Species Composition of Nebraska's Freshwater Gastropod Fauna: A Review of Historical Records

Author(s): Bruce J. Stephen
Source: American Malacological Bulletin, 33(1):1-11. 2015.
Published By: American Malacological Society
DOI: http://dx.doi.org/10.4003/006.033.0103
URL: http://www.bioone.org/doi/full/10.4003/006.033.0103

American Malacological Bulletin **Advanced Access published 29 December 2014**

Amer. Malac. Bull. **33**(1): 1–11 (2015)

Species composition of Nebraska's freshwater gastropod fauna: A review of historical records

Bruce J. Stephen

School of Natural Resources, University of Nebraska, Lincoln, Nebraska, 68583 U.S.A.

Correspondence, Bruce J. Stephen: bstephen@me.com

Abstract: Freshwater gastropods are important components of aquatic ecosystems yet little is known of their distribution and abundance in most states. To clarify historical species presence in Nebraska, I created a database from literature and museum records to catalog each species of freshwater gastropod. Records provided a list of more than 80 provisional species of freshwater snails in the state. I then evaluated each species for possible misidentification and/or synonyms based on known geographic ranges and systematic studies thereby reducing the number of species expected to be present in Nebraska to 31, including one non-indigenous species. I suspect eight species are rare based on the number of records.

Key words: Macroinvertebrates, freshwater snails, conservation, biogeography

Freshwater gastropods are central components of aquatic ecosystems. Most snails feed on periphyton and in turn are eaten by a number of invertebrate and vertebrate species, particularly waterfowl (Swanson and Duebbert 1989, Dillon 2000) and a diverse group of fishes from sunfishes to catfishes (Lauder 1983, Tiemann *et al.* 2011). A large amount of the energy throughput in aquatic systems involves snails (Newbold *et al.* 1983, Richardson *et al.* 1988, Brown 2001). These important ecosystem components are in a conservation crisis. The non-marine mollusks collectively are thought be one of the most threatened groups of organisms (Lydeard *et al.* 2004). Freshwater snails specifically head the list of endangered groups in some analyses with > 70% of the species imperiled or extinct (Lysne *et al.* 2008, Johnson *et al.* 2013). Yet current knowledge of their distribution and abundance in North America is lacking.

In Nebraska the most comprehensive list of freshwater gastropods, which contained 49 species, was recorded more than 100 years ago (Aughey 1877). Since this report systematic studies have reduced the array of valid species, merging synonymous species names within North America (Hubendick 1951, Dillon *et al.* 2002, Walther *et al.* 2006, Wethington and Lydeard 2007, Walther *et al.* 2010). For example in the Physidae, these studies have shown that what was once thought to be over forty species within North America (Burch 1989) is actually only about ten (Wethington and Lydeard 2007). The need to provide regional reviews with updated taxonomy of freshwater gastropods species is clear.

I have created a list of Nebraska's freshwater gastropod species based on historical and recent literature as well as natural history collection holdings. Each species is evaluated in light of taxonomic revisions and regional literature. This is the first comprehensive review of Nebraska's freshwater gastropods and is the starting point for assessing the current status of freshwater snails in Nebraska, U.S.A.

METHODS

Study region

Nebraska has an area of approximately 200,000 km^2 extending from 40°N to 43°N latitude and 95° to 104°W longitude (USGS 2009). In July–August the average high temperature range is from 26 to 33 °C while in January the average low temperature range is -12 to -8 °C (PCG 2014). Annual precipitation ranges from above 80 cm in the eastern part of the state to below 50 cm in the west (PCG 2014). Nebraska contains six level III ecoregions including the Western High Plains, Central Great Plains, Western Cornbelt Plains, and over 50,000 km^2 of Nebraska Sand Hill Plains (Chapman *et al.* 2001). Nebraska has fourteen level 3 hydrologic units (6-digit code) with major rivers including the White, the North and South Platte rivers, the Niobrara, the Republican River, the Loup and Dismal rivers, the Elkhorn, the Nemaha, and the Big Blue River (EPA 2014). The Missouri River forms the northeast border with South Dakota and continues to form the eastern border with Iowa. Wetlands of the state include valuable resources, such as the basin of the Platte River and the Rainwater Basin, for migrating waterfowl across the Central Flyway (LaGrange 2005).

Study design

I created a database of species presence records from published literature, The University of Nebraska State

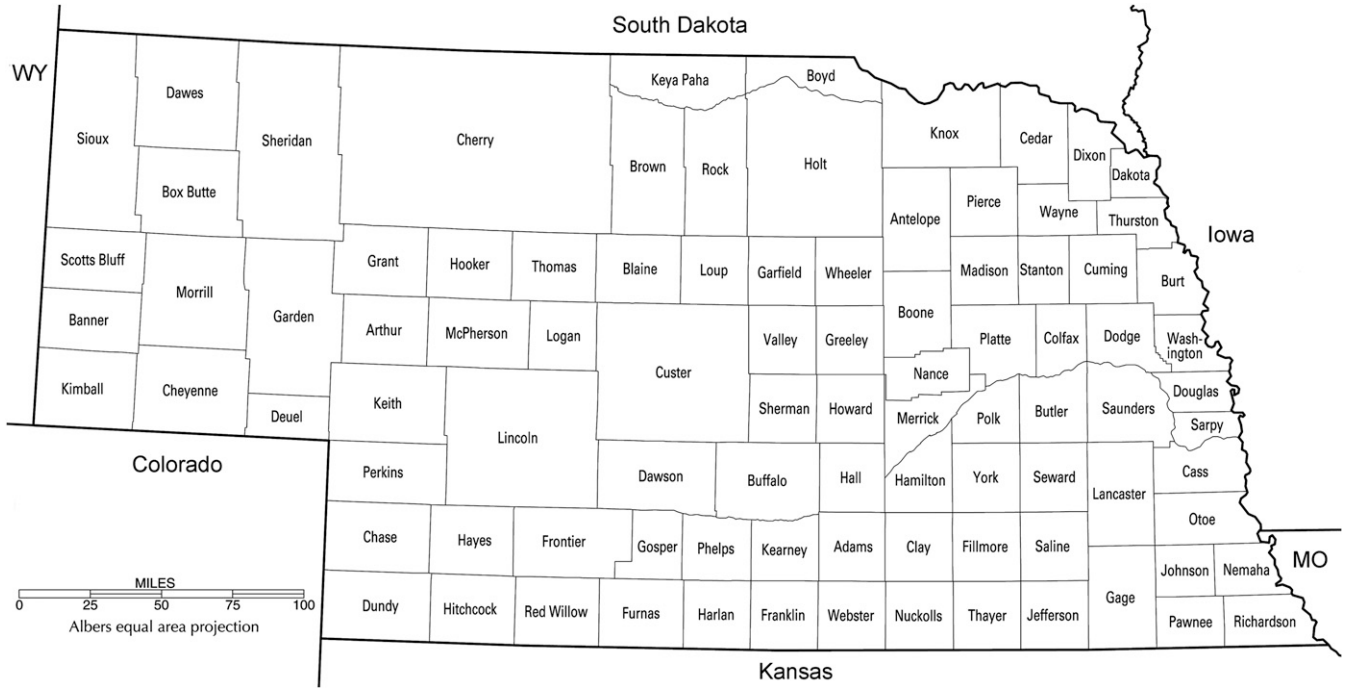

Figure 1. Map of Nebraska's 93 counties.

Museum collection (UNSM), and the online database of the Museum of Comparative Zoology at Harvard (MCZ). Other online databases were searched (the Florida Museum of Natural History, the Academy of Natural Sciences of Philadelphia, the North Carolina State Museum, the National Museum of Natural History (Smithsonian), the Yale Peabody Museum, the Illinois Natural History Survey (Mollusk Collection), and the University of Michigan Museum of Zoology) but none had records from Nebraska. The principal sources for species records were three historic studies (Tryon 1868, Aughey 1877, Walker 1906) and two reviews of regional fossils, which also include recent collections of live snails (Hibbard and Taylor 1960, Taylor 1960). More recent literature also provided records (Freeman and Perkins 1992, Freeman and Perkins 1997, Wu 2004–2005). The collections from the University of Nebraska State Museum (UNSM) are from a variety of collectors and are uncatalogued. Some historic and museum records contain a listing from a river or city without details. Each such listing was counted as a single record in the Nebraska snail database created.

I follow the taxonomy given in Johnson *et al.* (2013) with a few revisions. I use the two-genus system proposed by Wethington and Lydeard (2007) for the Physidae. Lumping or taxonomic changes of species were based primarily on the following studies: Planorbidae (Hubendick and Rees 1955), Physidae (Dillon and Wethington 2004, Wethington and Lydeard 2007), Lymnaeidae (Baker 1911, Hubendick 1951), Ancylidae (Walther *et al.* 2006, Walther *et al.* 2010), and Pleuroceridae (Goodrich 1939). Once I condensed species based on synonyms, I evaluated records for the likelihood of presence in Nebraska based on Burch (1989) and regional literature from the surrounding states of Kansas (Leonard 1959), Wyoming (Beetle 1989), South Dakota (Stephen and Winkler 2007), Iowa (Stewart 2006), Missouri (Wu *et al.* 1997), and Colorado (Harrold and Guralnick 2010).

RESULTS

My literature and museum survey returned over 80 nominal species from 296 records of freshwater snails within Nebraska. The database created is available as a MS Excel spreadsheet and can be found as supplemental material online at: 10.4003/006.033.0103.s1. Analysis, primarily by lumping species names due to systematic revision, reduces that number to a more realistic 31 species, including one non-indigenous species (Table 1). Discussed below, but not included in the table are species I suspect of being misidentifications placed within Nebraska in error. For each species the synonyms used in Nebraska studies, locality and regional presence is provided. County distribution maps are provided for species when this information is known (Figs. 2–5). Records that had no specific county locality are not mapped.

Table 1. Thirty-one species of freshwater gastropod recently or historically present in Nebraska. The non-indigenous *Bellamya chinensis* appears as a relative newcomer.

Family	Species	No. Records
Amnicolidae	*Amnicola limosus*	5
Hydrobiidae	*Cincinnatia integra*	1
Hydrobiidae	*Probythinella emarginata*	1
Lymnaeidae	*Galba bulimoides*	4
Lymnaeidae	*Galba humilis*	12
Lymnaeidae	*Lymnaea stagnalis*	1
Lymnaeidae	*Stagnicola caperata*	8
Lymnaeidae	*Stagnicola catascopium*	4
Lymnaeidae	*Stagnicola elodes*	23
Physidae	*Aplexa elongata*	18
Physidae	*Physa acuta*	38
Physidae	*Physa gyrina*	63
Physidae	*Physa jennessi*	3
Physidae	*Physa pomilia*	15
Planorbidae	*Ferrissia fragilis*	1
Planorbidae	*Ferrissia rivularis*	6
Planorbidae	*Gyraulus circumstriatus*	5
Planorbidae	*Gyraulus crista*	1
Planorbidae	*Gyraulus deflectus*	3
Planorbidae	*Gyraulus parvus*	5
Planorbidae	*Helisoma anceps*	7
Planorbidae	*Planorbella trivolvis*	12
Planorbidae	*Planorbula armigera*	3
Planorbidae	*Promenetus exacuous*	5
Planorbidae	*Promenetus umbilicatellus*	5
Pleuroceridae	*Pleurocera acuta*	1
Pomatiopsidae	*Pomatiopsis lapidaria*	1
Valvatidae	*Valvata sincera*	2
Valvatidae	*Valvata tricarinata*	7
Viviparidae	*Bellamya chinensis*	1
Viviparidae	*Campeloma decisum*	10

Species suspected of being misidentifications are also not included on maps.

Amnicolidae

Confusion among species in this family, the Hydrobiidae, and the Pomatiopsidae, all of which contain tiny to small conical snails, is common (Burch 1989). The family Amnicolidae was often placed as a subfamily of Hydrobiidae, however, recent molecular work separates the families into separate clades (Wilke *et al.* 2001, Bouchet and Rocroi 2005) but historical works on these families may contain overlapping identifications.

Amnicola limosus (Say, 1817). Synonym: *Amnicola limosa* (Say, 1817). This snail was listed by two studies (Aughey 1877, Walker 1906) from the Bow, Elkhorn, Blue, and Nemaha rivers, and the city of Lincoln. This species appears widespread

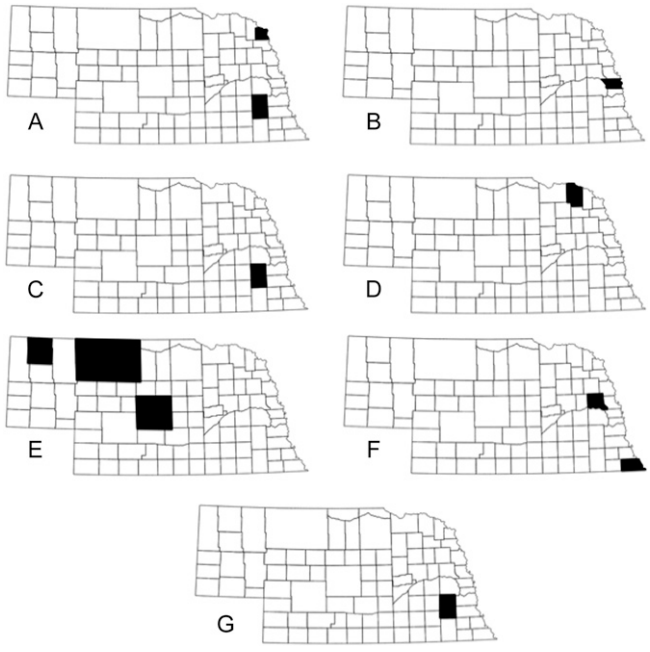

Figure 2. Distributions for **A,** *Amnicola limosus,* **B,** *Cincinnatia integra,* **C,** *Probythinella emarginata*, **D,** *Valvata sincera*, **E**, *Valvata tricarinata*, **F,** *Campeloma decisum*, and **G,** *Bellamya chinensis*. Shading indicates counties where taxa have been found.

regionally being recorded from Wyoming, Missouri, Iowa, South Dakota, and Colorado (Beetle 1989, Wu *et al.* 1997, Stewart 2006, Stephen and Winkler 2007, Harrold and

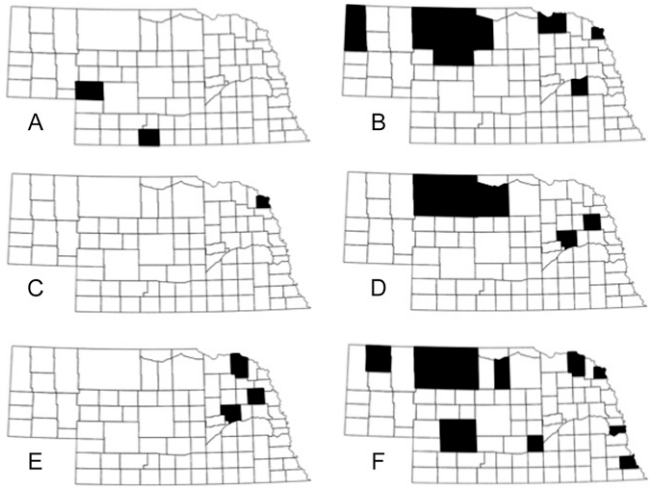

Figure 3. Distributions for **A,** *Galba bulimoides*, **B,** *Galba humilis*, **C,** *Lymnaea stagnalis,* **D,** *Stagnicola caperata*, **E**, *Stagnicola catascopium*, and **F,** *Stagnicola elodes*. Shading indicates counties where taxa have been found.

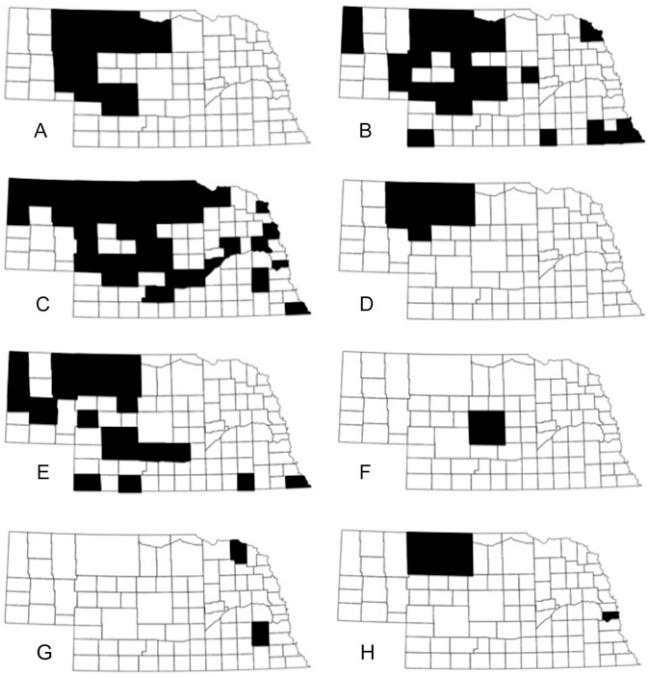

Figure 4. Distributions for **A,** *Aplexa elongata*, **B,** *Physa acuta*, **C,** *Physa gyrina*, **D,** *Physa jennessi*, **E**, *Physa pomilia*, **F,** *Ferrissia fragilis*, **G,** *Ferrissia rivularis*, and **H,** *Gyraulus deflectus*. Shading indicates counties where taxa have been found.

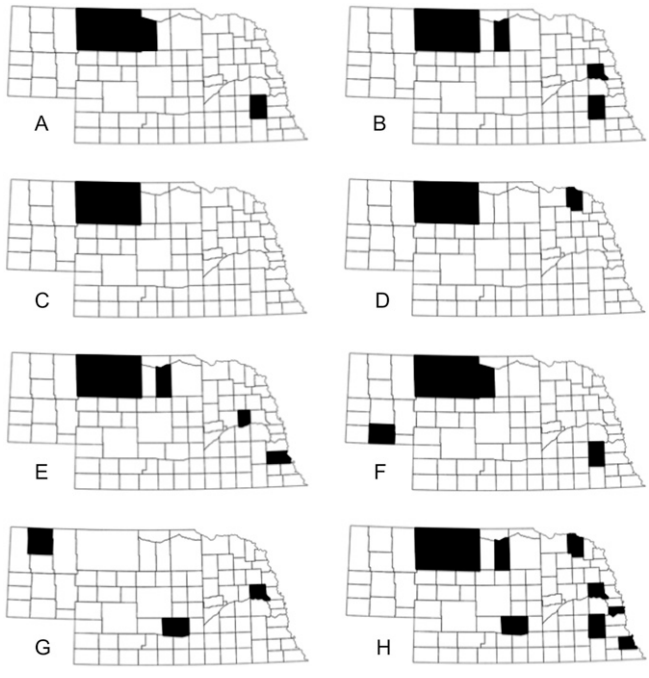

Figure 5. Distributions for **A,** *Gyraulus circumstriatus,* **B,** *Gyraulus parvus*, **C,** *Gyraulus crista*, **D,** *Planorbula armigera*, **E**, *Promenetus exacuous,* **F,** *Promenetus umbillicatellus,* **G,** *Helisoma anceps*, and **H,** *Planorbella trivolvis*. Shading indicates counties where taxa have been found.

Guralnick 2010). Kansas also has historic records but recent surveys failed to locate this species prompting a tentative listing of it being extirpated (Angelo *et al.* 2002). A total of five records from two Nebraska counties are listed in the database.

Lyogyrus granum (Say, 1822). Synonym: *Amnicola granum* (Say, 1822). This tiny snail was recorded only from the Nemaha River (Aughey 1877). It has not been reported from other states in this region (Leonard 1959, Wu *et al.* 1997, Stewart 2006, Stephen and Winkler 2007, Harrold and Guralnick 2010). Burch (1989) does not consider its range extending into this region and I suspect this species of being a misidentification in the historic literature. The database contains a single record of this species.

Hydrobiidae

Cincinnatia integra (Say, 1821). Synonym: *Amnicola cincinnatiensis* (Anthony 1865). This tiny snail is recorded as being present in Omaha (Tryon 1868). Found regionally in Kansas and Iowa (Leonard 1959, Stewart 2006). This species is widespread in eastern and northern North America (Burch 1989). The Nebraska snail database contains a single record of this species.

Probythinella emarginata (Küster, 1842). Synonym: *Probythinella lacustris* (Baker 1928). A single study lists this species from Salt Creek in Lincoln (Hibbard and Taylor 1960). Regionally they are found to the east in Missouri and Iowa (Wu *et al.* 1997, Stewart 2006). The database contains a single record of this species.

Lymnaeidae

Historic studies list twenty species of right-handed pond snail within Nebraska. I reduce the number of species expected to be present in Nebraska to eight by lumping synonyms primarily following Baker (1911) and Hubendick (1951). In addition I suspect two species listed herein as being misidentifications.

Acella haldemani (Binney, 1867). Synonym: *Limnaea gracilis* (Jay, 1839). This species is listed from the Bow and Elkhorn rivers (Aughey 1877). Regionally its range is considered to include Iowa but no regional records are evident (Stewart 2006). My database contains two records of this species. Though the thin elongate morphology of this species seems unmistakable this species is out of range in Nebraska (Burch 1989) and I consider this species record erroneous.

Galba bulimoides (Lea, 1841). Synonyms: *Lymnaea bulimoides* (Lea, 1841), *Lymnaea cockerelli* (Pilsbry and Ferriss, 1906), *Stagnicola bulimoides techella* (Haldeman, 1867), *Stagnicola cockerelli* (Pilsbry and Ferriss, 1906). I follow Baker (1911) in treating *G. techella* and *G. cockerelli* as subspecies of

G. bulimoides. This small snail is listed in Nebraska by a single study and two records are in the natural history collection at Harvard (Hibbard and Taylor 1960, MCZ). Regional listings are from Kansas, Wyoming, Missouri, Iowa and Colorado (Leonard 1959, Beetle 1989, Wu *et al.* 1997, Stewart 2006, Harrold and Guralnick 2010). The database contains a total of four records from two counties.

Galba humilis (Say, 1822). Synonyms: *Fossaria obrussa* (Say, 1825), *Fossaria dalli* (Baker, 1907), *Limnaea desidiosa* (Say, 1834), *Limnaea humilis* (Say, 1822). I lump *Fossaria dalli*, *Fossaria obrussa*, and *Limnaea desidiosa* under *G. humilis* following Baker (1911) and Hubendick (1951). Historic records of this species include a listing of "all the streams of Nebraska" (Aughey 1877) and a single county record (Walker 1906). More recent records include several western Nebraska streams and the Niobrara River (Taylor 1960, Freeman and Perkins 1997). In addition the University of Nebraska State Museum houses shells of this species from the Nebraska towns of Sidney, Chambers, and Ashland, as well as Pioneers Park within Lancaster County. Regional records for *G. humilis* include Kansas, Wyoming, Missouri, Iowa, South Dakota and Colorado (Leonard 1959, Beetle 1989, Wu *et al.* 1997, Stewart 2006, Stephen and Winkler 2007, Harrold and Guralnick 2010). The Nebraska snail database contains a total of 12 records from seven counties.

Lymnaea stagnalis (Linnaeus, 1758). Synonym: *Limnaea stagnalis* (Linnaeus, 1758). This large distinct species is listed by one study from a single locality, Smith's Lake in Dakota County (Aughey 1877). Regionally this species is more common being found in Wyoming, Iowa, South Dakota, and Colorado (Beetle 1989, Stewart 2006, Stephen and Winkler 2007, Harrold and Guralnick 2010). This species accounts for a single database record.

Pseudosuccinea columella (Say, 1817). Synonym: *Limnaea columella* (Say, 1817). This medium sized snail is listed from a single specimen from one locality, Smith's Lake in Dakota County (Aughey 1877). None of the references from surrounding states include this species with the exception of their presence in the Ozark lowlands in Southeast Missouri (Wu *et al.* 1997). I suspect this species of being erroneously placed within Nebraska.

Stagnicola caperata (Say, 1829). Synonym: *Lymnaea caperata* (Say, 1829). Records of this species are from the western part of the state (Walker 1906, Taylor 1960) and include an undated museum record (MCZ). Regional records are from Wyoming, Missouri, Iowa, South Dakota, and Colorado (Beetle 1989, Wu *et al.* 1997, Stewart 2006, Stephen and Winkler 2007, Harrold and Guralnick 2010). The database contains eight records from five counties.

Stagnicola catascopium (Say, 1816). Synonyms: *Limnaea catascopium* (Say, 1816), *Lymnaea emarginata* (Say, 1821), *Limnaea pallida* (Adams, 1840), *Limnaea sumassi* (Baird, 1863). This species was recorded from the Bow River (Aughey 1877) and Platte City (MCZ). Regionally records are from Wyoming and Iowa (Beetle 1989, Stewart 2006). Burch (1989) does not include Nebraska in the range of this species but includes Iowa and South Dakota. The Nebraska snail database contains four records of this species from two counties.

Stagnicola elodes (Say, 1821). Synonyms: *Lymnaea elodes* (Say, 1821), *Lymnaea palustris* (Müller, 1774), *Lymnaea reflexa* (Say, 1821), *Limnaea haydeni* (Lea, 1858). I lump *Lymnaea haydeni, L. reflexa and L. palustris*, into *Stagnicola elodes* following Baker (1911) and Hubendick (1951). All three primary historical studies, a natural history collection, and recent studies have records of this species in Nebraska (Tryon 1868, Aughey 1877, Walker 1906, MCZ, Freeman and Perkins 1992, Freeman and Perkins 1997). In addition the Nebraska State Museum collection houses uncatalogued shells of this species. Regionally it is common with records from Wyoming, Missouri, Iowa, South Dakota and Colorado (Beetle 1989, Wu *et al.* 1997, Stewart 2006, Stephen and Winkler 2007, Harrold and Guralnick 2010). Twenty three records of this species from ten counties are in the database.

Physidae

I follow the recommendation of Dillon *et al.* (2006), following Walker (1906) and more recent molecular work (Wethington and Lydeard 2007), and use a two-genus system for this family. The genera used are *Physa* (Draparnaud, 1801) and *Aplexa* (Fleming, 1820).

Aplexa elongata (Linnaeus, 1758). Synonyms: *Aplexa hypnorum* (Linnaeus, 1758), *Bulla hypnorum* (Linnaeus, 1758), *Bulinus distortus* (Haldeman, 1840). This large snail is listed historically by two authors from "all quiet waters of the state" and Cherry County (Aughey 1877, Walker 1906). More recent authors list this species from several western Nebraska locations including the Middle Loup River and roadside ditches (Taylor 1960, Wu 2004–2005). It is found regionally in Wyoming, Iowa, South Dakota, and Colorado (Beetle 1989, Stewart 2006, Stephen and Winkler 2007, Harrold and Guralnick 2010) but is not listed by Leonard (1959) from Kansas. This species is common in northern North America (Burch 1989). I have a total of 18 records from nine counties in the database.

Physa acuta (Draparnaud, 1805). Synonyms: *Physa anatine* (Lea, 1864), *Physa heterostropha* (Say, 1817), *Physa halei* (Lea, 1864), *Physa virgata* (Gould, 1855), *Physa whitei* (Lea, 1864). I follow Burch (1989) and Wethington and Lydeard (2007) in lumping five historically listed species into *Physa acuta*. This medium-sized snail is listed by two historical studies from "all streams from Nebraska" and the Roca and Platte rivers (Aughey 1877, Walker 1906). More recent studies and museum collections contain records from rivers and streams in western Nebraska but also include Nuckoll and

Richardson counties in eastern Nebraska (Taylor 1960, Wu 2004–2005, MCZ). This snail is abundant in the region, being found in Kansas, Wyoming, Missouri, Iowa, and Colorado (Leonard 1959, Beetle 1989, Wu *et al.* 1997, Stewart 2006, Harrold and Guralnick 2010). A total of 38 records from 25 counties within the database suggest this species is common.

Physa gyrina (Say, 1821). Synonyms: *Physella gyrina* (Say, 1821), *Physa ancillaria* (Say, 1825), *Physa gouldi* (Clench, 1935), *Physa lordi* (Baird, 1863), *Physa saffordi* (Lea, 1864), *Physa sayi* (Tappan, 1838), *Physa virginea* (Gold, 1847), *Physa warreniana* (Lea, 1864). I follow Wethington and Lydeard (2007) in lumping a large number of nominal species under *Physa gyrina*. This medium to large snail is recorded by the earliest historic studies from locations in eastern Nebraska (Aughey 1877, Walker 1906). More recent and museum records are from western Nebraska (Taylor 1960, Wu 2004–2005, MCZ). Recent studies also record this species from 22 sites along the Niobrara and Platte rivers (Freeman and Perkins 1992, 1997). Specimens of this species are also found in collections of the University of Nebraska State Museum. It is ubiquitous throughout North America (Burch 1989) and throughout the region with records from Wyoming, Missouri, Iowa, South Dakota, and Colorado (Beetle 1989, Wu *et al.* 1997, Stewart, 2006, Stephen and Winkler 2007, Harrold and Guralnick 2010). The database contains 63 records from 28 counties.

Physa jennessi (Dall, 1919). Synonym: *Physa skinneri* (Taylor, 1954). I use the oldest nomen in North America, *Physa jennessi*, described by Dall (1919) following Wethington and Lydeard (2007). This small species is not listed in any of the major historic studies examined and the only records come from the western Nebraska counties of Cherry, Grant, and Sheridan (Wu 2004–2005). This species is reported as widespread further north in North Dakota (Cvancara 1983). Listings from adjacent states are only from Wyoming (Beetle 1989) but also include the possibility, not confirmed, of their presence within the Iowa prairie potholes (Stewart 2006). The database contains only three records of this species from three counties.

Physa pomilia (Conrad, 1834). This small snail is not listed in any of the principal historical studies examined here. The records of this species come from collections of the University of Colorado Museum (Wu 2004–2005). Identification of this species is problematic as it is morphologically nearly identical to *Physa acuta.* This species is listed regionally only to the south and east in Kansas (Wu and Liu 2006) and Missouri (Wu *et al.* 1997). The database contains 15 records of this species from 13 counties.

Planorbidae

I follow Burch (1989) and Hubendick and Rees (1955) and eliminate two listed by Aughey (1877); *Gyraulus albus* (O. F. Müller, 1774) and *Planorbis glabratus* (Say, 1818). Neither species is historically found in the U.S.A. although *P. glabratus* is a recent invader to Florida (Burch 1989). The systematics of the limpets has benefited from recent molecular phylogenetic work (Walther *et al.* 2006, Walther *et al.* 2010). These analyses leave just three species of limpets in the U.S.A. all of which have records from Nebraska.

Ferrissia fragilis (Tryon, 1863). Synonym: *Ancylus shimekii* (Pilsbry, 1890). This small limpet is listed by a single study with a single locality in Nebraska, the town of Colloway (Walker 1906). Regional records of this species are found from Kansas, Missouri, Iowa, and Colorado (Leonard 1959, Wu *et al.* 1997, Stewart 2006, Harrold and Guralnick 2010).

Ferrissia rivularis (Say, 1817). Synonyms: *Ancylus rivularis* (Say, 1817), *Ancylus caurinus* (Binney, 1865). I follow Basch (1963) in lumping *Ancylus caurinus* under *Ferrissia rivularis.* This small limpet was listed by two historical studies (Aughey 1877, Walker 1906). Aughey (1877) lists them from Logan, Elkhorn, Nemaha, Blue, and Bow Rivers. Walker (1906) lists one locality, Dead Man's Run, which runs through Lincoln, Nebraska. Regional listings are from Wyoming, Missouri, Iowa, and Colorado (Beetle 1989, Wu *et al.* 1997, Stewart 2006, Harrold and Guralnick 2010). The Nebraska database contains six records from two counties.

Gyraulus circumstriatus (Tyron, 1866). Records for this tiny snail include Cherry, Brown, and Lancaster counties (Taylor 1960, Hibbard and Taylor 1960). Regional records are from Kansas, Wyoming, Iowa, and Colorado (Leonard 1959, Beetle 1989, Stewart 2006, Harrold and Guralnick 2010). The database contains five records from three counties.

Gyraulus crista (Linnaeus, 1758). Synonym: *Armiger crista* (Linnaeus, 1758). This tiny snail is recorded from a single site from a creek in Cherry County (Taylor 1960). Regionally this snail is listed just from Wyoming (Beetle 1989). Others records exist from further north in North Dakota (Cvancara 1983).

Gyraulus deflectus (Say, 1824). Synonym: *Planorbis deflectus* (Say, 1824). This small snail is recorded historically from "all streams in eastern Nebraska" (Aughey 1877). More recent records are from two localities in western Nebraska (Taylor 1960, Freeman and Perkins 1992). Regional records are found from Missouri and Iowa to the east (Wu *et al.* 1997, Stewart 2006). The database contains three records from two specific counties.

Gyraulus parvus (Say, 1817). Synonym: *Planorbis parvus* (Say, 1817). This small snail was recorded by Aughey (1877) and Walker (1906), from eastern Nebraska, and Taylor (1960), from western Nebraska. It is abundant in the region with records from Kansas, Wyoming, Missouri, Iowa, and Colorado (Leonard 1959, Beetle 1989, Wu *et al.* 1997, Stewart 2006, Harrold and Guralnick 2010). A total of nine records from five counties are in my database.

Helisoma anceps (Menke, 1830). Synonym: *Planorbis bicarinatus* (Say, 1819). This large snail is listed by all primary historical studies from eastern Nebraska and Cheyenne County (Tryon 1868, Aughey 1877, Walker 1906). This species was also found recently along the Niobrara River (Freeman and Perkins 1997). The Museum of Comparative Zoology contains two undated records and uncatalogued specimens are in collections of the University of Nebraska State Museum. Regionally this species is common in Kansas, Wyoming, Missouri, Iowa, South Dakota, and Colorado (Leonard 1959, Beetle 1989, Wu *et al.* 1997, Stewart 2006, Stephen and Winkler 2007, Harrold and Guralnick 2010). Though apparently abundant due to Aughey (1877) listing them from "all streams of eastern Nebraska" the Nebraska snail database contains just seven records from four counties.

Planorbella campanulata (Say, 1821). This large snail is recorded from the Bow River (Aughey 1877). It is reported from Iowa within this region but regional listings from other states are absent (Stewart 2006). The range of this species does not specifically include Nebraska (Burch 1989). Nebraska is either at the edge of its range or, as I suspect, it has been misidentified in the historic literature. The database contains a single record of this species.

Planorbella multivolvis (Case, 1847). This species is listed from a single historic study from the Bow River (Aughey 1877). *Planorbella multivolvis* is not listed as being found in the surrounding states of Kansas, South Dakota, Iowa, or Colorado (Leonard 1959, Stephen and Winkler 2007, Stewart 2006, Harrold and Guralnick 2010). I suspect this species of being erroneously placed within this region. One author thinks this species is now extinct (Bogan 2000). On the other hand this species has been treated as a subspecies of *Planorbella campanulata* (Say, 1821) (Clarke 1973, Burch 1989).

Planorbella trivolvis (Say, 1817). Synonyms: *Helisoma trivolvis* (Say, 1816), *Planorbis trivolvis* (Say, 1817). This large and common snail is recorded by all primary historical studies from eastern Nebraska and Dakota County (Tryon 1868, Aughey 1877, Walker 1906). It is represented in the UNSM and MCZ collections. Later records include western Nebraska and the Platte River (Taylor 1960, Freeman and Perkins 1992). It is widely distributed and abundant in adjacent states (Leonard 1959, Beetle 1989, Wu *et al.* 1997, Stewart 2006, Stephen and Winkler 2007, Harrold and Guralnick 2010). It is considered widespread in North America (Burch 1989). The database contains 12 records from nine counties.

Laevapex fuscus (Adams, 1841). Synonym: *Ancylus diaphanous* (Haldeman, 1841). This limpet was recorded from a single historical study from the Bow River (Aughey 1877). Regionally this species is listed from Missouri and Iowa (Wu *et al.* 1997, Stewart 2006). Burch (1989) considers Iowa the western edge of its range. Given the historic taxonomic uncertainty among limpets (Walther *et al.* 2006) and Nebraska being outside of its range I suspect this species of being misidentified.

Planorbula armigera (Say, 1821). Synonym: *Segmentina armigera* (Say, 1821). This small snail is recorded from the Bow, Loup, and Niobrara rivers (Aughey 1877, Taylor 1960). Regionally it is recorded from Missouri and Iowa (Wu *et al.* 1997, Stewart 2006). Burch (1989) lists this species specifically from Nebraska. The database contains three records of this species from two counties.

Promenetus exacuous (Say, 1821). Synonym: *Planorbis exacutus* (Say, 1821). This small snail is listed from "all streams in eastern Nebraska" (Aughey 1877) and four specific counties (Taylor 1960, Hibbard and Taylor 1960). This snail is found regionally in Kansas, Wyoming, Iowa, South Dakota and Colorado (Leonard 1959, Beetle 1989, Stewart 2006, Stephen and Winkler 2007, Harrold and Guralnick 2010). The database contains five records of this species.

Promenetus umbilicatellus (Cockerell, 1887). Records for this tiny snail are from Cherry, Brown, Cheyenne, and Lancaster counties (Hibbard and Taylor 1960, Taylor 1960). Regional records are from Kansas, Wyoming, Iowa, and Colorado (Leonard 1959, Beetle 1989, Stewart 2006, Harrold and Guralnick 2010). Four records of this species are within the database.

Pleuroceridae

Historically five species in this family are recorded in Nebraska (Aughey 1877). Goodrich (1939) in analyzing these records considered one species, *Leptoxis carinata* (Bruguiére, 1792), clearly an error as it is found only along the eastern seaboard. I lump the remaining four species into two following Goodrich (1939) and Tyron (1873).

Elimia semicarinata (Say, 1829). Synonyms: *Goniobasis larveaformis* (Lea, 1841), *Goniobasis occulta* (Anthony, 1860), *Goniobasis semicarinata* (Say, 1829). Records are from the Big Blue and Nemaha rivers (Aughey 1877). Listings of this species are not found in adjacent states. The database contains four records from two rivers but I suspect this species is a misidentification.

Pleurocera acuta (Rafinesque, 1831). Synonym: *Pleurocera neglectum* (Anthony, 1860). I follow the taxonomy in Johnson *et al.* (2013) although the Pleuroceridae express ecophenotypic plasticity and it may be that *Pleurocera canaliculata* (Say, 1821) is conspecific to *Pleurocera acuta* (Dillon *et al.* 2013). This species is listed only by one study (Aughey 1877). Regionally listings are from Kansas, Missouri, and Iowa (Leonard 1959, Wu *et al.* 1997, Stewart 2006). The database contains a single record from the Big Blue River without more specific locality and so the county distribution is not mapped.

Pomatiopsidae

There is confusion between snails of the families Hydrobidae and Pomatiopsidae, as mentioned earlier, because these snails are similar in appearance and very small (Burch 1989). This amphibious group is often found above the water line and, therefore, sometimes considered terrestrial rather than aquatic. A single species within this family appears in Nebraska.

Pomatiopsis lapidaria (Say, 1817). This tiny snail is listed from eastern Nebraska along the Missouri bluffs (Aughey 1877). Regionally this species is recorded from Kansas, Missouri, and Iowa but is not common (Leonard 1959, Wu *et al.* 1997, Stewart 2006). The database contains a single record of this species without specific locality data and so its county distribution is not mapped.

Valvatidae

Nebraska is at the southern edge of the distribution for this family (Burch 1989). I retain both species recorded historically.

Valvata sincera (Say, 1824). Aughey (1877) reported this tiny species from the Bow and Elkhorn rivers. Although *Valvata tricarinata* is widespread, *V. sincera* is less so and is a species of conservation interest in some regions (Smith 1984). It is listed in Wyoming, Iowa, and Colorado but is considered rare (Beetle 1989, Stewart 2006, Harrold and Guralnick 2010). Little other information exists for this species. The database contains two records of this species with only one specific county locale.

Valvata tricarinata (Say, 1817). This tiny snail was recorded in only one historical work from the Bow and Elkhorn rivers and was considered rare at the time (Aughey 1877). However, this species was found recently in a study of the Niobrara River (Freeman and Perkins 1997). It was also abundant enough in a western Nebraska lake for its use in studies of reproductive biology (Gugler 1969). It is a widespread snail in North America and is a common species in Iowa and South Dakota (Stewart 2006, Stephen and Winkler 2007). My database contains seven records from three counties.

Viviparidae

Historical records from Nebraska include five species within this family (Aughey 1877). However, Burch considers only *Campeloma decisum* (Say, 1817) as being in the region (Burch 1989). In addition Dillon *et al.* (2006) finding no consistent distinctions among the many nominal species of *Campeloma* (Rafinesque, 1819) reduces them to just one, *Campeloma decisum*, across North America. This assessment seems valid, and I follow it here. The other species listed here is a non-indigenous snail not reported in Nebraska until recently.

Bellamya chinensis (Reeve, 1863). Synonyms: *Cipangopaludina chinensis* (Gray, 1834), *Viviparus malleatus* (Reeve, 1863). This large non-indigenous Asian snail first invaded North America in the late 1800s and is now found in most U.S. States (Jokinen 1982). In Nebraska it is reported from the southeast of the state (Chaine *et al.* 2012). There is a single Nebraska record of this species from Lancaster County.

Campeloma decisum (Say, 1817). Synonyms: *Melantho decisa* (Say, 1817), *Melantho ponderosa* (Say, 1829), *Vivipara contectoides* (Binney, 1865), *Vivipara integra* (Say, 1829), *Vivipara intertexta* (Say, 1829), *Vivipara subpurpurea* (Say, 1829). This large snail has been recorded in "all the streams of Nebraska" (Aughey 1877). Typically it is found buried in river mud, which makes detection difficult (Burch 1989). Regionally this species is listed from Kansas, Missouri, and Iowa (Leonard 1959, Wu *et al.* 1997, Stewart 2006). Ten records from four rivers and two specific counties are in the database.

DISCUSSION

Systematic research reduces the number of species of freshwater snails in North America. In like form I have reduced the number of species of freshwater snail expected to be present in Nebraska. Historic and recent records provide 296 records and over 80 species names of freshwater gastropods in the state. By lumping species synonyms and excluding invalid records I reduce this to 31 species of freshwater snail within Nebraska (Table 1).

My list differs in a number of ways from that of a recent study listing the conservation status of all species of freshwater snail in Canada and the United States (Johnson *et al.* 2013). Amid taxonomic uncertainties I follow a conservative approach to elevating subspecies or nominal species to species status and, thus, *Galba cockerelli* (Pilsbry and Ferriss, 1906) and *Galba techella* (Haldeman, 1867) (the later listed in Nebraska studies as *Stagnicola bulimoides techella*) are lumped with *Galba bulimoides*. I also follow Baker (1911) in lumping *Galba dalli* (Baker 1907), *Galba modicella* (Say, 1825) and *Galba obrussa* (Say, 1825) into *Galba humilis*. I find no Nebraska records for two species of Lymnaeidae, *Galba parva* (Lea, 1841) and *Galba rustica* (Lea, 1841), listed in Johnson *et al.* (2013). I place *Physella virgata* (Gould, 1855) under *Physa gyrina* following Wethington and Lydeard (2007). My list contains seven species not included in Johnson *et al.* (2013); *Stagnicola catascopium*, *Lymnaea stagnalis*, *Physa acuta*, *Gyraulus crista*, *Pomatiopsis lapidaria*, *Valvata sincera* and the non-indigenous *Bellamya chinensis*. Among these species only *Physa acuta* appears abundant within the state.

Based on regional and known ranges I suspect several species discussed here of being placed within Nebraska in

error and I do not include them on my final list (Table 1). Suspected species are *Acella haldemani*, *Gyraulus albus*, *Planorbis glabratus*, *Laevapex fuscus, Pseudosuccinea columella, Planorbella campanulata*, *Planorbella multivolvis*, *Lyogyrus granum*, *Elimia semicarinata*, and *Leptoxis carinata* discussed under the Pleuroceridae. Aughey (1877) is the only author to list each of these species, most with a single record. Aughey's work in other areas has been criticized for not being reliable (Bolick 1993, Hoke 2000) but it is difficult to be certain that these species are not present in Nebraska when up-to-date sampling is lacking. Thus, this list acts as an incentive for current surveys and further analysis. Species richness of Nebraska freshwater snails is lower than that of adjacent Iowa, which was recently reviewed and shown to house 47 species historically (Stewart 2006). Though not as diverse as Iowa, Nebraska's 31 freshwater snail species include members from nine families. The majority of species (22) in Nebraska are pulmonate snails from the families Lymnaiedae, Physidae, and Planorbidae. At least four species appear to be abundant throughout Nebraska based on the number of historical listings and county distribution. These species are *Stagnicola elodes*, *Aplexa elongata*, *Physa gyrina*, and *Physa acuta*. All of these snails are pulmonates within the Heterobranchia.

Based on the number of records and localities I suspect eight species of being rare in Nebraska; *Cincinnatia integra*, *Probythinella emarginata*, *Lymnaea stagnalis*, *Ferrissia fragilis*, *Gyraulus crista*, *Pleurocera acuta*, *Pomatiopsis lapidaria*, and *Valvata sincera*. Some species, for example *Lymnaea stagnalis*, though rare in Nebraska appear to be at the edge of their range and more common in the broader region.

Though a conservation assessment of freshwater gastropods of North America has recently been completed (Johnson *et al.* 2013) the lack of attention to freshwater gastropods in general reduces the ability to provide worthwhile analysis of each species. In addition, the absence of recent data means rare species are difficult to distinguish from species erroneously listed. It is clear that field surveys are needed to clarify species in need of conservation and validate presence or extirpation.

ACKNOWLEDGMENTS

I thank Patricia Freeman and Dan Fogell for help in editing earlier versions of this manuscript. Thanks also to the anonymous reviewers who improved this manuscript in a variety of ways. Thanks to Rob Dillon for reviewing this manuscript and also, through the Freshwater Gastropods of North America project, creating the impetus for this study.

LITERATURE CITED

Angelo, R. T., M. S. Cringan, and J. E. Fry 2002. Distributional revision and new and amended occurrence records for prosobranch snails in Kansas. *Transactions of the Kansas Academy of Science* **105**: 246–57.

Aughey, S. 1877. Catalogue of the land and fresh-water shells of Nebraska. *Bulletin of the U.S. Geological and Geographical Survey of the Territories*. (Hayden Survey) **3**: 697–704.

Baker, F. C. 1911. *The Lymnaeidae of North and Middle America*. The Chicago Academy of Sciences, Chicago, Illinois.

Basch, P. F. 1963. A review of the recent freshwater limpet snails of North America (Mollusca: Pulmonata). *Bulletin of the Museum of Comparative Zoology at Harvard College* **129**: 399–461.

Beetle, D. E. 1989. Checklist of recent Mollusca of Wyoming, U.S.A. *Great Basin Naturalist* **49**: 637–645.

Bouchet, P., and J.-P. Rocroi. 2005. Classification and nomenclature of gastropod families. *International Journal of Malacology* **47**: 1–397.

Bogan, A. E. 2000. *Planorbella multivolvis*. *In*: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. Available at: www.iucnredlist.org 18 July 2012.

Bolick, M. R. 1993. Samuel Aughey, Jr.: The controversial first director of the University of Nebraska State Museum. *Museum Notes University of Nebraska State Museum* **84**: 1–4.

Brown, K. M. 2001. Mollusca: Gastropoda. *In*: J. H. Thorp, and A. P. Covich, eds., *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, San Diego, California. Pp. 297–329.

Burch, J. B. 1989. *North American Freshwater Snails*. Malacological Publications, Hamburg, Michigan.

Chaine N. M., C. R. Allen, K. A. Fricke, D. M. Haak, M. L. Hellman, R. A. Kill, K. T. Nemec, K. L. Pope, N. A. Smeenk, B. J. Stephen, D. R. Uden, K. M. Unstad, and A. E. VanderHam. 2012. Population estimate of Chinese mystery snail (*Bellamya chinensis*) in a Nebraska reservoir. *Bioinvasion Records* **1**: 283–287.

Chapman, S. S., J. M. Omernik, J. A. Freeouf, D. G. Huggins, J. R. McCauley, C. C. Freeman, G. Steinauer, R. T. Angelo, and R. L. Schlepp. 2001. Ecoregions of Nebraska and Kansas (color poster with map, descriptive text, summary tables, and photographs). U.S. Geological Survey (map scale 1:1,950,000), Reston, Virginia.

Clarke, A. H. 1973. The freshwater mollusks of the Canadian Interior Basin. *Malacologia* **13**: 1–509.

Cvancara, A. 1983. *Aquatic mollusks of North Dakota*. Report of Investigation No. 78. North Dakota Geological Survey. Kaye's Inc., Fargo, North Dakota.

Dall, W. H. 1919. *The Mollusca of the Arctic Coast of America collected by the Canadian Arctic Expedition West from Bathurat Inlet, with an appended report on a collection of Pleistocene fossil Mollusca*. Report of Canadian Arctic Expedition 1913–1918 No. 8A. F. A. Acland, Ottawa, Canada.

Dillon, R. T. 2000. *The Ecology of Freshwater Molluscs*. Cambridge University Press, Cambridge, England.

Dillon, R. T., S. J. Jacquemin, and M. Pyron. 2013. Cryptic phenotypic plasticity in populations of the freshwater prosobranch snail, *Pleurocera canaliculata*. *Hydrobiologia* **709**: 117–27.

Dillon, R. T., B. T. Watson, T. W. Stewart, and W. K. Reeves. 2006. The freshwater gastropods of North America. Available at: http://www.fwgna.org 28 April 2014.

Dillon, R. T. and A. R. Wethington. 2004. No-choice mating experiments among six nominal taxa of the subgenus *Physella* (Basommatophora: Physidae). *Heldia* **6**: 69–78.

Dillon, R. T., A. R. Wethington, J. M. Rhett, and T. P. Smith. 2002. Populations of the European freshwater pulmonate *Physa acuta* are not reproductively isolated from American *Physa heterostropha* or *Physa integra*. *Invertebrate Biology* **121**: 226–234.

EPA, 2014. U. S. Environmental Protection Agency. Surf your watershed. Available at: http://cfpub.epa.gov/surf/state.cfm?statepostal=NE 28 April 2014.

Freeman, P. W. and Perkins, K. 1992. *Survey of Mollusks of the Platte River: Final Report*. U.S. Fish and Wildlife Service. Grand Island, Nebraska.

Freeman, P. W. and Perkins, K. 1997. *Survey of Mollusks of the Niobrara River: Final Report*. U.S. Fish and Wildlife Service. Grand Island, Nebraska.

Goodrich, C. 1939. Pleuroceridae of the St. Lawrence River Basin. *Occasional Papers of the Museum of Zoology* **404**: 1–4.

Gugler, C. 1969. Notes on *Valvata tricarinata* from Central Nebraska. *American Malacological Union Inc. Annual Report* **36**: 61–62.

Harrold, M. N. and R. P. Guralnick. 2010. *A Field Guide to the Freshwater Mollusks of Colorado*, 2nd Edition. Colorado Division of Wildlife. Denver, Colorado.

Hibbard, C. W. and D. W. Taylor. 1960. Two late Pleistocene faunas from southwestern Kansas. *Contributions from the Museum of Paleontology* **16**: 1–223.

Hoke, E. 2000. A critical review of the unionid mollusks reported for Nebraska by Samuel Aughey (1877). *Central Plains Archeology* **8**: 35–47.

Hubendick, B. 1951. Recent Lymnaidae. Their variation, morphology, taxonomy, nomenclature, and distribution. *Kungliga Svenska Vetenskaps Akademies Handlingar* **3**: 1–223. [Swedish]. (Have only read translated summaries).

Hubendick, B. and W. J. Rees. 1955. Phylogeny in the Planorbidae. *The Transactions of the Zoological Society of London* **28**: 453–542.

Johnson, P. D., A. E. Bogan, K. M. Brown, N. M. Burkhead, J. R. Cordeiro, J. T. Garner, P. D. Hartfield, D. A. W. Lepitzki, G. L. Mackie, E. Pip, T. A. Tarpley, J. S. Tiemann, N. V. Whelan, and E. E. Strong. 2013. Conservation status of freshwater gastropods of Canada and the United States. *Fisheries* **38**: 247–282.

Jokinen, E. H. 1982. *Cipangopaludina chinensis* (Gastropoda: Viviparidae) in North America, review and update. *Nautilus* **96**: 89–95.

LaGrange, T. 2005. *Guide to Nebraska's Wetlands and Their Conservation Needs*. Nebraska Game and Parks Commission, Lincoln, Nebraska.

Lauder, G. V. 1983. Prey capture hydrodynamics in fishes: Experimental tests of two models. *Journal of Experimental Biology* **104**: 1–13.

Leonard, A. B. 1959. *Handbook of Gastropods in Kansas*. University of Kansas, Lawrence, Kansas.

Lydeard, C, R. H. Cowie, W. F. Ponder, A. E. Bogan, P. Bouchet, S. A. Clark, K. S. Cummings, T. J. Frest, O. Gargominy, and D. G. Herbert. 2004. The global decline of nonmarine mollusks. *BioScience* **54**: 321–330.

Lysne, S. J., K. E. Perez, K. M. Brown, R. L. Minton, and J. D. Sides. 2008. A review of freshwater gastropod conservation: Challenges and opportunities. *Journal of the North American Benthological Society* **27**: 463–70.

Museum of Comparative Zoology (MCZ), Harvard University. 2013. MCZbase: The database of the zoological collections. Available at: http://mcz.harvard.edu 24 March 2014.

Newbold, J. D., J. W. Elwood, R. V. O'Neill, and A. L. Sheldon. 1983. Phosphorus dynamics in a woodland stream ecosystem: A study of nutrient spiraling. *Ecology* **64**: 1249–1265.

PRISM Climate Group (PCG). 2014. Oregon State University, 30-year normals. Available at: http://www.prism.oregonstate.edu/normals 11 July 2014.

Richardson, T. D., J. F. Scheiring, and K. M. Brown. 1988. Secondary production of two lotic snails (Pleuroceridae: *Elimia*). *Journal of the North American Benthological Society* **7**: 234–245.

Smith, D. G. 1984. *Selected Freshwater Invertebrates Proposed for Special Concern Status in Massachusetts*, Part II. Massachusetts Department of Environmental Quality Engineering, Division of Water Pollution Control, Westborough, Massachusetts.

Stephen, B. J. and V. B. Winkler. 2007. A Survey of the Freshwater Snails of the Major Ecoregions of South Dakota. *Ellipsaria* **9**: 14–15.

Stewart, T. W. 2006. The freshwater gastropods of Iowa (1821–1998): Taxonomic composition, geographic distributions, and conservation concerns. *American Malacological Bulletin* **21**: 59–75.

Swanson, G. A. and H. F. Duebbert. 1989. Wetland Habitats of Waterfowl in the Prairie Pothole Region. *In*: A. van der Valk (ed.) *Northern Prairie Wetlands*. Iowa State University Press, Ames, Iowa. Pp. 228–267

Taylor, D. W. 1960. *Late Cenozoic Molluscan Faunas from the High Plains*. U.S. Geological Survey Professional Paper 337. United States Government Printing Office, Washington, D.C.

Tiemann, J. S., S. E. McMurray, M. C. Barnhart, and G. T. Watters. 2011. A Review of the Interactions Between Catfishes and Freshwater Mollusks in North America. Paper read at Conservation, ecology, and management of catfish: The second international symposium. *American Fisheries Society Symposium* **77**: 733–743.

Tryon, G. W. 1868. Notes on Mollusca collected by Dr. F. V. Hayden in Nebraska. *American Journal of Conchology* **4**: 150–51.

USGS, 2009. U. S. Geological Survey. Available at: http://www.usgs.gov/state/state.asp?State=NE 24 March 2014.

Walker, B. 1906. A list of shells from Nebraska. *Nautilus* **20**: 81–83.

Walther, A. C., J. B. Burch and D. Ó. Foighil. 2010. Molecular phylogenetic revision of the freshwater limpet genus *Ferrissia* (Planorbidae: Ancylinae) in North America yields two species: *Ferrissia (Ferrissia) rivularis* and *Ferrissia (Kincaidilla) fragilis*. *Malacologia* **53**: 25–45.

Walther, A. C., T. Lee, J. B. Burch, and D. Ó Foighil. 2006. E Pluribus Unum: A phylogenetic and phylogeographic reassessment of *Laevapex* (Pulmonata: Ancylidae), a North American genus of freshwater limpets. *Molecular Phylogenetics and Evolution* **40**: 501–516.

Wethington, A. R. and C. Lydeard. 2007. A molecular phylogeny of Physidae (Gastropoda: Basommatophora) based on mitochondrial DNA sequences. *Journal of Molluscan Studies* **73**: 241–257.

Wilke, T., G. M. Davis, A. Falniowski, F. Giusti, M. Bodon, and M. Szarowska. 2001. Molecular systematics of Hydrobiidae (Mollusca: Gastropoda: Rissooidea): Testing monophyly and phylogenetic relationships. *Proceedings of the Academy of Natural Sciences of Philadelphia* **151**: 1–21.

Wu, S.-K. 2004–2005. Nebraska Physidae (Gastropoda: Pulmonata: Hygrophila). *Malacological Review* **37/38**: 185–96.

Wu, S.-K. and H. P. Liu. 2006. Kansas Physidae (Gastropoda: Pulmonata: Hygrophila). *Malacological Review* **33/34**: 69–79.

Wu, S.-K., R. D. Oesch, and M. E. Gordon. 1997. Missouri aquatic snails. *Natural History Series* **5**: 1–97.

Submitted: 5 October 2013; **accepted:** 8 September 2014;
final revisions received: 25 November 2014