New mollusks associated with biogenic substrates in Cenozoic deep-water sediments of Washington State

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Cenozoic deep-water sediments of the Lincoln Creek, Makah, and Pysht formations in western Washington State, USA, contain sunken driftwood and whale bones that were colonized by invertebrates which largely depend on this type of transient habitat. These fossil wood- and whale-fall faunules yielded six new mollusk species that appear to have been endemic to these biogenic microhabitats, except for one species which also occurs in cold-seep limestones. The new gastropod species are the neomphalid *Leptogyra squiresi*, the buccinid *Colus sekiuensis*, the allogastropod *Xylodiscula okutanii*, and the new bivalve species are the protobranch "*Nuculana*" *posterolaevia*, the mytilid *Idas*? *olympicus*, and the heterodont *Thyasira xylodia*.

Key words: Gastropoda, Bivalvia, deep-sea, whale-fall, wood-fall, Eocene, Oligocene.

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Introduction

Whale carcasses and sunken wood in the deep-sea represent highly-localized but often large food items for the otherwise nutrient-poor deep-sea floor. These ephemeral habitats were coined whale- and wood-falls and support communities of highly specialized and largely endemic taxa (Dell 1987; Marshall 1988; Smith and Baco 2003). Most fossil examples of these microhabitats have so far been described from Eocene and Oligocene deep-water sediments of the Olympic Peninsula in western Washington State (Squires et al. 1991; Goedert et al. 1995; Lindberg and Hedegaard 1996; Kiel and Goedert 2006a, b). These fossil communities are very similar in their taxonomic composition to modern examples of these habitats, and ecologic relationships between the mollusks and the wood and bone can be established on actualistic grounds (Kiel and Goedert 2006b). The purpose of this paper is to provide detailed taxonomic descriptions of fossils representing six new species from these environments. Most of the species belong to groups with a considerable morphologic plasticity and a limited number of shell characters. Thus some uncertainty in our taxonomic assignments remains, but the present material does not allow a more reliable treatment.

Institutional abbreviations (all in USA).—CSUN, California State University Northridge; LACMIP, Los Angeles County Museum of Natural History, Invertebrate Paleontology; USGS, United States Geological Survey, Washington DC; USNM, National Museum of Natural History, Washington DC; UWBM, University of Washington, Burke Museum, Seattle.

Ecologic background

Time-series studies of whale carcasses on the bathyal seafloor off California indicate that dead whales pass through three successional stages (Smith and Baco 2003). These include a mobile scavenger stage during which most of the whale soft tissue is consumed by hagfish, sleeper sharks and other scavengers; an enrichment opportunist stage during which organically enriched sediments and bones are colonized by huge numbers of polychaetes and crustaceans; and a sulphophilic stage, during which trophically complex assemblages live on and around the skeleton as it emits sulfide from anaerobic breakdown of bone lipids (Smith and Baco 2003). The fauna of this third stage includes some chemosymbiotic and microbe-grazing species that also occur at hydrothermal vents and hydrocarbon seeps. Eocene and Oligocene whale bones most likely did not contain enough oil to sustain communities analogous to the "sulphophilic stage" of modern whale-falls or those of contemporaneous cold-seeps. Rather, these early whale-fall communities resembled wood-fall communities and represent a "chemosymbiotic opportunist stage" (Kiel and Goedert 2006a).

The nutrients stored in wood that sinks into the deep-sea are dispersed onto the surrounding seafloor mainly by xylophagaine and teredine bivalves, in the form of fecal pellets for detritus-feeders; the bivalves themselves are prey or carrion for predators and scavengers (Turner 1978). In addition, wood-degrading microbes and fungi are grazed upon by a variety of epifaunal gastropods, chitons, and limpets (Wolff 1979; Marshall 1985; Marshall 1986; Marshall 1988; Warén and Bouchet 2001; Sirenko 2004). Wood-fall bivalve taxa that host sulfide oxidizing endosymbionts include mytilids, thyasirids, and lucinids (Dell 1987; Kiel and Goedert 2006a; Janet R. Voight, personal communication 2005). The source of sulfides at wood-falls is not yet fully understood. They are most likely sequestered by a localized anoxic zone in the sediment underneath the wood resulting from the cover of fecal pellets around the wood which cuts off the oxygen supply derived from seawater causing anaerobic breakdown of the organic material (Kiel and Goedert 2006a, b).

Material and methods

The specimens were collected in seven localized areas in the Lincoln Creek, Makah, and Pysht formations on the Olympic Peninsula in Washington State, USA, depicted in Fig. 1. These formations are composed mainly of deep-water sediments and range in age from the late Eocene to the early Miocene (Armentrout 1973; Snavely et al. 1980; Moore 1984; Prothero and Armentrout 1985; Goedert and Squires 1993; Barnes and Goedert 2001). The stratigraphic positions of the various localities and the formations in which they occur are summarized in Fig. 2. Most whale- and wood-fall associations were found in concretions (Kiel and Goedert 2006a), and in one case in soft sediment (Kiel and Goedert 2006b). Larger specimens were photographed using the digital cameras Olympus Camedia C-3040 Zoom, and JVC KY-F75U; small specimens were photographed with a Philips XL30 ESEM scanning electron microscope.

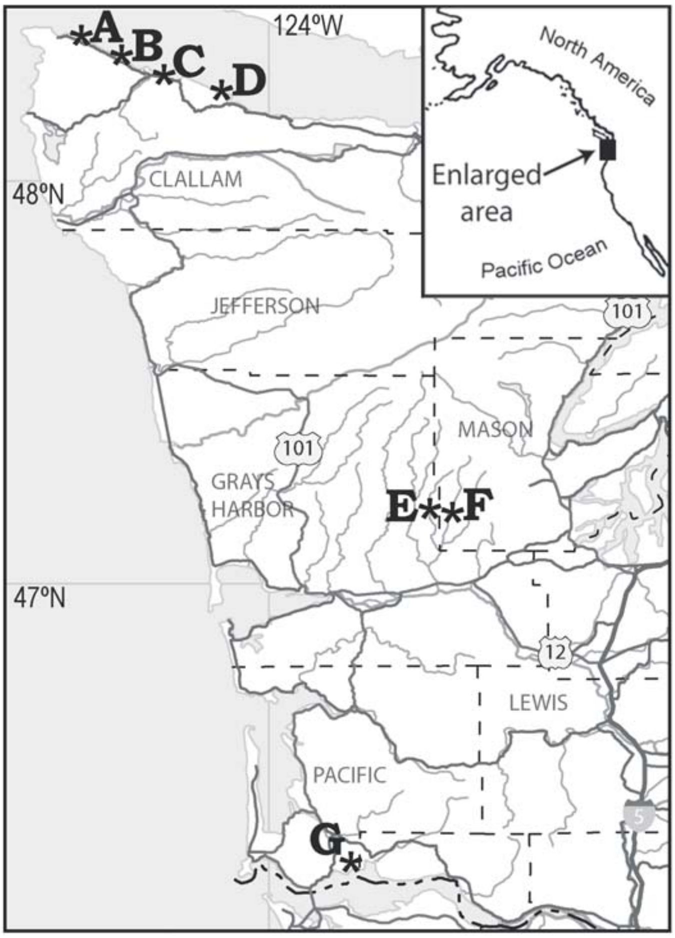

Fig. 1. Index map of western Washington State showing the fossil localities. **A**. Shipwreck Point (USGS loc. 26895). **B**. Sekiu River (USGS loc. 26896). **C**. Merrick's Bay (USGS loc. 26897). **D**. Murdock Creek (USGS loc. 26898). **E**. Canyon River sites (USGS locs. 26899–26901). **F**. Satsop River (USGS loc. 26902, 26905). **G**. Knappton (USGS locs. 26903–26904). Modified from Kiel and Goedert (2006a).

Systematic paleontology

Class Gastropoda Cuvier, 1797

Subclass uncertain

Family Neomphalidae McLean, 1981

Genus *Leptogyra* Bush, 1897

Type species: *Leptogyra verrilli* Bush, 1897; Recent, northwestern Atlantic.

Discussion.—*Leptogyra* has previously been placed in the Skeneidae Clark, 1851, a family that currently is a "dumping ground" for small, poorly studied deep-sea gastropods. Ongoing work indicates that *Leptogyra* belongs to the vent and seep endemic Neomphalidae (Kiel and Goedert 2006b; Steffen Kiel, Gerhard Haszprunar, and Yasunori Kano unpublished data).

Leptogyra squiresi sp. nov.

Figs. 3A–C.

2006 *Leptogyra* n. sp.; Kiel and Goedert 2006b: 549, fig. 2F, G.

Derivation of the name: For Richard L. Squires, Northridge.

Holotype: USNM 528923. Well-preserved specimen with slightly damaged apertural margin.

Paratypes: USNM 528922, 532037.

Type locality: USGS locality 26905, associated with wood fragments, Satsop River, Mason County, Washington State, USA.

Type horizon: Uppermost Eocene, Lincoln Creek Formation.

Material.—The type material and several unnumbered specimens from the type locality are deposited in the USNM.

Diagnosis.—Protoconch of one-half whorl, 190 µm diameter; with polygonal and spiral sculpture; a sinuous bulge near the aperture, transition to teleoconch marked by a fine ridge. Teleoconch low-spired skeneiform, apical angle about 125°, two and one-half convex, slightly shouldered whorls with fine spirals and prosocline axial ribs. Shell composed mainly of crossed-lamellar structure, with fine shell pores almost perpendicular to shell surface.

Description.—The protoconch is sculptured by a polygonal pattern on the first quarter whorl and spirally arranged wrinkles on the second quarter, the bulge near the aperture is approximately 15 microns wide. Suture of teleoconch deep; whorls sculptured by twelve fine spiral cords, with strongly prosocline ribs on earlier whorls, later whorls with strong

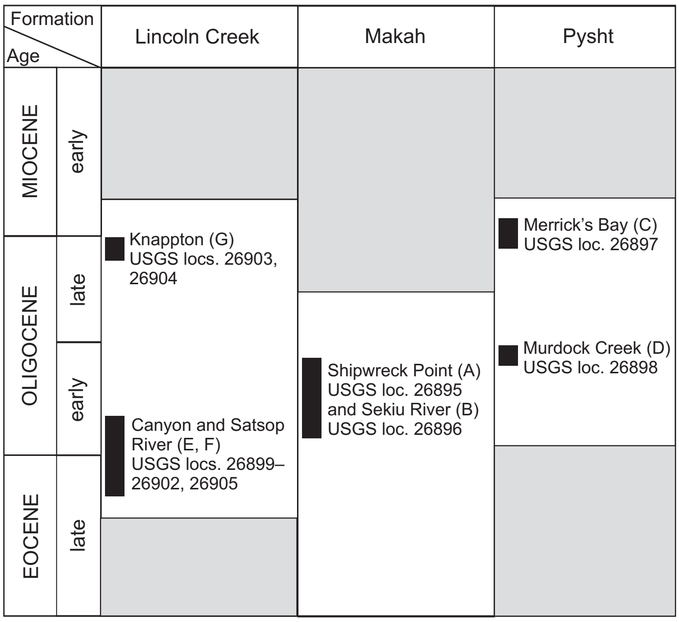

Fig. 2. Stratigraphic chart of the Lincoln Creek, Makah, and Pysht formations, indicating the stratigraphic position of the fossil localities discussed herein. Letters in parentheses refer to those in Fig. 1.

collabral growth lines only; the growth lines on the base are opisthocyrt; aperture broken, umbilical area covered by sediment in all specimens. Shell wall of the last whorl about 70 µm thick, composed of a thin (<10 µm) simple prismatic layer, and a thick layer of crossed-lamellar structure. The shell is perforated by thin (approximately 0.1 µm wide) pores. The holotype is 1.13 mm high and has a diameter of 1.61 mm.

Discussion.—This species is very close in shape to the Recent North Atlantic *Leptogyra verrilli* Bush, 1897 and *L. constricta* Marshall, 1988. From the latter it differs by its growth lines which are less prosocline. In *L. verrilli* the protoconch is larger (0.24 mm measured from Marshall 1988: fig. 2C) than in *L. constricta* and in *L. squiresi*. A *Leptogyra* species that inhabits hydrothermal vents rather than sunken wood is *L. inflata* Warén and Bouchet, 1993, which has finer sculpture than *L. squiresi*, and has, with 200 microns diameter, the smallest protoconch of the known recent species. The Recent Alaskan *L. alaskana* Bartsch, 1910, which is geographically the closest species to *L. squiresi*, has a lower spire than *L. squiresi*, but whether this species indeed belongs to *Leptogyra* is uncertain. Bartsch (1910) described the protoconch to consist of one-and-a-half whorls, which contradicts a position within *Leptogyra*, but the holotype is poorly preserved and the number of whorls of the protoconch was impossible to determine under a light microscope. However, Bartsch's (1910: 136) description of the protoconch as "light yellow horn color" cannot be confirmed. *Leptogyra squiresi* is the only species of *Leptogyra* known from the fossil record.

Stratigraphic and geographic range.—Known only from the uppermost Eocene in Washington State, USA.

Subclass Caenogastropoda Cox, 1959

Family Buccinidae Rafinesque, 1815

Genus *Colus* Röding, 1798

Type species: *Murex islandicus* Mohr, 1786; Recent, North Atlantic.

Colus sekiuensis sp. nov.

Fig. 3D, E.

2006 *Colus* sp.; Kiel and Goedert 2006a: 2626, fig. 2h.
2006 Buccind; Kiel and Goedert 2006b: 550, fig. 2M.

Derivation of the name: After the Sekiu River, near which many of the specimens were found.

Holotype: UWBM 97933. Complete specimen with 4.5 whorls.

Paratypes: USNM 531404, from USGS loc. 26898-A.

Type locality.—USGS locality 26898, Murdock Creek, Clallam County, Washington State, USA.

Type horizon: Upper lower Oligocene, lower part of Pysht Formation.

Material.—The type material and several specimens found at the following wood-fall sites: USGS locs. 26896-A, B, D, 26898-A, F, 26899, 26900, 26902, 26903, 26904, 26905. These specimens are deposited in the USNM.

Diagnosis.—Fusiform shell with at least five evenly convex whorls; sculpture of 12–13 subequal, broad, and almost flat-topped spiral cords, interspaces narrower than cords; same sculpture on siphonal column; aperture narrow-lenticular; siphonal canal short and twisted to the left.

Description.—Protoconch unknown; suture of teleoconch narrow and incised; in addition to spiral cords the whorls have numerous very fine opisthocyrt growth lines; the inner lip of the aperture is smooth. Height of holotype 23.5 mm, width 10 mm, apical angle ca. 35°.

Discussion.—This species has a rather generalized buccinid shell. It is placed here in *Colus* based on its overall similarity with the type species of this genus, but without radula or anatomical data some uncertainty remains. Similar shells are known from *Eosipho* Thiele, 1929, but most *Eosipho* species that we have seen either have additional axial ornament unlike *Colus sekiuensis*, or are smooth. Warén and Bouchet (2001) mentioned undescribed species of *Eosipho* from sunken wood in the tropical western Pacific. Also *Neptunea* Röding, 1798 builds similar shells, for example the Recent *Neptunea brevicauda* (Deshayes, 1832) which differs from *C. sekiuensis* only by its wider aperture and broader spiral cords. A very similar Recent buccind from deep water in the southern hemisphere is *Germonea rachelae* Harasewych and Kantor, 2004, which has the same spiral sculpture as *C. sekiuensis* but a more slender shell.

Two species of *Colus* have so far been reported from the Paleogene of the Pacific Northwest. A single specimen from the upper Eocene to lower Oligocene Keasey Formation in Oregon was named *Colus*? *precursor* Hickman, 1980. This specimen is slightly smaller than our largest specimens and has fewer but stronger and more erect spiral cords with very deep interspaces (Hickman 1980a). Kanno (1971) described *Colus* aff. *C. jordani* from the lower Oligocene and lowermost Miocene Poul Creek Formation in Alaska. *Colus* aff. *C.*

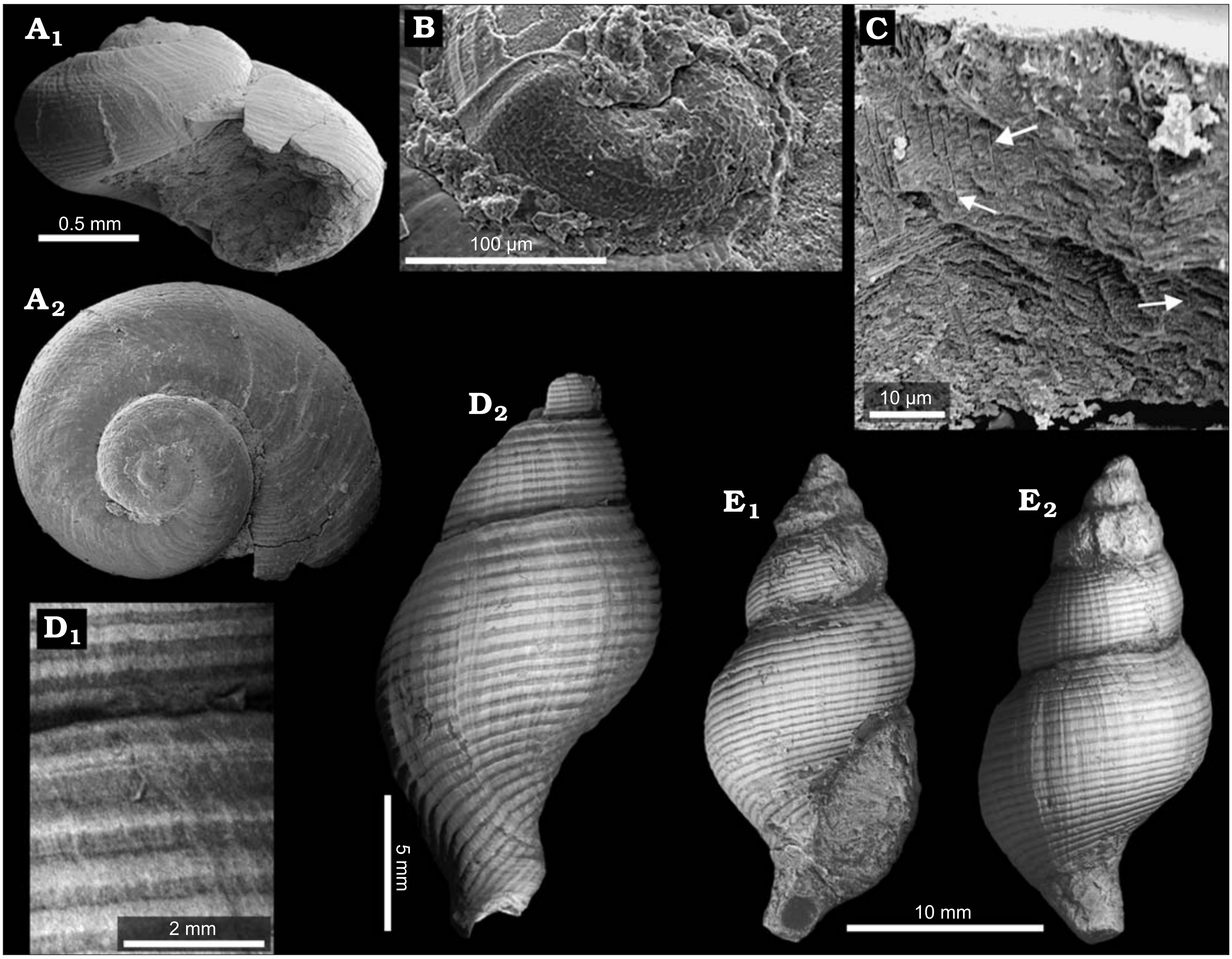

Fig. 3. Gastropods from Eocene to Miocene whale- and wood-falls in Washington State. **A**–**C**. Neomphalid *Leptogyra squiresi* sp. nov., from a uppermost Eocene wood-fall at the Satsop River (USGS loc. 26905). **A**. Holotype USNM 528923 in apertural (A_1) and apical (A_2) views. **B**. Protoconch of paratype, USNM 528922. **C**. Paratype showing shell microstructure, arrows indicate shell pores, USNM 532037. **D**, **E**. Buccinid *Colus sekiuensis* sp. nov. **D**. Paratype USNM 531404 from a upper lower Oligocene wood-fall at Murdock Creek (USGS loc. 26898-A); D_1, sculptural detail; D_2, lateral view. **E**. Holotype UWBM 97933 from a upper lower Oligocene whale-fall at Murdock Creek (USGS loc. 26898) in apertural (E_1) and lateral (E_2) views.

jordani differs from *Colus sekiuensis* in having numerous spiral threads with narrow interspaces, with a shorter and less twisted siphonal canal. On the western side of the North Pacific occurs *Colus* (*Aulacofusus*) *asagaensis* Makiyama, 1934 in Oligocene sediments in Japan, Sakhalin and Kamchatka (Oleinik 2001), a species in which the spiral ribs are more widely spaced than in *C. sekiuensis*.

Among the extant species of *Colus* from the North Pacific Ocean, *Colus herendeenii* (Dall, 1902) and *C. acosmius* (Dall, 1891) resemble *C. sekiuensis* regarding sculpture and the twisted siphonal canal, but differ by having less convex whorls and a less pronounced suture (Abbott 1974: figs. 2298, 2309). A very similar Recent species is *C. latericeus* Möller, 1842 from the North Atlantic (Bouchet and Warén 1985).

Neptunea has not been reported from Paleogene sediments in Washington, and the Neogene species all differ from *C. sekiuensis* by having shouldered whorls (Nelson 1978). A *Neptunea* that differs from *C. sekiuensis* by its broad last whorl and very weak spiral and axial sculpture was reported from the lower Oligocene Katalla district in Alaska (Oleinik and Marincovich 2003).

Stratigraphic and geographic range.—Uppermost Eocene to uppermost Oligocene, Lincoln Creek, Makah, and Pysht Formations, Washington State, USA.

Subclass Heterobranchia Gray, 1840
Order Allogastropoda Haszprunar, 1985
Family Xylodisculidae Warén, 1992
Genus *Xylodiscula* Marshall, 1988

Type species: *Xylodiscula vitrea* Marshall, 1988; Recent, bathyal, on sunken wood off New Zealand.

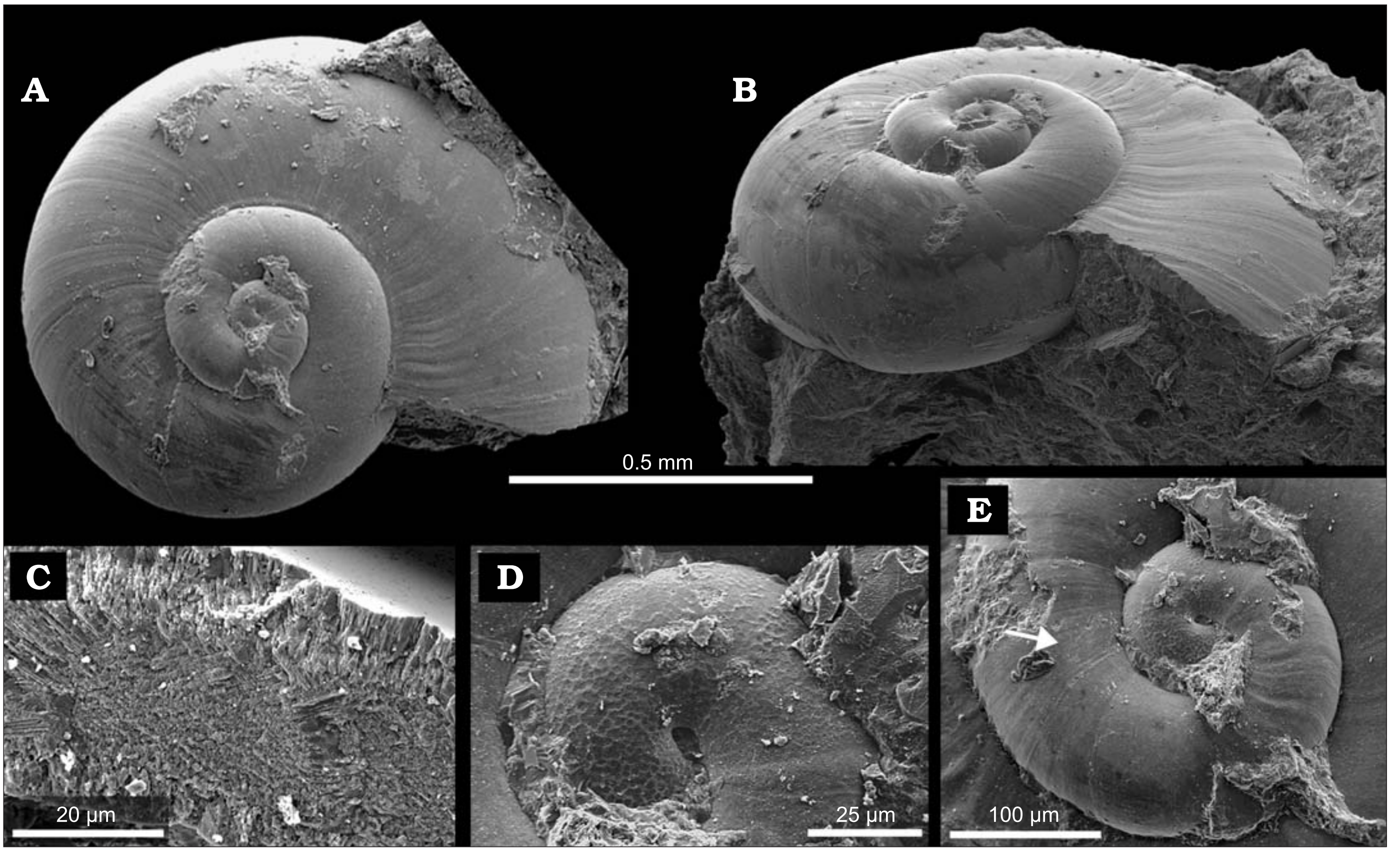

Fig. 4. Xylodisculid allogastropod *Xylodiscula okutanii* sp. nov., from a uppermost Oligocene or lowermost Miocene wood-fall in Merrick's Bay, holotype USNM 531406 from USGS loc. 26897-A. **A**. Apical view. **B**. Oblique view. **C**. Shell microstructure. **D**. Close-up of embryonic shell. **E**. Close-up of protoconch, arrow indicates transition from protoconch to teleoconch.

Xylodiscula okutanii sp. nov.

Fig. 4.

2006 *Hyalogyrina* n. sp.; Kiel and Goedert 2006a: 2626, fig. 2j, l.

Derivation of the name: After Takashi Okutani, Kanagawa.

Holotype: USNM 531406. Well-preserved specimen with lower half of aperture and base concealed by matrix.

Type locality: USGS loc. 26897-A, Merrick's Bay, Clallam County, Washington State, USA.

Type horizon: Uppermost Oligocene to lowermost Miocene, Pysht Formation.

Material.—Holotype only.

Diagnosis.—A *Xylodiscula* with almost three whorls, protoconch made of one and one-fifth whorls, 211 μm wide, initial part with fine polygonal pattern; teleoconch made of one and three-quarter well-rounded whorls, growth lines sinuous and well-visible near suture.

Description.—Embryonic part of protoconch heterostrophic, one-half whorl, 102 μm wide; larval shell smooth except for occasional broad, sinuous wrinkles. Teleoconch skeneiform, one and three-quarter whorls, smooth, growth lines sinuous near suture, otherwise prosocline. Shell composed of an inner and an outer layer of simple prismatic structure, and an intersected crossed-acicular layer in between. Diameter 1.03 mm.

Discussion.—We assigned this species earlier to the genus *Hyalogyrina* Marshall, 1988 because it resembles some low-spired species of this genus, like the Japanese *H. depressa* Hasegawa, 1997. But we are now convinced that this species rather belongs to *Xylodiscula*, because *Hyalogyrina* has a different type of protoconch, which usually consists of half or three-quarters of a whorl only, and has a larger whorl expansion rate than the protoconchs of *Xylodiscula*. Most Recent species of *Xylodiscula* differ from *X. okutanii* by having a more-or-less well developed shoulder. This includes the type species which has a strong shoulder. An additional difference to *X. okutanii* is the more pronounced transition from protoconch to teleoconch. *X. eximia* Marshall, 1988 is somewhat shouldered, although much weaker than *X. vitrea*, and the shoulder may be indicated by a spiral ridge only. Another species with slightly angular whorls is the vent-inhabiting *X. analoga* Warén and Bouchet, 2001. The shell microstructure of *X. okutanii* is very similar to that of *X. analoga* (Kiel 2004).

A somewhat similar heterobranch from the uppermost Eocene of western Washington, but with a planispiral shell is *Cyclostremella* (?) *chimaera* Hickman, 1980. That species has an entirely sinistrally coiled protoconch (Hickman 1980b), whereas in *Xylodiscula okutanii* only the embryonic shell is sinistral.

Stratigraphic and geographic range.—Uppermost Oligocene to lowermost Miocene, upper part of the Pysht Formation, Washington State, USA.

Class Bivalvia Linné, 1758
Subclass Protobranchia Pelseneer, 1889
Family Nuculanidae H. and A. Adams, 1858
Genus *Nuculana* Link, 1807

Type species: *Arca rostrata* Bruguière, 1789; Recent, Indo-Pacific.

Remarks.—*Nuculana* is used here in a broad sense. We are aware that many genera and subgenera are in use for nuculanids and *Nuculana* based on characters like shell shape, hinge dentition and muscle attachment scars (Coan et al. 2000; La Perna 2003; La Perna et al. 2004). The internal features of *Nuculana posterolaevia* sp. nov. are unknown and hence a more precise classification of the species than to "*Nuculana* sensu lato" is impossible at present. However, *Nuculana posterolaevia* has distinct external features on which it can readily be distinguished from other Recent and fossil nuculanids of this region.

"*Nuculana*" *posterolaevia* sp. nov.

Fig. 5.

1996 *Nuculana* sp.; Goedert and Campbell 1996: 25, fig. 2.

2003 "*Nuculana*" sp. aff. "*N.*" *grasslei* Allen; Goedert et al. 2003: 226, pl. 43: 8.

Derivation of the name: From Latin *laevis*, smooth, for its smooth posterior part.

Holotype: LACMIP 12310. Specimen with damaged central part of shell.

Paratype: UWBM 97315, from UWBM loc. B6753.

Type locality: USGS loc. 26895, Shipwreck Point, Clallam County, Washington State, USA.

Type horizon: Lower Oligocene, Makah Formation.

Material.—The type material and several specimens from the wood-fall sites USGS locs. 26896-D, 26897-A, 26898-B, and from a whale specimen (USNM 314545) from USGS loc. 26898. These specimens are deposited in the Cenozoic mollusk collection of the USNM.

Diagnosis.—A weakly rostrate *Nuculana* with orthogyrate umbo in anterior position (approx. 38% total length); sculpture of strong commarginal ribs and equally sized interspaces on anterior and central part of shell, ribs fade on posterior part of shell; rostrum smooth.

Description.—Shell moderately elongate, height/length ratio approx. 1.52–1.57; anterodorsal margin straight, anterior margin rounded and slightly pointed; posterodorsal margin convex near the umbo and becomes straight on the rostrum; lunule long, narrow, and only slightly excavated; ventral margin well-rounded; rostrum with growth lines only. Hinge unknown. The holotype is 7.0 mm long and 4.6 mm high, the paratype is 6.0 mm long and 3.8 mm high.

Discussion.—"*Nuculana*" *posterolaevia* sp. nov. is the most frequently found taxodont protobranch at cold seeps, whale- and wood-falls in the Cenozoic deep-water sediments in Washington. However, despite the overall similarity between these fossil communities and their modern analogs, this or a similar species has not yet been reported from extant seeps, whale- or wood-falls. The extant vent inhabiting *Nuculana grasslei* Allen, 1993 differs significantly by its sculptured posterior part of the shell.

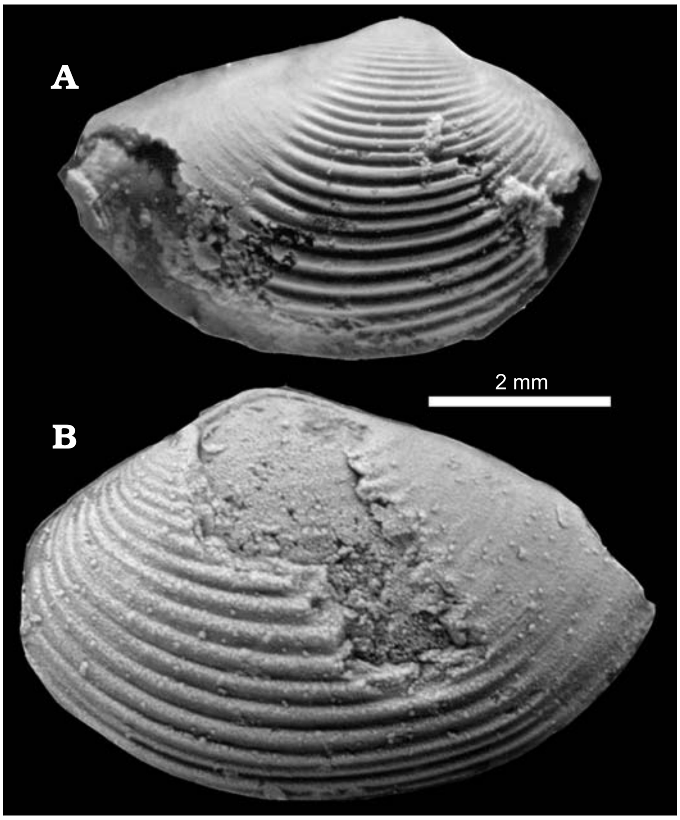

Fig. 5. Nuculanid bivalve "*Nuculana*" *posterolaevia* sp. nov. from Eocene and Oligocene seep carbonates, whale- and wood-falls in Washington State. **A**. Paratype UWBM 97315, from a uppermost Eocene seep-carbonate at Whiskey Creek (UWBM loc. B6753). **B**. Holotype LACMIP 12310, from a lower Oligocene seep-carbonate at Shipwreck Point (USGS loc. 26895).

The extant North Pacific *Nuculana* (*Jupiteria*) *taphira* (Dall, 1896) is similar to "*Nuculana*" *posterolaevia* in also having a smooth posterior part, but *N.* (*J.*) *taphira* differs by having more prosogyrate beaks, its smooth posterior part is shorter and more slender, and the posteroventral margin is concave (Coan et al. 2000: pl. 7), whereas it is convex in "*N.*" *posterolaevia*. *Nuculana ochsneri* var. *elmana* Etherington, 1931 from the Miocene Astoria Formation in Oregon and Washington State is more elongate and its smooth posterior part is much narrower than in "*N.*" *posterolaevia*.

Stratigraphic and geographic range.—Uppermost Eocene to lowermost Miocene, Washington State, USA, associated with wood, whale bones, and in cold-seep carbonates at Shipwreck Point, Makah Fm. (Goedert and Campbell 1995) and Whiskey Creek, Pysht Fm. (Goedert et al. 2003).

Subclass Pteriomorphia Beurlen, 1944
Family Mytilidae Rafinesque, 1815

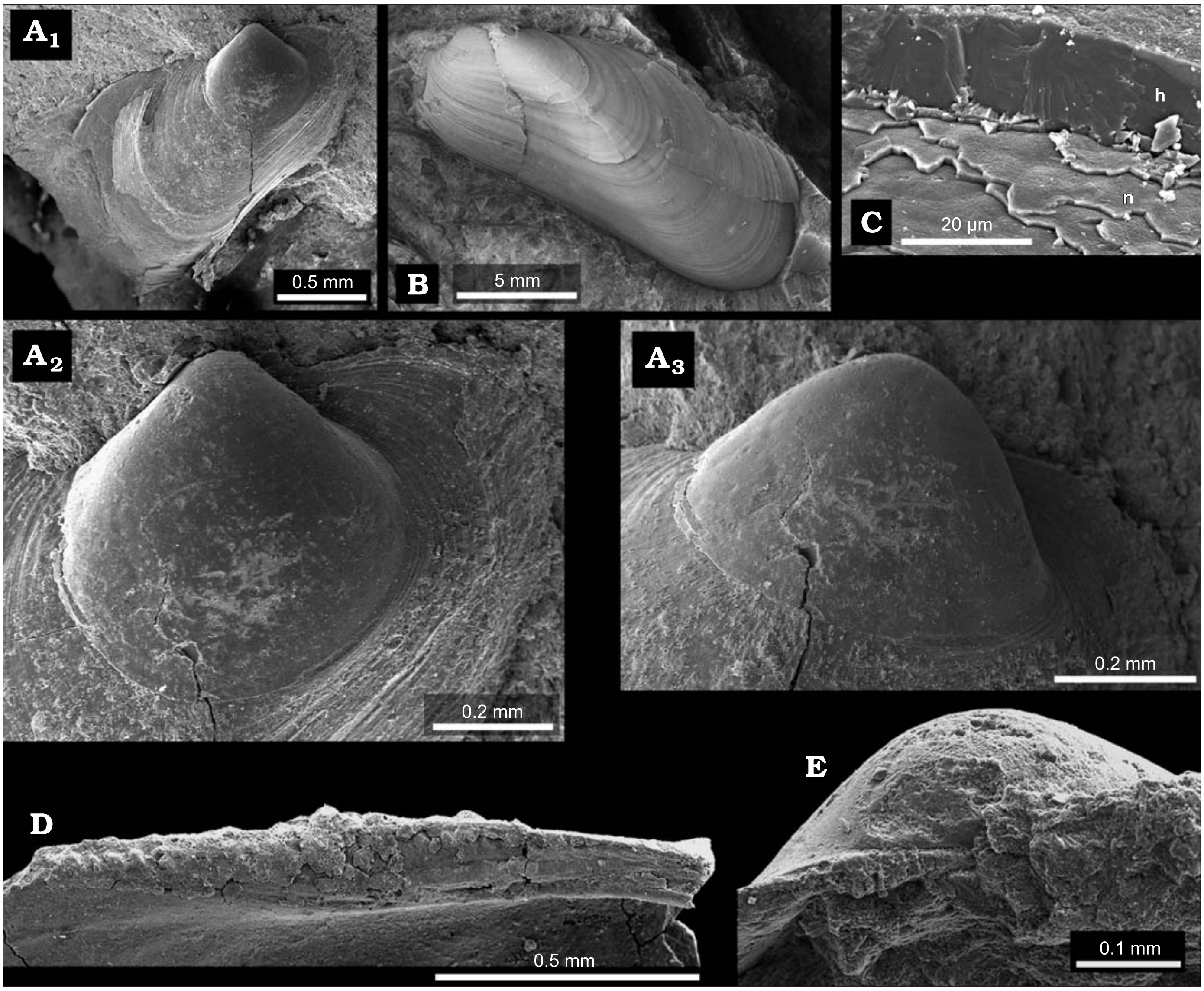

Fig. 6. Mytilid bivalve *Idas*? *olympicus* sp. nov. from Eocene to Miocene whale- and wood-falls in Washington State. **A**. Paratype USNM 532039, juvenile shell showing larval shell (A_1), from a uppermost Eocene wood-fall at the Satsop River (USGS loc. 26905), and two close-ups on the prodissoconch (A_2, A_3). **B**. Holotype USNM 532038, from a upper lower Oligocene wood-fall at Murdock Creek (USGS loc. 26898-A). **C**. Paratype USNM 532042, from an upper lower Oligocene whale-fall at Murdock Creek (USGS loc. 26898), showing shell microstructure (h = homogenous calcite, n = nacre). **D**. Paratype USNM 532040, showing hinge dentition anterior to umbo, from same locality as C. **E**. Paratype USNM 532041, showing hinge and hinge dentition, from same locality as C.

Genus *Idas* Jeffreys, 1876

Type species: *Idas argenteus* Jeffreys, 1876; Recent, Atlantic.

Idas? *olympicus* sp. nov.

Fig. 6.

2006 *Idas* n. sp.; Kiel and Goedert 2006a: 2626, fig. 2b.
2006 *Idas* n. sp.; Kiel and Goedert2006b: 549, fig. 2B.

Derivation of the name: For the Olympic Peninsula in western Washington State.

Holotype: USNM 532038. Well-preserved large specimen, inner side concealed by matrix.

Paratypes: USNM 532039–532041 from USGS loc. 26905, USNM 532042 from USGS loc. 26898.

Type locality: USGS loc. 26898, Murdock Creek, Clallam County, Washington State, USA.

Type horizon: Upper lowermost Oligocene, lower part of the Pysht Formation.

Material.—The type material and numerous specimens associated with wood-fall sites USGS locs. 26895, 26896-A, D, 26897-A to G, 26898-A to J, 26899, 26900, 26901, 26902, 26904; and with the whale specimens USNM 314593 and 314608 from USGS loc. 26896, and USNM 314545, 314556 at USGS loc. 26898. All specimens are deposited in the Cenozoic mollusk collection of the USNM.

Diagnosis.—Prodissoconch with round ventral margin and prominent, triangular umbo; adult shell modioliform, beak strongly prosogyrate, in subterminal position; posterodorsal margin straight or slightly convex, transition to posterior margin at an angulation at between 50 and 62 percent of entire shell length; ventral margin straight or slightly concave; posterior hinge area moderately broad, showing small denticles with 45° inclination; shell surface shows fine growth lines.

Description.—Prodissoconch 560 μm long and high, whitish, posterior side marginally more pointed than anterior side, margin flattened. Juvenile shell (1.3 mm) elongate-triangular in ventral view, highest at about three-quarters of total length, hinge line straight, posterior margin slightly angular at its middle, ventral margin straight to slightly convex, anterior margin short, pointed. Shell composed of three layers: a calcitic outer, homogenous or foliated layer with the sheets perpendicular to the shell's surface; a nacreous middle layer, and an inner layer of simple prismatic structure. The holotype is 17 mm long and 7 mm high, the largest specimen is 20 mm long.

Discussion.—The mineralogic composition of the shell (calcite and aragonite) was confirmed by X-ray analysis. Distinguishing *Idas* from small *Modiolus* on the limited shell features available for *Idas*? *olympicus* is difficult, because they can have very similarly shaped larval and adult shells, and also their hinge dentition can be similar. Ongoing work by SK and Luciana Génio (unpublished) indicates that *Modiolus* usually has a proportionally thinner outer calcitic layer than *Idas*. However, due to the poor preservation of the material available, our specimens are assigned to *Idas* with some hesitation.

Idas pelagicus (Woodward, 1854), *I. osseocolus* (Dell, 1987), *I. pacificus* (Dall, Bartsch, and Rehder, 1938), *I. coppingeri* (Smith, 1885), and *I. washingtonius* (Bernard, 1978) all differ from *I.*? *olympicus* by having the umbo in a more central position. *Idas japonicus* (Habe, 1976), *I. ghisottii* Warén and Carrozza, 1990, and *I. argenteus* Jeffreys, 1876 have the umbo in an anterior position similar to *I.*? *olympicus*, but differ by having a shorter posterior margin relative to the ventral margin. *Idasola*? sp. from an Oligocene whale-fall in Washington State has the umbo in a more central position, and has a more curved outline in ventral view (Goedert et al. 1995). The same is true for *Adipicola chikubetsuensis* (Amano, 1984) from a Miocene whale-fall in Japan (Amano and Little 2005). The "modiolids" reported earlier from whale-falls in this area (Goedert et al. 1995) most likely also belong to *Idas*? *olympicus*, as well as the "*Adula*" reported by Lindberg and Hedegaard (1996) from wood-fall concretions containing the acmaeoid *Pectinodonta palaeoxylodia* Lindberg and Hedegaard, 1996. *Idas*? *olympicus* may represent the earliest record for the genus.

Stratigraphic and geographic range.—Uppermost Eocene to lowermost Miocene, Makah, Lincoln Creek, and Pysht formations, Washington State, USA. Associated with wood and whale bones.

Subclass Heterodonta Neumayr, 1884
Family Thyasiridae Dall, 1901
Genus *Thyasira* Lamarck, 1818

Type species: *Tellina flexuosa* Montagu, 1803; Recent, North Sea.

Thyasira xylodia sp. nov.

Fig. 7.

1995 *Thyasira peruviana*? Olsson; Goedert et al. 1995: 154, table 1, figs. 4, 5.

2006 *Thyasira* n. sp.; Kiel and Goedert 2006a: 2626, fig. 2e, f.

Derivation of the name: From Greek *xylon*, wood; after its association with wood.

Holotype: LACMIP 13370. Large, articulate specimen with damaged posterior margin, right valve largely concealed by matrix.

Paratypes: USNM 532043 and 532857, both from USGS loc. 26898-B; LACMIP 12336, from USGS loc. 26898.

Type locality: USGS locality 26898, Clallam County, Washington State, USA.

Type horizon: Upper lowermost Oligocene, Pysht Formation.

Material.—The type material and specimens were found at the wood-fall sites USGS loc. 26896-C, 26898-B, 26901, and with the whale specimen USNM 314593 from USGS loc. 26896. These specimens are deposited in the USNM. Further specimens were found with whale bones at CSUN loc. 1578 (= USGS loc. 26898), the site from which (Goedert et al. 1995) described *Thyasira peruviana*? Olsson, 1931. These specimens are deposited in the UWBM.

Diagnosis.—Large *Thyasira* with equilateral obliquely-ovate outline; posterior margin truncate, posterior fold concave, sub-marginal sulcus very narrow, no auricle; lunule deeply excavated, broad, but not reaching the end of the anterodorsal margin.

Description.—Prodissoconch 132 μm wide, and 46 μm thick, smooth apart from very fine radial and concentric wrinkles. Dissoconch prosogyrate, 2nd posterior fold concave, forming a sharp edge with the narrow posterior sulcus; 1st posterior fold also with sharp inner edge, sub-marginal sulcus smooth and very narrow; length of lunule approx. 70% of anterodorsal margin; ventral margin in some specimens undulating, corresponding to a weak depression along the midline. Surface smooth apart from fine commarginal growth lines. The holotype is 21 mm high and long. The terminology used here follows that of Oliver and Killeen (2002).

Discussion.—Goedert et al. (1995) reported *Thyasira peruviana*? from Oligocene whale-falls in the Makah and Pysht Formations in western Washington, a species which had previously only been reported from suspected cold-seeps in northwestern Peru (Olsson 1931). Goedert et al. (1995) noted that some of the paratypes figured by Olsson (1931) do not show the sharp ridge in the posterodorsal area that characterizes the type specimen. Examination of Peruvian voucher material of *T. peruviana* in the USNM showed that this sharp ridge is in fact present in all examined specimens. The holotype figured by Olsson (1931) appears to lack the large posterodorsal area that is present in some of Olsson's paratypes. This was also observed among the USNM specimens, however, this lack can in all cases be attributed to corrosion.

Whereas the thyasirid *Conchocele bisecta* (Conrad, 1849) occurs throughout the siltstones and cold-seeps of the Lincoln Creek, Makah, and Pysht formations, *Thyasira xylodia*

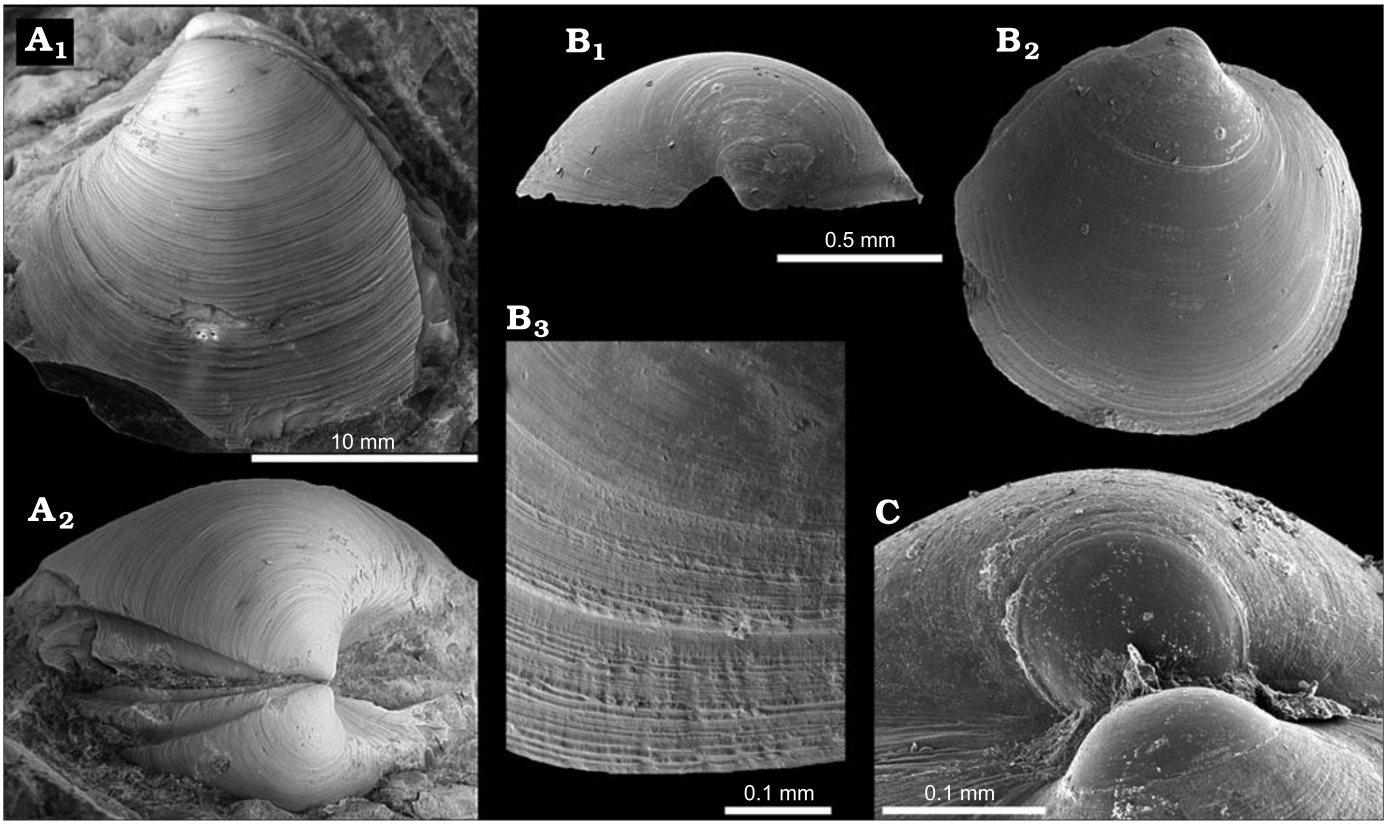

Fig. 7. Thyasirid bivalve *Thyasira xylodia* sp. nov. from Eocene to Miocene whale- and wood-falls in Washington State. **A**. Holotype LACMIP 13370, from a upper lower Oligocene wood-fall at Murdock Creek (USGS loc. 26898-J) in lateral (A_1) and umbonal (A_2) views. **B**. Paratype USNM 532043, juvenile specimen from a upper lower Oligocene wood-fall at Murdock Creek (USGS loc. 26898-B) in umbonal (B_1) and lateral (B_2) views, and close-up on microsculpture at ventral shell margin (B_3). **C**. Juvenile specimen USNM 532857, showing prodissoconch, from same locality as B.

has so far only been found associated with either wood or whale bones. It is distinguished from *Conchocele bisecta* by its truncate posterior margin with a very narrow sub-marginal sulcus. Goedert and Squires (1990) reported a large thyasirid from a upper middle to upper Eocene seep in the Humptulips Formation in Washington as *Thyasira folgeri* Wagner and Schilling, 1923, a species originally reported from the Wagonwheel and San Emigdio formations in California (Wagner and Schilling 1923; Squires and Gring 1996). *Thyasira xylodia* differs from these specimens by its truncate posterior margin with a very narrow sub-marginal sulcus. Although *T. folgeri* was not listed by Squires and Gring (1996) in their synonymy of *C. bisecta*, they mentioned that Smith (1956) and Jenkins (1931) both thought that *T. folgeri* was based on juvenile specimens of *C. bisecta*. However, observations by the senior author of material from the Humptulips and Wagonwheel seeps, and Recent specimens of *C. bisecta* in the USNM and LACM zoology collection indicate that the Humptulips specimens are consistently more inflated and proportionately shorter than *C. bisecta*. We thus consider the Humptulips species to be distinct from *C. bisecta*. Whether the Humptulips species does indeed belong to *T. folgeri* as initially proposed is not entirely certain, and is under study.

Stratigraphic and geographic range.—Uppermost Eocene to lower Oligocene, Makah, Lincoln Creek, and Pysht formations, Washington State, USA. Associated with wood and whale bones.

Conclusions

Careful sampling of sediments with high organic content, including bones and wood, can reveal small and fragile molluscan shells and other invertebrates associated with such substrates (Marshall 1985, 1986, 1994; and herein), contrary to earlier assumptions (Maddocks and Steineck 1987). The species described here are reported for the first time from biogenic substrates, and many of them have micrometer-scale features preserved, allowing a detailed taxonomic treatment.

The Neomphalidae were previously considered endemic to hydrothermal vents and cold seeps, and the discovery of these unusual gastropods in the 1980s contributed significantly to the idea that vent animals are “relics” and have remained virtually unchanged since the Paleozoic (McLean 1981; Newman 1985). However, Warén and Bouchet (2001) noted that there is virtually no variation in protoconch morphology among neomphalids, unlike in many other non-vent vetigastropods, and concluded that the radiation of neomphalids might be as recent as late Mesozoic or Cenozoic. Also, the protoconch of

Leptogyra squiresi does not deviate substantially from that of other neomphalids, including the Eocene *Retiskenea statura* (Kiel 2006). Thus the minimum age for the radiation of the modern neomphalids with this type of protoconch is late Eocene (approximately 37 Million years ago), but *Retiskenea* may be as old as Early Cretaceous (Campbell 2006). Other records of Cretaceous neomphalids still need to be confirmed and/or might represent an independent branch within the Neomphalina (Kiel and Campbell 2005).

The Cenozoic thyasirids from the Pacific Northwest are probably more diverse than previously thought. Due to the high morphological variability of *Conchocele bisecta*, Squires and Gring (1996) synonymized virtually all Cenozoic thyasirids from the Pacific Northwest. However, as shown herein, the Eocene to Oligocene wood- and whale-inhabiting thyasirid represents an independent species, and also the large thyasirid that occurs in Eocene seep carbonates in Washington can be distinguished from *C. bisecta*. Considering the large number of thyasirid species and subspecies that Kauffman (1967) was able to distinguish from a comparatively short time interval in the Late Cretaceous of the Western Interior Seaway of the US, detailed morphologic work may also reveal further species in the Cenozoic from the eastern North Pacific Ocean, perhaps with distinct ecological preferences.

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Appendix 1

Locality data

When more than one concretion with wood or bone was found at a locality, the concretions are individually labeled (e.g., USGS loc. 26898-A) to retain the faunal association.

USGS loc. 26895.—Shipwreck Point; Clallam County, Washington (= LACMIP loc. 8233). Makah Formation, lower Oligocene.

USGS loc. 26896.—West of the mouth of the Sekiu River, SE ¼ sec. 5, T. 32 N., R 13 W, Clallam County, Washington. Makah Formation, lower Oligocene.

USGS loc. 26897.—Merrick's Bay; beach outcrops exposed from the western boundary of Sec. 23 southeast for 700 m to the giant talus pile at the base of the cliff, SW ¼ Sec. 23, T. 32 N., R.12 W., Clallam County, Washington (= LACMIP loc. 8231). Top of Pysht Formation and base of Clallam Formation, uppermost Oligocene–lowermost Miocene.

USGS loc. 26898.—Murdock Creek; beach terrace to the west of the mouth of Murdock Creek, Clallam County, Washington. NW ¼ Sec. 29, T. 31 N., R. 9 W., Clallam County, Washington (= LACMIP loc. 6295 = LACMVP loc. 5412 = CSUN 1578). Lower part of Pysht Formation, upper lower Oligocene.

USGS loc. 26899.—Canyon River; found loose on gravel bar, approx. 240 meters east and 70 meters north of the southwest corner of Sec. 24, T. 21 N., R. 7 W., Grays Harbor County, Washington. Lincoln Creek Formation, Oligocene.

USGS loc. 26900.—Canyon River; east bank of Canyon River, approx. 30 meters upstream from sharp bend, approx. 600 meters north and 310 meters east of the southwest corner of Sec. 18, T. 21 N., R. 6 W., Mason County, Washington. Lincoln Creek Formation, uppermost Eocene to lowermost Oligocene.

USGS loc. 26901.—Canyon River; float concretion found on gravel bar just downstream from bridge, approximately 190 meters west and 95 meters north of the SE corner of Sec. 13, T. 21 N., R. 7 W., Grays Harbor County, Washington. Lincoln Creek Formation, uppermost Eocene?

USGS loc. 26902.—Satsop River; found loose on gravel bar along the Middle Fork of the Satsop River, in NE ¼ of SW ¼ of NE ¼ of Sec. 20, T. 21 N., R. 6 W., Mason County, Washington. Lincoln Creek Formation, lowermost Oligocene (minimum).

USGS loc. 26903.—Knappton; from landslide block between Knappton and Grays Point, 305 m south and 430 m east of NW corner of Sec. 9, T. 9 N., R. 9 W., on the Columbia River, Pacific County, Washington State (= LACMIP loc. 5843). Lincoln Creek Formation, uppermost Oligocene.

USGS loc. 26904.—Knappton; from landslide block between Knappton and Grays Point, 112 east and 520 m south of NW corner of Sec. 9, T. 9 N., R. 9 W., on the Columbia River, Pacific County, Washington State (= LACMIP loc. 5844). Lincoln Creek Formation, uppermost Oligocene.

USGS loc. 26905.—Satsop River; West bank of the Middle Fork of the Satsop River immediately south of where a small stream enters from the east, approx. 200 m south and 190 m west of the northeast corner of Sec. 20, T. 21 N., R. 6 W., Mason County, Washington. Lincoln Creek Formation, uppermost Eocene.

UWBM loc. B6753.—Whiskey Creek; near mouth of Whiskey Creek, limestone blocks on beach terrace, Clallam County, Washington State. Pysht Formation, uppermost Eocene.