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A systematic revision of the genus *Juga* from fresh waters of the Pacific Northwest, USA (Cerithioidea, Semisulcospiridae)

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Abstract. *Juga* is a genus of freshwater snails distributed from northern Washington to central California. The taxonomy and classification of the genus has a long and complex history, driven mainly by the features of their highly variable shells. The number of recognized species has fluctuated from ~9 to 11; however, it has been claimed that the actual diversity may be three times that number. We here present a systematic revision using a recently published molecular phylogeny as a framework, which supported the interpretation that there are only nine valid species. Comprehensive review of type material and original descriptions for all available species-group names indicates that almost all species previously considered valid were para- or polyphyletic grades of organization in shell morphology. Most species previously suggested to be putatively new were confirmed to be morphological variants of species already described. Species accounts include complete synonymies and partial chresonymies; the shells and radulae are illustrated and described. Lectotypes are designated for *Melania plicifera* Lea, 1838, *M. silicula* Gould, 1847, and *M. rudens* Reeve, 1860. Three species, *Juga caerulea* sp. nov., *J. canella* sp. nov., and *J. douglasi* sp. nov., are described as new and one species is excluded from the genus. The subgenera *Calibasis* D.W. Taylor, 1966 and *Idabasis* D.W. Taylor, 1966 are synonymized with *Juga*.

Keywords. Distributions, radular morphology, shell morphology, synonymy, conservation.

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Introduction

Juga H. & A. Adams, 1854 is a genus of large-bodied, freshwater snails from the Pacific Northwest of the United States. Adults are ~1.5–3.5 cm in shell length and are conspicuous members of their benthic macroinvertebrate communities. They prefer cold, oligotrophic, well oxygenated waters of perennial seeps and springs, spring runs, creeks, and rivers with stable bottoms, but some are tolerant of low energy conditions in lakes (Fig. 1). They can reach densities of 1500 individuals/m^2 and are found on a wide variety of substrates from mud to sand, deciduous leaf litter, stones, submerged wood, and the spray-moistened sides of boulders (Fig. 2) where they graze on periphyton and detritus. The sexes are separate, and females are oviparous, depositing thick, finger-like, gelatinous egg mass (Fig. 2B) containing hundreds of irregularly arranged eggs on the undersides of hard surfaces including stones and sunken logs. Hatchlings do not leave the egg mass immediately, often not before adding at least an additional two whorls to the shell. They reach sexual maturity after three years with life spans on the order of five to seven and possibly as many as nine years (Diamond 1982; Hawkins & Furnish 1987; Furnish 1990; Frest & Johannes 1995a, 1996, 1998, 2005, 2010; Furnish *et al.* 1997).

The name *Juga* also has been applied to semisulcospirids from the Russian Far East and adjacent regions of China and Korea (e.g., Zatravkin 1986; Bogatov & Zatravkin 1990; Prozorova 1990; Prozorova & Rasshepkina 2002, 2003). These were allocated to '*Parajuga*' Prozorova & Starobogatov, 2004 (Starobogatov *et al.* 2004), which is not a nomenclaturally available name (see Strong & Köhler 2009). Although its circumscription was unclear, the family-group name Jugidae Starobogatov, Prozorova, Bogatov & Sayenko, 2004 was also established apparently for Russian Far East species but is similarly nomenclaturally unavailable and considered a synonym of Semisulcospiridae J.P.E. Morrison, 1952 (Bouchet *et al.* 2017). Rasshepkina (2007) used this name at the rank of subfamily to unite '*Parajuga*' and *Juga*. Vinarski & Kantor (2016) followed Rasshepkina (2009) in returning the Russian species to *Juga*. However, molecular analyses have shown that at least one of these species, *Melania amurensis* Gerstfeldt, 1859, is more closely related to Asian species than to North American *Juga* (Strong & Köhler 2009; Köhler 2016, 2017). Köhler (2016) transferred this species to *Koreoleptoxis* Burch & Jung, 1988 and later (Köhler 2017) hypothesized that other East Asian semisulcospirids would also fall here. Since then, Du *et al.* (2019a, 2019b) have significantly expanded our understanding of relationships among semisulcospirids from China, but nominal taxa from the Russian Far East have yet to be comprehensively revised and remain in taxonomic limbo. We agree with Köhler (2017) that their affinities likely lie among Asian species and do not consider them further here.

The American species of *Juga* are distributed from northern Washington to central California, primarily in Pacific drainages to the west of the Cascades at low to medium elevations. The northern end of their distribution is roughly coincident with the southern limit of the Cordilleran ice sheet [Late Wisconsin (Fraser) glaciation] on the Olympic Peninsula and the southeastern edge of Puget Sound in Washington State and extends to southern Sonoma County in central California. In Oregon and Washington, verified records show they extend east along the Columbia River past the mouth of the John Day River. East of the Cascades in Oregon *Juga* is mostly absent, apart from the Deschutes and upper Klamath watersheds and the John Day headwaters in the northeastern part of the state. In California, they extend into the upper reaches of the Pit River drainage in the northeastern part of the state and south along the western flank of the Sierra Nevada primarily in the Sacramento River drainage, including the Feather, Yuba, and American Rivers, as well as the northern Mokelumne River drainage (Cosumnes River). They also occur sporadically in interior drainages of the northern Great Basin in northeastern California, south-central

Oregon, and northwestern Nevada. Reports of occurrences in British Columbia, Idaho, Colorado, Utah, Montana, and Wyoming (e.g., Bland & Cooper 1861; Tryon 1865; Ingersoll 1875, 1876; Dall 1910; Henderson 1924, 1929; Johnson *et al.* 2013) are erroneous (see e.g., Henderson 1936a; Frest & Johannes 2000b, 2010, and references therein; Campbell *et al.* 2016).

The fossil record of *Juga* reaches the early Tertiary (Taylor 1988) but does little to clarify the origins of the genus. In the most recent treatment, Frest & Johannes (2010) recognized 20 valid fossil species, not all of them formally described, ranging in age from Eocene to Pliocene. Reliable fossil occurrences

Fig. 1. Habitats of *Juga* H. Adams & A. Adams, 1854 in the Pacific Northwest. **A**. Springs and spring runs. Bitner Ranch, Nevada (*J. acutifilosa* (Stearns, 1890)). **B**. Spring runs. Phipps Meadow, Oregon (*J. caerulea* sp. nov.). **C**. Spring-fed creeks. Shoat Springs, Copco Rd, Oregon (*J. canella* sp. nov.). **D**. Creeks. Hat Creek, California (*J. douglasi* sp. nov.). **E**. Large rivers. Rogue River at Carpenter Island Park, Oregon (*J. nigrina* (I. Lea, 1856)). **F**. Lakes. Baum Lake, California (*J. occata* (Hinds, 1844)).

show that the genus was well established in what is now Washington State by the Late Eocene. At its peak during the Miocene and Pliocene, *Juga* extended beyond its present range into eastern Washington, Idaho, the Nevada Great Basin, to southern Central California (Frest & Johannes 2010). The most recent common ancestor of *Juga* is hypothesized to have ranged across the Beringean land bridge during warmer episodes of the Cenozoic and may have arrived in North America during the Paleocene-Eocene Thermal Maximum (Strong & Köhler 2009; Campbell 2019).

Fig. 2. Life habit. **A**. On leaves. Drift Creek on Cascade Highway NE, Oregon (*J. plicifera* (I. Lea, 1838)). **B**. Under submerged stones (with gelatinous egg masses). Youngs River Falls, just upstream of Youngs River Rd, Oregon (*J. plicifera*). **C**. On mud and leaves. Muddy Hollow, Oregon (*J. bulbosa* (A. Gould, 1847)). **D**. On submerged wood. Unnamed Creek at Skookum Creek Rd, Oregon (*J. canella* sp. nov.). **E**. On sand. Hat Creek, California (*J. douglasi* sp. nov.). **F**. On the spray-moistened sides of boulders. Pit River at U.S. Hwy 299, California (*J. occata* (Hinds, 1844)).

Juga was originally established at the rank of subgenus as *Vibex* (*Juga*) in the Melaniidae Children, 1823 [= Thiaridae Gill, 1871 (1823); see Bouchet *et al.* 2017], a large, polyphyletic assemblage of freshwater Cerithioidea J. Fleming, 1822. As summarized elsewhere (see Strong & Frest 2007; Strong & Köhler 2009; Frest & Johannes 2010; Campbell 2019; Strong & Whelan 2019), the family classification of the genus has a long, complex history and, until recently, it was placed in the Pleuroceridae P. Fischer, 1885 (1863), which united oviparous freshwater species from North America in the Pleurocerinae, with oviparous and ovoviviparous species from Asia in the Semisulcospirinae Morrison, 1952 (Bouchet & Rocroi 2005). However, from early on, the origins of western North American 'melanians' and their potential affinities to Asian species have been speculated (e.g., Tryon 1865; Walker 1900; Dall,1910; Morrison 1954; Branson 1970; Taylor 1988). Based on molecular data and anatomical synapomorphies of the kidney, prostate, and pallial oviduct, Strong & Köhler (2009) transferred *Juga* to the Semisulcospirinae and elevated the subfamily to family rank, thereby restricting Pleuroceridae to species from temperate and subtropical regions east of the Rocky Mountains (Strong & Lydeard 2019).

The earliest species of *Juga* to be described were established in the catchall genus *Melania* Lamarck, 1799, a junior objective synonym of *Thiara* Röding, 1798. As this genus began to be dismantled, early authors dispersed western North American species to informal subdivisions of melanians or to different genera, but the resulting assemblages were no less polyphyletic and united species that would be placed in Pleuroceridae, Semisulcospiridae or Pachychilidae Fischer & Crosse, 1892 today (e.g., Adams & Adams 1854; Chenu 1859; Brot 1862, 1868). Lea (1862) established *Goniobasis* I. Lea, 1862 for 82 new species of American Melanidae [sic], in which he explicitly included some members of *Elimia* H. & A. Adams, 1854 (Pleuroceridae), which had been established earlier but was not in common use. However, like *Juga* before, both *Elimia* and *Goniobasis* were established without designation of a type species. That for *Elimia* was only validly designated by Pilsbry & Rhoads (1896: 496), and for *Goniobasis* by Hannibal (1912: 17). This contributed to lasting confusion and instability surrounding the application of these names (see Burch 1999, 2001).

In his treatments of North American fluviatile gastropods, Tryon (1864, 1866, 1873) considered *Juga* and *Elimia* – among other genus-group names with nomenclatural priority – to be synonyms of *Goniobasis*. In a footnote, Tryon (1864: 4) explained that "Mr. Lea is the first naturalist who has properly defined this genus, and his name *Goniobasis* must therefore stand, in preference to any of the prior names given to artificial sections by the Messrs. Adams". Despite the fact that Pilsbry & Rhoads (1896) earlier had synonymized *Juga* and *Goniobasis* with *Elimia*, the name *Goniobasis* continued in prevailing usage for western North American species (e.g., Pilsbry 1899; Walker 1918; Henderson 1929, 1935a; Goodrich 1942, 1944), sometimes explicitly as a matter of nomenclatural convenience (e.g., Henderson 1935b, 1936b). In a significant departure, Morrison (1954) placed western species along with eastern North American pleurocerids and semisulcospirids from Korea, China, and Thailand in his highly polyphyletic *Oxytrema* Rafinesque, 1819, which is now considered a synonym of *Pleurocera* Rafinesque, 1818.

The modern era was ushered in by Baker's (1963, 1967) subsequent designation of *Melania silicula* A. Gould, 1847 as the type species of *Juga* which brought much needed stability to the application of the name. Taylor (1966, 1981) united the American species currently placed in *Juga* and justified their separation at the genus level from eastern North American species based on their unique oviduct and spawn morphology. Taylor (1966) recognized four subgenera, three of which occur in the Recent fauna, distinguished by the sculpture of the early teleoconch. The foundation for Taylor's subgeneric classification had been laid by Pilsbry (1899) and Henderson (1929, 1936b) who emphasized the importance of shape and sculpture of the early whorls as taxonomic characters (Frest & Johannes 2010). Goodrich (1942) recognized three informal groupings reflecting shell sculpture that anticipated Taylor's classification, which was adopted by Burch & Tottenham (1980) and Burch (1982, 1989). However, sporadic use of the name *Goniobasis* for western North American species continued to modern times (e.g., Branson & Branson 1984, 1991).

The number of species of *Juga* recognized as valid, and their rank as species or subspecies, has fluctuated dramatically over its history. This is exemplified to absurd extremes by Hannibal (1912) in his sweeping revision of North American Recent and Tertiary freshwater gastropods who synonymized almost all western North American species with *Ambloxus pliciferus* (Lea, 1838). However, as Hannibal (1912: 168) himself predicted, his treatment was not met with "general approval". Building on the work of Goodrich (1942, 1944) the classification of Burch & Tottenham (1980) and Burch (1982, 1989) was the standard for many years and which recognized 12 species and subspecies distributed among Taylor's three subgenera. This was followed by Turgeon *et al.* (1988, 1998) who recognized nine species but did not consider subspecies and subgenera as was the convention throughout those works. Eleven valid species were recognized in the taxonomic authority list of Johnson *et al.* (2013).

In contrast to the prevailing views of the last forty years, Frest & Johannes produced a series of reports and field guides (e.g., 1993, 1995a, 1995b, 1996, 1998, 1999, 2000a, 2000b, 2001, 2005, 2007) wherein they promoted the claim that there are many more undescribed than described species of *Juga*, and that others undoubtedly remain to be found. Many ostensibly new species were recognized in these works and left in open nomenclature, sometimes by different names in subsequent reports and, conversely, by application of the same name to different putative taxonomical entities. This confusion was compounded by the fact that species typically were not figured, sometimes were not accompanied by a description or diagnosis, and few specimens were deposited in vouchering institutions. Despite pervasive inconsistencies and ambiguity, some of these entities were recommended for protection at the state or federal level, and even petitioned for listing under the Endangered Species Act (Frest & Johannes 1993, 1995a; USFWS 2011). Moreover, these reports have informed state, federal, and non-profit agency strategy documents, environmental impact assessments, wildlife action plans, conservation assessments, and management plans (e.g., FEMAT 1993; Duncan 2005, 2008; Oregon Natural Heritage Advisory Council 2010; Abele 2011; Washington Department of Fish and Wildlife 2015; ISSSSP 2022; USDA 2022; Xerces Society 2022).

These disparate views on species diversity reflect widely differing opinions as to the significance of shell morphology and sculpture including size, color, and the strength and persistence of spiral and axial sculpture (e.g., Pilsbry 1899; Henderson 1929, 1935a, 1936b; Goodrich 1942; Taylor 1966, 1981; see Frest & Johannes 2010: table 2). These features are highly variable within species of *Juga* and frequently intergrade between them. Despite variation in sculpture with environment, and the lack of sharp distinctions between species (e.g., Henderson 1936b; Goodrich 1942), there is a propensity for recognizable forms to occupy different geographic areas (Henderson 1936b: 275). This pattern, combined with the assumption that each drainage should have its own unique assemblage of species (e.g., Branson & Barrett 1981), has encouraged a proliferation of names.

Like previous morphological estimates, two recent studies applied molecular data to resolve the diversity of *Juga* and came to very different conclusions. Campbell *et al.* (2016) assembled a dataset of partial COI sequences for 103 individuals and partial 16S sequences for 35 individuals from ~85 sites and recognized 33 operational taxonomic units (OTUs), none of which were geographically widespread, representing almost all available nominal species-group names and numerous undescribed forms. However, some populations were represented by only a single sequenced specimen, and not all OTUs were monophyletic on the resulting gene trees, sometimes separated by less than 1% uncorrected pairwise distances in COI. Overall, inadequate sampling prevented meaningful conclusions regarding what comprises intra- versus interspecific levels of genetic variation.

Strong & Whelan (2019) reassessed the conclusions of Campbell *et al.* (2016) with expanded population sampling and a three-gene mitochondrial and nuclear dataset. They included samples from ~100 sites and when possible sequenced at least five individuals per population; 560 individuals were sequenced for both COI and 16S and a subset of 272 individuals was also sequenced for ITS1. They explored the data using a range of phylogenetic and species delimitation methods. The preferred hypothesis (Fig. 3) supported the interpretation that there are only nine valid species, comprising a mixture of geographically widespread species and narrow-range endemics. These nine species corresponded to the nine clades recovered by Campbell *et al.* (2016: fig. 2, clades A–I) but differed in the interpretation of their composition and taxonomic rank. Features of the teleoconch traditionally relied upon for species

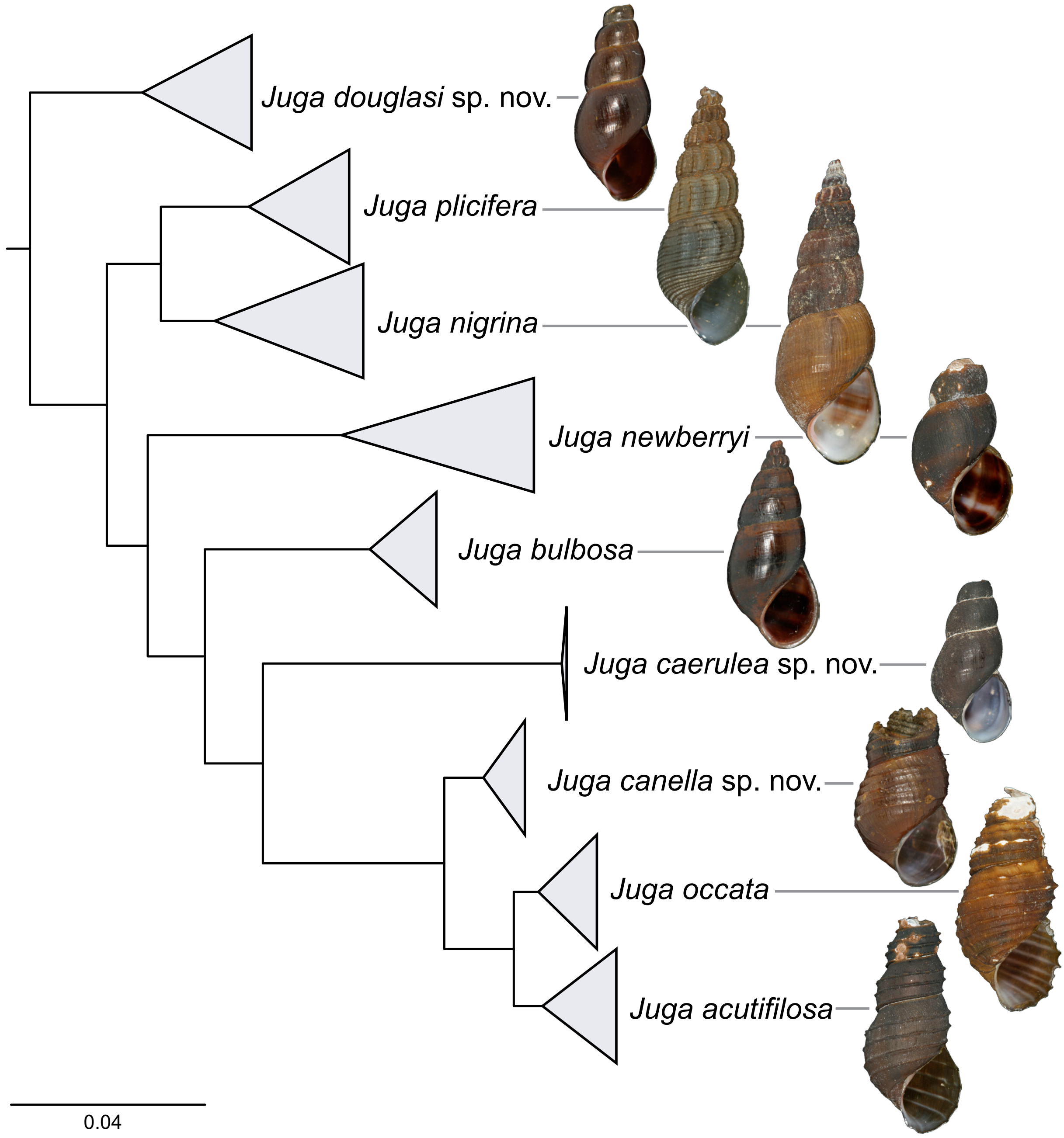


Fig. 3. Bayesian phylogram for 274 individuals based on a concatenated COI, 16S and ITS1 dataset, with nonconserved regions of the ITS1 dataset removed. Terminals collapsed and outgroups trimmed for simplicity. Scale bar indicates number of nucleotide substitutions per site. Modified from Strong & Whelan (2019). Shells shown to same scale.

diagnoses and subgeneric distinctions were confirmed to be variable within species, sometimes at a single site (Strong & Whelan 2019).

In anticipation of the molecular analyses that were eventually published in Campbell *et al.* (2016), Frest & Johannes (2010) prepared a review of the nominal taxa allocated to *Juga* and of their type localities, type material, and taxonomic status. This review appeared in volume 43/44 of *Malacological Review* (Museum of Zoology, University of Michigan) for 2010–2011; however, we have not been able to establish the actual date of publication. The existing physical and digital archives at the University of Michigan cannot refine the date of printing or distribution (T. Duda pers. com.). The volume has not been widely distributed and was not stamped upon receipt at the University of Michigan library. Volume 41/42 for 2008–2009 was stamped as "Dec 2011" (T. Duda pers. com.), but as far as we can determine, volume 43/44 may have appeared as late as 2018. There are no nomenclatural acts in this work and for simplicity we refer to it as 'Frest & Johannes 2010'.

In their review (Frest & Johannes 2010), nomina considered taxonomically valid were accompanied by descriptions of shell morphology and distribution, and occasional elaborations on the ecology and conservation status. Of the available species-group names for Recent *Juga*, they recognized 22 as taxonomically valid or potentially so, three as synonyms, and four as unrecognizable and/or not relocated. They also provided a list of names that they considered "invalid" or incorrectly used in combination with the genus-group name *Juga* and recognized 20 fossil species ranging in age from Eocene to Pliocene. While much valuable information was provided, the type material was not illustrated and the material examined was not listed or figured. The taxonomical framework was consistent with their previous works in considering that most nominal species represent distinct, valid species and that many records and historical museum lots, "do not fit readily into any named category" (Frest & Johannes 2010: 3). The information relevant for the nine species subsequently confirmed as valid in the molecular analyses of Strong & Whelan (2019) is highly fragmented and disorganized.

Thus, using the molecular phylogeny of Strong & Whelan (2019) as a framework, we here present a systematic revision of American species of the genus *Juga*. Species accounts include complete synonymies and partial chresonymies; the shells (including relevant type material) and radulae are illustrated and described. Distribution maps feature sequenced specimens, historical museum records, and type localities when well constrained. Three species are described as new.

Material and methods

We examined and photographed type material for almost all available species-group names for Recent *Juga*, and two species excluded from *Juga*. Material examined includes sequenced specimens from Strong & Whelan (2019) and specimens primarily in the collections of the U.S. National Museum (USNM) complemented by material in the Academy of Natural Sciences, Philadelphia (ANSP), California Academy of Natural Sciences (CASIZ), University of Michigan Museum of Zoology (UMMZ), and the Florida Museum of Natural History (UF) for geographic areas not well represented in the USNM collections. When possible, primary types are figured.

Synonymies are as comprehensive as possible given the limitations of ascribing some nominal taxa with vague or incorrect type localities to valid species. Chresonymies are not comprehensive. We have treated the recent classifications, identification guides, and authority lists in routine use (Burch & Tottenham 1980; Burch 1982, 1989; Turgeon *et al.* 1988, 1998; Johnson *et al.* 2013), and have allocated the species of *Juga* used in recent morphological and molecular analyses (Holznagel & Lydeard 2000; Lydeard *et al.* 2002; Prozorova & Rasshepkina 2004; Lee *et al.* 2006; Strong & Frest 2007; Ó Foighil *et al.* 2009; Strong & Köhler 2009; Strong *et al.* 2011; Köhler 2016, 2017). Apart from newly established nominal taxa, we have not comprehensively treated historical taxonomic rearrangements (e.g., Adams &

Adams 1854; Chenu 1859; Reeve 1860; Brot 1862, 1868; Tryon 1864, 1865, 1866, 1873; Pilsbry 1899; Hannibal 1912; Walker 1918; Henderson 1929, 1935a, 1935b, 1936b; Goodrich 1942; Taylor 1975a, 1981), which departed sometimes significantly from recent views and were often highly polyphyletic. Some of these rearrangements (Tryon 1865, 1873; Pilsbry 1899; Walker 1918; Henderson 1929, 1935a, 1936b; Goodrich 1942, 1944; Burch & Tottenham 1980; Burch 1982, 1989) were cross-referenced in Graf (2001) and in Frest & Johannes (2010: table 2). Frest & Johannes (2010 and references therein: table 3) also treated the popular works of Keep from 1887 to 1935.

In order to mitigate some of the profound confusion perpetuated by Frest & Johannes in their unpublished reports and field guides, we have attempted to place in synonymy the many taxa they recognized in open nomenclature, particularly those proposed to merit conservation action. These allocations should be considered tentative in areas where species ranges overlap given the aforementioned paucity of figures, lists of material examined, and of vouchers, but are robust when samples were sequenced by Campbell *et al.* (2016). Our coverage of their reports is not comprehensive as there are many and some are difficult to access. Frest & Johannes (1999) listed as “in press” a field guide that they had produced on “Northwestern US Sensitive nonmarine mollusks”, but it has never been published and was not examined for this work.

Radular and shell morphology was documented according to the methods described in Strong & Bouchet (2020). Distribution maps include sequenced specimens from Campbell *et al.* (2016) and Strong & Whelan (2019), historical museum records, and type localities when well constrained. Some of the sites referenced in Campbell *et al.* (2016) also were surveyed by Thomas Grace (Caithness Energy, Reno, Nevada) who deposited large series in CASIZ, UF, and USNM and which allow us to match sequenced OTUs with morphotypes. However, the lack of diagnostic shell characters makes identifying some historical museum specimens challenging, particularly those that are poorly or mislocalized. This is compounded by the fact that many historical lots are small, contain shells in poor condition, and do not preserve ontogenetic series. Given that the geographical ranges of recognized species are usually allopatric, and even when sympatric rarely co-occur at a site, historical specimens, including types, have been identified using a combination of geographical information and comparison of shell characters to sequenced vouchers. This approach is robust in most cases, but identification of historical specimens particularly from the Sierra Nevada should be regarded with caution given the few sequenced populations from this area.

Abbreviations

Repositories

ANSP = Academy of Natural Sciences, Philadelphia, PA, USA
CASIZ = California Academy of Natural Sciences, San Francisco, CA, USA
CMML = Canadian Museum of Nature, Ottawa, Canada
MCZ = Museum of Comparative Zoology, Cambridge, MA, USA
NHMUK = Natural History Museum, London, UK
SBMNH = Santa Barbara Museum of Natural History, Santa Barbara, CA, USA
UCM = University of Colorado Museum, Boulder, CO, USA
UF = Florida Museum of Natural History, Gainesville, FL, USA
UMMZ = University of Michigan Museum of Zoology, Ann Harbor, MI, USA
USNM = National Museum of Natural History, Washington D.C., USA

Other abbreviations

L = shell length
leg. = legit
spm/s = specimen/s

Results

Taxonomic account

Phylum Mollusca Linnaeus, 1758
Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Superfamily Cerithioidea J. Fleming, 1822
Family Semisulcospiridae J.P.E. Morrison, 1952

Genus ***Juga*** H. Adams & A. Adams, 1854

Vibex (*Juga*) H. & A. Adams, 1854. Type species: *Melania silicula* A. Gould, 1847, by subsequent designation (Baker 1963: 35).
Juga (*Calibasis*) D.W. Taylor, 1966. Type species: *Melania* (?*Goniobasis*) *acutifilosa* Stearns, 1890, by original designation. **Syn. nov.**
Juga (*Oreobasis*) D.W. Taylor, 1966. Type species: *Melania newberryi* I. Lea, 1860, by original designation.
Juga (*Idabasis*) D.W. Taylor, 1966†. Type species: *Juga chrysopylica* D.W. Taylor, 1966†, by original designation. **Syn. nov.**

Diagnosis

Shell dextral, smooth to strongly plicate, lirate or cancellate, medium to large in size, ~1.5–3.5 cm in length. Operculum corneous, brown, paucispiral with eccentric nucleus. Gonochoristic, oviparous, with broad, shallow, triangular ovipositor pore; convoluted gonoductal groove, proximal albumen gland u-shaped; seminal receptacle present; tightly interlocking folds of lateral and medial laminae of prostate gland; gelatinous, finger-like egg masses with large numbers of eggs. Radula taenioglossate, rachidian basal cusps weakly developed or lacking. Midgut with comparatively narrow glandular pad and wide, shallow, crescentic groove; digestive gland duct vestibule receiving several ducts of digestive gland.

Remarks

Until recently, extant species of *Juga* were distributed among three subgenera, based on the sculpture of the early whorls (Taylor 1966): *Juga* s. str. with strong and sometimes shouldered plications or ribs, *Calibasis* with spiral or lirate sculpture sometimes giving a frilled appearance, and *Oreobasis* with essentially smooth early whorls. Taylor (1966) also recognized a fourth subgenus with cancellate early sculpture, *Idabasis*, based on the Blancan fossil, *Juga chrysopylica* Taylor, 1966. According to Frest & Johannes (2010: 7), Taylor further subdivided *Oreobasis* into two sections in an unpublished checklist dated from 1977 which we have not seen.

Strong & Frest (2007) synonymized *Oreobasis* with *Juga* s. str. given their morphological similarity in reproductive and alimentary anatomy. Campbell *et al.* (2016) concluded that none of the three extant subgenera were monophyletic but that clades of equivalent rank merited recognition. The molecular analysis of Strong & Whelan (2019) confirmed that the strength and persistence of spiral and axial sculpture are variable within and between species, sometimes among conspecific individuals at a single site, and that subgeneric designations based primarily on shell sculpture are not meaningful. Moreover, the molecular phylogeny did not reveal clades that would merit recognition at the rank of subgenus. Thus, we here further synonymize *Calibasis* and *Idabasis* with *Juga*.

Juga plicifera (I. Lea, 1838)
Figs 4–6

Melania plicifera I. Lea, 1838: 93, pl. 23 fig. 90.
Melania silicula A. Gould, 1847: 224–225.
Melania rudens Reeve, 1860: unpaginated, species 224, pl. 33 fig. 224.
Goniobasis plicifera var. *bulimoides* Tryon, 1865: 238, pl. 24 figs 5–6.
Goniobasis plicifera var. *oregonensis* Tryon, 1865: 238, pl. 24 fig. 4.
Goniobasis hemphilli Henderson, 1935a: 96–97, pl. 4 fig. 1. **Syn. nov.**
Goniobasis hemphilli dallesensis Henderson, 1935a: 97, pl. 4 fig. 2. **Syn. nov.**

Melania silicula – Gould 1852: 141–142; “1856” [1860]: pl. 10 fig. 164–164a; 1862: 46.
Goniobasis hemphilli – Henderson 1936b, pl. 2 fig. 1.
Goniobasis hemphilli dallesensis – Henderson 1936b, pl. 2 fig. 2.
Juga (*Juga*) *plicifera* – Burch & Tottenham 1980: 152, fig. 448. — Burch 1982: 41, fig. 448; 1989: 152, fig. 448. — Holznagel & Lydeard 2000: 237.
Juga (*Juga*) *silicula* – Burch & Tottenham 1980: 152, fig. 449 (in part). — Burch 1982: 41, fig. 449 (in part); 1989: 152, fig. 449 (in part). — Neitzel & Frest 1992: B.25. — Holznagel & Lydeard 2000: 237. — Strong & Frest 2007: 45. — Johannes 2010b: 5.
Juga (*Juga*) *hemphilli dallesensis* – Burch & Tottenham 1980: 152, fig. 455. — Burch 1982: 41; 1989: 152, fig. 455. — Frest & Johannes 1993: 62; 1995a: 172; 2001: 59; 2010: 9, 26, fig. 2b. — Campbell *et al.* 2016: 160.
Juga silicula – Hawkins & Furnish 1987: 209. — Furnish 1990: 1; 2007: 14, fig. 6, lower left. — Turgeon *et al.* 1988: 65; 1998: 67. — Lee *et al.* 2006: 316. — Ó Foighil *et al.* 2009: 305. — Strong & Köhler 2009: 486. — Strong *et al.* 2011: 53. — Johnson *et al.* 2013: 282. — Köhler 2016: 270.
Juga plicifera – Turgeon *et al.* 1988: 65; 1998: 67. — Lee *et al.* 2006: 316. — Ó Foighil *et al.* 2009: 305. — Strong & Köhler 2009: 486. — Johnson *et al.* 2013: 263, 282, pl. 1.
Juga hemphilli – Turgeon *et al.* 1988: 65; 1998: 67. — Ó Foighil *et al.* 2009: 305. — Johnson *et al.* 2013: 282.
Juga (*Juga*) *plicifera plicifera* — Neitzel & Frest 1992: B.25 (in part). — Frest & Johannes 2001: 60; 2010: 11, 46 [as probably valid]. — Johannes 2015: 23. — Campbell *et al.* 2016: 160.
Juga (*Juga*) *hemphilli hemphilli* – Frest & Johannes 1993: 62; 1995a: 173; 2001: 59; 2010: 10, 35. — Campbell *et al.* 2016: 160.
Juga (*Juga*) *hemphilli* n. subsp. – Frest & Johannes 1993: 63.
Juga (*Juga*) n. sp. 1 – Frest & Johannes 1993: 63 (in part); 1995a: 175 (in part); 2001: 60 (in part).
Juga (*Juga*) n. sp. 3 – Frest & Johannes 1993: 63.
Juga (*Juga*) *hemphilli* n. subsp. 1 – Frest & Johannes 1995a: 174; 2001: 60.
Juga (*Juga*) *silicula silicula* – Frest & Johannes 2001: 60; 2010: 11, 50, fig. 2f. — Campbell *et al.* 2016: fig. 2c.
Juga nigrina – Lydeard *et al.* 2002: 401. — Strong & Köhler 2009: 486. — Strong *et al.* 2011: 53.
Juga sp. 1 – Prozorova & Rasshepkina 2004: 90, figs 1, 2.
Juga sp. 2 – Prozorova & Rasshepkina 2004: 91, figs 1, 3.
Juga sp. 3 – Prozorova & Rasshepkina 2004: 91, figs 1, 4.
Juga sp. 4 – Prozorova & Rasshepkina 2004: 91, figs 1, 5.
Juga sp. 5 – Prozorova & Rasshepkina 2004: 91, figs 1, 6.
Juga/*Elimia hemphilli* – Lee *et al.* 2006: 314–316, fig. 1a–c.
Juga/*Elimia hemphilli dallesensis* – Lee *et al.* 2006: 314–316, fig. 1a–c.
Juga hemphilli dallesensis – Ó Foighil *et al.* 2009: 305.
Juga (*Juga*) *draytonii* – Frest & Johannes 2010: 10, 34 (in part). — Campbell *et al.* 2016: 160.
Juga (*Juga*) *plicifera bulimoides* – Frest & Johannes 2010: 28 [as possibly valid].

Juga (*Juga*) *plicifera oregonensis* – Frest & Johannes 2010: 44 [as likely valid]. — Campbell *et al.* 2016: 160.
Juga (*Juga*) n. sp. – Johannes 2010a: 7.
Juga (*Juga*) cf. *plicifera* – Johannes 2013b: 16.
Juga (*Juga*) cf. *silicula* – Johannes 2013b: 19.
Juga (*Juga*) *hemphilli* n. subsp. 2 – Johannes 2015: 23.
Juga plicata – Köhler 2016: 270 (error for *J. plicifera*).
Juga (*Juga*) OTU 1 – Campbell *et al.* 2016: 160.
Juga (*Juga*) OTU 2 – Campbell *et al.* 2016: 160.
Juga plicifera group – Strong & Whelan 2019: 89.

non *Juga* (*Juga*) *hemphilli hemphilli* – Burch & Tottenham 1980: 152, fig. 454. — Burch 1982: 41, fig. 454; 1989: 152, fig. 454. — Frest & Johannes 2010: fig. 2c. [= *Juga bulbosa*]
non *Juga*/*Elimia hemphilli* – Lee *et al.* 2006: 316, fig. 1d. [= *Elimia doolyensis*; see Ó Foighil *et al.* 2009]
non *Juga*/*Elimia hemphilli dallesensis* – Lee *et al.* 2006: 316, fig. 1d. [= *Elimia doolyensis*; see Ó Foighil *et al.* 2009]

Material examined

Lectotype of *Melania plicifera* I. Lea, 1838 (here designated) (Fig. 4A)
USA • "Wahlamat [sic, Willamette River], near its junction with the Columbia River"; T. Nuttall leg.; USNM 119244.

Paralectotypes of *Melania plicifera* I. Lea, 1838
USA • 23 spms; same collection data as for lectotype; USNM 1665628 (formerly USNM 119244X) • 1 spm; same collection data as for lectoype; MCZ 161911.

Lectotype of *Melania silicula* A. Gould, 1847 (here designated) (Fig. 4B)
USA • "Nisqually, Oregon [Territory]" [possibly Sequalitchew Creek; Strong & Frest 2007; Frest & Johannes 2010]; U.S. Exploring Expedition leg.; USNM 12137.

Paralectotypes of *Melania silicula* A. Gould, 1847
USA • 2 spms; same collection data as for lectotype; USNM 1665633 (ex USNM 12137).

Lectotype of *Melania rudens* Reeve, 1860 (here designated) (Fig. 4C)
USA • locality unknown; H. Cuming collection; NHMUK 20110170/1.

Paralectotypes of *Melania rudens* Reeve, 1860
USA • 2 spms; same collection data as for lectotype; NHMUK 20110170/2, NHMUK 20110170/3.

Lectotype of *Goniobasis plicifera* var. *bulimoides* Tryon, 1865 (designated by Baker 1964: 180) (Fig. 4D)
USA • "Willamette River, at Eugene City"; W.M. Gabb leg.; ANSP 27542.

Paralectotypes of *Goniobasis plicifera* var. *bulimoides* Tryon, 1865
USA • 4 spms; same collection data as for lectotype; W.M. Gabb leg.; ANSP 453835 (ex ANSP 27542).

Lectotype of *Goniobasis plicifera* var. *oregonensis* Tryon, 1865 (designated by Baker 1964: 186) (Fig. 4E)
USA • "Willamette River, near its junction with the Columbia"; R.E.C. Stearns leg.; ANSP 27550.

Paralectotypes of *Goniobasis plicifera* var. *oregonensis* Tryon, 1865 (Fig, 4E)
USA • 6 spms; same collection data as for lectotype; ANSP 467223 (ex ANSP 27550).

Holotype of *Goniobasis hemphilli* Henderson, 1935 (Fig. 4F)
USA • "Near Portland, Oregon" [possibly Johnson Creek; Frest & Johannes 1993, 2010]; Hemphill collection; UCM 21167a.

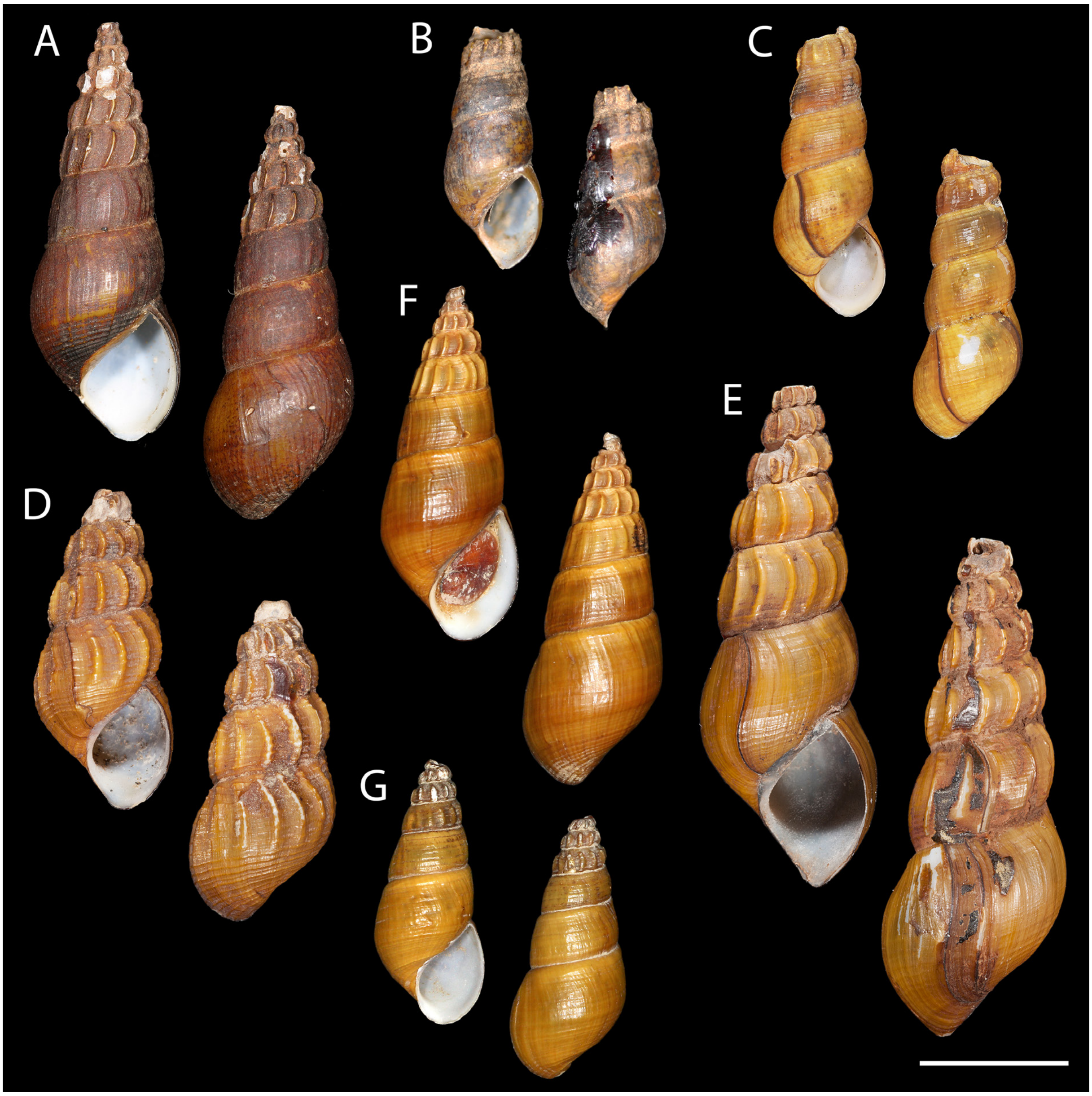


Fig. 4. Type material of *Juga plicifera* (I. Lea, 1838). **A**. *Melania plicifera* I. Lea, 1838. Lectotype, USNM 119244. **B**. *Melania silicula* A. Gould, 1847. Lectotype, USNM 12137. **C**. *Melania rudens* Reeve, 1860. Lectotype, NHMUK 20110170/1. **D**. *Goniobasis plicifera bulimoides* Tryon, 1865. Lectotype, ANSP 27542. **E**. *Goniobasis plicifera* var. *oregonensis* Tryon, 1865. Lectotype, ANSP 27550. **F**. *Goniobasis hemphilli* Henderson, 1935. Holotype, UCM 21167a. **G**. *Goniobasis hemphilli dallesensis* Henderson, 1935. Holotype, UCM 16016a. Scale bar = 1 cm.

Paratype of *Goniobasis hemphilli* Henderson, 1935
USA • 1 spm; same collection data as for holotype; UCM 21167b (Henderson 1935a: pl. 4 fig. 1, at right).

Holotype of *Goniobasis hemphilli dallesensis* Henderson, 1935 (Fig. 4G)
USA • "Mill Creek, The Dalles, Oregon"; 19 Aug. 1928; J. Henderson and Nelson leg.; UCM 16016a.

Paratypes of *Goniobasis hemphilli dallesensis* Henderson, 1935
USA • 3 spms; same collection data as for holotype; UCM 16016c (Henderson 1935a: pl. 4 fig. 2).

Remarks
Another paratype (UCM 16016b) was not examined (McCoy 1964).

Other material examined
352 lots, 3435 specimens, of which 200 were sequenced.

USA – **Washington** • 5 spms; Clallam Co., Lake Crescent; [48.0581, -123.8132]; 19 Jul. 1935; V. Scheffer leg.; USNM 756742 • 5 spms; Clark Co., Burnt Bridge Creek Bridge at NE 110th Ave, Vancouver; 45.6581, -122.5601; 23 Jun. 2015; K. Van Norman leg.; USNM 1413042 • 1 spm; same collection data as for preceding; GenBank: MK472579, MK464944; USNM 1413037 • 1 spm; same collection data as for preceding; GenBank: MK472580, MK464945, MK480955; USNM 1413038 • 1 spm; same collection data as for preceding; GenBank: MK472581, MK464946, MK480956; USNM 1413039 • 1 spm; same collection data as for preceding; USNM 1413040 • 1 spm; same collection data as for preceding; GenBank: MK472582, MK464947; USNM 1413041 • 38 spms; Clark Co., NW 179th St; 45.7503, -122.7146; 6 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295164 • 1 spm; same collection data as for preceding; GenBank: MK472553, MK464920; USNM 1295163 • 1 spm; same collection data as for preceding; GenBank: MK472549, MK464916; USNM 1295159 • 1 spm; same collection data as for preceding; GenBank: MK472550, MK464917; USNM 1295160 • 1 spm; same collection data as for preceding; GenBank: MK472551, MK464918, MK480948; USNM 1295161 • 1 spm; same collection data as for preceding; GenBank: MK472552, MK464919; USNM 1295162 • 12 spms; Clark Co., Washington River, Vancouver; Clench leg.; USNM 1501083 • 1 spm; Cowlitz Co., Abernathy Creek behind Abernathy Fish Technology Center; 46.2267, -123.1478; 1 Aug. 2017; M. Piteo leg.; GenBank: KF680626; USNM 1597945 • 1 spm; same collection data as for preceding; GenBank: KF680627; USNM 1597944 • 45 spms; Grays Harbor Co., Black River; 46.8299, -123.1859; 4 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413220 • 1 spm; same collection data as for preceding; GenBank: MK472616, MK464981; USNM 1413215 • 1 spm; same collection data as for preceding; GenBank: MK472617, MK464982; USNM 1413216 • 1 spm; same collection data as for preceding; GenBank: MK472618, MK464983, MK480970; USNM 1413217 • 1 spm; same collection data as for preceding; GenBank: MK472619, MK464984; USNM 1413218 • 1 spm; same collection data as for preceding; GenBank: MK472620, MK464985; USNM 1413219 • 9 spms; Grays Harbor Co., Lake Quinault; [47.4729, -123.8683]; United States Fish Commission (USFC); Rutter and Brady leg.; USNM 218271 • 1 spm; Grays Harbor Co., Lake Quinault, Falls Creek Campground, boat launch E of private docks along South Shore Rd; 47.4701, -123.8457; 11 Aug. 2015; C. Fallon and E. Blevins leg.; GenBank: MK472682, MK465049, MK481000; USNM 1413471 • 1 spm; same collection data as for preceding; GenBank: MK472683, MK465050, MK481001; USNM 1413472 • 1 spm; same collection data as for preceding; GenBank: MK472684, MK465051; USNM 1413473 • 1 spm; same collection data as for preceding; GenBank: MK472685, MK465052; USNM 1413474 • 1 spm; Grays Harbor Co., Lake Quinault at Gatton Creek Campground, along rocky beach; 47.4738, -123.8392; 11 Aug. 2015; C. Fallon and E. Blevins leg.; GenBank: MK472676, MK465043, MK480995; USNM 1413465 • 1 spm; same collection data as for preceding; GenBank: MK472677, MK465044, MK480996; USNM 1413466 •

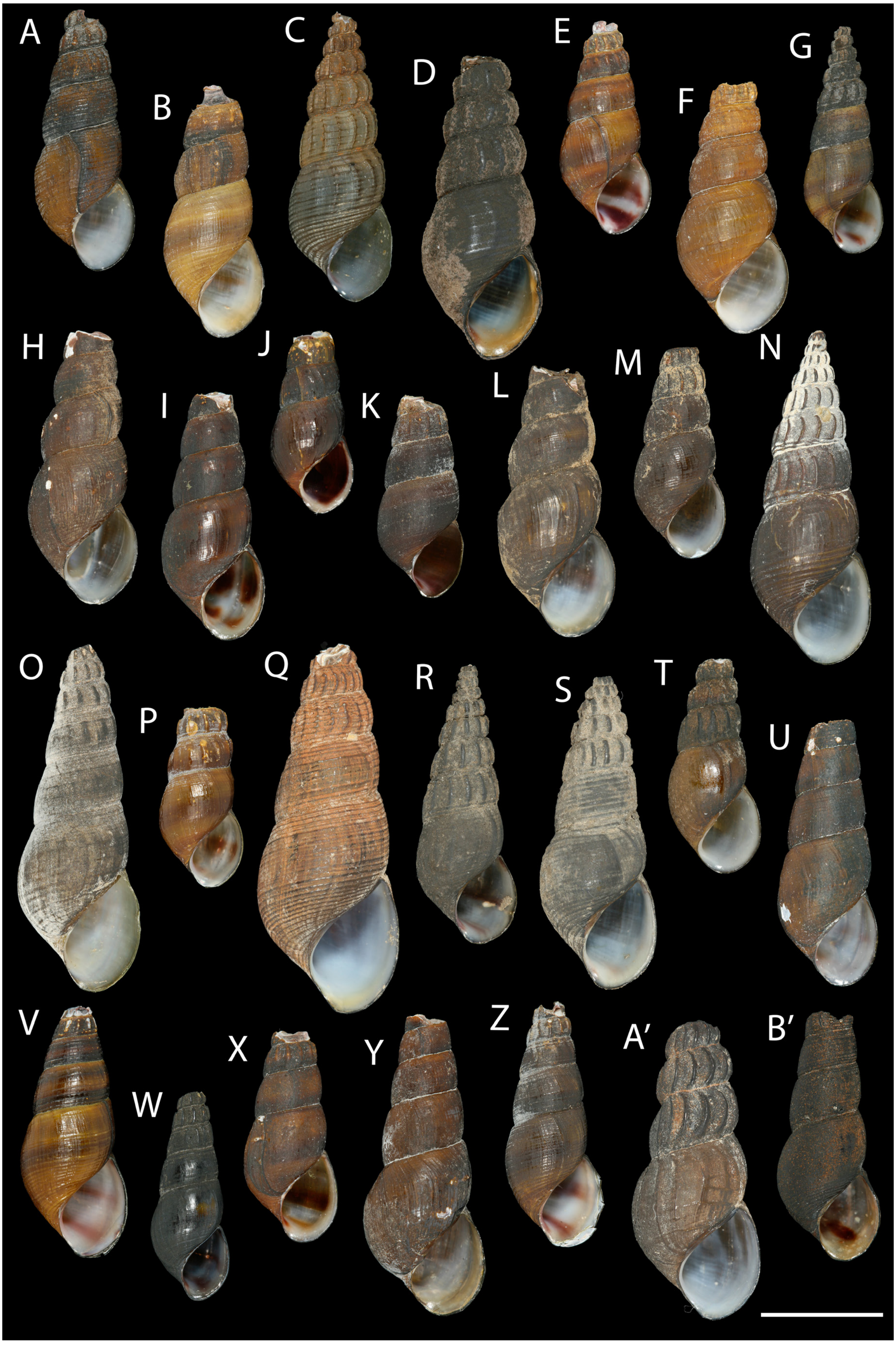
1 spm; same collection data as for preceding; GenBank: MK472678, MK465045, MK480997; USNM 1413467 • 1 spm; Jefferson Co., Quinault River, just N of S Shore Rd, between Fletcher and Bunch Canyons; 47.5297, -123.6987; 11 Aug. 2015; C. Fallon and E. Blevins leg.; GenBank: MK472679, MK465046, MK480998; USNM 1413468 • 1 spm; same collection data as for preceding; GenBank: MK472680, MK465047; USNM 1413469 • 1 spm; same collection data as for preceding; GenBank: MK472681, MK465048, MK480999; USNM 1413470 • 4 spms; King Co., L. Washington; [47.6214, -122.2557]; R.Z. Fahs leg.; USNM 169076 • 53 spms; Klickitat Co., Major Creek; 45.7154, -121.3509; 6 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413184 • 1 spm; same collection data as for preceding; GenBank: MK472604, MK464970, MK480965; USNM 1413182 • 1 spm; same collection data as for preceding; GenBank: MK472605, MK480966; USNM 1413183 • 41 spms; Lewis Co.. Ames Creek; 46.4516, -121.9929; 5 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413226 • 1 spm; same collection data as for preceding; GenBank: MK472621, MK464986, MK480971; USNM 1413221 • 1 spm; same collection data as for preceding; GenBank: MK472622, MK464987, MK480972; USNM 1413222 • 1 spm; same collection data as for preceding; GenBank: MK472623, MK464988; USNM 1413223 • 1 spm; same collection data as for preceding; GenBank: MK472624, MK464989; USNM 1413224 • 1 spm; same collection data as for preceding; GenBank: MK472625, MK464990; USNM 1413225 • 50 spms; Lewis Co., Cowlitz River at Spencer Rd Trout Hatchery; 46.4851, -122.7259; 5 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413175 • 1 spm; same collection data as for preceding; GenBank: MK472594, MK464960, MK480961; USNM 1413170 • 1 spm; same collection data as for preceding; GenBank: MK472595, MK464961; USNM 1413171 • 1 spm; same collection data as for preceding; GenBank: MK472596, MK464962; USNM 1413172 • 1 spm; same collection data as for preceding; GenBank: MK472597, MK464963; USNM 1413173 • 1 spm; same collection data as for preceding; GenBank: MK472598, MK464964, MK480962; USNM 1413174 • 46 spms; Lewis Co., Cowlitz River, at I-5 Crossing W of Toledo; [46.4149, -122.8897]; 24 May 1978; J. Landye leg.; on mud; USNM 892367 • 61 spms; Lewis Co., from stream in Lewis and Clark State Park [Lacamas Creek]; [46.5183, -122.8039]; 15 Jun. 1937; C.E. Burt leg.; USNM 473497 • 48 spms; Lewis Co., Little Falls [= Vader]; [46.395, -122.9578]; Arnold leg.; USNM 187284 • 49 spms; Lewis Co., Olequa Creek, tributary to Cowlitz River near Little Falls [= Vader]; [46.395, -122.9578]; R. Arnold leg.; USNM 181105 • 34 spms; Lewis Co., South Fork Newaukum River; 46.5751, -122.8353; 5 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413214 • 1 spm; same collection data as for preceding; GenBank: MK472611, MK464976, MK480968; USNM 1413209 • 1 spm; same collection data as for preceding; GenBank: MK472612, MK464977; USNM 1413210 • 1 spm; same collection data as for preceding; GenBank: MK472613, MK464978; USNM 1413211 • 1 spm; same collection data as for preceding; GenBank: MK472614, MK464979; USNM 1413212 • 1 spm; same collection data as for preceding; GenBank: MK472615, MK464980, MK480969; USNM 1413213 • 11 spms; Mason Co., Spider Lake, off of FR 23; 47.4068, -123.4372; 13 Aug. 2015; C. Fallon Mason and E. Blevins leg.; USNM 1413464 • 1 spm; same collection data as for preceding; GenBank: MK472675, MK465042, MK480994; USNM 1413463 • 5 spms; Pacific Co., Holcomb, Willapa River; [46.5699, -123.6154]; USFC; Rutter leg.; USNM 109895 • 1 spm; Pacific Co., Nasel, Nasel River [sic, Naselle, Naselle River]; [46.367, -123.8103]; USFC; Rutter leg.; USNM 109893 • 12 spms; Pierce Co., Ft Lewis, Sequalitchew Springs (main water source of Ft Lewis); [47.1116, -122.6016]; 19 Oct. 1951; Lt A. Mayfield leg.; USNM 598456 • 1 spm; Pierce Co., Lake George; [46.7878, -121.9036]; U.S. Exploring Expedition; USNM 5565 • 26 spms; Pierce Co., Roy; [47.0055, -122.5431]; 18 Aug. 1897; V. Bailey leg.; USNM 251946 • 6 spms; Pierce Co., S of Tacoma, in a brook; W.J. Eyerdam leg.; USNM 509403 • 6 spms; Pierce Co., Sequalitchew L., near creek; [47.1124, -122.6163]; 25 Apr. 1904; USFC; USNM 218270 • 9 spms; Pierce Co., Steilacoom Lake, near Tacoma; [47.1643, -122.5376]; 20 Oct. 1949; USNM 1294910 • 7 spms; Pierce Co., Steilacoon River [sic, Steilacoom = Chambers Creek]; [47.1948, -122.5528]; Smithsonian leg.; USNM 118931 • 2 spms; Pierce Co., Tacoma; [47.2538, -122.4349]; Hare leg.; USNM 133697 • 21 spms; Pierce Co., Tacoma, Steilacoom Lake; [47.1643, -122.5376]; 20 Oct. 1949; A.F. Bartsch leg.; USNM 601879 • 47 spms; Pierce Co., H.V. Chase leg.; USNM 742590 • 1 spm;

Sherman Co., at Biggs Junction, downstream from Wallula Gap, Columbia River; [45.6727, -120.8346]; 10 Feb. 1949; J.J. Davis leg.; USNM 653137 • 72 spms; Skamania Co., Le Bong Creek at Stevenson; 45.6976, -121.9128; 5 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413181 • 1 spm; same collection data as for preceding; GenBank: MK472599, MK464965; USNM 1413176 • 1 spm; same collection data as for preceding; GenBank: MK472600, MK464966; USNM 1413177 • 1 spm; same collection data as for preceding; GenBank: MK472601, MK464967, MK480963; USNM 1413178 • 1 spm; same collection data as for preceding; GenBank: MK472602, MK464968, MK480964; USNM 1413179 • 1 spm; same collection data as for preceding; GenBank: MK472603, MK464969; USNM 1413180 • 10 spms; Skamania Co., Skamania at Skelton Rd; 45.6219, -122.0505; 5 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413208 • 1 spm; same collection data as for preceding; GenBank: MK472606, MK464971; USNM 1413203 • 1 spm; same collection data as for preceding; GenBank: MK472607, MK464972; USNM 1413204 • 1 spm; same collection data as for preceding; GenBank: MK472608, MK464973; USNM 1413205 • 1 spm; same collection data as for preceding; GenBank: MK472610, MK464975, MK480967; USNM 1413207 • 1 spm; same collection data as for preceding; GenBank: MK472609, MK464974; USNM 1413206 • 3 spms; Skamania Co., Stevenson; [45.695, -121.8928]; V. Jackson leg.; USNM 169055 • 12 spms; Thurston Co., Black Lake; [46.9881, -122.9793]; USFC; Rutter leg.; USNM 109862 • 14 spms; Thurston Co., Black River, N of bridge along SE 128 Ave, Littlerock; 46.902, -123.0239; 28 Jun. 2015; K. Van Norman leg.; USNM 1413048 • 1 spm; same collection data as for preceding; GenBank: MK464948, MK480957; USNM 1413043 • 1 spm; same collection data as for preceding; GenBank: MK472583, MK464949; USNM 1413044 • 1 spm; same collection data as for preceding; GenBank: MK472584, MK464950; USNM 1413045 • 1 spm; same collection data as for preceding; GenBank: MK472585, MK464951; USNM 1413046 • 1 spm; same collection data as for preceding; GenBank: MK472586, MK464952, MK480958; USNM 1413047 • 1 spm; same collection data as for preceding; GenBank: MK472587, MK464953; USNM 1413049 • 1 spm; same collection data as for preceding; GenBank: MK472588, MK464954; USNM 1413050 • 16 spms; Thurston Co., creek on Evergreen State College, Snyder Cove; [47.0842, -122.9742]; 10 Aug. 1983; J. Landye leg.; USNM 1152454 • 5 spms; Thurston Co., creeks near Olympia; Randolph leg.; USNM 130099 • 24 spms; Thurston Co., McAllister Creek at Steilacoom Rd Bridge, near McAllister Creek Hatchery; 47.0501, -122.7262; 29 Sep. 2005; T. Frest and E. Johannes leg.; USNM 1100657 • 19 spms; Thurston Co., Millersylvania State Park, Deep Lake, in picnic area; [46.9088, -122.9109]; 24 May 1978; J. Landye leg.; USNM 892364 • 12 spms; Thurston Co., Muck Creek just upstream from Nisqually River; [46.9975, -122.6264]; 10 Aug. 1983; J. Landye leg.; USNM 1152371 • 54 spms; Thurston Co., Nisqually River; 46.9334, -122.5608; 4 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413239 • 1 spm; same collection data as for preceding; GenBank: MK472626, MK464991, MK480973; USNM 1413233 • 1 spm; same collection data as for preceding; GenBank: MK472627, MK464992, MK480974; USNM 1413234 • 1 spm; same collection data as for preceding; GenBank: MK472628, MK464993; USNM 1413235 • 1 spm; same collection data as for preceding; GenBank: MK472629, MK464994; USNM 1413236 • 1 spm; same collection data as for preceding; GenBank: MK472630, MK464995, MK480975; USNM 1413237 • 1 spm; same collection data as for preceding; GenBank: MK472631, MK464996; USNM 1413238 • 35 spms; Thurston Co., Skookumchuck River; 46.7954, -122.7609; 4 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413245 • 1 spm; same collection data as for preceding; GenBank: MK472632, MK464997; USNM 1413240 • 1 spm; same collection data as for preceding; GenBank: MK472633, MK464998, MK480976; USNM 1413241 • 1 spm; same collection data as for preceding; GenBank: MK472634, MK464999; USNM 1413242 • 1 spm; same collection data as for preceding; GenBank: MK472635, MK465000; USNM 1413243 • 1 spm; same collection data as for preceding; GenBank: MK472636, MK465001; USNM 1413244 • 15 spms; Thurston Co., Skookumchuck River, Bucoda Volunteer Park, Bucoda; 46.7961, -122.8672; 28 Jun. 2015; K. Van Norman leg.; USNM 1413060 • 1 spm; same collection data as for preceding; GenBank: MK472589, MK464955, MK480959; USNM 1413055 • 1 spm; same collection data as for preceding; GenBank: MK472590, MK464956; USNM 1413056 • 1 spm; same collection data as for preceding; GenBank: MK472591, MK464957; USNM 1413057 • 1 spm; same collection data as for preceding; GenBank: MK472592, MK464958, MK480960; USNM 1413058 • 1 spm; same collection data as for preceding; GenBank: MK472593, MK464959; USNM 1413059 • 13 spms; Walla Walla Co., Walla Walla; USNM 119156 • 9 spms; Walla Walla Co., Walula [sic, Wallula], Walla Walla River; USFC; USNM 109897 • 26 spms; Whitman Co.. Snake Riv. tributary between Wawawai and Bishop; [46.6022, -117.3548]; 1 Apr. 1958; Richards leg.; USNM 795562 • 16 spms; Coloting River [sic, mislocalized], Washington Territory; Suckley leg.; USNM 119152 • 2 spms; Salmon River; USNM 1294901. — **"Oregon" [Territory]** • 11 spms; USNM 58979 • 7 spms; same collection data as for preceding; USNM 59211 • 5 spms; same collection data as for preceding; USNM 58975 • 6 spms; same collection data as for preceding; USNM 12135 • 6 spms; same collection data as for preceding; Newcomb leg.; USNM 119285 • 9 spms; Columbia River; Drayton leg.; USNM 119158. – **Oregon** • 103 spms; Benton Co., 2 mi from Corvallis, Willamette River; [44.5291, -123.2538]; 5 Jul. 1929; L. Sinitsin leg.; USNM 531451 • 134 spms; Benton Co., Alsea River; 13 Apr. 1958; Walter leg.; USNM 795571 • 5 spms; Benton Co., Corvallis; [44.5655, -123.2555]; 22 Jul. 1949; A.L. Mehring leg.; USNM 715700 • 48 spms; Benton Co., Corvallis, Mr. Little's Ranch; 31 Jul. 1929; L. Sinitsin leg.; USNM 531205 • 1 spm; Benton Co., Corvallis, Oak Creek; [44.557, -123.282]; 14 Jul. 1929; L. Sinitsin leg.; USNM 531114 • 21 spms; Benton Co., Mary's River, Mary's River Park, Philomath; 44.5343, -123.3735; 14 Jul. 2015; K. Van Norman leg.; USNM 1413036 • 1 spm; same collection data as for preceding; GenBank: MK472575, MK464940; USNM 1413031 • 1 spm; same collection data as for preceding; GenBank: MK472576, MK464941, MK480953; USNM 1413032 • 1 spm; same collection data as for preceding; USNM 1413033 • 1 spm; same collection data as for preceding; GenBank: MK472577, MK464942, MK480954; USNM 1413034 • 1 spm; same collection data as for preceding; GenBank: MK472578, MK464943; USNM 1413035 • 1 spm; Clackamas Co., left bank of Clackamas River, 100 ft south (upstream) of mouth of Whale Creek; 45.1109, -122.0725; 19 May 2014; J. Williamson leg.; USNM 1413021 • 1 spm; same collection data as for preceding; GenBank: MK472569; USNM 1413022 • 1 spm; same collection data as for preceding; USNM 1413023 • 1 spm; same collection data as for preceding; USNM 1413024 • 4 spms; Clackamas Co., near Estacada, N fork of Molalla River [sic, possibly Clackamas River]; Jul. 1943; D. Macfarlane leg.; USNM 518284 • 12 spms; Clackamas Co., Oregon City; [45.3586, -122.6092]; L.B. Elliott leg.; USNM 509456 • 62 spms; Clackamas Co., Oswego, from a creek [possibly Tryon Creek]; [45.424, -122.661]; L. Bruner and H.F. Wickham leg.; USNM 504256 • 20 spms; Clackamas Co., small creek near Tawney's Hotel [Tawney's Mountain Home], 12 mi from Mount Hood; [45.3165, -121.9475]; Aug. 1916; J.G. Malone leg.; ANSP 115580 • 1 spm; Clackamas Co., Whale Creek, between confluence with Clackamas River and upstream 45 feet; 45.111, -122.0731; 19 May 2014; J. Williamson leg.; USNM 1413019 • 1 spm; same collection data as for preceding; USNM 1413020 • 5 spms; Clatsop Co., Astoria; [46.1882, -123.8275]; ANSP 264447 • 7 spms; same collection data as for preceding; ANSP 27546 • 15 spms; Clatsop Co., Astoria, Columbia River; [46.1882, -123.8275]; W.H. Dall leg.; USNM 119012 • 41 spms; Clatsop Co., at confluence with Bear Creek, Maki Rd; 46.1543, -123.6672; 7 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295182 • 1 spm; same collection data as for preceding; GenBank: MK472559, MK464926; USNM 1295177 • 1 spm; same collection data as for preceding; GenBank: MK472560, MK464927; USNM 1295178 • 1 spm; same collection data as for preceding; GenBank: MK472561, MK464928, MK480949; USNM 1295179 • 1 spm; same collection data as for preceding; GenBank: MK472562, MK464929; USNM 1295180 • 1 spm; same collection data as for preceding; GenBank: MK472563; USNM 1295181 • 2 spms; Clatsop Co., Columbia River, near Astoria; [46.1882, -123.8275]; H. Hemphill leg.; UF 80844 • 4 spms; same collection data as for preceding; E. White leg.; UF 80863 • 41 spms; Clatsop Co., Green Mountain Rd, ca 300 m upstream of confluence of North Fork and South Fork Klaskanine Rivers; 46.0865, -123.741; 7 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295069 • 1 spm; same collection data as for preceding; GenBank: MK472535, MK464901; USNM 1295064 • 1 spm; same collection data as for preceding; GenBank: MK472536, MK464902; USNM 1295065 • 1 spm; same collection data as for preceding; GenBank: MK472537, MK464903, MK480940; USNM 1295066 • 1 spm; same collection data as for preceding;

GenBank: MK472538, MK464904, MK480941; USNM 1295067 • 1 spm; same collection data as for preceding; GenBank: MK472539, MK464905, MK480942; USNM 1295068 • 13 spms; Clatsop Co., just downstream of Gnat Creek Fish Hatchery, along U.S. Hwy 30; 46.177, -123.5034; 7 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295006 • 1 spm; same collection data as for preceding; GenBank: MK472519, MK464885, MK480933; USNM 1295001 • 1 spm; same collection data as for preceding; GenBank: MK472520, MK464886, MK480934; USNM 1295002 • 1 spm; same collection data as for preceding; GenBank: MK472521, MK464887, MK480935; USNM 1295003 • 1 spm; same collection data as for preceding; GenBank: MK472522, MK464888, MK480936; USNM 1295004 • 1 spm; same collection data as for preceding; GenBank: MK472523, MK464889; USNM 1295005 • 19 spms; Clatsop Co., old U.S. Hwy 30; 46.1663, -123.673; 7 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1294987 • 1 spm; same collection data as for preceding; GenBank: MK472513; USNM 1294981 • 1 spm; same collection data as for preceding; GenBank: MK472514, MK464880; USNM 1294982 • 1 spm; same collection data as for preceding; GenBank: MK472515, MK464881, MK480930; USNM 1294983 • 1 spm; same collection data as for preceding; GenBank: MK472516, MK464882; USNM 1294984 • 1 spm; same collection data as for preceding; GenBank: MK472517, MK464883, MK480931; USNM 1294985 • 1 spm; same collection data as for preceding; GenBank: MK472518, MK464884, MK480932; USNM 1294986 • 25 spms; Clatsop Co., Tweedle Rd; 45.8963, -123.5544; 7 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1294980 • 1 spm; same collection data as for preceding; GenBank: MK472507, MK464874, MK480928; USNM 1294974 • 1 spm; same collection data as for preceding; GenBank: MK472508, MK464875; USNM 1294975 • 1 spm; same collection data as for preceding; GenBank: MK472509, MK464876; USNM 1294976 • 1 spm; same collection data as for preceding; GenBank: MK472510, MK464877, MK480929; USNM 1294977 • 1 spm; same collection data as for preceding; GenBank: MK472511, MK464878; USNM 1294978 • 1 spm; same collection data as for preceding; GenBank: MK472512, MK464879; USNM 1294979 • 22 spms; Clatsop Co., Youngs River Falls, just upstream of Youngs River Rd; 46.0675, -123.7888; 7 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295023 • 1 spm; same collection data as for preceding; GenBank: MK472524, MK464890; USNM 1295018 • 1 spm; same collection data as for preceding; GenBank: MK472525, MK464891; USNM 1295019 • 1 spm; same collection data as for preceding; GenBank: MK472526, MK464892; USNM 1295020 • 1 spm; same collection data as for preceding; GenBank: MK472527, MK464893; USNM 1295021 • 1 spm; same collection data as for preceding; GenBank: MK472528, MK464894, MK480937; USNM 1295022 • 20 spms; Columbia Co., McBride Creek, Smith Rd; [45.8912, -122.8178]; 29 Jun. 2002; T. Frest and E. Johannes leg.; USNM 1270862 • 29 spms; Columbia Co., Scappoose Creek on road to Pittsburg and Vernonia; [45.7638, -122.88]; J. Landye leg.; USNM 1152453 • 53 spms; Columbia Co., U.S. Hwy 30, Scapoose; 45.7708, -122.8791; 7 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295043 • 1 spm; same collection data as for preceding; GenBank: MK472529, MK464895; USNM 1295037 • 1 spm; same collection data as for preceding; GenBank: MK472530, MK464896, MK480938; USNM 1295038 • 1 spm; same collection data as for preceding; GenBank: MK472531, MK464897; USNM 1295039 • 1 spm; same collection data as for preceding; GenBank: MK472532, MK464898; USNM 1295040 • 1 spm; same collection data as for preceding; GenBank: MK472533, MK464899, MK480939; USNM 1295041 • 1 spm; same collection data as for preceding; GenBank: MK472534, MK464900; USNM 1295042 • 28 spms; Deschutes Co., just downstream of U.S. Hwy 20 (FS campground); 44.3567, -121.6107; 16 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1294973 • 1 spm; same collection data as for preceding; GenBank: MK472504, MK464871; USNM 1294970 • 1 spm; same collection data as for preceding; GenBank: MK472503, MK464870, MK480926; USNM 1294969 • 1 spm; same collection data as for preceding; GenBank: MK472502, MK464869; USNM 1294968 • 1 spm; same collection data as for preceding; GenBank: MK472505, MK464872, MK480927; USNM 1294971 • 1 spm; same collection data as for preceding; GenBank: MK472506, MK464873; USNM 1294972 • 55 spms; Gilliam Co., Columbia River, 5 mi W of Arlington; [45.7109, -120.3043]; 17 Oct. 1960; D. Bauer leg.; UF 545965 • 23 spms; same collection data as for preceding; UF 545985 • 26 spms; Hood River Co., just downstream of the mouth of Hood River; 45.7149, -121.5135; 15 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1294961 • 1 spm; same collection data as for preceding; GenBank: MK472495, MK464862, MK480924; USNM 1294959 • 1 spm; same collection data as for preceding; GenBank: MK472494, MK464861; USNM 1294958 • 1 spm; same collection data as for preceding; GenBank: MK472493, MK464860; USNM 1294957 • 1 spm; same collection data as for preceding; GenBank: MK472492, MK464859; USNM 1294956 • 1 spm; same collection data as for preceding; GenBank: MK472496, MK464863; USNM 1294960 • 23 spms; Lane Co., 29 mi E of Eugene, near Vida, McKenzie River; [44.1425, -122.5633]; 12 Aug. 1929; L. Sinitsin leg.; USNM 531104 • 6 spms; Lane Co., 4 mi N of Sea Lion Cave, large creek [sic, likely Big Creek]; [44.1744, -124.1153]; 27 May 1971; A.W. Vazquez leg.; USNM 758161 • 22 spms; Lane Co., end of Crossroads Lane (boat ramp); 44.1879, -123.1443; 15 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295176 • 1 spm; same collection data as for preceding; GenBank: MK472554, MK464921; USNM 1295171 • 1 spm; same collection data as for preceding; GenBank: MK472555, MK464922; USNM 1295172 • 1 spm; same collection data as for preceding; GenBank: MK472556, MK464923; USNM 1295173 • 1 spm; same collection data as for preceding; GenBank: MK472557, MK464924; USNM 1295174 • 1 spm; same collection data as for preceding; GenBank: MK472558, MK464925; USNM 1295175 • 10 spms; Lane Co., Eugene; [44.0455, -123.1254]; USNM 431330 • 4 spms; Lane Co., Eugene, Mackenzie River; [44.1124, -123.0468]; USFC; Cramer and Otaki leg.; USNM 109896 • 13 spms; Lane Co., Eugene, Willamette River; [44.0638, -123.1007]; D.T. Jones leg.; USNM 510720 • 38 spms; Lane Co., Long Tom River at Poodle Creek Rd; 44.1434, -123.4298; 16 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413341 • 1 spm; same collection data as for preceding; GenBank: MK472637, MK465002, MK480977; USNM 1413336 • 1 spm; same collection data as for preceding; GenBank: MK472638, MK465003; USNM 1413337 • 1 spm; same collection data as for preceding; GenBank: MK472639, MK465004; USNM 1413338 • 1 spm; same collection data as for preceding; GenBank: MK472640, MK465005; USNM 1413339 • 1 spm; same collection data as for preceding; GenBank: MK472641, MK465006, MK480978; USNM 1413340 • 8 spms; Lane Co., N of Marchfield [sic, Marshfield], Ten Mile Creek; [44.2241, -124.1096]; J. Henderson leg.; USNM 425498 • 88 spms; Lane Co., near Mapleton, Sheverton opposite electric station; [44.0213, -123.8555]; Jul. 1929; L. Sinitsin leg.; where river very slow and shallow; USNM 531107 • 29 spms; Lane Co., Riverlet opp. Mapleton; [44.0333, -123.855]; Jul. 1929; L. Sinitsin leg.; USNM 531105 • 46 spms; Lane Co., Siuslaw Hatchery, creek ca 1 mi from office; [44.0939, -123.7739]; Jul. 1929; L. Sinitsin leg.; USNM 531106 • 28 spms; Lane Co., Siuslaw River at Brickerville; 44.0606, -123.8852; 16 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413395 • 1 spm; same collection data as for preceding; GenBank: MK472662, MK465027; USNM 1413390 • 1 spm; same collection data as for preceding; GenBank: MK472663, MK465028, MK480988; USNM 1413391 • 1 spm; same collection data as for preceding; GenBank: MK472664, MK465029; USNM 1413392 • 1 spm; same collection data as for preceding; GenBank: MK472665, MK465030; USNM 1413393 • 1 spm; same collection data as for preceding; GenBank: MK472666, MK465031; USNM 1413394 • 31 spms; Lane Co., Siuslaw River, ca 1 mi from hatchery in the forest; [44.0939, -123.7739]; Jul. 1929; L. Sinitsin leg.; USNM 531074 • 24 spms; Lane Co., Siuslaw River, Siuslaw hatchery, opp. the house; [44.0939, -123.7739]; Jul. 1929; L. Sinitsin leg.; USNM 531108 • 1 spm; Lane Co., Siuslaw Salmon Hatchery; [44.0939, -123.7739]; 22 May 1929; L. Sinitsin leg.; USNM 531098 • 5 spms; Lane Co., Sutton Lake; [44.0586, -124.0899]; 27 May 1971; A.W. Vazquez leg.; USNM 758160 • 66 spms; Lane Co., Swisshome, Siuslaw Riv.; [44.0553, -123.8014]; Jul. 1929; L. Sinitsin leg.; USNM 531273 • 3 spms; Lincoln Co., Devils Lake; [44.9808, -123.9921]; E.C. Huffman leg.; USNM 593063 • 13 spms; Lincoln Co., just below Nashville, Yaquina River; [44.6531, -123.6077]; 8 Sep. 1977; C. Simmons leg.; USNM 771822 • 21 spms; Lincoln Co., near Eddyville, mi 21 on US20, large creek (Mary's Riv.?) [= Little Elk Creek]; [44.6287, -123.7674]; 31 May 1971; A.W. Vasquez leg.; USNM 758152 • 52 spms; Linn Co., Albany; [44.6384, -123.1065]; 1900; H.F. Wickham leg.; USNM 509443 • 37 spms; Linn Co., Calapooia River at McKercher Park; 44.3585, -122.8763; 16 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413347 • 1 spm; same collection data as for preceding; GenBank: MK472642, MK465007; USNM 1413342 •

1 spm; same collection data as for preceding; GenBank: MK472643, MK465008; USNM 1413343 • 1 spm; same collection data as for preceding; GenBank: MK472644, MK465009, MK480979; USNM 1413344 • 1 spm; same collection data as for preceding; GenBank: MK472645, MK465010, MK480980; USNM 1413345 • 1 spm; same collection data as for preceding; GenBank: MK472646, MK465011, MK480981; USNM 1413346 • 52 spms; Linn Co., Thomas Creek at Chapin Park in Scio; 44.7044, -122.8472; 16 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413413 • 1 spm; same collection data as for preceding; GenBank: MK472670, MK465037; USNM 1413408 • 1 spm; same collection data as for preceding; GenBank: MK472671, MK465038; USNM 1413409 • 1 spm; same collection data as for preceding; GenBank: MK472672, MK465039, MK480993; USNM 1413410 • 1 spm; same collection data as for preceding; GenBank: MK472673, MK465040; USNM 1413411 • 1 spm; same collection data as for preceding; GenBank: MK472674, MK465041; USNM 1413412 • 58 spms; Marion Co., Drift Creek on Cascade Highway NE; 44.9693, -122.8094; 16 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413371 • 1 spm; same collection data as for preceding; GenBank: MK472652, MK465017, MK480984; USNM 1413366 • 1 spm; same collection data as for preceding; GenBank: MK472653, MK465018; USNM 1413367 • 1 spm; same collection data as for preceding; GenBank: MK472654, MK465019; USNM 1413368 • 1 spm; same collection data as for preceding; GenBank: MK472655, MK465020, MK480985; USNM 1413369 • 1 spm; same collection data as for preceding; GenBank: MK472656, MK465021, MK480986; USNM 1413370 • 1 spm; Marion Co., Mehama; [44.7889, -122.618]; C.V. Piper leg.; USNM 225925 • 15 spms; Marion Co., Salem; [44.9446, -123.0461]; M. Witter leg.; USNM 509400 • 8 spms; same collection data as for preceding; A.K.F. leg.; USNM 509454 • 2 spms; Marion Co., Salem; [44.9446, -123.0461]; USNM 534927 • 2 spms; Multnomah Co., Benson State Recreation Area, along Interstate 84, near Multnomah Falls; 45.577, -122.1262; 8 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295075 • 1 spm; same collection data as for preceding; GenBank: MK472540, MK464906, MK480943; USNM 1295070 • 1 spm; same collection data as for preceding; GenBank: MK472541, MK464907, MK480944; USNM 1295071 • 1 spm; same collection data as for preceding; GenBank: MK472542, MK464908; USNM 1295072 • 1 spm; same collection data as for preceding; GenBank: MK472543, MK464909; USNM 1295073 • 1 spm; same collection data as for preceding; GenBank: MK472544, MK464910, MK480945; USNM 1295074 • 30 spms; Multnomah Co., Benson State Recreation Area, along Interstate 84, near Multnomah Falls; 45.5767, -122.13; 8 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295200 • 1 spm; same collection data as for preceding; GenBank: MK472564, MK464930; USNM 1295195 • 1 spm; same collection data as for preceding; GenBank: MK472565, MK464931; USNM 1295196 • 1 spm; same collection data as for preceding; GenBank: MK472566, MK464932; USNM 1295197 • 1 spm; same collection data as for preceding; GenBank: MK472567, MK464933; USNM 1295198 • 1 spm; same collection data as for preceding; GenBank: MK472568, MK464934, MK480950; USNM 1295199 • 18 spms; Multnomah Co., Coopey Creek above falls at Angels Rest trail crossing, Columbia River Gorge Natl Scenic Area; [45.5616, -122.1629]; 22 Jul. 2015; R. Wisseman leg.; USNM 1438822 • 2 spms; Multnomah Co., E of Portland; H. Hemphill leg.; USNM 30585 • 5 spms; Multnomah Co., near Horse Tail Falls; [45.5896, -122.0687]; E.C. Huffman leg.; USNM 593061 • 3 spms; Multnomah Co., Portland; Lewis leg.; USNM 715183 • 22 spms; same collection data as for preceding; L.B. Elliott leg.; USNM 509453 • 16 spms; same collection data as for preceding; H. Hemphill leg.; USNM 59132 • 51 spms; same collection data as for preceding; 27 Jun. 1905; M.W. Lyon Jr. leg.; USNM 187283 • 12 spms; same collection data as for preceding; May 1895; W. Palmer leg.; USNM 184298 • 4 spms; same collection data as for preceding; B. Shimek leg.; USNM 512975 • 2 spms; same collection data as for preceding; H. Hemphill leg.; USNM 30582 • 2 spms; Multnomah Co., Portland, Johnson Creek; [45.4686, -122.5657]; 14 May 1905; J.E. Benedict leg.; USNM 184189 • 16 spms; Multnomah Co., tributary of Young Creek at old highway crossing, Columbia River Gorge Natl Scenic Area; [45.5466, -122.1978]; 22 Jul. 2015; R. Wisseman leg.; USNM 1665621 (formerly USNM 1438822) • 31 spms; Polk Co., Mill Creek at Mill Creek Park; 44.9866, -123.4259; 16 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413389 • 1 spm; same collection data as for preceding; GenBank: MK472657, MK465022, MK480987; USNM 1413384 •

1 spm; same collection data as for preceding; GenBank: MK472658, MK465023; USNM 1413385 • 1 spm; same collection data as for preceding; GenBank: MK472659, MK465024; USNM 1413386 • 1 spm; same collection data as for preceding; GenBank: MK472660, MK465025; USNM 1413387 • 1 spm; same collection data as for preceding; GenBank: MK472661, MK465026; USNM 1413388 • 34 spms; Polk Co., Mill Creek, Buell County Park, near Sheridan; 45.0229, -123.4181; 14 Jul. 2015; K. Van Norman leg.; USNM 1413030 • 1 spm; same collection data as for preceding; GenBank: MK472570, MK464935, MK480951; USNM 1413025 • 1 spm; same collection data as for preceding; GenBank: MK472571, MK464936, MK480952; USNM 1413026 • 1 spm; same collection data as for preceding; GenBank: MK472572, MK464937; USNM 1413027 • 1 spm; same collection data as for preceding; GenBank: MK472573, MK464938; USNM 1413028 • 1 spm; same collection data as for preceding; GenBank: MK472574, MK464939; USNM 1413029 • 48 spms; Polk Co., Willamette River at Salem Wallace Marine Park; 44.946, -123.044; 16 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413353 • 1 spm; same collection data as for preceding; GenBank: MK472647, MK465012, MK480982; USNM 1413348 • 1 spm; same collection data as for preceding; GenBank: MK472648, MK465013, MK480983; USNM 1413349 • 1 spm; same collection data as for preceding; GenBank: MK472649, MK465014; USNM 1413350 • 1 spm; same collection data as for preceding; GenBank: MK472650, MK465015; USNM 1413351 • 1 spm; same collection data as for preceding; GenBank: MK472651, MK465016; USNM 1413352 • 12 spms; Tillamook Co., 8.7 mi N of Beaver, Fawcett Creek, on U.S. Hwy 101; [45.3897, -123.8031]; 28 May 1971; A.W. Vasquez leg.; USNM 758162 • 7 spms; Tillamook Co., Bewley Creek; [45.3864, -123.8549]; E.C. Huffman leg.; USNM 593060 • 6 spms; Tillamook Co., Farmer Creek; [45.2542, -123.8616]; E.C. Huffman leg.; USNM 593067 • 3 spms; Tillamook Co., Hoquarton Slough; [45.4621, -123.8338]; E.C. Huffman leg.; USNM 593065 • 2 spms; Tillamook Co., Lake Lytle; [45.6239, -123.9401]; E.C. Huffman leg.; USNM 593064 • 10 spms; Tillamook Co., Rockaway, Lake Lytle; [45.6239, -123.9401]; 28 May 1971; A.W. Vazquez leg.; USNM 758159 • 2 spms; Tillamook Co., Trask River; E.C. Huffman leg.; USNM 593066 • 5 spms; Tillamook Co., Wilson River; E.C. Huffman leg.; USNM 593062 • 2 spms; Wasco Co., The Dalles; [45.6030, -121.1800]; H. Hemphill leg.; USNM 30548 • 4 spms; same collection data as for preceding; USNM 30564 • 1 spm; same collection data as for preceding; USNM 509426 • 138 spms; same collection data as for preceding; H.F. Wickham leg.; USNM 509449 • 32 spms; Wasco Co., Thompson City Park, just upstream of Interstate 84, The Dalles; 45.6046, -121.1894; 9 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1294967 • 1 spm; same collection data as for preceding; GenBank: MK472497, MK464864; USNM 1294962 • 1 spm; same collection data as for preceding; GenBank: MK472498, MK464865; USNM 1294963 • 1 spm; same collection data as for preceding; GenBank: MK472499, MK464866, MK480925; USNM 1294964 • 1 spm; same collection data as for preceding; GenBank: MK472500, MK464867; USNM 1294965 • 1 spm; same collection data as for preceding; GenBank: MK472501, MK464868; USNM 1294966 • 52 spms; Washington Co., Tualatin Hills Park, Cedar Mills; 45.5214, -122.8377; 7 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295152 • 1 spm; same collection data as for preceding; GenBank: MK472545, MK464911; USNM 1295147 • 1 spm; same collection data as for preceding; GenBank: MK464912; USNM 1295148 • 1 spm; same collection data as for preceding; GenBank: MK472546, MK464913, MK480946; USNM 1295149 • 1 spm; same collection data as for preceding; GenBank: MK472547, MK464914; USNM 1295150 • 1 spm; same collection data as for preceding; GenBank: MK472548, MK464915, MK480947; USNM 1295151 • 2 spms; Yamhill Co., near McMinnville, Muddy Creek; [45.127, -123.3029]; Jun. 1943; A.W. Macy leg.; USNM 518283 • 48 spms; Yamhill Co., South Yamhill River at McMinnville City Park; 45.2071, -123.1805; 16 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413401 • 1 spm; same collection data as for preceding; GenBank: MK472667, MK465032, MK480989; USNM 1413396 • 1 spm; same collection data as for preceding; GenBank: MK465033, MK480990; USNM 1413397 • 1 spm; same collection data as for preceding; GenBank: MK472668, MK465034, MK480991; USNM 1413398 • 1 spm; same collection data as for preceding; GenBank: MK472669, MK465035, MK480992; USNM 1413399 • 1 spm; same collection data as for preceding; GenBank: MK465036; USNM 1413400 • 2 spms; Willamette River;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H.E. Dore leg.; USNM 99305 • 2 spms; same collection data as for preceding; S. Smith leg.; USNM 321801 • 2 spms; same collection data as for preceding; USNM 218569.

Description

Shell. Thick, large, reaching ~3.5 cm in length; turriform, narrowly conical to cylindrical in shape, spire high, highly variable in sculpture, color, and banding (Fig. 5). Whorls somewhat flattened to moderately convex, occasionally weakly shouldered or with a subsutural ramp, suture weakly to moderately impressed. Aperture oval in shape, lip smooth, slightly sinuous. Spiral sculpture of numerous, fine striae, typically moderately to strongly developed and rarely indistinct, highly variable in strength and number; sporadic slightly elevated lirae. Axial sculpture of fine, sinuous growth lines, and plications on early whorls when preserved; plications regular and even, moderately to strongly developed, occasionally shouldered, orthocline, opisthocline, to strongly opisthocyrt, sometimes extending full length of shell, but frequently obsolete on body whorl; may be thickened or beaded at intersections with spiral striae. Shell black, dark brown, to olive or tan in color. Bands present or absent, one to three in number and variable in width, reddish-purple in color. Interior of aperture white or cream to dark purple in color, occasionally with yellowish-orange rim inside lip; bands when present visible inside aperture. Base of columella occasionally tinged reddish-purple.

Radula. Rachidian narrowly rectangular, wider than tall, with convex lower margin and a small, pointed, basal denticle at lower, outer corners (Fig. 6). Upper margin slightly concave with cutting edge bearing central, elongate conical cusp and two to three stout, conical denticles on each side. Lateral teeth with prominent triangular cusp flanked by two to three inner and two to three outer, triangular denticles, and frequently a membranous outermost denticle. Marginal teeth with broadly rounded cutting edges and long, slender, flattened shafts with membranous flanges along inner and outer edges. Narrow inner flanges along distal third to half of shafts; outer flanges extending almost to tooth bases, narrow on inner marginal teeth, broadening towards cutting edges on outer marginal teeth. Inner marginal teeth with five to six, and outer marginal teeth with six to seven flattened denticles.

Distribution and ecology

In small creeks to large rivers primarily west of the Cascades from the Olympic Peninsula of Washington in the north (Branson 1977) to the Willamette River drainage in south-central Oregon (Fig. 7A).

Remarks

Frest & Johannes (2010) refined the type locality of *M. plicifera* to the Multnomah Channel, which is indicated on some early maps as the second mouth of the 'Wahlamat' or Multnomah River. The terminal portion of the Willamette River near its confluence with the Columbia is also the type locality of *Goniobasis plicifera* var. *oregonensis*. Near topotypic specimens have been sequenced from Waterhouse Creek, Tualatin Hills, Washington County (Strong & Whelan 2019) (Fig. 5R–S), and were conspecific with specimens from nearby Johnson Creek, Multnomah County (Campbell *et al.* 2016), which may have

Fig. 5 (previous page). Shell morphology of *Juga plicifera* (I. Lea, 1838). Sequenced vouchers, arranged roughly from North to South. **A**. Near topotypic (*Melania silicula* A. Gould, 1847), USNM 1413235. **B**. USNM 1413244. **C**. USNM 1413471. **D**. USNM 1413219. **E**. USNM 1413170. **F**. USNM 1413171. **G**. USNM 1413222. **H**. USNM 1413183. **I**. USNM 1413177. **J**. USNM 1413204. **K**. USNM 1295003. **L**. USNM 1295178. **M**. USNM 1295022. **N**. USNM 1294958. **O**. Topotypic (*Goniobasis hemphilli dallesensis* Henderson, 1935), USNM 1294964. **P**. USNM 1295070. **Q**. USNM 1295196. **R–S**. Near topotypic (*Melania plicifera* I. Lea, 1838; *Goniobasis plicifera* var. *oregonensis* Tryon, 1865) **R**. USNM 1295147. **S**. USNM 1295150. **T**. USNM 1413397. **U**. USNM 1413028. **V**. USNM 1413386. **W**. USNM 1413370. **X**. USNM 1413409. **Y**. USNM 1413344. **Z**. USNM 1294972. **A'**. Near topotypic (*Goniobasis plicifera* var. *bulimoides* Tryon, 1865), USNM 1295172. **B'**. USNM 1413394. Scale bar = 1 cm.

produced Henderson's type specimens of *Goniobasis hemphilli* (Frest & Johannes 2010). Sequalitchew Creek is considered a possible source of Gould's type material of *Melania silicula*, a Puget Sound tributary which flowed just to the north of the site of Fort Nisqually between 1833 and 1843, the Hudson's Bay Co. outpost on the shores of Puget Sound. It was the only settlement in the area at the time and was the first port of call for the U.S. Exploring Expedition, which was the source of Gould's types (Strong & Frest 2007; Frest & Johannes 2010). *Juga* no longer occurs in Sequalitchew Creek, but near topotypic specimens from McAllister Creek (Campbell *et al.* 2016) and the Nisqually River (Strong & Whelan 2019) (Fig. 5A) also placed in this clade. *Melania silicula* was synonymized with *plicifera* by Pilsbry (1899), a view not followed by later authors. In earlier treatments, *silicula* was considered widespread

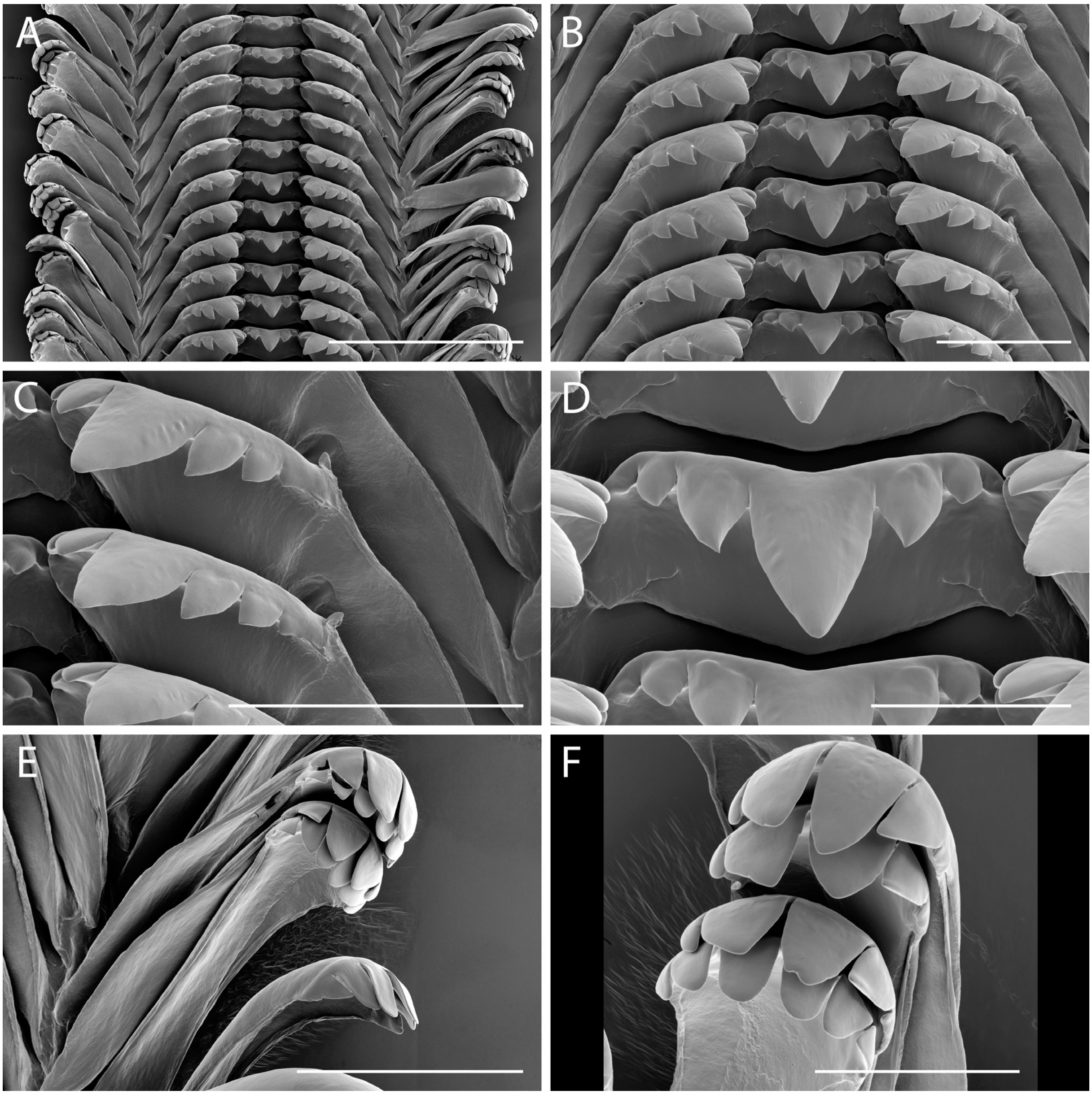


Fig. 6. Radular morphology of *Juga plicifera* (I. Lea, 1838) (USNM 1295041). **A**. View of the anterior radular ribbon. **B**. Detail of cutting edge of rachidian and lateral teeth. **C**. Detail of lateral teeth cusps. **D**. Detail of rachidian cusps. **E**. Inner and outer marginal teeth. **F**. Detail of inner and outer marginal teeth cusps. Scale bars: A = 300 µm; B–C, E = 100 µm; D, F = 50 µm.

in Washington and Oregon (e.g., Goodrich 1942; Burch & Tottenham 1980, Burch 1982, 1989), but more recently was considered a narrow-range endemic of southeastern Puget Sound (Strong & Frest 2007; Frest & Johannes 2010; Johannes 2010b). *Juga hemphilli hemphilli* and *J. h. dallesensis* were regarded as species incerta by Goodrich (1942) but recognized as valid by Burch & Tottenham (1980) and Burch (1982, 1989). Campbell *et al.* (2016) noted the low genetic divergence of *dallesensis* from the nominotypical form but did not address their taxonomic status apart from concluding the small morphological differences in the latter could represent individual variation. Frest & Johannes (2010) also considered both as valid, but the inclusion of the name *J. h. dallesensis* in a heading indicated that they had apparently considered it a possible synonym of *J.* (*O.*) *bulbosa* (Frest & Johannes 2010: 26). *Juga hemphilli* was recognized without subdivision by Turgeon *et al.* (1988, 1998) and Johnson *et al.* (2013). Thus, the synonymy of these two nominal species with *plicifera* here is new.

Melania rudens Reeve, 1860 was established without a locality. Tryon (1864) synonymized it with *Goniobasis silicula* but was later (Tryon 1865: 239) convinced of its validity and considered the species to range from Oregon to California in the Columbia and Sacramento Rivers. *Goniobasis silicula rudens* was recognized as valid by Henderson (1935a, 1936b) as a form from the Olympic Peninsula. However, most authors have synonymized it with *silicula* (e.g., Tryon 1873; Henderson 1929; Goodrich 1942; Burch & Tottenham 1980; Burch 1982, 1989) except Pilsbry (1899) who synonymized it with *plicifera*. Frest & Johannes (2010) considered *Juga* (*Juga*) *rudens* a "dubious taxon", probably a synonym of *J. silicula*, and based on the original illustration of Reeve (1860: pl. 33 fig. 224) found the morphology closely comparable to that of specimens from the Nisqually River watershed and nearby tributaries of Puget Sound, the source of the types of *Melania silicula*. We agree and retain it here.

Tryon (1865) established the varieties *Goniobasis plicifera* var. *bulimoides* and *G. p.* var. *oregonensis*, distinguished by the length of the shell and the density of revolving striae. He abandoned them soon thereafter, omitting them as either varieties or synonyms (Tryon 1866, 1873). Henderson (1935a, 1936b: 273) acknowledged the "interminably intergrading varieties" and their rather arbitrary separation, yet inexplicably found the names useful, "in order to keep our ideas somewhat clear". Apart from Goodrich

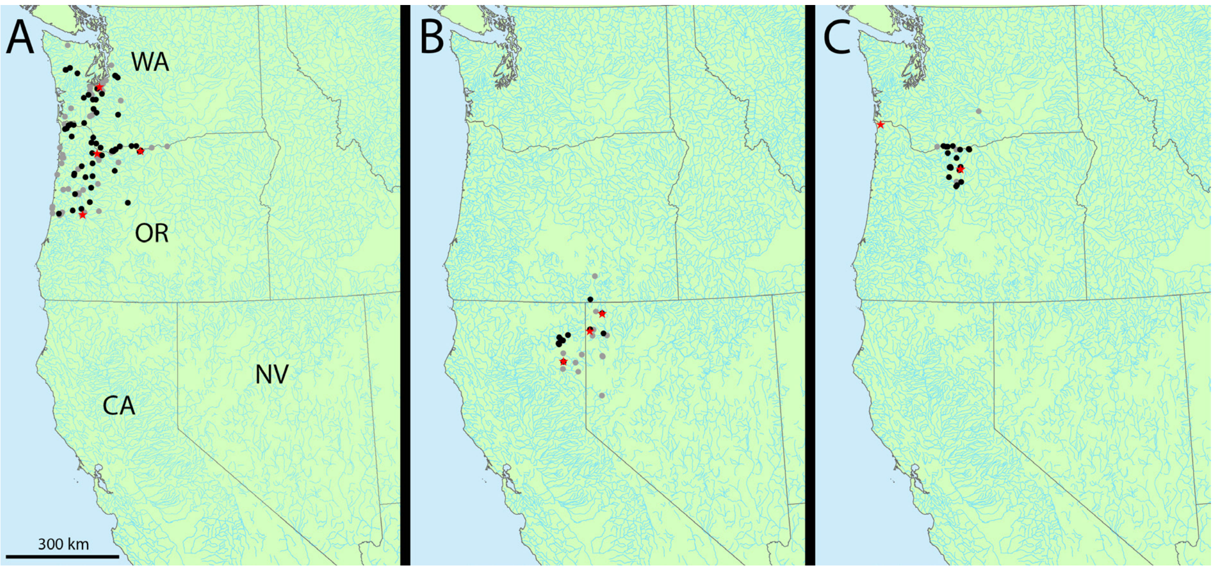


Fig. 7. Distribution maps. **A**. *Juga plicifera* (I. Lea, 1838). **B**. *Juga acutifilosa* (Stearns, 1890). **C**. *Juga bulbosa* (A. Gould, 1847). Red stars, type localities; black dots, sequenced specimens; gray dots, unsequenced museum material. Abbreviations: CA = California; NV = Nevada; OR = Oregon; WA = Washington.

(1942) who synonymized the two with *G. plicifera*, other 20th century authors have ignored the names. Frest & Johannes (2010) thought *Juga* (*Juga*) *plicifera bulimoides* could be a valid large, slow river form, and *J.* (*J.*) *p. oregonensis* also likely to be valid. Campbell *et al.* (2016) noted the low genetic divergence of *bulimoides* and *oregonensis* from the nominotypical form and supported the synonymy of *J. bulimoides* with *plicifera* but did not address the taxonomic status of *J.* (*J.*) *p. oregonensis*, apart from concluding the small morphological differences could represent individual variation. Analysis of near topotypic specimens consistent with the morphology of the types (Strong & Whelan 2019) indicates that both subspecies represent morphological variation within the range of *plicifera.*

Frest & Johannes' (1993, 1995a, 2010) concept of *Juga* (*Juga*) *draytonii* [= "*J.* (*J.*) n. sp. 1 (Brown Juga)"], and possibly of "*J.* (*J.*) *hemphilli* n. subsp." and "*J.* (*J.*) n. sp. 3 (Tall Juga)" are composite. All three occur in the central and western Columbia Gorge in both Oregon and Washington, including the Mt. Hood National Forest, and would include individuals of both *J. plicifera* and *J. bulbosa* (Gould, 1847) as circumscribed here. The specimen sequenced as *J.* (*J.*) *draytonii* by Campbell *et al.* (2016) placed in the same clade with *J.* (*J.*) *plicifera plicifera*; however, the morphology of the type material of *draytonii* is more consistent with the interpretation that it is a synonym of *J. bulbosa* (see account below).

Distribution

Several historical records suggest that *J. plicifera* may once have occurred, at least sporadically, in the Columbia River drainage of southeastern Washington. Two of these date from the late 1800's and early 1900's [Walla Walla (USNM 119156; Lea Collection, Lady K. Douglas) and Wallula (USNM 109897; U.S. Fish Commission)] and their provenance is unreliable (Carpenter 1857: 162). Another lot collected in 1958 (USNM 795562; identified as *J. hemphilli*) places the species in a spring alongside the Snake River, a Columbia River tributary, in Whitman County of far eastern Washington, which lies far to the east of the known distribution. Moreover, this lot contains only preserved soft parts lacking shells, so the identification cannot be confirmed. However, an iNaturalist record from 2019 east of Pendleton, Oregon, shows a plicate specimen that appears to be this species (https://www.inaturalist.org/observations/28180434) and demonstrates the species extends farther east than museum records suggest. Given the non-contiguous distribution of *Juga* in eastern Oregon and western Nevada, the occurrence of *Juga* at these distant sites should not be immediately discounted (Frest & Johannes 2010: 18), but we do not include them on our distribution map until they can be confirmed in modern surveys.

Common name

The common name for this species is the Pleated Juga (Turgeon *et al.* 1988, 1998; Johnson *et al.* 2013; Johannes 2015). It has also been referred to as the Plicate Juga (Frest & Johannes 2001, 2010). Synonyms have been referred to as the Glass or Glassy Juga (*J. silicula*), the Barren Juga (*J. hemphilli hemphilli*), Dalles Juga (*J. hemphilli dallesensis*), and the Washougal Juga (*J.* (*J.*) *hemphilli* n. subsp. 1) (Turgeon *et al.* 1988, 1998; Frest & Johannes 1993, 1995a, 2001, 2010; Duncan 2008; Johannes 2010b, 2015; Johnson *et al.* 2013). Also conspecific with *J. plicifera* is the Indian Ford Juga [= *Juga* (*Juga*) *hemphilli* n. subsp. 2], known from Indian Ford Creek near Black Butte in the Deschutes National Forest, Deschutes County, Oregon (Frest & Johannes 1995a; Duncan 2008; Johannes 2015). This corresponds to the site "just downstream of U.S. Hwy 20 (FS campground)" in Strong & Whelan (2019) (Fig. 5Z) and represents an unusual incursion of *J. plicifera* into the Deschutes River system; it is also the farthest occurrence of *Juga* up the Deschutes basin (Johannes 2015).

Juga acutifilosa (Stearns, 1890)

Figs 8–9

Melania (?*Goniobasis*) *acutifilosa* Stearns, 1890: 211–212, pl. 15 fig. 9.
Goniobasis laurae Goodrich, 1944: 2–3, fig. 1. **Syn. nov.**
Goniobasis interioris Goodrich, 1944: 3–4, fig. 2. **Syn. nov.**

Juga (*Calibasis*) *acutifilosa acutifilosa* – Burch & Tottenham 1980: 152, fig. 450. — Burch 1982: 41, fig. 450; 1989: 152, fig. 450.
Juga (*Oreobasis*) *laurae* – Burch & Tottenham 1980: 154, fig. 467. — Burch 1982: 42, fig. 467; 1989: 154, fig. 467. — Frest & Johannes 2010: 10, 38. — Campbell *et al.* 2016: 160.
Juga (*Oreobasis*) *interioris* – Burch & Tottenham 1980: 154, fig. 466. — Burch 1982: 42, fig. 466; 1989: 154, fig. 466. — Frest & Johannes 2010: 10, 38. — Campbell *et al.* 2016: 160.
Juga acutifilosa – Turgeon *et al.* 1988: 65; 1998: 67. — Johnson *et al.* 2013: 282. — Johannes & Clark 2016: 23–24.
Juga laurae – Turgeon *et al.* 1988: 65; 1998: 67. — Johnson *et al.* 2013: 282.
Juga interioris – Turgeon *et al.* 1988: 65; 1998: 67. — Johnson *et al.* 2013: 282.
Juga (*Calibasis*) *acutifilosa* – Frest & Johannes 1993: 61 (in part); 1995b: 37 (in part); 2000a: 283 (in part); 2005: 160 (in part); 2010: 9, 22, fig. 2a (in part). — Strong & Frest 2007: 51. — Campbell *et al.* 2016: 160, fig. 2a.
Juga (*Calibasis*) n. sp. 1 – Frest & Johannes 1995b: 38 (in part).
Juga (*Calibasis*) OTU 1 – Campbell *et al.* 2016: 160.
Juga (*Calibasis*) OTU 2 – Campbell *et al.* 2016: 160.
Juga acutifilosa group – Strong & Whelan 2019: 89.

non *Juga interioris* – Lee *et al.* 2006: 316. — Ó Foighil *et al.* 2009: 305. [= *Juga douglasi* sp. nov.]
non *Juga* (*Calibasis*) *acutifilosa* – Furnish 2007: 14, fig. 6, above left. [= *Juga occata*]
non *Juga acutifilosa* – Johnson *et al.* 2013: pl. 4. [= *Elimia arachnoidea*]

Material examined

Lectotype of *Melania* (?*Goniobasis*) *acutifilosa* Stearns, 1890 (designated by Strong & Frest 2007: 51) (Fig. 8A)
USA • "Eagle Lake, California"; Jun. 1877; H.W. Henshaw leg.; USNM 60596.

Paralectotypes of *Melania* (?*Goniobasis*) *acutifilosa* Stearns, 1890
USA • 14 spms; same collection data as for lectotype; USNM 1665625 (formerly USNM 60596X) • 25 spms; same collection data as for lectotype; USNM 1665626 (formerly USNM 60596).

Paratypes of *Goniobasis laurae* Goodrich, 1944 (Fig. 8B)
USA • 10 spms; "Spring west of Home Camp, Long Valley, Washoe County, Nevada"; 1934; C.L. Hubbs leg.; MCZ 221159 • 1 spm; "In springs of Grasshopper Valley, Lassen County, California"; 1942; C.L. Hubbs leg.; SBMNH 35483.

Remarks
Holotype (UMMZ 160002, "Spring west of Home Camp, Long Valley, Washoe County, Nevada". 1934. C.L. Hubbs leg.); 100 spms, paratypes (UMMZ 63452, "Spring west of Home Camp, Long Valley, Washoe County, Nevada"; 1934; C.L. Hubbs leg.), possibly lost (Taehwan Lee pers. com.); and 75 spms, paratypes (UMMZ 63453, "In Boulder Springs, Long Valley"; 1934; C.L. Hubbs leg.) not examined.

Paratypes of *Goniobasis interioris* Goodrich, 1944
USA • 2 spms; "Badger Creek, Bitner Ranch, Washoe County, Nevada"; 1942; C.L. Hubbs leg.; MCZ 221163 (Fig. 8C) • 1 spm; same collection data as for preceding; SBMNH 35482.

Remarks
Holotype (UMMZ 160005, "Badger Creek, Bitner Ranch, Washoe County, Nevada"; 1942; C.L. Hubbs leg.) and 1 spm, paratype (UMMZ 160007, "Outlet of artesian wells 9 miles west of Gerlach, Washoe County, Nevada"; 1942; C.L. Hubbs leg.) not examined.

Other material examined
83 lots, 3896 specimens, of which 43 were sequenced.

USA – **Oregon** • 24 spms; Lake Co., adjacent to Coleman Lake (dry); 42.0698, -119.8405; 11 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295054 • 1 spm; same collection data as for preceding; GenBank: MK472270, MK464638, MK480797; USNM 1295053 • 1 spm; same collection data as for preceding; GenBank: MK472261, MK464629; USNM 1295044 • 1 spm; same collection data as for preceding; GenBank: MK472262, MK464630, MK480795; USNM 1295045 • 1 spm; same collection data as for preceding; GenBank: MK472263, MK464631; USNM 1295046 • 1 spm; same collection data as for preceding; GenBank: MK472264, MK464632; USNM 1295047 • 1 spm; same collection data as for preceding; GenBank: MK472265, MK464633; USNM 1295048 • 1 spm; same collection data as for preceding; GenBank: MK472266, MK464634; USNM 1295049 • 1 spm; same collection data as for preceding; GenBank: MK472267, MK464635; USNM 1295050 • 1 spm; same collection data as for preceding; GenBank: MK472268, MK464636; USNM 1295051 • 1 spm; same collection data as for preceding; GenBank: MK472269, MK464637, MK480796; USNM 1295052 • 4 spms; Lake Co., Stone Corral; [42.6206, -119.6913]; C.C. Engberg leg.; USNM 363039. – **California** • 218 spms; Lassen Co., Ash Creek, 2600′ E, 2500′ S, 33-38N-11E, NK 10-9 A-3; [41.0903, -120.7133]; 4 Jul. 1972; D.W. Taylor leg.; CASIZ 183594 • 151 spms; Lassen Co., Ash Creek, 2600’W, 1500’N, 4-38N-10E, NK 10-9 A-4; [41.1592, -120.8272]; 30 Aug. 1981; D.W. Taylor leg.; CASIZ 183597 • 6 spms; Lassen Co., Ash Creek, east side of FS R39N50, at Dan Ryan Place; [41.1499, -120.8176]; 18 Aug. 2007; T. Grace leg.; USNM 1111962 • 12 spms; Lassen Co., Ash Creek, Modoc Natl Forest, Dan Ryan Place, E of FS39N50; 41.1499, -120.8176; 18 Aug. 2007; T. Grace leg.; UF 520305 • 6 spms; same collection data as for preceding; UF 520310 • 4 spms; Lassen Co., Ash Creek, NW of Ash Creek Campground, just below FS22; 41.1604, -120.8292; 18 Aug. 2007; T. Grace leg.; UF 520306 • 49 spms; Lassen Co., Big Spring; [40.7574, -120.1233]; 3 Nov. 1986; D. Sada leg.; USNM 858178 • 9 spms; Lassen Co., Eagle Lake [sic, likely Willow Creek]; [40.6043, -120.6936]; Horn leg.; USNM 59145 • 192 spms; Lassen Co., in spring in Murrers Lower Meadow, approx. 2 mi E of Eagle Lake; [40.5897, -120.6993]; 28 Aug. 1979; J. Landye and L. Eng leg.; on rocks; USNM 892378 • 14 spms; Lassen Co., Modoc Natl Forest, Route 139 Willow Creek, NE side of road, just N of the end of Lower McBride Springs and ca 0.64 km E of Hayden Hill Rd; 41.0176, -120.8379; 16 Sep. 2007; T. Grace leg.; USNM 1111797 • 21 spms; Lassen Co., Modoc Natl Forest, Willow Creek, off Route 139 and just upstream from Hayden Hill Rd (Lassen CR 534, FS 37N42) junction, along W side; 41.0192, -120.8517; 16 Sep. 2007; T. Grace leg.; USNM 1111791 • 3 spms; Lassen Co., N end of Murrers Lower Meadow, S-most of 3 springs and E of Eagle Lake; 40.5848, -120.6959; 10 Sep. 1993; T. Frest and E. Johannes leg.; USNM 1100659 • 248 spms; Lassen Co., Sellicks Springs; [40.5668, -120.321]; 27 Aug. 1979; J. Landye and L. Eng leg.; on rocks and sand; USNM 892370 • 42 spms; Lassen Co., spring in Murrer’s Lower Meadow; 40.5875, -120.6973; 10 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413158 • 1 spm; same collection data as for preceding; GenBank: MK472276, MK464644; USNM 1413152 • 1 spm; same collection data as for preceding; GenBank: MK472277, MK464645, MK480803; USNM 1413153 • 1 spm; same collection data as for preceding; GenBank: MK472278, MK464646; USNM 1413154 • 1 spm; same collection data as for preceding; GenBank: MK472279, MK464647; USNM 1413155 • 1 spm; same collection data as for preceding; GenBank: MK472280, MK464648; USNM 1413156 • 1 spm; same collection data as for preceding; GenBank: MK472281, MK464649; USNM 1413157 • 103 spms; Lassen Co., Spring near Susanville, drains into Honey Lake [possibly Cady Spring]; [40.4158, -120.7106]; W.H. Dall leg.; 4700 ft; USNM 118564 • 17 spms; Lassen Co., Wendel, Secret Valley; [40.3495, -120.2341]; Henshaw leg.; USNM 198875 • 35 spms; Lassen Co., Willow Creek; 10 Oct. 1959; D.W. Taylor leg.; USNM 1151932 • 107 spms; Lassen Co., Willow Creek at Hayden Hill Rd; 41.0202, -120.8526; 10 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413078 • 1 spm; same collection data as for preceding; GenBank: MK472271, MK464639, MK480798; USNM 1413073 • 1 spm; same collection data as for preceding; GenBank: MK472272, MK464640, MK480799; USNM

1413074 • 1 spm; same collection data as for preceding; GenBank: MK472273, MK464641, MK480800; USNM 1413075 • 1 spm; same collection data as for preceding; GenBank: MK472274, MK464642, MK480801; USNM 1413076 • 1 spm; same collection data as for preceding; GenBank: MK472275, MK464643, MK480802; USNM 1413077 • 40 spms; Lassen Co., Willow Creek off dirt road to east, and 0.4 km S of Murrers Lower Meadow; 40.5722, -120.6963; 10 Sep. 1993; T. Frest and E. Johannes leg.; USNM 1100658 • 239 spms; Lassen Co., Willow Creek, S of Adin on Hwy 139 near Willow Creek campground; [41.0131, -120.826]; 31 Jul. 1983; J. Landye leg.; USNM 1152451 • 6 spms; Lassen Co., Willow Fork; Ex.+ Surv. W of 100 Merid.; USNM 198955a • 7 spms; same collection data as for preceding; USNM 198955 • 22 spms; Modoc Co., Ash Creek, Modoc Natl Forest, S of FS39N50 bridge; 41.1499, -120.8176; 8 Oct. 2007; T. Grace leg.; UF 520304 • 14 spms; Modoc Co., Likely, W side of Modoc CR 63, 2.6 mi W of Hwy 395, Smokey Charley Spring run, 0.24 km E of source; 1360 m a.s.l.; [41.2248, -120.5533]; 18 Aug. 2007; T. Grace leg.; on stones and among weeds; USNM 1111961. _ **Nevada** • 12 spms; Humboldt Co., Cabin Springs, Area B, W of cabins 150 m; 30 Aug. 1979; J. Landye *et al.* leg.; on stones; USNM 892377 • 115 spms; Humboldt Co., Little Smoky Creek No. 1; [41.2082, -119.3235]; 16 Jun. 1991; Great Basin Spring Snail Project; G. Vinyard leg.; USNM 874224 • 411 spms; Humboldt Co., Little Smoky Creek No. 3; [41.2082, -119.3235]; 16 Jun. 1991; Great Basin Spring Snail Project; G. Vinyard leg.; USNM 874222 • 20 spms; Humboldt Co., Paiute Canyon, Upper Paiute Creek; [39.7772, -119.5049]; 9 Aug. 1991; Great Basin Spring Snail Project; G. Vinyard leg.; USNM 874271 • 222 spms; Washoe Co., Big Hole Spring, 8 mi NW of Gerlach; [40.7076, -119.4692]; 6 Aug. 1991; Great Basin Spring Snail Project; G. Vinyard leg.; USNM 874273 • 35 spms; Washoe Co., Bitner Ranch; 41.7364, -119.469; 9 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413195 • 1 spm; same collection data as for preceding; GenBank: MK472282, MK464650; USNM 1413189 • 1 spm; same collection data as for preceding; GenBank: MK472283, MK464651, MK480804; USNM 1413190 • 1 spm; same collection data as for preceding; GenBank: MK472284, MK464652, MK480805; USNM 1413191 • 1 spm; same collection data as for preceding; GenBank: MK472285, MK464653; USNM 1413192 • 1 spm; same collection data as for preceding; GenBank: MK472286, MK464654; USNM 1413193 • 1 spm; same collection data as for preceding; GenBank: MK472287, MK464655, MK480806; USNM 1413194 • 405 spms; Washoe Co., Boulder Reservoir Spring; [41.3462, -119.7473]; 2 Aug. 1991; Great Basin Spring Snail Project; G. Vinyard leg.; USNM 874265 • 211 spms; Washoe Co., Deep Hole Spring, 9 mi WNW of Gerlach; [40.7211, -119.4828]; 30 Aug. 1979; J. Landye *et al.* leg.; in areas of flow on rocks and vegetation; USNM 892369 • 34 spms; Washoe Co., Divine Spring run near Home Camp; 41.354, -119.854; 9 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413202 • 1 spm; same collection data as for preceding; GenBank: MK472288, MK464656; USNM 1413196 • 1 spm; same collection data as for preceding; GenBank: MK472289, MK464657, MK480807; USNM 1413197 • 1 spm; same collection data as for preceding; GenBank: MK472290, MK480808; USNM 1413198 • 1 spm; same collection data as for preceding; GenBank: MK472291, MK464658, MK480809; USNM 1413199 • 1 spm; same collection data as for preceding; GenBank: MK472292, MK464659; USNM 1413200 • 1 spm; same collection data as for preceding; GenBank: MK472293, MK464660, MK480810; USNM 1413201 • 23 spms; Washoe Co., Hays Canyon Range, E side of range, unnamed spring; 3 Aug. 1991; Great Basin Spring Snail Project; G. Vinyard leg.; USNM 874267 • 22 spms; Washoe Co., Long Valley, 1 mi NE of Middle Lake, unnamed spring; [41.7801, -119.6705]; 12 Nov. 1992; Great Basin Spring Snail Project; G. Vinyard leg.; USNM 854634 • 339 spms; Washoe Co., N of Little High Rock Reservoir, unnamed spring; [41.2545, -119.4295]; 17 Jun. 1991; Great Basin Spring Snail Project; G. Vinyard leg.; USNM 874220 • 15 spms; Washoe Co., North Little High Rock Canyon Wilderness, Black Rock Desert; 41.2594, -119.4344; 29 Sep. 2011; D. Sada leg.; USNM 1239164 • 1 spm; same collection data as for preceding; GenBank: MK472257; USNM 1239160 • 1 spm; same collection data as for preceding; GenBank: MK472255, MK464625; USNM 1239158 • 1 spm; same collection data as for preceding; GenBank: MK472259; USNM 1239162 • 1 spm; same collection data as for preceding; GenBank: MK472254, MK464624, MK480791; USNM 1239156 • 1 spm; same collection data as for preceding; GenBank: MK472251, MK464621, MK480788; USNM 1239153 • 1 spm; same collection data as for preceding; GenBank: MK472253, MK464623, MK480790; USNM 1239155 • 1 spm; same collection data as for preceding; GenBank: MK472258, MK464627, MK480793; USNM 1239161 • 1 spm; same collection data as for preceding; GenBank: MK472260, MK464628, MK480794; USNM 1239163 • 1 spm; same collection data as for preceding; GenBank: MK472252, MK464622, MK480789;

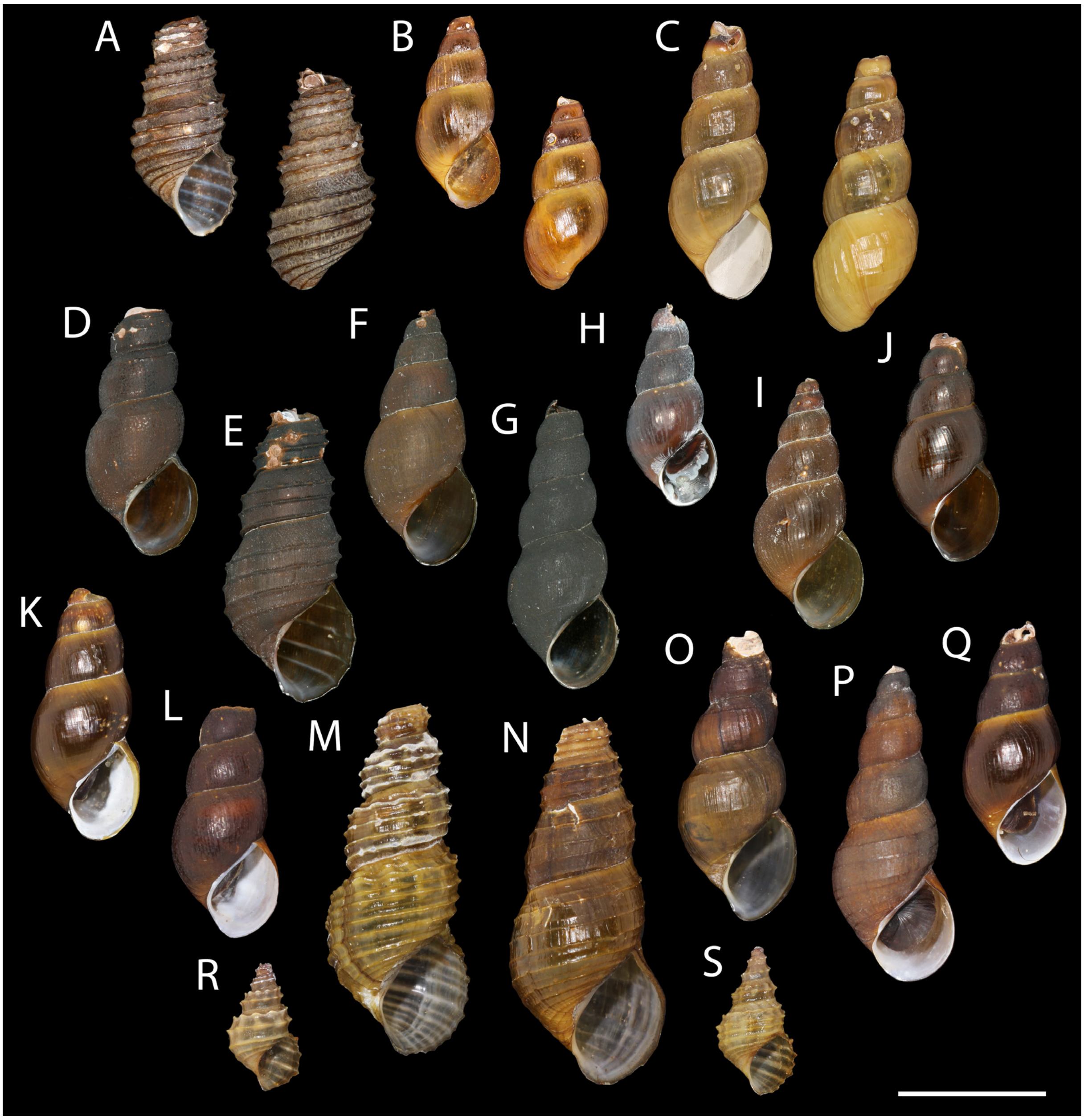


Fig. 8. Shell morphology of *Juga acutifilosa* (Stearns, 1890). **A–C**. Type material. **D–J**. Sequenced vouchers. **A**. *Melania acutifilosa* Stearns, 1890. Lectotype, USNM 60596. **B**. *Goniobasis laurae* Goodrich, 1944. Paratype, MCZ 221159. **C**. *Goniobasis interioris* Goodrich, 1944. Paratype, MCZ 221163. **D–E**. Topotypic (*Melania acutifilosa* Stearns, 1890). **D**. USNM 1413153. **E**. USNM 1413156. **F**. Topotypic (*Goniobasis laurae* Goodrich, 1944), USNM 1413201. **G**. Topotypic (*Goniobasis interioris* Goodrich, 1944), USNM 1413191. **H**. USNM 1239161. **I**. USNM 1295048. **J**. USNM 1413073. **K**. USNM 854634. **L**. USNM 1152451. **M**. CASIZ 183594. **N**. CASIZ 183597. **O**. UF 520310. **P**. USNM 858178. **Q**. USNM 874271. **R–S**. CASIZ 183594. Scale bar = 1 cm.

USNM 1239154 • 1 spm; same collection data as for preceding; GenBank: MK472256, MK464626, MK480792; USNM 1239159 • 396 spms; Washoe Co., Wall Canyon Reservoir, 3 mi above canyon, unnamed spring; [41.2048, -119.7822]; 2 Aug. 1991; Great Basin Spring Snail Project; G. Vinyard leg.; USNM 874269.

Description

Shell. Thin to moderately thick, large, reaching ~2.85 cm in length; turriform, narrowly conical to cylindrical in shape, spire height moderate to tall (Fig. 8). Whorls somewhat flattened to convex or angulate with a subsutural ramp, suture weakly to deeply impressed. Aperture oval in shape, lip smooth to crenate, simple to slightly sinuous. Spiral sculpture absent or present, of thickened, scalloped lirae, barely elevated to prominent, highly variable in number and sinuosity, dividing whorl into intervening flattened areas or grooves. Axial sculpture of fine, orthocline, or weakly opisthocyrt to sinuous growth lines; plications lacking. Shell black, brown or reddish brown, rarely yellowish green in color, occasionally with a lighter subsutural band; bands otherwise lacking. Interior of aperture light brown to white in color.

Radula. Rachidian narrowly rectangular, wider than tall, basal margin slightly concave between bluntly rounded median and lateral projections; basal denticles lacking or vestigial (Fig. 9). Upper margin slightly concave with cutting edge bearing central, elongate conical cusp, and two stout, conical denticles on each side. Lateral teeth with prominent triangular cusp flanked by two inner and three to four outer, triangular denticles, and occasionally a membranous outermost denticle. Marginal teeth with broadly rounded cutting edges and long, slender, flattened shafts with membranous flanges along inner and outer edges. Narrow inner flanges along distal third to half of shafts; broad outer flanges extending almost to tooth bases. Inner marginal teeth with five and outer marginal teeth with six flattened denticles. See also Strong & Frest (2007).

Distribution and ecology

In springs, spring runs, and spring-fed creeks from Modoc and Lassen Counties in the upper Pit River drainage in northern California and in Great Basin drainages from northeastern California (Lassen County, Honey Lake basin), southeastern Oregon (Lake County), and northwestern Nevada, primarily in Washoe County, and adjacent parts of western Humboldt County (Fig. 7B).

Remarks

The type material of *Melania acutifilosa* was collected during the geographical surveys of the territory of the United States west of the 100th meridian (Wheeler 1879). The type locality is “Eagle Lake” (Stearns 1890), later corrected by Taylor (1981) to head of Willow Creek without justification. Strong & Frest (2007) followed this, explaining that no populations are currently found in Eagle Lake or in the small tributaries that flow into the lake during winter. Moreover, specimens of *Juga* have not been recorded from the lake itself during subsequent collecting efforts (e.g., by J. Maillard in 1923; Hanna 1924) nor from drift and dredged material (Frest & Johannes 2010) but have been reported from several unnamed springs and creeks nearby in collections made by R.C. McGregor in 1898 (Pilsbry 1899; in the collections of the ANSP). Frest & Johannes (2010) noted that Taylor (1981) did not distinguish between the “headwaters” or “Murrer’s Meadows” as the source of the types. Given their view that different taxonomical species are found in the headwaters versus further downstream, they concluded the lirate types were most likely from the head of Willow Creek. This is likely correct, as Willow Spring at the head of Willow Creek in Murrer’s Upper Meadow was the site of an altitude measurement taken during the survey (Wheeler 1879: 130) and lies roughly two miles to the east of the shore of Eagle Lake. Frest & Johannes (2010) considered USNM 198955 from “Willow Fork” also collected during the expedition as possible topotypes; the lot was annotated “Eagle Lake vicinity” by J.P.E. Morrison who separated the original lot into lirate and smooth forms (USNM 198955 and USNM 198955a), which are here considered conspecific.

This is a highly variable species, ranging from lirate to smooth forms, and like *J. canella* sp. nov. with which this species has been frequently confused, these forms can co-occur at a single site. *Juga laurae* and *J. interioris* have been considered valid species in recent classifications (Burch & Tottenham 1980; Burch 1982, 1989; Turgeon *et al.* 1988, 1998; Frest & Johannes 2010; Johnson *et al.* 2013). However, molecular data (Strong & Whelan 2019) show that topotypic specimens (Fig. 8F–G) of these two

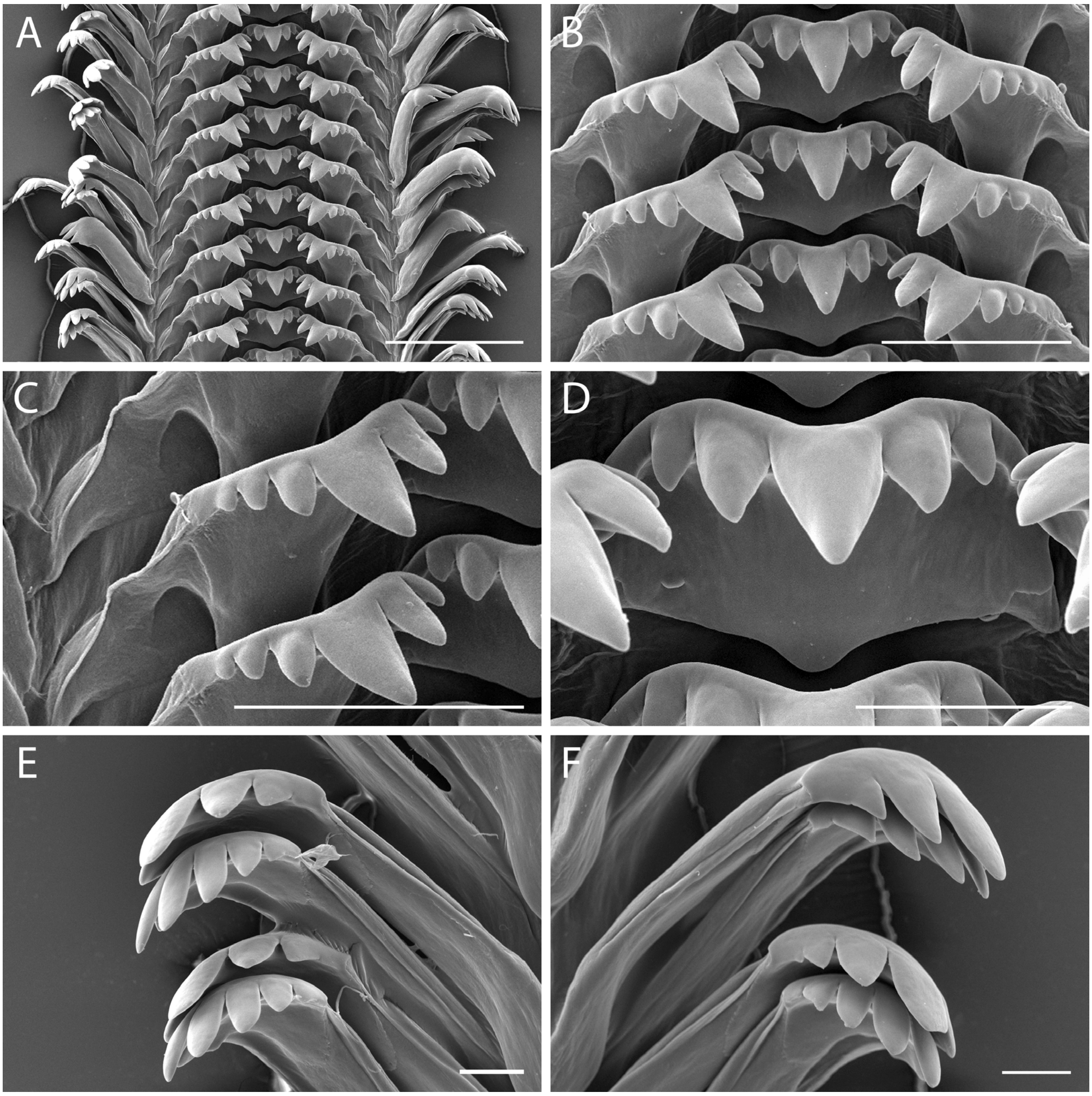


Fig. 9. Radular morphology of *Juga acutifilosa* (Stearns, 1890). **A**. View of the anterior radular ribbon. **B**. Detail of cutting edge of rachidian and lateral teeth. **C**. Detail of lateral teeth cusps. **D**. Detail of rachidian cusps. **E**. Inner and outer marginal teeth. **F**. Detail of inner and outer marginal teeth cusps. (D and F modified from Strong & Frest 2007). Scale bars: A = 200 µm; B–C = 100 µm; D = 50 µm; E–F = 20 µm.

nominal species are conspecific with disjunct populations from adjacent parts of Oregon and California, including from the type locality of *M. acutifilosa* (Fig. 8D–E), and their synonymy with *J. acutifilosa* here is new. *Juga laurae* and *J. interioris* were established by Goodrich (1944), who found them so wanting in definite characters of the shell, operculum, and radula that he was at first hesitant to describe them as new (Goodrich 1935), but later upon doing so, felt unable to ascertain their affinities (Goodrich 1944: 1). Despite statements to the contrary (Frest & Johannes 2010: 38), Taylor (1981) did not mention nor explicitly synonymize the two with *J. nigrina* in his checklist of freshwater mollusks of California. The range for *nigrina*, given by Taylor (1981: 149) as "northern California and adjacent parts of Oregon and Nevada", might imply inclusion of *laurae* and *interioris*, but is ambiguous.

Distribution

The species as redefined herein occurs in the upper Pit River drainage in northern California and Great Basin drainages in northeastern California, southeastern Oregon, and northwestern Nevada. Based on the presence of elevated spiral lirae, *J. acutifilosa* erroneously has been considered to extend to Siskiyou County, California, and Jackson County in south-central Oregon (Frest & Johannes 1993, 2000a, 2010; Furnish 2007; Johnson *et al.* 2013), although Frest & Johannes (2010) acknowledged the species to be composite. As defined by Frest & Johannes (1993, 2000a, 2005, 2010: table 5), *J. acutifilosa* would contain species referable to *J. acutifilosa*, *J. occata*, and *J. canella* sp. nov. as redefined herein.

USNM 1296706 is a lot of 11 specimens ostensibly collected in Jun. 1948 from Convict Creek, a Great Basin tributary of the Owens River in Mono County, California. This record lies far to the south of the currently accepted distribution of *Juga* and its provenance is unreliable. A lot from Paiute Canyon in southern Humboldt County, Nevada, collected in 1991 under the auspices of the Great Basin Spring Snail Project, represents a southern extension of the range as reported elsewhere (Strong & Frest 2007; Frest & Johannes 2010; Campbell *et al.* 2016). The species is more broadly distributed than previously appreciated and includes populations of smooth, dark morphs attributed to *J. interioris* and *J. laurae* from northwestern Nevada.

Common name

The common name for this species is the Scalloped Juga (Frest & Johannes 1993, 2000a). Turgeon *et al*. (1988, 1998) incorrectly referred to this species as the Topaz Juga (= *J. occata*) which was followed by Frest & Johannes (1995b, 2010) and Johnson *et al.* (2013). This may have been the result of the erroneous synonymy of *Goniobasis acutifilosa pittensis* with the frequently reddish-brown *J. acutifilosa* rather than with *J. occata*, for which a green- or yellow-brown coloration is more typical (Frest & Johannes 2010; see *J. occata* below). Synonyms have been known as the Oasis Juga (for *J. laurae*) and Smooth Juga (for *J. interioris*) (e.g., Turgeon *et al.* 1988, 1998; Frest & Johannes 2010; Johnson *et al.* 2013). As mentioned above, populations from south-central Oregon (Frest & Johannes 1993, 2000a, 2005) referred to as the Scalloped Juga represent a different species (= *Juga canella* sp. nov.; see account below). A composite species comprised of *J. acutifilosa* and *J. occata* as circumscribed herein has been referred to as the Willow Creek Juga (= *Juga* (*Calibasis*) n. sp. 1; Frest & Johannes 1995b). The specimen with a prominent spiral keel figured as *J. acutifilosa* (USNM 425495) in Johnson *et al.* (2013), is *Elimia arachnoidea* (Anthony, 1854) (USNM 28749) from Tennessee.

Juga bulbosa (A. Gould, 1847)
Figs 10–11

Melania bulbosa A. Gould, 1847: 225.
Goniobasis bairdiana I. Lea, 1862: 267. **Syn. nov.**
Goniobasis draytonii I. Lea, 1862: 264. **Syn. nov.**
Goniobasis hemphilli maupinensis Henderson, 1935a: 97. **Syn. nov.**

Melania bulbosa – Gould 1852: 142; "1856" [1860]: pl. 10 fig. 163–163a; 1862: 46–47.
Goniobasis bairdiana – Lea 1863a: 317–318, pl. 37 fig. 164; 1863b: 139–140, pl. 37 fig. 164.
Goniobasis draytonii – Lea 1863a: 300, pl. 37 fig. 134; 1863b: 122, pl. 37 fig. 134.
Juga (*Oreobasis*) *bulbosa* – Burch & Tottenham 1980: 152 (in part) . — Burch 1982: 41 (in part); 1989: 152 (in part). — Frest & Johannes 2010: 9, 26. — Johannes 2015: 24.
Juga (*Juga*) *silicula* – Burch & Tottenham 1980: 152 (in part). — Burch 1982: 41 (in part); 1989: 152 (in part).
Juga (*Juga*) *hemphilli hemphilli* – Burch & Tottenham 1980: 152, fig. 454. — Burch 1982: 41, fig. 454; 1989: 152, fig. 454. — Frest & Johannes 2010: fig. 2c.
Juga (*Juga*) *hemphilli maupinensis* – Neitzel & Frest 1992: B.25. — Frest & Johannes 1995a: 173; 2010: 10, 37. — Johannes 2015: 23. — Campbell *et al.* 2016: 160.
Juga (*Juga*) *plicifera plicifera* – Neitzel & Frest 1992: B.25 (in part).
Juga (*Oreobasis*) n. sp. 1 – Frest & Johannes 1993: 64; 1995a: 178; 2001: 60.
Juga (*Oreobasis*) n. sp. 2 – Frest & Johannes 1993: 65; 1995a: 179; 1996: 43, 131; 1999: 85, figs 33–34. — Johannes 2015: 23.
Juga (*Juga*) n. sp. 1 – Frest & Johannes 1993: 63 (in part); 1995a: 175 (in part); 2001: 60 (in part).
Juga (*Juga*?) *bairdiana* – Frest & Johannes 1995a: 246.
Juga (*Juga*) *rubiginosa* – Frest & Johannes 1995a: 246.
Juga (*Oreobasis*?) *draytonii* – Frest & Johannes 1995a: 247.
Juga (*Juga*) n. sp. 2 – Frest & Johannes 1995a: 176; 2001: 60. — Johannes 2015: 23.
Juga bulbosa – Strong & Frest 2007: 56. — Johnson *et al.* 2013: 282.
Juga (*Juga*) *draytonii* – Frest & Johannes 2010: 10, 34 (in part).
Juga (*Juga*) *bairdiana* – Campbell *et al.* 2016: 160.
Juga species 2 – Strong & Whelan 2019: 89, fig. 4a-e.

non *Oxytrema bulbosa* – Morrison 1954: 361, 384, pl. 11 fig. 5. [= *Juga caerulea* sp. nov.]
non *Juga bulbosa* – Turgeon *et al.* 1988: 65; 1998: 67. [= *Juga newberryi*]
non *Juga* (*Oreobasis*) *bulbosa* – Neitzel & Frest 1992: B.25. — Frest & Johannes 1995a: 177. [= *Juga newberryi*]
non *Juga* (*Oreobasis*) n. sp. 1 – Frest & Johannes 1995b: 39; 2005: 179. — Johannes 2013a: 24. [= *Juga canella* sp. nov.]
non *Juga* (*Oreobasis*) n. sp. 2 – Frest & Johannes 2005: 179. [= *Juga canella* sp. nov.]
non *Juga* (*Juga*) *draytonii* – Campbell *et al.* 2016: 160. [= *Juga plicifera*]

Material examined

Lectotype of *Melania bulbosa* A. Gould, 1847 (designated by Graf 2001: 18) (Fig. 10A)
USA • "Columbia River" [label: "Oregon"]; U.S. Exploring Expedition; J. Drayton leg.; MCZ 169067.

Paralectotypes of *Melania bulbosa* A. Gould, 1847
USA • 9 spms; same collection data as for lectotype; MCZ 169068 • 1 spm; [labels: "Oregon"]; MCZ 216750 • 2 spms; "Oregon" [Territory]; U.S. Exploring Expedition; USNM 5563.

Lectotype of *Goniobasis bairdiana* I. Lea, 1862 (designated by Graf 2001: 14) (Fig. 10B)
USA • "Columbia River, at Fort George, Oregon [Territory]"; J. Drayton leg.; USNM 119069.

Paralectotype of *Goniobasis bairdiana* I. Lea, 1862
USA • 1 spm; same collection data as for lectotype; USNM 1665627 (formerly USNM 119069X).

Lectotype of *Goniobasis draytonii* I. Lea, 1862 (designated by Graf 2001: 38) (Fig. 10C)
USA • "Fort George, Oregon"; J. Drayton leg.; USNM 118993.

Paralectotypes of *Goniobasis draytonii* I. Lea, 1862

USA • 6 spms; same collection data as for lectotype; USNM 1665629 (formerly USNM 118993X) • 12 spms; "Walla, Oregon" [sic, Walla Walla, Oregon Territory]; received from Lady K. Douglas; USNM 119124.

Holotype of *Goniobasis hemphilli maupinensis* Henderson, 1935 (Fig. 10D)

USA • "Deschutes River, Maupin, Oregon"; 11 Aug. 1931; J. and B.R. Henderson leg.; UCM 17754a.

Remarks

1 paratype (UCM 17754b, same collection data as for holotype) not examined (McCoy 1964).

Other material

114 lots, 678 specimens, of which 75 were sequenced.

USA – **Washington** • 32 spms; Klickitat Co., Major Creek; 45.7154, -121.3509; 6 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413188 • 1 spm; same collection data as for preceding; GenBank: MK472168, MK464540; USNM 1413185 • 1 spm; same collection data as for preceding; GenBank: MK472169, MK464541; USNM 1413186 • 1 spm; same collection data as for preceding; GenBank: MK472170, MK464542; USNM 1413187 • 40 spms; Skamania Co., Dog Creek; 45.7106, -121.6715; 5 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413232 • 1 spm; same collection data as for preceding; GenBank: MK472171, MK464543; USNM 1413227 • 1 spm; same collection data as for preceding; GenBank: MK472172, MK464544; USNM 1413228 • 1 spm; same collection data as for preceding; GenBank: MK472173, MK464545; USNM 1413229 • 1 spm; same collection data as for preceding; GenBank: MK472174, MK464546; USNM 1413230 • 1 spm; same collection data as for preceding; GenBank: MK472175, MK464547; USNM 1413231 • 8 spms; Yakima Co., Ahtanum Creek, south of Union Gap; [46.5369, -120.4751]; UCM 15814. – **"Oregon" [Territory]** • 1 spm; USNM 59058 • 3 spms; same collection data as for preceding; USNM 56427 • 1 spm; same collection data as for preceding; USNM 36948 • 2 spms; same collection data as for preceding; USNM 12141 • 6 spms; same collection data as for preceding; USNM 12209. – **Oregon** • 10 spms; Hood River Co., Post Canyon Dr; 45.697, -121.5749; 8 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295063 • 1 spm; same collection data as for preceding; GenBank: MK472148, MK464520; USNM 1295056 • 1 spm; same collection data as for preceding; GenBank: MK472149, MK464521; USNM 1295057 • 1 spm; same collection data as for preceding; GenBank: MK472150, MK464522; USNM 1295058 • 1 spm; same collection data as for preceding; GenBank: MK472151, MK464523, MK480749; USNM 1295059 • 1 spm; same collection data as for preceding; GenBank: MK472158, MK464530; USNM 1295060 • 1 spm; same collection data as for preceding; GenBank: MK472159, MK464531; USNM 1295061 • 1 spm; same collection data as for preceding; GenBank: MK472160, MK464532; USNM 1295062 • 1 spm; same collection data as for preceding; GenBank: MK472147, MK464519; USNM 1295055 • 20 spms; Hood River Co., SH 281, Hood River; 45.6971, -121.5231; 8 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295095 • 1 spm; same collection data as for preceding; GenBank: MK472152, MK464524; USNM 1295087 • 1 spm; same collection data as for preceding; GenBank: MK472153, MK464525; USNM 1295088 • 1 spm; same collection data as for preceding; GenBank: MK472154, MK464526; USNM 1295089 • 1 spm; same collection data as for preceding; GenBank: MK472155, MK464527, MK480750; USNM 1295090 • 1 spm; same collection data as for preceding; GenBank: MK472156, MK464528; USNM 1295091 • 1 spm; same collection data as for preceding; GenBank: MK472161, MK464533; USNM 1295092 • 1 spm; same collection data as for preceding; GenBank: MK472162, MK464534; USNM 1295093 • 1 spm; same collection data as for preceding; GenBank: MK472163, MK464535; USNM 1295094 • 28 spms; Hood River Co., West Fork Neal Creek at 1700 Rd; 45.5421, -121.5222; 5 Aug. 2015; Jennings leg.; USNM 1413445 • 1 spm; same collection data as for preceding; GenBank: MK472202; USNM 1413438 • 1 spm; same collection data as for preceding;

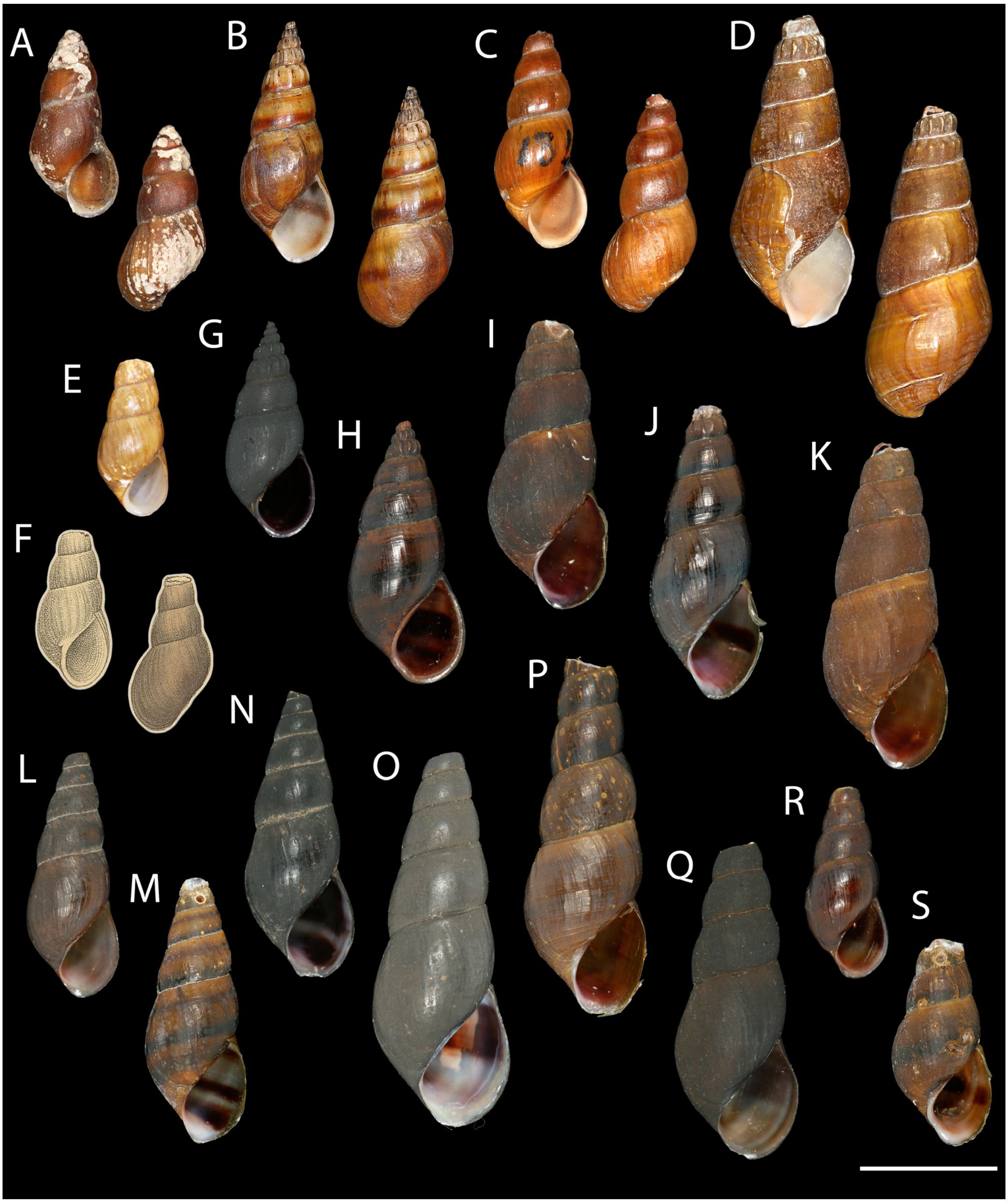


Fig. 10. Shell morphology of *Juga bulbosa* (A. Gould, 1847). **A–D**. Type material. **G–S**. Sequenced vouchers. **A**. *Melania bulbosa* A. Gould, 1847. Lectotype, MCZ 169067. **B**. *Goniobasis bairdiana* I. Lea, 1862. Lectotype, USNM 119069. **C**. *Goniobasis draytonii* I. Lea, 1862. Lectotype, USNM 118993. **D**. *Goniobasis hemphilli maupinensis* Henderson, 1935. Holotype, UCM 17754a. **E**. *Melania bulbosa*. Figured specimen, USNM 5563. **F**. *Melania bulbosa.* Original figure (Gould 1860: pl. 10 fig. 163–163a). **G**. USNM 1413315. **H**. USNM 1413307. **I–J**. Near topotypic (*Goniobasis hemphilli maupinensis* Henderson, 1935). **I**. USNM 1413300. **J**. USNM 1413301. **K**. USNM 1413426. **L**. USNM 1413186. **M**. USNM 1413230. **N**. USNM 1295091. **O**. USNM 1295055. **P**. USNM 1413165. **Q**. USNM 1413458. **R**. USNM 1413435. **S**. USNM 1295201. Scale bar = 1 cm.

GenBank: MK472203, MK464574; USNM 1413439 • 1 spm; same collection data as for preceding; GenBank: MK472204, MK464575; USNM 1413440 • 1 spm; same collection data as for preceding; GenBank: MK472205; USNM 1413441 • 1 spm; same collection data as for preceding; GenBank: MK472206, MK464576; USNM 1413442 • 1 spm; same collection data as for preceding; USNM 1413443 • 1 spm; same collection data as for preceding; GenBank: MK472207, MK464577; USNM 1413444 • 1 spm; Jefferson Co., Deschutes River at junction with Dry Creek; 44.7844, -121.1959; 8 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413422 • 25 spms; Jefferson Co., Deschutes River, 100 yds. S of Hwy 26 bridge at Warm Springs; [44.7595, -121.2277]; 2 Aug. 1971; J. Landye leg.; USNM 892362 • 1 spm; Jefferson Co., U.S. Hwy 26; 44.7584, -121.2272; 9 Jul. 2014; J.T. Garner and N.V. Whelan leg.; GenBank: MK472157, MK464529; USNM 1295201 • 59 spms; Sherman Co., confluence of Muddy Hollow and China Hollow; 45.6471, -120.8086; 6 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413310 • 1 spm; same collection data as for preceding; GenBank: MK472181, MK464553; USNM 1413305 • 1 spm; same collection data as for preceding; GenBank: MK472182, MK464554, MK480751; USNM 1413306 • 1 spm; same collection data as for preceding; GenBank: MK472183, MK464555; USNM 1413307 • 1 spm; same collection data as for preceding; GenBank: MK472184, MK464556; USNM 1413308 • 1 spm; same collection data as for preceding; GenBank: MK472185; USNM 1413309 • 54 spms; Sherman Co., Muddy Hollow 2; 45.6311, -120.7933; 6 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413316 • 1 spm; same collection data as for preceding; GenBank: MK472186, MK464557, MK480752; USNM 1413311 • 1 spm; same collection data as for preceding; GenBank: MK472187, MK464558, MK480753; USNM 1413312 • 1 spm; same collection data as for preceding; GenBank: MK472188, MK464559, MK480754; USNM 1413313 • 1 spm; same collection data as for preceding; GenBank: MK472189, MK464560; USNM 1413314 • 1 spm; same collection data as for preceding; GenBank: MK472190, MK464561; USNM 1413315 • 1 spm; Wasco Co., Oak Springs; 45.2216, -121.0827; 8 Sep. 2015; E.E. Strong and P. Bouchet leg.; GenBank: MK472164, MK464536; USNM 1413165 • 1 spm; same collection data as for preceding; GenBank: MK472165, MK464537; USNM 1413166 • 1 spm; same collection data as for preceding; GenBank: MK472166, MK464538; USNM 1413167 • 1 spm; same collection data as for preceding; GenBank: MK472167, MK464539; USNM 1413168 • 4 spm; Skamania Co., above Bonneville Dam, Sullivan's Id., Columbia River; [45.6916, -121.882]; H.W. Krieger leg.; USNM 468428 • 23 spms; Wasco Co., Chenoweth Creek on Chenoweth Rd; [45.6289, -121.2283]; 1 Aug. 1983; J. Landye leg.; USNM 1152452 • 45 spms; Wasco Co., Fifteenmile Creek; 45.4309, -121.2249; 6 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413359 • 1 spm; same collection data as for preceding; GenBank: MK472191, MK464562; USNM 1413354 • 1 spm; same collection data as for preceding; GenBank: MK472192, MK464563; USNM 1413355 • 1 spm; same collection data as for preceding; GenBank: MK472193, MK464564, MK480755; USNM 1413356 • 1 spm; same collection data as for preceding; GenBank: MK472194, MK464565; USNM 1413357 • 1 spm; same collection data as for preceding; GenBank: MK472195, MK464566; USNM 1413358 • 1 spm; Wasco Co., Gate Creek at the 4820 Rd; 45.2193, -121.4305; 9 Jul. 2015; Jennings leg.; GenBank: MK472215; USNM 1413455 • 1 spm; Wasco Co., Gate Creek at the 4820 Rd; 45.2193, -121.4305; 9 Jul. 2015; Jennings leg.; USNM 1413462 • 19 spms; Wasco Co., Gate Creek at the 4820 Rd; 45.2192, -121.4305; 5 Aug. 2015; Jennings leg.; USNM 1413454 • 1 spm; same collection data as for preceding; GenBank: MK472211, MK464581, MK480757; USNM 1413450 • 1 spm; same collection data as for preceding; GenBank: MK472212, MK464582; USNM 1413451 • 1 spm; same collection data as for preceding; GenBank: MK472213, MK464583; USNM 1413452 • 1 spm; same collection data as for preceding; GenBank: MK472214, MK464584; USNM 1413453 • 40 spms; Wasco Co., Harpham Flat; 45.1375, -121.122; 8 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413304 • 1 spm; same collection data as for preceding; GenBank: MK472176, MK464548; USNM 1413299 • 1 spm; same collection data as for preceding; GenBank: MK472177, MK464549; USNM 1413300 • 1 spm; same collection data as for preceding; GenBank: MK472178, MK464550; USNM 1413301 • 1 spm; same collection data as for preceding; GenBank: MK472179, MK464551; USNM 1413302 • 1 spm; same collection data as for preceding; GenBank: MK472180, MK464552; USNM 1413303 • 26 spms; Wasco Co., I-84 eastbound at The Dalles Dam just past exit 88 (Frest spring #3 site); 45.6256, -121.1059; 18 May 2017; K. Van Norman leg.; USNM 1592625 • 1 spm; same collection data as for preceding; USNM 1592629 • 1 spm; same collection data as for preceding; USNM 1592626 • 1 spm; same collection data as for preceding; USNM 1592627 • 1 spm; same collection data as for preceding; USNM 1592628 • 1 spm; Wasco Co., South Fork Gate Creek at the 4830 Rd; 45.196, -121.4132; 15 Jul. 2015; Jennings leg.; GenBank: MK472216, MK464585, MK480758; USNM 1413456 • 29 spms; Wasco Co., South Fork Gate Creek at the 4830 Rd; 45.196, -121.4132; 5 Aug. 2015; Jennings leg.; USNM 1413461 • 1 spm; same collection data as for preceding; GenBank: MK472217, MK464586; USNM 1413457 • 1 spm; same collection data as for preceding; GenBank: MK472218, MK464587; USNM 1413458 • 1 spm; same collection data as for preceding; GenBank: MK464588; USNM 1413459 • 1 spm; same collection data as for preceding; GenBank: MK472219, MK464589; USNM 1413460 • 1 spm; Wasco Co., South Junction; 44.8602, -121.0604; 8 Sep. 2015; E.E. Strong and P. Bouchet leg.; GenBank: MK472196, MK464567; USNM 1413423 • 1 spm; same collection data as for preceding; GenBank: MK472197, MK464568; USNM 1413424 • 1 spm; same collection data as for preceding; GenBank: MK472198, MK464569; USNM 1413425 • 1 spm; same collection data as for preceding; GenBank: MK472199, MK464570; USNM 1413426 • 1 spm; same collection data as for preceding; GenBank: MK472200, MK464571; USNM 1413427 • 1 spm; Wasco Co., Souva Creek off the 4830120 Rd; 45.2081, -121.448; 8 Jul. 2015; Jennings leg.; GenBank: MK472201, MK464573; USNM 1413437 • 1 spm; Wasco Co., Souva Creek off the 4830120 Rd; 45.2085, -121.4483; 8 Jul. 2015; Jennings leg.; USNM 1413448 • 1 spm; same collection data as for preceding; GenBank: MK472210, MK464580; USNM 1413449 • 1 spm; Wasco Co., Souva Creek off the 4830120 Rd; 45.209, -121.4493; 8 Jul. 2015; Jennings leg.; GenBank: MK472208, MK464578; USNM 1413446 • 1 spm; Wasco Co., Souva Creek off the 4830120 Rd; 45.2094, -121.45; 8 Jul. 2015; Jennings leg.; GenBank: MK472209, MK464579; USNM 1413447 • 25 spms; Wasco Co., Souva Creek off the 4830120 Rd; 45.2081, -121.4481; 5 Aug. 2015; Jennings leg.; USNM 1413436 • 1 spm; same collection data as for preceding; GenBank: MK464572, MK480756; USNM 1413435 • 48 spms; Wasco Co., Warm Springs River; 44.9672, -121.4687; 6 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413407 • 1 spm; same collection data as for preceding; USNM 1413402 • 1 spm; same collection data as for preceding; USNM 1413403 • 1 spm; same collection data as for preceding; USNM 1413404 • 1 spm; same collection data as for preceding; USNM 1413405 • 1 spm; same collection data as for preceding; USNM 1413406 • 33 spms; Wasco Co., Warm Springs River, at Hwy 26 Crossing NW of Warm Springs River; [44.9669, -121.4678]; 2 Aug. 1971; J. Landye leg.; on rocks; USNM 892374 • 7 spms; Wasco Co., Warm Springs River, near Kah-Nee-Ta Warm Spring Area by highway bridge; [44.8664, -121.2164]; 23 Apr. 1975; J. Landye leg.; on sand; USNM 892376 • 2 spms; Willamette River [sic, mislocalized]; S. Smith leg.; USNM 321825.

Description

Shell. Thick, large, reaching ~2.75 cm in length; turriform, narrowly conical in shape, spire height moderate to tall (Fig. 10). Whorls somewhat flattened to moderately convex, suture weakly to moderately impressed. Aperture oval in shape, lip smooth and simple. Spiral sculpture of numerous fine striae, usually indistinct but occasionally weakly to moderately developed, variable in strength and number; sporadic indistinct elevated lirae. Axial sculpture of fine, sinuous growth lines; plications present or absent, confined to upper part of spire; plications regular and even, weakly to moderately developed, occasionally shouldered, orthocline to weakly opisthocyrt, variable in strength and number. Shell black, dark or reddish brown, to tan in color, occasionally with a lighter subsutural band; reddish brown bands present or absent, one to three in number and variable in width. Interior of aperture white, yellowish-brown to dark purple in color; bands when present visible inside aperture.

Radula. Rachidian narrowly rectangular, wider than tall, basal margin flattened between bluntly rounded median and lateral projections; basal denticles lacking or vestigial (Fig. 11). Upper margin slightly concave with cutting edge bearing central elongate, conical cusp, and two stout, conical denticles on each side. Lateral teeth with prominent triangular cusp flanked by two inner and two to three outer, triangular denticles, and occasionally a membranous outermost denticle. Marginal teeth with broadly rounded cutting edges and long, slender, flattened shafts with membranous flanges along inner and outer edges. Narrow inner flanges along distal third of inner marginal teeth and extending almost to tooth bases of outer marginal teeth; broad outer flanges extending almost to tooth bases. Inner marginal teeth with four and outer marginal teeth with four to five flattened denticles.

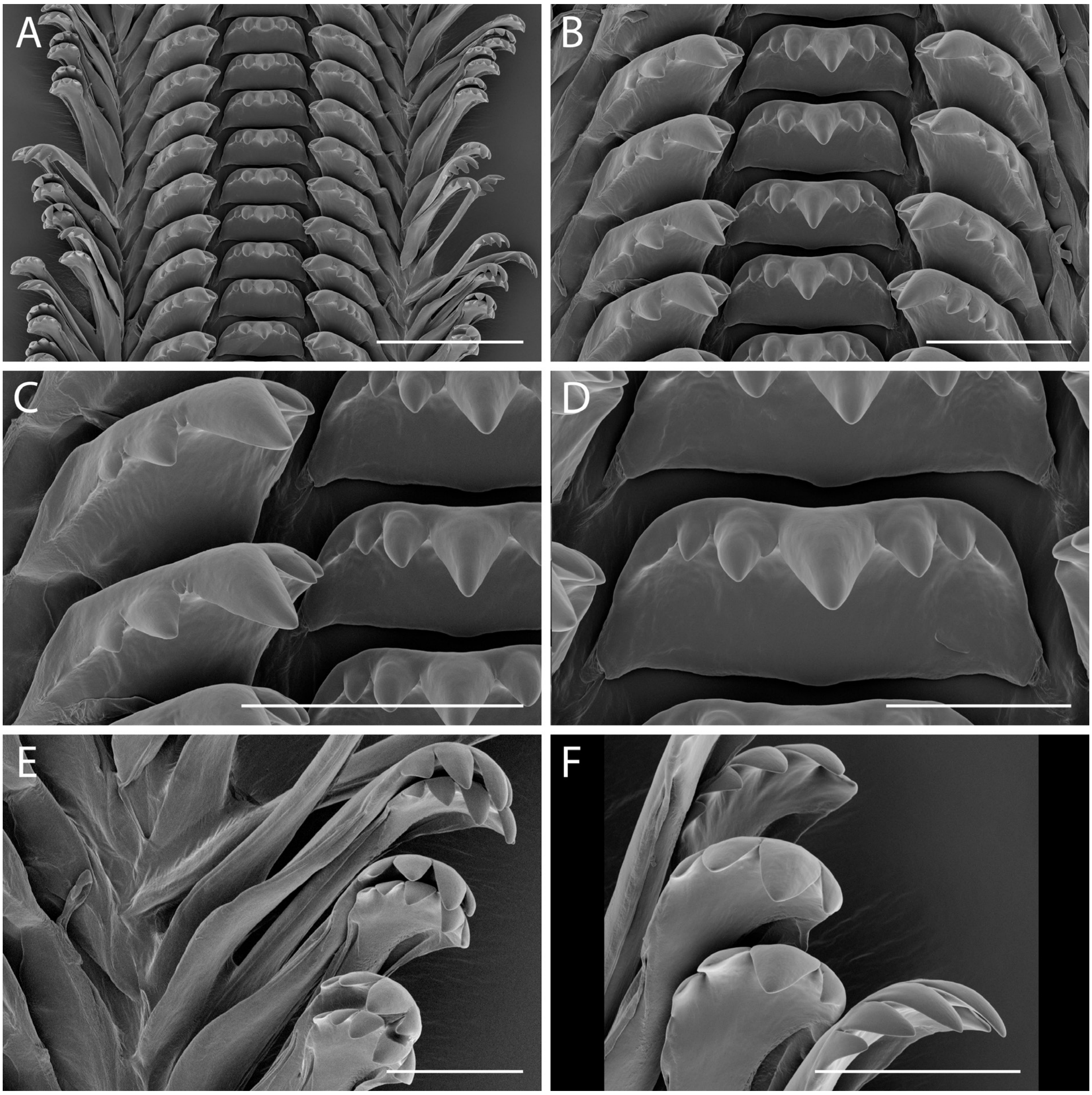


Fig. 11. Radular morphology of *Juga bulbosa* (A. Gould, 1847) (USNM 1413186). **A**. View of the anterior radular ribbon. **B**. Detail of cutting edge of rachidian and lateral teeth. **C**. Detail of lateral teeth cusps. **D**. Detail of rachidian cusps. **E**. Inner and outer marginal teeth. **F**. Detail of inner and outer marginal teeth cusps. Scale bars: A = 200 µm; B–C = 100 µm; D–F = 50 µm.

Distribution and ecology

In springs, spring runs, and spring-fed creeks to large rivers in the central and eastern Columbia River Gorge drainages in north-central Oregon and south-central Washington, including the Mt. Hood National Forest, Columbia Gorge National Scenic Area, and Lower Deschutes River below Pelton Dam (Fig. 7C).

Remarks

The type locality of *Goniobasis bairdiana* and *G. draytonii*, both ostensibly from the Columbia River at Fort George [= Astoria] collected by J. Drayton, is likely erroneous (Frest & Johannes 2010), as the species does not extend to the western Columbia Gorge and there is no evidence it ever has. All sequenced specimens and historical lots in museum collections from the terminal part of the Columbia River are conspecific with *Juga plicifera* (e.g., Fig. 5K–M). Joseph Drayton was the expedition's artist and travelled up the Columbia Gorge as far as Fort Walla Walla with a Hudson Bay Company boat bringing supplies to the forts up the river (Smith 1937; Frest & Johannes 2010), and thus the types could have come from anywhere along this route, likely from tributaries of the main stem Columbia in the central to eastern part of the gorge. The paralectotype lot of *draytonii* from "Walla" [sic, Walla Walla] (USNM 119124) received via Lady K. Douglas lies well to the east of the known range but its provenance is unreliable (Carpenter 1857: 162).

Intensive sequencing effort along the Columbia Gorge has revealed only two species (Strong & Whelan 2019), *Juga plicifera* and a second species that Strong & Whelan (2019) referred to as *Juga* species 2 and for which we consider *Melania bulbosa* to be the earliest available name. The type locality of *M. bulbosa*, vaguely attributed to the "Columbia River", is not in conflict with this interpretation. Although considered valid in most historical taxonomical treatments (see Frest & Johannes 2010; table 2), the erroneous synonymy of *M. newberryi* with *bulbosa* (see *J. newberryi*, below), resulted in enormous confusion in the application of the name and most usages of *bulbosa* in the literature in fact refer to *J. newberryi* (e.g., Tryon 1865: fig. 17, 1866: fig. 217, 1873: fig. 496; Roscoe 1963: pl. 4 figs 5–6; Burch & Tottenham 1980: fig. 452; Burch 1982, 1989: fig. 452; Turgeon *et al.* 1988, 1998) (see below). This confusion was caused, at least in part, by the paucity of historical material in museum collections, and what little there is in some cases contains mixtures of the two species. For example, the paralectotype lot MCZ 169068 is a mixture of *bulbosa* and *newberryi*, as is USNM 5563 which contains Gould's (1860: pl. 10 fig. 163–163a) figured specimen of *bulbosa* (Fig. 10E–F). Strong & Frest (2007) removed *newberryi* from the synonymy of *bulbosa*, leaving the status of the latter somewhat unresolved as a likely valid species; this was followed by Frest & Johannes (2010) who reported that they had been unable to recollect this form anywhere in the Deschutes River drainage or Columbia Gorge; accordingly, Campbell *et al.* (2016) reported they could not assess its status. Johnson *et al.* (2013) considered *bulbosa* a valid species and it was indicated to be endangered under AFS criteria and critically imperiled under NatureServe's global conservation status ranks but tallied as extinct (Johnson *et al.* 2013: table 1) (Campbell *et al.* 2016; Campbell 2019).

After comprehensive review of the type material in comparison to the morphology of sequenced specimens, we consider the smooth, unbanded lectotypes of *Melania bulbosa* (Fig. 10A) and *Goniobasis draytonii* (Fig. 10C) to fall within the range of variation of *Juga* species 2 sensu Strong & Whelan (2019) in size, proportion, profile, and sculpture. However, populations precisely matching the distinctive morphology of the types of *bulbosa* have not been recollected thus far (Strong & Frest 2007; Frest & Johannes 2010) and may no longer be extant. Frest & Johannes (2010: 26) noted the similarity of the types of *bulbosa* and of *draytonii* but distinguished the latter on the basis of its more elongate spire and more numerous whorls after decollation. Frest & Johannes (1993, 1995a, 2001) considered that their *J.* (*J.*) n. sp. 1 (Brown Juga) could match Lea's types of *draytonii*, but their composite concept of the species was distributed from the central and western Columbia Gorge in both Oregon and Washington, including the Mt. Hood National Forest, and thus would include individuals of both *J. bulbosa* and *J. plicifera* as circumscribed here. The specimen sequenced as *J.* (*J.*) *draytonii* by Campbell *et al.* (2016)

placed in the same clade with *J.* (*J.*) *plicifera plicifera*; however, the morphology of the type material of *draytonii* is consistent with the interpretation that it is a synonym of *J. bulbosa*. Even the comparatively smooth forms of *J. plicifera* in small Columbia River tributaries from Washington (e.g., Fig. 5H–J) can be readily distinguished from *J. bulbosa* by their larger size at adulthood, more cylindrical shape, higher spire, and more shouldered whorls. In Columbia River tributaries on the Oregon side, *plicifera* tends to be quite large and heavily sculptured (e.g., Fig. 5N–O, R–S) and that much more distinct from *bulbosa*. When preserved, the plications in *bulbosa* are less conspicuous and confined to the upper spire.

Juga bulbosa also includes what has been referred to as *J.* (*Juga*) *bairdiana* by Frest & Johannes (2010) and Campbell *et al.* (2016). With its plicate early whorls, *bairdiana* has been viewed as a synonym of *plicifera* (Pilsbry 1899; Walker 1918) or *silicula* (Goodrich 1942) or as a subspecies of *silicula* (Henderson 1935a, 1936b), but sequenced specimens morphologically identical to the type of *bairdiana* (e.g., Fig. 10H) (Strong & Whelan 2019) confirm it is conspecific with *bulbosa* as circumscribed here. Near topotypic specimens (Fig. 10I–J) from the Deschutes River of what has been referred to as *J.* (*J.*) *hemphilli maupinensis* (Burch & Tottenham 1980; Burch 1982, 1989; Frest & Johannes 2010; Campbell *et al.* 2016) are also conspecific with *bulbosa*.

Distribution

As mentioned, well localized, historical specimens of this species are uncommon in museum collections. In the USNM, apart from the material collected for this study, it is represented by four lots collected between 1971 and 1983. The remaining 13 lots, including the type material, were collected in the early 1900's or earlier and are all poorly or mislocalized: six lots are localized simply to "Oregon", and one lot said to be from the Willamette River (USNM 321825) is mislocalized. Another lot from Sullivan's Island in the Columbia River (USNM 468428) was catalogued in late 1936 with no collecting date and occurs slightly farther west than the species' known range, but is comprised of bleached and worn, dead-collected specimens that may have been transported. *Goniobasis bulbosa* was erroneously reported by Pilsbry (1899) to occur in the Owyhee River, a Snake River tributary, based on a mislocalized specimen record in the ANSP (ANSP 27561), an error perpetuated until recently (e.g., Burch & Tottenham 1980; Burch 1982, 1989; see Frest & Johannes 1995a). This lot was interpreted as *nigrina* sensu lato by Frest & Johannes (2010) but is a mixed lot of *bulbosa* and *newberryi*. Surveys in the Owyhee River drainage and from archeological sites in this drainage have not produced any *Juga* (Frest & Johannes 2010: 26). A lot cited by Henderson (1929, 1936b; UCM 15814) from Ahtanum Creek, Union Gap, in Yakima County, Washington, that he attributed to *Goniobasis draytonii* and *G. rubiginosa*, appears to be *J. bulbosa* as circumscribed herein, and which Frest & Johannes (2010: 35) stated to resemble specimens from the Klickitat Plateau, Washington. One lot of 50 specimens in the ANSP database, from Union Gap in the Yakima area, could not be found (P. Callomon, pers. com.). Attempts to recollect *Juga* in this area were unsuccessful (Frest & Johannes 1995a: 246). Campbell *et al.* (2016: fig. 1) show a specimen record from the Imnaha River, a Snake River tributary in the northeastern corner of Oregon, coded with the same pattern as the point from Ahtanum Creek. Frest and Johannes (2010: 41) have claimed there are no *Juga* present in any Snake River tributaries, and the map published in their 2010 work (Frest & Johannes 2010: fig. 1) does not include this point. Campbell *et al.* (2016) do not provide any information about the basis for this record, and we are unaware of any specimens in museum collections from this drainage.

Common name

The common name for this species is the Bulb Juga (Frest & Johannes 2010; Johnson *et al.* 2013; Johannes 2015). Synonyms have been referred to as the Three-Band Juga [= *Juga* (*Juga*) n. sp. 2], the One-Band Juga, Brown Juga (*J. draytonii*/*J.* (*J.*) n. sp. 1), and the Deschutes or Purple-Lipped Juga (= *J. hemphilli maupinensis*) (e.g., Frest & Johannes 1993, 1995a, 2001, 2010; Furnish 2005; Duncan 2008; Johannes 2015). *Juga bulbosa* also includes what has been referred to as the Basalt Juga [= *Juga* (*Oreobasis*) n. sp. 2] (Frest & Johannes 1999; Duncan 2008; Johannes 2015), which has been afforded federal protection under the "survey and manage" provisions of the Northwest Forest Plan (USDA and USDI 1994, 2000) and petitioned for federal listing under the U.S. Endangered Species Act (USFWS 2011). However, the 12-month finding on the petition concluded that the species could not be considered a listable entity pending the necessary genetic comparisons to establish its taxonomic validity (USFWS 2012). Given placement of the Basalt Juga as a synonym of this wider-ranging species, a listing decision can now be made but will require consideration of the full range of *J. bulbosa*.

Juga caerulea sp. nov.
urn:lsid:zoobank.org:act:B1DFDF9D-9B8B-471B-822A-80F281835610
Figs 12–13

Oxytrema bulbosa – Morrison 1954: 361, 384, pl. 11 fig. 5.
Juga (*Oreobasis*) n. sp. 5 – Frest & Johannes 1995a: 181. — Johannes 2015: 27.
Juga (*Oreobasis*) OTU 4 – Campbell *et al.* 2016: 160.
Blue Mountains Juga – Strong & Whelan 2019: 89.

Etymology

'*Caeruleus -a -um*', Latin for 'blue', in reference to the Blue Mountains where it is found, and to the bluish to purplish appearance of the aperture interior of fresh collected shells.

Type material

Holotype

USA • 1 spm (L = 15.02 mm); Oregon, Grant County, Phipps Meadow along U.S. Hwy 26; 44.5816, -118.4419; 10 Jul. 2014; J.T. Garner and N.V. Whelan leg.; GenBank: MK472115, MK464487, MK480730; USNM 1294988.

Other material examined

13 lots, 66 specimens, of which 11 were sequenced.

USA – **Oregon** • 37 spms; Grant Co., 10 mi E of Austin, Blue Mountains, stream, John Day River drainage; [44.5987, -118.3364]; alt. 4000 ft; 25 May 1939; V.B. Scheffer leg.; USNM 473801 • 18 spms; Grant Co., Phipps Meadow along U.S. Hwy 26; 44.5816, -118.4419; 10 Jul. 2014; J.T. Garner and

Fig. 12. Shell morphology of *Juga caerulea* sp. nov. **A**. Holotype (USNM 1294988). **B–E** Sequenced vouchers. **B**. USNM 1294991. **C**. USNM 1294994. **D**. USNM 1294996. **E**. USNM 1294999. **F–G**. USNM 473801. Scale bar = 1 cm.

N.V. Whelan leg.; USNM 1295000 • 1 spm; same collection data as for preceding; GenBank: MK472116, MK464488; USNM 1294989 • 1 spm; same collection data as for preceding; GenBank: MK472117, MK464489, MK480731; USNM 1294990 • 1 spm; same collection data as for preceding; GenBank: MK472118, MK464490, MK480732; USNM 1294991 • 1 spm; same collection data as for preceding; GenBank: MK472119, MK464491; USNM 1294992 • 1 spm; same collection data as for preceding; GenBank: MK472120, MK464492; USNM 1294993 • 1 spm; same collection data as for preceding; GenBank: MK472121, MK464493; USNM 1294994 • 1 spm; same collection data as for preceding; GenBank: MK472122, MK464494, MK480733; USNM 1294995 • 1 spm; same collection data as for

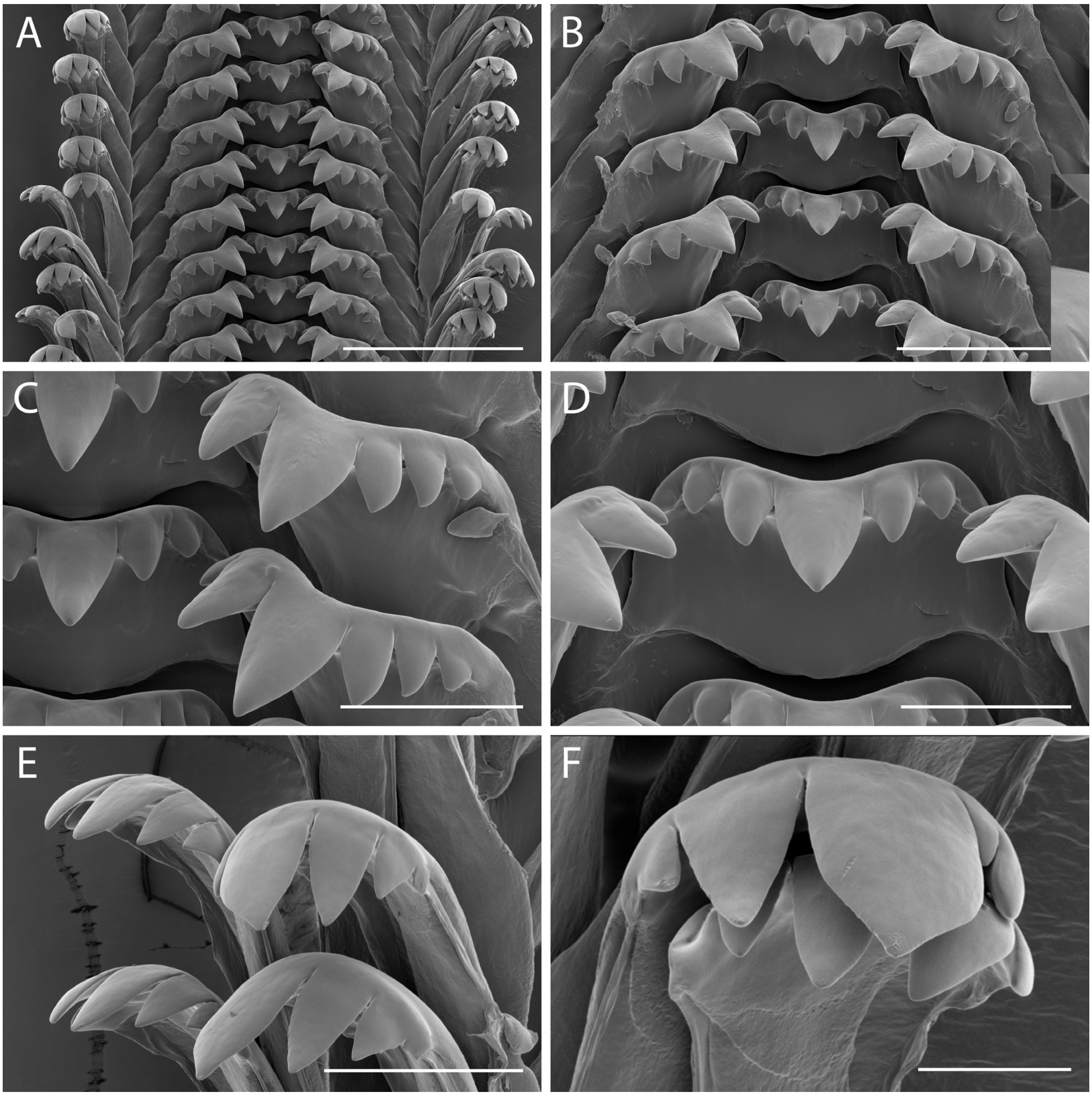


Fig. 13. Radular morphology of *Juga caerulea* sp. nov., holotype (USNM 1294988). **A**. View of the anterior radular ribbon. **B**. Detail of cutting edge of rachidian and lateral teeth. **C**. Detail of lateral teeth cusps. **D**. Detail of rachidian cusps. **E**. Cutting edges of inner and outer marginal teeth. **F**. Detail of inner and outer marginal teeth cusps. Scale bars: A = 200 µm; B = 100 µm; C, E = 50 µm; D = 40 µm; F = 20 µm.

preceding; GenBank: MK472123, MK464495, MK480734; USNM 1294996 • 1 spm; same collection data as for preceding; GenBank: MK472124, MK464496, MK480735; USNM 1294997 • 1 spm; same collection data as for preceding; GenBank: MK472125, MK464497, MK480736; USNM 1294998 • 1 spm; same collection data as for preceding; GenBank: MK472126, MK464498; USNM 1294999.

Description

Shell. Thin, moderate in size, reaching ~1.5 cm in length; turriform, conical in shape, spire height moderate (Fig. 12). Whorls convex, suture moderately impressed. Aperture oval in shape, lip smooth, simple to slightly sinuous. Spiral sculpture of indistinct, fine striae, variable in strength and number. Axial sculpture of fine, orthocline to weakly opisthocyrt or sinuous growth lines; plications lacking. Shell dark brown to black, occasionally with a lighter subsutural band. Interior of aperture bluish in color, occasionally tinged with purple.

Radula. Rachidian broadly rectangular, wider than tall, with convex lower margin and projecting outer corners; basal denticles lacking or vestigial (Fig. 13). Upper margin slightly concave with cutting edge bearing central, elongate conical cusp, and two to three stout, conical denticles on each side. Lateral teeth with prominent triangular cusp flanked by two inner and two to three outer, triangular denticles, and frequently a membranous outermost denticle. Marginal teeth with broadly rounded cutting edges and long, slender, flattened shafts with membranous flanges along inner and outer edges. Narrow inner flanges along distal half to two-thirds of shafts; broad outer flanges extending almost to tooth bases. Inner marginal teeth with ~four and outer marginal teeth with ~five flattened denticles.

Distribution and ecology

In springs and spring runs of the John Day River drainage, northeastern Oregon (Fig. 14A).

Remarks

This species is characterized by its simple, smooth, dark, lightly constructed shell, without distinguishing sculpture; the only known populations are rather uniform in shape and size.

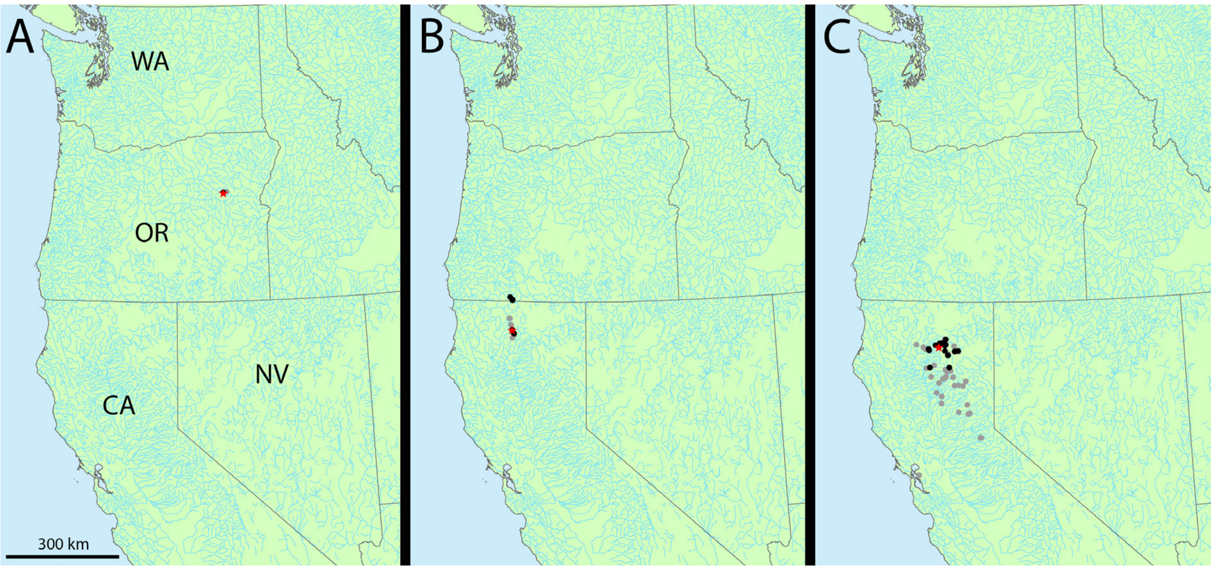


Fig. 14. Distribution maps. **A**. *Juga caerulea* sp. nov. **B**. *Juga canella* sp. nov. **C**. *Juga douglasi* sp. nov. Red stars, type localities; black dots, sequenced specimens; gray dots, unsequenced museum material. Abbreviations: CA = California; NV = Nevada; OR = Oregon; WA = Washington.

Distribution

Juga caerulea sp. nov. is a highly disjunct and restricted species, occurring in springs and spring runs from a few sites within a single spring complex in Phipps Meadow, the headwaters of the Middle Fork of the John Day River in the Malheur National Forest. One lot collected in 1939 (USNM 473801) indicates that historically it may have occurred in small streams in the area; Morrison (1954: 361, 384, pl. 11 fig. 5) identified these specimens as *Oxytrema bulbosa* and provided a sketch of the head-foot of a female to show the egg laying groove and ovipositor. However, recent efforts to locate the species elsewhere in the Blue Mountains have been unsuccessful (Frest & Johannes 1995a). Phipps Meadow, the source of the type material, has been heavily affected by grazing and Frest & Johannes (1995a) considered existing surveys were sufficient to merit a status of Endangered at the Federal or State level. The Blue Mountain Land Trust recently purchased Phipps Meadow with the goal of protecting and restoring the meadow's riparian habitat (https://bmlt.org/news/phipps-meadow).

Common name

The common name for this species is the Blue Mountain Juga (Johannes 2015). It has also been referred to as the Blue Mountains Juga (Frest & Johannes 1995a; Duncan 2008; Strong & Whelan 2019).

Juga canella sp. nov.

urn:lsid:zoobank.org:act:36573E63-B6D8-49D0-84D4-C1BE0FDD59D8

Figs 15–16

Juga (*Calibasis*) *acutifilosa* – Frest & Johannes 1993: 61 (in part); 1995b: 37 (in part); 2000a: 283 (in part); 2005: 160 (in part); 2010: 9, 22 (in part).
Juga (*Oreobasis*) n. sp. 3 – Frest & Johannes 1993: 65; 1996: 44, 132; 1999: 89, figs 35–36.
Juga (*Oreobasis*) "*nigrina*" – Frest & Johannes 1995b (in part): 39; 2005: 179.
Juga (*Oreobasis*) n. sp. 1 – Frest & Johannes 1995b: 39; 2005: 179. — Johannes 2013a: 24.
Juga (*Oreobasis*) n. sp. 2 – Frest & Johannes 2005: 179. — Johannes 2013a: 24.
Juga (*Calibasis*) n. sp. – Johannes 2013a: 24.
Juga (*Oreobasis*) n. sp. – Johannes 2013a: 24.
Juga (*Calibasis*) OTU 6 – Campbell *et al.* 2016: 160.
Juga (*Calibasis*) OTU 7 – Campbell *et al.* 2016: 160.
Juga species 3 – Strong & Whelan 2019: 89, fig. 4r–w.

non *Juga* (*Oreobasis*) n. sp. 3 – Frest & Johannes 1995a: 179. — Johannes 2015: 23. [= *Juga newberryi*]
non *Juga* (*Oreobasis*) n. sp. 1 – Frest & Johannes 1993: 64; 1995a: 178; 2001: 60. [= *Juga bulbosa*]
non *Juga* (*Oreobasis*) n. sp. 2 – Frest & Johannes 1993: 65; 1995a: 179; 1996: 43, 131; 1999: 85, figs 33–34. — Johannes 2015: 23. [= *Juga bulbosa*]

Etymology

'*Kanéla*' in Greek, and '*canella*' in Medieval Latin, for 'cinnamon', in reference to the reddish-brown color of many specimens, and to the common name 'Cinnamon Juga' that has been applied to members of the species in the southern part of its range. Used as a noun in apposition.

Type material

Holotype

USA • 1 spm (L = 16.87 mm); California, Siskiyou County, headwaters of Sacramento River at Mount Shasta City Park; 41.3287, -122.3271; 11 Sep. 2015; E.E. Strong and P. Bouchet leg.; GenBank: MK472233, MK464603, MK480770; USNM 1413106.

Other material examined

46 lots, 929 specimens, of which 30 were sequenced.

USA – **Oregon** • 23 spms; Jackson Co., Shoat Springs, Copco Rd; 42.046, -122.3362; 11 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295017 • 1 spm; same collection data as for preceding; GenBank: MK472220, MK464590; USNM 1295007 • 1 spm; same collection data as for preceding; GenBank: MK472221, MK464591, MK480759; USNM 1295008 • 1 spm; same collection data as for preceding; GenBank: MK472222, MK464592, MK480760; USNM 1295009 • 1 spm; same collection data as for preceding; GenBank: MK472223, MK464593; USNM 1295010 • 1 spm; same collection data as for preceding; GenBank: MK472224, MK464594, MK480761; USNM 1295011 • 1 spm; same collection data as for preceding; GenBank: MK472225, MK464595, MK480762; USNM 1295012 • 1 spm; same collection data as for preceding; GenBank: MK472226, MK464596, MK480763; USNM 1295013 • 1 spm; same collection data as for preceding; GenBank: MK472227, MK464597, MK480764; USNM 1295014 • 1 spm; same collection data as for preceding; GenBank: MK472228, MK464598, MK480765; USNM 1295015 • 1 spm; same collection data as for preceding; GenBank: MK472229, MK464599, MK480766; USNM 1295016 • 61 spms; Jackson Co., Keene Creek at Lincoln; 42.1047, -122.4129; 15 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413293 • 1 spm; same collection data as for preceding; GenBank: MK472243, MK464613, MK480780; USNM 1413285 • 1 spm; same collection data as for preceding; GenBank: MK472244, MK464614, MK480781; USNM 1413286 • 1 spm; same collection data as for preceding; GenBank: MK472245, MK464615, MK480782; USNM 1413287 • 1 spm; same collection data as for preceding; GenBank: MK472246, MK464616, MK480783; USNM 1413288 • 1 spm; same collection data as for preceding; GenBank: MK472247, MK464617, MK480784; USNM 1413289 • 1 spm; same collection data as for preceding; GenBank: MK472248, MK464618, MK480785; USNM 1413290 • 1 spm; same collection data as for preceding; GenBank: MK472249, MK464619, MK480786; USNM 1413291 • 1 spm; same collection data as for preceding; GenBank: MK472250, MK464620, MK480787; USNM 1413292 • 73 spms; Jackson Co., unnamed creek at Skookum Creek Rd; 42.029, -122.3383; 15 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413284 • 1 spm; same collection data as for preceding; GenBank: MK472235, MK464605, MK480772; USNM 1413276 • 1 spm; same collection data as for preceding; GenBank: MK472236, MK464606, MK480773; USNM 1413277 • 1 spm; same collection data as for preceding; GenBank: MK472237, MK464607, MK480774; USNM 1413278 • 1 spm; same collection data as for preceding; GenBank: MK472238, MK464608, MK480775; USNM 1413279 • 1 spm; same collection data as for preceding; GenBank: MK472239, MK464609, MK480776; USNM 1413280 • 1 spm; same collection data as for preceding; GenBank: MK472240, MK464610, MK480777; USNM 1413281 • 1 spm; same collection data as for preceding; GenBank: MK472241, MK464611, MK480778; USNM 1413282 • 1 spm; same collection data as for preceding; GenBank: MK472242, MK464612, MK480779; USNM 1413283. – **California** • 5 spms; Shasta Co., Conant [Castella], from Sacramento River; [41.1381, -122.3176]; Aug. 1937; T. Burch and J.Q. Burch leg.; UF 192876 • 150 spms; Siskiyou Co., 2 mi NE of Weed, near source (spring) of Carrick Creek; [41.4467, -122.3661]; 30 Jul. 1967; A.G. Smith leg.; CASIZ 30027 • 17 spms; Siskiyou Co., 2 mi N of Weed, Hwy 97; [41.4467, -122.3661]; 18 Jul. 1948; M.L. Walton leg.; ANSP 346015 • 8 spms; Siskiyou Co., Big Springs Creek; [41.6001, -122.428]; 18 Jun. 1958; Wales leg.; USNM 791508 • 288 spms; Siskiyou Co., Big Springs, Nature Conservancy property; 41.5981, -122.4069; 2 Sep. 2015; J.L. Furnish and R. Lis leg.; CASIZ 223498 • 24 spms; same collection data as for preceding; CASIZ 223572 • 1 spm; Siskiyou Co., Dunsmuir; [41.2027, -122.2751]; 1891; H.F. Wickham leg.; USNM 509469 • 28 spms; Siskiyou Co., headwaters of Sacramento River at Mount Shasta City Park; 41.3287, -122.3271; 11 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413108 • 1 spm; same collection data as for preceding; GenBank: MK472230, MK464600, MK480767; USNM 1413103 • 1 spm; same collection data as for preceding; GenBank: MK472231, MK464601, MK480768; USNM 1413104 • 1 spm; same collection data as for preceding; GenBank: MK472232, MK464602, MK480769; USNM 1413105 • 1 spm; same collection data as for preceding; GenBank: MK472234, MK464604, MK480771; USNM 1413107 • 74 spms; Siskiyou Co., Shasta River; 1884; R.E. Call leg.; USNM 63494 • 45 spms; Siskiyou Co., Shasta River, base of Mt Shasta; R.E. Call leg.; USNM 63495 • 3 spms; Siskiyou Co., Sisson [Mount Shasta City]; [41.3108, -122.331]; ANSP 185617 • 18 spms; same collection data as for preceding; UF 80824 • 81 spms; Siskiyou Co.; H.F. Wickham leg.; USNM 509452.

Description

Shell. Thin, small to moderate in size, usually not exceeding ~1.5 cm in length, rarely up to ~2.4 cm; turriform, broadly to elongately conical in shape, spire height low to moderate (Fig. 15). Whorls convex to

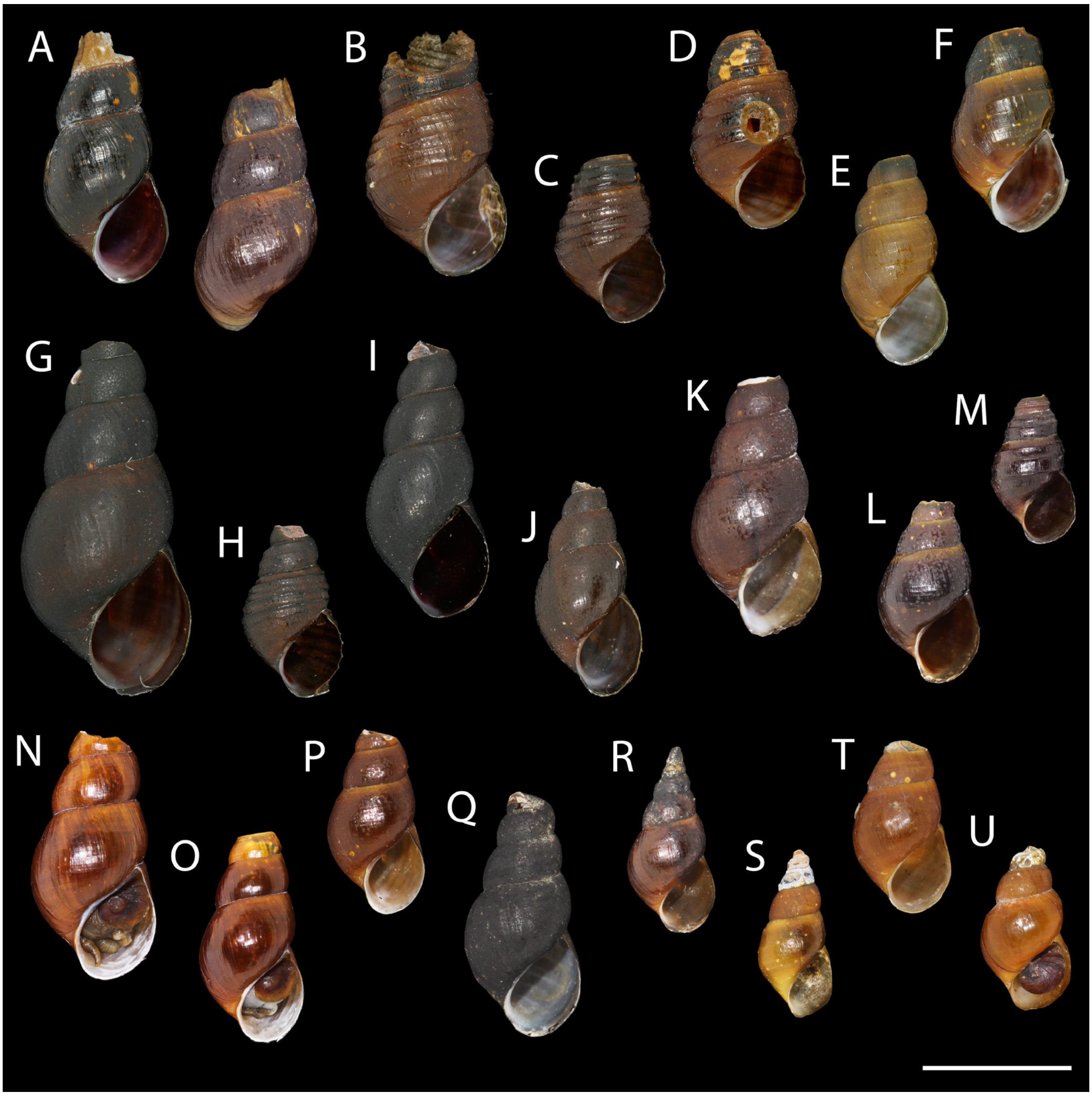


Fig. 15. Shell morphology of *Juga canella* sp. nov. **A**. Holotype, USNM 1413106. **B–J**. Sequenced vouchers. **B**. USNM 1295010. **C**. USNM 1295012. **D**. USNM 1295016. **E**. USNM 1413103. **F**. USNM 1413107. **G**. USNM 1413276. **H**. USNM 1413280. **I**. USNM 1413281. **J**. USNM 1413288. **K**. USNM 791508. **L**. CASIZ 223498. **M**. CASIZ 223572. **N–O**. CASIZ 30027. **P**. ANSP 346015. **Q–R**. UF 80824. **S**. USNM 63495. **T**. USNM 509469. **U**. UF 192876. Scale bar = 1 cm.

angulate with a subsutural ramp, occasionally shouldered, suture moderately to deeply impressed. Body whorl usually inflated. Aperture oval in shape, lip smooth to crenate, simple to weakly sinuous. Spiral sculpture absent or present, of thickened lirae, smooth to slightly sinuous, barely elevated to prominent, variable in number, dividing whorl into intervening flattened areas or grooves. Axial sculpture of fine, weakly prosocline to opisthocyrt or sinuous growth lines; plications lacking. Shell black, dark purplish to reddish cinnamon brown or tan in color, infrequently with irregular streaks of reddish purple or a lighter subsutural band. Interior of aperture cream to dark purple in color.

Radula. Rachidian squarish, slightly wider than tall, with weakly v-shaped lower margin and projecting outer corners; basal denticles lacking (Fig. 16). Upper margin slightly concave with cutting edge bearing central, elongate conical cusp, and two to four stout, conical denticles on each side. Lateral teeth with prominent triangular cusp flanked by two to three inner and three to four outer, triangular denticles, and frequently a membranous outermost denticle. Marginal teeth with broadly rounded cutting edges and long, slender, flattened shafts with membranous flanges along inner and outer edges. Narrow inner flanges along distal half to two-thirds of shafts; broad outer flanges extending almost to tooth bases. Inner marginal teeth with ~three and outer marginal teeth with three to five flattened denticles.

Distribution and ecology

Primarily in springs, spring runs, and spring-fed creeks of northern California in Shasta River drainages and adjacent parts of the upper Sacramento River drainage in Siskiyou and Shasta Counties, and of south-central Oregon in upper Klamath River drainages in Jackson County, including sites in the Cascade-Siskiyou National Monument (Fig. 14B).

Remarks

Juga canella sp. nov. is comprised of smooth and lirate forms that can co-occur at the same site and possess the same COI haplotype (Strong & Whelan 2019: fig. 4). In the northern part of its range, *J. canella* can be distinguished from *J. nigrina*, which is typically banded and sculptured with spiral striae and plications on the upper whorls, more cylindrical with a narrower spire angle, and larger in size at adulthood (see *J. nigrina* below).

Distribution

Based on sequenced specimens, the confirmed southern extent of the range is from springs north of Mossbrae Falls in the vicinity of Dunsmuir in southern Siskiyou County, California (Campbell *et al.* 2016). At least historically, the species extended slightly further south as represented by one lot of five specimens collected in 1937 at Conant [= Castella] in northern Shasta County (UF 192876). In the southern part of the range, the species occurs in the part of the Sacramento River drainage affected by the Cantara Loop chemical spill in 1991 (Frest & Johannes 1993, 2005). The species is associated primarily with springs and spring runs where it survived the disaster, but Frest & Johannes (1999) noted rare populations associated with subaqueous springs in the main stem of the Sacramento River which would have been extirpated by the spill.

Common name

The common name for this species is the Cinnamon Juga (Frest & Johannes 1995b, 1999; Duncan 2008; Johannes 2015) (= *Juga* (*Oreobasis*) n. sp. 3: Frest & Johannes 1993; = *Juga* (*Oreobasis*) n. sp. 1: Frest & Johannes 1995b), which previously was considered restricted to the upper Sacramento River drainage in Siskiyou County, California, and had been afforded federal protection under the "survey and manage" provisions of the Northwest Forest Plan (USDA and USDI 1994, 2000) and petitioned for federal listing (USFWS 2011). However, the 12-month finding on the petition concluded that the species could not be considered a listable entity pending the necessary genetic comparisons to establish its taxonomic validity (USFWS 2012).

This species also includes putatively new taxa in the Cascade-Siskiyou National Monument, although these were never figured or diagnosed, including *Juga* (*Oreobasis*) n. sp. 1 (Close Butte Juga) and *J.* (*O.*) n. sp. 2 (Rattlesnake Spring Juga) (Frest & Johannes 2005; Johannes 2013a). The OTU referred to as *J.* (*O.*) "*nigrina*" (Frest & Johannes 2005 = Schoolhouse Meadow Juga) and later as *J.* (*O.*) n. sp. (Johannes 2013a = Spring Creek Juga) from the Cascade-Siskiyou National Monument comprises smooth forms of *J. canella* sp. nov. The OTU referred to as *J.* (*O.*) "*nigrina*" (Frest & Johannes 1995b = Smooth River Juga) from the Upper Sacramento System is a mixture of *J. canella* and *J. douglasi* sp. nov. as circumscribed here. The lirate forms of *J. canella* were referred to *J.* (*Calibasis*) *acutifilosa*,

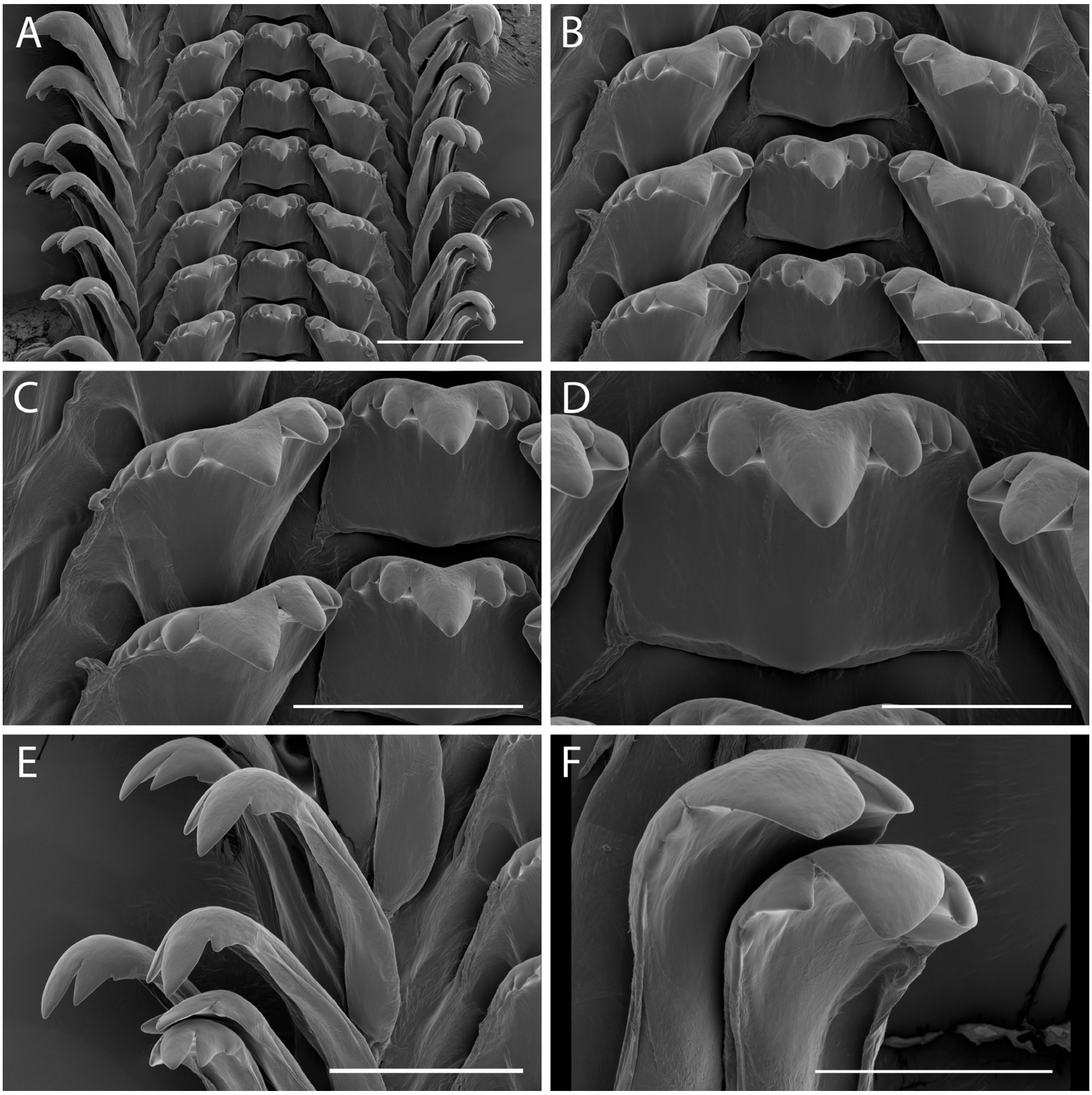


Fig. 16. Radular morphology of *Juga canella* sp. nov., holotype (USNM 1413106). **A**. View of the anterior radular ribbon. **B**. Detail of cutting edge of rachidian and lateral teeth. **C**. Detail of lateral teeth cusps. **D**. Detail of rachidian cusps. **E**. Inner and outer marginal teeth. **F**. Detail of inner and outer marginal teeth cusps. Scale bars: A = 200 µm; B–C, E = 100 µm; D, F = 50 µm.

or Scalloped Juga (Frest & Johannes 2005), and later to *J.* (*C.*) n. sp., or Fall Creek Juga (Johannes 2013a).

Juga douglasi sp. nov.
urn:lsid:zoobank.org:act:8EA208D9-9CE9-4521-8381-7411439C8E1F
Figs 17–18

Juga (*Oreobasis*) *nigrina* – Frest & Johannes 1995b*:* 38 (in part).
Juga (*Oreobasis*) "*nigrina*" – Frest & Johannes 1995b*:* 39 (in part).
Juga interioris – Lee *et al.* 2006: 316. — Ó Foighil *et al.* 2009: 305.
Juga n. spp. – Frest & Johannes 2007: table 4.
Juga (*Oreobasis*) OTU 2 – Campbell *et al.* 2016: 160.
Juga (*Oreobasis*) OTU 3 – Campbell *et al.* 2016: 160.
Juga species 1 – Strong & Whelan 2019: 89, fig. 4g–l.

Etymology

Named in honor of the father of the first author, Douglas Wayne Strong. A native Californian, Doug shared with his family his deep appreciation for the natural beauty of northern California, and always enjoyed hearing about the snails that also make their home amongst the majestic redwoods.

Type material

Holotype

USA • 1 spm (L = 15.74 mm); California, Shasta County, Goose Valley Spring; 40.9295, -121.726; 11 Sep. 2015; E.E. Strong and P. Bouchet leg.; GenBank: MK472138, MK464510, MK480745; USNM 1413130.

Other material examined

64 lots, 818 specimens, of which 19 were sequenced.

USA – **California** • 13 spms; Alameda Co., Strawberry Creek, Berkeley; [37.871, -122.2635]; 18 Aug. 1926; E. Caruthers leg.; ANSP 145847 • 1 spm; Butte Co., Paradise; [39.7522, -121.6143]; J. Rowell leg.; ANSP 105056 • 51 spms; Butte Co., spring on Chico Creek [possibly Richardson Springs] tributary of Sacramento River; [39.8395, -121.7798]; Henshaw leg.; USNM 128206 • 5 spms; Butte Co., Table Mountain; [39.5831, -121.6192]; W.M. Gabb leg.; ANSP 27568 • 6 spms; same collection data as for preceding; USNM 119284 • 9 spms; El Dorado Co., small stream 24.5 mi E of Placerville; [38.7737, -120.3949]; 10 May 1946; M.L. Walton leg.; ANSP 346017 • 9 spms; Lassen Co., Bob Creek, at crossing of Little Valley Rd (CR 404), Beaver Creek Ranch, 5.5 mi NW of Little Valley; 40.9467, -121.2534; 1 Sep. 2007; T. Grace leg.; USNM 1111865 • 20 spms; Lassen Co., Lassen Natl Forest, Davis Spring, upstream ca 1.5 mi from FS 22 crossing, ca 19 air mi WNW of Spalding; [40.8233, -121.1026]; 15 Jun. 2001; USFS Lassen Natl Forest Mollusk Survey 2001; CASIZ 165974 • 27 spms; Nevada Co., 1 mi NW of North San Juan, small stream between South and North Forks of the Yuba River on Hwy 49 [= Clear Creek]; [39.3792, -121.091]; Jun. 1971; D.D. Chivers leg.; CASIZ 30310 • 8 spms; Nevada Co., Tahoe National Forest, East Fork Creek, 1 mi S of Washington [sic, possibly East Fork Washington Creek]; 22 Aug. 1997; J. Vindum and C. Spencer leg.; CASIZ 113099 • 2 spms; Nevada Co., Tahoe Natl Forest, S fork of Yuba River, E of Washington along Maybert Rd, Golden Quartz picnic area; [39.356, -120.7466]; 28 Aug. 1997; E.J. Kools leg.; on rocks; CASIZ 113100 • 30 spms; Nevada Co., Tahoe Natl Forest, Washington Creek, 1 mi S of Washington; 39.3446, -120.7948; 28 Aug. 1997; E.J. Kools leg.; CASIZ 112152 • 3 spms; Placer/El Dorado Counties, Middle Fork American River; H. Moores leg.; USNM 118854 • 20 spms; Plumas Co., Butterfly Creek, near Keddie; [40.0071, -120.9624]; Chace and H.N. Lowe leg.; ANSP 212242 • 24 spms; Plumas Co., Domingo Springs, off CR Route 311 (approx.

7 air mi NW of Chester); [40.3609, -121.3473]; 19 Jun. 2001; USFS Lassen Natl Forest Mollusk Survey 2001; J. Brim Box leg.; CASIZ 165953 • 10 spms; Plumas Co., East Fork of Feather River [East Branch North Fork]; [40.0193, -121.1048]; 1898; R.C. McGregor leg.; ANSP 73510 • 5 spms; Plumas Co., Howells [possibly Howells Bridge, along East Branch North Fork Feather River, Belden]; [40.0142, -121.2258]; 29 Aug. 1946; H.P. Chandler leg.; CASIZ 170000 • 8 spms; Plumas Co., Indian Valley; [40.1186, -120.8791]; USNM 58981 • 68 spms; Plumas Co., Lassen Natl Forest, Soldier Creek, off FS Rd 28N36, ca 7 air mi SSW of Chester; [40.2123, -121.2717]; 25 Jun. 2001; USFS Lassen Natl Forest Mollusk Survey 2001; J. Brim Box leg.; CASIZ 165371 • 3 spms; Sacramento Co., spring on Placerville Rd, ca 23 mi E of Placerville; [38.774, -120.4271]; 1916; H.N. Lowe leg.; ANSP 114784 • 14 spms; Shasta Co., Battle Creek 10 mi above mouth, tributary to Sacramento River; [40.4147, -122.0988]; 1898; R.C. McGregor leg.; ANSP 73522 • 30 spms; Shasta Co., Blackberry Creek, Shasta NF, N side of FS50, 5.87 km E of Pit 5 Dam; 40.9669, -121.8284; 16 Sep. 2007; T. Grace leg.; UF 520318 • 23 spms; Shasta Co., Goose Valley Spring; 40.9295, -121.726; 11 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413139 • 1 spm; same collection data as for preceding; GenBank: MK472137, MK464509; USNM 1413129 • 1 spm; same collection data as for preceding; GenBank: MK472139, MK464511; USNM 1413131 • 1 spm; same collection data as for preceding; GenBank: MK472140, MK464512, MK480746; USNM 1413132 • 1 spm; same collection data as for preceding; GenBank: MK472141, MK464513, MK480747; USNM 1413133 • 1 spm; same collection data as for preceding; GenBank: MK472142, MK464514, MK480748; USNM 1413134 • 1 spm; same collection data as for preceding; GenBank: MK472143, MK464515; USNM 1413135 • 1 spm; same collection data as for preceding; GenBank: MK472144, MK464516; USNM 1413136 • 1 spm; same collection data as for preceding; GenBank: MK472145, MK464517; USNM 1413137 • 1 spm; same collection data as for preceding; GenBank: MK472146, MK464518; USNM 1413138 • 12 spms; Shasta Co., Goose Valley, unnamed spring run on W side of Goose Valley Rd and Goose Valley, ca 0.8 km N of Goose Creek, approx. 4.5 mi N of Route 299; 40.9329, -121.7264; 16 Sep. 2007; T. Grace leg.; USNM 1111796 • 15 spms; Shasta Co., Grace Lake [near Shingletown]; [40.4833, -121.8636]; 9 Nov. 1963; CASIZ 57480 • 30 spms; Shasta Co., Hat Creek at Bridge Campground; 40.73, -121.4371; 10 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413102 • 1 spm; same collection data as for preceding; GenBank: MK472127, MK464499; USNM 1413092 • 1 spm; same collection data as for preceding; GenBank: MK472128, MK464500, MK480737; USNM 1413093 • 1 spm; same collection data as for preceding; GenBank: MK472129, MK464501; USNM 1413094 • 1 spm; same collection data as for preceding; GenBank: MK472130, MK464502, MK480738; USNM 1413095 • 1 spm; same collection data as for preceding; GenBank: MK472131, MK464503, MK480739; USNM 1413096 • 1 spm; same collection data as for preceding; GenBank: MK472132, MK464504, MK480740; USNM 1413097 • 1 spm; same collection data as for preceding; GenBank: MK472133, MK464505, MK480741; USNM 1413098 • 1 spm; same collection data as for preceding; GenBank: MK472134, MK464506, MK480742; USNM 1413099 • 1 spm; same collection data as for preceding; GenBank: MK472135, MK464507, MK480743; USNM 1413100 • 1 spm; same collection data as for preceding; GenBank: MK472136, MK464508, MK480744; USNM 1413101 • 6 spms; Shasta Co., Lamoine, side creek going into Sacramento River; [40.9753, -122.4311]; Aug. 1937; T. Burch and J.Q. Burch leg.; UF 192866 • 5 spms; Shasta Co., Lost Creek, in lava field on N of Wilcox Ranch Rd, W of Hat Creek rim, E of Hat Creek and Hwy 44/89, lower fishing access.; 40.7628, -121.4347; 12 Aug. 2007; T. Grace leg.; USNM 1111863 • 23 spms; Shasta Co., Pit River Canyon (small spring), W side of river 4 mi below Fall River Mills; [40.9851, -121.5126]; C.H. Merriam leg.; USNM 361546 • 108 spms; Shasta Co., Potem Creek, in tributary to Pit River after falls by road; [40.8368, -122.0222]; 17 May 1978; J. Landye leg.; USNM 892366 • 3 spms; Shasta Co., Rainbow Springs, at headwaters of Fall Mill Creek on Lazy S Ranch adjacent to Thousand Springs Ranch; [41.1111, -121.5511]; 16 May 1978; J. Landye leg.; USNM 1665622 (ex USNM 892373) • 1 spm; Shasta Co., S side of Hwy 299, Pit River, Lion's Club picnic area, W of Pit River camping grounds; 40.9866, -121.513; 1 Sep. 2007; T. Grace leg.; USNM 1665623 (ex USNM 1111864) • 14 spms; Shasta Co., S side of Pit River, water source spring at Pacific Gas and Electric plant; [40.9896, -121.5021];

16 May 1978; J. Landye leg.; USNM 1665624 (ex USNM 892372) • 18 spms; Shasta Co., Salt Creek Rd, 1 km S of Fenders Ferry Rd [Salt Ck]; 40.8646, -122.1395; 360 m a.s.l.; 18 Oct. 2011; J. Slapcinsky leg.; UF 448882 • 35 spms; Shasta Co., tributary to Shasta Reservoir, 4.7 road mi from McCloud Bridge, E of McCloud arm [= Nosoni Creek]; [40.9113, -122.2078]; 1 Jul. 1997; J.L. Furnish leg.; CASIZ 223387 • 1 spm; Sierra Co., Downieville, Fiddle Creek [sic]; 20 Sep. 1946; H.P. Chandler leg.; CASIZ 170002 • 26 spms; Sierra Co., North Fork, Yuba River, Downieville; [39.5583, -120.8275]; ANSP 125085 • 1 spm; Siskiyou Co., headwaters of Fall River; 1896; R.C. McGregor leg.; ANSP 332330 • 17 spms; Tehama Co., Deer Creek, off FS Rd 28N29, ca 10 air mi NNW of Forest Ranch; [40.0702, -121.7048]; 25 Jul. 2001; USFS Lassen Natl Forest Mollusk Survey 2001; J. Brim Box leg.; CASIZ 165961 • 24 spms; Tehama Co., Deer Creek, off Potato Patch Campground, off SR 32, ca 12 air mi SSE of Mineral; [40.1873, -121.5323]; 23 Jul. 2001; USFS Lassen Natl Forest Mollusk Survey 2001; CASIZ 166030 • 7 spms; Tehama Co., Deer Creek, off SR 32, 0.5 mi N of Alder Creek Campground, ca 11 air mi SE of Mineral; [40.2163, -121.4917]; 23 Jul. 2001; USFS Lassen Natl Forest Mollusk Survey 2001; CASIZ 166361 • 21 spms; Tehama Co., Lassen Natl Forest, Deer Creek, at lower falls, off FS Rd 27N08, approx. 13 air mi S of Mineral; [40.168, -121.5814]; 24 Jul. 2001; USFS Lassen Natl Forest Mollusk Survey 2001; J. Brim Box leg.; CASIZ 165372 • 15 spms; Tehama Co., unnamed spring off [Tehama] County Rd 769, ca 0.4 mi E of SR 36/89, ca 13 air mi WNW of Chester; [40.3406, -121.4605]; 21 Jun. 2001; USFS Lassen Natl Forest Mollusk Survey 2001; CASIZ 166013 • 26 spms; Tehama Co., W Branch of Feather River, Morgan Springs; [40.3846, -121.5137]; 1898; R.C. McGregor leg.; ANSP 73512 • 2 spms; Shaw Creek, at Fire Creek Fire Control Station, Shasta Co. [sic, possibly Shaw Creek, Tehama Co.]; [40.2096, -121.9511]; 17 May 1978; J. Landye leg.; USNM 892381.

Description

Shell. Thin, moderate in size, reaching ~2 cm in length; turriform, conical in shape, spire height moderate (Fig. 17). Whorls convex, suture moderately impressed. Aperture oval in shape, lip smooth, simple to weakly sinuous. Spiral sculpture of numerous, indistinct, fine striae. Axial sculpture of fine, weakly prosocline to opisthocyrt or sinuous growth lines; irregular varices occasionally present confined to upper spire. Shell light brown to dark purplish- or reddish-brown, occasionally with a lighter subsutural band. Interior of aperture light, yellowish brown to dark purple.

Radula. Rachidian narrowly rectangular, wider than tall, basal margin flattened, with slight, bluntly rounded median and lateral projections; basal denticles lacking or vestigial (Fig. 18). Upper margin slightly concave with cutting edge bearing central, elongate conical cusp, and two to three stout, conical denticles on each side. Lateral teeth with prominent triangular cusp flanked by ~three inner and three to five outer, triangular denticles, and frequently a membranous outermost denticle. Marginal teeth with broadly rounded cutting edges and long, slender, flattened shafts with membranous flanges along inner and outer edges. Narrow inner flanges along distal half to third of inner marginal teeth and extending almost to tooth bases of outer marginal teeth; broad outer flanges extending almost to tooth bases. Inner marginal teeth with ~four and outer marginal teeth with ~five flattened denticles.

Distribution and ecology

Primarily in springs, spring runs, and small creeks in the southern Pit River system; possibly extending into larger creeks and rivers in eastern Sacramento River tributaries and the northern Mokelumne River watershed of the Sierra Nevada (Fig. 14C).

Remarks

Given the uncertainty of the circumscription of this species in the southern part of its range (see below), the preceding description is based on sequenced and topotypic specimens. Although not present in all specimens, the species may be distinguished by the presence of irregular varices on the upper whorls

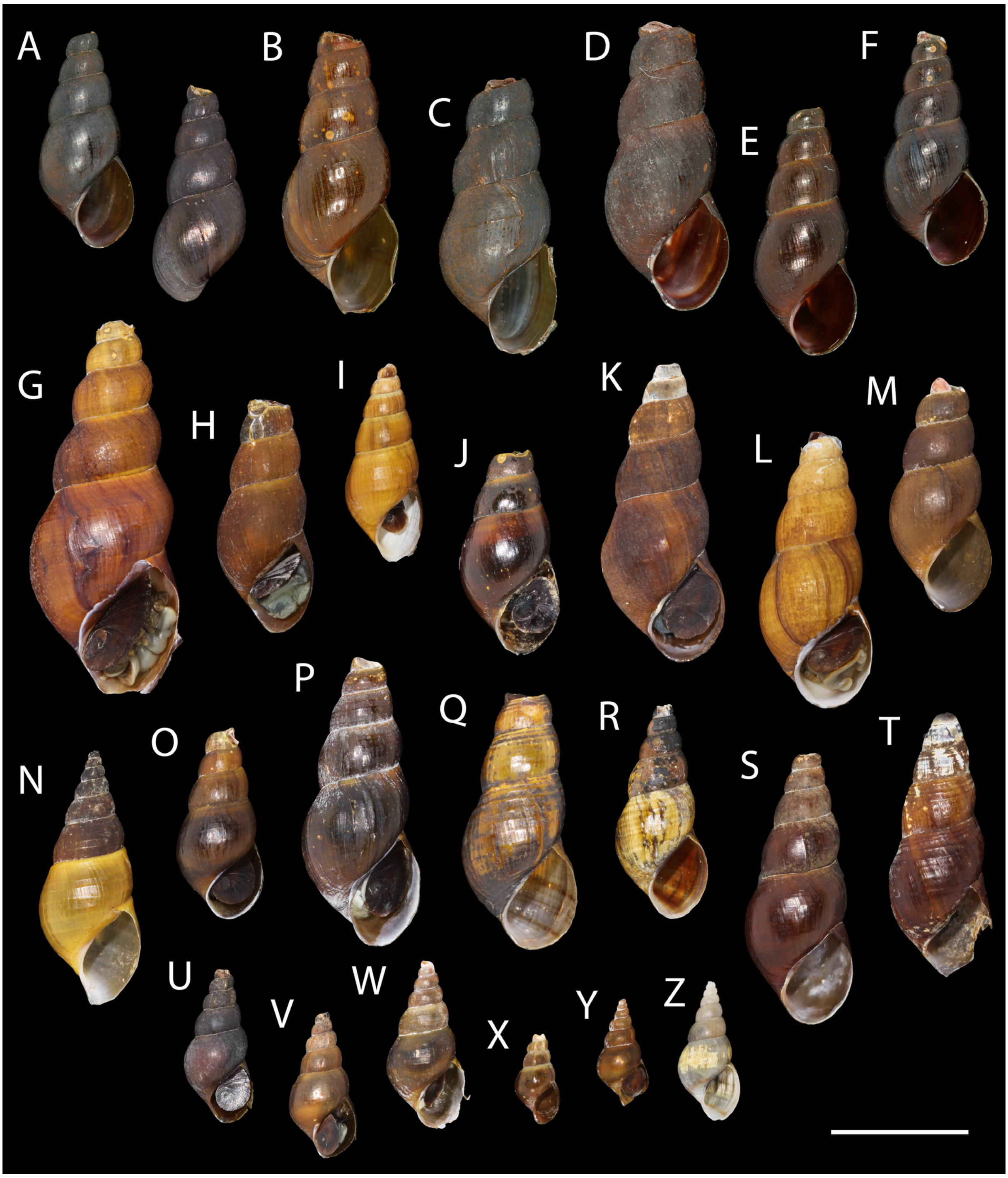


Fig. 17. Shell morphology of *Juga douglasi* sp. nov. **A**. Holotype, USNM 1413130. **B–F**. Sequenced vouchers. **B**. USNM 1413138. **C**. USNM 1413133. **D**. USNM 1413095. **E**. USNM 1413096. **F**. USNM 1413093. **G**. USNM 1665624 (ex USNM 892372). **H**. UF 448882. **I**. CASIZ 223387. **J**. UF 520318. **K**. USNM 892366. **L**. CASIZ 57480. **M**. ANSP 73522. **N**. ANSP 73510. **O**. CASIZ 166013. **P**. CASIZ 165372. **Q**. USNM 119284. **R**. CASIZ 30310. **S–T**. ANSP 145847. **U**. USNM 1413139. **V**. CASIZ 166013. **W**. CASIZ 165372. **X**. UF 520318. **Y**. UF 448882. **Z**. CASIZ 30310. Scale bar = 1 cm.

of some specimens (e.g., Fig. 17V, X–Y). These can be seen in the sequenced holotype and topotypic specimens (Fig. 17A, U) and are more irregular and widely spaced than the plications seen in *J. nigrina* with which it overlaps in distribution in the western part of its range (see *J. nigrina* below).

Distribution

The main part of the distribution of *J. douglasi* sp. nov. lies in the southern Pit River drainages in Shasta and Lassen Counties where it overlaps with *J. occata*, although individuals of the two species are rarely found in syntopy; only three lots with mixtures of the two were found in the USNM collections [USNM 1111864, USNM 1665623 (ex USNM 1111864); USNM 892372, USNM 1665624 (ex USNM

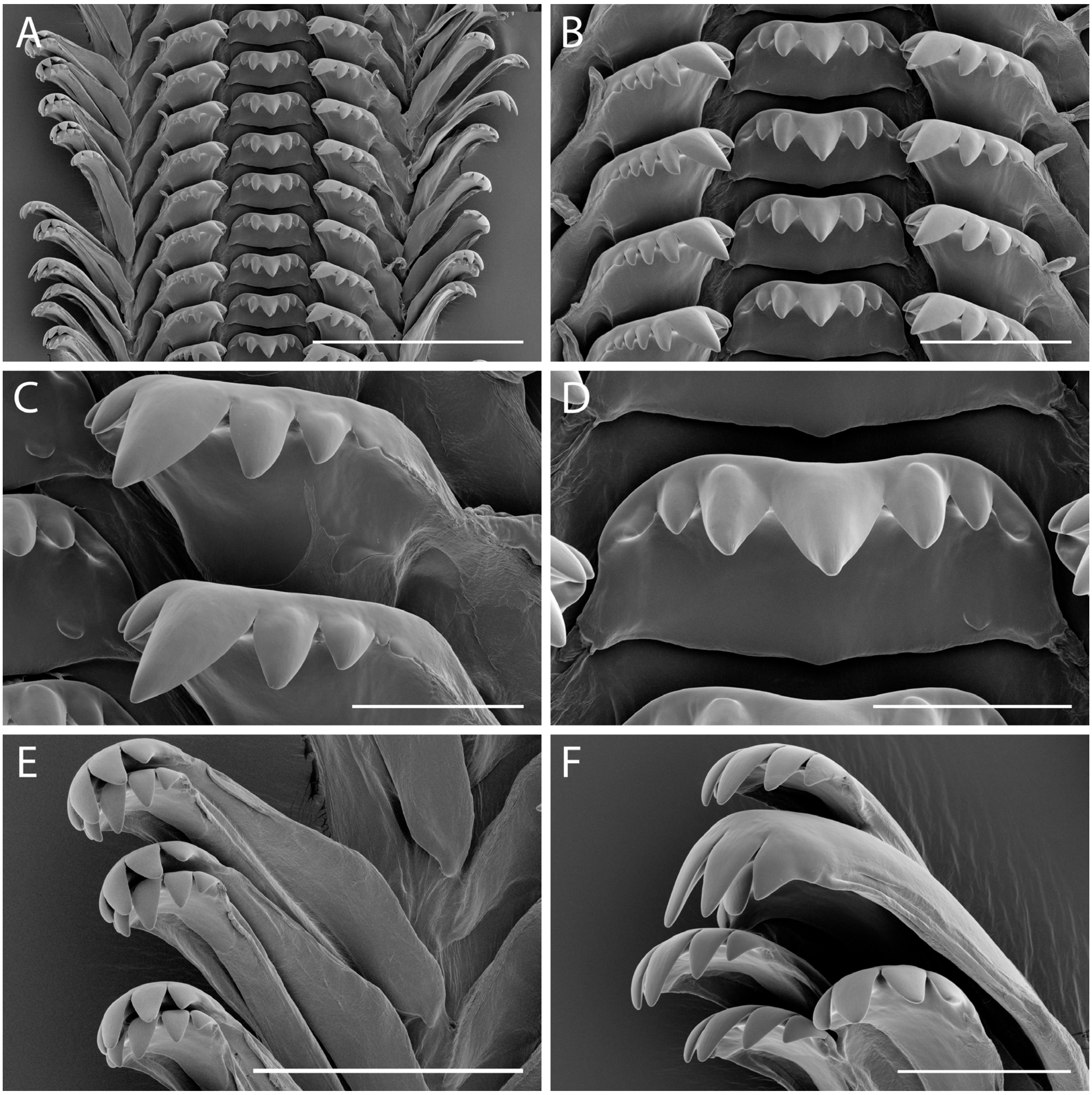


Fig. 18. Radular morphology of *Juga douglasi* sp. nov., holotype (USNM 1413130). **A**. View of the anterior radular ribbon. **B**. Detail of cutting edge of rachidian and lateral teeth. **C**. Detail of lateral teeth cusps. **D**. Detail of rachidian cusps. **E**. Inner and outer marginal teeth. **F**. Detail of inner and outer marginal teeth cusps. Scale bars: A = 300 µm; B, E = 100 µm; C–D, F = 50 µm.

892372); USNM 892373, USNM 1665622 (ex USNM 892373)], and one species is always numerically dominant. Sequenced specimens reported in Campbell *et al.* (2016) expand the distribution into the eastern Sacramento River tributaries of southern Lassen County and northern Plumas County. Specimens consistent with the *J. douglasi* sp. nov. morphotype from McCloud River (Nosoni Creek; CASIZ 223387) and upper Sacramento River drainages (Lamoine; UF 192866) extend the distribution slightly to the west where it overlaps with *J. nigrina*, but this should be confirmed with sequenced specimens.

Populations from Sacramento River drainages of the western foothills of the Sierra Nevada have been attributed primarily to *J. nigrina* (e.g., Lowe 1916; Taylor 1981; Frest & Johannes 1995b; Brim Box 2002; Brim Box *et al.* 2005), rarely to *J. interioris* (e.g., Lee *et al.* 2006; Ó Foighil *et al.* 2009), and more recently were noted to comprise at least one new species (Frest & Johannes 2007). These are difficult to identify with certainty in the absence of molecular data but are here cautiously interpreted as representing *J. douglasi* sp. nov. When preserved, the early teleoconch is typically smooth, narrow, with convex whorls and a deeply impressed suture, and sometimes (CASIZ 165961, CASIZ 166013) shows the varices seen more frequently in the northwest part of the range. The teleoconchs are usually smooth, but occasionally spirally grooved or with indistinct spiral striae and are rarely banded. If these records can be verified as conspecific with *J. douglasi*, scattered museum records place the species, at least historically, in eastern Sacramento River drainages in Butte, Sierra, Nevada, El Dorado, and Sacramento Counties in the Feather River, Yuba River, and American River Basins. These areas coincide with the Sierra Nevada goldfields and were heavily affected by placer mining activities including hydraulic mining and dredging. However, modern museum records from the mid 1990's and surveys by Frest & Johannes (2007; as *Juga* n. spp.) confirm that *Juga* is surviving in highly fragmented populations in the southern Lassen National Forest, the Plumas National Forest, and the Tahoe National Forest in Nevada County (CASIZ 112152, 113099, 113100). A 2018 iNaturalist record (https://www.inaturalist.org/observations/15172449) from the Cosumnes River, El Dorado County, indicates that *Juga* populations are persisting in the Mokelumne River watershed, which borders the Sacramento River watershed to the south. One historical lot (ANSP 145847) from Strawberry Creek on the UC Berkeley campus in the East San Francisco Bay Area contains spirally grooved specimens (Fig. 17T) similar to some from Table Mountain in Butte County [USNM 119284 (Fig. 17Q), ANSP 27568] and North San Juan in Nevada County [CASIZ 30310 (Fig. 17R, Z)] and is hypothesized also to be conspecific with *J. douglasi*. However, given the range of morphological variation seen in species of *Juga*, it is possible that populations from the Sierra Nevada represent mixtures of *J. occata* and *J. douglasi*, or an as yet undescribed form.

Common name

The common name for this species is the Douglas Juga. The OTU referred to as *J.* (*O.*) *nigrina* (Frest & Johannes 1995b = Black Juga) from the Upper Sacramento System is a mixture of true *J. nigrina* and *J. douglasi* sp. nov. as circumscribed here. The OTU referred to as *J.* (*O.*) "*nigrina*" (Frest & Johannes 1995b = Smooth River Juga) from the Upper Sacramento System is a mixture of *J. canella* sp. nov. and *J. douglasi* as circumscribed here.

Juga newberryi (I. Lea, 1860)
Figs 19–20

Melania newberryi I. Lea, 1860: 93.

Goniobasis newberryi – Lea 1863a: 300–301, pl. 37 fig. 135; 1863b: 122–123, pl. 37 fig. 135.
Juga (*Oreobasis*) *bulbosa* – Burch & Tottenham 1980: 152, fig. 452 (in part). — Burch 1982: 41, fig. 452 (in part); 1989: 152, fig. 452 (in part). — Neitzel & Frest 1992: B.25. — Frest & Johannes 1995a: 177.
Juga bulbosa – Turgeon *et al.* 1988: 65; 1998: 67.

Juga (*Oreobasis*) n. sp. 3 – Frest & Johannes 1995a: 179. — Johannes 2015: 23.
Juga (*Oreobasis*) n. sp. 4 – Frest & Johannes 1995a: 180. — Johannes 2015: 23.
Juga (*Oreobasis*) *newberryi* – Strong & Frest 2007: 54. — Frest & Johannes 2010: 10, 39. — Johannes 2015: 23. — Campbell *et al.* 2016: 160.
Juga newberryi – Johnson *et al.* 2013: 282. — Strong & Whelan 2019: 89.
Juga (*Oreobasis*) OTU 1 – Campbell *et al.* 2016: 160.

non *Juga* (*Oreobasis*) n. sp. 3 – Frest & Johannes 1993: 65; 1996: 44, 132; 1999: 89, figs 35–36. [= *Juga canella* sp. nov.]
non *Juga newberryi* – Strong & Köhler 2009: 486. [= *Juga nigrina*]

Material examined

Lectotype of *Melania newberryi* I. Lea, 1860 (designated by Graf 2001: 70) (Fig. 19A)
USA • "Upper des Chutes [sic, Deschutes] River, Oregon Territory"; J.S. Newberry, M.D. leg.; USNM 118961.

Paralectotypes of *Melania newberryi* I. Lea, 1860
USA • 12 spms; same collection data as for lectotype; USNM 1665630 (formerly USNM 118961X).

Other material examined
42 lots, 380 specimens, of which 27 were sequenced.

USA – **"Oregon" [Territory]** • 2 spms; U.S. Exploring Expedition; USNM 12174. – **Oregon** • 24 spms; Jefferson Co., Deschutes River at junction with Dry Creek; 44.7844, -121.1959; 8 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413421 • 1 spm; same collection data as for preceding; USNM 1413414 • 1 spm; same collection data as for preceding; USNM 1413415 • 1 spm; same collection data as for preceding; USNM 1413416 • 1 spm; same collection data as for preceding; USNM 1413417 • 1 spm; same collection data as for preceding; USNM 1413418 • 1 spm; same collection data as for preceding; USNM 1413419 • 1 spm; same collection data as for preceding; USNM 1413420 • 56 spms; Jefferson Co., Deschutes River at Rainbow Landing; 44.7578, -121.2272; 6 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413434 • 1 spm; same collection data as for preceding; GenBank: MK472315, MK464682, MK480826; USNM 1413428 • 1 spm; same collection data as for preceding; GenBank: MK472316, MK464683, MK480827; USNM 1413429 • 1 spm; same collection data as for preceding; GenBank: MK472317, MK464684, MK480828; USNM 1413430 • 1 spm; same collection data as for preceding; GenBank: MK472318, MK464685, MK480829; USNM 1413431 • 1 spm; same collection data as for preceding; GenBank: MK472319, MK464686, MK480830; USNM 1413432 • 1 spm; same collection data as for preceding; GenBank: MK472320, MK464687, MK480831; USNM 1413433 • 30 spms; Jefferson Co., Deschutes River at RM 97.2 to 97.4 on east side channel, ca 0.3–0.6 km S of U.S. 526 bridge and mouth of Shitike Creek at Rainbow Landing; 44.7575, -121.2267; 13 Aug. 2000; T. Frest leg.; USNM 1100660 • 67 spms; Jefferson Co., Opal Springs; 44.4905, -121.2981; 7 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413335 • 1 spm; same collection data as for preceding; GenBank: MK472312, MK464679, MK480823; USNM 1413332 • 1 spm; same collection data as for preceding; GenBank: MK472313, MK464680, MK480824; USNM 1413333 • 1 spm; same collection data as for preceding; GenBank: MK472314, MK464681, MK480825; USNM 1413334 • 1 spm; same collection data as for preceding; GenBank: MK472311, MK464678; USNM 1413331 • 1 spm; same collection data as for preceding; GenBank: MK472310, MK464677, MK480822; USNM 1413330 • 33 spms; Jefferson Co., U.S. Hwy 26; 44.7584, -121.2272; 9 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295086 • 1 spm; same collection data as for preceding; GenBank: MK472303, MK464670, MK480820; USNM 1295085 • 1 spm; same collection data as for preceding; GenBank: MK472301, MK464668, MK480818; USNM 1295083 • 1 spm; same collection data as for preceding; GenBank: MK472302, MK464669, MK480819; USNM 1295084 • 1 spm; same collection data as for preceding; GenBank: MK472299, MK464666, MK480816; USNM 1295081 • 1 spm; same collection data as for preceding; GenBank: MK472300, MK464667, MK480817; USNM 1295082 • 1 spm; same collection data as for preceding; GenBank: MK472296, MK464663, MK480813; USNM 1295078 • 1 spm; same collection data as for preceding; GenBank: MK472298, MK464665, MK480815; USNM 1295080 • 1 spm; same collection data as for preceding; GenBank: MK472297, MK464664, MK480814; USNM 1295079 • 1 spm; same collection data as for preceding; GenBank: MK472294, MK464661, MK480811; USNM 1295076 • 1 spm; same collection data as for preceding; GenBank: MK472295, MK464662, MK480812; USNM 1295077 • 25 spms; Jefferson Co., Willow Creek, at inflow to Lake Simtustus, Madras West, 2400 ft S, 1800 ft E of NW corner; [44.6718, -121.2278]; 2 Aug. 1971; J. Landye leg.; in substrate; USNM 905120 • 109 spms; Wasco Co., Oak Springs; 45.2216, -121.0827; 8 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413323 • 1 spm; same collection data as for preceding; GenBank: MK472305, MK464672; USNM 1413318 • 1 spm; same collection data as for preceding; GenBank: MK472306, MK464673; USNM 1413319 • 1 spm; same collection data as for preceding; GenBank: MK472307, MK464674; USNM 1413320 • 1 spm; same collection data as for preceding; GenBank: MK472308, MK464675; USNM 1413321 • 1 spm; same collection data as for preceding; GenBank: MK472309, MK464676; USNM 1413322 • 1 spm; same collection data as for preceding; GenBank: MK472304, MK464671, MK480821; USNM 1413317.

Description

Shell. Moderately thick, small for the genus, reaching ~1.5 cm in length; broadly to elongately conical in shape, spire height low to moderate (Fig. 19). Whorls convex to somewhat flattened, shouldered, suture deeply impressed, body whorl usually inflated. Aperture broadly oval in shape, lip smooth, simple. Spiral sculpture lacking. Axial sculpture of fine, weakly prosocline to opisthocyrt growth lines; plications lacking. Shell dark purple to tan in color, usually with three reddish brown bands, variable in width. Interior of aperture white to dark purple in color; bands when present visible inside aperture. Columella occasionally tinged reddish-purple.

Radula. Rachidian narrowly rectangular, wider than tall, with angular to convex lower margin and projecting outer corners; basal denticles lacking or vestigial (Fig. 20). Upper margin slightly concave with cutting edge bearing central, elongate conical cusp, and two to three stout, conical denticles on each side. Lateral teeth with prominent triangular cusp flanked by two to three inner and two to three outer, triangular denticles, and frequently a membranous outermost denticle. Marginal teeth with broadly rounded cutting edges and long, slender, flattened shafts with membranous flanges along inner and outer edges. Narrow inner flanges along distal half to two-thirds of shafts; broad outer flanges extending almost to tooth bases. Inner marginal teeth with four to five and outer marginal teeth with six to seven flattened denticles. See also Strong & Frest (2007).

Distribution and ecology

In the lower Middle and Lower Deschutes River in central Oregon, and associated springs, spring runs and spring-fed creeks in the Deschutes River drainage (Fig. 21A).

Remarks

Tryon (1864, 1865, 1866, 1873) viewed *Goniobasis newberryi* as valid and distinct but remarked that this species and *G. bulbosa* were "exactly similar in outline" (Tryon 1864: 53; 1865: 246; 1873: 255) and "certainly extremely closely allied" (Tryon 1865: 245), differing only in the presence or absence of bands (Tryon 1866: 34). Pilsbry (1899) subsequently synonymized the two, which was followed by most authors and resulted in confusion about the identity and distribution of *Juga newberryi* for over 100 years (see Strong & Frest 2007). Most usages of the name *bulbosa* in the literature in fact refer to *J. newberryi* (e.g., Tryon 1865: fig. 17; 1866: fig. 217; 1873: fig. 496; Roscoe 1963: pl. 4 figs 5–6; Burch & Tottenham 1980: fig. 452; Burch 1982, 1989: fig. 452; Turgeon *et al.* 1988, 1998). This confusion was compounded by the fact that the species is inexplicably rare in museum collections (see e.g., Henderson 1936b) despite occurring in abundance at some sites. Apart from the types and material collected for the present research, holdings of *newberryi* in the USNM collections include only three lots, one from the U.S. Exploring Expedition, one collected in 1971 and one in 2000. What little museum material there is in some cases contains mixtures of the two species (see account for *J. bulbosa*, above).

Although Frest & Johannes (2010: 26) could not determine its identity, the specimen figured by Tryon as *Goniobasis bulbosa* (1865: fig. 17; 1866: fig. 217; 1873: fig. 496) is the larger of the two specimens in USNM 12174 (Fig. 19N), entered in the handwritten ledger catalogue on May 10, 1876, identified as "*Strepoma bulbosa* Gould" with no other information than being from "Oregon" [Territory]. Tryon (1865: 246) claimed the specimen to be, "the largest I have seen, and considerably exceeds the dimensions of Dr. Gould's type specimen". There can be no doubt that it represents a specimen of *J. newberryi* given the low spire and inflated body whorl. Paralectotype lot MCZ 169068 comprises a mixture of *bulbosa* and *newberryi*, as does USNM 5563 which contains Gould's (1860: fig. 163–163a) figured specimen of *bulbosa* (Fig. 10E–F).

The erroneous synonymy of *newberryi* with *bulbosa* notwithstanding, this is a distinctive Deschutes River endemic, particularly the low spired, inflated morph. However, banded subadults of *J. bulbosa* (e.g., Fig. 10S) may be confused for *J. newberryi* without careful scrutiny when they co-occur (e.g.,

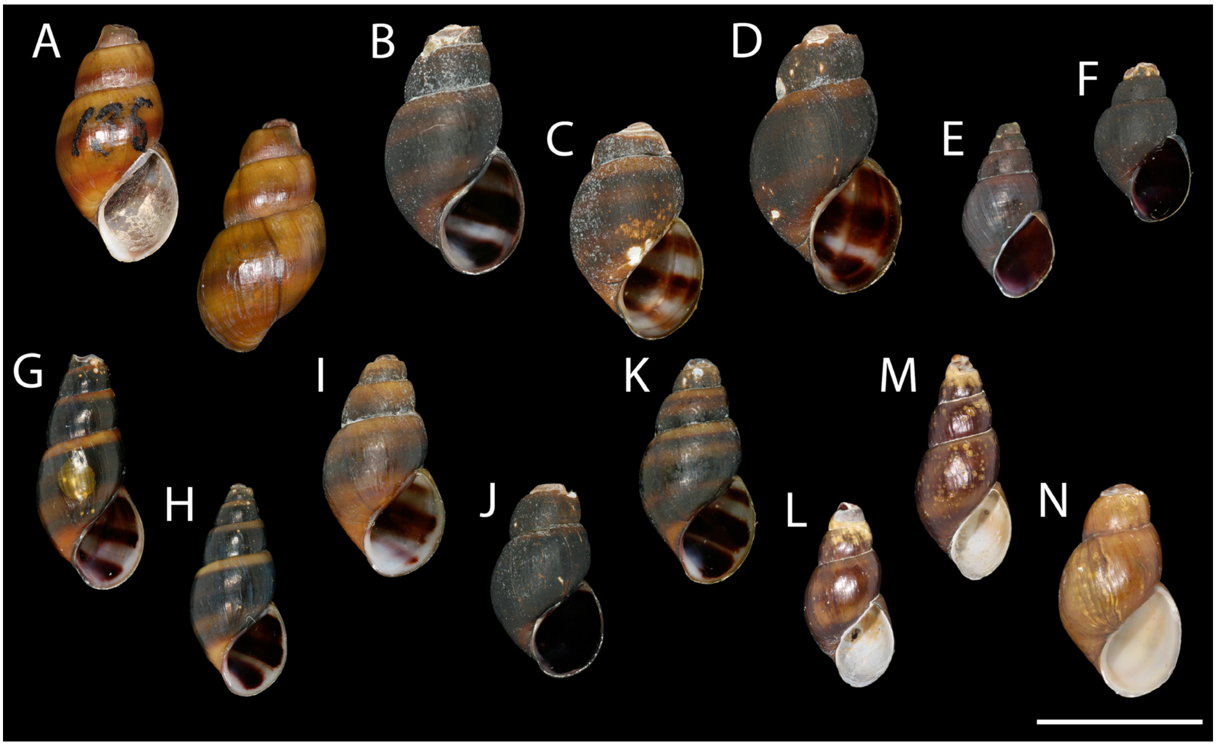


Fig. 19. Shell morphology of *Juga newberryi* (I. Lea, 1860). **A**. *Melania newberryi* I. Lea, 1860. Lectotype, USNM 118961. **B–K**. Sequenced vouchers. **B**. USNM 1295080. **C**. USNM 1295084. **D**. USNM 1295085. **E**. USNM 1413317. **F**. USNM 1413321. **G**. USNM 1413332. **H**. USNM 1413334. **I**. USNM 1413428. **J**. USNM 1413429. **K**. USNM 1413430. **L–M**. USNM 905120. **N**. USNM 12174. Scale bar = 1 cm.

Fig. 19C–D) but can be distinguished by the degree of banding, spire height, and inflation of the body whorl. The early teleoconchs of *bulbosa* are frequently eroded but when preserved may be plicate, whereas they are invariably smooth in *newberryi*. The tall slender morph of *newberryi* (Fig. 19G–H, L–M) also may be difficult to differentiate from *bulbosa* as the banding patterns can be quite similar. One lot containing dead-collected specimens from the confluence of Willow Creek and the Deschutes River (USNM 905120; Fig. 19L–M) compares favorably in size and proportion with specimens sequenced from Opal Springs (Fig. 19G–H) and are considered to represent *newberryi*. Specimens of *bulbosa* sequenced nearby generally have a less deeply impressed suture and are larger in size at adulthood (e.g., Fig. 10P). There are banded and unbanded morphs of both species, even at a single site, but unbanded

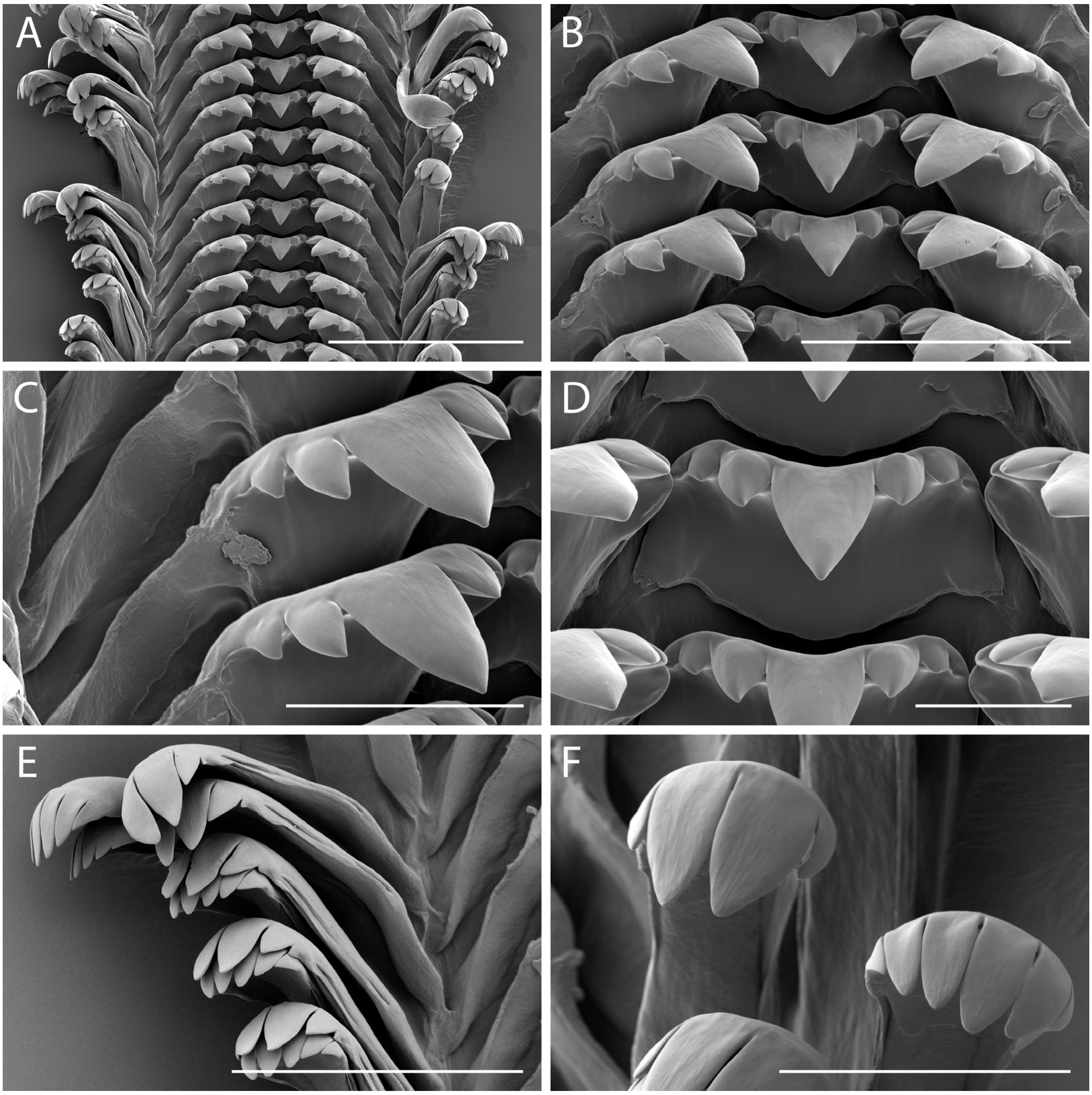


Fig. 20. Radular morphology of *Juga newberryi* (I. Lea, 1860) (USNM 1413317). **A**. View of the anterior radular ribbon. **B**. Detail of cutting edge of rachidian and lateral teeth. **C**. Detail of lateral teeth cusps. **D**. Detail of rachidian cusps. **E**. Inner and outer marginal teeth. **F**. Detail of inner and outer marginal teeth cusps. Scale bars: A = 200 µm; B, E = 100 µm; C, F = 50 µm; D = 30 µm.

morphs of *newberryi* are rare and are usually quite dark, not the tan to golden base color as seen in most historical lots. It is uncertain whether these golden, unbanded forms are merely faded or represent a local variant that has not been recollected.

Distribution

The type locality of *newberryi* is the Upper Deschutes River, which is considered the region upstream of Bend, Oregon, but there is no evidence it ever extended this far upriver. Frest & Johannes (1995a, 2010) and Strong & Frest (2007) considered the types to have originated from near Bend without justification and indicated the species occurs sporadically below Pelton Dam to roughly 6 miles above the mouth where it is replaced by "*J.* (*J.*) *plicifera*" (= *J. bulbosa* as circumscribed herein). However, some spring dwelling forms (e.g., Opal Springs, Oak Springs) previously considered an undescribed species (see below) are conspecific with *J. newberryi* (Strong & Whelan 2019) and place the species above Pelton Dam.

Common name

The common name for this species is the Banded Juga (Johnson *et al.* 2013). It has been referred to as the Newberry Juga (Johannes 2015) and the Bulb Juga (Frest & Johannes 1995a; Turgeon *et al.* 1988, 1998), the latter reflecting the erroneous synonymy with *J. bulbosa*. Putatively new species that are conspecific with *J. newberryi* have been referred to as the Crooked River or Opal Springs Juga [= *J.* (*Oreobasis*) n. sp. 4] (Fig. 19G–H) and the Oak Springs or Purple Juga (e.g., Frest & Johannes 1995a; Duncan 2008; Johannes 2015; Fallon *et al.* 2020). The latter is a dark, unbanded form (Fig. 19E–F).

Juga nigrina (I. Lea, 1856)
Figs 22–24

Melania nigrina I. Lea, 1856: 80.
Melania shastaensis I. Lea, 1856: 80. **Syn. nov.**
Goniobasis circumlineata Tryon, 1865: 244–245, pl. 24 figs 14–15.
Melania californica Clessin, 1882: 189–190, pl. 4 fig. 8 [sic, fig. 9]. No type material located. "California".
Goniobasis chacei Henderson, 1935a: 132–134, pl. 4 fig. 8. **Syn. nov.**

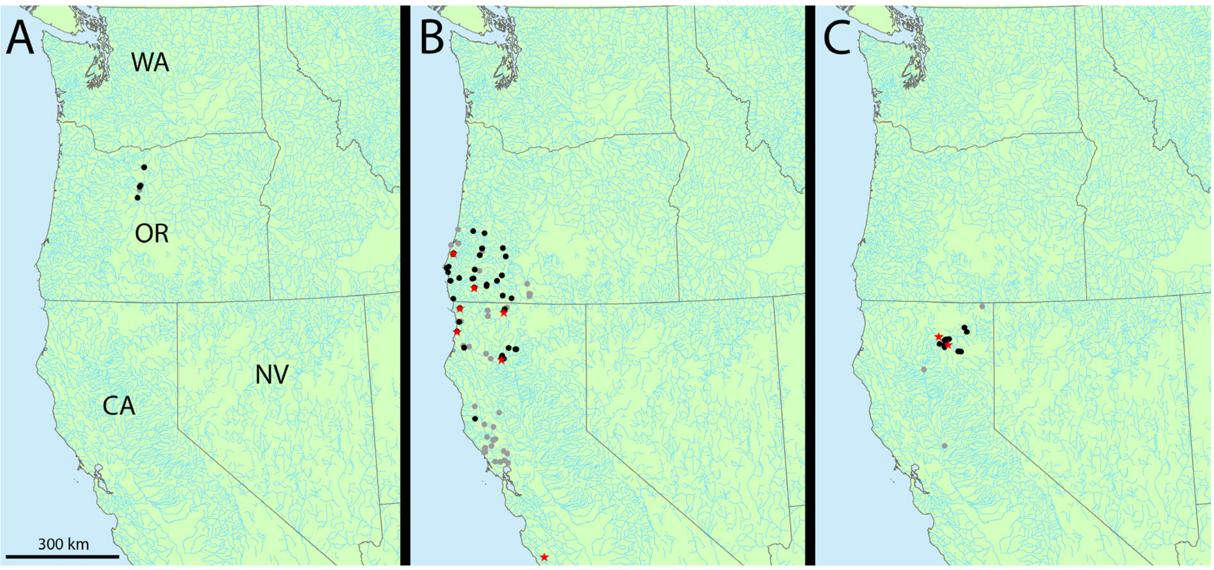


Fig. 21. Distribution maps. **A**. *Juga newberryi* (I. Lea, 1860). **B**. *Juga nigrina* (I. Lea, 1856). **C**. *Juga occata* (Hinds, 1844). Red stars, type localities; black dots, sequenced specimens; gray dots, unsequenced museum material. Abbreviations: CA = California; NV = Nevada; OR = Oregon; WA = Washington.

Goniobasis coquillensis Henderson, 1935a: 131–132, pl. 4 fig. 6. **Syn. nov.**
Goniobasis orickensis Henderson, 1935a: 130–131, pl. 4 fig. 10. **Syn. nov.**
Goniobasis yrekaensis Henderson, 1935a: 97–98, pl. 4 figs 3–4. **Syn. nov.**
Goniobasis yrekaensis obscura Henderson, 1935a: 98–99. **Syn. nov.**

Goniobasis nigrina – Lea 1863a: 302, pl. 37 fig. 137; 1863b: 124, pl. 37 fig. 137.
Goniobasis shastaensis – Lea 1863a: 337, pl. 38 fig. 199; 1863b: 159, pl. 38 fig. 199.
Goniobasis circumlineata – Tryon 1866: 36, figs 237–238.
Goniobasis chacei – Henderson 1936b: pl. 2 fig. 8.
Goniobasis coquillensis – Henderson 1936b: pl. 2, fig. 6.
Goniobasis orickensis – Henderson 1936b: pl. 2 fig. 10.
Goniobasis yrekaensis – Henderson 1936b: pl. 2 figs 3–4.
Juga (*Oreobasis*) *nigrina* – Burch & Tottenham 1980: 154, fig. 453. — Burch 1982: 42, fig. 453; 1989: 154, fig. 453. — Frest & Johannes 1995b*:* 38 (in part); 2010: 10, 42, fig. 2d. — Holznagel & Lydeard 2000: 237 [identification later corrected in GenBank to *Juga bulbosa*]. — Campbell *et al.* 2016: fig. 2b.
Juga (*Juga*) *silicula* – Burch & Tottenham 1980: 152 (in part). — Burch 1982: 41 (in part); 1989: 152 (in part).
Juga nigrina – Turgeon *et al.* 1988: 65; 1998: 67. — Johnson *et al.* 2013: 282. — Köhler 2016: 270; 2017: 252.
Juga (*Oreobasis*) *chacei* – Frest & Johannes 1993: 64; 2000a: 305; 2010: 9, 29. — Campbell *et al.* 2016: 160.
Juga (*Oreobasis*) *orickensis* – Frest & Johannes 1993: 65; 2000a: 306; 2010: 11, 45. — Campbell *et al.* 2016: 160.
Juga (*Oreobasis*) "*nigrina*" – Frest & Johannes 1998: 28. — Johannes 2015: 30.
Juga (*Juga*) *silicula shastaensis* – Frest & Johannes 2005: 179; 2010: 48 [as possibly valid]. — Johannes 2013a: 24. — Campbell *et al.* 2016: 160.
Juga newberryi – Strong & Köhler 2009: 486.
Juga (*Oreobasis*) *coquillensis* – Frest & Johannes 2010*:* 31 [as possibly valid].
Juga (*Juga*) *yrekaensis yrekaensis* – Frest & Johannes 2010: 51 [as likely valid]. — Campbell *et al.* 2016: 160.
Juga (*Juga*) *yrekaensis obscura* – Frest & Johannes 2010: 43 [as dubiously valid].
Juga chacei – Johnson *et al.* 2013*:* 282.
Juga (*Juga*) *coquillensis* – Campbell *et al.* 2016: 160.
Juga shastaensis – Johannes & Clark 2016: 23–24.
Juga nigrina group – Strong & Whelan 2019: 89.

non *Melania shastaensis* – Reeve 1860: unpaginated, species 318, pl. 44 fig. 318. [= *Juga occata*]
non *Juga* (*Oreobasis*) "*nigrina*" – Frest & Johannes 1995b: 39. [= *Juga canella* sp. nov. and *J. douglasi* sp. nov.]; 2005: 179. [= *Juga canella* sp. nov.]
non *Juga nigrina* – Lydeard *et al.* 2002: 401. — Strong & Köhler 2009: 486. — Strong *et al.* 2011: 53. [= *Juga plicifera*]

Material examined

Lectotype of *Melania nigrina* I. Lea, 1856 (designated by Graf 2001: 71) (Fig. 22A)
USA • "Clear Creek, Shasta County, California"; Dr Trask leg.; USNM 118992.

Paralectotypes of *Melania nigrina* I. Lea, 1856
USA • 23 spms; same collection data as for lectotype; USNM 1665631 (formerly USNM 118992X).

Lectotype of *Melania shastaensis* I. Lea, 1856 (designated by Graf 2001: 94) (Fig. 22B)
USA • "Shasta and Scott Rivers, California" [type locality possibly erroneous; Henderson 1935a, 1936b]; Dr Trask leg.; USNM 119283.

Paralectotypes of *Melania shastaensis* I. Lea, 1856
USA • 26 spms; same collection data as for lectotype; USNM 1665632 (formerly USNM 119283X).

Lectotype of *Goniobasis circumlineata* Tryon, 1865 (designated by Baker 1964: 181) (Fig. 22C)
USA • "Mission San Antonio, California"; W. Newcomb leg.; ANSP 27573.

Paralectotypes of *Goniobasis circumlineata* Tryon, 1865
USA • 1 spm; "Shasta Co., California"; W. Newcomb leg.; ANSP 27574 • 2 spms; "California"; W. Newcomb leg.; USNM 12185.

Holotype of *Goniobasis chacei* Henderson, 1935 (Fig. 22D)
USA • "Small tributary of Smith River, Adams Station, Del Norte Co., Calif" [possibly Mary's Creek; Frest & Johannes 2010]; Oct. 1931; E.P. Chace leg.; UCM 18058a.

Paratype of *Goniobasis chacei* Henderson, 1935
USA • 1 spm (Henderson 1935a: pl. 2 fig. 8, at right); same collection data as for holotype; UCM 18058b.

Holotype of *Goniobasis coquillensis* Henderson, 1935 (Fig. 22E)
USA • "A creek at Riverton, on Coquille River, Oregon" [possibly Alder Creek fide Frest & Johannes 2010]; Hannibal collection; UCM 21168a (incorrectly cited as 21167a in the original description).

Paratype of *Goniobasis coquillensis* Henderson, 1935
USA • 1 spm (Henderson 1935a: pl. 4 fig. 6, at right); same collection data as for holotype; UCM 21168b.

Holotype of *Goniobasis orickensis* Henderson, 1935 (Fig. 22F)
USA • "Redwood Creek, Orick, California"; J. and B.R. Henderson leg.; UCM 17710a.

Paratypes of *Goniobasis orickensis* Henderson, 1935
USA • 2 spms (Henderson 1935a: pl. 4 fig. 10, at left and right); "A creek 26 miles east of Arcata, California, by winding mountain road, almost certainly Redwood Creek"; J. and B.R. Henderson leg.; UCM 17703a.

Holotype of *Goniobasis yrekaensis* Henderson, 1935 (Fig. 22G)
USA • "Shasta River, Calif., about 4 miles above the mouth, below Yreka"; 6 Aug. 1931; J. and B.R. Henderson leg.; UCM 17735a.

Paratypes of *Goniobasis yrekaensis* Henderson, 1935
USA • 3 spms (Henderson 1935a: pl. 4 fig. 4); same collection data as for holotype; UCM 17735b.

Holotype of *Goniobasis yrekaensis obscura* Henderson, 1935 (Fig. 22H)
USA • "A creek two miles southwest of Wonder, Oregon" [possibly Slate Creek or Butcherknife Creek; Frest & Johannes 2010]; 4 Aug. 1931; J. and B.R. Henderson leg.; UCM 17724a.

Other material examined
244 lots, 2062 specimens, of which 150 were sequenced.

USA – **Oregon** • 4 spms; Coos Co., Charleston, Sunset Bay State Park, Sunset Creek [sic, likely Big Creek]; [43.331, -124.3717]; 1951; I. Pratt leg.; USNM 598151 • 19 spms; Coos Co., Coos River;

[43.3768, -124.1325]; USNM 56462 • 2 spms; same collection data as for preceding; USNM 56462a • 32 spms; Coos Co., SH 425, just south of Riverton; 43.1162, -124.2901; 14 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295188 • 1 spm; same collection data as for preceding; GenBank: MK472387, MK464754, MK480861; USNM 1295185 • 1 spm; same collection data as for preceding; GenBank: MK472388, MK464755; USNM 1295186 • 1 spm; same collection data as for preceding; GenBank: MK472389, MK464756, MK480862; USNM 1295187 • 1 spm; same collection data as for preceding;

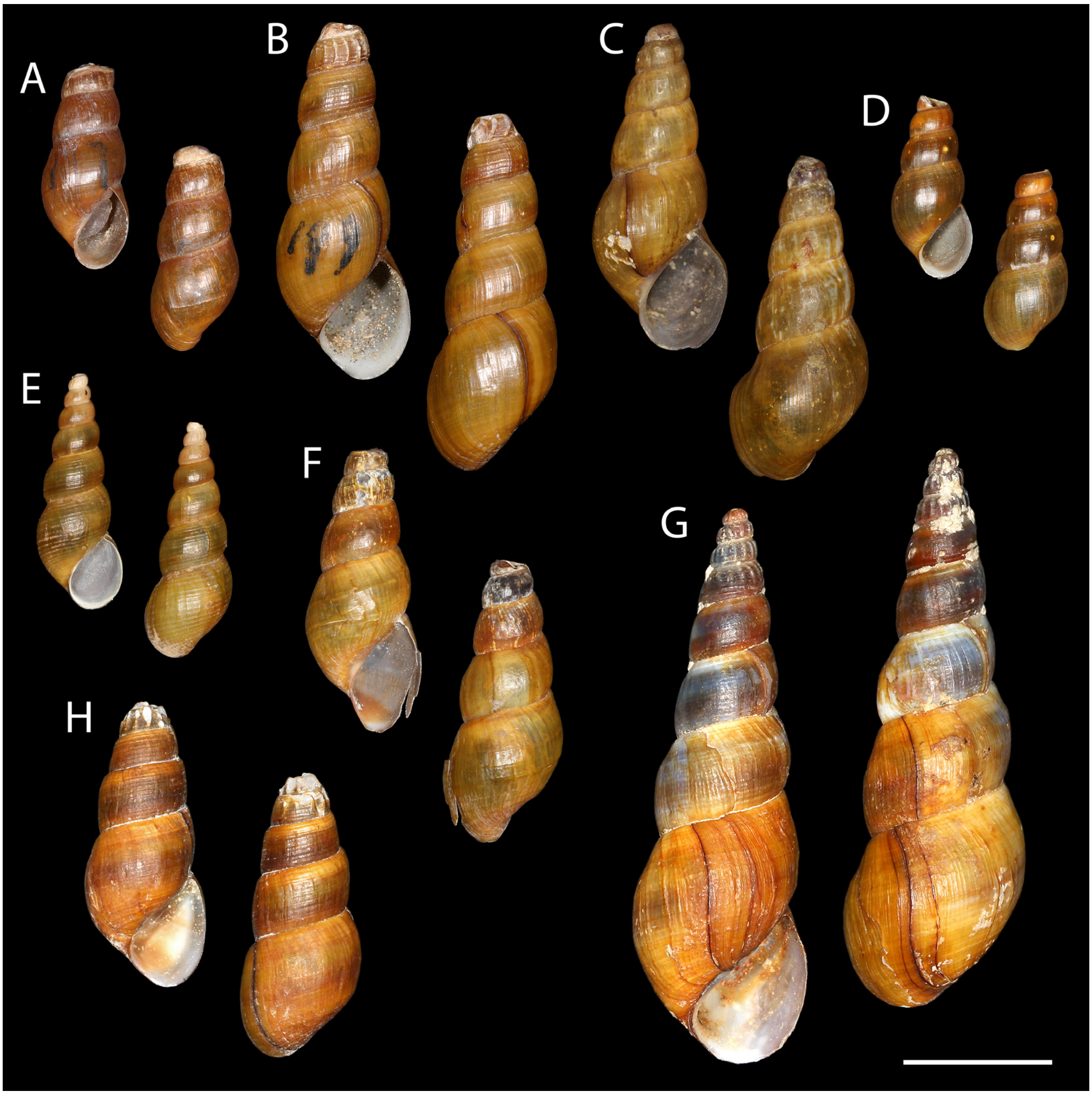


Fig. 22. Type material of *Juga nigrina* (I. Lea, 1856). **A**. *Melania nigrina* I. Lea, 1856. Lectotype, USNM 118992. **B**. *Melania shastaensis* I. Lea, 1856. Lectotype, USNM 119283. **C**. *Goniobasis circumlineata* Tryon, 1865. Lectotype, ANSP 27573. **D**. *Goniobasis chacei* Henderson, 1935. Holotype, UCM 18058a. **E**. *Goniobasis coquillensis* Henderson, 1935. Holotype, UCM 21168a. **F**. *Goniobasis orickensis* Henderson, 1935. Holotype, UCM 17710a. **G**. *Goniobasis yrekaensis* Henderson, 1935. Holotype, UCM 17735a. **H**. *Goniobasis yrekaensis obscura* Henderson, 1935. Holotype, UCM 17724a. Scale bar = 1 cm.

GenBank: MK472386, MK464753; USNM 1295184 • 1 spm; same collection data as for preceding; GenBank: MK472385, MK464752; USNM 1295183 • 37 spms; Curry Co., Edson Campground; 42.8152, -124.4109; 13 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295102 • 1 spm; same collection data as for preceding; GenBank: MK472336, MK464703, MK480837; USNM 1295100 • 1 spm; same collection data as for preceding; GenBank: MK472337, MK464704; USNM 1295101 • 1 spm; same collection data as for preceding; GenBank: MK472332, MK464699; USNM 1295096 • 1 spm; same collection data as for preceding; GenBank: MK472333, MK464700; USNM 1295097 • 1 spm; same collection data as for preceding; GenBank: MK472334, MK464701; USNM 1295098 • 1 spm; same collection data as for preceding; GenBank: MK472335, MK464702; USNM 1295099 • 12 spms; Curry Co., Elk River Rd, just upstream of U.S. Hwy 101; 42.7861, -124.4811; 13 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295114 • 1 spm; same collection data as for preceding; GenBank: MK472346, MK464713, MK480841; USNM 1295112 • 1 spm; same collection data as for preceding; GenBank: MK472347, MK464714, MK480842; USNM 1295113 • 1 spm; same collection data as for preceding; GenBank: MK472343, MK464710, MK480839; USNM 1295109 • 1 spm; same collection data as for preceding; GenBank: MK472344, MK464711; USNM 1295110 • 1 spm; same collection data as for preceding; GenBank: MK472345, MK464712, MK480840; USNM 1295111 • 32 spms; Curry Co., Jack Creek; 42.062, -124.219; 14 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413269 • 1 spm; same collection data as for preceding; GenBank: MK472437, MK464804, MK480884; USNM 1413264 • 1 spm; same collection data as for preceding; GenBank: MK472438, MK464805, MK480885; USNM 1413265 • 1 spm; same collection data as for preceding; GenBank: MK472439, MK464806, MK480886; USNM 1413266 • 1 spm; same collection data as for preceding; GenBank: MK472440, MK464807, MK480887; USNM 1413267 • 1 spm; same collection data as for preceding; GenBank: MK472441, MK464808, MK480888; USNM 1413268 • 29 spms; Curry Co., Rogue River at Agness; 42.5578, -124.0595; 14 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413251 • 1 spm; same collection data as for preceding; GenBank: MK472422, MK464789; USNM 1413246 • 1 spm; same collection data as for preceding; GenBank: MK472423, MK464790, MK480874; USNM 1413247 • 1 spm; same collection data as for preceding; GenBank: MK472424, MK464791; USNM 1413248 • 1 spm; same collection data as for preceding; GenBank: MK472425, MK464792; USNM 1413249 • 1 spm; same collection data as for preceding; GenBank: MK472426, MK464793, MK480875; USNM 1413250 • 71 spms; Curry Co., Rogue River at Huntley Park; 42.4802, -124.3303; 14 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413257 • 1 spm; same collection data as for preceding; GenBank: MK472427, MK464794, MK480876; USNM 1413252 • 1 spm; same collection data as for preceding; GenBank: MK472428, MK464795, MK480877; USNM 1413253 • 1 spm; same collection data as for preceding; GenBank: MK472429, MK464796, MK480878; USNM 1413254 • 1 spm; same collection data as for preceding; GenBank: MK472430, MK464797, MK480879; USNM 1413255 • 1 spm; same collection data as for preceding; GenBank: MK472431, MK464798; USNM 1413256 • 14 spms; Curry Co., U.S. Hwy 101, Humbug Mountain State Park; 42.6837, -124.4222; 13 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295121 • 1 spm; same collection data as for preceding; GenBank: MK472348, MK464715; USNM 1295115 • 1 spm; same collection data as for preceding; GenBank: MK472349, MK464716, MK480843; USNM 1295116 • 1 spm; same collection data as for preceding; GenBank: MK472350, MK464717; USNM 1295117 • 1 spm; same collection data as for preceding; GenBank: MK472351, MK464718, MK480844; USNM 1295118 • 1 spm; same collection data as for preceding; GenBank: MK472352, MK464719, MK480845; USNM 1295119 • 1 spm; same collection data as for preceding; GenBank: MK472353, MK464720, MK480846; USNM 1295120 • 15 spms; Douglas Co., ~.35 mi S of Hwy 138 (south of junction of NF4714 and NF4720); 43.3018, -122.6817; 13 Aug. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295029 • 1 spm; same collection data as for preceding; GenBank: MK472321, MK464688, MK480832; USNM 1295024 • 1 spm; same collection data as for preceding; GenBank: MK472322, MK464689; USNM 1295025 • 1 spm; same collection data as for preceding; GenBank: MK472323, MK464690; USNM 1295026 • 1 spm; same collection data as for preceding; GenBank: MK472324, MK464691; USNM 1295027 •

1 spm; same collection data as for preceding; GenBank: MK472325, MK464692; USNM 1295028 • 25 spms; Douglas Co., along SH 42, just SW of Winston; 43.1177, -123.4268; 14 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295170 • 1 spm; same collection data as for preceding; GenBank: MK472380, MK464747; USNM 1295165 • 1 spm; same collection data as for preceding; GenBank: MK472381, MK464748; USNM 1295166 • 1 spm; same collection data as for preceding; GenBank: MK472382, MK464749, MK480860; USNM 1295167 • 1 spm; same collection data as for preceding; GenBank: MK472383, MK464750; USNM 1295168 • 1 spm; same collection data as for preceding; GenBank: MK472384, MK464751; USNM 1295169 • 39 spms; Douglas Co., Cow Creek Rd at FS Rd 32-7-19; 42.7724, -123.5737; 14 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295194 • 1 spm; same collection data as for preceding; GenBank: MK472390, MK464757; USNM 1295189 • 1 spm; same collection data as for preceding; GenBank: MK472391, MK464758; USNM 1295190 • 1 spm; same collection data as for preceding; GenBank: MK472392, MK464759; USNM 1295191 • 1 spm; same collection data as for preceding; GenBank: MK472393, MK464760; USNM 1295192 • 1 spm; same collection data as for preceding; GenBank: MK472394, MK464761; USNM 1295193 • 11 spms; Douglas Co., Fort Umpqua; [43.7028, -124.1675]; Smithsonian leg.; USNM 119286 • 12 spms; Douglas Co., Glendale, Cow Creek; [42.7401, -123.4168]; W. Westgate leg.; USNM 334393 • 55 spms; Douglas Co., North Umpqua River at Amacher Park; 43.2816, -123.3564; 15 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413383 • 1 spm; same collection data as for preceding; GenBank: MK472466, MK464833; USNM 1413378 • 1 spm; same collection data as for preceding; GenBank: MK472467, MK464834, MK480904; USNM 1413379 • 1 spm; same collection data as for preceding; GenBank: MK472468, MK464835; USNM 1413380 • 1 spm; same collection data as for preceding; GenBank: MK472469, MK464836; USNM 1413381 • 1 spm; same collection data as for preceding; GenBank: MK472470, MK464837, MK480905; USNM 1413382 • 7 spms; Douglas Co., Roseburg, Umpqua River; [43.2108, -123.3525]; J. Henderson leg.; USNM 425496 • 19 spms; Douglas Co., Umpqua River; Andrus leg.; USNM 134591 • 48 spms; Douglas Co., Umpqua River at Sawyers Rapids; 43.6822, -123.6684; 15 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413377 • 1 spm; same collection data as for preceding; GenBank: MK472461, MK464828; USNM 1413372 • 1 spm; same collection data as for preceding; GenBank: MK472462, MK464829, MK480902; USNM 1413373 • 1 spm; same collection data as for preceding; GenBank: MK472463, MK464830, MK480903; USNM 1413374 • 1 spm; same collection data as for preceding; GenBank: MK472464, MK464831; USNM 1413375 • 1 spm; same collection data as for preceding; GenBank: MK472465, MK464832; USNM 1413376 • 14 spms; Douglas Co., Upstream of NF2823 bridge (downstream of log jam); 43.1071, -122.585; 12 Aug. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295036 • 1 spm; same collection data as for preceding; GenBank: MK472331, MK464698; USNM 1295035 • 1 spm; same collection data as for preceding; GenBank: MK472326, MK464693, MK480833; USNM 1295030 • 1 spm; same collection data as for preceding; GenBank: MK472327, MK464694, MK480834; USNM 1295031 • 1 spm; same collection data as for preceding; GenBank: MK472328, MK464695; USNM 1295032 • 1 spm; same collection data as for preceding; GenBank: MK472329, MK464696, MK480835; USNM 1295033 • 1 spm; same collection data as for preceding; GenBank: MK472330, MK464697, MK480836; USNM 1295034 • 7 spms; Douglas Co., Winchester, Umpqua River; [43.283, -123.3552]; J. Henderson leg.; USNM 425497 • 29 spms; Douglas Co., Yoncalla Creek at Boswell Rd; 43.6408, -123.2983; 15 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413365 • 1 spm; same collection data as for preceding; GenBank: MK472456, MK464823, MK480897; USNM 1413360 • 1 spm; same collection data as for preceding; GenBank: MK472457, MK464824, MK480898; USNM 1413361 • 1 spm; same collection data as for preceding; GenBank: MK472458, MK464825, MK480899; USNM 1413362 • 1 spm; same collection data as for preceding; GenBank: MK472459, MK464826, MK480900; USNM 1413363 • 1 spm; same collection data as for preceding; GenBank: MK472460, MK464827, MK480901; USNM 1413364 • 10 spms; Douglas Co.; T.J.L. leg.; USNM 509447 • 41 spms; Jackson Co., Jenny Creek at Pinehurst; 42.118, -122.366; 15 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413329 • 1 spm; same collection data as for preceding; GenBank: MK472451, MK464818, MK480894; USNM 1413324

• 1 spm; same collection data as for preceding; GenBank: MK472452, MK464819; USNM 1413325 • 1 spm; same collection data as for preceding; GenBank: MK472453, MK464820; USNM 1413326 • 1 spm; same collection data as for preceding; GenBank: MK472454, MK464821, MK480895; USNM 1413327 • 1 spm; same collection data as for preceding; GenBank: MK472455, MK464822, MK480896; USNM 1413328 • 28 spms; Jackson Co., near jct of Birdseye Creek Rd and Birdseye West Rd (37-4-4); 42.3845, -123.1748; 12 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295134 • 1 spm; same collection data as for preceding; GenBank: MK472360, MK464727, MK480847; USNM 1295129 • 1 spm; same collection data as for preceding; GenBank: MK472361, MK464728, MK480848; USNM 1295130 • 1 spm; same collection data as for preceding; GenBank: MK472362, MK464729, MK480849; USNM 1295131 • 1 spm; same collection data as for preceding; GenBank: MK472363, MK464730, MK480850; USNM 1295132 • 1 spm; same collection data as for preceding; GenBank: MK472364, MK464731, MK480851; USNM 1295133 • 18 spms; Jackson Co., Neil Creek; 42.1765, -122.6504; 15 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413298 • 1 spm; same collection data as for preceding; GenBank: MK472447, MK464814, MK480891; USNM 1413294 • 1 spm; same collection data as for preceding; GenBank: MK472448, MK464815, MK480892; USNM 1413295 • 1 spm; same collection data as for preceding; GenBank: MK472449, MK464816; USNM 1413296 • 1 spm; same collection data as for preceding; GenBank: MK472450, MK464817, MK480893; USNM 1413297 • 6 spms; Jackson Co., Rogue River at Rogue River City; 42.4313, -123.1711; 14 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413275 • 1 spm; same collection data as for preceding; GenBank: MK472442, MK464809; USNM 1413270 • 1 spm; same collection data as for preceding; GenBank: MK472443, MK464810, MK480889; USNM 1413271 • 1 spm; same collection data as for preceding; GenBank: MK472444, MK464811, MK480890; USNM 1413272 • 1 spm; same collection data as for preceding; GenBank: MK472445, MK464812; USNM 1413273 • 1 spm; same collection data as for preceding; GenBank: MK472446, MK464813; USNM 1413274 • 30 spms; Jackson Co., SH 234, Dodge Bridge County Park; 42.5261, -122.8427; 12 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295158 • 1 spm; same collection data as for preceding; GenBank: MK472377, MK464744; USNM 1295155 • 1 spm; same collection data as for preceding; GenBank: MK472378, MK464745, MK480859; USNM 1295156 • 1 spm; same collection data as for preceding; GenBank: MK472379, MK464746; USNM 1295157 • 1 spm; same collection data as for preceding; GenBank: MK472375, MK464742; USNM 1295153 • 1 spm; same collection data as for preceding; GenBank: MK472376, MK464743, MK480858; USNM 1295154 • 11 spms; Jackson Co., SH 62 just upstream of Casey State Recreation Area, Takelma Dr, near McGregor Park; 42.6589, -122.694; 12 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295140 • 1 spm; same collection data as for preceding; GenBank: MK472365, MK464732, MK480852; USNM 1295135 • 1 spm; same collection data as for preceding; GenBank: MK472366, MK464733, MK480853; USNM 1295136 • 1 spm; same collection data as for preceding; GenBank: MK472367, MK464734; USNM 1295137 • 1 spm; same collection data as for preceding; GenBank: MK472368, MK464735, MK480854; USNM 1295138 • 1 spm; same collection data as for preceding; GenBank: MK472369, MK464736, MK480855; USNM 1295139 • 35 spms; Josephine Co., North Fork Galice Creek; 42.5553, -123.6388; 14 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413169 • 35 spms; Josephine Co., North Fork Galice Creek Rd; 42.5531, -123.6324; 14 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295108 • 1 spm; same collection data as for preceding; GenBank: MK472340, MK464707; USNM 1295105 • 1 spm; same collection data as for preceding; GenBank: MK472341, MK464708; USNM 1295106 • 1 spm; same collection data as for preceding; GenBank: MK472342, MK464709; USNM 1295107 • 1 spm; same collection data as for preceding; GenBank: MK472338, MK464705, MK480838; USNM 1295103 • 1 spm; same collection data as for preceding; GenBank: MK472339, MK464706; USNM 1295104 • 23 spms; Josephine Co., Rogue River at Carpenter Island Park; 42.5595, -123.5984; 14 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413263 • 1 spm; same collection data as for preceding; GenBank: MK472432, MK464799, MK480880; USNM 1413258 • 1 spm; same collection data as for preceding; GenBank: MK472433, MK464800, MK480881; USNM 1413259 • 1 spm; same collection data as for preceding; GenBank: MK472434, MK464801; USNM

1413260 • 1 spm; same collection data as for preceding; GenBank: MK472435, MK464802, MK480882; USNM 1413261 • 1 spm; same collection data as for preceding; GenBank: MK472436, MK464803, MK480883; USNM 1413262 • 38 spms; Josephine Co., SH 199, 1.4 mi SW of Wonder; 42.348, -123.5594; 12 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295146 • 1 spm; same collection data as for preceding; GenBank: MK472370, MK464737, MK480856; USNM 1295141 • 1 spm; same collection data as for preceding; GenBank: MK472371, MK464738; USNM 1295142 • 1 spm; same collection data as for preceding; GenBank: MK472372, MK464739; USNM 1295143 • 1 spm; same collection data as for preceding; GenBank: MK472373, MK464740, MK480857; USNM 1295144 • 1 spm; same collection data as for preceding; GenBank: MK472374, MK464741; USNM 1295145 • 3 spms; Klamath Co., 16 mi NE of Dorris; [42.174, -121.7985]; USNM 404252 • 17 spms; Klamath Co., 2 mi N of Modoc Point; [42.4711, -121.8728]; 13 Aug. 1929; L. Sinitsin leg.; ditch by the highway; USNM 531428 • 2 spms; Klamath Co., Klamath Falls, L. Klamath; [42.2389, -121.8051]; W. Westgate leg.; USNM 334391 • 81 spms; Klamath Co., Klamath Falls, small creek by lab at Biological Survey on the lake; [42.2292, -121.7769]; 14 Aug. 1929; L. Sinitsin leg.; USNM 531319. – **California** • 4 spms; USNM 12140a • 5 spms; same collection data as for preceding; USNM 56464 • 1 spm; same collection data as for preceding; H. Hemphill leg.; USNM 504245 • 2 spms; same collection data as for preceding; S. Smith leg.; USNM 218589 • 7 spms; Del Norte Co., 4 mi E of Klamath; [41.5378, -123.9379]; J. Henderson leg.; USNM 425495 • 15 spms; Del Norte Co., along SH 199, south side of Gasquette, former site of Adams Station; 41.8428, -123.9948; 13 Jul. 2014; J.T. Garner and N.V. Whelan leg.; USNM 1295128 • 1 spm; same collection data as for preceding; GenBank: MK472355, MK464722; USNM 1295123 • 1 spm; same collection data as for preceding; GenBank: MK472356, MK464723; USNM 1295124 • 1 spm; same collection data as for preceding; GenBank: MK472357, MK464724; USNM 1295125 • 1 spm; same collection data as for preceding; GenBank: MK472358, MK464725; USNM 1295126 • 1 spm; same collection data as for preceding; GenBank: MK472359, MK464726; USNM 1295127 • 1 spm; same collection data as for preceding; GenBank: MK472354, MK464721; USNM 1295122 • 13 spms; Del Norte Co., Klamath; [41.5257, -124.0426]; 7 Jul. 1951; USNM 665461 • 24 spms; Del Norte Co., Klamath River at Klamath Glen; 41.5152, -124.0003; 13 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413145 • 1 spm; same collection data as for preceding; USNM 1413140 • 1 spm; same collection data as for preceding; USNM 1413141 • 1 spm; same collection data as for preceding; USNM 1413142 • 1 spm; same collection data as for preceding; USNM 1413143 • 1 spm; same collection data as for preceding; USNM 1413144 • 31 spms; Del Norte Co., tributary of the Smith Creek [sic, Smith River]; 9 May 1929; L. Sinitsin leg.; USNM 531452 • 102 spms; Glenn Co., Brittain Ranch [sic, Brittan Ranch]; [39.3968, -122.6636]; 22 Mar. 1970; K.E. Lucas leg.; CASIZ 30022 • 7 spms; Humboldt Co., E of Willow Creek Campground, Hwy 299; [40.9452, -123.6566]; 16 Jun. 2015; B. Norman leg.; USNM 1436667 • 8 spms; Humboldt Co., near Orick, near hatchery; 9 May 1929; L. Sinitsin leg.; USNM 531473 • 84 spms; Humboldt Co., Redwood Creek at Chezem Rd; 40.9129, -123.8137; 13 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413066 • 1 spm; same collection data as for preceding; GenBank: MK472395, MK464762, MK480863; USNM 1413061 • 1 spm; same collection data as for preceding; GenBank: MK472396, MK464763; USNM 1413062 • 1 spm; same collection data as for preceding; GenBank: MK472397, MK464764; USNM 1413063 • 1 spm; same collection data as for preceding; GenBank: MK472398, MK464765, MK480864; USNM 1413064 • 1 spm; same collection data as for preceding; GenBank: MK472399, MK464766; USNM 1413065 • 47 spms; Humboldt Co., Redwood Creek at Orick; 41.2888, -124.0571; 13 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413122 • 1 spm; same collection data as for preceding; GenBank: MK472411, MK464778; USNM 1413116 • 1 spm; same collection data as for preceding; GenBank: MK472412, MK464779, MK480870; USNM 1413117 • 1 spm; same collection data as for preceding; GenBank: MK472413, MK464780; USNM 1413118 • 1 spm; same collection data as for preceding; GenBank: MK472414, MK464781; USNM 1413119 • 1 spm; same collection data as for preceding; GenBank: MK472415, MK464782, MK480871; USNM 1413120 • 1 spm; same collection data as for preceding; GenBank: MK472416, MK464783, MK480872; USNM 1413121 • 1 spm; Humboldt Co., Redwood

Creek, Bair's Ranch; [40.9638, -123.8405]; H.S. Barber leg.; USNM 193865 • 1 spm; Lake Co., Clear Lake; [39.0616, -122.8272]; Pease leg.; USNM 30647 • 4 spms; Mendocino Co., 10 mi N of Willets; [39.536, -123.4162]; 26 Jun. 1951; USNM 665462 • 11 spms; Mendocino Co., Cow Mountain; [39.1122, -123.109]; W.M. Gabb leg.; ANSP 27579 • 4 spms; Mendocino Co., Montgomery Creek at Montgomery Woods State Reserve; 39.2347, -123.3961; 12 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413072 • 1 spm; same collection data as for preceding; GenBank: MK472400, MK464767, MK480865; USNM 1413067 • 1 spm; same collection data as for preceding; GenBank: MK472401, MK464768, MK480866; USNM 1413068 • 1 spm; same collection data as for preceding; GenBank: MK472402, MK464769; USNM 1413069 • 1 spm; same collection data as for preceding; GenBank: MK472403, MK464770; USNM 1413070 • 1 spm; same collection data as for preceding; GenBank: MK472404, MK464771; USNM 1413071 • 2 spms; Mendocino Co.; H. Hemphill leg.; USNM 30552 • 6 spms; Mendocino Co.; USNM 59028 • 9 spms; Napa Co., Huichica Creek; [38.2145, -122.3564]; 8 Jul. 1980; L. Eng leg.; CASIZ 80989 • 12 spms; Napa Co., Oakville; [38.441, -122.395]; Brannan leg.; USNM 59040 • 17 spms; Napa Co., White Sulphur Springs; [38.49, -122.498]; Jul. 1877; J. Le Conte leg.; USNM 58932 • 25 spms; Shasta Co., Clear Creek at French Gulch; 40.7048, -122.6366; 11 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413115 • 1 spm; same collection data as for preceding; GenBank: MK472405, MK464772, MK480867; USNM 1413109 • 1 spm; same collection data as for preceding; GenBank: MK472406, MK464773; USNM 1413110 • 1 spm; same collection data as for preceding; GenBank: MK472407, MK464774, MK480868; USNM 1413111 • 1 spm; same collection data as for preceding; GenBank: MK472408, MK464775; USNM 1413112 • 1 spm; same collection data as for preceding; GenBank: MK472409, MK464776; USNM 1413113 • 1 spm; same collection data as for preceding; GenBank: MK472410, MK464777, MK480869; USNM 1413114 • 6 spms; Siskiyou Co., 4 mi above mouth of Shasta River; [41.7863, -122.6017]; J. Henderson leg.; USNM 425494 • 4 spms; Siskiyou Co., Klamath River at Klamathton; [41.8999, -122.505]; 1899; R.C. McGregor leg.; ANSP 76792 • 7 spms; Siskiyou Co., O'Neil Creek; [41.8105, -123.1158]; W.B. Murbarger leg.; USNM 467207 • 8 spms; Siskiyou Co., Scott River, 8 mi above Scott Bar; [41.6767, -123.1016]; L. Shapovalor leg.; ANSP 179318 • 7 spms; Siskiyou Co., Scott River, Scott River Resort [Scott River Lodge]; [41.6795, -123.1]; 23 Jun. 1948; M.L. Walton leg.; ANSP 347189 • 46 spms; Siskiyou Co., Shasta River below Hwy 263 Bridge; 41.807, -122.5938; 14 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413128 • 1 spm; same collection data as for preceding; GenBank: MK472417, MK464784; USNM 1413123 • 1 spm; same collection data as for preceding; GenBank: MK472418, MK464785; USNM 1413124 • 1 spm; same collection data as for preceding; GenBank: MK472419, MK464786; USNM 1413125 • 1 spm; same collection data as for preceding; GenBank: MK472420, MK464787; USNM 1413126 • 1 spm; same collection data as for preceding; GenBank: MK472421, MK464788, MK480873; USNM 1413127 • 12 spms; Sonoma Co., Adobe Creek; [38.2343, -122.5978]; ANSP 120900 • 1 spm; Sonoma Co., Austin Creek State Recreation Area, East Austin Creek, Black Rock Creek to road crossing in Recreation Area; [38.5594, -123.0564]; 10 Jul. 1979; L. Courtois leg.; CASIZ 169957 • 2 spms; Sonoma Co., Austin Creek State Recreation Area, East Austin Creek, vicinity of road crossing; [38.5359, -123.0721]; 10 Jul. 1970; L. Eng leg.; CASIZ 85269 • 18 spms; Sonoma Co., Buckeye Spring, on The Geysers Rd; [38.7414, -122.8289]; 28 Aug. 1979; J. Landye leg.; on rocks and sand; USNM 892379 • 6 spms; Sonoma Co., Cloverdale; [38.816, -123.0111]; USNM 58994 • 3 spms; same collection data as for preceding; USNM 56426 • 207 spms; Sonoma Co., Cold Springs, S of Sulphur Creek, The Geysers, 0.5 km S, 0.8 km E from NW corner; [38.7531, -122.8242]; 26 Aug. 1979; J. Landye leg.; on rocks, leaves, dead wood; USNM 903672 • 8 spms; Sonoma Co., Duncans Mills; [38.4541, -123.0495]; USNM 56425 • 27 spms; Sonoma Co., Gualala River, Wheatfield Fork; USFC; Gilbert leg.; USNM 109894 • 12 spms; Sonoma Co., Healdsburg; W. Gregg leg.; USNM 1501084 • 13 spms; Sonoma Co., in spring on E Side of U.S. Hwy 101, 0.9 mi N of Hwy 101 bridge over Russian River; [38.6055, -122.8708]; 25 Aug. 1979; J. Landye leg.; USNM 892371 • 53 spms; Sonoma Co., Mr Martin's Ranch [Silas W Martin Dairy, in Two Rock, near Petaluma]; [38.2426, -122.7525]; 17 Apr. 1929; L. Sinitsin leg.; USNM 531206 • 4 spms; Sonoma Co., 1.15 mi NE of junction of California Hwy 1 and 12, 550 ft

NW of BM 27, Duncans Mills Area; [38.4495, -123.0948]; 21 Sep. 1966; J. Landye and D.W. Taylor leg.; in spring trickle on N side of Russian River; USNM 905121 • 9 spms; Sonoma Co., Sonoma Creek; [38.2773, -122.4719]; W. Sutton leg.; USNM 509435 • 4 spms; same collection data as for preceding; J. Rowell leg.; ANSP 27575 • 3 spms; Sonoma Co., The Geysers; [38.7748, -122.7552]; Kelsey leg.; USNM 153054 • 3 spms; Sonoma Co.; H. Hemphill leg.; USNM 30556 • 7 spms; Sonoma Co.; J.G. Cooper leg.; USNM 28929 • 1 spm; Trinity Co., North Fork of the Trinity River, East Fork of the North Fork of the Trinity River, tributary, Brock Creek [sic, Brock Gulch]; [40.7881, -123.1242]; 6 Jun. 1978; Del Sarto leg.; CASIZ 85263 • 2 spms; Trinity Co., Trinity River, tributary, Dutton Creek; [40.675, -122.9704]; 20 Jun. 1978; Del Sarto leg.; CASIZ 85222 • 81 spms; 3 mi N of Golden Beach [sic]; 15 Aug. 1951; USNM 665463.

Description

Shell. Thin to moderately thick, large, usually not exceeding ~2.5 cm, exceptionally reaching ~3.75 cm in length; turriform, narrowly conical to cylindrical in shape, spire moderate to high, highly variable in sculpture, color, and banding (Fig. 23). Whorls somewhat flattened to convex, occasionally weakly shouldered or with a subsutural ramp, suture weakly to deeply impressed. Aperture oval in shape, occasionally flattened at the base, lip smooth, simple to slightly sinuous. Spiral sculpture of fine striae, indistinct to moderately developed, highly variable in strength and number; later whorls occasionally with few, indistinct elevated lirae. Axial sculpture of fine, orthocline, weakly opisthocyrt to sinuous growth lines; plications present or absent, confined to upper part of spire; plications regular to somewhat irregular, weakly to moderately developed, occasionally shouldered, orthocline to moderately opisthocyrt; may be thickened or beaded at intersections with spiral striae. Shell black, dark brown, to olive, tan or yellowish in color. Bands present or absent, one to three in number and variable in width, reddish-purple in color. Interior of aperture white or cream to dark purple in color. Base of columella occasionally tinged reddish-purple

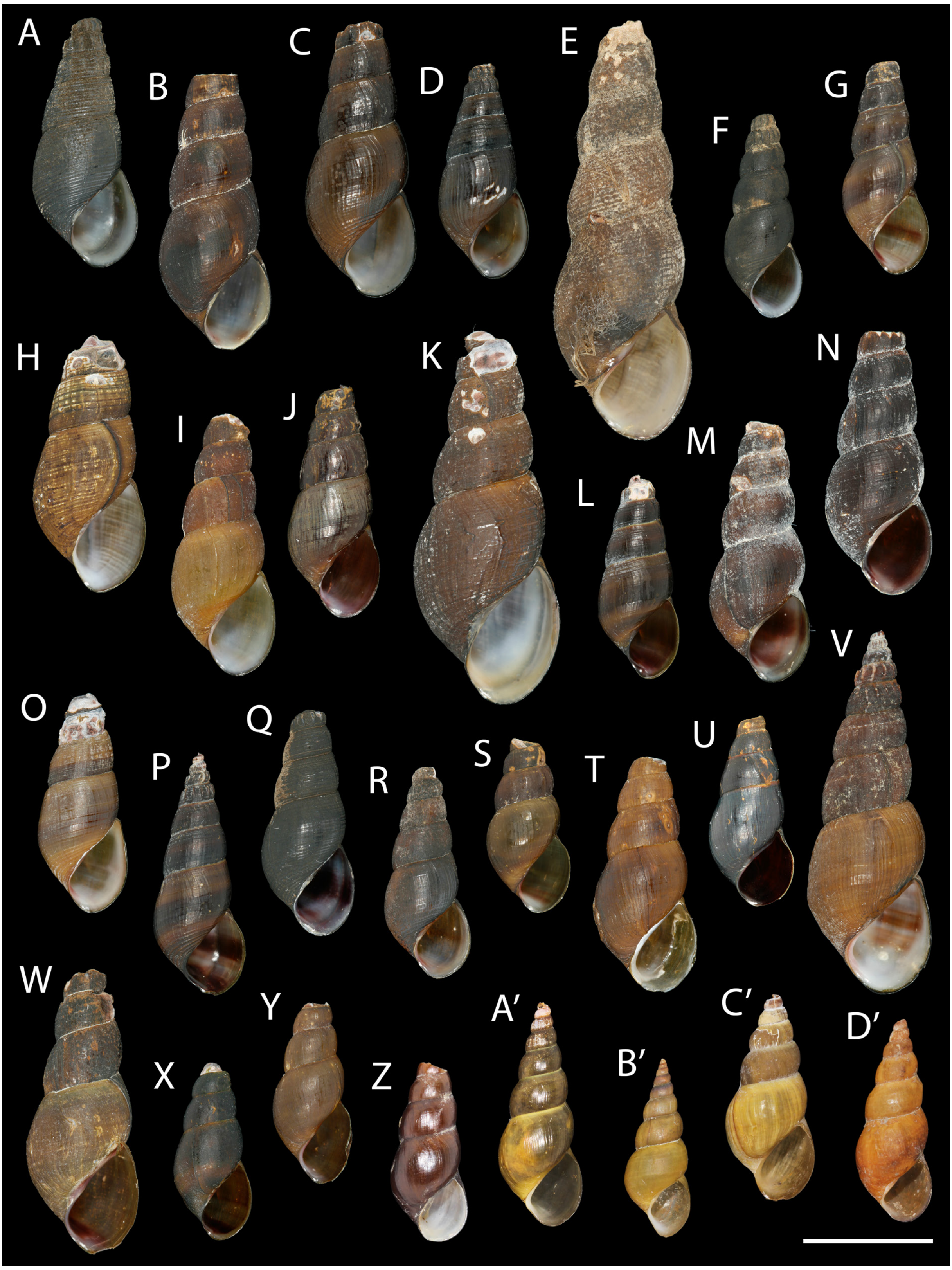
Radula. Rachidian narrowly rectangular, wider than tall, with convex lower margin and small, bluntly pointed, basal denticles at lower, outer corners (Fig. 24). Upper margin slightly concave with cutting edge bearing central, elongate conical cusp, and two to three stout, conical denticles on each side. Lateral teeth with prominent triangular cusp flanked by two to three inner and two to three outer, triangular denticles, and occasionally a membranous outermost denticle. Marginal teeth with broadly rounded cutting edges and long, slender, flattened shafts with membranous flanges along inner and outer edges. Narrow inner flanges along distal half to two-thirds of shafts; broad outer flanges extending almost to tooth bases. Inner marginal teeth with ~five, and outer marginal teeth with six to seven flattened denticles.

Distribution and ecology

In small creeks to large rivers primarily in coastal drainages from south-central Oregon to central California (Fig. 21B).

Remarks

Melania nigrina and *M. shastaensis* were established simultaneously by Lea (1856). *Melania shastaensis* was first synonymized with *Goniobasis occata* by Reeve (1860), followed by Brot (1862), an error resulting from a misidentified specimen that was labeled as originating from the author ("authentic"; Tryon 1865: 237; 1873: 146). Tryon (1864) synonymized *shastaensis* with *silicula* which has been followed by most subsequent authors (Tryon 1865, 1866, 1873; Henderson 1929; Goodrich 1942; Burch & Tottenham 1980; Burch 1982, 1989), apart from Pilsbry (1899) who synonymized the species with *plicifera*. Henderson (1935a, 1936b) recognized the species as a distinct variety of *silicula* which was followed by Frest & Johannes (2010). Campbell *et al.* (2016: 167) noted that their sequenced specimen of *J.* (*J.*) *silicula shastaensis* was supported in a different clade from *J.* (*J.*) *silicula silicula*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but did not address its taxonomic status. Thus, the fact that *nigrina* and *shastaensis* represent the same taxonomical species is new. We here take the right of First Reviser (Art. 24.2.2; ICZN, 1999), and establish the precedence of *nigrina* over *shastaensis*.

Although it is not known precisely where in Clear Creek the types of *Melania nigrina* originated, this creek has been severely affected by impoundment and gold dredging and many sites still lack *Juga* (Frest & Johannes 2010). However, refugial populations in several large tributaries seem to be repopulating the main course near their junctions with Clear Creek. Frest & Johannes (2010) noted the discrepancy between Lea's (1856, 1863a, 1863b) description and the type specimens (Fig. 22A), which do not appear as nearly black and polished with a dark purple interior as the description would suggest. Near topotypic specimens from Clear Creek at French Gulch (Fig. 23T) were included in the analysis of Strong & Whelan (2019), which showed a range of variation from those yellow-brown in color with a light interior similar to the type, to those black in color with a dark purple interior (Fig. 23U) matching the original description.

The type locality of *Melania shastaensis* was indicated to be Shasta and Scott Rivers, California (Lea 1856). Lea (1863a, 1863b) later added "Fort Umpqua, O.T. [Oregon Territory]" to the list of habitats with the Smithsonian as collector, which refers to USNM 119286 from the Lea collection. However, this material has no type status as it was not originally included. Henderson (1935a, 1936b) questioned whether the original type locality was erroneous, having seen no material from the Shasta River that matched the description, and considered the types more similar to material from the Umpqua River, an opinion shared by Frest & Johannes (2010). Henderson submitted specimens from the Shasta, Klamath and Umpqua Rivers to the USNM for comparison with the type of *shastaensis* and received the following reply from curator Harald Rehder, "[the types of *Goniobasis shastaensis* Lea] are more like those from the Umpqua River. […] Whether Lea's type lot (from Scott and Shasta Rivers) really came from either or both of those rivers, or whether we are here dealing with a confusion of localities, I cannot tell" (Henderson 1935a: 95; 1936b: 276). Owing to his doubts over the precision of the type locality, Henderson (1935a) described material in his possession from the Shasta River as *Goniobasis yrekaensis*. Henderson (1936b) later reported receiving specimens from the Scott River that agreed well with the original description of *shastaensis*, as did specimens from the Umpqua River drainage and elsewhere in western Oregon. Efforts to recollect from the Scott River were unsuccessful (Frest & Johannes 2010). Ultimately, however, the ambiguity is of little consequence as the same taxonomical species (*J. nigrina*) is found in both the Klamath and Umpqua River drainages.

The type locality of *Melania circumlineata* is the Mission San Antonio in Monterey County, California, but is widely assumed to be in error (Henderson 1932; Taylor 1981; Frest & Johannes 2010) as it lies far to the south of the documented distribution of Recent *Juga* (Fig. 21B). It was not infrequent in those times that specimens brought back to natural history museums "from the seats of trade" (Carpenter

Fig. 23 (previous page). Shell morphology of *Juga nigrina* (I. Lea, 1856). **A–Y**. Sequenced vouchers, arranged roughly from North to South. **A**. USNM 1413363. **B**. USNM 1295028. **C**. USNM 1413381. **D**. USNM 1413379. **E**. USNM 1295167. **F**. Topotypic (*Goniobasis coquillensis* Henderson, 1935), USNM 1295185. **G**. USNM 1295096. **H**. USNM 1295110. **I**. USNM 1413249. **J**. USNM 1413264. **K**. USNM 1413259. **L**. USNM 1295103. **M–N**. Topotypic (*Goniobasis yrekaensis obscura* Henderson, 1935). **M**. USNM 1295142. **N**. USNM 1295145. **O**. USNM 1413273. **P**. USNM 1295129. **Q**. USNM 1413294. **R**. USNM 1413327. **S**. Topotypic (*Goniobasis chacei* Henderson, 1935), USNM 1295125. **T–U**. Topotypic (*Melania nigrina* I. Lea, 1856). **T**. USNM 1413110. **U**. USNM 1413109. **V**. Topotypic (*Goniobasis yrekaensis* Henderson, 1935), USNM 1413125. **W**. Topotypic (*Goniobasis orickensis* Henderson, 1935), USNM 1413121. **X**. USNM 1413063. **Y**. USNM 1413068. **Z**. USNM 531319. **A'**. USNM 58932. **B'**. USNM 59040. **C'**. USNM 85269. **D'**. USNM 120900. Scale bar = 1 cm.

1857: 162), or from the seats of worship (e.g., Neubert *et al.* 2009), took incorrect provenance. Cooper (1894) indicated San Antonio Creek as the southern extent of *Goniobasis circumlineata*. This creek, which forms part of the boundary between Marin and Sonoma Counties, is a tributary of the Petaluma River, which flows into the northwestern corner of San Pablo Bay. Henderson (1932) quoted a personal communication from G.D. Hanna who pointed out that there are many San Antonio Creeks in California, but agreed that the one cited by Cooper may be the source of the type material. Hanna referred to an unconfirmed report of a chapel on the San Antonio Rancho at the head of the creek.

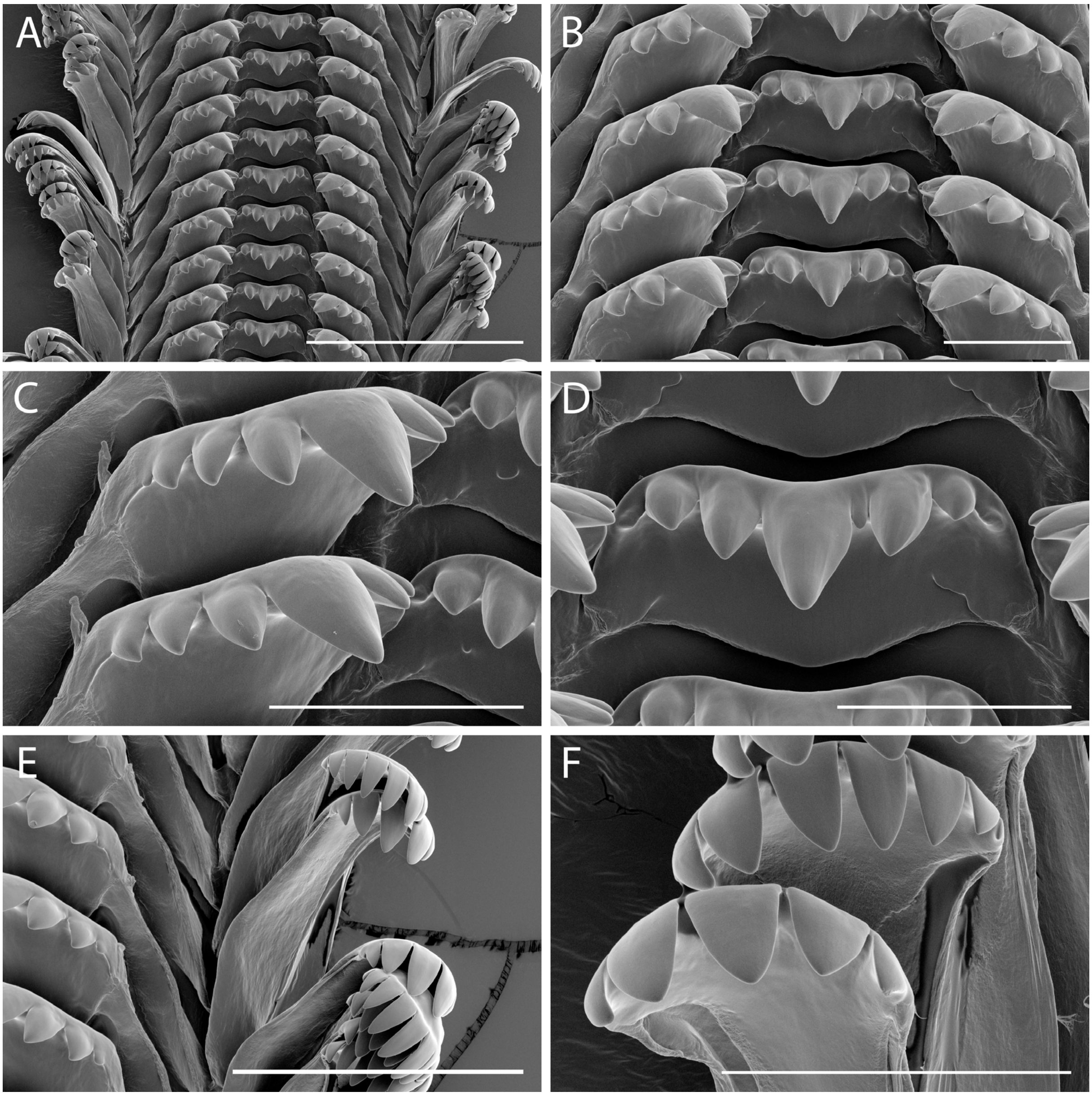


Fig. 24. Radular morphology of *Juga nigrina* (I. Lea, 1856) (USNM 1413111, topotypic). **A**. View of the anterior radular ribbon. **B**. Detail of cutting edge of rachidian and lateral teeth. **C**. Detail of lateral teeth cusps. **D**. Detail of rachidian cusps. **E**. Inner and outer marginal teeth. **F**. Detail of inner and outer marginal teeth cusps. Scale bars: A = 200 µm; B–C = 50 µm; D, F = 40 µm; E = 100 µm.

Several museum lots (e.g., Fig. 23A') collected in southern Sonoma and Napa Counties are morphologically similar in size, shape, color and proportion to the lectotype of *circumlineata*. Pilsbry (1899) and Walker (1918) considered it to be likely only a variety of *nigrina*; Frest & Johannes (2010) agreed that the type may be a decollate "*nigrina*" s. lat. Campbell *et al.* (2016: supp. file 1) reported this species could represent a number of smooth-shelled forms but were not able to analyze it. In addition to specimens from Mission San Antonio and Shasta County, California, both received from W. Newcomb, Tryon's (1865) concept of *Goniobasis circumlineata* included specimens collected by J.S. Newberry from the Pit River, and specimens from J.H. Thomson from the Feather River. Possible type material from the latter two localities has not been located and could potentially represent *Juga occata*, *J. douglasi* sp. nov., or both, but not *J. nigrina*, which does not extend that far east. Tryon (1873) later omitted *circumlineata* without comment and did not reproduce his earlier figures.

Attempts to locate type material of *Melania californica* have been unsuccessful. Clessin's collection was in Stuttgart, Germany, and was reportedly destroyed during World War II (Tomlin 1947: 288). Although parts of the collection evidently remain intact in the Stuttgart Museum, no types of this species are found there (I. Richling, pers. com.). Clessin (1882) attributed the locality information ("California") as communicated ("*com.*" = communicavit) from H. von Heimburg of Oldenburg. Parts of von Heimburg's collection, particularly the freshwater parts, were purchased and re-assembled by C. Bosch, whose collection was received by the Senckenberg in 1962 (Zilch 1967). However, there is no type or topotypic material of this species in the Senckenberg (J. Sigwart, R. Janssen, pers. com.). Thus, on the merits of the originally published figure, we tentatively consider *californica* to be a synonym of *nigrina*. This synonymy was first proposed by Pilsbry (1899) and followed by Walker (1918), Henderson (1929, 1935a, 1936b), and Taylor (1981). Frest & Johannes (2010) found Taylor's (1981) synonymy with *nigrina* to be plausible but noted that it could be a *nigrina*-like form and suggested the common name California Juga. Campbell *et al.* (2016: supp. file 1) reported this species could represent a number of smooth-shelled forms but were not able to analyze it. Other authors have ignored the name.

Topotypic or near topotypic specimens for all five of Henderson's (1935a) nominal species established from northern California (*Goniobasis chacei*, *G. coquillensis*, *G. orickensis*, *G. yrekaensis*, and *G. y. obscura*) were included in the molecular analysis of Strong & Whelan (2019) (Fig. 23F, M–N, S, V–W) and are conspecific with topotypic specimens of *nigrina* (Fig. 23T–U). All five were regarded as species incerta by Goodrich (1942). Burch & Tottenham (1980) and Burch (1982, 1989) did not mention any of them; nor did Turgeon *et al.* (1988, 1998). Taylor (1981) considered only *Juga* (*Oreobasis*) *chacei* and *J.* (*O.*) *orickensis* as valid, of which only the former was retained in the list of Johnson *et al.* (2013). Frest & Johannes (2010) considered all as valid, or potentially so, except *yrekaensis obscura*, which they synonymized with *yrekaensis*. Campbell *et al.* (2016: supp. file 1) supported the synonymy of *obscura* with *yrekaensis* but they did not address the taxonomic status of Henderson's other nominal species. Thus, the explicit synonymy of all five nominal species with *nigrina* here is new.

Specimens identified as *Juga* (*Oreobasis*) "*nigrina*" from the Upper Klamath River drainage by Frest & Johannes (1998) and Johannes (2015) are hypothesized here to represent true *nigrina*, but this will require confirmation with molecular data. Frest & Johannes (1998, 2005) reported that they had found no ribbed forms in this area. However, USNM 334391 from Klamath Falls is a lot of two juvenile specimens which display regular plications typical of *nigrina*. The other three historical lots from Klamath County are all eroded but are rather high spired and cylindrical with a moderately impressed suture and are cautiously interpreted as representing true *nigrina* as well. However, it is possible they could represent a mixture of *nigrina* and smooth forms of *J. canella* sp. nov., which would extend the distribution of the latter to the east. The OTU referred to as *Juga* (*Oreobasis*) "*nigrina*" (Frest & Johannes 2005 = Schoolhouse Meadow Juga) and later as *Juga* (*O.*) n. sp. (Johannes 2013a = Spring Creek Juga) from the Cascade-Siskiyou National Monument comprises smooth forms of *J. canella*. The OTU referred to as

J. (*O.*) "*nigrina*" (Frest & Johannes 1995b = Smooth River Juga) from the Upper Sacramento System is a mixture of *J. canella*. and *J. douglasi* sp. nov. as circumscribed here. The axially ribbed forms of true *nigrina* that occur in the Cascade-Siskiyou National Monument have been referred to as *J.* (*J.*) *silicula shastaensis* (Frest & Johannes 2005; Johannes 2013a). Populations from Sacramento River drainages of the western foothills of the Sierra Nevada have been attributed primarily to *J. nigrina* (e.g., Lowe 1916; Taylor, 1981; Frest & Johannes 1995b; Brim Box 2002; Brim Box *et al.* 2005) or to a potentially new species (Frest & Johannes 2007) and are interpreted here as representing *J. douglasi* (see account above). As confirmed by sequenced specimens, *J. nigrina* is known only as far east in California as the McCloud River drainage in northwestern Shasta County and does not occur in the Sierra Nevada.

Distribution

Historical museum records place the species in southern Sonoma and Napa Counties, California, in the north San Pablo Bay watershed. The southernmost populations previously documented were from Salmon Creek and nearby Occidental in Pacific drainages of western Sonoma County (Henderson 1932). Taylor (1981) noted that the population in Salmon Creek was presumed extirpated. However, an observation record in iNaturalist (https://www.inaturalist.org/observations/11249251) has documented an extant population in Salmon Creek, an observation we have confirmed; this record and others from the area indicate that isolated populations in southern Sonoma and Napa Counties are still extant.

Common name

The common name for this species is the Black Juga (Turgeon *et al.* 1988, 1998; Frest & Johannes 1995b, 2010; Johnson *et al.* 2013). Synonyms have been referred to as the Shasta Juga (*J.* (*J.*) *silicula shastaensis*), Chace Juga (*J. chacei*), and Redwood Juga (*J. orickensis*) (Frest & Johannes 1993, 2005, 2010; Johannes 2013a; Johnson *et al.* 2013). The OTU referred to as *J.* (*O.*) *nigrina* (Frest & Johannes 1995b = Black Juga) from the Upper Sacramento System is a mixture of true *J. nigrina* and *J. douglasi* sp. nov. as circumscribed here.

Juga occata (Hinds, 1844)
Figs 25–26

Melania occata Hinds, 1844: 9.
Goniobasis acutifilosa var. *siskiyouensis* Pilsbry, 1899: 65–66.
Goniobasis acutifilosa pittensis Henderson, 1935a: 134, pl. 4 fig. 11.

Melania occata – Hinds 1845: 56–57, pl. 15 fig. 5.
Melania shastaensis – Reeve 1860: unpaginated, species 318, pl. 44 fig. 318.
Goniobasis acutifilosa pittensis – Henderson 1936b, pl. 2 fig. 11.
Juga (*Calibasis*) *occata* – Burch & Tottenham 1980: 152, fig. 451. — Burch 1982: 41, fig. 451; 1989: 152, fig. 451. — Frest & Johannes 1993: 61; 1995b: 38; 2010: 10, 44, fig. 2e. — Furnish 2007: 16, fig. 6, above right. — Campbell *et al.* 2016: 160.
Juga (*Calibasis*) *acutifilosa siskiyouensis* – Burch & Tottenham 1980: 152. — Burch 1982: 41; 1989: 152.
Juga (*Calibasis*) *acutifilosa pittensis* – Burch & Tottenham 1980: 152. — Burch 1982: 41; 1989: 152.
Juga occata – Turgeon *et al.* 1988: 65; 1998: 67. — Johannes & Clark 2016: 24. — Johnson *et al.* 2013: 282. — Strong & Whelan 2019: 89, fig. 4m–q.
Juga (*Calibasis*) *acutifilosa* – Frest & Johannes 1993: 61 (in part); 1995b: 37 (in part); 2000a: 283 (in part); 2005: 160 (in part); 2010: 9, 22 (in part). — Furnish 2007: 14, fig. 6, above left.
Juga (*Calibasis*) n. sp. 1 – Frest & Johannes 1995b: 38 (in part).
Juga (*Calibasis*) OTU 3 – Campbell *et al.* 2016: 160.
Juga (*Calibasis*) OTU 4 – Campbell *et al.* 2016: 160.
Juga (*Calibasis*) OTU 5 – Campbell *et al.* 2016: 160.

Material examined

***Melania occata* Hinds, 1844**

USA • 1 spm (possible syntype, Fig. 25A); "River Sacramento, California"; R.B. Hinds leg.; NHMUK 4.9.23.34.

Lectotype of *Goniobasis acutifilosa* var. *siskiyouensis* Pilsbry, 1899 (designated by Baker 1964: 187)

USA • "Headwaters of Fall River, S.-E. [southeast] Siskiyou Co."; R.C. McGregor leg.; ANSP 73508.

Paralectotypes of *Goniobasis acutifilosa* var. *siskiyouensis* Pilsbry, 1899 (Fig. 25B)

USA • 90 spms; same collection data as for lectotype; ANSP 466291 (ex ANSP 73508).

Holotype of *Goniobasis acutifilosa pittensis* Henderson, 1935 (Fig. 25C)

USA • "Fall River Mills, on Pitt [sic, Pit] River, California"; Ellsworth Bethel leg.; UCM 12080a.

Paratypes of *Goniobasis acutifilosa pittensis* Henderson, 1935

USA • 2 spms; same collection data as for holotype; UCM 12080b.

Other material examined

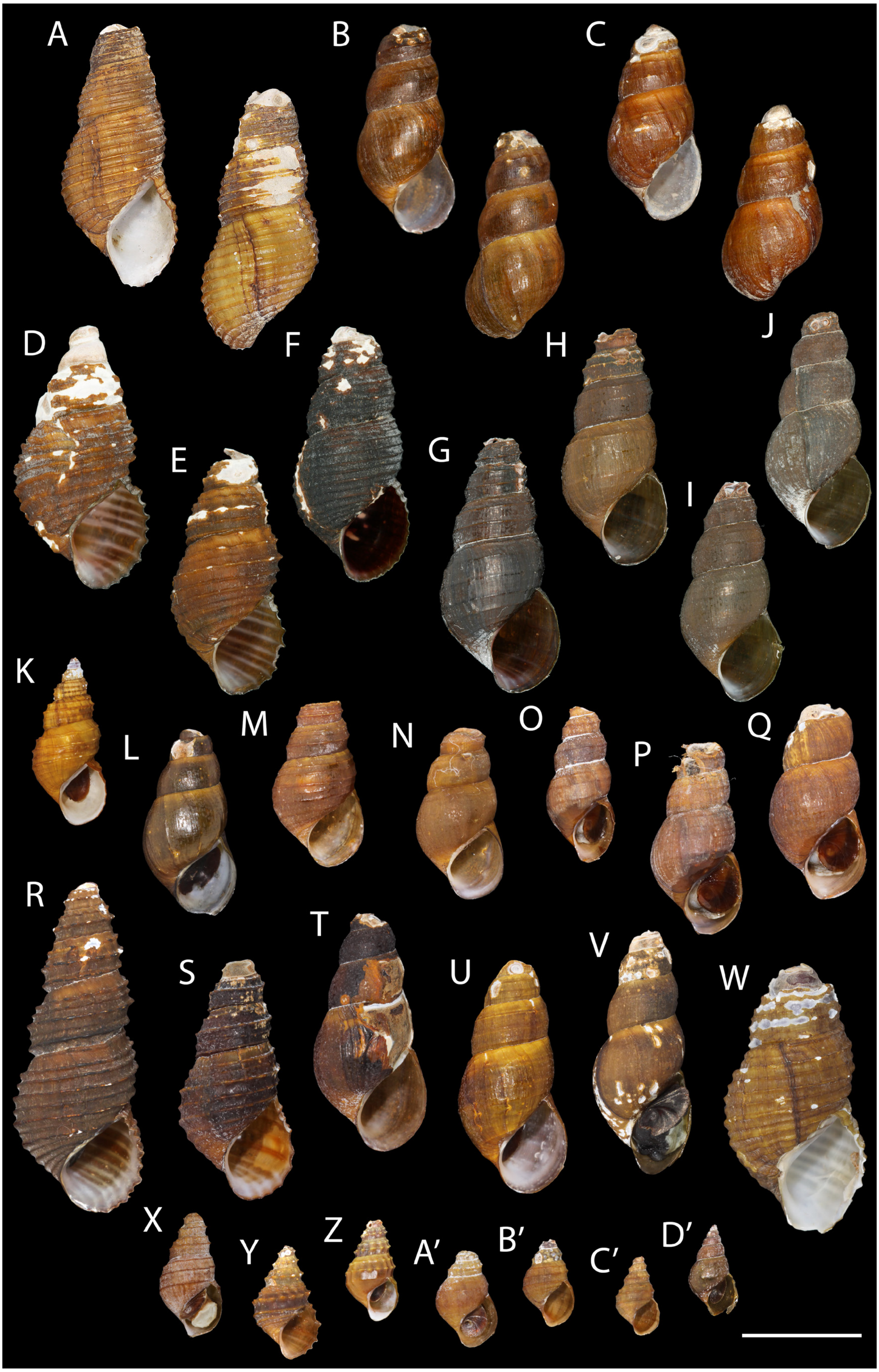
48 lots, 898 specimens, of which 21 were sequenced.

USA – **California** • 5 spms; Lassen Co., Davis Creek, Lassen NF, above FS22; 40.8325, -121.1183; 1 Sep. 2007; T. Grace leg.; UF 520312 • 54 spms; Lassen Co., Lassen Natl Forest, Davis Creek, on FS Rd 22; [40.8375, -121.1183]; 5 Jun. 2001; USFS Lassen Natl Forest Mollusk Survey 2001; CASIZ 166015 • 39 spms; Lassen Co., Lassen Natl Forest, Davis Creek, on FS Rd 22 [= FS Rd 35N05]; [40.8375, -121.1183]; 5 Jun. 2001; USFS Lassen Natl Forest Mollusk Survey 2001; CASIZ 165958 • 199 spms; Lassen Co., Lassen Natl Forest, Russell Dairy Spring, on 35N85 [= FS Rd 35N05]; [40.8277, -121.0281]; 2001; USFS Lassen Natl Forest Mollusk Survey 2001; CASIZ 166008 • 35 spms; Lassen Co., Russell Dairy Spring Run, Lassen NF, FS22 and 34N2, S side of road; 40.8253, -121.0268; 1 Sep. 2007; T. Grace leg.; UF 520309 • 12 spms; Modoc Co., Goose Lake; [41.9067, -120.3652]; 26 Sep. 1979; CASIZ 85267 • 2 spms; Modoc Co., Modoc Natl Forest, W end of Upper Rush Creek Campground, 3.2 km N of Lower Rush Creek Campground; [41.3015, -120.8461]; 8 Oct. 2007; T. Grace leg.; small spring run, among water cress and on rocks and twigs; UF 548146 • 1 spm; Sacramento Co., Sacramento; [38.5833, -121.5064]; Wetherby leg.; USNM 118914 • 2 spms; Shasta Co., Battle Creek, S boundary of county; [40.3921, -122.1787]; 1898; R.C. McGregor leg.; ANSP 73521 • 49 spms; Shasta Co., Baum Lake; 40.9345, -121.5485; 10 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413151 • 1 spm; same collection data as for preceding; GenBank: MK472482, MK464849, MK480916; USNM 1413146 • 1 spm; same collection data as for preceding; GenBank: MK472483, MK464850, MK480917; USNM 1413147 • 1 spm; same collection data as for preceding; GenBank: MK472484, MK464851, MK480918; USNM 1413148 • 1 spm; same collection data as for preceding; GenBank: MK472485, MK464852, MK480919; USNM 1413149 • 1 spm; same collection data as for preceding; GenBank: MK472486, MK464853, MK480920; USNM 1413150 • 34 spms; Shasta Co., Fall River at Spinner Fall Lodge; 41.0972, -121.5491; 11 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413084 • 1 spm; same collection data as for preceding; GenBank: MK472471, MK464838, MK480906; USNM 1413079 • 1 spm; same collection data as for preceding; GenBank: MK472472, MK464839, MK480907; USNM 1413080 • 1 spm; same collection data as for preceding; GenBank: MK472473, MK464840, MK480908; USNM 1413081 • 1 spm; same collection data as for preceding; GenBank: MK472474, MK464841, MK480909; USNM 1413082 • 1 spm; same collection data as for preceding; GenBank: MK472475, MK464842, MK480910; USNM 1413083 • 29 spms; Shasta Co., Hat Creek Park, Hat Creek, E of Burney at highway bridge; [40.9767, -121.5565]; 16 May 1978; J. Landye leg.; sand and emergent vegetation; USNM 892368 • 50 spms; Shasta Co., Hat Creek Park, Hat Creek, E of Burney at highway crossing; [40.9767, -121.5565]; 16 May 1978; J. Landye leg.; on sand and vegetation; USNM 892375 • 9 spms; Shasta Co., near border of Modoc County, N of McArthur, Big Lake, Crystal Springs; [41.1118, -121.4494]; 16 Jul. 1980; CASIZ 85274 • 55 spms; Shasta Co., Pit River at U.S. Hwy 299; 40.9807, -121.5473; 11 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413091 • 1 spm; same collection data as for preceding; GenBank: MK472476, MK464843, MK480911; USNM 1413085 • 1 spm; same collection data as for preceding; GenBank: MK472477, MK464844, MK480912; USNM 1413086 • 1 spm; same collection data as for preceding; GenBank: MK472478, MK464845; USNM 1413087 • 1 spm; same collection data as for preceding; GenBank: MK472479, MK464846, MK480913; USNM 1413088 • 1 spm; same collection data as for preceding; GenBank: MK472480, MK464847, MK480914; USNM 1413089 • 1 spm; same collection data as for preceding; GenBank: MK472481, MK464848, MK480915; USNM 1413090 • 57 spms; Shasta Co., Pit River, above Lake Britton and upstream from Hat Creek; [40.9805, -121.5476]; 16 May 1978; J. Landye leg.; in pockets along rocky shore in eddies; USNM 892363 • 16 spms; Shasta Co., Rainbow Springs, at headwaters of Fall Mill Creek on Lazy S Ranch adjacent to Thousand Springs Ranch; [41.1111, -121.5511]; 16 May 1978; J. Landye leg.; USNM 892373 • 75 spms; Shasta Co., Rainbow Springs, in headspring on Lazy S Ranch in Thousand Springs Area; [41.1111, -121.5511]; 16 May 1978; J. Landye leg.; on rocks; USNM 892380 • 15 spms; Shasta Co., S side of Hwy 299, Pit River, Lion's Club picnic area, W of Pit River camping grounds; 40.9866, -121.513; 1 Sep. 2007; T. Grace leg.; USNM 1111864 • 2 spms; Shasta Co., S side of Pit River, water source spring at Pacific Gas and Electric plant; [40.9896, -121.5021]; 16 May 1978; J. Landye leg.; USNM 892372 • 58 spms; Shasta Co., S side of Pit River, water source spring at Pacific Gas and Electric Plant #1; [40.9896, -121.5021]; 16 May 1978; J. Landye leg.; USNM 892365 • 46 spms; Shasta Co., Spring Creek at Spring Creek Rd; 41.1018, -121.5189; 11 Sep. 2015; E.E. Strong and P. Bouchet leg.; USNM 1413164 • 1 spm; same collection data as for preceding; GenBank: MK472487, MK464854, MK480921; USNM 1413159 • 1 spm; same collection data as for preceding; GenBank: MK472488, MK464855; USNM 1413160 • 1 spm; same collection data as for preceding; GenBank: MK472489, MK464856, MK480922; USNM 1413161 • 1 spm; same collection data as for preceding; GenBank: MK472490, MK464857, MK480923; USNM 1413162 • 1 spm; same collection data as for preceding; GenBank: MK472491, MK464858; USNM 1413163 • 18 spms; Sacramento River; Trask leg.; USNM 119157 • 2 spms; same collection data as for preceding; U.S. Exploring Expedition; USNM 16251 • 7 spms; Upper Sacramento; USNM 58982 • 3 spms; Sacramento River, headwaters [sic, likely mislocalized]; USNM 56463. – **Oregon** • 3 spms; Clatsop Co., Astoria [sic, mislocalized]; White leg.; USNM 126074.

Description

Shell. Thin to moderately thick, large, reaching ~2.75 cm in length; turriform, narrowly or broadly conical to cylindrical in shape, spire height moderate to tall (Fig. 25). Whorls somewhat flattened to convex or angulate with a subsutural ramp, suture weakly to deeply impressed. Aperture oval in shape, lip smooth to crenate, simple to slightly sinuous. Spiral sculpture absent or present, of thickened,

Fig. 25 (next page). Shell morphology of *Juga occata* (Hinds, 1844). **A–C**. Primary type material. **D–J**. Sequenced vouchers. **A**. *Melania occata* Hinds, 1844. Possible syntype, USNM 4.9.23.34. **B**. *Goniobasis acutifilosa* var. *siskiyouensis* Pilsbry, 1899. Lectotype, ANSP 73508. **C**. *Goniobasis acutifilosa pittensis* Henderson, 1935. Holotype, UCM 12080a. **D**. USNM 1413088. **E**. USNM 1413085. **F**. USNM 1413086. **G**. USNM 1413146. **H–J**. Near topotypic (*Goniobasis acutifilosa* var. *siskiyouensis* Pilsbry, 1899; *Goniobasis acutifilosa pittensis* Henderson, 1935). **H**. USNM 1413159. **I**. USNM 1413082. **J**. USNM 1413079. **K**. CASIZ 85267. **L**. UF 548146. **M–N**. Paralectotype, ANSP 466291 (ex ANSP 73508). **O–Q**. USNM 892373. **R**. USNM 892363. **S–T**. CASIZ 85274. **U**. USNM 892368. **V**. CASIZ 165958. **W**. ANSP 73521. **X**. USNM 892380. **Y**. USNM 892363. **Z**. USNM 1111864. **A'**. USNM 892372. **B'**. USNM 892368. **C'**. USNM 892375. **D'**. CASIZ 166015. Scale bar: 1 cm.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scalloped lirae, barely elevated to prominent, highly variable in number and sinuosity, dividing whorl into intervening flattened areas or grooves. Axial sculpture of fine, weakly opisthocyrt to sinuous growth lines; plications lacking. Shell dark to reddish brown, to yellowish green in color, occasionally with a lighter subsutural band; bands otherwise lacking. Interior of aperture light brown to white in color.

Radula. Rachidian squarish, slightly wider than tall, with weakly v-shaped lower margin and projecting outer corners; basal denticles lacking or vestigial (Fig. 26). Upper margin slightly concave with cutting edge bearing central, elongate conical cusp, and two to three stout, conical denticles on each side. Lateral teeth with prominent triangular cusp flanked by two to three inner and two to three outer, triangular denticles, and frequently a large, membranous outermost denticle. Marginal teeth with broadly rounded cutting edges and long, slender, flattened shafts with membranous flanges along inner and outer edges. Narrow inner flanges along distal third to quarter of inner marginal teeth and distal two-thirds of outer marginal teeth; broad outer flanges extending almost to tooth bases. Inner marginal teeth with three to four and outer marginal teeth with four to five flattened denticles.

Distribution and ecology

In spring-fed creeks to large rivers and lakes, currently restricted to the Pit River system in Lassen, Shasta, and Modoc Counties of northern California (Fig. 21C).

Remarks

Taylor (1981) emended the type locality of *Melania occata* to "Sacramento River, California (between American River and mouth)" given that the types were collected during the voyage of the HMS Sulphur which traveled no further upstream than the mouth of the American River. Museum records (e.g., UMMZ 40420, UMMZ 134037) indicate that the species once inhabited the Sacramento River and the lower part of the San Joaquin River watershed to Antioch, California (Henderson 1935a: 96), but was extirpated in the 19th century from the lower Sacramento River system owing to the effects of mining, pollution, and impoundment (Taylor 1981; Frest & Johannes 1993, 2010; Furnish 2007). Only three river miles of the Upper Sacramento River were unaffected by the Cantara chemical spill in 1991, but surveys found it already extirpated there as well; there are no museum records from the Upper Sacramento River since at least 1940 (Frest & Johannes 1993).

The type locality of *G. a.* var. *siskiyouensis* was indicated to be the headwaters of the Fall River in southeastern Siskiyou County. However, the Fall River is considered to originate at Thousand Springs in northeastern Shasta County. Bear Creek is a major tributary that joins the river near its origin and flows from southeastern Siskiyou County and may have been the source of the type material. Attempts to collect from Bear Creek by the authors were unsuccessful. The type locality of *G. a. pittensis* at the confluence of the Fall and Pit Rivers is now impounded, heavily polluted, and eutrophic from agricultural runoff and *Juga* no longer occurs there.

Juga occata has been considered a robust, heavily sculptured, large river form (Fig. 25D–F) (Burch & Tottenham 1980; Taylor 1981; Burch 1982, 1989; Frest & Johannes 1993, 2010), but molecular analyses indicate that this form is conspecific with less heavily sculptured populations that occur in lakes and spring-fed creeks (Strong & Whelan 2019). This includes near topotypic specimens (Fig. 25H–J) of *Goniobasis acutifilosa* var. *siskiyouensis* and *G. a. pittensis*. The classifications of Burch & Tottenham (1980) and Burch (1982, 1989) recognized these two subspecies as valid, but recent classifications (Turgeon *et al.* 1988, 1998; Johnson *et al.* 2013) did not consider the rank of subspecies. Frest & Johannes (2010) followed Taylor (1981) in synonymizing *siskiyouensis* with *J. acutifilosa*, and *pittensis* with *J. occata*, while Campbell *et al.* (2016: supp. file 1) synonymized both with *occata*.

Distribution

The main part of the distribution of *Juga occata* lies in southern Pit River drainages in Shasta and Lassen Counties where it overlaps with *J. douglasi* sp. nov., although individuals of the two species are rarely found in syntopy; only three lots with mixtures of the two were found in the USNM collections, and one species is always numerically dominant [USNM 1111864, USNM 1665623 (ex USNM 1111864); USNM 892372, USNM 1665624 (ex USNM 892372); USNM 892373, USNM 1665622 (ex USNM 892373)]. In contrast to *J. douglasi*, juveniles of *occata* are lirate, although not always prominently so, and erosion frequently obscures details of the spire; the spire angle in *occata* is also generally broader and the suture less impressed (Fig. 25X–D'). Sequenced specimens from two sites sampled by Campbell

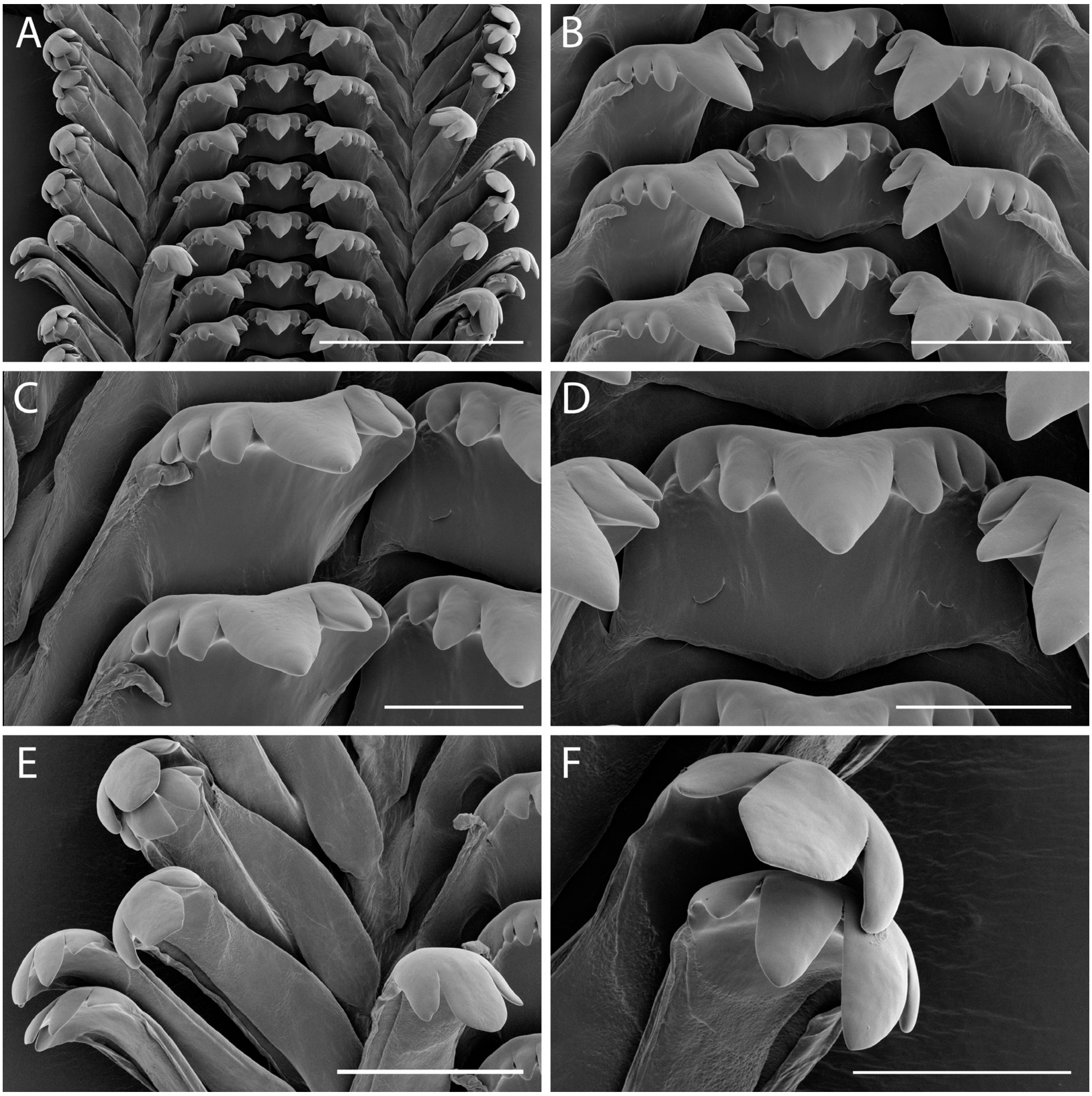

Fig. 26. Radular morphology of *Juga occata* (Hinds, 1844) (USNM 1413085). **A**. View of the anterior radular ribbon. **B**. Detail of cutting edge of rachidian and lateral teeth. **C**. Detail of lateral teeth cusps. **D**. Detail of rachidian cusps. **E**. Inner and outer marginal teeth. **F**. Detail of inner and outer marginal teeth cusps. Scale bars: A = 300 µm; B, E = 100 µm; C–D, F = 50 µm.

et al. (2016) and lirate museum specimens collected nearby (UF 520309, UF 520312, CASIZ 165958, CASIZ 166008, CASIZ 166015) confirm that the current range of *occata* extends as far south as central western Lassen County. If reliable, one historical lot (ANSP 73521) collected in the late 19th century from Battle Creek along the southern border of Shasta County indicates that the well-sculptured form also extended into smaller tributaries of the Sacramento River. Most historical lots from the lower Sacramento and San Joaquin Rivers, including the types, are poorly localized specimens of the typical, sculptured, large river form. We could find no evidence of early teleoconchs with the characteristic lirae south of the Pit watershed and, thus, records in the Sierra Nevada are tentatively hypothesized to represent *Juga douglasi*. However, given the range of morphological variation seen in species of *Juga*, it is possible that populations from the Sierra Nevada represent mixtures of *J. occata* and *J. douglasi*, or an as yet undescribed form.

Common name

The common name for this species is the Topaz Juga (Frest & Johannes 1993), erroneously referred to as the Scalloped Juga by Turgeon *et al.* (1988, 1998), which was followed by Frest & Johannes (2010) and Johnson *et al.* (2013) (see *J. acutifilosa*, above). A composite species comprised of *J. acutifilosa* and *J. occata* as circumscribed herein has been referred to as the Willow Creek Juga (= *Juga* (*Calibasis*) n. sp. 1; Frest & Johannes 1995b).

The fossil record of Juga H. & A. Adams, 1854

Given that names of fossil taxa described from late Pliocene to Pleistocene (Blancan) age might be applicable to Recent species, several observations on these forms are relevant here. Taylor (1966) was the first to revise the fossil taxa attributed to *Juga* in the Blancan fauna of North America and recognized *J. kettlemanensis kettlemanensis* (Arnold, 1909), *J. k. woodringi* (Pilsbry, 1934), *J. chrysopylica* Taylor, 1966 and *J. arnoldiana* (Pilsbry, 1934). At the same time, he established the subgeneric classification of *Juga* based on the ontogeny of teleoconch sculpture with *J. chrysopylica* as the type of the extinct subgenus *Idabasis*. Given the implications of the molecular analyses for the subgeneric classification of extant forms (Strong & Whelan 2019), we infer that subgeneric distinctions based on shell sculpture similarly would not be meaningful for the fossils and have here synonymized *Idabasis* with *Juga*. Likewise, we consider recognition of subspecies of *J. kettlemanensis* (e.g., Pilsbry 1934; Taylor 1966; Frest & Johannes 2010) to be unjustified and recommend synonymizing *J. k. woodringi* with *kettlemanensis*. Furthermore, we consider none of these nominal fossil species to be conspecific with any in the modern fauna and thus none of these names should be considered as available for one of the Recent species, including those described here as new. In addition to the four fossil species treated by Taylor (1966), Frest & Johannes (2010) included *J. sculptilis* (Meek, 1870) and *J. subsculptilis* (Meek, 1870) as valid species of Blancan age. However, we follow Taylor (1975b, and references therein) who indicated the species not to be of Blancan age but of early or middle Pliocene age, and who considered *J. sculptilis* to be a synonym of *J. subsculptilis*.

Nomina nuda and taxa excluded from Juga H. & A. Adams, 1854

Frest & Johannes (2010: table 6) provided a list of names that are "invalid" or have been incorrectly used in combination with the genus-group name *Juga*. However, they included several names that have not been used in combination with *Juga* but were simply described from the West Coast of North America in genera that are now considered to be pleurocerids or viviparids. They also summarized incorrect subsequent spellings, lapsus calami, incorrect author attributions, and nomina nuda; while some are synonyms and hence not taxonomically valid, nomina nuda and incorrect subsequent spellings are not available names and hence cannot be taxonomically invalid. To their list we make the following additions and corrections.

***Melania buschiana* Reeve, 1860**

This species was established by Reeve (1860) based on material said to be from California. Carpenter (1872) included it on his list of mollusks from western North America and noted that it resembled the young of *Melania scipio* Gould, 1847. As noted by Graf (2001), Tryon (1873: 340) included it on his list of "Doubtful and Spurious Species" and considered it to be of East Indian provenance. Both species are now in the synonymy of *Stenomelania aspirans* (Hinds, 1844) (Thiaridae) (Starmühlner 1993). This species was omitted by Frest & Johannes (2010).

***Goniobasis columbiensis* Whiteaves, 1905**

Frest & Johannes (2010) treated this nominal species elsewhere in their text but omitted it from their list of taxa incorrectly assigned to *Juga*. It was described from "headwaters of the Columbia River, at Upper Columbia Lake, in the East Kootenay District of British Columbia" (Whiteaves 1905: 61–62, pl. 2 figs 11–12). Attempts to recollect it at the type locality and nearby sites were unsuccessful (Frest & Johannes 2010), and it is known only from the type material (Fig. 27A). It is considered a mislocalized specimen of the eastern North American pleurocerid, *Elimia livescens* (Menke, 1830) (Walker 1918; Goodrich 1937, 1942; LaRocque 1953; Frest & Johannes 2010).

***Anculosa fusca* Haldeman, 1841**

This species was described from "Oregon" in the genus *Anculosa* Say, 1821, a junior synonym of *Leptoxis* Rafinesque, 1819 (Pleuroceridae), where it was retained by Brot (1862, 1868). It was included by Graf (2001) but from early on (e.g., Cooper 1867) was recognized to belong to the genus *Fluminicola*, where it remains today (Hershler & Frest 1996). It was omitted by Frest & Johannes (2010).

"*Goniobasis plicifera* var. *leai* Hemphill, 1890"

This was correctly listed by Frest & Johannes (2010) as a nomen nudum, but only on the authority of Coan & Roth (1987). This name was listed in Hemphill's (1890: 18) catalogue of North American shells for sale as originating from "Oregon". Taylor (1975a) included it as *Juga leai* with no indication that it was not an available name. Wu & Brandauer (1982) listed "cotypes" UCM 17779 and UCM 17780 collected by H. Hemphill from the Willamette River in Oregon, which have no type status (Coan & Roth 1987). Given the locality, the specimens would be referable to *J. plicifera* as circumscribed here, not *J.* (*J.*) *plicifera oregonensis* as suggested by Frest & Johannes (2010).

"*Juga maluccinosa* Quoy"

One of the species originally included in the subgenus *Juga* by Adams & Adams (1854), this was listed as an extralimital cerithioidean by Frest & Johannes (2010) with no additional information. This is an incorrect subsequent spelling by Adams & Adams (1854) for *Melania moluccensis* Quoy & Gaimard, 1834, and is a synonym of *Stenomelania erosa* (Lesson, 1831) (Glaubrecht & Podlacha 2010).

***Anculotus nuttalii* Reeve, 1861**

Described from "Oregon", Hershler & Frest (1996) considered this to be an incorrect subsequent spelling of *nuttaliana* Lea, 1838. Reeve attributed the name *Anculotus nuttalii* to "Lea MS", and did not refer to *Paludina nuttaliana* I. Lea, 1838. The name is thus neither an incorrect subsequent spelling nor an emendation, but a newly established nominal species founded on its own type material. It was included by Graf (2001), who did not examine the type material. We follow Hershler & Frest (1996) in placing it in the synonymy of *Fluminicola nuttalianus* (Lithoglyphidae Tryon, 1866). *Anculotus* Conrad, 1834 is an incorrect subsequent spelling of *Anculosa.* This species was omitted by Frest & Johannes (2010).

"*Juga obruta* Lea"

One of the species originally included in the subgenus *Juga* by Adams & Adams (1854), this was incorrectly listed as a possible nomen nudum by Frest & Johannes (2010). This species was established without a locality as *Melania obruta* I. Lea & H.C. Lea, 1851 and was placed in the Hemisinidae P. Fischer & Crosse, 1891 as *Aylacostoma obrutum* by Berning (2020).

Goniobasis rubiginosa I. Lea, 1862

This name was established by Lea (1862: 270; 1863a: 333–334, pl. 38 fig. 193; 1863b: 155–156, pl. 38 fig. 193) based on two specimens sent to him by Wesley Newcomb, M.D., from "Oregon". Tryon (1864, 1865, 1866, 1873) considered the species to be valid, despite having seen specimens only from Lea's collection, and was confident they would be plicate if the initial whorls were not eroded (Tryon 1865: 244). Pilsbry (1899) also considered the species to be valid. Henderson (1929) identified two specimens as this species in a lot of eight from Ahtanum Creek, Union Gap, in Yakima County, Washington; the other specimens in the lot were identified as *Goniobasis draytonii*. Henderson (1936b: 274) later admitted that one of the specimens was quite young, and in the other the carina was evidently the "result of disease or injury". As mentioned above, the lot in question (UCM 15814) appears to be *J. bulbosa* as circumscribed herein and it does not resemble Lea's (1863a, 1863b: pl. 38 fig. 193) original illustration of *rubiginosa* (Fig. 27B). Frest & Johannes (1995a: 246) provided the common name "Rusty Juga", and listed *J.* (*J.*) *rubiginosa* among species of uncertain status but considered it a potentially valid species and local endemic of conservation concern owing to agricultural impacts in the Yakima Valley. Later, Frest & Johannes (2010: 6) indicated it could be *J. plicifera*, but again expressed doubts as to its identity as a *Juga*. Other authors have considered the species to be conspecific with *J. silicula* (Goodrich, 1942; Burch & Tottenham 1980; Burch 1982, 1989). J.P.E. Morrison annotated the label of the lectotype, USNM 119297 (Graf 2001; Fig. 27B), that the locality was incorrect, and was "probably North or South Carolina". Given that no *Juga* species are known to possess a single, prominent spiral keel, we agree with the interpretation of Morrison that this species is a mislocalized eastern North American pleurocerid. The paralectotype is filed under *Elimia symmetrica* (Haldeman, 1841) in the USNM collections. Three

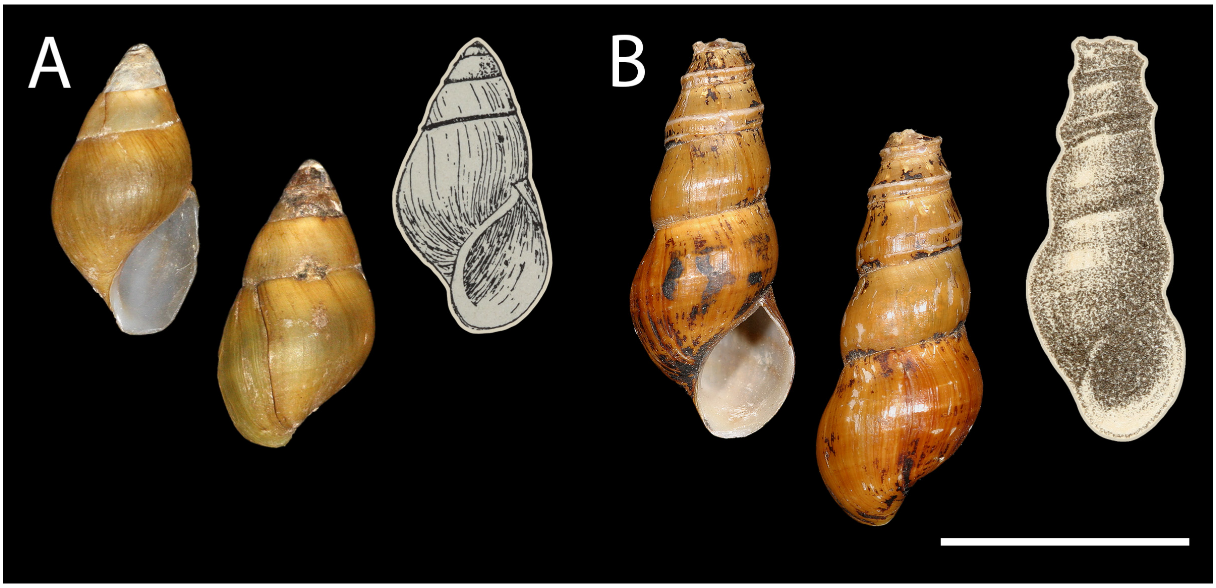

Fig. 27. Species erroneously attributed to *Juga* H. Adams & A. Adams, 1854. **A**. *Goniobasis columbiensis* Whiteaves, 1905, syntype (CMML 2042), original figure (Whiteaves 1905: pl. 2 fig. 11). **B**. *Goniobasis rubiginosa* I. Lea, 1862, lectotype (Graf 2001: 91) (USNM 119297), original figure (Lea 1863a, 1863b: pl. 38 fig. 193). Scale bar = 1 cm.

paralectotypes in the Newcomb collections at the Paleontological Research Institute (PRI 21730) appear conspecific with the specimens in the USNM.

"*Juga schiedeana* Phillipi" (sic, Philippi)

One of the species originally included in the subgenus *Juga* by Adams & Adams (1854), this was listed by Frest & Johannes (2010) as an extralimital cerithioidean with no additional information. It was established as *Melania schiedeana* Philippi, 1843 from Mexico and is currently placed in the Pachychilidae as *Pachychilus schiedeanus* (Thompson 2011).

"*Juga striata* Lea"

One of the species originally included in the subgenus *Juga* by Adams & Adams (1854), Frest & Johannes (2010) correctly indicated the status of *Melania striata* I. Lea, 1841 as a junior homonym [non *Melania striata* Sowerby, 1814 (nomen dubium); *Melania striata* Perry, 1811; *Melania striata* Schumacher, 1817], for which Lea (1842) himself provided the replacement name, *Melania striatula* I. Lea, 1842. However, the current taxonomic placement is *Elimia striatula* (Pleuroceridae) (Burch & Tottenham 1980; Burch 1982, 1989; Johnson *et al.* 2013; Bieler 2021), not *E. perstriata perstriata* (I. Lea, 1852) as suggested by Frest & Johannes (2010). The latter was the placement of "*Goniobasis striatula* Lea" of Wheeler (1912) (see Goodrich 1930: 17), which Graf (2001) reported as a nomen nudum.

"*Melania wahlamatensis* Lea"

This was correctly listed as a nomen nudum (Frest & Johannes 2010), but only on the authority of Graf (2001), who attributed it to Binney (1860) while noting that Hannibal (1912: 178) gave the authority as "'Lea,' Carpenter, 1857 (nude name)". Indeed, the first mention we can find is Carpenter (1857: 211, 325), who listed it from the Sacramento River and credited it to a draft manuscript of Gould on the U.S. Exploring Expedition shells. Given the locality, it would be referable to *J. occata*, not a "form of *plicifera*" as speculated by Frest & Johannes (2010). The name was listed by Taylor (1975a) as *Juga wahlamatensis* with no indication that it was not an available name.

Finally, the list of Frest & Johannes (2010; table 6) included two species described by Lea in the Viviparidae J.E. Gray, 1847, *Paludina virens* I. Lea, 1838 and *P. nuclea* I. Lea, 1838, from the "Wahlamat [sic, Willamette River], near its junction with the Columbia River", T. Nuttall leg. Both were placed in the pleurocerid genus *Leptoxis* by Haldeman (1847–1848: 5), which was followed by Brot (1862, 1868). Tryon (1873: 421) included them in his list of "Doubtful and Spurious Species" as *Amnicola*, and they were listed by Graf (2001) in his pleurocerid lexicon. However, both had already been recognized as members of *Fluminicola* Carpenter, 1864 (see Carpenter 1872), where they remain today (Hershler & Frest 1996). Frest & Johannes (2010) were correct that both are considered to represent Lithoglyphidae but neither has been used in combination with *Juga.*

Discussion

The present new systematic framework has revealed that almost all species previously considered valid were para- or polyphyletic grades of organization in shell morphology and ornament. This includes the many putative new species abandoned in open nomenclature by Frest & Johannes, most of which represent morphological variants of species already described. Only one of the species they recognized (Frest & Johannes 1995a; Johannes 2015) as new was a distinct, monophyletic OTU in molecular analyses (Strong & Whelan 2019), the Blue Mountain Juga = *J. caerulea* sp. nov. Of the species previously established, only the distinctive *J. newberryi* has no available synonyms.

Much like their island-like population genetic structure (Strong & Whelan 2019: 100), the propensity of morphologically recognizable forms to occupy discrete geographic areas has contributed to the proliferation of species-group names and recognized OTUs. For example, one of the species described here as new, *Juga canella* sp. nov., represents a mixture of at least five morphotypes each occupying a different drainage and previously hypothesized to each represent a distinct and undescribed new species (see chresonymy, above). This pattern also explains the challenge in allocating some poorly localized historical specimens, including types, to recognized species. The dense population sampling and sequencing effort of Strong & Whelan (2019) has alleviated this to some extent; however, surveys have failed to locate the source population(s) of the distinctive type material of *bulbosa*, which may no longer be extant (Strong & Frest 2007; Frest & Johannes 2010). By the same token, most species, even those whose morphological range intergrades with other species, include distinctive forms that cannot be confused for any other species (e.g., the low spired, broadly conical morph of *newberryi*, the "*bairdiana*" morph of *bulbosa*, and the heavily sculptured, large river morphs of *occata* and *plicifera*). However, the sequenced populations of *J. caerulea* sp. nov. and *J. douglasi* sp. nov. are rather simple, smooth, dark, lightly constructed, mostly without distinguishing sculpture; *J. acutifilosa*, *bulbosa*, *canella*, and *nigrina* all possess forms that have converged on this basic morphotype. In the absence of precise locality information or sequence data, many of these morphs cannot be reliably identified to species.

Given this complicated morphological landscape, it is unsurprising that the two most wide-ranging and morphologically variable species, *J. plicifera* and *J. nigrina*, are the most taxonomically complex. As circumscribed herein, they overlap in color, banding, and strength and persistence of spiral and axial sculpture, and as such, these two species and their many synonyms have been widely confused and variably interpreted. The molecular analyses of Strong & Whelan (2019) confirmed that the two species have allopatric distributions, with *plicifera* occurring in the Willamette River drainage and northwards, and *nigrina* occurring in the Umpqua River drainage and southwards. The break in their distribution coincides with the boundary between the Klamath and Oregonian biogeographic provinces for land and freshwater mollusks (*sensu* Frest & Johannes 2000a, 2000b) at the southern end of the Willamette River drainage and adjoining Pacific drainages. Despite the lack of discrete, diagnosable differences between the two, plications tend to be more strongly developed in *plicifera* and can extend farther down the shell than in *nigrina*, sometimes reaching the body whorl. The shell of *plicifera* is typically more heavily constructed than *nigrina*, but large river forms of both species are thicker and more sculptured than those found in small creeks and streams. Larger, more robust specimens of *nigrina* with more prominent sculpture are usually found in larger rivers in the northern part of the range, while specimens from the southern part of the range are more lightly constructed, often lighter in color, and typically lack plications (Fig. 23Y–D').

While the molecular analyses of Strong & Whelan (2019) clarified the diversity of species of *Juga*, mitochondrial and nuclear gene trees did not agree on the relationships between them. Additional sequencing effort with more nuclear loci is needed to resolve internal nodes and to clarify the identities of the Sierra Nevada populations. Population genomics could better illuminate intraspecific relationships among shell morphs and patterns of gene flow across the landscape. Surveys are also needed to clarify the status of isolated observation records in the eastern Columbia Gorge. Furthermore, many populations have not been revisited in years if not decades and may be no longer extant. Efforts by the authors to recollect some populations that had been sampled by Frest & Johannes were unsuccessful, evidently the victim of drought, trampling from grazing, eutrophication, and other human-mediated impacts.

Conservation

A reliable and accurate taxonomic framework is essential for meaningful interpretations and comparisons of past, present, and future anatomical, physiological, ecological, biogeographical, and life history studies, which are all needed to devise effective conservation management plans. Both locally and globally, freshwater mollusks are facing increasing threats from human-mediated impacts, including climate change, and rank among the most threatened animals on Earth with the highest rates of modern extinction (Johnson *et al.* 2013). However, understanding of their biodiversity continues to be plagued by significant knowledge shortfalls (Lydeard *et al.* 2004; Strong *et al.* 2008; Johnson *et al.* 2013; Böhm *et al.* 2021; Lopes-Lima *et al.* 2021). Knowledge shortfalls are now even more pronounced for *Juga*, as the new systematic framework has redrawn species boundaries to cut across almost all species as previously defined. The implications are that much of the conventional knowledge of *Juga* species, what little we do know, in terms of their life histories, distributions, population size and structure, ecological tolerances, and habitat preferences will require reassessment. Basic demographic, life history, and ecological information is essential for updating the conservation status of these species.

Despite the need to generate conservation-relevant data on the species recognized here, some generalizations are possible. *Juga* species are found predominantly in groundwater-dependent habitats including springs, spring runs, and spring-fed creeks. These fragile ecosystems face increasing threats from climate change as temperatures increase, precipitation declines, and droughts and wildfires become more severe (Johannes 2015). These threats are compounding other human-mediated impacts from pollution (urban runoff, agriculture), eutrophication, recreation, water diversions and groundwater extraction (irrigation and livestock), dam construction, sedimentation, and habitat fragmentation and loss. Many populations have declined in size, and for some species (e.g., *J. occata*) the range has contracted markedly (Taylor 1981; Duncan 2005; Furnish 2007; Frest & Johannes 2010; Blackburn *et al.* 2021). However, some entities thought to require federal protection are now known to be part of much wider ranging species (e.g., the undescribed Basalt Juga), which may make management actions less necessary. On the other hand, one newly described species, *J. caerulea* sp. nov., has an extremely restricted current range and may warrant immediate protection.

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