proposed mechanism for the postglacial connection between the Red and Lower Mississippi River systems is stream-head capture. Most tributaries of the eastern Red River basin generally trend E to W. The Otter Tail River, however, runs N to S above the mouth of the Pelican River at Fergus Falls, Otter Tail County, Minnesota. Earlier in postglacial time, the Upper Otter Tail River (that portion of the present-day Otter Tail River above the mouth of the Pelican River) continued S across the present continental divide to the Pomme de Terre River, a tributary of the Minnesota River, while the Pelican River drained S to the Mustinka River, another tributary of the Red River of the North System. The Lower Otter Tail River flowed in its present stream channel at that time, beginning at a point to the W of its present junction with the Upper Otter Tail River System. Headward migration of the Lower Otter Tail River eventually led to the capture of the Pelican and Upper Otter Tail rivers and the beheading of the Pomme de Terre River.

According to this hypothesis, with the abandonment of the southern outlet around 9500 ybp and the withdrawal of Lake Agassiz from the study area ca. 8600 ybp, the five drainage systems of the region were isolated much as they are today. Pearly mussels from southern refugia migrated throughout the Lower Mississippi River System. When the Upper Otter Tail River System was captured, the unionoideans present in those streams dispersed downstream into the Red River of the North and its tributaries, and the new species introduced by this mechanism were those species of the Red River Fauna. This hypothesis accounts for the absence of the Red River Fauna from the Lake of the Woods and Lake Superior systems.

The postglacial invasion of the Red River Fauna is supported by the fossil record of the region. From sediments dated from before 12,000 ybp to ca. 8000 years ago, the only mussel species present in Lake Agassiz sediments are widespread species of the Upper Mississippi River Fauna. In sediments dated after 4000 ybp, the species of the Red River Fauna appear (Ashworth and Cvancara, 1983).

The postglacial invasion of Lower Mississippi River and Lake Superior faunas.—The last unionoideans to invade the region via the Mississippi River are those of the Lower Mississippi River Fauna. If the Red River Fauna did migrate into the Red River System in postglacial time, there is no way to know whether members of the Lower Mississippi River Fauna were present in the Lower Mississippi River System at that time or not. The upper reaches of the Pomme de Terre River presently support a mussel community very similar to that of the Red River System (Bright *et al.,* 1995). Thus, the Red River Fauna may have been part of the larger migration of mussel species from southern refugia in postglacial time; since they were the only species located in the Pomme de Terre River at that time, they were the only species captured.

The most recent species to invade the region is *Elliptio complanata* of the Lake Superior Fauna. According to historical records (Walker, 1913; Goodrich and van der Schalie, 1932; Dawley, 1947), the Lake Superior Fauna likely migrated into Minnesota portions of Lake Superior from the eastern Great Lakes in the last 80 yr or so.

The distributional hypotheses presented here require further testing. Radke's (1992) stream-capture hypothesis is by far the most challenging new idea presented, and the dispersal chronologies of the fishes and the mussels have been revised because of it. Biogeographical studies of other aquatic taxa (*e.g.,* the freshwater decapods) will undoubtedly further clarify the hypotheses presented through their own reflection of the history of interbasin connections in the region.

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