New taxa, records, and data for vesicomyid bivalves from Cenozoic strata of the North Pacific region

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New discoveries of Cenozoic deep-water hydrocarbon seep deposits and continued collecting at previously documented sites in the North Pacific region have resulted in additional fossils of vesicomyid bivalves and necessitate a systematic review. We report five new vesicomyid species, including four species from western Washington State, USA: *Isorropodon humptulipsense* sp. nov. from middle to upper Eocene strata of the Humptulips Formation and the "Siltstone of unit B", the oldest record for *Isorropodon*, *Pleurophopsis thieli* sp. nov. from upper Eocene to lowermost Oligocene strata of the Lincoln Creek, Makah, and Pysht formations, and *Pliocardia*? *guthrieorum* sp. nov. and *Squiresica plana* sp. nov. from Oligocene strata of the Lincoln Creek and Pysht formations. The new species *Squiresica yooni* sp. nov. is from the Middle Miocene Duho Formation in South Korea. We report possibly the as-yet oldest *Vesicomya* from a lower Oligocene seep deposit in the Lincoln Creek Formation in western Washington. *Pliocardia kawadai* was previously only known from Lower to Middle Miocene strata in Japan; with our new record from the Lower to Middle Miocene Astoria Formation in western Washington, this species represents the first fossil vesicomyid species with a trans-Pacific distribution. The large and elongated *Pleurophopsis chinookensis* is restricted to upper Eocene strata; previous Oligocene records are shown to belong to other species.

Key words: Bivalvia, chemosymbiosis, deep-sea, Japan, South Korea, USA, Washington.

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Introduction

Vesicomyid bivalves are common in deep-water habitats around the world, especially around hydrothermal vents, hydrocarbon seeps, and sunken whale carcasses (Krylova and Sahling 2010). Most of them live in symbiosis with sulfide–oxidizing bacteria, hosted in their gills, from which they derive most of their nutrition (Fisher 1990). More than 100 extant species have been described, and more than 40 fossil species, ranging back in time to the middle Eocene (Amano and Kiel 2007; Krylova and Sahling 2010; Amano et al. 2022). However, there are still gaps in our understanding of taxonomic and phylogenetic relationships, especially among the geochronologically early members of the family.

Cenozoic deep-water strata of the North Pacific region proved to be particularly rich in vesicomyid fossils, including the oldest record of the family (Amano and Kiel 2007; Hryniewicz 2022). On the east coast of the North Pacific Ocean, most vesicomyid fossils are from western Washington State, USA (e.g., Goedert and Squires 1990, 1993; Squires and Goedert 1991; Goedert and Campbell 1995), with a few additional records from California (Crickmay 1929; Woodring 1938; Squires 1991; Squires and Gring 1996). Farther north, vesicomyid fossils are known from Alaska (Kanno 1971), including the oldest record of the genus *Calyptogena* (Amano and Kiel 2007; Kiel and Amano 2010). Along the western coast of the North Pacific, Japan has a rich and well-investigated record of fossil vesicomyids with 19 described species (Amano et al. 2013, 2019a). One species has been reported as *Calyptogena* cf. *elongata* from South Korea (Yoon 1976a) and there are some potential records described as species of *Macrocallista* Meek, 1876, from Miocene rocks of eastern Kamchatka (Krishtofovich 1969).

In the present contribution, we use extensive collections made in western Washington over the last few decades to describe new vesicomyid species and to clarify the identity of those previously described. Furthermore, the identity of the South Korean "*Calyptogena* cf. *elongata*" is clarified, the largest specimens of the Japanese species *Hubertschenckia ezoensis* are illustrated, and the biogeographic history and relationships of these species are discussed.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:251DFB5C-149C-4629-B960-7128B1B34AE8

Institutional abbreviations.—CSUN, California State University at Northridge, California, USA; LACM and LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology, Los Angeles, California, USA; NRM, Swedish Museum of Natural History, Stockholm, Sweden; UWBM, University of Washington, Burke Museum of Natural History and Culture, Seattle, Washington, USA.

Other abbreviations.—aams, anterior adductor muscle scar; H, height; L, length; LV, left valve; pams, posterior adductor muscle scar; RV, right valve; W, width.

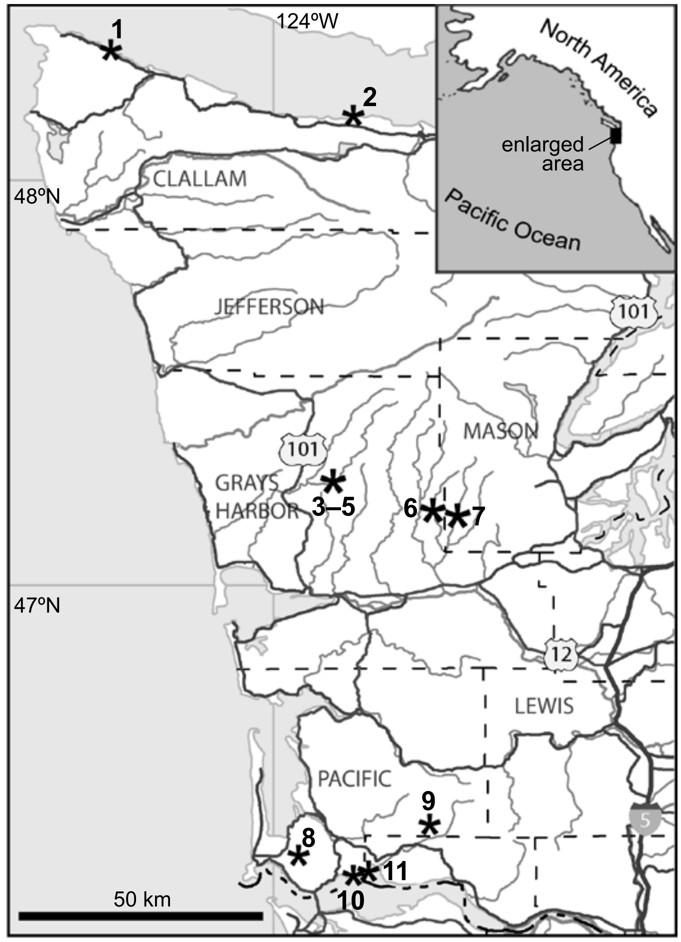

Fig. 1. Map showing localities in western Washington State, USA. 1, coastal sites between Rasmussen Creek and Jansen Creek (Makah Formation); 2, Whiskey Creek site (Pysht Formation); 3–5, sites LACMIP loc. 12385, CSUN loc. 1583, "East Fork Bridge site" (Humptulips Formation); 6, UWBM loc. B7452 in the Canyon River (Lincoln Creek Formation); 7, SR2 and SR4, Satsop River (Lincoln Creek Formation); 8, Bear River seep deposit; 9, West Fork of Grays River (Siltstone of Unit B); 10, Frankfort (Astoria Formation); 11, sites around Rocky Point (Astoria Formation).

Material and methods

Specimens were mechanically extracted from the rock matrix using hammers and chisels, and pneumatic fossil preparation tools. Casts were made using colored silicone rubber. Some fossil specimens were used to produce polished surfaces. Specimens were coated with ammonium chloride prior to photography, unless noted otherwise. One articulated specimen was scanned with an Xradia Versa 520 x-ray microscope at the Stockholm University Brain Imaging Center (SUBIC). Most specimens are deposited at the Swedish Museum of Natural History (NRM), some are stored in the Natural History Museum of Los Angeles County (LACMIP) and the Burke Museum, University of Washington (UWBM).

Localities

Washington State, USA.—The material from Washington State, USA (Fig. 1), was collected by JLG over the last decades; some of it jointly with SK. GPS coordinates are given using the WGS84 datum (World Geodetic System). Standard locality descriptions, based upon US Geological Survey topographic maps, refer to section, township, and range according to the USA Public Land Survey System.

Astoria Formation: The material reported here was collected from the Lower to Middle Miocene, thin-bedded mudstone unit of the Astoria Formation ("Tasu" of Wolfe and McKee 1968; Unit III of Wolfe and McKee 1972; Bald Ridge unit of Wells 1989) cropping out along the north shore of the Columbia River in Pacific County. Fossils were found in float seep limestone and concretions (Amano and Kiel 2007; Kuechler et al. 2012) found on intertidal platforms at three sites between the ghost town of Frankfort in the west and the mouth of Deep River in the east. These include the previously published site LACMIP 6132 just to the east of Frankfort (Kiel 2010b) and two new sites just east and west of Rocky Point. The concretions contain mostly the vesicomyid *Pliocardia kawadai* and are accompanied by small-sized specimens (up to 40 mm in length) of the thyasirid *Conchocele* spp. and a few indeterminable gastropods. Paleodepths for these strata are poorly constrained, ranging 16–650 m or possibly deeper based on foraminiferans (e.g., Wolfe and McKee 1968, 1972), and bottom water temperatures may have been near zero (Qu et al. 2017). Deposition was in part by turbidity flows (Wolfe and McKee 1972). Other fossils are generally rare, but include a few crustaceans and a variety of terrestrial plants (Berglund and Goedert 1992), propeamussiid bivalves coined "mud pectens" (Wolfe and McKee 1972), pteropod gastropods (Squires 1989), and a marine mammal (Peredo et al. 2018). The seep deposits are not common but are conspicuous because they contain abundant, densely packed, large and mostly articulated bivalves.

Bear River seep deposit: We document further specimens of *Pleurophopsis chinookensis* from its type locality, a well-described, upper Eocene seep deposit at Bear River (Goedert and Squires 1990; Squires and Goedert 1991; Goedert and Benham 2003; Kiel 2006; Kiel and Amano 2013). There is much more research to be done on this site but currently, Weyerhaeuser Company owning the land does not allow access.

Humptulips Formation: This formation consists mainly of upper middle Eocene deep-water mudstone (Rau 1984, 1986; Prothero et al. 2001; Goedert et al. 2013). The only molluscan fossils not found in seep deposits were rare wood-fall taxa (Kiel 2008b). The material reported here comes from four different blocks of seep carbonate found along, or in the vicinity of, the Humptulips River: (i) LACMIP locality 12385, a large seep deposit with a diverse fauna (Goedert and Squires 1990; Squires and Goedert 1991; Kiel 2006; Kiel and Amano 2013; Hryniewicz et al. 2017); (ii) CSUN loc. 1583, a seep deposit also known as the "Raui site" for its most conspicuous gastropod, *Humptulipsia raui* (Goedert and Kaler, 1996) (Saul et al. 1996; Goedert and Kaler 1996; Squires and Goedert 1996; Kiel 2008a; Jakubowicz et al. 2020); (iii) a seep deposit named "East Fork Bridge site" in a recent isotopic study (Jakubowicz et al. 2020), with a fauna consisting mainly of an as-yet unidentified lucinid bivalve and the vesicomyid reported herein; (iv) an as-yet undescribed block found as float on the same gravel bar (at 47.2469°N, 123.8409°W) as the previous deposit, but with a nodular, micritic lithology, with narrow vugs filled by calcite spar, and a diverse fauna including worm tubes, thyasirid bivalves, and the herein reported vesicomyid. Much more work remains to be done at these sites, but currently Rayonier Corporation owning the land no longer allows access.

Lincoln Creek Formation: This formation is composed of the upper Eocene to lowest Miocene strata, mainly deep-water deposits, and crops out between the southern foothills of the Olympic Mountains and the Columbia River. The material reported here is from four seep deposits, from the Oligocene part of the formation, exposed along the Canyon and Satsop rivers as mapped by Rau (1966). The in situ deposits from the Satsop River were previously described as SR2 (= UWBM loc. B6702; earliest Oligocene age) and SR4 (= LACMIP loc. 17426; late Oligocene age) (Peckmann et al. 2002). Those from the Canyon River were blocks found as float on gravel bars along the river, among them several from UWBM loc. B7452 that include specimens of *Bathymodiolus inouei* Amano and Jenkins, 2011b, and *Lucinoma* sp. (Kiel and Amano 2013) in addition to the vesicomyid reported herein; the other was found at about 47.267522° N, 123.526238° W and is probably of late Oligocene age. Some of the Satsop and Canyon river in situ seep deposits are very small in size (e.g., Peckmann et al. 2002; Kiel 2006; Yamaguchi et al. 2016) and because the rivers generally flow perpendicular to strike and dip with the oldest strata exposed upstream, the ages given for deposits found as float should be regarded as minimums because there is the possibility they are older.

Makah Formation: The Makah Formation crops out along the shore of the Strait of Juan de Fuca in northwestern Washington (Snavely et al. 1980). Between Whiskey Creek and the Lyre River are extensive outcrops of deep-water siltstone with abundant concretions, originally mapped (Brown and Gower 1958; Tabor and Cady 1978) as the middle member of the Twin River Formation. The middle member of the Twin River Formation was later named the Makah Formation by Snavely et al. (1980), although they do not specifically mention the strata exposed between Whiskey Creek and the Lyre River. These rocks yield a crab, *Macroacaena alseana* (Rathbun, 1932), only found in upper Eocene rocks in Oregon and Washington (Feldman 1989; Tucker 1998), but except for foraminifers (Rau 1964), a marine bird (e.g., Goedert and Cornish 2002), and a terrestrial plant (Crabtree and Miller 1989), other fossils have not yet been described. Rocks between the Lyre River and Whiskey Creek were later mapped in error as the Pysht Formation by Nesbitt et al. (2010) (Elizabeth A. Nesbitt, personal communication to JLG, 2011). Seep carbonates are present as float along these coastal outcrops and include thyasirids and possibly a vesicomyid (discussed herein), but these carbonates have not yet been fully investigated.

Farther to the west, seep carbonate from the Shipwreck Point area west of the Sekiu River contains vesicomyids (Goedert and Campbell 1995) and these are further discussed herein. Two float seep carbonate blocks containing vesicomyids were sampled from coastal outcrops of the uppermost Eocene or lowermost Oligocene Jansen Creek Member between the mouth of Rasmussen Creek eastward to a point about 500 m southeast of Jansen Creek. The Jansen Creek Member is an olistostrome (Snavely et al. 1980) and contains both deep and shallow water marine deposits. This olistostrome contains a complex of seep carbonates that are either in situ within large (up to 100 m long; Snavely et al. 1980) blocks of marine sediment, allochthonous (Goedert and Campbell 1995), or perhaps even in part precipitated within and on top of the rubble pile after submarine slumping, but this awaits further analyses and detailed mapping. Goedert and Squires (1993) reported vesicomyids from a turbidite deposit belonging to the Jansen Creek Member. The Jansen Creek Member seep carbonates yield a distinct species of *Bathymodiolus* that differs from other known fossil bathymodiolins in western Washington (Kiel and Amano 2013). Thyasirids were reported from Jansen Creek Member seep deposits (Hryniewicz et al. 2017) as were provannid gastropods (Squires 1995). A recently described seep site has abundant echinoids (Müller et al. 2023).

Pysht Formation: Sampling sites for this study include the highly fossiliferous, upper Eocene Whiskey Creek seep deposit (Goedert et al. 2003; Peckmann et al. 2003; Hryniewicz et al. 2017) probably from the basal part of the formation. Additional specimens of a previously published vesicomyid from an lower upper Oligocene seep deposit at LACMIP loc. 15621, in the lower part of the Pysht Formation west of the mouth of Murdock Creek, Clallam County (Goedert and Squires 1993) are re-evaluated.

Siltstone of unit B: Several float carbonate concretions and an in situ site from this upper Eocene rock unit (Wolfe and McKee 1968) were collected along West Fork of Grays River, upstream from the mouth of Beaver Creek in Pacific County. Although this siltstone is locally highly fossiliferous, the fossils have not yet been described in detail (i.e., Wolfe and McKee 1968, 1972; Kiel 2010a). Limacinid pteropods were documented by Garvie et al. (2020). A deep water crab, *Macroacaena alseana* from this rock unit was discussed by Feldman (1989). This crab fossil is also found in the upper Eocene Hoko River and Makah formations (between Whiskey Creek and the Lyre River, see discussion above) in northwestern Washington and the upper Eocene Nestucca Formation in Oregon (Feldman 1989; Tucker 1998). Based on benthic foraminifers, the deposition of this siltstone unit was estimated to have occurred at depths of ca. 150–750 m (Wolfe and McKee 1968, 1972). In addition to the vesicomyids reported herein, an unidentified thyasirid was reported from these seep deposits (Hryniewicz et al. 2017).

South Korea.—Duho Formation: The Middle Miocene Duho Formation of the Euichang Group in the Pohang Basin, is exposed in and around Pohang City, near the southeast coast of Korea (Yun 1986). It is composed of deep-water mudstone and has produced a diverse fauna of deep-water taxa, including various mollusks (Yoon 1976a, b), brittlestars (Seong et al. 2009; Ishida et al. 2022), sharks (Yun 2020, 2021; Malyshkina et al. 2022), and a pleuronectiform flatfish (Ko 2016). The specimens documented here were collected by the late Professor Sun Yoon at a hill-side cut for the foundation of a house, about 400 m southeast of Goedong-dong, Daesong-myeon, Yeongil-gun, South Korea. This is loc. 18 of Yoon (1976b).

Japan.—Poronai Formation: Five specimens of *Hubertschenckia ezoensis* were collected by the late Saburo Kanno, who was an Emeritus Professor at the University of Tsukuba and Joetsu University of Education, from the upper Eocene Poronai Formation. The exact locality is unknown but was most likely either in Yubari City or Mikasa City, in central Hokkaido.

Systematic palaeontology

Class Bivalvia Linnaeus, 1758

Subclass Heteroconchia Gray, 1854

Order Venerida Gray, 1854

Family Vesicomyidae Dall and Simpson, 1901

Subfamily Vesicomyinae Dall and Simpson, 1901

Genus *Vesicomya* Dall, 1886

Type species: *Callocardia atlantica* Smith, 1885, by original designation; Recent, North Atlantic Ocean.

Vesicomya? sp. 1

Fig. 2A–G.

Material.—One articulated specimen (NRM Mo 204811) from the SR2 seep deposit of Peckmann et al. (2002) [= UWBM loc. B6702], in the lower Oligocene part of the Lincoln Creek Formation, western Washington State, USA.

Dimensions (in mm).—NRM Mo 204811: L = 17.0, H = 14.5, W = 12.8.

Description.—Large for genus, well inflated; umbones large, blunt, strongly raised, displaced anteriorly to approximately 30% of total shell length; anterior margin truncate, acutely rounded; ventral margin very slightly convex; posterodorsal margin gently sloping, accompanied by submarginal ridge and weak sulcus to its anterior; lunular incision short, heart-shaped; escutcheon short, lanceolate; surface with irregular growth lines. Hinge plate narrow, with teeth oriented subparallel to dorsal margin, as is typical for *Vesicomya*.

Vesicomya? sp. 2

Fig. 2H–K.

Material.—One articulated specimen and two isolated RV (NRM Mo 204701–03) from the SR4 seep deposit of Peckmann et al. (2002) [= UWBM loc. 17426], in the upper Oligocene part of the Lincoln Creek Formation, western Washington State, USA.

Dimensions (in mm).—NRM Mo 204701: L = 6.5, H = 5.0; NRM Mo 204702: L = 5.6; NRM Mo 204703: L = 4.3.

Description.—Average size for genus, well inflated; umbones subcentral, raised, prosogyrate; posterior margin angular due to weak ridge from umbones to posteroventral corner; surface with irregular growth lines; lunular incision deeply incised, broad, short.

Remarks.—*Vesicomya*? sp. 1 and sp. 2 reported here are potentially the oldest fossil records of the *Vesicomya* (sensu stricto). Unfortunately, in neither of the two species the pallial line or muscle scars are visible, thus some doubt about their assignments to *Vesicomya* remain (cf., Cosel and Salas 2001; Krylova et al. 2018). The only other fossil species that can confidently be assigned to *Vesicomya* sensu stricto is *Vesicomya margotae* Beets, 1953, from the Upper Miocene of Indonesia (Buton Island, Beets 1953) and the Pliocene of the Philippines (Leyte Island, Kiel et al. 2020a).

A lower Oligocene record of a putative *Vesicomya* sp. was published by Goedert and Campbell (1995: 26, fig. 3), a single valve approximately 12 mm long with a convexity of 4.8 mm, from the Makah Formation. However, that

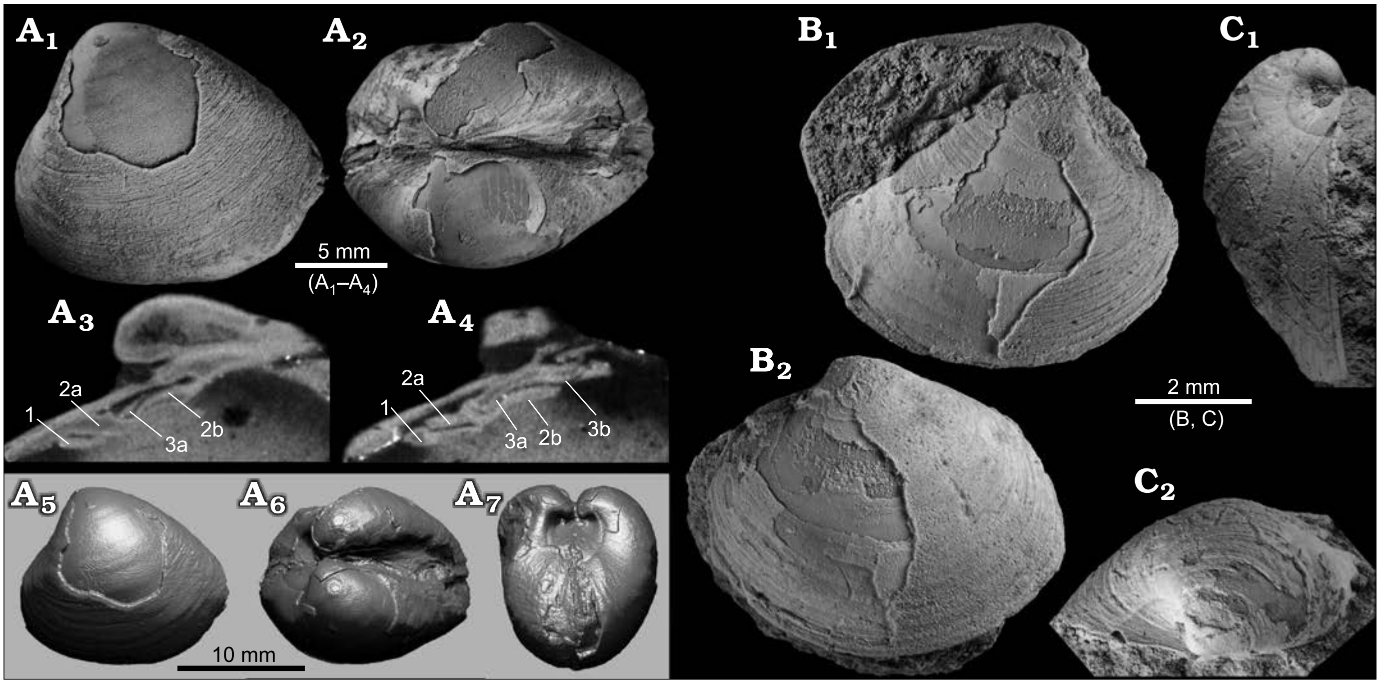

Fig. 2. The small vesicomyid bivalves *Vesicomya*? sp. 1 and sp. 2, from Oligocene seep deposits in the Lincoln Creek Formation, western Washington State, USA. **A**. *Vesicomya*? sp. 1 from the early Oligocene SR2 site, Satsop River. NRM Mo 204811, left side view (A_1) and dorsal view on LV and dorsal side of actual specimen (A_2); A_3, A_4, X-ray section through the hinge area, with our interpretations; A_5–A_7, 3D renderings of the specimen. **B**, **C**. *Vesicomya*? sp. 2 from the late Oligocene SR4 site, Satsop River. **B**. NRM Mo 204701, disarticulated specimen, view on RV with naticid drill hole on the umbo (B_1) and on the LV showing the truncate posterior margin (B_2). **C**. NRM Mo 204702, RV in anterior view, showing inflation and lunular incision (C_1) and dorsal view, showing lunular incision (C_2).

specimen is more elongate than a typical *Vesicomya* and the hinge is not observable in the only known specimen. If the Makah Formation fossil is indeed a vesicomyid, it is more likely a juvenile *Squiresica* or *Isorropodon*.

Subfamily Pliocardiinae Woodring, 1925

Genus *Isorropodon* Sturany, 1896

Type species: *Isorropodon perplexum* Sturany, 1896, by monotypy; Recent, eastern Mediterranean Sea.

Isorropodon humptulipsense sp. nov.

Fig. 3.

1996 *Vesicomya* sp.; Squires and Goedert 1996: 270.
1996 *Vesicomya* sp.; Goedert and Kaler 1996: 67.
2007 *Archivesica* cf. *tschudi* (Olsson, 1931); Amano and Kiel 2007: 282, figs. 24–29.

ZooBank LCID: urn:lsid:zoobank.org:act:A03AC3DA-5702-4AA3-8099-D69460782E1F.

Etymology: After the Humptulips Formation, the type horizon of the species.

Type material: Holotype: NRM Mo 204723 from CSUN loc. 1583, an internal mold showing muscle scars and pallial line. Paratypes: NRM Mo 204722 from CSUN loc. 1583; NRM Mo 204724, 25 from LACMIP loc. 12385; NRM Mo 204733, from as-yet undescribed boulders found near the East Fork Bridge site (reported here as site (iv) for the Humptulips Formation). Eocene, Washington State, USA.

Type locality: The seep deposit at CSUN loc. 1583, Washington State, USA.

Type horizon: Humptulips Formation, Eocene.

Material.—39 specimens; 29 specimens from Humptulips Formation: two specimens from CSUN loc. 1583 (NRM Mo 204722, 23), 9 specimens from LACMIP loc. 12385 (NRM Mo 204724–32), 10 specimens from a block found near the East Fork Bridge site, (NRM Mo 204733–42), 8 specimens from the East Fork Bridge site (NRM Mo 204753–60), and 10 specimens from Siltstone of unit B, Grays River mudstone (NRM Mo 204743–52). Eocene, Washington State, USA.

Dimensions.—See Table 1.

Diagnosis.—Well-inflated shells reaching nearly 35 mm in length, umbones elevated, prosogyrate; lunule deeply incised; broad escutcheon bordered by blunt ridges; pallial line distinct, anteriorly narrow, posteriorly broadening, curving upward, either evenly or with slight indentation, no pallial sinus; RV hinge with elongate cardinal teeth 1 and 3a running parallel to shell margin, 3b pointing posteroventrally; LV hinge with cardinal teeth 2a and 2b elongate, parallel to shell margin, 2b with small posterior peg.

Description.—Shells reaching nearly 35 mm in length and 25 mm in height, inflated, umbones elevated, strongly prosogyrate, at anterior 16–18% of shell length; lunule deeply incised, elongate-heart shaped, escutcheon broad, demarcated by blunt ridges; anterior adductor muscle scar bean-shaped, fused with pedal retractor scar; pallial line entire, distinct, anteriorly narrow, broadening posteriorly, starting at posterodorsal corner of anterior adductor muscle scar,

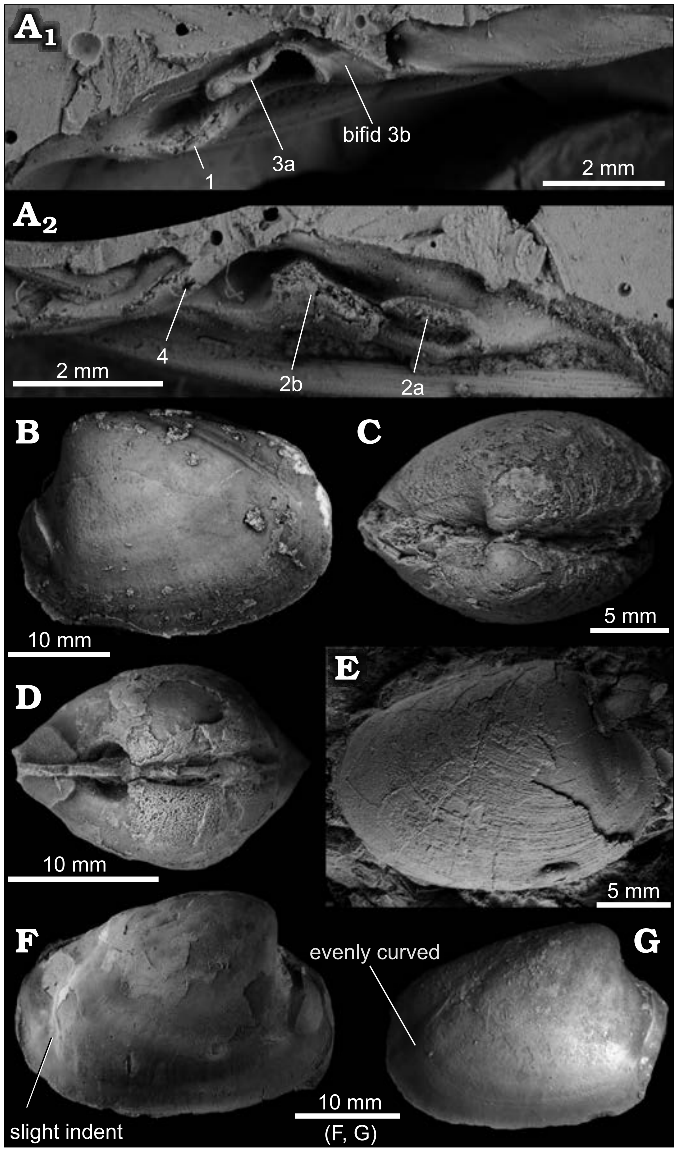

Fig. 3. The vesicomyid bivalve *Isorropodon humptulipsense* sp. nov., from middle to upper Eocene strata in western Washington State, USA. **A**. Rubber cast of the paratype, NRM Mo 204722, Humptulips Formation, CSUN loc. 1583, hinge area, RV (A_1), LV (A_2). **B**. Holotype, NRM Mo 204723, Humptulips Formation, CSUN loc. 1583, internal mold, view on LV. **C**. NRM Mo 204724, Humptulips Formation, LACMIP loc. 12385, articulated specimen, view on anterodorsal margin showing lunular incision. **D**. Paratype, NRM Mo 204733, Humptulips Formation, near East Fork Bridge site, view on anterodorsal margin and anterior adductor muscle scars. **E**. Paratype, NRM Mo 204744, Siltstone Unit B along Grays River, specimen with partially preserved shell. **F**. Paratype, NRM Mo 204743, Siltstone Unit B along Grays River, internal mold showing pallial line with slight indentation on RV. **G**. Internal mold, USNM 534952, Humptulips Formation, CSUN loc. 1583, view on RV with pallial line curving evenly into posterior adductor muscle scar (re-illustrated from Amano and Kiel 2007).

running close and parallel to ventral shell margin, posteriorly curving upward, either evenly or with slight indentation, to join posterior adductor muscle scar at its base; no pallial sinus; distinct interior ridge running from umbones to ventral side of posterior adductor muscle scar; hinge with three cardinals in each valve; RV with elongate cardinal teeth 1 and 3a running parallel to shell margin, 3b bifid with raised edges, pointing posteroventrally; in LV cardinal teeth 2a and 2b elongate, parallel to shell margin, 2b with small posterior peg, cardinal tooth 4b thin, short.

Remarks.—For a more detailed description see Amano and Kiel (2007). The small, circular and deep subumbonal pit figured earlier (Amano and Kiel 2007: figs. 24, 25) was likely an artifact because we have not seen it in additional specimens. Small-sized specimens reaching 2.5 mm in length were reported as "unidentified vesicomyid bivalve" from the middle Eocene Weatherwax seep deposit of the Humptulips Formation (Hybertsen and Kiel 2018); these oval specimens have an almost *Vesicomya*-like hinge dentition and might be juveniles of *Isorropodon humptulipsense* sp. nov.

The pallial line of *Isorropodon humptulipsense* shows some variation in thickness and in its posterior-most part before reaching the posterior adductor muscle scar. In some specimens the pallial line curves evenly upward into the posterior adductor muscle scar (Fig. 3B, G), in others, it

Table 1. Measurements (in mm) of *Isorropodon humptulipsense* sp. nov. ** holotype; * paratype; na, measurement not possible.

Specimen no.	Length	Height	Width	Locality
NRM Mo 204722*	20.6	15.3	11.8	CSUN loc. 1583
NRM Mo 204723**	31.0	23.8	15.8	CSUN loc. 1583
NRM Mo 204724*	11.0	9.6	7.0	LACMIP loc. 12385
NRM Mo 204725*	13.8	11.4	11.7	LACMIP loc. 12385
NRM Mo 204726	18.3	11.9	na	LACMIP loc. 12385
NRM Mo 204727	15.2	12.0	7.1	LACMIP loc. 12385
NRM Mo 204728	15.3	11.7	9.0	LACMIP loc. 12385
NRM Mo 204729	12.8	10.8	7.8	LACMIP loc. 12385
NRM Mo 204730	12.1	8.5	5.7	LACMIP loc. 12385
NRM Mo 204731	11.1	8.8	6.0	LACMIP loc. 12385
NRM Mo 204732	8.4	6.8	4.5	LACMIP loc. 12385
NRM Mo 204733*	22.8	18	13.7	near East Fork Bridge
NRM Mo 204734	34.6	24.7	na	near East Fork Bridge
NRM Mo 204735	17.0	13.5	11.0	near East Fork Bridge
NRM Mo 204737	16.2	12.0	na	near East Fork Bridge
NRM Mo 204739	12.6	12.3	na	near East Fork Bridge
NRM Mo 204740	11.2	11.7	na	near East Fork Bridge
NRM Mo 204741	10.6	7.6	na	near East Fork Bridge
NRM Mo 204743	30.3	20.0	na	Grays River
NRM Mo 204744	23.5	18.8	na	Grays River
NRM Mo 204745	32.0	25.0	19.6	Grays River
NRM Mo 204746	30.8	22.8	19.0	Grays River
NRM Mo 204747	25.0	20.8	17.8	Grays River
NRM Mo 204748	25.0	19.0	15.2	Grays River
NRM Mo 204749	24.5	19.5	na	Grays River
NRM Mo 204750	25.5	22.0	13.3	Grays River
NRM Mo 204751	na	21.5	16.6	Grays River
NRM Mo 204753	na	21.4	15.0	East Fork Bridge site
NRM Mo 204755	19.5	14.6	na	East Fork Bridge site
NRM Mo 204756	19.7	16.0	12.0	East Fork Bridge site

shows a slight indentation (but not a sinus) on its way upward (Fig. 3F). Other species of *Isorropodon* also show some variation of this feature. In *I. megadesmum* Oliver, Rodrigues, and Cunha, 2011, the pallial line joins the posterior adductor muscle scar after a sinuous swing (Oliver et al. 2011: fig. 9C); in *I. bigoti* Cosel and Salas, 2001 (their fig. 55) and *I. curtum* Cosel and Salas, 2001 (their fig. 59) both join after a straight section followed by an angulation of the pallial line, and this angulation can point either posteriorly (*I. bigoti*) or anteriorly (*I. curtum*). In *I. nyeggaense* Krylova, Gebruk, Portnova, Todt, and Haflidason, 2011 (Krylova et al. 2011: figs. 6D, 7D), the pallial line just has a straight section before reaching the posterior adductor muscle scar.

Compared to other species of *Isorropodon*, *I. humptulipsense* is relatively large and has a distinct lunular incision. *Isorropodon bigoti* reaches only 21 mm in length, has a straighter ventral margin, and an indistinct lunular incision. The type species *I. perplexum* reaches a maximum of 15 mm in length, its hinge teeth are arranged mostly parallel to each other in contrast to the radiating teeth of *I. humptulipsense*, and it lacks a lunular incision. *Isorropodon curtum* is not only much smaller, it also has a shorter shell. Of similar size as *I. humptulipsense* is *I. striatum*, but its hinge teeth are arranged in a parallel fashion and its lunular incision is indistinct. *Isorropodon megadesmum* reaches only 12 mm in length and has an indistinct lunular incision, and *I. nyeggaense*: is up to 21 mm long, is less inflated than *I. humptulipsense*, and has an indistinct lunular incision. *Isorropodon arguinense* Hoffman, Cosel, and Freiwald, 2019, is smaller and much more elongate than *I. humptulipsense* (i.e., Hoffman et al. 2019). The Miocene *I. frankfortense* Kiel and Amano, 2007 (originally introduced as *I. frankfortensis*) from the Astoria Formation in southwestern Washington State is much smaller and has a more convex ventral margin than *I. humptulipsense*, and has the hinge teeth arranged in a parallel fashion (Amano and Kiel 2007).

Somewhat similar is *Cytherocardia cytheroides* (Mayer, 1868), type of the little-known genus *Cytherocardia* Sacco, 1900, from Miocene of Italy (Mayer 1868; Sacco 1900), which has been suggested to be a member of Vesicomyidae (Janssen and Krylova 2012). The shells are oval with strong, elevated, prosogyrate umbones, thus somewhat have a similar shape to *Isorropodon humptulipsense* (i.e., Janssen and Krylova 2012: pl. 5: 19). However, the taxonomically important dentition of the right valve of *C. cytheroides* remains unknown, as are internal features such as pallial line and muscle scars. We find the allocation of *Cytherocardia* to the Vesicomyidae doubtful, and the lack of a lunular incision in *C. cytheroides* clearly distinguishes it from *Isorropodon humptulipsense*.

Stratigraphic and geographic range.—Seep carbonate deposits within the middle Eocene Humptulips Formation and upper Eocene Siltstone of unit B, Washington State, USA.

Genus *Pliocardia* Woodring, 1925

Type species: *Anomalocardia bowdeniana* Dall, 1903, by original designation; Pliocene, Bowden Formation, Jamaica (Dall 1903).

Pliocardia kawadai (Aoki, 1954)

Figs. 4, 5.

1954 *Lamelliconcha kawadai* sp. nov.; Aoki 1954: 36–37, pl. 2: 1–13, 22.
1962 *Vesicomya kawadai* (Aoki); Kamada 1962: 88–89, pl. 8: 2a–b.
2001 *Vesicomya kawadai* (Aoki); Amano et al. 2001: 192, figs. 3–5, 8–11.
2007 *Vesicomya kawadai* (Aoki); Amano et al. 2007: figs. 3D, E, G, J.
2012 *Pliocardia kawadai* (Aoki); Amano and Kiel 2012: 80–83, figs. 2–4, 6, 7, 9–12.
2019 *Pliocardia kawadai* (Aoki); Amano et al. 2019b: fig. 4 C, E, J–O.
2022 *Pliocardia kawadai* (Aoki); Amano et al. 2022: fig. 10.9 f, g.

Material.—Eight specimens from LACM 6132 (NRM Mo 204715–18, 21, LACMIP 6132.2–6132.4); seven specimens from northeast of Rocky Point (NRM Mo 204709–13, 19, 20); 27 mostly fragmentary specimens from west of Rocky Point (NRM Mo 204714 [1 specimen], 204812 [26 specimens]). Miocene, Astoria Formation, Bald Ridge unit, north shore of the Columbia River, Pacific County, Washington State, USA.

Dimensions.—See Table 2.

Remarks.—The specimens of *Pliocardia kawadai* from the Lower to Middle Miocene Columbia River seep deposits resemble those from the Lower Miocene Honya Formation of Joban coalfield in Japan in every aspect (Aoki 1954; Kamada 1962). The topotype specimens subsequently reported (Amano and Kiel 2012) show no discernable difference in hinge structure compared with the specimens from Washington, though they appear slightly less inflated and have sharper (more angular) posterodorsal ridges. The Japanese specimens of *Pliocardia kawadai* reach 43.1 mm in length (i.e., Amano et al. 2019b), which is similar to the average size of the specimens from Washington, with the exception of one specimen that is nearly 50 mm long.

Table 2. Measurements (in mm) of *Pliocardia kawadai* (Aoki, 1954). na, measurement not possible.

Specimen no.	Length	Height	Width	Locality
NRM Mo 204709	39.7	25.0	na	Frankfort
NRM Mo 204710	27.4	19.8	na	Frankfort
NRM Mo 204711	49.8	39.6	na	Frankfort
NRM Mo 204712	36.0	30.4	na	Frankfort
NRM Mo 204714	40.0	24.5	18.4	Rocky Point
NRM Mo 204719	34.0	20.5	18.4	Frankfort
NRM Mo 204720	31.7	22.4	17.4	Frankfort
NRM Mo 204715	37.0	22.7	18.8	LACM 6132
NRM Mo 204716	34.6	25.2	na	LACM 6132
NRM Mo 204717	36.0	22.3	19.0	LACM 6132
NRM Mo 204718	34.0	32.5	27.3	LACM 6132
NRM Mo 204721	31.6	22.8	20.0	LACM 6132
LACMIP 6132.2	39.5	24.7	23.3	LACM 6132
LACMIP 6132.3	45.0	33.8	25.2	LACM 6132
LACMIP 6132.4	37.0	23.2	na	LACM 6132

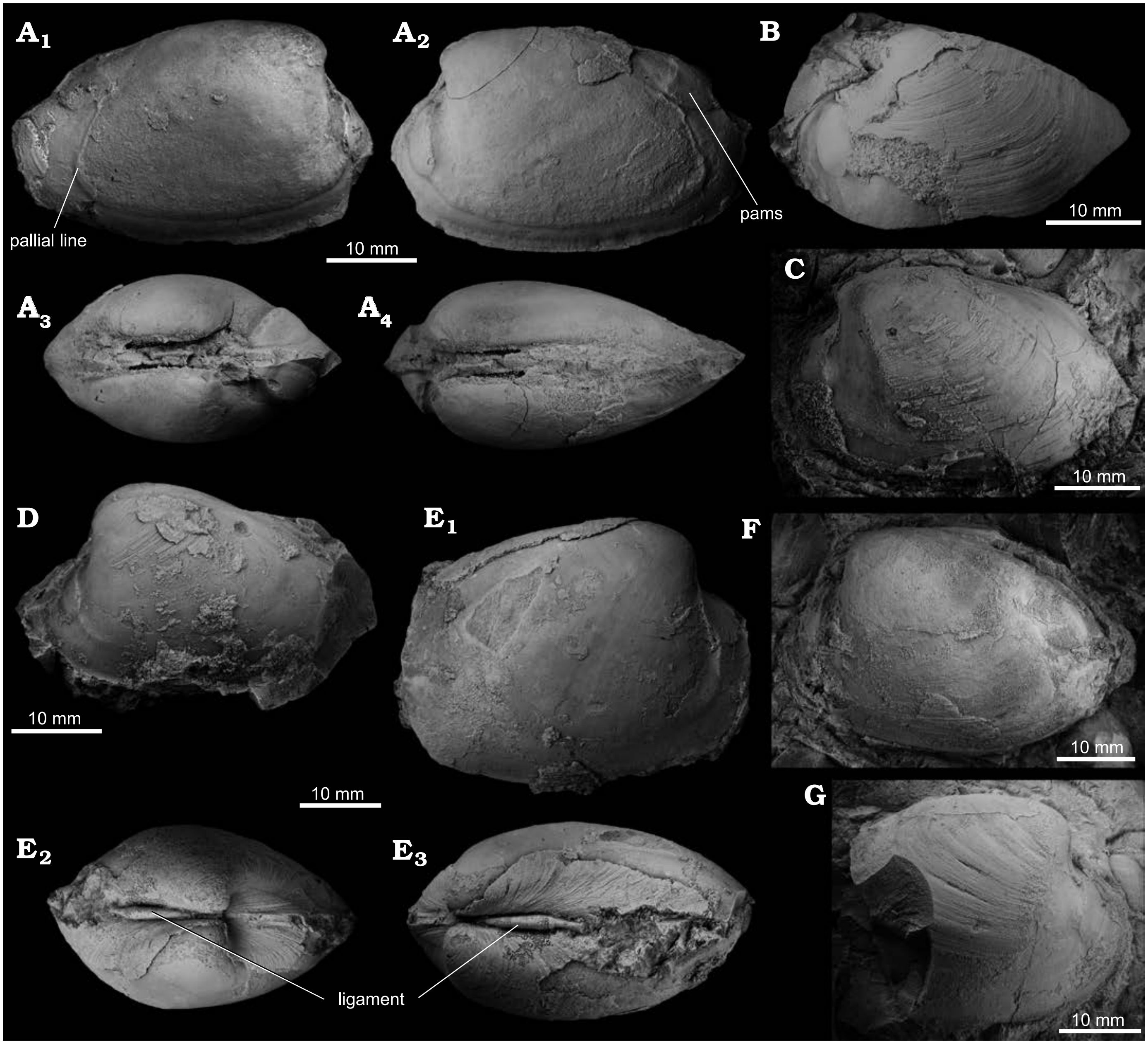

Fig. 4. The vesicomyid bivalve *Pliocardia kawadai* (Aoki, 1954), from Middle Miocene seep deposits of the Astoria Formation in western Washington State, USA. **A**. NRM Mo 204714, Rocky Point, internal mold showing muscle scars and pallial line. **B**. NRM Mo 204719, Frankfort, specimen with partially preserved shell (LV) showing the fine, irregular growth lines and the anterior adductor muscle scar. **C**. NRM Mo 204709, Frankfort, mostly an internal mold, showing the anterior adductor muscle scar and the posterior ridge. **D**. NRM Mo 204720, Frankfort, mostly an internal mold, note naticid drill hole on posterodorsal margin. **E**. LACMIP 6132.2, LACMIP loc. 6132, specimen with partially preserved shell; view of RV showing muscle scars (E_1); anterodorsal view showing elongate lunular incision (E_2); posterodorsal view showing ligament (E_3). **F**. NRM Mo 204711, Frankfort, internal mold of left valve, showing pallial line and posterior adductor muscle scar. **G**. NRM Mo 204712, Frankfort, specimen with partially preserved shell (RV) showing the fine, irregular growth lines and the anterior adductor muscle scar.

As pointed out previously (Amano and Kiel 2012), the most similar extant species is the West Pacific *P. crenulomarginata* (Okutani, Kojima, and Iwasaki, 2002), which differs from *P. kawadai* mainly by having less prosogyrate umbones and fine crenulations on the posterior margin.

Stratigraphic and geographic range.—Lower–Middle Miocene of Hokkaido and Honshu, Japan, and seep deposit in southwestern Washington State, USA.

Pliocardia? *guthrieorum* sp. nov.

Fig. 6.

ZooBank LCID: urn:lsid:zoobank.org:act:EEDC380D-91CD-44E9-A722-6096971A8D9C.

Etymology: In honor of Lloyd S. and Kay Guthrie (Olympia, USA), for their help over several fieldtrips that produced some of these specimens.

Type material: Holotype: NRM Mo 204785 (Fig. 6G); paratypes: NRM

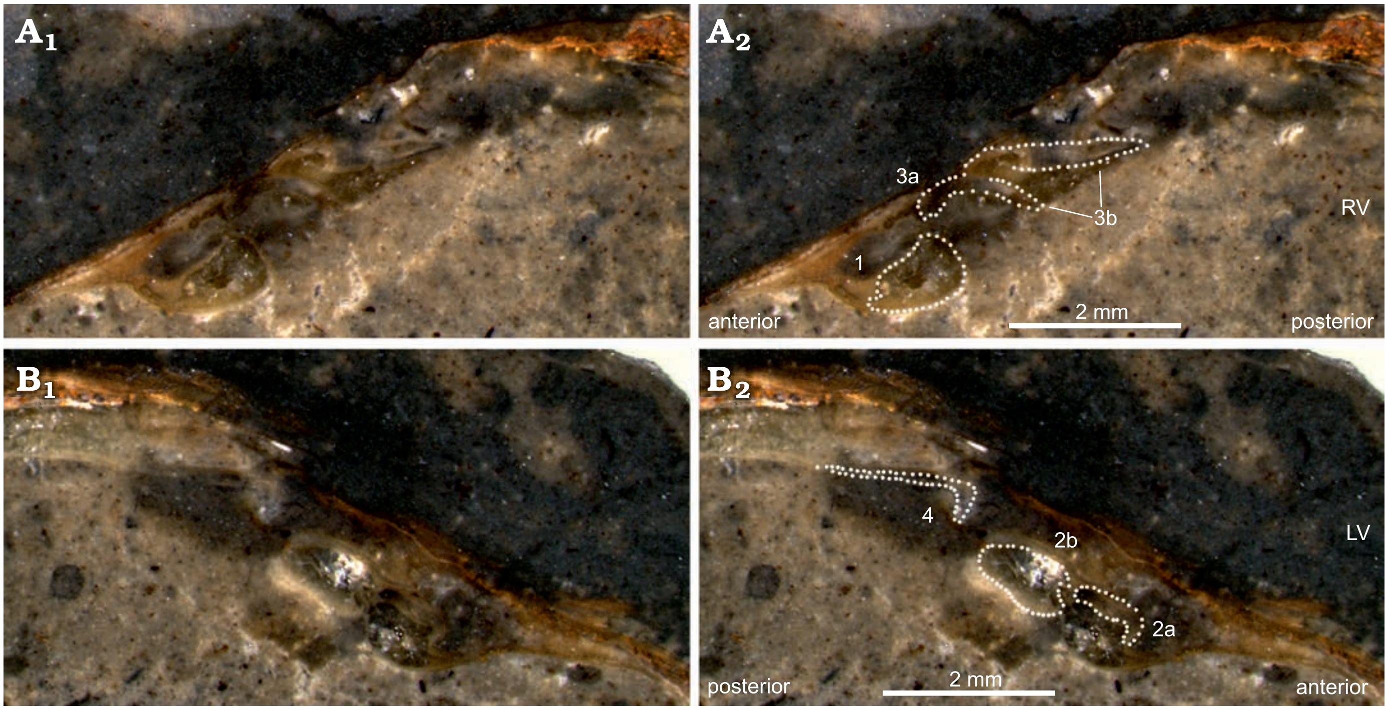

Fig. 5. The vesicomyid bivalve *Pliocardia kawadai* (Aoki, 1954), from Middle Miocene seep deposit at Frankfort of the Astoria Formation in western Washington State, USA. NRM Mo 204713, polished sections of the hinge area in the RV (**A**) and LV (**B**). Photographs (A_1, B_1) and their interpretation (A_2, B_2).

Mo 204779–82, 204784, 204813, 14, UWBM IP 117930, 31. All specimens from the type locality and horizon.

Type locality: UWBM loc. B7452 in the Canyon River in western Washington State, USA.

Type horizon: Lincoln Creek Formation, Oligocene.

Material.—73 specimens from UWBM loc. B7452 (NRM Mo 204779–89, 92, 93, 204813, 14, UWBM IP 117930–31), and four from UWBM loc. B6702 (NRM Mo 204790), all Lincoln Creek Formation. One specimen from the Makah Formation, west of Whiskey Creek (NRM Mo 204791). Oligocene, Washington State, USA.

Dimensions.—See Table 3.

Diagnosis.—Shell oval to elongate-oval, moderately inflated, reaching nearly 50 mm in length; blunt, submarginal posterior ridge; umbones prominent, elevated, prosogyrate; lunular incision very elongate, often indistinct; ligament short.

Table 3. Measurements (in mm) of *Pliocardia*? *guthrieorum* sp. nov. ** holotype; * paratype; na, measurement not possible.

Specimen no.	Length	Height	Width	Locality
NRM Mo 204779*	48.6	37.5	22.7	UWBM loc. B7452
NRM Mo 204780*	37.0	24.0	14.8	UWBM loc. B7452
NRM Mo 204781*	47.2	31.5	na	UWBM loc. B7452
NRM Mo 204784*	46.0	30.4	19.4	UWBM loc. B7452
NRM Mo 204785**	46.5	29.8	19.0	UWBM loc. B7452
NRM Mo 204788	44.9	39.4	16.8	UWBM loc. B7452
NRM Mo 204789	16.8	12.4	7.2	UWBM loc. B7452
NRM Mo 204791	24.0	16.2	na	W of Whiskey Creek
NRM Mo 204813*	30-	25+	15.8	UWBM loc. B7452
NRM Mo 204814*	32+	17.5+	13.5	UWBM loc. B7452
UWBM 117930	36.1	21.8	13.4	UWBM loc. B7452
UWBM 117931	47.0	33.0	18+	UWBM loc. B7452

Description.—Shell medium-sized, broadly oval-elongate, moderately inflated (max. L = 48.6 mm, H = 37.5 mm, W = 22.7 mm); umbones elevated, prosogyrate, positioned anterior at about 21% of total shell length; blunt ridge close to posterodorsal margin; elongate lunular incision present but not very deep; short and narrow ligament, no escutcheon. Anterior adductor muscle scar D-shaped, posterior margin shallow; pallial line starting at posteroventral corner of anterior adductor scar, extending mostly parallel to ventral shell margin, near posterior end of shell bending upward to continue nearly straight into the base of the posterior adductor muscle scar; posterior adductor muscle scar round, with weak but distinct ridge running from umbo to ventral margin where it meets the pallial line. Hinge plate narrow, with three teeth in each valve; teeth in RV subparallel to dorsal shell margin, 1 thin, elongate, just anterior of umbo, 3a and 3b both short, thin, originating underneath umbo; LV with thin 2a, subparallel to dorsal shell margin, 2b nearly perpendicular to 2a, thick and short.

Remarks.—All specimens are from the Oligocene part of the Lincoln Creek Formation in the Canyon and Satsop rivers area. One specimen from limestone deposits found in upper Eocene rocks mapped as Makah Formation, just west of Whiskey Creek, may also belong here. It is a small (c. 25 mm long) right valve that externally resembles *Pliocardia*? *guthrieorum*, but it is embedded in rock matrix so neither hinge nor pallial line or muscle scars are visible, hampering a reliable identification.

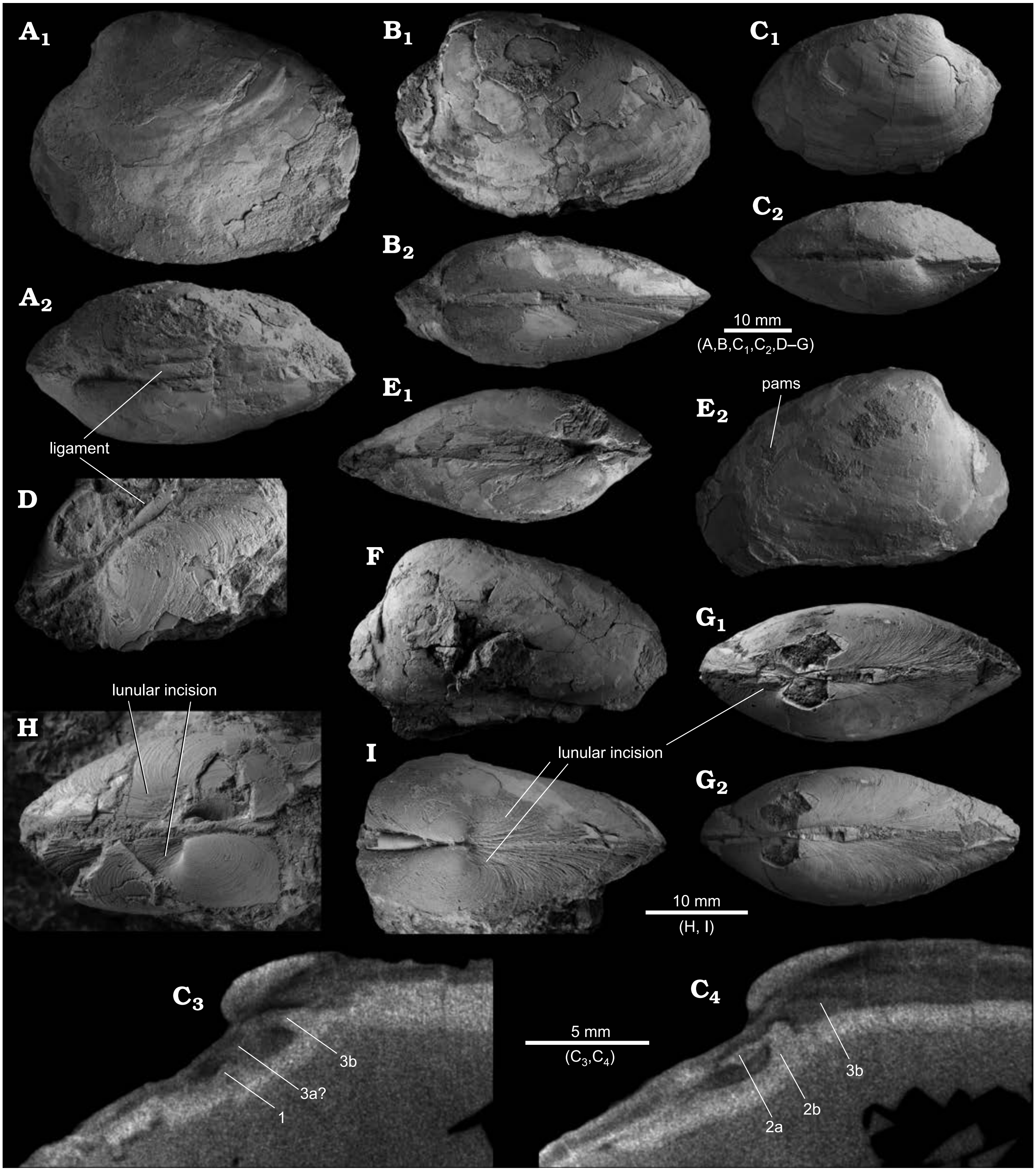

Fig. 6. The vesicomyid bivalve *Pliocardia*? *guthrieorum* sp. nov., from the Oligocene seep deposits at UWMB loc. B7452, Lincoln Creek Formation, western Washington State, USA. **A**. Paratype, NRM Mo 204779, large specimen showing outline, inflation, and ligament; left valve (A_1) and dorsal (A_2) views. **B**. Paratype, NRM Mo 204784, showing outline, inflation, and anterior adductor muscle scar; left valve (B_1) and dorsal (B_2) views. **C**. Paratype, NRM Mo 204780, small, elongate specimen; right valve (C_1) and dorsal (C_2) views; digital sections through the hinge area, with our interpretation of the hinge teeth indicated (C_3, C_4). **D**. Paratype, NRM Mo 204782, showing ligament. **E**. Holotype, NRM Mo 204785, showing inflation (E_1) and both adductor muscle scars and the pallial line in the RV (E_2). **F**. Paratype, NRM Mo 204781, large specimen with particularly large and blunt umbo. **G**. Paratype, NRM Mo 204814, small specimen in dorsal view, showing inflation and lunular incision (G_1) and the lack of an escutcheon (G_2). **H**. Paratype, NRM Mo 204786, showing lunular incision. **I**. Paratype, NRM Mo 204813, showing lunular incision. Abbreviation: pams, posterior adductor muscle scar.

We hesitantly assign this species to *Pliocardia* because it resembles some of the larger-sized extant species assigned to this genus, as well as for example *P. kawadai* reported above. However, virtually all species of *Pliocardia* are more strongly inflated than *Pliocardia*? *guthrieorum*. Furthermore, our interpretation of the hinge dentition is based on x-ray scanning of a specimen with an only moderately preserved hinge, and some uncertainty remains, in particular about cardinal 3a. Extant species of the genus *Wareniconcha* Cosel and Olu, 2009, have shells with similar minimal inflation, but they have more convex ventral margins and less elevated umbones, and they have an escutcheon (Smith 1906; Prashad 1932; Cosel and Olu 2009; Krylova and Sahling 2010), which *Pliocardia*? *guthrieorum* lacks.

Stratigraphic and geographic range.—Upper Eocene? to Oligocene seep deposits; Olympic Peninsula, western Washington State, USA.

Genus *Squiresica* Hybertsen, Goedert, and Kiel, 2022

Type species: *Archivesica knapptonensis* Amano and Kiel, 2007, by original designation; Oligocene, western Washington State, USA (Hybertsen et al. 2022).

Remarks.—Some species of *Squiresica* show a dimorphism in shell shape. The posterior part of the shell either has an evenly rounded posterior margin (i.e., *S. yooni* sp. nov., Fig. 9C$_2$) or a sloping posterodorsal margin (i.e., *S. yooni* sp. nov., Fig. 9A$_3$, B$_2$). This dimorphism has been reported from extant vesicomyid taxa such as *Calyptogena* (Krylova and Sahling 2006). Although it occurs in fossil vesicomyids too (SK personal observation), it is rarely explicitly described.

Squiresica cf. *knapptonensis* (Amano and Kiel, 2007)

Fig. 7.

Material.—Eleven numbered specimens (NRM Mo 204773–78; 204805–09) and numerous additional fragments (NRM

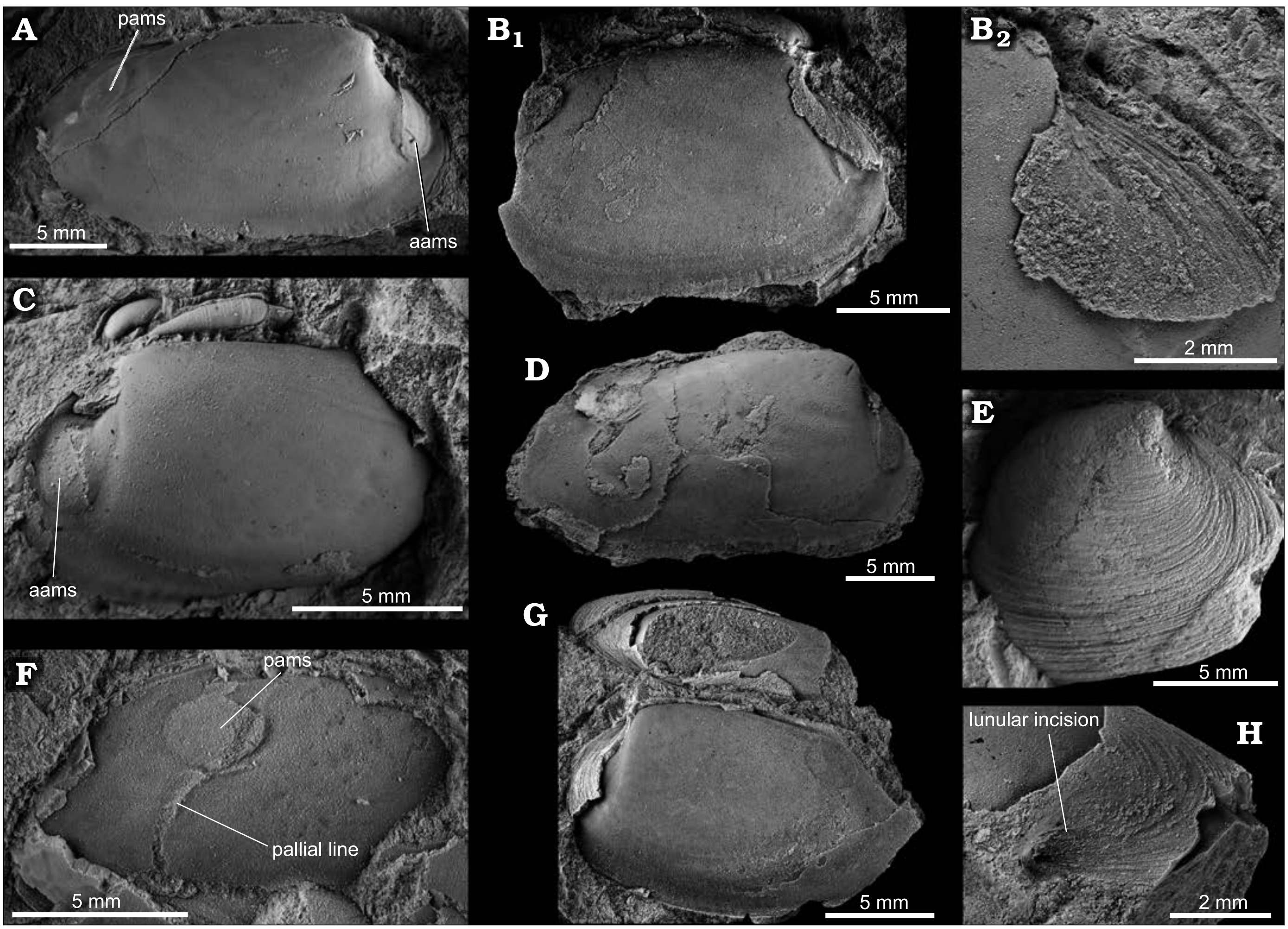

Fig. 7. The vesicomyid bivalve *Squiresica* cf. *knapptonensis* (Amano and Kiel, 2007) from upper Eocene seep deposits of the Siltstone Unit B along the West Fork of Grays River in western Washington State, USA. **A**. NRM Mo 204773, internal mold of RV showing adductor muscle scars and pallial line. **B**. NRM Mo 204808, internal mold of semi-articulated specimen; view on RV (B$_1$); close-up on lunular incision (B$_2$). **C**. NRM Mo 204776, internal mold of LV showing anterior adductor muscle scar, onset of pallial line, and the short ligament. **D**. NRM Mo 204775, internal mold of RV showing adductor muscle scars and pallial line. **E**. NRM Mo 204809, anterior half of RV showing external shell sculpture. **F**. NRM Mo 204805, view on internal mold of posterior adductor muscle scar. **G**. NRM Mo 204807I, internal mold of semi-articulated specimen, view on LV. **H**. NRM Mo 204806, close-up on lunular incision of LV.

Table 4. Measurements (in mm) of *Squiresica* cf. *knapptonensis* (Amano and Kiel, 2007). na, measurement not possible.

Specimen no.	Length	Height	Width	Locality
NRM Mo 204773	23.6	12.0	na	Grays River
NRM Mo 204774	21.7	10.0	na	Grays River
NRM Mo 204775	23.5	12.3	8.0	Grays River
NRM Mo 204776	13.5+	10.7	na	Grays River
NRM Mo 204777	21.7	12.2	na	Grays River
NRM Mo 204778	23.7	11.5	na	Grays River
NRM Mo 204807	16.3	10.0	na	Grays River
NRM Mo 204808	18.0	12.0	na	Grays River

Mo 204810) from the Eocene Siltstone of Unit B in the Grays River area, western Washington State, USA.

Dimensions.—See Table 4.

Remarks.—The visible features of the late Eocene age specimens from the Siltstone of unit B fall within the variation seen in the early to late Oligocene age specimens of *S. knapptonensis* from various deposits of the Lincoln Creek Formation (Amano and Kiel 2007; Hybertsen et al. 2022). However, their hinge dentition remains unknown and therefore we assign these specimens only preliminarily to *S. knapptonensis*.

Stratigraphic and geographic range.—Upper Eocene, Siltstone of unit B, southwestern Washington State, USA.

Squiresica plana sp. nov.

Fig. 8.

1993 *Calyptogena chinookensis* Squires and Goedert, 1991; Goedert and Squires 1993: fig. 5.

1995 *Calyptogena* (*Calyptogena*) *chinookensis* Squires and Goedert, 1991; Goedert and Campbell 1995: 24, table 1.

Zoobank LCID: urn:lsid:zoobank.org:act:82DEC36A-45E3-438D-9AF0-99BBD8F1A5D4.

Etymology: From Latin *plana*, flat; in reference to the minimal inflation of the species.

Type material: Holotype: articulated specimen with shell material (NRM Mo 204704). Paratypes: single valves or semi-articulated specimens embedded in rock matrix (NRM Mo 204705, 06, 204770–72) from the type locality and horizon.

Type locality: UWBM loc. B7452, Canyon River, Washington State, USA.

Type horizon: The Lincoln Creek Formation, Oligocene.

Material.—Four specimens (NRM Mo 204769–72) and numerous fragments from Canyon River (UWBM loc. B7452), five specimens from LACMIP loc. 17426 (NRM Mo 204704–08); all Lincoln Creek Formation. About ten fragmentary specimens showing external features only (NRM Mo 204834) from LACMIP loc. 15621, Pysht Formation. Oligocene, Washington State, USA.

Diagnosis.—Small for genus, minimally inflated, lunular incision very indistinct, ligament short, anterior adductor muscle scar circular.

Description.—Small, elongate, little inflated shells reaching 21 mm in length; umbones only slightly elevated, slightly prosogyrate, pointed, situated anteriorly at about 20% total shell length; surface covered by fine, dense growth increments; escutcheon and ligament short, narrow, no lunular incision. Anterior adductor muscle scar roundish with acute dorsal side; pallial line starting just anterior of posteroventral corner of anterior adductor muscle scar, running parallel to ventral margin, at posterior end curving upward into circular posterior adductor muscle scar. Hinge plate moderately wide, LV with three radiating teeth, cardinal tooth 2a thin, pointing anteriorly, 2b thick, short, pointing posteroventrally, cardinal tooth 4b short, thin, subparallel to 2b; subumbonal pit small, triangular.

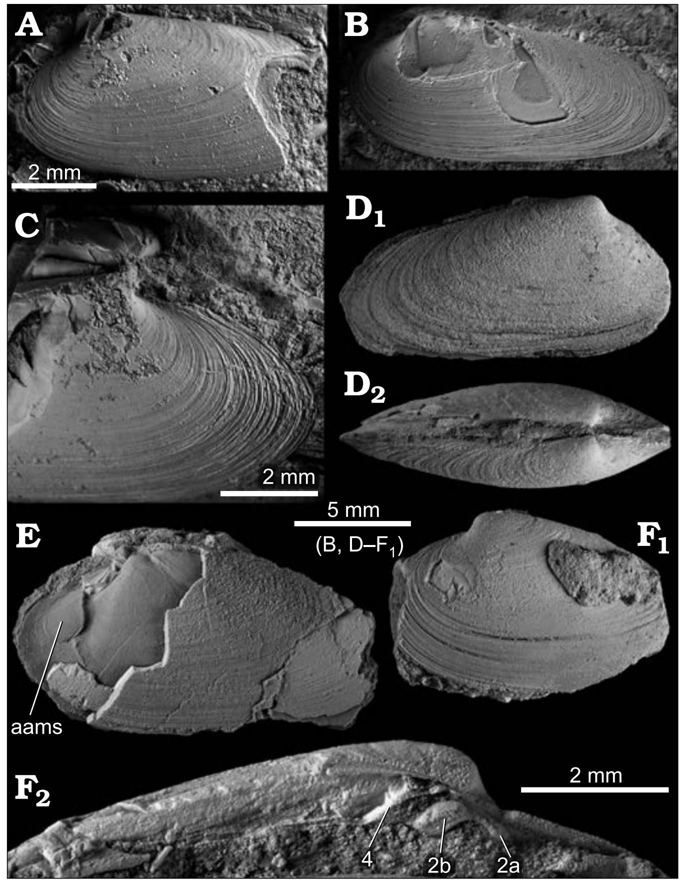

Fig. 8. The vesicomyid bivalve *Squiresica plana* sp. nov., from Oligocene seep deposits in the Lincoln Creek Formation in western Washington State, USA. Specimens from UWBM loc. B7452 (A–C) and LACMIP loc. 17426 (= SR4) (D–F). **A**. Paratype, NRM Mo 204772, exterior of LV showing fine growth increments. **B**. Paratype, NRM Mo 204771, exterior of LV showing shell outline and fine growth increments. **C**. Paratype, NRM Mo 204770, close-up on anterior part of RV showing near absence of a lunular incision. **D.** Holotype, NRM Mo 204704, articulated specimen with preserved shell; lateral view on RV (D_1) and dorsal view, showing inflation and ligament (D_2). **E**. Paratype, NRM Mo 204705, specimen with partially preserved shell, showing anterior adductor muscle scar and onset of pallial line. **F**. Paratype, NRM Mo 204706, semi-articulated specimen; F_1, close-up on LV hinge area; F_2, lateral view on LV.

Dimensions.—See Table 5.

Remarks.—*Squiresica plana* sp. nov. differs from *Squiresica knapptonensis* mainly by having a smaller, less inflated shell with posteriorly directed 2b tooth and very indistinct, elon-

Table 5. Measurements (in mm) of *Squiresica plana* sp. nov. ** holotype; * paratype; na, measurement not possible.

Specimen no.	Length	Height	Width	Locality
NRM Mo 204704**	14.2	7.0	4.4	LACMIP loc. 17426
NRM Mo 204705*	15.7	10.0	5.4	LACMIP loc. 17426
NRM Mo 204706*	12.0	7.8	4.0	LACMIP loc. 17426
NRM Mo 204707	14.8	9.0	5.0	LACMIP loc. 17426
NRM Mo 204708	12.8	7.6	4.0	LACMIP loc. 17426
NRM Mo 204769	20.8	8.7	na	UWBM loc. B7452
NRM Mo 204770*	12.4+	7.8	na	UWBM loc. B7452
NRM Mo 204771*	14.5	6.3	na	UWBM loc. B7452
NRM Mo 204772*	7.5	3.3	na	UWBM loc. B7452

gate and narrow lunular incision. The Miocene *Squiresica yooni* sp. nov. from Korea described below is more inflated and has a wider escutcheon. Oligocene specimens previously reported as *Calyptogena chinookensis* Squires and Goedert, 1991, from the Pysht and Makah formations in northwestern Washington State (Goedert and Squires 1993; Goedert and Campbell 1995) have the general shape and size of *S. plana* and are here considered as belonging to this species. They are quite different from the large type specimens of *Pleurophopsis chinookensis* (discussed below) that reach 80 mm in length.

Stratigraphic and geographic range.—Seep deposits in the Oligocene parts of the Pysht, and Lincoln Creek formations, western Washington State, USA.

Squiresica yooni sp. nov.

Fig. 9.

1976 *Calyptogena* cf. *elongata* Dall; Yoon 1976a: 13, pl. 3: 3, 7, 9.

Zoobank LCID: urn:lsid:zoobank.org:act:74536D5A-3B34-4763-B4E0-89FC7DD33241.

Etymology: In honor of Sun Yoon, who donated the illustrated specimens to the late Professor Kanno, who in turn passed them on to KA.

Type material: Holotype: partially damaged internal mold, showing hinge characters (NRM Mo 204829). Paratypes: three articulated specimens, mostly internal molds (NRM Mo 204830–32) from the type locality and horizon.

Type locality: Loc. 18 of Yoon (1976b), hillside cut for the foundation of house building, about 400 m southeast of Goedong-dong, Daesong-myeon, Yeongil-gun, South Korea.

Type horizon: Duho Formation, uppermost part of Yeonil Group, Middle Miocene.

Material.—The type material only.

Dimensions.—See Table 6.

Diagnosis.—Small *Squiresica* having some rough commarginal ribs in posterior surface, umbo strongly displaced anteriorly, convex ventral margin, very indistinct lunular incision, and rather strong cardinal tooth 1 of RV.

Table 6. Measurements (in mm) of *Squiresica yooni* sp. nov. from loc. 18 of Yoon (1976b), South Korea; ** holotype; * paratype.

Specimen no.	Length	Height	Width
NRM Mo 204829**	30.0	17.0	8.2
NRM Mo 204830*	24.4	13.0	8.0
NRM Mo 204831*	19.8	9.6	6.0
NRM Mo 204832*	19.4	11.2	6.0

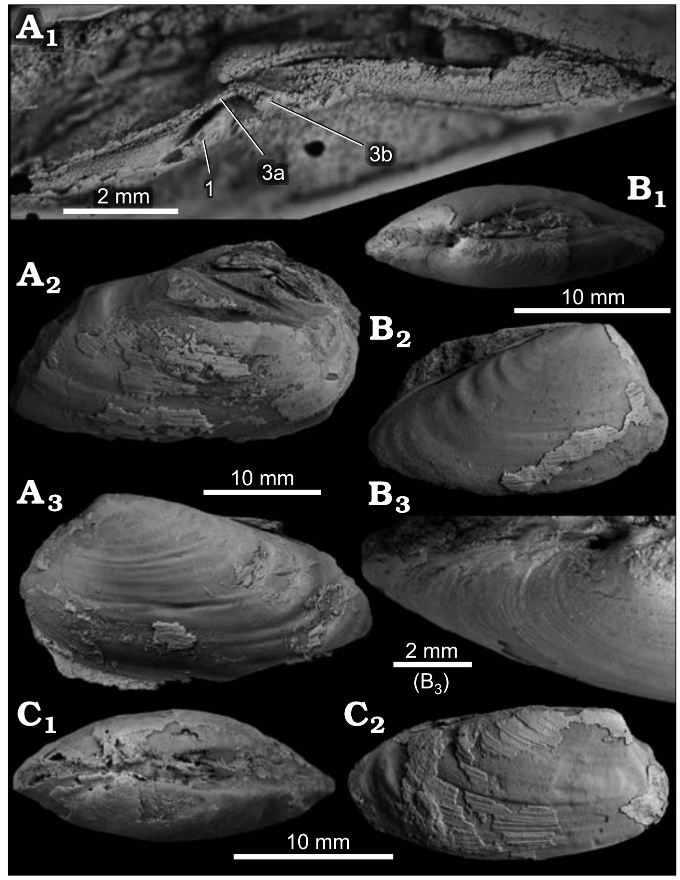

Fig. 9. The vesicomyid bivalve *Squiresica yooni* sp. nov., from the Middle Miocene Duho Formation, loc. 18 of Yoon (1976b), South Korea. **A**. Holotype, NRM Mo 204829, an articulated specimen with preserved cast of RV hinge area; close-up on hinge area (A_1), view on right valve and exposed hinge of left valve (A_2), and view on left valve (A_3). **B**. Paratype, NRM Mo 204832, articulated specimen, mostly an internal mold; dorsal view showing inflation (B_1); view on exterior of RV (B_2); close-up on anterior part of LV showing the lack of a lunular incision (B_3). **C**. Paratype, NRM Mo 204831, articulated specimen with some shell preserved; dorsal view showing inflation (C_1); lateral view on RV showing fine growth increments (C_2).

Original description.—“Shell small to medium in size, ovate, transversely elongated, thin. Beaks low, small, situated at about one-fourth of shell length anteriorly. No lunule, but escutcheon long, excavated; ligament external. Antero-dorsal margin short; anterior end rather narrowly rounded; posterodorsal margin long, almost straightly sloping down and passing into posterior end which is more narrowly rounded than the anterior one; ventral margin almost straight except for the both ends. Surface sculptured-with fine, somewhat rough, concentric growth lines.” (Yoon 1976a).

Supplemental description.—Hinge plate narrow, RV hinge with strong, elongate, forward-directed cardinal tooth 1, cardinal tooth 3a very thin, long, parallel to dorsal margin, cardinal tooth 3b short, bifid with raised edges, radiating posteroventrally, subumbonal pit elongate-triangular, very distinct.

Slight dimorphism in shell outline: posterior margin either evenly rounded or with sloping posterodorsal margin.

Remarks.—According to Yoon (1976b), specimens of *Squiresica yooni* sp. nov. occur in dense aggregations of articulated valves in the siltstone of the type locality, associated with specimens of a thyasirid identified as *Conchocele bisecta*. Yoon's (1976a) largest specimen was 34.5 mm long.

The main differences between *Squiresica yooni* and *S. knapptonensis* (Amano and Kiel, 2007) are the shorter anterior portion of the shell, the stronger cardinal tooth 1, and the virtual lack of a lunular incision in *S. yooni*. The Eocene–Oligocene *Squiresica plana* sp. nov. described above differs from *S. yooni* by being smaller (length up to 20.8 mm in *S. plana* vs. up to 30 mm in *P. yooni*), possessing a more distinct lunular incision and having more parallel dorsal and ventral shell margins.

Notably similar to *Squiresica yooni* regarding size, elongation, and inflation is the early Oligocene age *Pleurophopsis lithophagoides* Olsson, 1931, from Peru, which is also similar to the Oligocene *Squiresica knapptonensis*. With the pallial sinus and lunule of *P. lithophagoides* being unknown, its relation to *Squiresica* remains uncertain (i.e., Kiel et al. 2020b; Hybertsen et al. 2022).

Stratigraphic and geographic range.—Middle Miocene Duho Formation, South Korea.

Genus *Pleurophopsis* Van Winkle, 1919

Type species: *Pleurophopsis unioides* Van Winkle, 1919, by monotypy; Middle Miocene, Trinidad.

Pleurophopsis chinookensis (Squires and Goedert, 1991)

Fig. 10.

1990 *Calyptogena* n. sp.; Goedert and Squires 1990: fig. 20p, o.

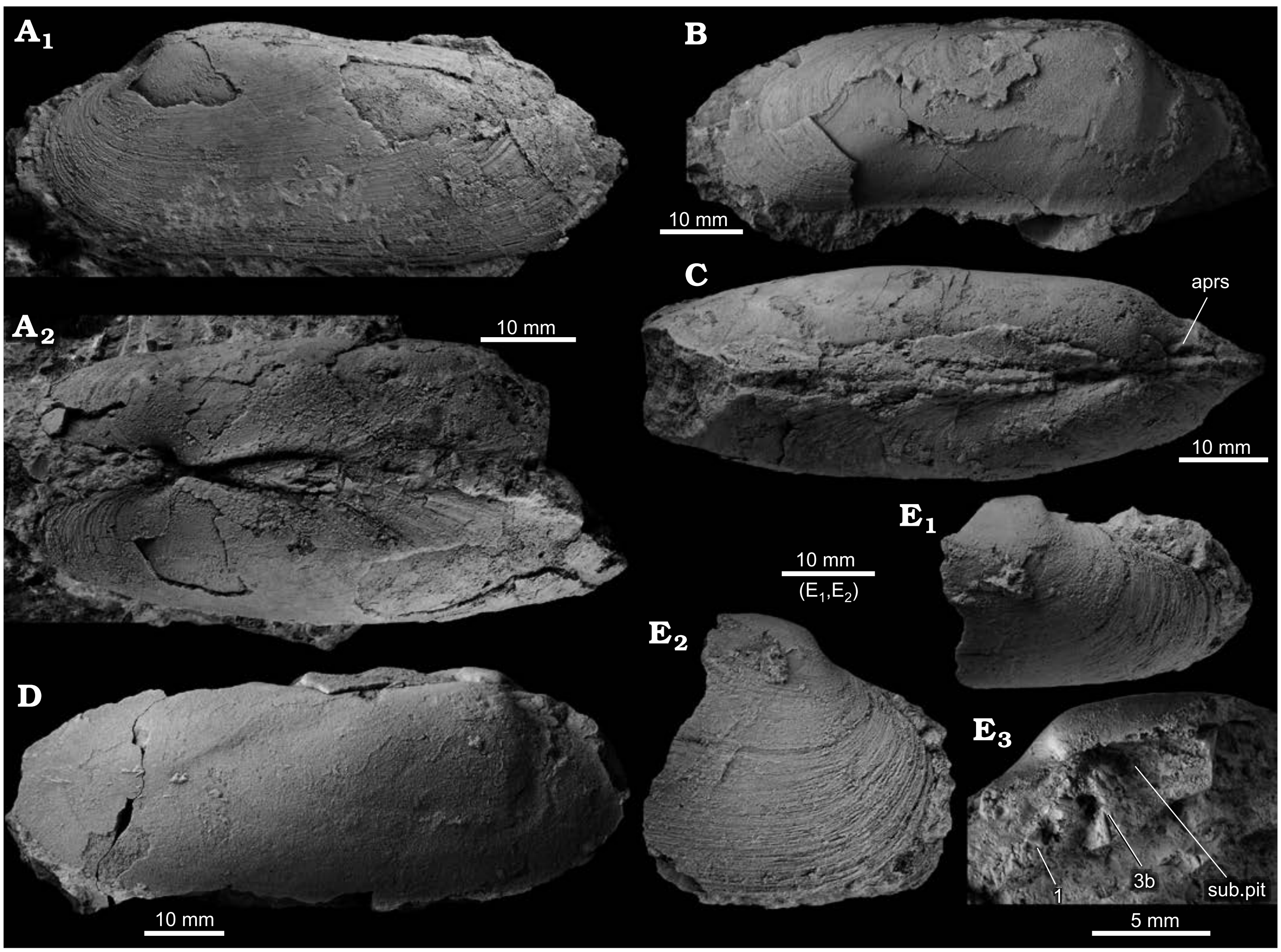

Fig. 10. The vesicomyid bivalve *Pleurophopsis chinookensis* (Squires and Goedert, 1991), from the upper Eocene Bear River seep deposit in western Washington State, USA. **A**. NRM Mo 204815, semi-articulated specimen with preserved shell material; view on LV (A_1); dorsal view showing short ligament (A_2). **B**. NRM Mo 204816, largely an internal mold, view on LV showing anterior adductor muscle scar. **C**. NRM Mo 204817, closely articulated specimen in dorsal view, showing true width. **D**. NRM Mo 204818, view on RV of internal mold showing internal posterior ridge. **E**. NRM Mo 204819, anterior part of RV with preserved shell, showing lack of lunular incision (E_1, E_2) and hinge dentition (E_3). Abbreviations: aprs, anterior pedal retractor scar; sub. pit., subumbonal pit.

Table 7. Measurements (in mm) of *Pleurophopsis chinookensis* (Squires and Goedert, 1991) from the Bear River seep deposit. na, measurement not possible.

Specimen no.	Length	Height	Width
NRM Mo 204815	65.8	25.5	na
NRM Mo 204816	71.3	25.9	na
NRM Mo 204817	70.4	33.6	23.4
NRM Mo 204818	78.4	28.2	na

1991 *Calyptogena chinookensis* Squires and Goedert, 1991: 414, figs. 2.7–2.11.

non 1993 *Calyptogena chinookensis* Squires and Goedert; Goedert and Squires 1993: 53, figs. 3–5.

non 1995 *Calyptogena* (*Calyptogena*) *chinookensis* Squires and Goedert; Goedert and Campbell 1995: 24, table 1.

2007 *Adulomya chinookensis* (Squires and Goedert, 1991); Amano and Kiel, 2007: 279, figs. 19–23.

Material.—15 specimens (NRM Mo 204815–20) from the upper Eocene Bear River seep deposit, Washington State, USA.

Dimensions.—See Table 7.

Remarks.—To supplement previous documentations and descriptions of this species (Squires and Goedert 1991; Amano and Kiel 2007), here we illustrate (i) features of the shell surface (Fig. 10A) including the absence of a lunular incision (Fig. $10E_1$, E_2); (ii) a fully articulated specimen in dorsal view to show its true inflation (Fig. 10C); (iii) the short ligament (Fig. $10A_2$); (iv) the small, elongate anterior pedal retractor scar that is distinct from the adductor muscle scar (Fig. 10C); and (v) the hinge of a right valve showing two strong, radiating cardinal teeth, namely cardinals 1 and 3b, and a large and deep subumbonal pit (Fig. $10E_3$). This species was originally reported from middle to upper Eocene strata. Oligocene specimens previously assigned to *P. chinookensis* differ from those from the upper Eocene type locality by being notably smaller, less inflated, having a different arrangement of the hinge teeth, and possessing a lunular incision. These specimens belong to either *Squiresica knapptonensis* (Amano and Kiel, 2007) or *S. plana* sp. nov., as discussed above.

Stratigraphic and geographic range.—Humptulips Formation and Bear River seep deposit, Middle to upper Eocene, southwestern Washington State, USA.

Pleurophopsis thieli sp. nov.

Figs. 11, 12.

2002 *Vesicomya* (*Calyptogena*) sp.; Peckmann et al. 2002: 861, fig. 3C.

2003 *Vesicomya* (*Calyptogena*) sp.; Goedert et al. 2003: pl. 42: 6, 7.

Zoobank LCID: urn:lsid:zoobank.org:act:C3DAEBBE-2844-4BDB-BEA4-3C1C01A76A69.

Etymology: In honor of Bruce Thiel (Portland, Oregon), in recognition of his help with fieldwork related to this project.

Type material: Holotype: articulated internal mold showing pallial line and muscle scars (NRM Mo 204761). Paratypes: mostly internal molds (NRM Mo 204762–65, 204826) from Jansen Creek Member; articulated or semi-articulated specimens with shell material (Mo 204794–797) and internal molds (Mo 204798–802 from Whiskey Creek seep deposit. Upper Eocene to lower Oligocene, Washington State, USA.

Type locality: Shoreline exposures approximately 800 m southeast of the mouth of Rasmussen Creek, Clallam County, Washington State, USA.

Type horizon: Jansen Creek Member of the Makah Formation, lower Oligocene.

Material.—About 25 specimens and fragments from the Whiskey Creek site, Pysht Formation (NRM Mo 204794–204802, UWBM 97305, 06). About 34 specimens from the Jansen Creek Member of the Makah Formation, including four from near Rasmussen Creek (NRM Mo 204761–64) and about 30 from near the mouth of Jansen Creek, many in butterfly preservation (NRM Mo 204765–68, 204828). Nine specimens from UWBM loc. B6702 (= SR2 in Peckmann et al. 2002), Lincoln Creek Formation (NRM Mo 204826, 27). Upper Eocene to lower Oligocene, Washington State, USA. UWBM 97038 was previously reported as *Vesicomya* (*Calyptogena*) sp. by Peckmann et al. (2002).

Diagnosis.—Shell average size for genus, inflation slight to moderate, posterior side tapering, often bent downward due to concave ventral margin; anterior adductor muscle scar bean or D-shaped; posterior adductor muscle scar rather small, displaced anteriorly, near posterodorsal margin; hinge with two strong, radiating teeth in right valve and three in left valve; subumbonal pit large and deep.

Description.—Shell elongate, up to 57.6 mm long; umbones anterior, at about 20% of total shell length; blunt, low ridge running from umbones to posterior margin; no lunular incision or escutcheon; anterior margin evenly to acutely rounded; anterior half of ventral margin straight, posterior half slightly concave, giving shell curved appearance; posterodorsal margin either straight and slightly tapering (Fig. 11D), or anterior half straight and parallel to ventral margin, and posterior half more strongly inclined toward the ventral (Fig. 12E); posterior margin evenly rounded. Anterior adductor muscle scar bean to D-shaped with posterior edge, pallial line starting at its posteroventral corner, extending subparallel to ventral shell margin, and bending upward and anteriorly near the posterior shell margin, to merge into ventral margin of posterior adductor muscle scar; posterior adductor muscle scar positioned at about 30% of total shell length, relatively small, with broad trapezoid area including the pedal retractor scar to its anterior; hinge plate short and moderately broad, with two strong, radiating cardinal teeth in each valve; RV with short cardinal tooth 1 originating under umbo, running oblique to anterodorsal shell margin, cardinal tooth 3a reduced, 3b originating under umbo, short, running oblique to posterodorsal shell margin; LV with short, thin cardinal tooth 2a running subparallel to anterodorsal shell margin, 2b thick, triangular or bifid, directly under umbo, 4b very short and thin, or reduced; oval subumbonal pit present in each valve.

Dimensions.—See Table 8.

Remarks.—Most similar to *Pleurophopsis thieli* sp. nov.

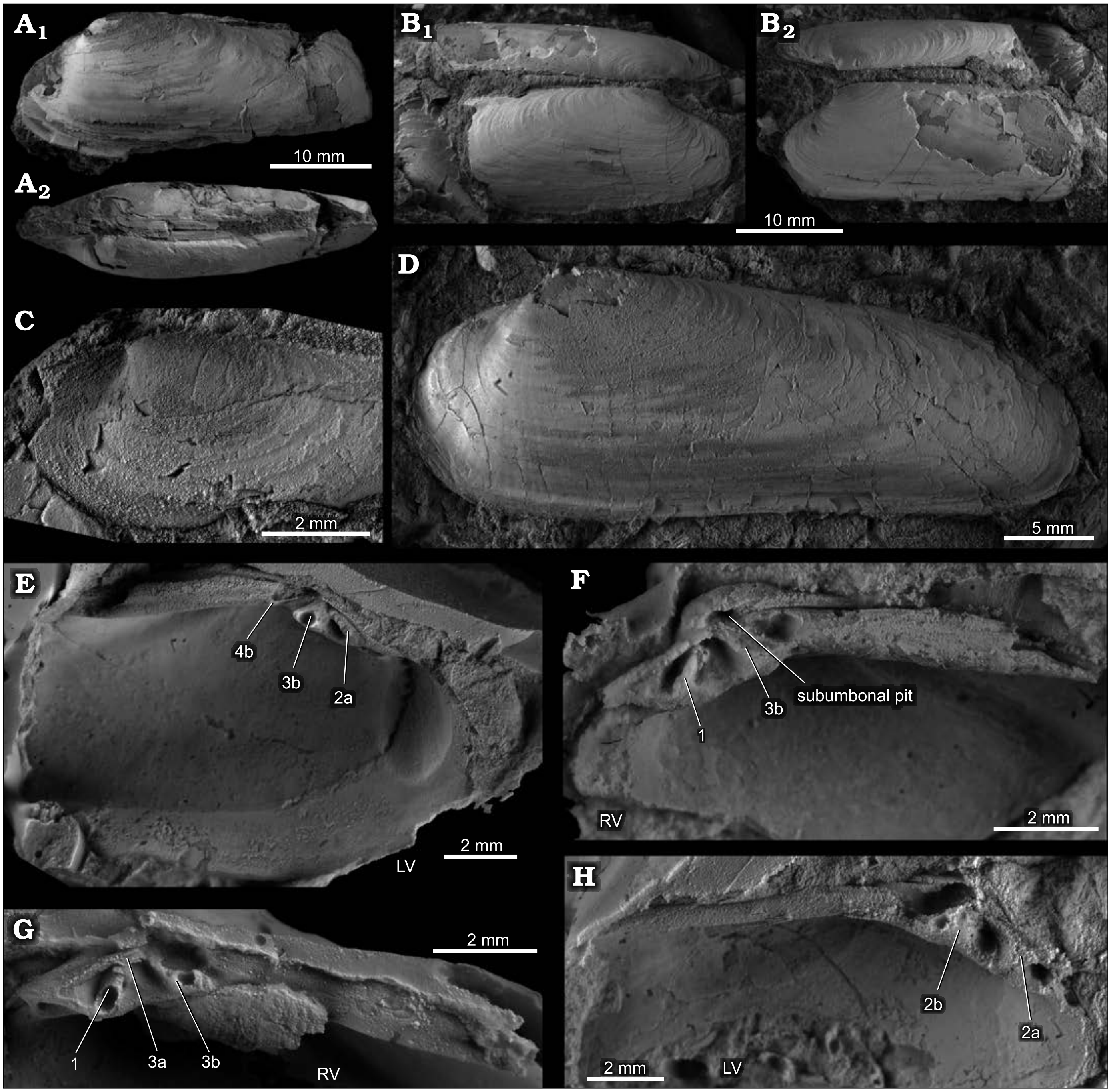

Fig. 11. The vesicomyid bivalve *Pleurophopsis thieli* sp. nov., from the upper Eocene Whiskey Creek seep deposit in the Pysht Formation in western Washington State, USA. **A**. NRM Mo 204797, small articulated specimen, showing inflation; left valve (A_1) and dorsal (A_2) views. **B**. NRM Mo 204795, semi-articulated specimen; left valve (B_1) and right valve (B_2) views. **C**. NRM Mo 204796, small left valve, showing lack of lunular incision. **D**. NRM Mo 204794, LV showing shell outline. **E**. NRM Mo 204799, hinge area and anterior adductor muscle scar of LV. **F**. NRM Mo 204800, hinge plate of right valve. **G**. NRM Mo 204801, hinge plate and ligament nymph of RV. **H**. NRM Mo 204802, hinge plate and ligament nymph of LV. All specimens are paratypes.

Fig. 12. The vesicomyid bivalve *Pleurophopsis thieli* sp. nov., from lower Oligocene, western Washington State, USA. Jansen Creek Member, Makah Formation (A–C, G); "Big slide", Jansen Creek Member, Makah Formation (D–F); UWBM loc. B6702, Lincoln Creek Formation (H). **A**. Paratype, NRM Mo 204762, internal mold of articulated specimen, showing anterior adductor muscle scar (aams), inflation, and long ligament; left valve (A_1) and dorsal (A_2) views. **B**. Holotype, NRM Mo 204761, internal mold of articulated specimen, showing muscle scars and pallial lin; dorsal view of posterior part (B_1) and right valve (B_2). **C**. Paratype, NRM Mo 204764, internal mold of LV, showing anterior adductor muscle scar and course of anterior part of pallial line. **D**. Paratype, NRM Mo 204768, RV with preserved shell material, showing external sculpture. **E**. Paratype, NRM Mo 204765, RV with preserved shell material, showing external sculpture. **F**. Paratype, NRM Mo 204828, block with numerous specimens in butterfly preservation. **G**. Paratype, NRM Mo 204763, rubber cast of LV hinge area. **H**. Paratype, NRM Mo 204826, anterior part of RV showing hinge dentition. B and C not coated with ammonium chloride. →

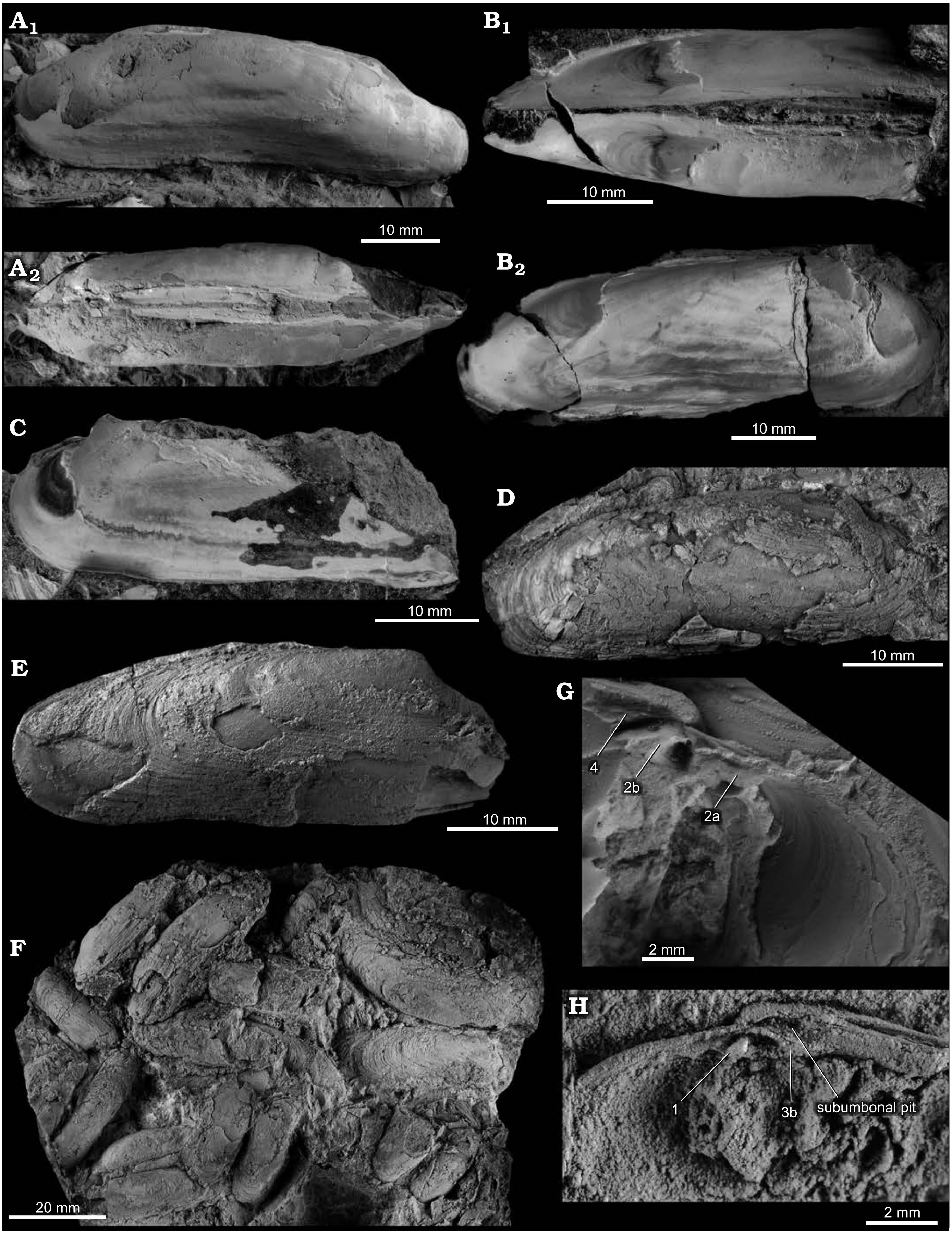
A1
B1
10 mm
10 mm
A2
B2
10 mm
C
D
10 mm
10 mm
E
G
4
2b
2a
10 mm
2 mm
F
H
1
3b
subumbonal pit
20 mm
2 mm

Table 8. Measurements (in mm) of *Pleurophopsis thieli* sp. nov. ** holotype; * paratype; na, measurement not possible.

Specimen no.	Length	Height	Width	Locality
NRM Mo 204794*	35.7	13.5	na	Whiskey Creek
NRM Mo 204795*	31.3	11.4	na	Whiskey Creek
NRM Mo 204796*	9.2	4.5	na	Whiskey Creek
NRM Mo 204797*	26.0	10.4	na	Whiskey Creek
NRM Mo 204798*	38.8	16.0	na	Whiskey Creek
NRM Mo 204761**	57.0	20.0	19.0	Jansen Creek area
NRM Mo 204762*	57.6	16.4	15.0	Jansen Creek area
NRM Mo 204764*	45.6	na	na	Jansen Creek area
NRM Mo 204765*	44.4	16.8	na	Jansen Creek area
NRM Mo 204766	37.8	13.3	na	Jansen Creek area
NRM Mo 204767	36.6	14.0	na	Jansen Creek area
NRM Mo 204768	43.8	15.0	na	Jansen Creek area

is *Pleurophopsis chitanii* (Kanehara, 1937) from Lower to Middle Miocene strata in Japan (Kanehara 1937; Hirayama 1973; Amano and Jenkins 2007; Amano and Kiel 2011). The main difference is in the posterior adductor muscle scar, which is smaller and more anteriorly positioned in *P. thieli*, whereas *P. chitanii* has a very large posterior adductor muscle scar in an almost terminal posterior position.

Specimens resembling *P. thieli* have been reported as *P. chitanii* from presumably Lower to Middle Miocene strata on Kayak Island, Alaska (Kanno 1971). In our view, the identity and relation of the Kayak Island specimens to either *P. chitanii* or *P. thieli* are somewhat uncertain. The size and morphological range of the specimens sketched and illustrated by Kanno (1971) suggests that they perhaps belong to more than one species. One illustrated specimen (Kanno 1971: pl. 7: 6) shows a pams that appears to be in a somewhat intermediate position between those seen in *P. chitanii* and *P. thieli*. Confusingly, although Kanno (1971) lists *P. chitanii* only from USGS loc. M1769 in the upper part of the Yakataga Formation on Kayak Island, Plafker (1974) lists only one mollusk from that locality, a sareptid bivalve. Plafker (1974) does, however, list *P. chitanii* from the upper and lower Yakataga Formation at four other localities on Kayak Island. Plafker (1974) lists *Calyptogena* n. sp.? from five additional localities, one of which (USGS loc. 15861), approximately 1.8 km east of Cape St. Peter is apparently the same, or very near loc. M1769 according to the map. Additional collecting effort is needed to clarify how many species of *Pleurophopsis* (or possibly other vesicomyid genera) are present in the strata on Kayak Island, including the upper and lower Katalla Formation because Plafker (1974) also recorded ?*Hubertschenckia* and a "vesicomyacid" from those strata. We also do not at present know anything about the local detailed geologic context for each of the sites listed and mapped by Plafker (1974); much more could be learned if these are discreet ancient seep sites. According to Addicott (1976: 123), the age of the Yakataga Formation on Kayak Island is Early Miocene, whereas the exposures on the mainland are Middle Miocene.

Pleurophopsis thieli differs from the late Eocene *P. chinookensis* by having a lower shell, more curved outline, resulting from its often slightly concave ventral margin and its sloping posterodorsal margin, whereas *P. chinookensis* has nearly straight and subparallel posterodorsal and posteroventral margins. The Middle Miocene type species *P. unioides* also has straighter and subparallel posterodorsal and posteroventral margins compared to *P. thieli*, and furthermore has larger and more round anterior and posterior adductor muscle scars (Van Winkle 1919; Kiel 2007; Krylova et al. 2010).

Stratigraphic and geographic range.—Seep deposits within the Pysht and Makah formations, upper Eocene to lowermost Oligocene, western Washington State, USA.

Genus *Hubertschenckia* Takeda, 1953

Type species: *Tapes ezoensis* Yokoyama, 1890, by monotypy; Poronai Formation, upper Eocene, Hokkaido, Japan.

Remarks.—A species named *Hubertschenckia quisquiliae* Hu, 1995, was reported from Eocene–Oligocene strata in south-central Taiwan, near Yakou village along Nankeng road (Hu 1995: 2020–2021, pl. 369: 1, 5; pl. 370: 9, 16; pl. 371: 1, 6, 8, 9). The shell was described as follows: "The shell is unequal triangular in shape, moderately swollen, with a short and concave front, a long and slight arc in the back, and a slightly boat-bottom-shaped ventral side. The umbo is located in front of the vertical midline, protruding and slightly inclined to the front. The front end of the shell is short and small, and the rear end is long and round. The surface is sculptured by evenly spaced commarginal ribs." (Hu 1995, translated from Chinese by Liping Liu).

The illustrated specimens, some of which were examined by SK in the National Museum of Natural Sciences in Taichung (NMNS 007556), bear some resemblance to *Hubertschenckia ezoensis* in outline, showing a large, round anterior adductor muscle scar and reaching 70 mm in length. Some have distinctive, equally spaced commarginal ribs with smooth, rounded surfaces (similar to those of an *Astarte*). Although these ribs match those on the sketch reconstruction by Hu (1995: 2021, text-fig. 7), several illustrated specimens are far more elongated (like *H. ezoensis*) than on Hu's (1995) sketch reconstruction. Whether all of those specimens belong to the same species, and whether any of the specimens belong to *Hubertschenckia*, remains questionable.

Hubertschenckia snatolensis Sinelnikova in Sinelnikova et al., 1991, was described from the middle Eocene Snatol Formation in western Kamchatka (Sinelnikova et al. 1991: 157, pl. 39: 14, pl. 40: 20). The species was described as "Shell elongate, flat, rather small, with almost parallel dorsal and ventral margin, and much anteriorly located umbo. Umbo very wide and weakly bending. Sculpture only consisting of growth lines. Hinge ill-preserved, but two cardinal teeth well visible on each valve. Pallial sinus wide, very short and high, with round top, located near muscle scar. Measurements (in mm); length = 35, height = 19, thickness = 8. Comparison; This species is distinguished from *Hubertschenckia ezoensis* (Yok.) by having much smaller size, longer and more flat shell." (Sinelnikova et al. 1991, translated from Russian by KA).

The description and illustrations of this species are insufficient to accept or reject affinities to Vesicomyidae. Considering its size and outline, the specimens resemble *Squiresica* rather than *Hubertschenckia*; however, the reported two cardinal teeth in each valve would preclude a placement in either of these genera.

As noted in the discussion of *Pleurophopsis thieli*, an unidentified species questionably assigned to *Hubertschenckia* was listed from upper Oligocene to Lower Miocene localities in the Katalla Formation on Kayak Island, Alaska (Plafker 1974).

Hubertschenckia ezoensis (Yokoyama, 1890)

Fig. 13.

1890 *Tapes ezoënsis* sp. nov.; Yokoyama 1890: 197, pl. 25: 6–8.

non 1928 *Meretrix* (*Macrocallista*) *ezoensis* (Yokoyama). Yokoyama 1928: 77, pl. 8: 1.

1951 *Tapes* (new gen.?) *ezoensis* Yokoyama; Minato and Uozumi 1951: 150, pl. 13: 108a–c.

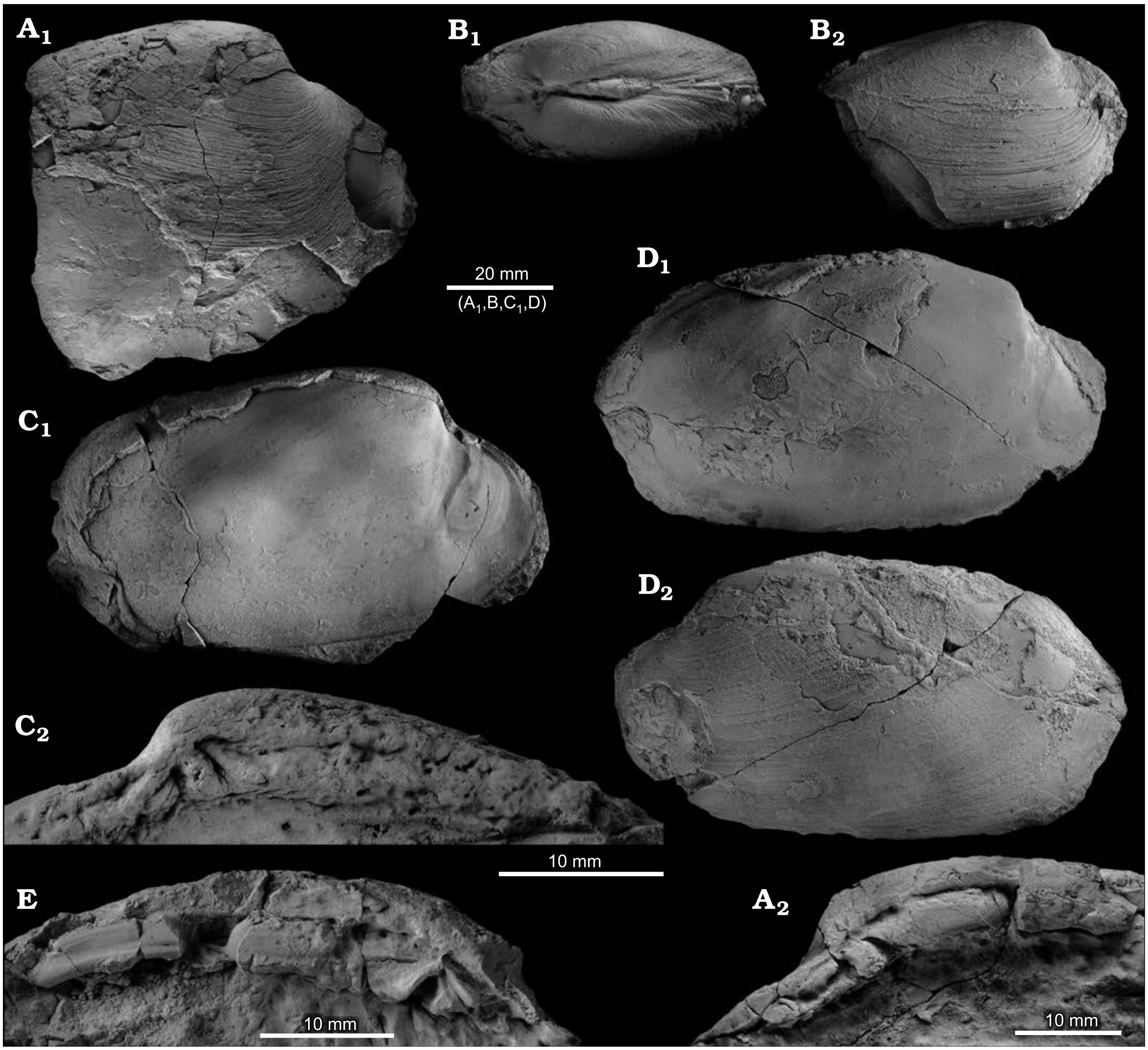

Fig. 13. The vesicomyid bivalve *Hubertschenckia ezoensis* (Yokoyama, 1890), from the upper Eocene Poronai Formation in Hokkaido, Japan. **A**. NRM Mo 204823, very large RV; external sculpture (A_1) and hinge (A_2) views. **B**. NRM Mo 204821, small articulated specimen; showing ligament (B_1) and external ornament and posterior ridge (B_2). **C**. NRM Mo 204824, internal mold of large RV, showing anterior adductor muscle scar; view on right valve (C_1) and close-up on hinge area (C_2). **D**. NRM Mo 204825, large articulated specimen, mostly an internal mold; view on right valve (D_1) and left valve (D_2). **E**. NRM Mo 204822, hinge of LV.

Table 9. Measurements (in mm) of *Hubertschenckia ezoensis* (Yokoyama, 1890) from the Poronai Formation; na, measurement not possible.

Specimen no.	Length	Height	Width
NRM Mo 204821	55.8+	38.8	25.5
NRM Mo 204822	85.0	44.0	na
NRM Mo 204823	na	65.0	na
NRM Mo 204824	90.4	52.6	na
NRM Mo 204825	92.4	50.5	na

1953 *Hubertschenckia ezoensis* (Yokoyama); Takeda 1953: 85, pl.13: 5.
1960 *Hubertschenckia ezoensis* (Yokoyama); Oyama et al. 1960: 188–189, pl. 58: 2a–d.
non 1989 *Hubertschenckia ezoensis* (Yokoyama); Honda 1989: 79: 13, 14.
2007 *Hubertschenckia ezoensis* (Yokoyama); Amano and Kiel 2007: 275–277, figs. 6–12.
2007 *Hubertschenckia ezoensis* (Yokoyama); Amano and Jenkins 2007: fig. 2B.
2013 *Hubertschenckia ezoensis* (Yokoyama); Amano et al. 2013: figs. 6K–M.
2016 *Hubertschenckia ezoensis* (Yokoyama); Nobuhara et al. 2016: figs. 2–16.
2016 *Hubertschenckia ezoensis* (Yokoyama); Kiel et al. 2016: fig. 1G.
2022 *Hubertschenckia ezoensis* (Yokoyama); Amano et al. 2022: figs. 10.9a, k.

Material.—Five large specimens (NRM Mo 204821–25) from the upper Eocene Poronai Formation in Hokkaido, Japan.

Dimensions.—See Table 9.

Remarks.—We illustrate several very large specimens of *Hubertschenckia ezoensis* to further document the characteristics of this species and their variability. The largest previously published specimen measured 74.6 mm in length (Amano and Kiel 2007); the largest specimen reported here exceeds 90 mm in length. One of our specimens has a height of 65 mm. Considering the L/H ratio of ca. 1.8 known from other specimens of *Hubertschenckia ezoensis*, this specimen could have been almost 120 mm in length, making it the largest Eocene vesicomyid known to date.

Stratigraphic and geographic range.—Upper Eocene to lower Oligocene, Hokkaido, Japan.

Discussion

The two *Vesicomya*? spp. reported here from the Oligocene are potentially the geologically oldest members of this genus. They would significantly extend the fossil record of *Vesicomya* compared to the next oldest records from Upper Miocene rocks of Buton Island, Indonesia (Beets 1953). *Vesicomya* is considered the sister taxon to all other vesicomyids (Johnson et al. 2017). Small, thin-shelled deep-water bivalves such as *Vesicomya* are particularly prone to have an incomplete fossil record (Valentine et al. 2006), and hence an even longer fossil record could be expected.

The new records and species of *Squiresica*, *S. plana* and *S. yooni*, expand the stratigraphic range of this genus, from the upper Eocene to the mid-Miocene. They also expand the geographic range of the genus, which now includes both sides of the North Pacific Ocean. The genus is not known from seep deposits of similar age in the Caribbean region, despite a relatively good fossil record (Gill et al. 2005; Kiel and Hansen 2015).

The decrease in vesicomyid species diversity in western Washington State after the Oligocene (Fig. 14) is likely a facies bias because most Neogene sediments in this region were deposited in increasingly shallower water (Kiel 2010c), where vesicomyids are uncommon. The Lower Miocene deep-water strata on Kayak Island, Alaska (Plafker 1974), may therefore be uniquely informative in this respect.

Several vesicomyid species today have broad geographic ranges including trans-Pacific occurrences (Kojima et al. 2004; Audzijonyte et al. 2012). There is no evidence for shared species or even genera between the eastern and western North Pacific during the Eocene and most of the Oligocene. The late Oligocene–Early Miocene *Pleurophopsis matsumotoi* Amano, Miyajima, Jenkins, and Kiel, 2019, from Japan is the first western Pacific occurrence of a vesicomyid genus that occurred earlier only in the eastern Pacific Ocean (Amano et al. 2019a). The first vesicomyid species with a trans-Pacific distribution is the Early to Middle Miocene *Pliocardia kawadai*, initially described from Japan and here reported from western Washington State, USA. However, the Oligocene record of seep deposits

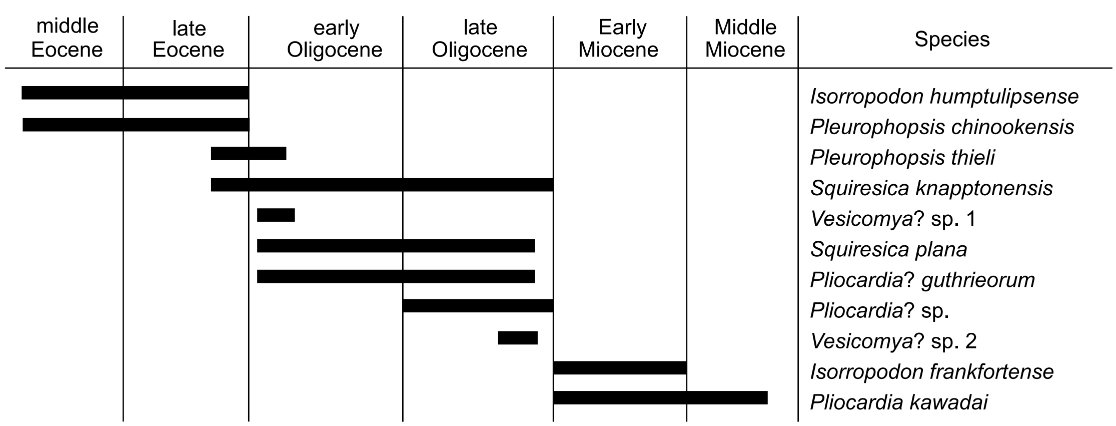

Fig. 14. Stratigraphic ranges of vesicomyid bivalve species in western Washington State, USA (reported herein and by Amano and Kiel 2007).

and vesicomyids of Japan is rather poor, with only three reported occurrences: *Hubertschenckia ezoensis* from upper Eocene to possibly lower Oligocene seep carbonates in southern Honshu (Amano et al. 2013) and from lower Oligocene seep deposit in eastern Hokkaido (Amano and Jenkins 2013; Kiel et al. 2016), and an upper Oligocene to Lower Miocene carbonate nodule with *Pleurophopsis matsumotoi* (Amano et al. 2019a). Thus, increased sampling in the Paleogene of Japan could potentially change this picture of shared, trans-Pacific vesicomyid species.

The fossil record of Late Miocene and younger deep-water faunas in western North America becomes rather poor, and a thorough comparison with the much better record of Japan is not feasible. *Calyptogena* first appears in the Oligocene of Alaska and is known from Japan from the Late Miocene and younger rocks (Kiel and Amano 2010; Amano et al. 2019a), suggesting a Northeastern Pacific origin of this genus. Furthermore, the Plio-Pleistocene *Archivesica gibbera* (Crickmay, 1929) and *A. lasia* (Woodring, 1938) from California (e.g., Squires 1991) seem to have quite close relatives in coeval strata in Japan, such as the Pliocene *A. kannoi* Amano and Kiel, 2010. *Archivesica* is regarded as having a warm-water origin (Amano and Jenkins 2011a; Amano et al. 2019a), and with *Archivesica* being unknown from Oligocene–Miocene deposits in the Caribbean region (Gill et al. 2005; Kiel and Hansen 2015) but present in Miocene to Pleistocene deposits of the Philippines (Kiel et al. 2020a, 2022), a western Pacific source area for the East Pacific, present-day *Archivesica* seems plausible.

Among other families of chemosymbiotic bivalves, the eastern and western North Pacific regions shared the bathymodiolin mussel *Bathymodiolus inouei* Amano and Jenkins, 2011, the lucinid *Lucinoma acutilineatum* (Conrad, 1849), and the thyasirid *Conchocele taylori* Hickman, 2015, during the late Eocene to Oligocene (Majima et al. 2005; Kiel 2010c; Amano and Jenkins 2011b; Kiel and Amano 2013; Hickman 2015; Hryniewicz et al. 2017). Whether the Neogene *Conchocele bisecta* (Conrad 1849) indeed occurs on both sides of the North Pacific (Weaver 1942; Majima et al. 2005; Kiel 2010a), or represents an as-yet undifferentiated garbage-bin taxon, remains to be tested.

Conclusions

Five new species and one new genus of Vesicomyidae are described from Cenozoic deep-water deposits in the North Pacific region. These include the oldest known vesicomyid, the middle to late Eocene *Isorropodon humptulipsense*, and the oldest records of the genera *Squiresica* (late Eocene), and possibly *Vesicomya* (early Oligocene). Our new findings document a rapid early morphological diversification among vesicomyids, starting with the short, strongly inflated *Isorropodon humptulipsense* and the elongate, inflated *Pleurophopsis chinookensis* in the middle Eocene. By the late Eocene, two further morphologies had appeared: the small, little inflated, elongated *Squiresica*, and the large, oval-elongate, moderately inflated *Hubertschenckia*. During the Eocene and most of the Oligocene there was apparently little faunal exchange among vesicomyids between the eastern and western North Pacific. Colonization from east to west appears to have commenced in the late Oligocene with the genus *Pleurophopsis*, and the Early to Middle Miocene occurrence of *Pliocardia kawadai* in both Japan and western Washington State is currently the oldest record of a vesicomyid species with a trans-Pacific distribution.

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