A new genus of chemosymbiotic vesicomyid bivalves from the Oligocene of western North America

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We describe a new genus of the chemosymbiotic bivalve family Vesicomyidae, *Squiresica*, for two Oligocene species, previously assigned to *Archivesica*, from western North America. *Squiresica* is characterized by a small and weakly inflated shell, a small to nearly absent pallial sinus, an *Archivesica*-like hinge dentition, with an indistinct to well incised lunular incision. Two species are assigned to this new genus: the type species, *S. knapptonensis* from western Washington State, USA, and *S. marincovichi* from Oligocene strata of Alaska, USA. *Squiresica knapptonensis* had previously been described from the upper Oligocene of the Lincoln Creek Formation; further specimens are here reported from a newly discovered seep deposit in the lower Oligocene part of the Lincoln Creek Formation.

Key words: Bivalvia, Vesicomyidae, cold-seep, deep-water, Oligocene, North America.

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Introduction

The Vesicomyidae is a species-rich family of chemosymbiotic marine bivalves found worldwide in deeper water, especially in reducing habitats such as hydrothermal vents, methane-seeps, and decaying whale carcasses (Boss and Turner 1980; Sasaki et al. 2005; Cosel 2006; Krylova and Sahling 2010). The larger vesicomyids of the subfamily Pliocardiinae all live in a symbiotic association with sulfur-oxidizing bacteria housed in their hypertrophied gills, from which they derive most, if not all, of their nutrition (Felbeck et al. 1981; Arp et al. 1984; Childress et al. 1993; Fisher 1995). Most species live half buried in soft substrates and simultaneously mine hydrogen sulfide from sediment pore water and extract oxygen from the water column (Dubilier et al. 2008; Krylova and Sahling 2010). The only exceptions are the hydrothermal vent species *Turneroconcha magnifica* (Boss and Turner, 1980), which lives on pillow lavas and extents its foot into the crevices between pillows to access the diffusing hydrogen sulfide (Krylova and Sahling 2020) and *Laubiericoncha puertodeseadoi* Signorelli and Pastorino, 2015, of which empty shells have been found at active hydrothermal sites in the South Atlantic Ocean (Linse et al. 2020).

The family has an extensive fossil record, extending back to the middle Eocene, with the oldest record coming from Washington State (Goedert and Squires 1990; Amano and Kiel 2007). Many fossil species have been described, though the generic assignments of some of them remain contentious because their shell characters are insufficiently known. One particularly troublesome genus is *Archivesica* Dall, 1908, based on the large, extant *Archivesica gigas* Dall, 1896. Numerous fossil species of Eocene to Pleistocene age have been assigned to it (Amano and Kiel 2007, 2010; Amano and Suzuki 2010; Kiel and Taviani 2017; Hansen et al. 2017; Kiel et al. 2020), at some point even the as-yet oldest vesicomyid, though that species was subsequently considered as more likely belonging to *Pliocardia* (Amano and Kiel 2007, 2012). In molecular phylogenetic studies, species clustering with *Archivesica gigas* are often referred to as the "*gigas*"-group and include species assigned in other studies to the genera *Archivesica*, *Phreagena* Woodring, 1938, *Laubiericoncha* Cosel and Olu, 2008, *Ectenagena* Woodring, 1938, and *Akebiconcha* Kuroda, 1943 (Audzijonyte et al. 2012; Decker et al. 2012; Johnson et al. 2017).

Ongoing phylogenetic work on the Vesicomyidae using morphologic characters, by us, indicates that two small-sized, fossil species previously assigned to *Archivesica*, *A. knapptonensis* Amano and Kiel, 2007 and *A. marincovichi*

Kiel and Amano, 2010, are closely related to each other, but are quite distant to the type species *Archivesica gigas*. A re-examination of the shell characters of these two species indeed revealed several features inconsistent with those of *A. gigas*, including their small size, slender shape, and often the presence of a lunular incision. A new genus is here introduced for these two species, and additional material of *A. knapptonensis* from a recently discovered late early Oligocene seep deposit in western Washington State, USA, is reported.

Institutional abbreviations.—NRM, Swedish Museum of Natural History, Stockholm, Sweden; UCMP, University of California, Museum of Paleontology, Berkeley, USA; USNM, Smithsonian Museum of Natural History, Washington, DC, USA.

Other abbreviations.—H, height; L, length; W, width.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:C706ED1A-0393-4414-9BDA-CC0AF38FCF56

Material and methods

The new seep deposit was discovered by JLG and SK in August 2019 in bedrock of the Lincoln Creek Formation on the east side of the West Fork Satsop River, Grays Harbor County, Washington (WGS84 datum GPS coordinates: 47.268247° N, 123.562015° W, Fig. 1). Based on Rau's stratigraphy of the West Fork Satsop section (Rau 1966) and the magnetostratigraphy of the Canyon River section of Prothero and Armentrout (1985), the deposit was found in the upper lower Oligocene part of the Lincoln Creek Formation (at C10r, around 31 million years ago).

The nodular, fossiliferous limestone block measures at least 1.5 × 1.0 m. In addition to the vesicomyid species reported here, we collected two large specimens of *Acharax* sp. (height 30 mm), common mussels resembling *Bathymodiolus* (sensu lato) *satsopensis* Kiel and Amano, 2013 (up to 40 mm length), *Conchocele* sp. (30 mm long), a small *Lucinoma acutilineata* Conrad, 1849, a fragment probably belonging to a species of large lucinid (cf. *Elliptiolucina*), the naticid *Polinices washingtonensis* Weaver, 1916, and poorly preserved fragments possibly belonging to *Provanna antiqua* Squires, 1995. Specimens were mechanically extracted from the rock matrix using hammers and chisels, and pneumatic fossil preparation tools. Specimens were coated with ammonium chloride prior to photography.

Systematic palaeontology

Class Bivalvia Linnaeus, 1758

Family Vesicomyidae Dall and Simpson, 1901

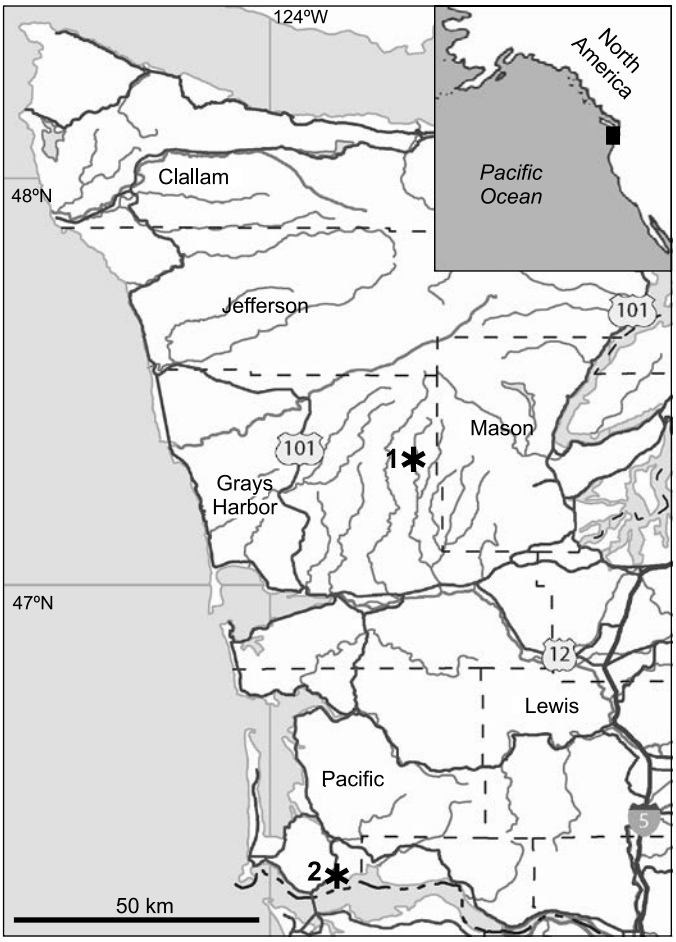

Fig. 1. Map showing location of the studied localities in North America (inset) and western Washington State, USA. 1, the new West Fork Satsop seep deposit; 2, Knappton, the type locality of *Squiresica knapptonensis*.

Genus *Squiresica* nov.

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Type species: *Archivesica knapptonensis* Amano and Kiel, 2007, Oligocene part of the Lincoln Creek Formation, western Washington State, USA.

Species included: The type species and *Archivesica marincovichi* Kiel and Amano, 2010, from the Oligocene Kulthieth Formation in Alaska, USA.

Etymology: In honor of Richard L. Squires (Northridge, USA), who pioneered work on fossil vesicomyids from the US West Coast, and the ending of the related vesicomyid genus *Archivesica*.

Diagnosis.—Shell small (L up to 50 mm), elongate, weak to moderately inflated; escutcheon narrow, lunular incision indistinct to well incised, narrow to moderately broad; umbo elevated. Pallial line impressed anteriorly; pallial sinus small and shallow, or even just a slight forward sloping of the pallial line before meeting the posterior adductor muscle scar; hinge plate moderately broad, with thick cardinal 1 radiating anteriorly, cardinal 3a thin, short and parallel to shell margin or reduced, cardinal 3b small, pointing posteroventrally, with parallel or somewhat diverging raised edges; subumbonal pit elongate or deep.

Table 1. Comparison of diagnosable features of the pliocardiin genera discussed herein. Shell size describes the length (L) of the shell: small (S) L <50 mm, medium (M) L 50–120 mm, large (L) L >120 mm. Cardinal 3a has three different character states, it can be separated from cardinal 3b, fused with 3b or reduced which refers to an absent state.

Genus	Shell size	Umbo	Inflation	Posterior ridge	Pallial sinus	Escutcheon	Lunular incision	Cardinal 3a	Cardinal 3b
Archivesica Dall, 1908	M–L	low	strong	absent	present	absent	absent	separate	semi-triangular shape
Austrogena Krylova, Sellanes, Valdés and D'Elía, 2014	S	elevated	moderate	present	absent	present	present	reduced	broad
Hubertschenckia Takeda, 1953	M	elevated	moderate	absent	small indentation	present	absent	fused	oblique state
Isorropodon Cosel and Olu, 2008	S	elevated	strong	absent	absent	present	present	fused	semi-triangular shape
Pleurophopsis Van Winkle, 1919	M	low	moderate	absent	absent	absent	absent	reduced	semi-triangular shape
Pliocardia Woodring, 1925	S	elevated	strong	present	small indentation	present	present	fused	semi-triangular shape
Squiresica gen. nov.	S	elevated	strong	absent	small indentation	present	present	separate	oblique state

Remarks.—The new genus *Squiresica* has an *Archivesica*-like hinge dentition, but differs from *Archivesica* by (i) being much smaller, (ii) having an elevated umbo with strongly coiled beaks, (iii) its pallial sinus, which is only a small indentation, whereas *Archivesica* in general, and the type species *A. gigas* in particular, has a large and broad pallial sinus, (iv) possessing an escutcheon and typically a lunular incision, both of which are absent from *Archivesica gigas*. *Archivesica redwoodia* Kiel and Amano, 2010, a small species from Alaska, shares the small pallial sinus with the species of *Squiresica*, but differs by having a long anterior cardinal 3a parallel to the dorsal shell margin, a more ventrally pointing cardinal 3b, and a much broader and deeper pallial sinus (see Table 1 for comparison to other pliocardiin genera).

Austrogena nerudai Krylova, Sellanes, Valdés, and D'Elía, 2014, type species of *Austrogena* from the Southeastern Pacific, shares the presence of an escutcheon, a lunular incision, a subumbonal pit and an elongate cardinal 4b with species of *Squiresica*; however, it can be distinguished from these by the complete lack of a pallial sinus (Krylova et al. 2014). The oldest vesicomyid, "*Archivesica* cf. *tschudi*" from the middle Eocene of western Washington (Amano and Kiel 2007) is very small and *Archivesica*-like, but it has a low umbo and lacks a pallial sinus. *Hubertschenckia* Takeda, 1953, reaches 90 mm in length and is thus much larger than *Squiresica*. Further differences include the cardinal 3b, which points downwards or slightly anteriorly in *Hubertschenckia*, but posteriorly in *Squiresica*, and *Hubertschenckia* has a posterior nymphal ridge, absent in *Squiresica* (Takeda 1953; Amano and Kiel 2007). Other pliocardiins sharing the small sized shell with *Squiresica* are *Pliocardia* Woodring, 1925, and *Isorropodon* Sturany, 1896. Both genera have an elevated umbo and a lunular incision, but *Isorropodon* lacks a pallial sinus and *Pliocardia* has a posterior ridge (Sturany 1896; Woodring 1925; Cosel and Salas 2001; Krylova and Janssen 2006; Amano and Kiel 2007). *Isorropodon* is less elongate than *Squiresica*, and all cardinal teeth of *Isorropodon* are thin and more or less parallel to the dorsal shell margin (e.g., Cosel and Salas 2001), in contrast to the radiating teeth of *Squiresica*. *Pliocardia* is more rounded than *Squiresica*, it features a posterior ridge on the outside of the shell, lacking in *Squiresica*, and its cardinal 3b is shorter and more compressed than that of *Squiresica*. The Pleistocene Arctic species *Archivesica arctica* Hansen, Hoff, Sztybor, and Rasmussen, 2017, has stronger and more radiating teeth than the species of *Squiresica*, a very distinct, pointed pallial sinus, and reaches much larger size (55–67 mm compared to 40 mm in the species of *Squiresica*).

A further species that could potentially belong to *Squiresica* is *Pleurophopsis lithophagoides* Olsson, 1931, from the lower Oligocene of northern Peru (Olsson 1931). That species is notably smaller than most other species of *Pleurophopsis* Van Winkle, 1919 (see Kiel et al. 2020: table 1) but is in the size range of the species of *Squiresica*. It also has a similar elongate shape and is rather flat like *Squiresica knapptonensis*. The cardinal 3a of *Pleurophopsis lithophagoides* remains unknown, as well as the presence or absence of a pallial sinus (Olsson 1931; Kiel et al. 2020), and hence a potential assignment to *Squiresica* remains unresolved.

Stratigraphic and geographic range.—Oligocene, Pacific Coast of North America, from Alaska to Washington State.

Squiresica knapptonensis (Amano and Kiel, 2007) comb. nov.

Figs. 2, 3.

1993 *Calyptogena* (*Calyptogena*) *chinookensis* Squires and Goedert, 1991; Goedert and Squires 1993: 74, fig. 4.

2007 *Archivesica knapptonensis* sp. nov.; Amano and Kiel 2007: 284, figs. 30–43.

Type material: Fragment of right valve with preserved hinge dentition, length 13.5 mm+, height 7.0 mm, USNM 534954.

Type locality: LACMIP loc. 5843, beach terrace of the Columbia River near Knappton, Washington State, USA.

Type horizon: Upper Oligocene part of the Lincoln Creek Formation.

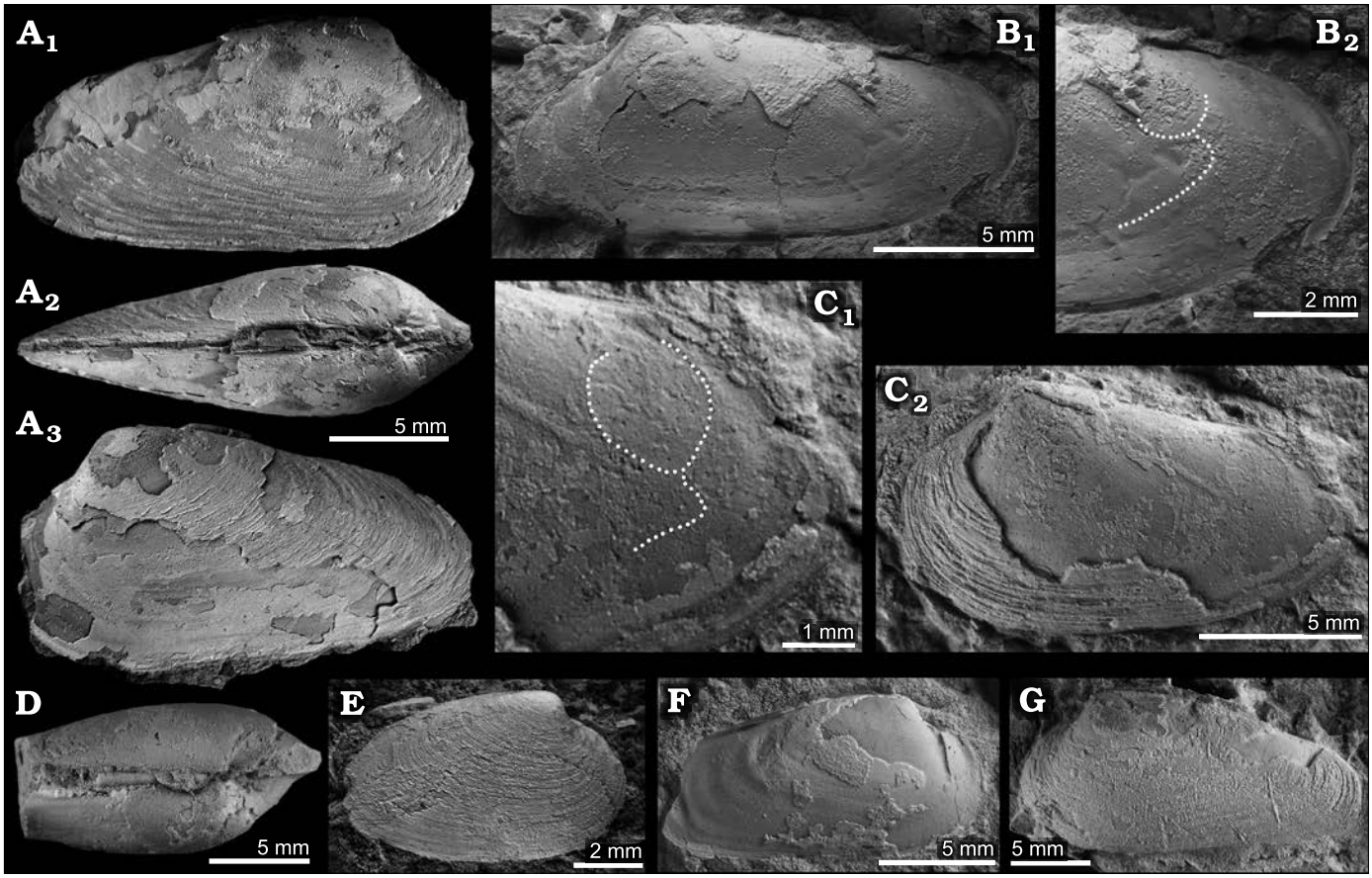
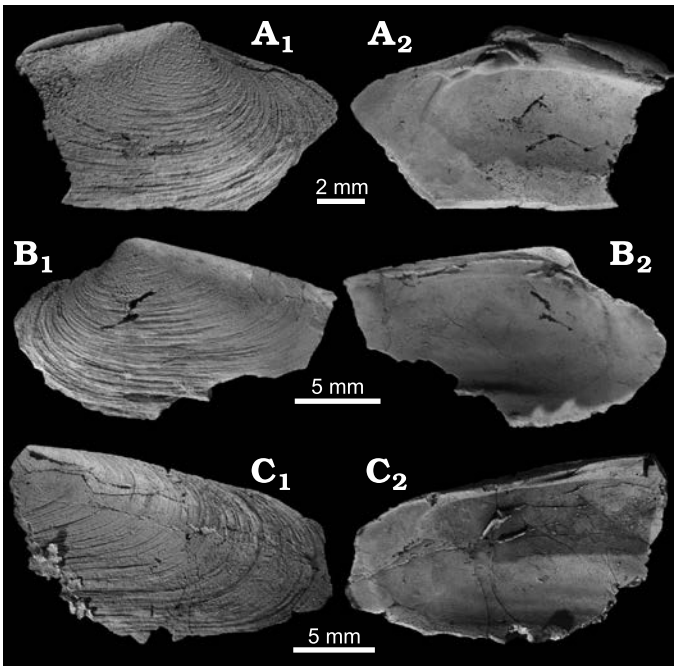


Fig. 2. The vesicomyid bivalve *Squiresica knapptonensis* (Amano and Kiel, 2007) from the West Fork Satsop seep deposit, lower Oligocene, Lincoln Creek Formation, western Washington, USA. **A**. NRM PAL Mo 195149, articulated specimen with partially preserved shell, in lateral (A_1, A_3) and dorsal (A_2) views. **B**. NRM PAL Mo 195150, left valve embedded in matrix, with partially preserved shell; B_2, close-up showing pallial line and anterior adductor muscle scar (dotted line). **C**. NRM PAL Mo 195151, left valve embedded in matrix, with partially preserved shell (C_2) and with posterior adductor muscle scar barely visible (dotted line in C_1). **D**. NRM PAL Mo 195153, articulated specimen showing inflation and ligament. **E**. NRM PAL Mo 195152, small specimen with fully preserved shell, view on outer shell surface. **F**. NRM PAL Mo 195154, right valve embedded in matrix, with partially preserved shell, showing pallial line and anterior adductor muscle scar. **G**. NRM PAL Mo 195155, left valve with mostly preserved shell.



Material.—Numerous specimens (figured: NRM PAL Mo 195149–195155) from the West Fork Satsop seep deposit, lower Oligocene, Lincoln Creek Formation, western Washington, USA.

Description.—Elongated, weakly inflated, small shell, reaching little over 20 mm in length, H/L-ratio 0.46–0.60, W/H-ratio 0.61–0.65; umbo slightly elevated and moderately coiled, positioned at anterior 20–25% of shell length; external ligament opisthodetic, occupying >60% of postero-dorsal margin; anterior adductor scar D-shaped, its posterior margin thick; posterior adductor scar nearly round; pallial line impressed anteriorly, commarginal, forming a small indentation right beneath posterior adductor scar.

Fig. 3. The vesicomyid bivalve *Squiresica knapptonensis* (Amano and Kiel, 2007) from the upper Oligocene part of the Lincoln Creek Formation at Knappton, along the Columbia River, western Washington, USA. **A**. Holotype USNM 534954, left valve showing external surface (A_1) and hinge (A_2). **B**. Paratype USNM 534956, left valve showing external surface (B_1) and hinge (B_2). **C**. USNM 534955, posterior part of a left valve showing external surface (C_1) and the posterior end of the nymphal ridge (C_2). All images (except C_2) from Amano and Kiel (2007).

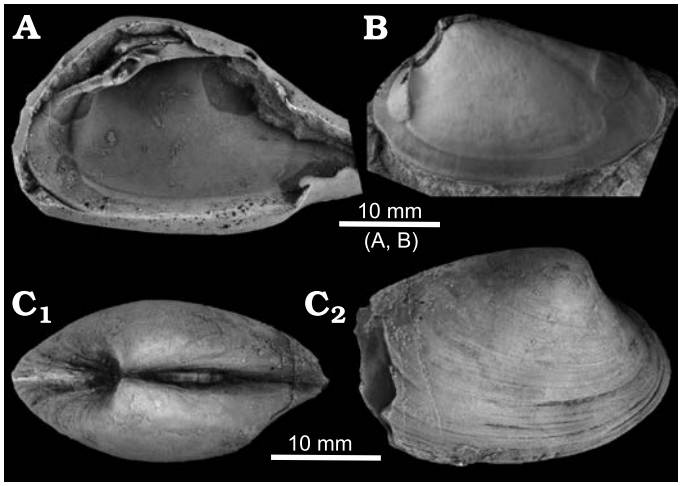


Fig. 4. The vesicomyid bivalve *Squiresica marincovichi* (Kiel and Amano, 2010), from the Oligocene Kulthieth Formation, Alaska, USA. **A**. Rubber peel of holotype UCMP 555221 showing internal features including hinge dentition of the right valve. **B**. Paratype UCMP 555223, internal mold of a left valve, showing adductor muscle scars and small pallial sinus. **C**. Paratype UCMP 555224, an articulated specimen showing inflation, lunular incision, and escutcheon (C_1) and external sculpture of right valve (C_2). All images from Kiel and Amano (2010).

Remarks.—Goedert and Squires (1993) reported *Calyptogena chinookensis* Squires and Goedert, 1991 from the Pysht and Makah formations along the northern coast of Washington state, and from the upper Oligocene part of the Lincoln Creek Formation on the southern side of Washington state. Among their illustrated specimens, that from the Lincoln Creek Formation (Goedert and Squires 1993: fig. 4) shows a lunular incision and a different hinge morphology than *C. chinookensis* and instead belongs to *Squiresica knapptonensis* (i.e., Amano and Kiel 2007). The newly collected material from the West Fork of Satsop River shows all characters possessed by specimens from the upper Oligocene type locality of *S. knapptonensis* and thus extends the stratigraphic range of this species down into the lower Oligocene.

The second species assigned here to the new genus, *Squiresica marincovichi* (Kiel and Amano 2010: 80–81, figs. 17–25) from the Oligocene Kulthieth Formation in Alaska, differs from *S. knapptonensis* by being less elongated, having a broader escutcheon, lacking irregular growth lines on the outer surface, and a less distinct subumbonal pit (see Fig. 4 for a re-illustration of the type material). *Squiresica marincovichi* reaches almost 40 mm in length and it thus notably larger than *S. knapptonensis*.

Stratigraphic and geographic range.—Oligocene, Lincoln Creek Formation, western Washington State, USA.

Concluding remarks

Regarding shell characters, the species of *Squiresica* share more with the geochronologically oldest vesicomyid, "*Pliocardia* cf. *tschudi*" (formerly identified as *Archivesica* cf. *tschudi*) than with the type species of *Archivesica*, *A. gigas*. Presently, *Squiresica* is restricted to Oligocene strata of the northeast Pacific region, with a potential extension to northern Peru (*Pleurophopsis lithophagoides*). Notably, no species assignable to *Squiresica* is known from the well-investigated fossil record of Japan, where the dominant vesicomyid at Oligocene seep deposits is the much larger (up to 90 mm long) genus *Hubertschenckia* (Majima et al. 2005; Amano and Kiel 2007, 2010, 2011; Amano et al. 2013, 2019). This emphasizes the differences among vesicomyids between eastern and western Pacific seep communities during Cenozoic times (Amano et al. 2019), contrary to the present-day situation with several vesicomyid species known from both sides of the North Pacific Ocean (Kojima et al. 2004; Audzijonyte et al. 2012). This is in remarkable contrast to the bathymodiolin mussels, the other major group of seep-inhabiting bivalves. At least one bathymodiolin species, "*Bathymodiolus*" *inouei* Amano and Jenkins, 2011, occurred in both Japan and Washington during the Oligocene (Amano and Jenkins 2011; Kiel and Amano 2013), but no bathymodiolin species is shared between the two regions today (Duperron 2010; Lorion et al. 2013; McCowin et al. 2020). Reasons for these contrasting patterns remain to be investigated.

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