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Interdisciplinary Approaches Improve Understanding of Cryptogenic Species: A Historical Case Study of Crayfish in Montana, USA

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Received: 30 April 2024 | **Revised:** 1 February 2025 | **Accepted:** 15 February 2025

Associate Editor: Christian Torgersen | **Editor-in-Chief:** Wendy Jepson | **Senior Editor:** Jan Seibert

Funding: This work supported by the USDA Forest Service (USFS) Southern Research Station and the Montana Department of Fish, Wildlife and Parks (MFWP). Kennedy was supported, in part, by an appointment to the USFS Research Participation Program administered by the Oak Ridge Institute for Science and Education (ORISE) through an interagency agreement between the U.S. Department of Energy (DOE) and the National Institute of Environmental Health Sciences. ORISE is managed by ORAU under DOE contract number DE-SC0014664. All opinions expressed in this paper are the authors' and do not necessarily reflect the policies and views of USDA, USFS, DOE, or ORAU/ORISE.

Keywords: crayfish | cryptogenic species | historical sources | Montana | nonnative species

ABSTRACT

Cryptogenic species are those that are not yet "demonstrably native or introduced" in a given area, such as crayfish in western Montana, USA. Delving into evidence from diverse fields can help clarify the status of cryptogenic species. Primary historical sources and indigenous knowledge have informed various ecological questions but are seldom used to clarify the status of cryptogenic species, especially aquatic taxa. We summarize types of evidence used to illuminate species status and offer a case study applying historical sources to cryptogenic crayfish in Montana. We searched for crayfish mentions in dictionaries of indigenous languages and primary historical documents (e.g., travel journals, newspaper accounts, early biological surveys). Early explorer accounts we examined did not mention crayfish in Montana, though they noted them in the nearby Snake River drainage of Idaho and Wyoming. The first mention of crayfish in Montana that we found was from an 1868 newspaper account, probably referencing the upper Missouri River. The species was not noted, but an 1887 article suggested signal crayfish *Pacifastacus leniusculus* introductions near Bozeman, where non-native signal crayfish still persist. The earliest crayfish mention we found west of the Great Divide in Montana was from 1934 in Ninepipes and probably referred to non-native virile crayfish (*Faxonius virilis*). Signal crayfish were not mentioned west of the Divide until a 1944 newspaper account noted their 1937 introduction to the Bitterroot River drainage. The case study demonstrates the value of historical sources in identifying the absence of species and documenting their presence or introduction during periods predating scientific data.

1 | Introduction

Historical ecology, including the use of primary historical documents and indigenous knowledge, has been applied in interesting ways to understand and contextualize diverse ecological questions (Szabó 2010; Beller et al. 2017). Ziembicki et al. (2013) applied indigenous knowledge to understanding Australian mammal declines in a long temporal context. In the USA, archaeological evidence indicated the presence of now-extirpated large mammals in eastern Washington and Oregon (Osborne 1953),

and historical accounts from the Meriwether Lewis and William Clark expedition (Corps of Discovery, 1804–6) were used to argue that some mammal extirpations had occurred prior to European colonization (Laliberte and Ripple 2003). In Australia, historical documents were used to place recent plant community changes in the context of early-European-colonization conditions (Franco and Morgan 2007). And in Oregon, historical accounts served to illustrate a contraction in summer distributions of Chinook salmon (*Oncorhynchus tshawytscha*), as well as changes in river channel geomorphology, since the 1800's (Torgersen 1996; Torgersen et al. 1999). Matteson (1960) used mussel-shell middens to understand prehistoric river hydrology and habitat.

Both historical information and indigenous knowledge can also inform investigations of the native versus non-native (Soto et al. 2024) status of species. Cryptogenic species are those that are not yet "demonstrably native or introduced" (crypto = hidden; genic = origin) to an area (Carlton 1996). The number of species considered non-native, or even cryptogenic, seems to be greatly underestimated (Jarić et al. 2019), in part due to a tendency to presume species native until proven otherwise (Carlton 2009; Haydar 2012). Resolving whether species are native to a particular area is critical to understanding biogeographic, evolutionary, and ecological patterns and may profoundly influence management inferences and actions (Carlton 2009). Among 12 reasons offered for underestimation of the number of invasive species was "uninvestigated taxa;" that is, "species groups that are not or rarely studied" (Carlton 2009). Quantitative, historical, biological collection data are usually lacking for cryptogenic species, although sometimes such data exist but have led to conflicting conclusions. Historical information can add to evidence from other disciplines indicating whether a cryptogenic species is native to an area (Essl et al. 2018). We review approaches that have been used to investigate the origins of cryptogenic species, with emphasis on historical sources and indigenous knowledge. We then offer a case study in which we review and apply historical information to the question of whether crayfish are native to western Montana, USA.

2 | Approaches to Resolving the Status of Cryptogenic Species

Numerous approaches have been used to investigate the status of cryptogenic species, but because one cannot prove a negative (e.g., the absence of a species), certainty can be hard to come by when a species is not native to an area. Such uncertainty can lead to conflict within and beyond the scientific community (e.g., Clavero 2022; Clavero et al. 2016; Jussila et al. 2021; Matallanas et al. 2016a; Roche 2019) (Sidebar 1). Historical accounts and indigenous knowledge can be informative in some situations, especially where species in question were useful to, or problematic for, humans (e.g., Ens et al. 2015; Gilchrist et al. 2005; Laliberte and Ripple 2003).

The origin of cryptogenic species should be addressed using as many independent approaches as possible (Clavero 2019), and conclusions based on a preponderance of evidence. Investigators have used biological, paleontological, and social science approaches to assessing the native status of species, with various information sources being more or less available and relevant depending on the taxon and location in question (Table 1). In fortunate cases, paleoecological, or archaeological data presents irrefutable evidence of prehistoric presence of a species (Cooper 2000; but see Clavero 2019), but again, proving absence is problematic (Cooper 2000). Moreover, with archaeological evidence, one might consider the possibility that prehistoric people moved (i.e., introduced) species. In such cases, some have suggested incorporating a time-frame into the definition of native versus non-native, whereas others argue that the conceptual distinction between native and non-native depends only on the role of humans in overcoming a species' biogeographic boundaries, regardless of when anthropogenic influences occurred (Oficialdegui et al. 2024; Soto et al. 2024; Willis and Birks 2006). Evidence from all potential information types will rarely be available, and all types of evidence do not carry the same weight. Definitively categorizing a species as non-native requires clear evidence of a human role in overcoming a species' biogeographic boundaries (e.g., reported introductions or escapes), although observation and documentation of such events is seldom available (Essl et al. 2018). Genetic results, in particular, may often be inconclusive (Haydar et al. 2011), and evidence from different disciplines may conflict (Matallanas et al. 2016b; Willis and Birks 2006). However, if all evidence from multiple sources points to the same answer, "it is reasonable to accept it as decisive" (Webb 1985). Essl et al. (2018) proposed criteria that incorporate uncertainty into terminology relating to categorizations of potentially non-native species. Acknowledging both uncertainty and the possibility that additional evidence could change conclusions (e.g., Clavero 2019; Essl et al. 2018) may minimize conflict and encourage risk-assessment approaches to related management decisions.

Challenges in using historical records differ between areas recently colonized by Europeans (e.g., the Americas and Australia) and those where written records extend back much further. In regions with long written histories, a greater possibility exists that ever-older documents providing different information will eventually be found (Clavero et al. 2016; Matallanas et al. 2016a). In most inland parts of the western USA, in contrast, one can be fairly certain that few detailed written records will emerge that predate Lewis and Clark's Corps of Discovery, 1804–6[1]. The most powerful historical evidence supporting claims that species were introduced are documents (e.g., eyewitness accounts or newspaper articles) contemporary with the introduction that "provide reference points for inferring likely routes, sources, times, and numbers of introductions" (Campbell et al. 2018).

2.1 | Application of Indigenous Knowledge and Historical Documents

Indigenous knowledge seems to have been applied to understanding ecological processes or extirpations of native species more often than to understanding the provenance of cryptogenic species (e.g., Ens et al. 2015; Jessen et al. 2022). Indigenous knowledge may provide unique perspectives in solving questions about cryptogenic species, especially those that are useful in some way to the indigenous people (Ens et al. 2015) or that occur in regions where European colonization was more recent. One caution about relying solely on indigenous knowledge as

TABLE 1 | Examples of the types of evidence that have been demonstrated or proposed as useful for determining whether species are native or non-native. Examples of taxa to which the criteria have been applied or proposed for use with, and the information sources are included.

Criteria or nature of evidence	Taxa	Source
Human-related		
Archaeology	Various; mussels	(Clavero et al. 2016; Grayson 2001; Savoya et al. 2015)
Linguistics	Crayfish	(Clavero et al. 2016; Lucey 1999)
Historical evidence (scientific or otherwise)	Plants; mammals; crayfish	(Campbell et al. 2018; Clavero 2022; Clavero et al. 2016; Matallanas et al. 2016b; Reynolds 1997; Thompson 1843; Webb 1985; Wester 1992)
Supposed means of introduction/known human modes of dispersal	Plants; small marine crustaceans	(Chapman and Carlton 1991; Webb 1985)
Biological or ecological		
Paleoecology (e.g., fossils, sediment cores, pollen analyses)	Plants; birds; general	(Cooper 2000; Roche 2019; Webb 1985; Willis and Birks 2006)
Genetics	Various (including plants; mammals; birds; fish; crayfish; marine invertebrates)	(Blakeslee and Moore 2023; Campbell et al. 2018; Clavero et al. 2016; Fok et al. 2002; Geller et al. 2010; Gouin et al. 2003; Grandjean et al. 1997, 2001; Matallanas et al. 2016a, 2016b; Saltonstall 2002; Santucci et al. 1997; Taylor et al. 2007; Webb 1985)
Morphology	Marine mussels	(Savoya et al. 2015)
Biogeography	Plants; crayfish	(Clavero et al. 2016; Larson and Williams 2015; Lucey 1999; Reynolds 1997; Webb 1985; Wester 1992)
Symbiotic organisms	Invertebrates; crayfish; general	(Blakeslee and Moore 2023; Clavero et al. 2016; Füreder et al. 2009; Gagne et al. 2022; Larson and Williams 2015)
Habitat associations	Plants	(Webb 1985; Wester 1992)
Species' active or passive dispersal abilities that cannot explain current distribution	Small marine crustaceans; plants	(Chapman and Carlton 1991; Wester 1992)
Reproductive pattern	Plants	(Webb 1985)
Ease of known naturalization elsewhere	Plants; crayfish	(Larson and Williams 2015; Webb 1985)

proof that a species is native is that indigenous peoples, too, moved and exploited species and altered habitats in numerous ways, and so prehistoric or early historic conditions do not necessarily reflect ecologically "pristine" conditions (Grayson 2001; Truett 1996). Some authors have suggested using different terms for species introduced by indigenous people prior to European colonization [e.g., "Polynesian introductions" (Wester 1992); "archaeophytes" or "neophytes" (central Europe, Pyšek et al. 2004)]. Alternatively, one may need to consider how far back in time to assess anthropogenic introductions (Willis and Birks 2006).

Biologists have used historical documents to inform biological and ecological questions, including the provenance of cryptogenic species (e.g., Sidebar 1), across a broad array of taxa (Table 1). In Ireland, multiple approaches were used to address contention about whether Scots pine (*Pinus sylvestris*) was native and, if so, was ever extinct in the country. Historical sources supplemented ecological and paleoecological results, indicating that pine woodlands were historically and continuously present at one site examined (Roche 2019). In Catalonia, Spain, a historic record supported an argument that the status of brown trout (*Salmo trutta*) should be changed from introduced to uncertain (i.e., cryptogenic) (Benejam et al. 2008). In that case, considering the fish as native versus non-native qualitatively altered the outcomes of fish biotic indices used to assess the ecological status of streams, and so had potentially important implications for habitat management. Historical documents contributed to understanding native crayfish distributions in the upper Great Basin and Snake River Basin in Yellowstone National Park, Wyoming, USA (Dean et al. 1974), and the provenance of crayfish in Ireland (Lucey 1999).

SIDEBAR 1 | Application of diverse approaches to resolving the status of a cryptogenic crayfish in Spain.

Several groups of scientists have used diverse approaches to resolve the status of the cryptogenic white-clawed crayfish (*Austropotomobius pallipes*) in the Iberian Peninsula but have come to opposing conclusions (Clavero 2022; Clavero et al. 2016; Clavero and Villero 2014; Jussila et al. 2021; Martínez-Ríos et al. 2023; Matallanas et al. 2016a, 2016b). Clavero et al. (2016) used paleoecological, biogeographical, genetic, historical, and linguistic information to counter earlier work and conclude that the species was not native to Spain, but rather was introduced from Italy beginning in the 1500s. Others have refuted that conclusion, asserting that the authors misinterpreted genetic and linguistic results (Jussila et al. 2021; Martínez-Ríos et al. 2023; Matallanas et al. 2016a) and overlooked other historical accounts that indicate the species is native (Matallanas et al. 2016b). This example illustrates that while diverse approaches offer important insights, they do not always provide definitive, uncontested answers (Essl et al. 2018). Multidisciplinary investigations are most powerful and convincing when all results point to the same conclusion about a species' geographic origin (Essl et al. 2018; Webb 1985).

3 | Case Study With Freshwater Crayfish in Montana, USA

In Montana, prior to 2021, only one systematic survey of crayfishes had been conducted, and that was restricted to the Columbia River Basin (CRB) west of the Continental Divide (hereafter, Divide) in the late 1980s (Sheldon 1989). Two species occurred there (Figure 1): virile (or northern) crayfish (*Faxonius virilis*) (Figure 1A), native east of the Divide and introduced to the CRB, and signal crayfish (*Pacifastacus leniusculus*) (Figure 1B), native west of the Divide in at least portions of the CRB (Larson et al. 2012). In recent sampling, we found a third taxon, *Pacifastacus* sp. (Figure 1C) in one location west and one location east of the Divide (unpublished data, Adams et al.; Figure 2). Preliminary genetic and morphometric results indicate that these individuals belong to the cryptic Okanagan lineage defined by Larson et al. (2012, 2016). Sheldon (1989) assumed *P. leniusculus* to be native to Montana, as have other biologists (Lewis 2002; Thomas 1991); however, contemporaneously, Horton Hobbs Jr. the pre-eminent US crayfish biologist at the time, did not include Montana in the native range of *P. leniusculus* (Hobbs Jr. 1988, 1989). Subsequent work indicated that *P. leniusculus* may be native only to the lower Columbia River and tributaries, possibly restricted to below Celilo Falls (now inundated by The Dalles Dam), with several *Pacifastacus* cryptic groups occurring in small areas of Oregon, Washington, and British Columbia (Larson and Williams 2015); however, previous phylogenetic work did not assess crayfish from northern Idaho or Montana (Larson et al. 2012, 2016). *Pacifastacus* crayfishes also occur in a handful of Montana locations east of the Divide, where they are assumed by most to be introduced, despite a presumably erroneous historic record of *Pacifastacus gambelii* in far-eastern Montana (Faxon 1885; Larson and Williams 2015; and see Section 3.5).

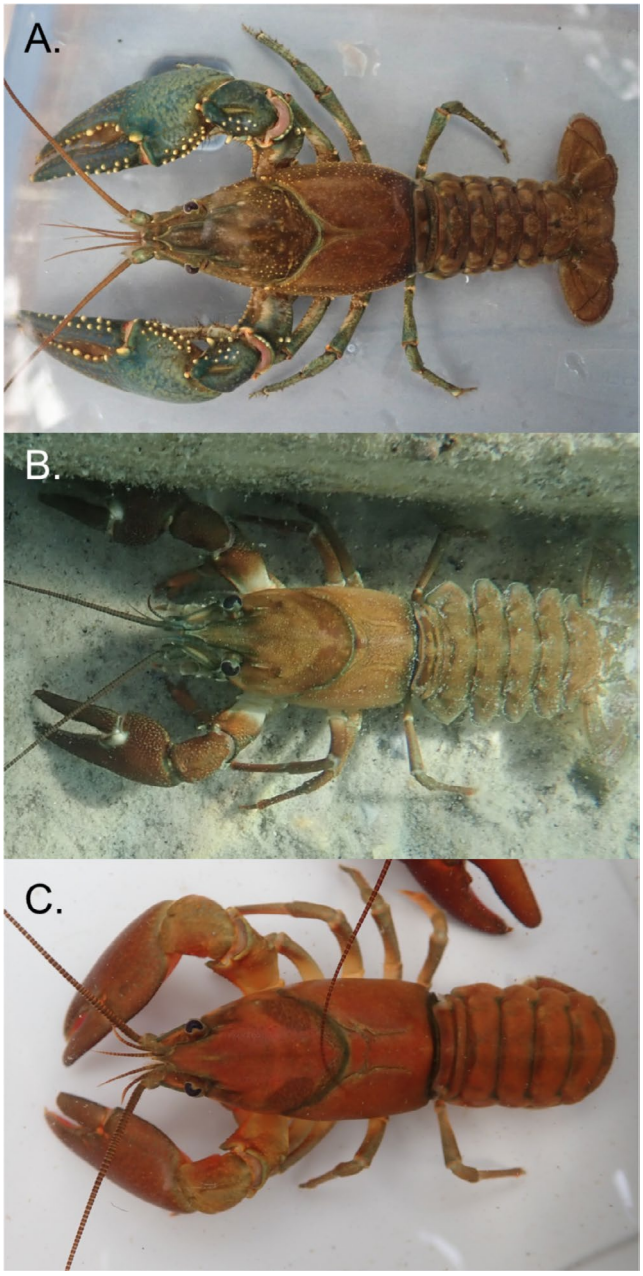

FIGURE 1 | Photographs of three crayfish taxa found in western Montana, USA, in 2021–2022 (unpublished data): (A) *Faxonius virilis*, (B) *Pacifastacus leniusculus*, and (C) *Pacifastacus* sp.

P. leniusculus has been widely introduced globally (Kouba et al. 2014; Mrugała et al. 2017), including to extralimital locations in western North America (Girdner et al. 2018; Larson et al. 2012; Larson and Williams 2015; Riegel 1959). The species has repeatedly established and spread, readily becoming invasive on several continents (Kouba et al. 2014). In the western USA, the species has apparently contributed to the endangerment (Light et al. 1995) or extinction (Bouchard 1977) of congeners, but the greatest ecological impacts likely occur in ecosystems historically lacking native crayfish (Twardochleb et al. 2013). In such ecosystems, non-native *P. leniusculus* has dramatically reduced or extirpated native fauna, including fish (Velema et al. 2012), amphibians, and aquatic macroinvertebrates, especially snails (Girdner et al. 2018; Scordo et al. 2023);

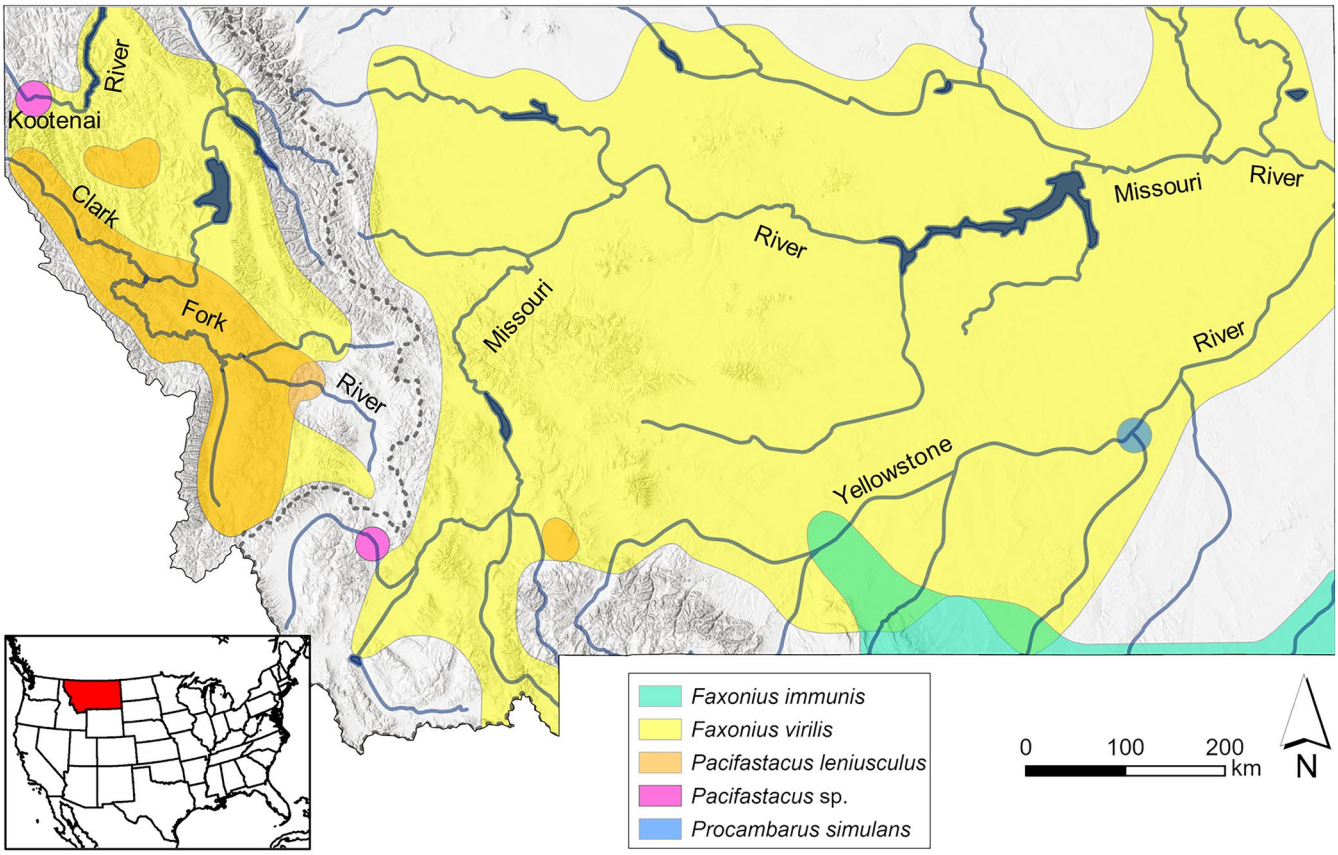

FIGURE 2 | General distributions of crayfish species sampled in Montana in 2021 and 2022 (Adams et al. unpublished data). Dashed line indicates the Great Divide. Prior to this study, most biologists presumed *Pacifastacus leniusculus* to be native west of the Divide and *Faxonius virilis* to the east in Montana, and considered *Faxonius immunis* to be non-native or cryptogenic. Neither *Pacifastacus* sp. nor *Procambarus simulans* (Schmidt et al. 2023) had been reported from the state prior to this sampling effort. Inset shows the location of Montana within the USA.

has altered nutrient cycles and algal and periphyton communities (Scordo et al. 2023); and has reduced or extirpated aquatic macrophytes (Nyström et al. 1996), among other effects (Lodge et al. 2000; Twardochleb et al. 2013).

East of the Divide, although *F. virilis* is now widespread throughout much of the Missouri River basin in Montana (Figure 2), the species may be native to the state only in the lower portion of the basin (Williams 2012). Based on preliminary results, *F. virilis* farther upstream in the Missouri River drainage lacks mitochondrial DNA variation and, thus, might be non-native (unpublished data). However, the extent to which native *F. virilis* may have been present but subsequently displaced by introduced genotypes versus historically absent is unknown (Williams 2012). Field observations have suggested a recent arrival of *F. virilis* in the upper Madison River drainage (Stagliano 2022). A rapid range expansion of the species was suspected in Alberta, Canada, probably due to a combination of natural upstream expansion as Pleistocene glaciers receded and introductions by humans in the 20th century, especially to popular fishing lakes (Williams 2012; Williams et al. 2011). After widespread introductions, *F. virilis* has readily invaded many waters across the USA and Canada well beyond its large native range in the eastern part of the continent (Adams et al. 2015; Larson and Olden 2011; Riegel 1959; Martinez 2012; Williams et al. 2011). Similar to most other established non-native crayfish, *F. virilis* causes dramatic ecosystem changes where introduced (Dorn and Wojdak 2004), especially in areas lacking native crayfish, although their impacts are less well documented relative to *P. leniusculus* impacts (Twardochleb et al. 2013).

As one prong of a multidisciplinary effort to investigate native distributions of crayfish in Montana, we explored historical documents seeking insight into two questions: (1) Are any crayfish native to the CRB in western Montana? and (2) Are *F. virilis* native to the Marias River or the upper Missouri River basin (i.e., upstream of Great Falls, Montana)? Most historical sources referencing crayfish do not identify species, but this lack of detail is not surprising given the types of sources in the historical record. Nonetheless, we hoped that historical documents would prove useful in establishing an estimated time of crayfish introduction to, or arrival in, the areas in question if they are not native.

3.1 | Approach to Reviewing Historical Documents

We began our historical investigations by searching for crayfish (or crawdad, crawfish, or écrevisse) references in the journals from the Corps of Discovery expedition (Lewis 1805; Ordway 1805; Whitehouse 1805) and then established a chronology of European-American movement across Northwest USA, and to a lesser extent, Western Canada, which furnished us with a list of individuals who may have recorded accounts of their travels through

Montana. Chittenden (1902) and Merk (1968) surveyed economic ventures, primarily by the American Fur Company, Missouri Fur Company, North West Company, and Hudson's Bay Company, which was the largest enterprise in the region during the early 19th century. Topping (1883) offered a historical overview of the eastern half of the state, and Horstman (1984) summarized indigenous and commercial history farther west, within the upper Clark Fork River drainage. Ten volumes of *The Contributions to the* Historical Society of Montana (1876–1940) added significantly to our search, particularly regarding individual memoirs. A bibliography compiled by Knowles and Knowles (1993) provided the most comprehensive list of sources addressing pre-settlement wildlife and habitat conditions for our chronology.

We also examined dictionaries of indigenous languages written by settlers, as encounters between settlers and indigenous groups offered insights where indigenous oral histories were silent. Ronan (1890), Grinnell (1892), and McClintock (1910) recounted the fishing practices of the Salish, Flathead, and Blackfeet peoples, respectively. The memoirs of a missionary (Palladino 1922), covering the years 1831–1891, also described the fishing practices of the Salish and Flathead in detail. Mackenzie (1911) traversed North America, in what is now Canada, between 1789 and 1793, noting many indigenous words, and Howse (1844) produced a dictionary of the Cree more localized to the West. Giorda and Mengarini (1877) wrote dictionaries of the Kalispell and Flathead languages. Supporting Information includes bibliographies of additional significant (Appendix S1) and minor (Appendix S2) sources that we searched without finding references to crayfish in Montana.

3.2 | Indigenous Languages

Dictionaries of indigenous languages provided no evidence of crayfish in western Montana. None of the dictionaries or reports of interactions with the Crow, Flathead, Salish, or Blackfeet peoples that lived in or near Montana mention crayfish or include words for crayfish (Grinnell 1892; McClintock 1910; Palladino 1922; Ronan 1890). The absence of crayfish from Palladino's (1922) account is particularly telling because he described the Salish and Flathead fishing practices in detail. Mackenzie (1911) noted that the Knisteneaux, or Cree, had a word for crayfish: "A-shag-gee;" however, traditional Cree lands extend east into present-day Quebec, and their influence in Montana was minimal. Howse's (1844) more western-focused Cree dictionary did not include "A-shag-gee," despite abundant translations for other wildlife (e.g., "umisk" for beaver and "nummáis" for fish). Dictionaries for the Kalispel and Flathead peoples, whose traditional lands include western Montana, similarly did not list a word for crayfish but provided translations for other aquatic animals (e.g., "aizchst" for "salmon trout") (Giorda and Mengarini 1877). The omission of crayfish in these documents suggests that crayfish were absent from western Montana at the time or were present but unimportant to indigenous cultures and diets.

3.3 | Early Historical Travel Accounts

Most early 19th century accounts of Northwest USA are in frontiersmen journals and missionary reports. Meriwether Lewis and members of the Corps of Discovery expedition were the first to document crayfish in the CRB, although they did not mention crayfish in Montana (Lewis 1805; Ordway 1805; Whitehouse 1805).[2] On September 21, 1805, after 11 days traversing the Bitterroot Mountains from present-day Montana west into Idaho, Lewis wrote of an abundance of game: pheasants[3], a "Prairie Wolfe" and "some crawfish which we obtained in the creek enabled us to make one more hearty meal, not knowing where the next was to be found" (Lewis 1805). On the same day, John Ordway (1805) wrote, "we ... caught a fiw craw fish in the creek and eat them". The campsite, known as "Pheasant Camp" among historians, is marked on Lolo Creek, Idaho (46° 17.325′ N, 115° 45.534′ W) (Figure 3). Expedition members did not record crayfish in Montana on either their outbound or return journeys (Figure 3).

Peter Ogden's expeditions throughout Idaho and Montana provide further evidence of native crayfish in the Idaho portion of the CRB. His 1824–1825 expedition beginning at Flathead Post (Saleesh House), near present-day Thompson Falls, Montana, canvassed portions of the Clark Fork, Bitterroot, Beaverhead, and Jefferson rivers. Ogden did not report crayfish in his Montana accounts (Rich 1950), though he did document their presence on a separate expedition down the Snake River in Idaho. Recounting his Idaho travels from April 26–28, 1826, Ogden wrote "it is almost incredible the number of Craw fish we took in this River sufficient to give all a good meal which all appeared to relish on this stream which is not more than 3 miles in length..." (Rich 1950). Journal entries bracketing those dates place him near the Portneuf River ("three-mile stream" in Figure 3), a tributary of the Snake River. Nathaniel Wyeth also documented historical presence of crayfish in the Snake River while establishing trade operations across the Pacific Northwest on two expeditions between 1832 and 1834[4]. On August 1, 1832, several of his men returned to camp "with about a peck of craw fish and a dozen of trout these average about 1 lb and are fine eating...", and on August 15, he noted "there are also in the streams abundance of craw-fish" (Young 1899). The group was "encamped on a small creek running into one called Blackfoot this latter is the second stream we have passed which emties into S. fork of Lewis River the first was called Grays River and is also small (this since crossing Lewis River)" (Young 1899) (Figure 3). Mentions of the Blackfoot, Portneuf, and Raft rivers suggest the party was moving southwest from the Teton Mountains. Merriam (1891) later confirmed these private reports and identified the crayfish species as *P. gambelii*.

Although Ogden's and Wyeth's expeditions were economic ventures, unlike the Corps of Discovery expedition that had a scientific and cartographic focus, all three welcomed the discovery of crayfish. Most fur trappers did not leave records behind, and those that did had little reason to record crayfish presence. Only when they were unable to procure game did they turn to the waterways for sustenance. These writers were observant but rarely sedentary; their observations offer only a glimpse of the biodiversity they encountered. Other prominent expeditions through western Montana in the early 1800s were similarly void of any mention of crayfish. The Hudson's Bay Company maintained the earliest and largest permanent settlements of Europeans in Montana west of the Divide. We found no crayfish mentions in the records of notable figures from any expedition or venture in that early period for example, David

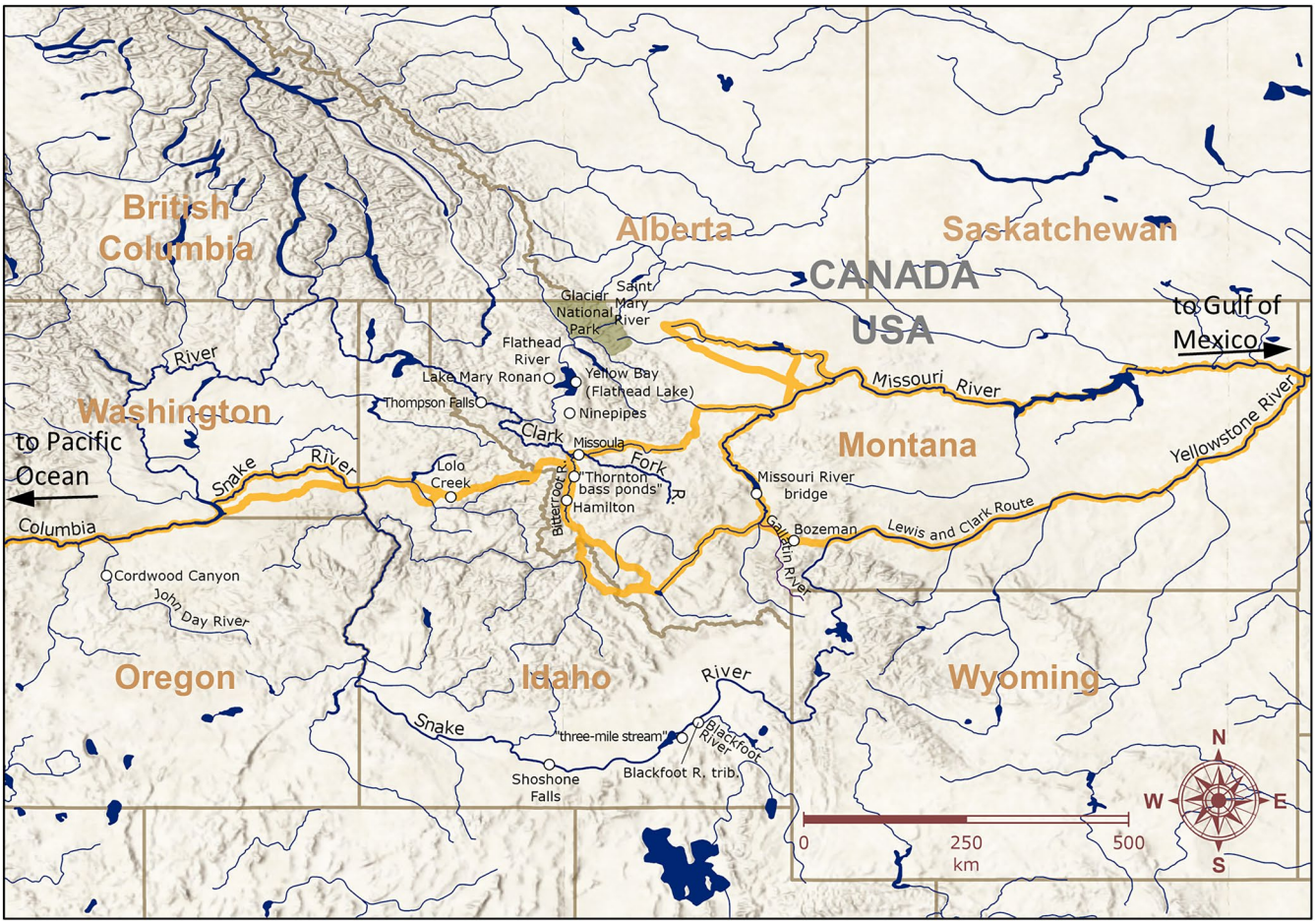

FIGURE 3 | Northwestern USA and southwestern Canada with current political boundaries, major rivers, and locations mentioned in text. Orange lines indicate Lewis and Clark's Corps of Discovery routes on their outgoing and return journeys, 1804–6. Florence, Montana (MT), is just north of the "Thornton bass ponds" location, and the St. Mary's Mission is just south of it. The Flathead Post is near the town of Thompson Falls, MT. The Missoula Valley area that Woodward (1934) studied is not indicated but surrounds Missoula, MT, and was "bounded by the top of Mount Sentinel on the East, the mouth of Pattee Canyon on the South, the fairgrounds on the West, and Cherry Creek on the North." R = River.

Thompson (White 1950), William (Ashley 1825), Jedediah Smith (Sullivan 1934), James (Stuart 1902), and Major John Owen (Dunbar 1927) (Appendix S1)[5]. Other references to crayfish further west in the CRB do appear, such as in Simpson's journals of his 1824–25 expedition to Oregon (Merk 1968). He noted the Chinook people's fishing practices and gave a detailed description of crayfish; "they collect Shell Fish on the shore resembling Lobster in shape and colour also in taste but much smaller, in fact they are the Lobster in miniature" (Merk 1968). Other traders documented various indigenous groups in Oregon, like the Tualatin, as including crayfish in their diet (Meyer-Arendt and Henderson 2020). Although early 19th century sources confirm the historical presence of crayfish in the CRB, none of these travelers recorded their presence in Montana.

By the early 1850s, the US War Department sought a railroad route from the Mississippi River to the Pacific Ocean (U.S. War Department, 1857–1860)[6]. Their expedition's 12-volume compilation of exhaustive reptile, mammal, bird, and fish data of Western USA did not mention crayfish. The War Department's surveys of neighboring Wyoming and Idaho territories (Hayden 1883), where crayfish were already documented, likewise did not mention crayfish.

Pinpointing species' presence historically can be difficult, as place names have changed over time, and locations that texts refer to can be vague. Father Pierre-Jean DeSmet proselytized to the Flathead people and recorded his missionary work and observations in a series of letters between 1841 and 1842[7]. He wrote one letter, dated September 1, 1841, at an encampment at Beaverhead (near present-day Dillon) and another, dated September 21, at Hells Gate (present-day Missoula). Therefore, his letter dated September 10, written at the "St. Ignatius River" (likely a reference to the Bitterroot River), must have been written between the two localities and described the feeding habits of opossums, notably their unique way of catching crayfish: "Opossums are common *here* [emphasis added]. They are generally found near marshes and ponds that abound in small crawfish, of which they are extremely fond" (Chittenden and Richardson 1905). We can only assume what DeSmet meant by "here," but the context is telling. The September 10th letter recalled natural observations around the Black Hills (South Dakota), and in the western country more generally. His letters describe both precise locations and the broader region. His mention of opossums offers a valuable clue that he was referencing a much broader region because opossums had not yet been introduced to Montana (Gardner 1982; MNHP and MFWP 2024), and that makes geolocating the crayfish reference challenging.

3.4 | Popular Media Accounts

The earliest reference we found to crayfish apparently in Montana was in an 1868 newspaper article (From Our Bucolic Correspondent 1868). A Bozeman-area correspondent wrote "wait a little my friend; if you are not afraid of getting your fingers a little pinched, you can catch ecrivisses, or crawfish, from the brook." This appears to refer to somewhere in the upper Missouri River basin, as the author mentioned Radersburg and the East and West Gallatin rivers prior to the crayfish comment. These could have been introduced signal crayfish (see below, 3.6.1).

Many sources, including newspapers and local high school course descriptions as early as 1904, mention crayfish used for classroom studies (Silloway 1905; Halvorson 1917). Some refer to crayfish shipments, and it is generally not specified if the crayfish ordered were live or preserved, but we assume the latter in most early cases. A Butte, MT, school purchased crayfish from Ward Natural Science for dissection (Specimens Received 1903). Halvorson (1917) mentioned students in Cut Bank (on the Marias River) experimenting with crayfish, which suggests they were alive, but did not indicate if they were sourced locally. Other schools obtained specimens from local waters; for example, a class in the Great Falls area "took a field trip to Black Eagle Dam ... to catch live crayfish" (High School News Notes 1940) (Figure 3). Such mentions confirm the dispersed presence of crayfish east of the Divide by the mid-1900s, but do not indicate the species. Also, schools have been sources of crayfish introductions elsewhere (Campbell 2012; Larson and Olden 2008).

One article suggests that crayfish either inhabited northern Idaho's Coeur d'Alene River drainage, or were transported there as bait, in 1914 (In the Days of Real Sport 1914): "The biggest trout brought into Kellogg this year ... was caught yesterday ... in the North Fork at Freeman's eddy ... Dominick baited his hook with a crawfish..." Articles referring to mammals such as muskrat and otter feeding on crayfish are numerous (Muskrat Lore 1919; Sherman 1951), though discerning how specific the references are to Montana without a specific location mentioned is difficult to ascertain. Regular angler reports of crayfish as bait do not appear until the early 1950s, and many of these articles are general and meant to educate the reader on fishing tactics (Fly Fishing Hints 1950).

3.5 | Historical Biological Research

Faxon (1885), a biologist, reported that the first crayfish specimen from Montana was a *P. gambelii* "collected by the Hayden survey [likely the first Hayden expedition, 1854–1855] at the mouth of the Yellowstone River, which joins the Missouri River at the western boundary of Dakota."[8] All other *P. gambelii* specimens from the time period were taken west of the Divide (Faxon 1885, 1898), and yet Faxon (1885) added that "The correctness of the ticket accompanying the Yellowstone River specimens is at any rate unquestioned." This record has created much confusion, with others (e.g., Holthuis 1962; Larson and Williams 2015) arguing that the locality on the label is indeed questionable because if *P. gambelii* occurred east of the Continental Divide, it was probably restricted to headwaters of the Missouri River drainage near the Snake River headwaters (Larson and Williams 2015). The suggestion of an incorrectly labeled specimen gains merit when considering that Hayden (1872), himself, did not mention collecting these specimens in his geological report of Montana, and that other government reports contemporary to Hayden's (Forsyth 1875; Raynolds 1866; Stanley 1874) did not mention crayfish either[9]. Although Hobbs (1988) did not include eastern Montana in the *Pacifastacus* range, the following year he listed the state in the *P. gambelii* range (Hobbs Jr. 1989).

Aquatic biological research conducted at specific Montana localities over extended time periods began with Morton Elrod's surveys of Flathead Lake (Figure 3) between 1899 and 1916. His surveys, and those that subsequent researchers conducted nearby, support the absence of crayfish inferred from earlier accounts of the northern Flathead and Blackfeet territories. Elrod's (1902) biological reconnaissance of Flathead Lake in 1899 concluded that "the banks of the lake do not afford as much shelter for invertebrate life as would at first seem apparent." In summer 1916, Elrod (1916) examined stomach contents of various fishes (including bull trout *Salvelinus confluentus* and northern pikeminnow *Ptychocheilus oregonensis* [formerly northern squawfish]; see Appendix S1 for others) in Flathead Lake, primarily in Yellow Bay (Figure 3). None of the stomach contents included crayfish remains. Farther downstream in the CRB, northern pikeminnow larger than 200 or 240 mm fed heavily on crayfish in rivers (Shively et al. 1996; Tabor et al. 1993; Thompson 1959) and lakes (Jeppson and Platts 1959), making the historical absence of crayfish from pikeminnow stomachs in Flathead Lake all the more noteworthy. Other early aquatic surveys in northwest Montana (Muttkowski 1925) in Glacier National Park, and (Young 1935) in Flathead Lake likewise did not report crayfish.

To the south and farther upstream in the Clark Fork River drainage, Woodward (1934) hypothesized how species may have colonized the Missoula Valley (Figure 3), concluding that most species, both in aquatic and terrestrial environments, arrived "by way of the Columbia and Clark Fork" rivers. Woodward's omission of crayfish is interesting considering that the Missoulian was publishing reports of locals finding crayfish in western Montana waters at around the same time (see 3.6.1 below).

In 1947, Holthuis (1962) collected the first scientifically documented Cambarid crayfish in Montana—an *F. virilis* from a Missouri River tributary north of Townsend—after learning that Bozeman State College zoology students collected crayfish from Missouri River tributaries. He documented three more *F. virilis* localities in 1960. The Smithsonian National Museum of Natural History online database indicated that their holdings included only 13 crayfish lots from Montana collected prior to 1980 (Table 2).

3.6 | Probable Crayfish Introductions

3.6.1 | *Pacifastacus* Spp.

The first reference that we found to signal crayfish from the Clark Fork River drainage was in a 1944 article in The Missoulian newspaper reporting surprised reactions to finding a crayfish (Crayfish Caught 1944).

> Hamilton, Sept. 18. - Lawrence Humble and Fred Ward, fishing in the Bitter Root river near Florence, hooked a lobster-like "critter of the deep" that is said to be a Columbia river crayfish. How the crayfish ever found its way into the Bitter Root is a mystery. The specimen has been placed on exhibition at the Roberts book store. It fills an ordinary fruit jar.

A follow-up article the next day solved the mystery (Crayfish Planted 1944).

> The Columbia river crayfish, caught by Hamilton fishermen near Florence ... undoubtedly is one of, or the offspring of one of a thousand such crayfish planted in the Thornton bass ponds[10] about seven years ago by Dr. Charles Thornton and the late Thomas Marlowe. Sportsmen have long recognized the value of the crayfish as food for bass and these sportsmen purchased 1,000 of them to add to the bass plant made in the Thornton ponds in the Bitter Root. Undoubtedly one or more of these crayfish escaped the ponds and this particular fellow was unfortunate enough to be caught (Figure 3).

The newspaper timeline places the introduction to the ponds in about 1937. "Columbia river crayfish" would have been a *Pacifastacus* species—probably *P. leniusculus*, which is native to the lower Columbia River drainage (Larson et al. 2012). Commercial fisheries for *P. leniusculus* in the lower Columbia River began in 1893 and were still ongoing in 1956, with crayfish sold for human consumption and bait and exported as far east as St. Louis (Miller and Van Hyning 1970). Therefore, *P. leniusculus* were commercially available in the 1930s, and we found no other crayfish species documented in the Bitterroot River drainage prior to 2021 (Sheldon 1989; and unpublished data).

In an earlier account east of the Divide, "Merino Mike" appears to have introduced crayfish to the Bozeman, Montana, area from the Cordwood Canyon area, John Day River, Oregon (Yerkes 1887): "Merino Mike, who used to live in Cordwood canyon, where he caught crawfish for the Heppner market ... traveled to Bozeman ... He has introduced the culture of crawfish, securing the seed from canned lobsters ..." Any crayfish native to Oregon would have been a *Pacifastacus* species. In 2022, a nonnative population of *P. leniusculus* still occupied a short segment of the East Gallatin River near Bozeman (unpublished data). In the 2000s, the John Day River contained both an undescribed, cryptic lineage of *Pacifastacus* (the Central Oregon lineage, endemic to central Oregon) and *P. leniusculus* (Larson et al. 2012). Whether the *P. leniusculus* were native in the drainage is unknown. So, Merino Mike might have introduced *P. leniusculus* or the Central Oregon lineage of *Pacifastacus* from the John Day or Columbia rivers to the Bozeman area. In addition, crayfish from the Portland, Oregon, area were also being sold to biological supply houses by the 1950's (Miller and Van Hyning 1970), and are one of several other possible sources of introductions. So, the relationship between the present-day *Pacifastacus* near Bozeman and those that Merino Mike may have introduced is unclear.

3.6.2 | *Faxonius virilis*

In 1934, a resident new to Montana (west of the Divide) expressed dissatisfaction at finding no "craw-daddies" in the local creeks and rivers (Dingerville 1934) (Figure 3). Learning of this, a coworker, Tom Cummings, "brought one to the cubicle the other day. It was a vigorous specimen, of medium size. He got it at Nine Pipes [in the CRB], where, he says, there are many more. How did they get to Montana? Did some lonesome Middle-Westerner import them, as another did the dandelion long ago?" In 1950, an article noted that "crayfish are just beginning to gather on the screen this week ... The crayfish ... are good feed for the larger game fish in Lake Ronan[11] ... A fish was caught in the lake last year that had 11 crayfish inside of it" (Sunfish Raked 1950) (Figure 3). The only species now known from those water bodies is *F. virilis*, which is nonnative west of the Divide (unpublished data; Table 2).

East of the Divide, a newspaper article (Untitled article 1940a) made crayfish seem like a novelty in the upper Missouri River drainage (upstream of Great Falls) in 1940: "Frank Rose, Ennis grocer, this week found a living crayfish on the banks of the Madison River, the only one ever known to have been found in the river. The small fresh water lobster is very plentiful in the south and middle west but is practically unknown in this part of the country. Consequently, the Rose grocery has been a popular place during the past week while the crayfish or "crawdad" as he is popularly known has been on display." A contemporary article added that Ernest Vetter Jr. also found a crayfish in the Gallatin River (Untitled article 1940b). These reports suggests that *F. virilis* may have been introduced to the Madison and Gallatin rivers prior to 1940. If the crayfish had gradually moved up the river on their own, finding one in the region probably would not have seemed a novelty. An introduction to Ennis Lake seems likely. Stories in newspapers of crayfish presence, using specimens in biology classrooms, and advocating for their use in fishing, became common across the state by the mid-twentieth century.

4 | Conclusion

Knowing whether species are native or nonnative, or recognizing them as cryptogenic (or data deficient, sensu Essl et al. 2018) when uncertainty exists, is essential to making appropriate management and conservation decisions and valid scientific inferences (Essl et al. 2018; Haydar 2012). Bringing multiple lines of evidence to bear on the provenance of cryptogenic species is likely to lead to better inferences about species' origins (Essl et al. 2018). Historical and indigenous knowledge are two types of evidence that have been underutilized in addressing questions of species' origins, especially for aquatic fauna. While such sources have limitations that should be acknowledged, they can provide valuable insights, especially when used in conjunction with other types of information. While conclusions drawn from historical evidence have engendered controversy in some cases,

TABLE 2 | All Montana crayfish specimens collected prior to 1980 that were in the Smithsonian National Museum of Natural History online database as of 18 March 2022.

USNM catalog number	Scientific name	Year collected	River basin	County	Locality	Latitude	Longitude
117,901	*Faxonius virilis*	1948	Columbia	Lake	Lake Mary Ronan	47.9294	−114.392
89,815	*Faxonius virilis*	1949	Columbia	Lake	Near Charlo, irrigation ditches	47.4369	−114.17
310,561	*Faxonius virilis*	1949	Columbia	Lake	Reservoir on Ninepipe Bird Refuge; 6 miles South Ronan	n/a	n/a
96,235	*Faxonius virilis*	1949	Columbia	Lake	Lake Mary Ronan Tuffin Camp	47.943	−114.395
310,560	*Pacifastacus leniusculus trowbridgii*	1954	Columbia	Ravalli	Bitter Root River		
192,827	*Faxonius virilis*	1958	Columbia	Flathead	Lake Mary Ronan	47.9333	−114.383
310,559	*Pacifastacus leniusculus trowbridgii*	1959	Columbia	Ravalli	Bitter Root River	n/a	n/a
117,904	*Faxonius virilis*	1946?	Missouri	Gallatin	Logan, Gallatin River, tributary of Missouri River	45.8855	−111.418
85,501	*Faxonius virilis*	Pre-1949	Missouri	Broadwater	Missouri River near Highway and Ry. bridge north of Townsend	48.0225	−105.809
96,224	*Faxonius virilis*	1951	Missouri	Broadwater	Missouri River just North of Townsend, at town park	48.0225	−105.809
117,165	*Faxonius virilis*	Pre-1960	Missouri	Lewis and Clark	Missouri River near Hansen Dam	46.6098	−111.698
105,888	*Faxonius virilis*	1960	Missouri	Daniels	Middle fork of Poplar River, near Karst Beach, 26 miles NW of Scobey near International border	48.8177	−105.483
105,889	*Faxonius virilis*	1960	Missouri	Cascade	Sun River West of Great Falls	47.509	−111.999

Note: Records are sorted by river basin then year collected. The *Pacifastacus leniusculus trowbridgii* specimens collected in the 1950s were identified in 2001, presumably using the Miller and Van Hyning (1970) guidance, suggesting that they were morphologically similar to either the Chehalis group or *P. leniusculus*, as characterized by Larson et al. (2012). One of us (SBA) re-examined the specimens and concluded that they fell within the range of morphological variation seen in *P. leniusculus* that we collected from the Clark Fork River drainage and differed from the *Pacifastacus* sp. that we collected. Locality spellings remain as they appeared in the database, and missing coordinates are indicated by "n/a."

overall, the literature substantiates the value of historic sources in multidisciplinary approaches to biological queries.

Our case-study review of historical documents from 1789 to about 1950, and of dictionaries of indigenous languages, allowed us to make inferences about the origins of crayfishes in Montana. Natural scientists must recognize "history as an inveterate and iterative methodology" (Santana-Cordero et al. 2024) and so realize that one potential drawback of relying on historical sources is that earlier documents may be unearthed that controvert results found to date (e.g., Clavero et al. 2016; Lucey 1999; Matallanas et al. 2016a). However, because of the relatively short historical record in Montana, older written historical sources are unlikely to be uncovered in this case. Moreover, we found several smoking guns of crayfish introductions: news reports that stated or implied that crayfish were not known to be present in various areas of the state prior to the report, or that explicitly reported crayfish introductions. Documented evidence of actual introductions is rare but powerful in investigations of cryptogenic species' origins (Essl et al. 2018). We found no historical evidence of crayfish in Montana's CRB or Marias River drainage prior to the early twentieth century. In the upper Missouri River Basin, historical reports are less clear, with some indicating crayfish in the area by 1868, but others suggesting they were a novelty in 1940. If the 1868 article referred to a geographically-restricted population of *Pacifastacus* crayfish introduced by "Merino Mike" near Bozeman (a *Pacifastacus* population persists to the present day in a short segment of the East Gallatin River), then the novelty of crayfish in the Madison and Gallatin rivers in 1940 might make sense. Now, additional types of information should be applied to the question of crayfish origins in the state.

We encourage biologists to more regularly consider whether species are cryptogenic, rather than assuming that they are native just because they were present when biologists first turned their attention to them. This will likely result in more frequent application of the label cryptogenic. We also encourage a greater fusion of biological and ecological research with other types of information, such as historical research and indigenous knowledge, whether to address species' native status or other biological or ecological questions. In the case of Montana crayfish origins, potentially informative future research could incorporate: the genetics of crayfish (ongoing), as well as of their parasites and commensals (Füreder et al. 2009; Larson and Williams 2015); biogeography; archaeology; and collaborations with interested indigenous peoples across the state to incorporate their traditional knowledge about the issue. As we approach 90 years since the reported introduction of *Pacifastacus* to the Bitterroot River drainage, oral histories with long-time residents of the area could be informative. While answers to questions about cryptogenic species' origins will often be tentative (Essl et al. 2018), responsible conservation decision-making requires scientists to bring all possible resources to bear in critically examining questions about species' native distributions.

Author Contributions

Hampton L. Kennedy: conceptualization (equal), investigation (equal), methodology (equal), project administration (supporting), resources (equal), writing – original draft (equal), writing – review and editing (equal). **Susan B. Adams:** conceptualization (equal), investigation (equal), methodology (equal), project administration (lead), resources (equal), writing – original draft (equal), writing – review and editing (equal).

Acknowledgments

The historical research benefited from conversations with David Schmetterling and Stacy Schmidt (MFWP), David Stagliano (Montana Biological Survey), and Chris Frissell and students in his Introduction to Hydrology class, Fall 2023 (Salish-Kootenai College, Ronan, MT). Bill Whitfield (Ravalli County Museum) researched the location of the Thornton Bass Ponds. Carl Smith (FS) prepared GIS maps. Stacy Schmidt and David Schmetterling were integral to the statewide crayfish project that was the genesis of this manuscript, and numerous MFWP personnel, most notably Lindsey Gilstrap, partnered in sampling. Many, many others, including biologists with the Crow Nation, Blackfeet Nation, Confederated Salish and Kootenai Tribes, USFS, and US Bureau of Land Management, American Fisheries Society Hutton Scholars, and more, assisted with crayfish sampling within their jurisdictions.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Related WIREs Articles

Identifying anthropogenic legacy in freshwater ecosystems

Endnotes

[1] William Broughton's mapping of 100 miles of the Columbia River from its mouth as part of George Vancouver's expedition in 1792 proved valuable to the Corps of Discovery Expedition (Vancouver 1984). Robert Gray named the river in 1792 as part of his Columbia Rediviva Expedition (Howay 1990). But neither Vancouver's nor Gray's expedition journeyed far inland.

[2] See Figure 1 in Knowles and Knowles (1993). A bibliography of literature and papers pertaining to pre settlement wildlife and habitat of Montana and adjacent areas. FaunaWest Wildlife Consultants. p.4.

[3] "Pheasants" probably referred to ruffed grouse (*Bonasa umbellus*), and "prairie Wolfe" to coyote (*Canis latrans*).

[4] For Wyeth's route, see Figure 6 in Knowles and Knowles (1993). A bibliography of literature and papers pertaining to pre settlement wildlife and habitat of Montana and adjacent areas. FaunaWest Wildlife Consultants. p.13.

[5] For Thompson's route through Montana, see Figure 3 in Knowles and Knowles (1993). A bibliography of literature and papers pertaining to pre settlement wildlife and habitat of Montana and adjacent areas. FaunaWest Wildlife Consultants. p. 10.

[6] For the War Department survey route, See Figure 13 in Knowles and Knowles (1993). A bibliography of literature and papers pertaining to pre settlement wildlife and habitat of Montana and adjacent areas. FaunaWest Wildlife Consultants. p. 26.

[7] For DeSmet's travels, See Figure 8 in Knowles and Knowles (1993). A bibliography of literature and papers pertaining to pre settlement wildlife and habitat of Montana and adjacent areas. FaunaWest Wildlife Consultants. p.16.

[8] For Hayden's survey route, See Figure 14 iKnowles and Knowles (1993). A bibliography of literature and papers pertaining to pre

settlement wildlife and habitat of Montana and adjacent areas. FaunaWest Wildlife Consultants. p. 26.

[9] For Raynold's route, See Figure 16 in Knowles and Knowles (1993). A bibliography of literature and papers pertaining to pre settlement wildlife and habitat of Montana and adjacent areas. FaunaWest Wildlife Consultants. p. 28.

[10] "On Thornton Farm" The Missoulian, Oct 6, 1939, placed the Thornton bass ponds just north of the "old Bitter Root Inn," and the inn appears to have been between Stevensville and Florence, MT (https://flwright.org/explore/bitter-root-inn [accessed Mar. 8, 2024]). Steiner (2009) noted that Porter Hill Road passes through the north end of the inn site Steiner, DM. 2009 Bitter Root Inn, near Stevensville, Montana (1908—S.145). http://www.steinerag.com/flw/Artifact%20Pages/PhRtS145.htm. [Accessed Apr. 24, 2024].

[11] Presumably refers to Lake Mary Ronan.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.