

TWO NEW SPECIES OF *RETISKENEA*? (GASTROPODA: NEOMPHALIDAE) FROM LOWER CRETACEOUS HYDROCARBON-SEEP CARBONATES OF NORTHERN CALIFORNIA

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ABSTRACT—Two new Mesozoic gastropod species, provisionally attributed to the minute (height < 5 mm) coiled neomphalid genus *Retiskenea*?, are described from three geographically isolated, Early Cretaceous, hydrocarbon seep-carbonate sites at Wilbur Springs, Rice Valley, and Cold Fork of Cottonwood Creek, northern California (USA). A fourth paleo-seep locality at Paskenta, of probable Upper Jurassic age, also yielded a single specimen of a morphologically similar microgastropod that may be a neomphalid with affinities to the Lower Cretaceous specimens described herein. The limestone lenses are ~2–260 m in length, ~1–5 m in diameter, and surrounded by forearc siliciclastics of bathyal turbidites or sedimentary serpentinites in the Upper Jurassic to Lower Cretaceous (Tithonian–Albian) Great Valley Group and its equivalents. The Lower Cretaceous microgastropods are tentatively placed in *Retiskenea*? based on similar shell characters: size, globose shape, inflated reticulate protoconch, number and distinct inflation of the body whorls, and fine, prosocline sculpture of the final body whorl. The fossils occur in carbonate microbialites that formed in seafloor sediments during archaeal anaerobic oxidation of methane in the zone of bacterial sulfate reduction, associated with H₂S- and CH₄-rich fluid seepage. The California *Retiskenea*? fossils commonly are found in gregarious clusters, or closely affiliated with thin worm tubes or, in one case, a larger gastropod.

These Mesozoic records increase the total known species attributable to this cold-seep endemic genus from two to four. Its spatial and temporal distribution thus may have spanned ~9,000 km around the Pacific Rim from at least ~133 m.y. to the present in 10 subduction-related seep sites from California (possibly Upper Jurassic–Lower Cretaceous), Washington (middle Eocene–Upper Oligocene), and modern offshore Oregon, the eastern Aleutians, and the Japan Trench. If the generic placement of these microgastropod fossils is correct, the California records are the oldest-known occurrences of *Retiskenea*, consistent with an estimated minimum Mesozoic origin for the ‘hot vent’ Neomphalidae, as inferred from molecular analyses published on other living members of the family.

INTRODUCTION

ALL LIVING members of the gastropod family Neomphalidae (nine genera, 15 species) are endemic to hydrothermal vents except *Retiskenea diploura* Warén and Bouchet, 2001, a deep-water, cold-seep taxon from the eastern Aleutian convergent margin and slope of the Japan Trench (Fig. 1; Warén and Bouchet, 2001; Okutani and Fujikura, 2002). A single specimen of *Retiskenea* cf. *diploura* Warén and Bouchet, 2001 also has been reported from methane/sulfide seeps in the subduction zone offshore of Oregon (Fig. 1; Warén and Bouchet, 2001). Fossil hydrothermal vent deposits have yet to yield neomphalids (Little, 2002; Little and Vrijenhoek, 2003). However, a growing record in ancient hydrocarbon seep-carbonates is emerging for this unusual family of vent/seep gastropods (Goedert and Benham, 1999; Warén and Bouchet, 2001; Kiel and Campbell, 2005; Kaim, personal commun., 2006).

Living neomphalids contain an odd mixture of morphological characteristics of both the Archaeogastropoda and Caenogastropoda, and their discovery in hydrothermal vents and hydrocarbon seeps has stimulated much research on gastropod phylogeny by molluscan neontologists (cf. Haszprunar, 1988; Ponder and Lindberg, 1997; McArthur and Koop, 1999; Warén and Bouchet, 2001). In general, living Gastropoda display the most extensive endemism at hydrothermal vents and other sulfide-rich habitats (McArthur and Tunnicliffe, 1998). The Neomphalina, in particular, represent one of the largest in situ evolutionary radiations in these extreme environments (McArthur and Tunnicliffe, 1998).

Cold-seep communities of low to moderate diversity and high abundance are known from many passive and active margins around the world, from modern sites to fossil deposits as old as Silurian in age (e.g., Sibuet and Olu, 1998; Peckmann et al., 2001; Campbell, 2006 and references therein). Criteria for recognition of ancient hydrocarbon seeps are discussed elsewhere (e.g., Campbell et al., 2002; Peckmann et al., 2002; Peckmann and Thiel, 2004), and include paleontologic, (bio)geochemical, sedimentologic, stratigraphic, and structural assessment. The four microgastropod-bearing deposits of this study—Wilbur Springs, Rice Valley, Cold Fork of Cottonwood Creek, and Paskenta (Figs.

1, 2)—were identified previously as isolated Upper Jurassic to Lower Cretaceous hydrocarbon seep-carbonates preserved in deepwater, Great Valley Group forearc strata and equivalents, northern California (cf. “white limestones” of Stanton, 1895; Campbell and Bottjer, 1993, 1995a; Campbell et al., 1993, 2002; Campbell, 1995). These and several other seep-carbonate localities in Great Valley and Franciscan accretionary prism rocks of western California are generally gastropod rich (e.g., Campbell, 1996, 2006). For example, a new genus and species of Neomphalidae has been described recently from the Lower Cretaceous Rocky Creek and Bear Creek seep-carbonates (Great Valley Group; Kiel and Campbell, 2005). Numerous other fossil gastropod taxa from seep deposits in the region are currently under further study (Kiel et al., unpublished data). Results of this research suggest that minute neomphalid gastropods, tentatively placed in *Retiskenea*? herein, appear to have been associated with Pacific hydrocarbon-seep environments (Fig. 1) from at least as long ago as early in the Cretaceous (~133 Ma).

MATERIAL AND METHODS

Types and partially prepared, or unprepared bulk, fossiliferous limestone samples relevant to this study are housed at three institutions: California Academy of Sciences (CAS), Los Angeles County Museum Invertebrate Paleontology Collection (LACMIP), and University of California at Berkeley (UCMP), where U.S. Geological Survey Mesozoic invertebrate collections (USGS M# locations) presently reside. Mesozoic ages cited here are averages for each international Age, as listed in Gradstein et al. (2004), because ages are only grossly known for the Great Valley Group strata studied here. The recent claim that no Jurassic strata exist in these rocks based on zircon analyses (Surpless et al., 2006), thus challenging the long-standing buchiid bivalve zones of the region (Jones et al., 1969), is currently under reevaluation (R. McLaughlin, personal commun., 2006). We choose to follow established Great Valley biostratigraphy until the age controversy is resolved.

The study fossils were hand-picked with a pin-vise under a binocular microscope, measured with calipers, and coated with

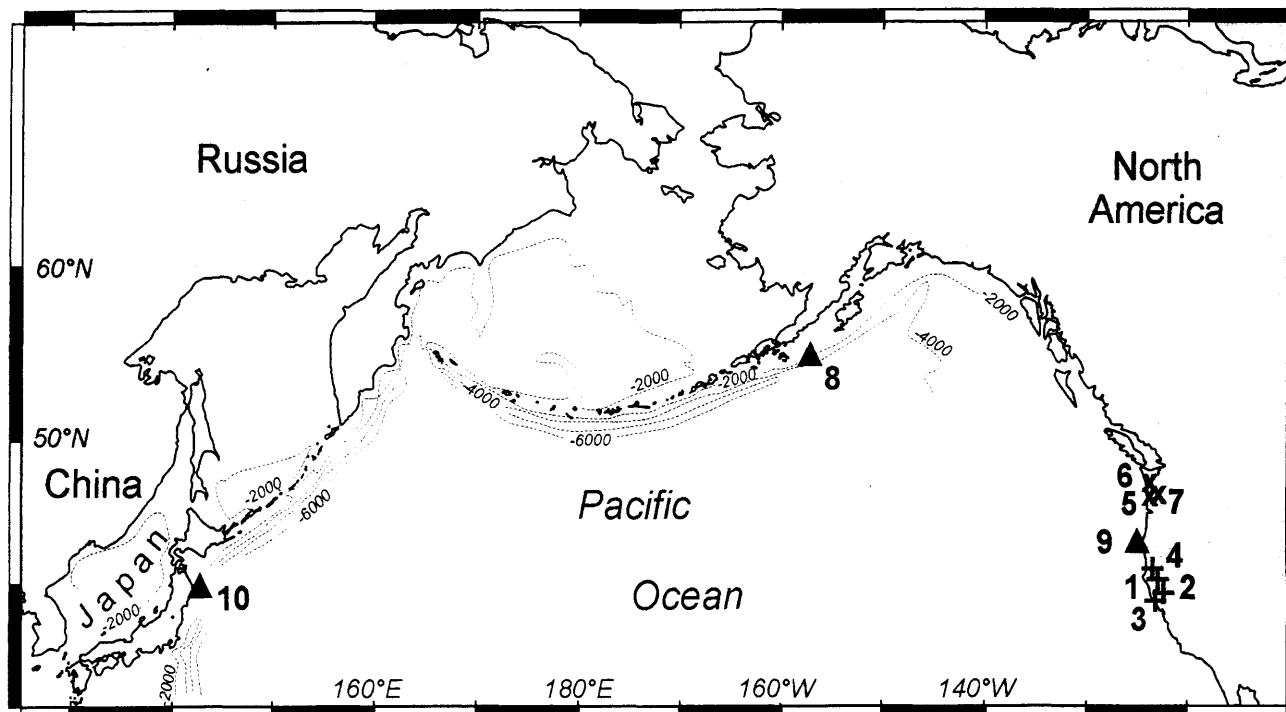


FIGURE 1—Geographic distribution map of occurrences of neomphalids with affinities to or ascribed to *Retiskenea* in hydrocarbon-seep settings of the Pacific Rim, ~148 Ma to present. From oldest to youngest: 1, Indeterminate coiled neomphalid microgastropod, Upper Jurassic (Tithonian, ~148 m.y.) Great Valley Group, Paskenta, California; 2, 3, *Retiskenea? tuberculata* n. sp., Lower Cretaceous (Hauterivian, ~133 m.y.) Great Valley Group, Wilbur Springs and Rice Valley, California, respectively; 4, *Retiskenea? kieli* n. sp., Lower Cretaceous (Albian, ~106 m.y.) Great Valley Group, Cold Fork of Cottonwood Creek, California; *Retiskenea statura* (Goedert and Benham, 1999) in 5, middle Eocene (~48 m.y.) Humptulips Formation; 6, Lower Oligocene (~32 m.y.) Makah Formation, and 7, Upper Oligocene (~26 m.y.) Lincoln Creek Formation, Washington; 8, modern *Retiskenea diploura* Warén and Bouchet, 2001, Shumagin site, Aleutian forearc, offshore Alaska; 9, modern *Retiskenea* cf. *diploura*, Oregon convergent margin (Warén and Bouchet, 2001); 10, modern *R. diploura*, Japan Trench (Okutani and Fujikura, 2002).

platinum (Polaron SC7640 sputter coater) for scanning electron microscopy using a Phillips (FEI) XL20S field emission gun scanning electron microscope, at an accelerating voltage of 5 keV and a working distance of 5 mm. Paleoecological relationships were studied using a petrographic microscope and standard polished thin sections.

SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA
Class GASTROPODA

Clade VETIGASTROPODA Salvini-Plawen, 1980,
sensu Ponder and Lindberg, 1997

Superfamily NEOMPHALOIDEA McLean, 1981

Discussion.—The higher-order systematic position of superfamily Neomphaloidea is uncertain (McArthur and Koop, 1999; Bouchet and Rocroi, 2005), a group also known collectively as the “Hot Vent Taxa,” sensu Ponder and Lindberg (1997). Proposed suborder names have included Euomphalina, Neomphalina and Neomphaloidei (McLean, 1990; Bouchet and Rocroi, 2005). McLean (1981) allied living vent *Neomphalus* McLean, 1981 with the extinct Paleozoic group Euomphaloidea, and erected a new suborder Euomphalina (Neomphaloidea + Peltospiroidea) to accommodate this “living fossil” (McLean, 1981, 1989, 1990). Neomphalids and peltospirids such as *Depressigyra* Warén and Bouchet, 1989 share broadly similar shell microstructure, as well as other anatomical and molecular characters (Warén and Bouchet, 1989; Kiel, 2004, and references therein). Warén and Bouchet (1993) synonymized Neomphaloidea with Neomphalina, the informal name they assigned to modern hydrothermal vent relatives of *Neomphalus* (summarized in McArthur and Koop, 1999). Morphological character analysis of living hot vent neomphalids yielded different phylogenetic tree positions, probably because of

a lack of ultrastructural soft-part data and parallelism of many characters (Ponder and Lindberg, 1997). Specifically, Ponder and Lindberg (1997) found that paraphyly or monophyly were not fully resolved among the Neomphalidae and concluded that the family either resides at or near the base of the vetigastropods or is in a clade with the neritopsines and cocculinoideans. In a recent working classification of gastropods that is followed herein, Bouchet and Rocroi (2005) cited both molecular and morphological affinities to confirm and place superfamily Neomphaloidea (comprising families Neomphalidae, Melanodrymiidae and Peltospiridae) within the clade Vetigastropoda.

Family NEOMPHALIDAE McLean, 1981

Genus RETISKENEWA Warén and Bouchet, 2001

Type species.—*Retiskenea diploura* Warén and Bouchet, 2001.

Diagnosis.—Shell small, globular, narrowly umbilicate, with delicate net sculpture on protoconch.

Discussion.—Warén and Bouchet (2001, p. 157) found the genus difficult to classify because of a “strange combination” of archaeogastropod and caenogastropod characters but placed *Retiskenea* in Neomphalidae owing to similarities in soft-part anatomy and protoconch sculpture. In particular, the genus name was chosen to convey the net-like (*rete*, Latin) character of the protoconch, and to acknowledge a similar shell-shape to the trochoidean genus *Skenea* Fleming, 1825. The protoconch sculpture differs between *Retiskenea* and other neomphalids, in that the ridges forming the net of the latter are of a fairly uniform size, whereas in *Retiskenea*, their strength is more variable (Warén and Bouchet, 2001). Other vent/seep groups of microgastropods display gross morphological similarity to *Retiskenea* but can be distinguished from it based on details of shell shape, extent of coiling, protoconch shape/ornament, apertural shape and degree of

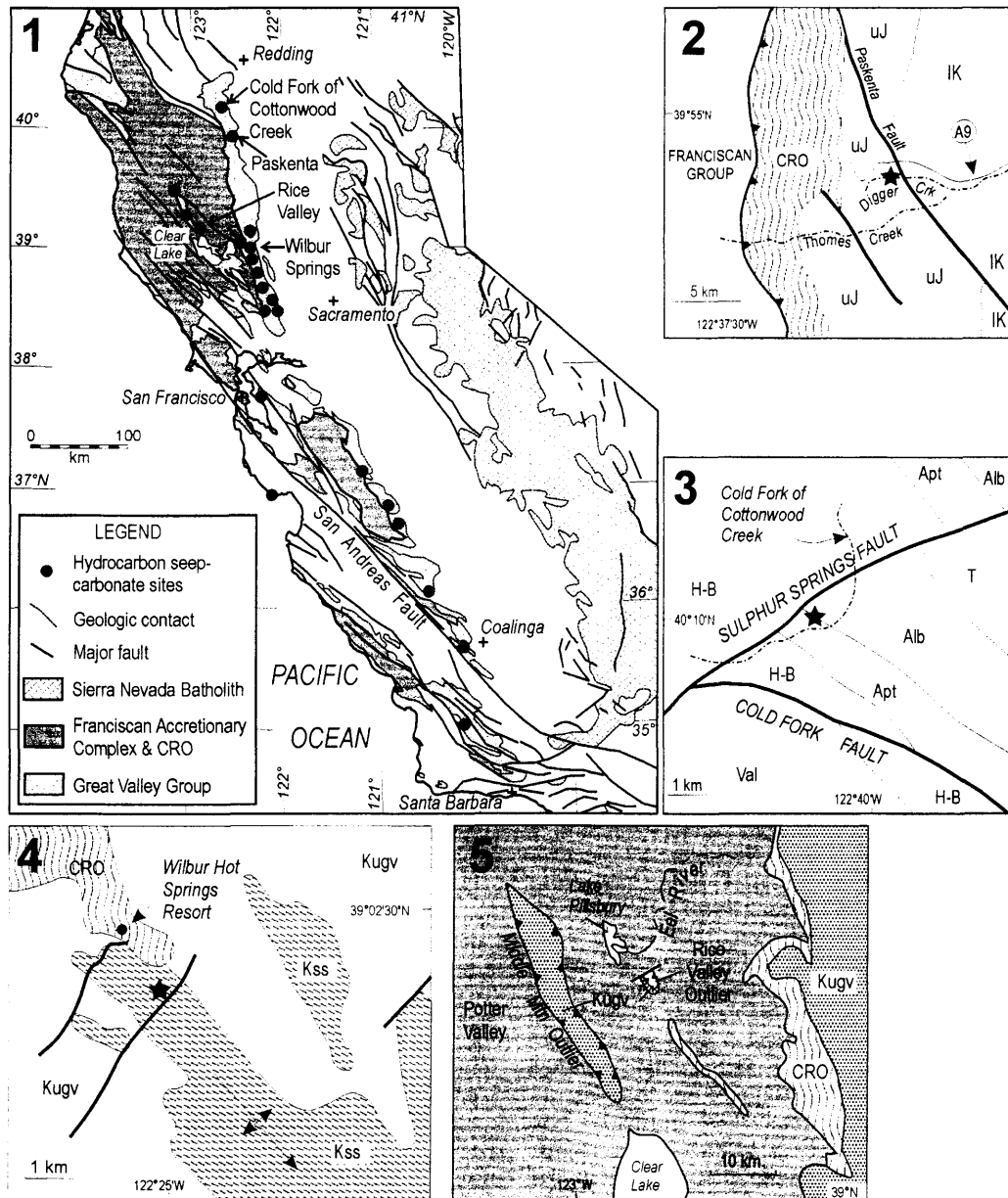


FIGURE 2—Geologic and location maps of sites of this study. 1. Simplified geology of the north-south-trending Mesozoic convergent margin system includes, from west to east: undifferentiated Franciscan Accretionary Complex (Jurassic to Cretaceous)—belts of mélangé, broken formation—and Coast Range Ophiolite (CRO); Great Valley Group (GV, Jurassic to Paleogene)—siliciclastic forearc turbidites and sedimentary serpentinites; and Sierra Nevada batholith—present-day roots of Mesozoic volcanic arc. Mesozoic and Cenozoic seep-carbonates shown as black circles. Taxa described herein include a possible neomphalid? from the Paskenta deposit with some morphological similarities to *Retiskenea?*, *Retiskenea? kieli* n. sp., from the Cold Fork of Cottonwood Creek deposit, and *Retiskenea? tuberculata* n. sp., from the Wilbur Springs and Rice Valley deposits. 2–5 show simplified geology and locations of fossiliferous seep-carbonates (stars) containing the neomphalid microgastropods of this study. 2. Paskenta, uJ, Upper Jurassic (Tithonian), GV slope turbidites; IK, Lower Cretaceous GV turbidites east of the synsedimentary Paskenta Fault. 3. Cold Fork of Cottonwood Creek area; Val, Valanginian; H-B, Hauterivian-Barremian; Apt, Aptian; Alb, Albian; T, Tertiary. 4. Wilbur Springs area; Kss, diapir-associated sedimentary serpentinites (Hauterivian); Kugv, undifferentiated GV Group turbidites (Cretaceous). 5. Rice Valley area; fault-bounded outlier of GV-equivalent strata and seep-carbonates enclosed within eastern belt of Franciscan Group. Geologic maps simplified from U.S. Geological Survey and California Division of Mines and Geology (1966), Jones et al. (1969), Jones and Bailey (1973), Berkland (1973), and Carlson (1984b).

inflation, and teleoconch decoration. For example, the thin-shelled vetigastropod *Sahlingia* Warén and Bouchet, 2001 is somewhat larger in size, shows more rapid whorl expansion, has a wider umbilicus, and displays spiral sculpture (Warén and Bouchet, 2001, fig. 8a, 8b, p. 130). Compared to *Retiskenea*, the protoconch of *Depressigyra* Warén and Bouchet, 1989 has a different shape (cf. Warén and Bouchet, 2001, fig. 15j vs. 15o, p. 144), and shows an axial rather than tangential aperture position. Hyalogyrinids and the skeneids *Protolira* Warén and Bouchet, 1993 and *Bruceiella* Warén and Bouchet, 1993 also possess distinctly different

protoconchs, more open umbilici, and either greater or lesser apical expansion of the whorls, as compared to *Retiskenea* (cf. Warén and Bouchet, 1993).

RETISKENEIA DIPLOURA Warén and Bouchet, 2001

- Retiskenea diploura* WARÉN AND BOUCHET, 2001, p. 144, fig. 15j; p. 157–159, fig. 24c.
Retiskenea diploura WARÉN AND BOUCHET, 2001, p. 213, fig. 2 (Okutani and Fujikura, 2002).
Retiskenea diploura WARÉN AND BOUCHET, 2001, p. 174, fig. 19 (Kiel, 2004).

TABLE 1.—List of height and diameter measurements (in mm) for *Retiskenea? kieli* n. sp., Cold Fork of Cottonwood Creek, California; *R.? tuberculata* n. sp., Wilbur Springs and Rice Valley, California; neomphalid?, Paskenta, California; and *R. diploura*, Aleutian and Japan trenches. Museum numbers indicate collection localities, as described in text. Cross-plot of size data shown in Figure 4 and depicted in a principal components analysis in Figure 6.

<i>Retiskenea? kieli</i> n. sp., Cold Fork of Cottonwood Creek, California (CAS 68044, 68059, 68064)		<i>R.? tuberculata</i> n. sp., Wilbur Springs, California (CAS 68061)		Neomphalid? sp. indet., Paskenta, California (LACMIP 15917)		<i>R. statura</i> (Goedert and Benham, 1999), Washington (LACMIP 8233, 15911, 12385, 16504)		<i>R. diploura</i> Warén and Bouchet, 2001, Japan Trench	
Height (mm)	Diameter (mm)	Height (mm)	Diameter (mm)	Height (mm)	Diameter (mm)	Height (mm)	Diameter (mm)	Height (mm)	Diameter (mm)
2.11	2.75	2.16	2.85	~1.85	~2.57	2.9	2.6	3.5	3.4
3.85	4.41	1.79	2.62			2.9	2.7	2.0	1.9
1.06	1.58	3.86	4.35			3.1	2.8	2.6	2.6
1.42	2.25	1.64	2.95			3.4	3.1	1.7	1.8
1.70	2.60	1.73	2.39			2.5	2.0	3.0	2.8
1.71	2.54	1.98	2.73			3.0	2.4	2.0	2.0
2.00	2.38	1.37	2.15			2.6	2.5	1.7	1.7
2.30	3.18	2.14	2.75					2.8	2.8
1.25	1.80							2.2	2.2
0.45	0.90							2.2	2.6
1.15	1.67							1.8	1.7
1.54	2.52							2.3	2.4
2.63	3.29							1.9	1.9
1.90	2.85							2.5	2.9
1.81	2.74							2.2	1.9
1.75	3.00							3.2	2.9
2.00	2.90							2.2	2.0
2.21	3.16							2.3	2.1
2.12	2.44							2.2	2.1
1.55	2.40							1.8	1.8
1.50	2.30								
2.82	3.05								
2.40	3.09								
2.00	2.85								
1.86	2.64								
1.95	2.35								
1.50	2.11								
1.12	1.50								
1.27	2.00								
1.41	2.09								

Diagnosis.—Shell small, thin, of a moderately tall skeneiform shape; body whorl large and globose, narrowly umbilicate with oval aperture; delicate net sculpture on protoconch, 300 μ m diameter.

Description.—The protoconch consists of two-thirds of a whorl, has a large initial portion, and is completely covered in fine ridges, forming a network with slightly variable mesh size. The teleoconch consists of up to three distinctly convex whorls, sculptured by irregularly spaced growth lines of variable strength, and united by a deep suture. A micro-ornament of evenly distributed small pits (1–2 μ m diameter) extends over the surface. The aragonitic shell microstructure (approximately 50 μ m total thickness) comprises three layers: outer homogeneous, simple prismatic, and innermost intersected crossed platy structure. The outer lip is thin and sharp; the peristome is almost round. The umbilicus is narrow and deep.

Material examined.—K. Fujikura and T. Okutani kindly provided shell measurements for 20 *R. diploura* from the Japan Trench.

Occurrence.—Living *Retiskenea diploura* is known from the Shumagin cold-seep locality, Aleutian Trench, at lat. 54°18.17'N, long. 157°11.82'W, 4,808 m (Warén and Bouchet, 2001, p. 223). In addition, 39 specimens were collected from the Japan Trench at lat. 39°06.47'N, long. 143°53.49'W, 5,379 m (Okutani and Fujikura, 2002).

Discussion.—Warén and Bouchet (2001) attributed the small size range of their Aleutian material (1.2–2.2 mm diameter, 27 specimens) to immature, corroded individuals. Specifically protoconchs were perfectly preserved in all live-collected specimens (e.g., Warén and Bouchet, 2001, fig. 15j, p. 144) but were dissolved in old shells and in other small gastropods from the same locality. Okutani and Fujikura (2002, fig. 2b, p. 213) illustrated the finely reticulate protoconch ornament for a specimen collected from the Japan Trench. They noted that the thin shells are covered by a yellowish periostracum, which is commonly roughened with patches of black, flaky material.

Japanese *R. diploura* shows a nearly 1:1 height:diameter ratio (Fig. 4, Table 1) compared to the three fossil species attributed to

Retiskenea, including the two *Retiskenea?* described below. The 20 well-preserved Japanese shells are moderately tall (mean height 2.31 mm) compared to the two new Mesozoic species of *Retiskenea?* described here, but are lower spired compared to the reported heights of Cenozoic *R. statura* (see below; Tables 1, 2). In addition, a principal component analysis of height and diameter size data for all four species (Fig. 6) displays the distinctiveness of the Japanese specimens.

RETISKENEIA STATURA (Goedert and Benham, 1999)

Depressigyra? statura GOEDERT AND BENHAM, 1999, fig. 2a–g, p. 115.

Retiskenea statura (Goedert and Benham, 1999). WARÉN AND BOUCHET, 2001, p. 157–158; (Goedert and Benham, 1999). KIEL, 2006, shell microstructure, fig. 3.6; protoconch detail, fig. 3.7–3.9.

Diagnosis.—A *Retiskenea* with a spire elevated well above the body whorl; protoconch 250 μ m in diameter, larger in initial portion, with sculpture of somewhat irregular, polygonal pits.

Description.—Shell small, globose, thin (~25 μ m), nearly smooth except for numerous fine, sinuous, prosocline growth lines; aperture rounded, prosocline, outer lip thin; whorls convex, suture impressed, spire elevated above the body whorl; protoconch (~½–1 whorl) knob-like, commonly corroded; largest shell with 2 ¼ post-larval whorls. Shell microstructure comprises an inner layer with simple crossed lamellar structure and a homogeneous outer layer.

Material examined.—Morphologic comparisons in this study were made with 19 unprepared or partially prepared specimens of *Retiskenea statura* from CAS 69122.01, upper Oligocene Knappton locality, Pacific County, Washington, kindly supplied by J. L. Goedert.

Occurrence.—*Retiskenea statura* occurs at three cold-seep carbonate sites, enclosed in bathyal siltstones of western Washington State, including the middle Eocene Humpulips Formation, the lower Oligocene part of the Makah Formation, and the upper Oligocene Knappton locality (Goedert and Benham, 1999, and references therein).

TABLE 2—Basic statistics for each species (*Retiskenea? kieli* n. sp., *R.? tuberculata* n.sp., *R. statura*, and *R. diploura*), including sample size (N), mean (\pm SE) and range of heights and diameters, Pearson correlation coefficient (r), p-value for correlation, and mean (\pm SE) and range of height-to-diameter ratios.

Species	N	Mean (\pm SE) (mm)		Range (mm)		r	p
		H	D	H	D		
CFCC <i>R.? kieli</i> n. sp.	39	1.8 (0.1)	2.5 (0.1)	0.4–3.8	0.9–4.4	0.94	<0.01
WS <i>R.? tuberculata</i> n. sp.	10	2.3 (0.3)	3.1 (0.3)	1.4–3.9	2.2–4.6	0.96	<0.01
WA <i>R. statura</i>	7	2.9 (0.1)	2.6 (0.1)	2.5–3.4	2.0–3.1	0.87	<0.05
Japan <i>R. diploura</i>	20	2.3 (0.1)	2.3 (0.1)	1.7–3.5	1.7–3.4	0.93	<0.01
<i>Height-to-Diameter Ratios</i>							
		Mean (\pm SE) (mm)		Range (mm)			
CFCC <i>R.? kieli</i> n. sp.		0.7 (0.0)		0.5–0.9			
WS <i>R.? tuberculata</i> n. sp.		0.7 (0.0)		0.6–0.9			
WA <i>R. statura</i>		1.1 (0.0)		1.0–1.3			
Japan <i>R. diploura</i>		1.0 (0.0)		0.8–1.2			

Discussion.—Warén and Bouchet (2001) transferred *Depressigyra? statura* to *Retiskenea* because the shape of the protoconch and teleoconch closely resemble that found in *R. diploura*. Kiel (2006) later illustrated a specimen with protoconch sculpture, confirming its reticulate nature (Kiel, 2006, fig. 3.9, p. 123). *Retiskenea statura* also exhibits a tangential position of the aperture; whereas, *Depressigyra* possesses a strongly ridged protoconch and radial position of the aperture. Of the four named species of *Retiskenea*, including those tentatively placed in the genus and described below, *R. statura* possesses a spire of greater height, or stature (*statura*, Latin; mean height 2.91 mm, Tables 1 and 2; cf. Fig. 4). It also shows somewhat coarser reticulation of the protoconch than *R. diploura* (Kiel, 2006).

RETISKENEAE? KIELI new species Figure 3

Diagnosis.—A skeneiform neomphalid, thin shelled, low spired, with a net-like, moderately coarse reticulate protoconch, ~250 μ m diameter; sutures deeply incised; body whorl inflated, with fine, sinuous, incremental growth lines; prosocline aperture flared, with shallow labial notch; umbilicus deep and narrow.

Description.—Shell small, thin-walled, low spired, skeneiform (Fig. 3.1–3.3, 3.5–3.7, 3.9, 3.10); protoconch of one whorl, knob-like, strongly reticulate, becoming less distinct toward the peristome (Fig. 3.4, 3.8). Teleoconch comprises three convex whorls with deeply incised sutures and shows fine, variably spaced, sinuous prosocline growth lines. Body whorl inflated, compressed, flaring (Fig. 3.2) toward aperture, with obliquely rounded shoulder. Aperture prosocline, obliquely rounded, narrowly indented by preceding whorl; lip thin, tangential, with sinuous, shallow labial notch. Umbilicus is deep and narrow (Fig. 8.1). Shell microstructure is recrystallized in all specimens examined under SEM, and therefore is presently unknown for this fossil species.

Etymology.—Named after paleontologist Steffen Kiel.

Types.—Holotype CAS specimen 69162 (2.75 mm diameter; 2.11 mm height), and paratypes CAS specimens 69163–69191 are designated (Fig. 3). All were collected from one ~260-m-long limestone lens in lower Cretaceous, Great Valley Group slope-turbidites of the Cold Fork of Cottonwood Creek, from three different sites along the southern half of the lens (CAS localities 68064, 68059, 68044; detailed below). Listed in Tables 1 and 2 and plotted in Figure 4 are the diameter and height measurements for the 30 individual type specimens. In addition, 97 prepared fossils from CAS locality 68044 were examined. They are included as bulk paratype CAS 69201, and stored with the type collection.

Other material examined.—Other unprepared supplementary material housed in the CAS stratigraphic collection includes bulk limestone with numerous *Retiskenea?* microgastropods from CAS localities 68064, 68059, 68044.

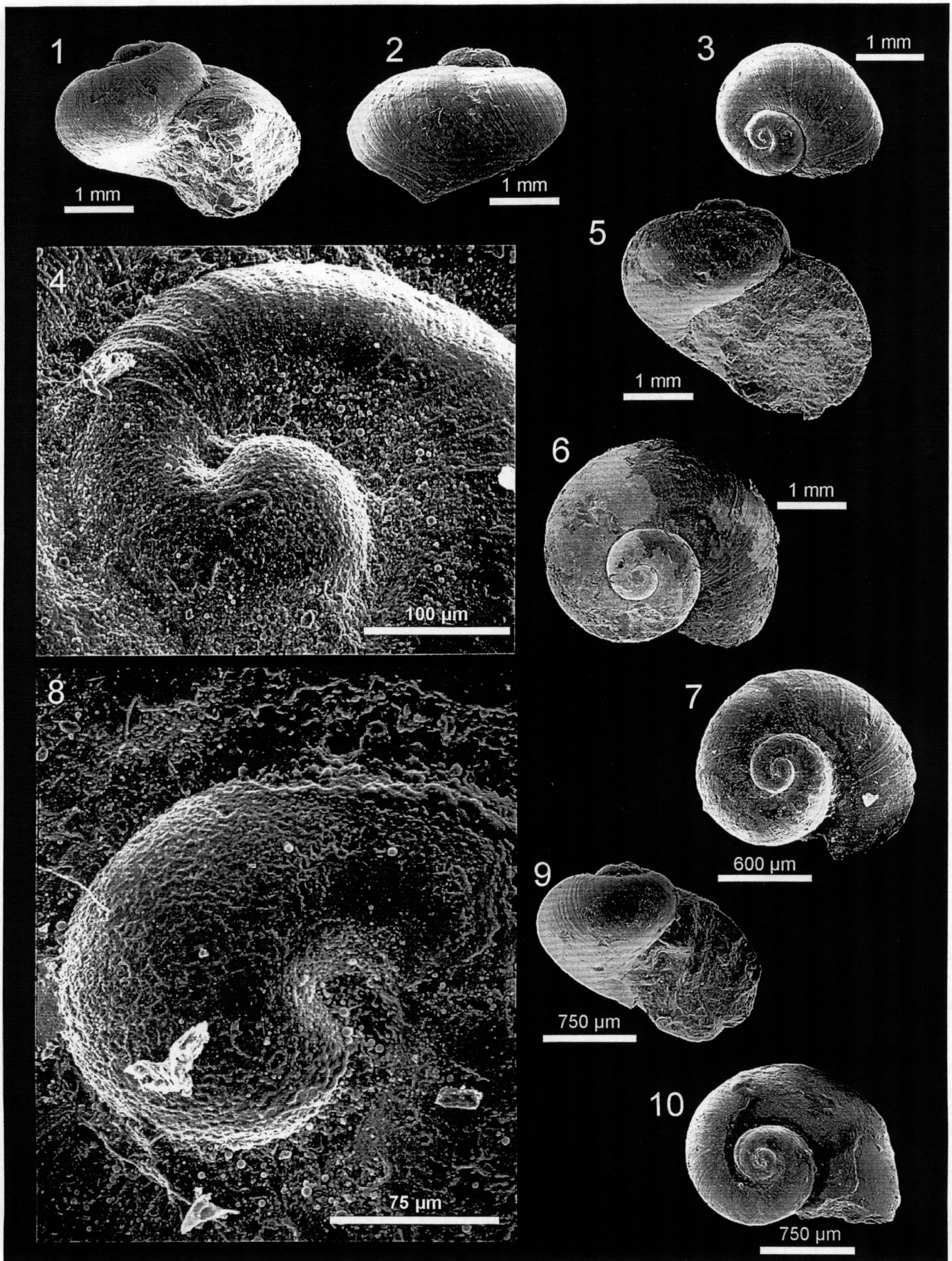
Occurrence.—The in situ hydrocarbon-seep carbonates that contain *Retiskenea? kieli* n. sp. are enclosed in Lower Cretaceous slope turbidites of the Lodoga Formation, Great Valley Group, Cold Fork of Cottonwood Creek, 20 km west of Red Bluff on the Pettyjohn Ranch, northern California (Stanton, 1895; Jones and Bailey, 1973; Ingersoll, 1983; Campbell and Bottjer, 1993; Campbell et al., 1993, 2002). Jones and Bailey (1973) mapped the northwest-southeast-trending Cold Fork limestone lens adjacent to the Sulphur Springs Fault (Fig. 2.3), and assigned an Albian age (~106 m.y.) to the deposit based on the occurrence of ammonite *Leconteites* cf. *L. deansi* (Whiteaves, 1893). Three CAS localities were sampled northward and parallel to bedding along the ~260-m-long (~1.3-m-thick) Cold Fork carbonate lens: from the southernmost exposure (0 m) of a dark gray limestone adjacent to Pettyjohn Road (CAS 68064), a gray limestone outcrop ~60 m up the hillslope (CAS 68059), and a light-gray recrystallized limestone ~130 m up the hillslope (“midlens,” CAS 68044), Tehama County, 1.7 km upstream along road from Pettyjohn ranch house, Cold Fork of Cottonwood Creek, northeast of Stevenson Peak and due west of Wilcox Flat, NW quarter of sec. 29, T27N, R7W, U.S. Geological Survey 15-minute Colyear Springs Quadrangle (USGS 1957; see also geologic map of Jones and Bailey, 1973). The Cold Fork of Cottonwood Creek “white limestone” deposit of this study is the same location as USGS M2676 and M1070 (see also Stanton, 1895).

Associated fauna.—Taxa associated with *R.? kieli* include worm tubes, a lucinid bivalve, large mussel *Modiola major* (Gabb, 1869), limpets, a high-spired, round-shouldered gastropod, and foraminifera and ostracodes (Stanton, 1895; Campbell, 1996; Campbell et al., 2002).

Discussion.—The systematic position of the Neomphalidae has been the subject of considerable discussion. The lack of soft parts in fossil neomphalids creates serious difficulties for correct taxonomic placement, including the present material, because soft anatomy provides the majority of diagnostic features for living neomphalid genera and species, and hence affinities based on shell characters alone are problematic. Another issue arising is in regard to the potential longevity of the genus *Retiskenea*. A time range jumping from Lower Cretaceous for the *Retiskenea?* species described here, to Eocene-Oligocene for *R. statura*, and then to modern settings for *R. diploura*, illustrates the considerable gaps currently present in the known fossil record for this group. A similar situation exists for Paleozoic-Mesozoic “lineages” of seep-restricted rhynchonellide brachiopods (cf. Campbell and Bottjer, 1995a; Gischler et al., 2003). In light of these uncertainties, we can only tentatively place this species and the following one in *Retiskenea*.

Retiskenea? kieli possesses moderately coarse reticulation, becoming less distinct toward the peristome, and teleoconch characters that suggest assignment to the Neomphalidae. Such shell features as the inflated body whorl, obliquely rounded, prosocline, tangential aperture, and narrow umbilicus are characters shared

FIGURE 3—*Retiskenea? kieli* n. sp., scanning electron micrographs. Figured types sampled from the midlens portion (~130 m, CAS locality 68044) of the ~260-m-long hydrocarbon-seep carbonate at Cold Fork of Cottonwood Creek, Great Valley Group. 1–4. Holotype CAS specimen 69162: 1, oblique apertural view; 2, side view; 3, apical view; 4, protoconch and early teleoconch. 5–6. Paratype CAS specimen 69163: 5, apertural view; 6, apical view. 7, 8. Paratype CAS 69164: 7, apical view; 8, protoconch detail, showing irregular reticulate ornament. 9, 10. Paratype 69195: 9, apertural view; 10, apical view.



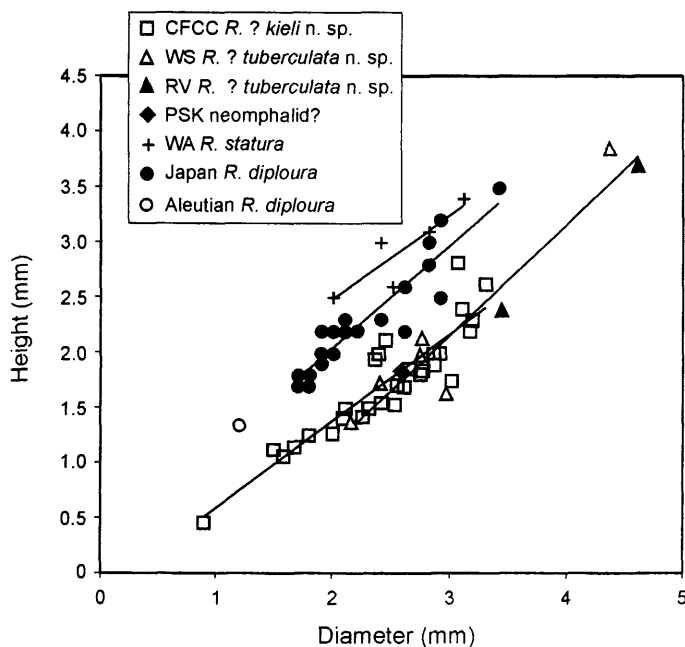


FIGURE 4—Graph of measured height (mm) versus diameter (mm) of two Mesozoic species of *Retiskenea*?, the Cenozoic species, *Retiskenea statura*, and modern *R. diploura*. Trend lines are shown for each species. Open squares, *R.? kieli*, Cold Fork of Cottonwood Creek (CFCC); black triangles, *R.? tuberculata*, Wilbur Springs (WS); open triangles, *R.? tuberculata*, Rice Valley (RV); +, *R. statura* (Goedert and Benham, 1999), Washington (WA); black circles, *R. diploura*, Japan Trench (Okutani and Fujikura, 2002); open circle, *R. diploura* holotype, Aleutian Trench (Warén and Bouchet, 2001). Also shown is the approximate height and diameter measurement for the single specimen of a neomphalid? from Paskenta, California (black diamond), which has not been prepared from the carbonate matrix (cf. Fig. 7).

by *Retiskenea* and *Retiskenea?* *Retiskenea? kieli* has a lower mean shell height (1.81 mm) than measurements for the other three species attributed to *Retiskenea* (Table 2). *R.? kieli* differs from *R. diploura* Warén and Bouchet, 2001 in its somewhat more compressed shell profile, more obliquely rounded aperture, and slightly larger mean diameter of complete shells (Fig. 4, Table 2). *Retiskenea? kieli* differs from *R. statura* in possessing a lower spire, shallower apical angle, less globose lateral body profile, more deeply incised sutures, and more obliquely rounded aperture. Recently, Kiel (2006, fig. 3.7–3.9) illustrated well-preserved protoconchs of *R. statura* from the Lincoln Creek Formation, showing relatively deep polygonal pits. By contrast, the protoconch ornament of *R.? kieli* (Fig. 3.4, 3.8) is more net-like and similar in overall form to the living *Retiskenea* species, with irregular low ridges separating shallow depressions of variable size and shape. *Retiskenea? kieli* differs from *R.? tuberculata* n. sp., described below, by smaller size, possession of a smaller, net-like protoconch rather than a larger, tuberculate protoconch, a slightly more obliquely rounded aperture profile, and finer growth lines.

RETISKENEAE? TUBERCULATA new species Figure 5

Diagnosis.—A skeneiform neomphalid, thin shelled, low spired, with a coarsely reticulate to granular protoconch, to ~400

µm diameter; body whorl inflated, relatively wide, with distinct beaded growth lines in first 1/3 of teleoconch; remainder of teleoconch displays fine evenly spaced growth lines, with sinuous labial notch; prosocline aperture flared and almost circular; umbilicus deep and narrow.

Description.—Shell small, thin-walled, low spired, skeneiform (Fig. 5.1, 5.4, 5.6–5.8, 5.10, 5.11); protoconch measuring two-thirds of a whorl, knob-like, inflated in its initial area, tuberculate, vaguely reticulate and becoming less distinct toward the peristome (Fig. 5.2, 5.9). Teleoconch of two and a half convex whorls with deeply incised sutures, and evenly spaced, coarsely beaded, sinuous growth lines in its initial portion (1/3 of whorl past the protoconch; Fig. 5.2, 5.3). Body whorl inflated, with a well-rounded shoulder, gently flared approaching the aperture (Fig. 5.10), with fine evenly spaced growth lines. Aperture prosocline, nearly round, with shallowly sinuous labial notch (Fig. 5.4), tangential to the body whorl, in narrow contact with the preceding whorl. The umbilicus is deep and narrow.

Etymology.—Latin *tuber* for bump, swelling, alluding to the coarse granular protoconch, vague reticulation, and beading of the early teleoconch growth lines.

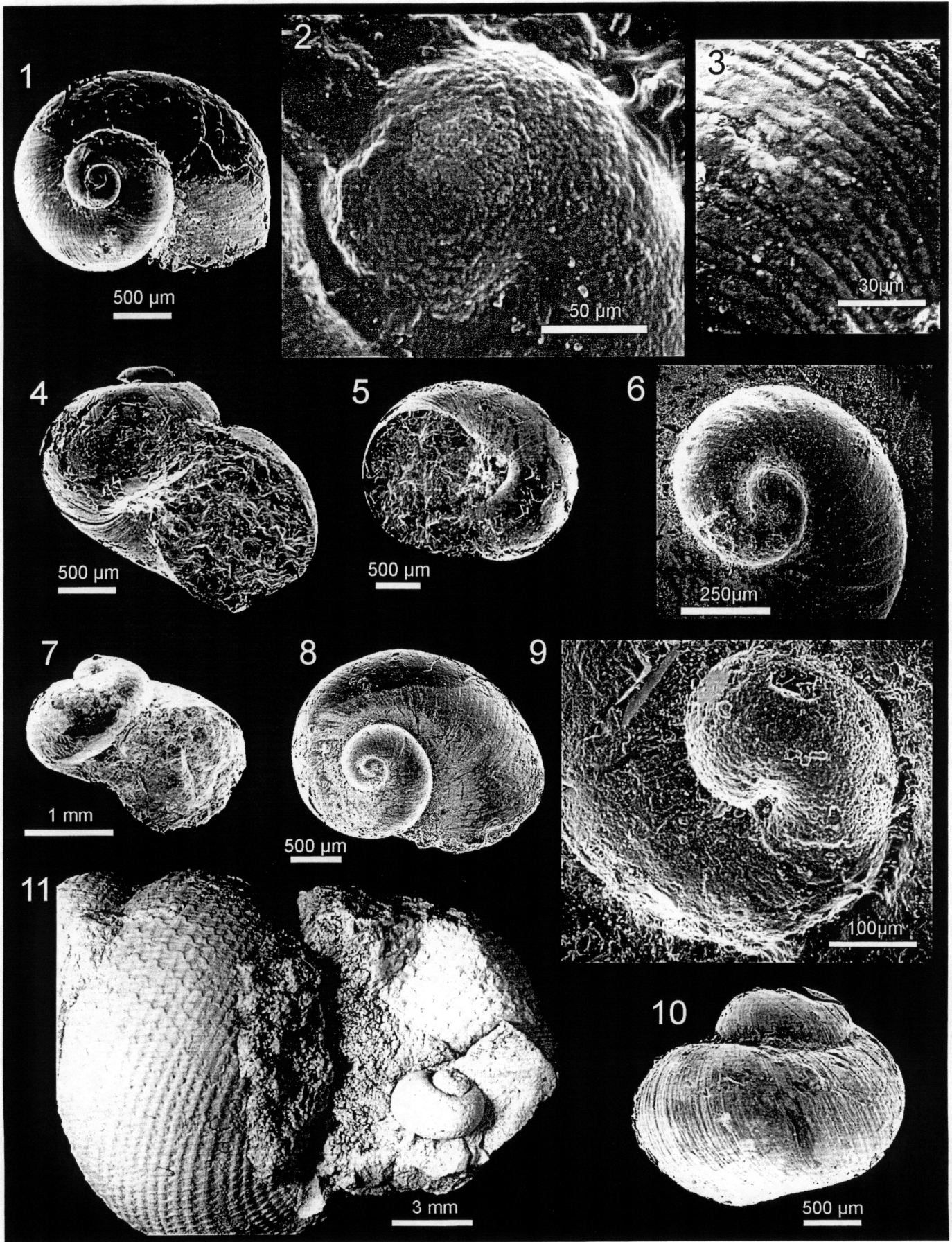
Types.—Holotype CAS specimen 69192 (2.85 mm diameter; 2.16 mm height) was recovered from the main Wilbur Hot Springs Resort limestone deposit, in the lower Cretaceous Stony Creek Formation, comprising Great Valley Group slope-turbidites and intercalated sedimentary serpentinites (CAS locality 68061; detailed below). Also designated were paratypes CAS 69193–69200 and UCMP type no. 154112 (Fig. 5.11), collected from lower Cretaceous white limestones at Wilbur Springs (Colusa County, CAS locality 68061) and Rice Valley (Lake County, CAS location 68079, USGS locality M6010), respectively. Height and diameter measurements are listed in Tables 1 and 2 and depicted in Figure 4 for these 10 individual type specimens.

Other material examined.—One specimen of *Retiskenea?* cf. *tuberculata* (2.80 mm diameter; 2.55 mm height) was recognized in a small collection from UCMP locality A-4658, a volumetrically minor limestone deposit exposed near the main Wilbur Springs Resort Limestone (CAS locality 68061, see below). The collection also contains two indeterminate microgastropods and one broken larger gastropod in recrystallized micrite. It was made by the Fall 1948 Paleo 103 class from the University of California, Berkeley. The locality description card for UCMP A-4658 reads: "Colusa County, about 0.8 km south (S 10°W) of Wilbur Hot Springs Resort, and 100 m from top-of-hill float boulders of whitish fossiliferous limestone located near Digger pine tree on fence line; in basal Paskenta Formation, 39°N, 122.1°W, SE 1/4 of NW 1/2 of sec. 28, T14N, R5W, 15-minute Wilbur Springs Quadrangle (1944 edition)."

Occurrence.—*Retiskenea? tuberculata* was recovered from quarried float blocks of a hydrocarbon-seep carbonate deposit (Campbell et al., 2002) enclosed in Lower Cretaceous slope turbidites and foliate serpentine breccias of the Great Valley Group at Wilbur Springs (Colusa County, CAS 68061; Fig. 2.4). It also has been found in a Lower Cretaceous seep limestone surrounded by Great Valley-equivalent siliciclastic strata and serpentinite of the Rice Valley outlier, situated in the eastern belt of the Franciscan Group (Lake County, CAS 68079; Fig. 2.5). A Hauterivian age (~133 m.y.) was assigned to both limestone deposits based on co-occurrence of the brachiopod, *Peregynella whitneyi* Gabb, 1869, and stratigraphic position above *Buchia pacifica* Lawton, 1856 (Berkland, 1973; Carlson, 1984a), although this age is not certain (discussed in Campbell and Bottjer, 1995a). Wilbur Springs, CAS locality 68061, Colusa County: white limestone on hill 1.5 km south/southeast of Wilbur Hot Springs Resort (= "Resort limestone"), above Sulphur Creek, lat. 39°N, long. 122°W, 1,000 ft. N, 300 ft. east of the southwest corner of sec. 28, T14N, R5W, U.S. Geological Survey 7.5-minute Wilbur Springs Quadrangle (USGS, 1989). The main Wilbur Springs white limestone deposit of this study is the same location as USGS M7012. Rice Valley CAS locality 68079, Lake County: white limestone in Rice Valley (= "SW Rice Valley Wall"), 650 m north, 530 m west of the southeast corner of sec. 10, T17N, R9W, U.S. Geological Survey 7.5-minute Potato Hill Quadrangle (USGS, 1967). The Rice Valley limestone deposit of this study is the same location as USGS M6010.

Associated fauna.—Taxa associated with *R.? tuberculata* include worm tubes, a moderately globose gastropod with squamose ornament (Fig. 5.11).

FIGURE 5—*Retiskenea? tuberculata* n. sp., scanning electron micrographs. 1–3, Holotype CAS specimen 69192 from main Resort limestone at Wilbur Springs (lower Cretaceous, CAS locality 68061): 1, apical view; 2, detail view of tuberculate, vaguely reticulate protoconch; 3, detail view of granular, beaded texture of early teleoconch. 4–6, paratype CAS specimen 69193 from Rice Valley limestone deposit (lower Cretaceous, CAS locality 68079): 4, apertural view; 5, umbilical view; 6, protoconch area. 7–9, Paratype CAS specimen 69194 from main Resort limestone at Wilbur Springs (CAS locality 68061): 7, oblique apertural view; 8, apical view; 9, detail of granular protoconch. 10, Paratype CAS specimen 69195 from CAS locality 68061 at Wilbur Springs, side view. 11, Paratype UCMP specimen 154112, closely associated with a larger gastropod with squamose ornament (UCMP specimen 154113), at its folded aperture, from Rice Valley limestone deposit (USGS locality M6010 = CAS locality 68079).



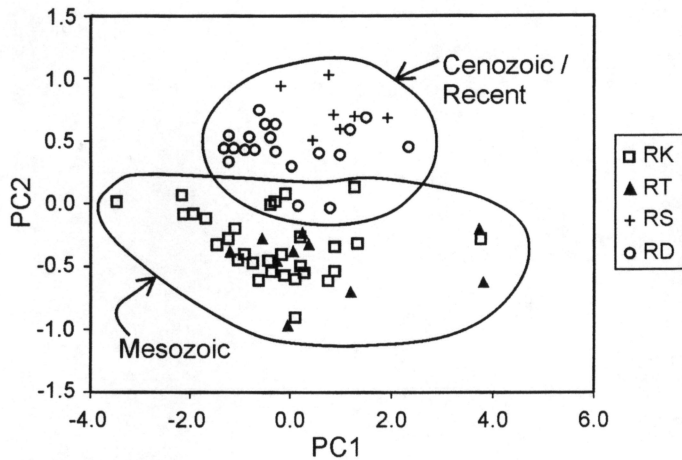


FIGURE 6—Principal component analysis using the height and diameter for four neomphalid microgastropod species, including *Retiskenea? kieli* n. sp. (RK), *R.? tuberculata* n. sp. (RT), *R. statura* (RS), and *R. diploura* (RD).

the cold-seep-restricted brachiopod *Peregrinella whitneyi*, and mytilid, solemyid, lucinid and pectinid (*Pecten complexicosta* Gabb, 1869) bivalves (Gabb, 1869; Stanton, 1895; Berkland, 1973; Campbell, 1996; Campbell and Bottjer, 1995a).

Discussion.—Shell characters of this fossil species, especially the inflated, vaguely reticulate protoconch, number of shell whorls, inflated body whorl and shell sculpture, suggest inclusion within the neomphalid genus *Retiskenea*. *Retiskenea? tuberculata* has a larger mean shell diameter (3.1 mm) than the other three species of the genus (Table 2). The present species differs from *R. diploura* Warén and Bouchet, 2001 in its more compressed shell profile, more obliquely rounded aperture, and larger, granular protoconch. *Retiskenea? tuberculata* differs from *R. statura* (Goedert and Benham, 1999) in possessing a lower spire, a larger, granular protoconch, shallower apical angle, less globose shell profile, more deeply incised sutures, and more obliquely rounded aperture. *Retiskenea? tuberculata* differs from *R.? kieli* n. sp. in possessing a larger, tuberculate protoconch, beaded early teleconch, slightly more circular aperture, and stronger growth lines.

NEOMPHALIDAE? sp. INDET.

Figure 7

Discussion.—A single individual fossil microgastropod (LACMIP specimen 12925) is broadly similar to the two new Mesozoic *Retiskenea?* species described herein. The specimen was recovered from the Paskenta hydrocarbon seep-carbonate (~1.85 mm high, ~2.57 mm wide; Figs. 4, 7). The white limestone lens is enclosed in Upper Jurassic (Tithonian, ~148 m.y.), Great Valley slope-turbidites of the Stony Creek Formation, adjacent to the synsedimentary Paskenta Fault (Fig. 2.2, LACMIP locality 15917, = “Keyserling’s Gate”—cf. Stanton, 1895; Jones et al., 1969; Ingersoll, 1983; Moxon, 1990; Campbell et al., 1993, 2002). It is associated with Tithonian *Buchia piochii* (Gabb, 1869). The compressed globose shape, size, whorl proportions, flaring aperture, and fine growth lines suggest the specimen may be a neomphalid related to *Retiskenea*. The specimen was not prepared further because additional material has not yet been uncovered from the rock matrix of the Paskenta deposit, and the site is currently not accessible.

Occurrence.—The site is located 4.8 km northwest of Paskenta along Thomas Camp Road, on a knoll between the road and Digger Creek, southeast quarter of sec. 25, T24N, R7W, U.S. Geological Survey 7.5-minute Paskenta Quadrangle (USGS 1967), Tehama County, California.

Associated fauna.—Stanton (1895) made the first invertebrate fossil collection from the Paskenta locality (USNM 23205, 23245, 23051). Additional material acquired during Campbell’s (1995) dissertation study resides in LACMIP collections (localities 15912–15928). The associated fauna enclosed in

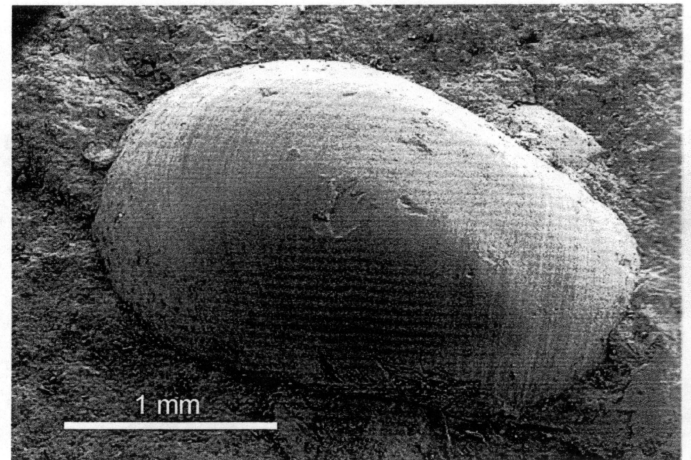


FIGURE 7—Undescribed neomphalid? (LACMIP specimen 12925) from Paskenta hydrocarbon seep-carbonate (Upper Jurassic, LACMIP locality 15917). Side view, unprepared in carbonate matrix.

micrites includes thin worm tubes, solemyid, lucinid, nuculid, mytilid, inoceramid and astartiid bivalves, belemnites, as well as the cold-seep-affiliated brachiopod, *Cooperhynchia schucherti* Sandy and Campbell, 1994, and several gastropods (cf. Stanton, 1895; Sandy and Campbell, 1994). Age-diagnostic taxa include ammonites, *Phylloceras? knoxvillensis* Stanton, 1895 and *Paradontoceras? storrsi* (Stanton, 1895), and the bivalves, *Buchia piochii* (Gabb, 1864) and *B. fisheriana* (d’Orbigny, 1845) (W. P. Elder, personal comm., 1992).

COMPARATIVE SIZE DATA AMONG *RETISKENEA* SPECIES

Correlation analyses of shell height and diameter data resulted in significant linear relationships for all four species attributed to *Retiskenea* and *Retiskenea?* (Fig. 4, Table 2), hence showing general isometric growth in the modern and fossil populations sampled. The height-to-diameter ratios for *R. statura* and *R. diploura* display a similar 1:1 relationship as compared to *R.? kieli* and *R.? tuberculata*, which both have a lower ratio of 0.7 ± 0.0 (Table 2). Thus, the Mesozoic microgastropods are more compressed than the Cenozoic and modern species. A principal component analysis, using the height and diameter size data for the two *Retiskenea* and two *Retiskenea?* species, resulted in a good separation between Mesozoic and the Cenozoic/Recent groups (Fig. 6). However, based on height and diameter data alone, the two Mesozoic species cannot be separated from one another, nor can the two Cenozoic/Recent species be differentiated. In the principal component analysis, the height and diameter loadings for the first component were both 0.937, and for the second component they were 0.35 and -0.35 , respectively. The first component explained 87.8% of the variation while the second component explained the remaining 12.2%. In summary, the two Cretaceous *Retiskenea?* species, and the single Upper Jurassic neomphalid? microgastropod specimen, are clearly more similar to one another in these shell dimensions (Figs. 4, 6). The younger species also are similar to one another, but statistically discrete from the microgastropods of the Mesozoic localities. It is unknown why the neomphalid microgastropods from the two Eras cluster in two distinctive groupings (cf. Fig. 6).

PALEOECOLOGY AND PRESERVATION OF MESOZOIC *RETISKENEA?* FROM NORTHERN CALIFORNIA

At the northern California localities studied, *Retiskenea?* microgastropods occur in microbialites. These carbonates are typified by a “structure grumeleuse” fabric of micritic clots with indistinct margins, surrounded by more coarsely crystalline, translucent cement spar (cf. Bathurst, 1975; MacIntyre, 1985; Fig. 8.1–8.4). Similar clotted micrite fabrics are common in ancient seep-carbonates worldwide, and have been inferred as microbial in

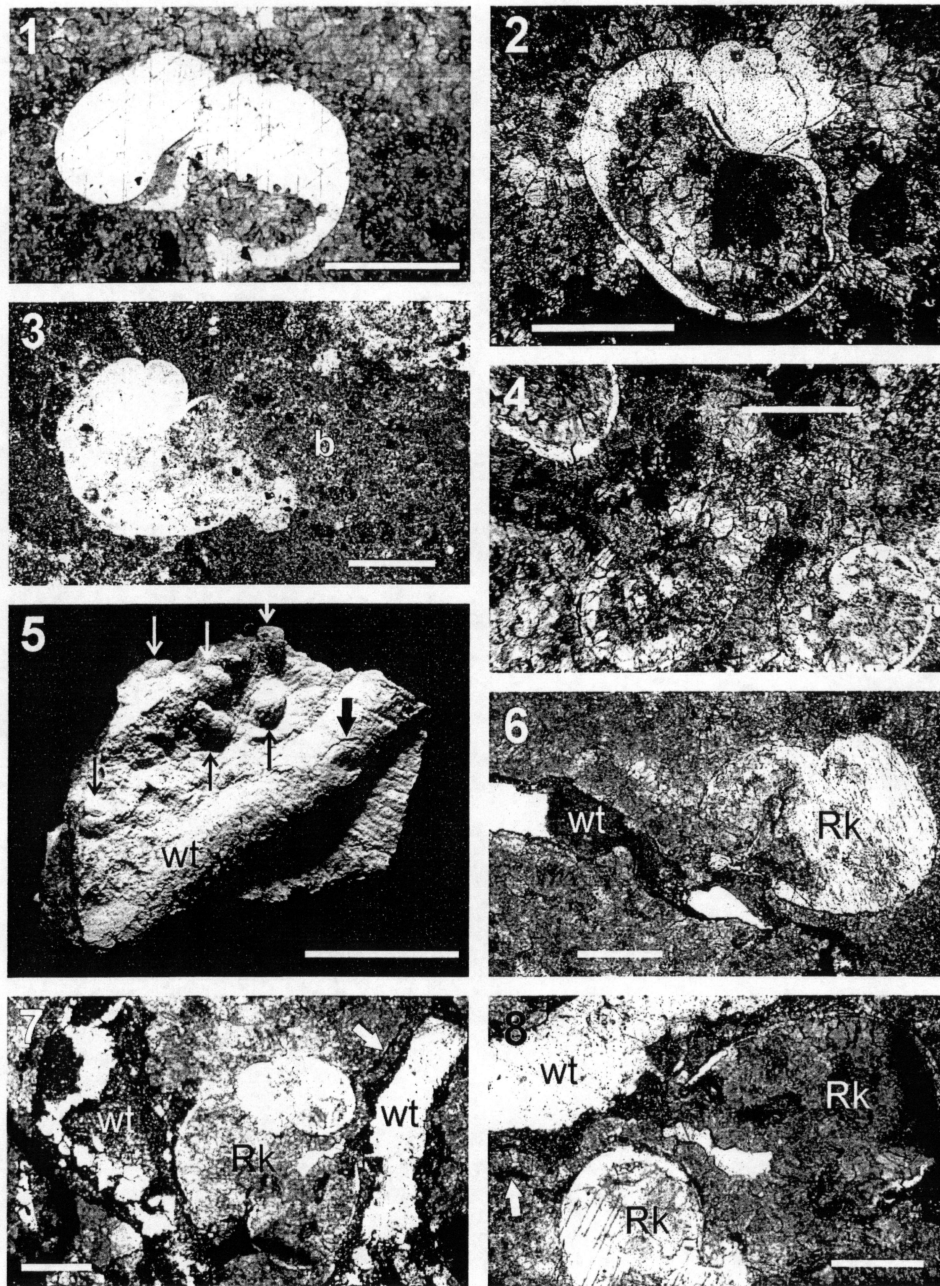


FIGURE 8—Paleocological and sedimentological associations of the *Retiskenia? kieli* n. sp., Cold Fork of Cottonwood Creek locality. Scale bars all 1 mm. 1. Apertural view of snail in cross section showing typical depressed-globular shell form, inflated aperture, and narrow, deep umbilical slit. Whorls partially filled with geopetal early cement; remaining pore space occluded by late diagenetic calcite spar (white), which also replaced original shell material. Plane-polarized light; CC-200-1. 2. Side view of snail in cross section showing shape of protoconch and globose but slightly compressed body whorls, flaring toward aperture. Plane-polarized light; CC-0-1. 3. Side view of snail in cross section displaying peloids and bioturbated micrite (b) around apertural opening. Plane-polarized light; CC-0-1. 4. Three snails showing gregarious clustering in "structure grumeleuse" (microbial) fabric; plane-polarized light; CC-160-4. 5. Several juvenile? snails (thin arrows) and a possible homing scar (thick arrow) closely associated with a worm tube (wt); hand specimen photograph. 6. Recrystallized *R. kieli* (Rk) attached to carbonate-cemented worm tube (wt); plane-polarized light; CC-1. 7. Recrystallized *R. kieli* (Rk) nestled in between two carbonate-cemented worm tubes (wt) that are encrusted by a dark microbial laminite (arrow) of micrite, and filled with late-stage, barite-rich, silty clay (dark), and blocky calcite spar (white); plane-polarized light; CC-160-4. 8. Two microgastropods (Rk) attached to worm tube (wt), coated in places by a dark microbial laminite (arrow); upper-right gastropod has corroded or broken left margin. Plane-polarized light; CC-160-4.

origin, formed in association with the activities of Archaea performing anaerobic methane oxidation (AOM) in the zone of bacterial sulfate reduction (e.g., Cavagna et al., 1999; Peckmann et al., 1999, 2002; Thiel et al., 1999; Clari and Martire, 2000; Peckmann and Thiel, 2004). Molecular analyses of several *Retiskenia?*-bearing micritic carbonates of this study confirm the presence of key biomarkers for AOM, specifically ^{13}C -depleted crocetane and PMI (Birgel et al., 2006). Hence, the microgastropods were adapted to living in oxygen-poor conditions, also suggested by co-occurrence of framboidal pyrite (Campbell et al.,

2002), where chemically reduced fluids rich in dissolved sulfide and methane seeped to the seafloor.

Mesozoic *Retiskenia?* appear to have produced peloids with sharp boundaries, which are possible fecal pellets, and they locally disturbed the micritic sediments with bioturbation activities (e.g., Fig. 8.3), indicating that the gastropods were interacting with the surrounding soft sediments prior to cementation. They may have been feeding on microbial biofilms, as radulae of modern neomphalids indicate that they are grazers (e.g., Warén and Bouchet, 2001).

The *Retiskenea?* fossils from the Cold Fork of Cottonwood Creek locality typically occur in clusters (e.g., Fig. 8.4, 8.5, 8.8), and/or were associated spatially with other mega-invertebrates, notably worm tubes (Fig. 8.5–8.8). Thin micrite laminae on some worm tubes of this study (Fig. 8.7, 8.8) may represent preserved microbial biofilms. Therefore, the close spatial association between the fossil microgastropods and these fabrics suggests that the snails were feeding on seafloor substrates or worm tube surfaces encrusted with microbes in areas of active hydrocarbon seepage. Similar clusterings of gastropods have been reported from western Pacific hydrothermal-vent sites, where living neomphalid limpets adapted to hard substrates aggregate on basalt boulders and *Riftia* Jones, 1981 tube worms (e.g., McLean 1981, 1990). Clustering of the living coiled neomphalids, *Retiskenea diploura*, also occur in the Japan Trench, where they have been observed crawling upon *Calyptogena* Dall, 1891 shells, or found in the silty sediments adjacent to these bivalves (Fujikura et al., 2002).

One large *R.?* *tuberculata* from the Rice Valley locality is closely associated with a larger gastropod with a thin, folded shell bearing scaly ornament (Fig. 5.11). The folding suggests a decalcified shell of an animal that was living in a corrosive, H₂S-rich paleoenvironment. Decalcified gastropod shells have been reported for modern *Retiskenea* on the Oregon continental margin (Warén and Bouchet, 2001).

The microgastropod shells of this study are recrystallized, preventing us from making shell microstructural comparisons with younger *Retiskenea* (cf. Kiel, 2004). Recrystallization (Fig. 8.1–8.4, 8.6–8.8) occurred late in diagenesis, as is evident from the bright orange color of the shells under cathodoluminescence (CL). This CL pattern matches that of a pore-filling, blocky calcite spar, the last-formed cement developed during burial of the Californian seep deposits (cf. Campbell et al., 2002).

PACIFIC RIM HYDROCARBON-SEEP ASSOCIATIONS OF *RETISKENEA*

The geological settings and biotic associations of all known microgastropods ascribed to *Retiskenea* or *Retiskenea?*, modern and fossil, have been found exclusively in seep (paleo)environments of the Pacific region (Fig. 1), in moderately diverse faunal assemblages. In particular, the genus and type species of living *Retiskenea diploura* was described by Warén and Bouchet (2001) from 4,808-m-deep waters of the eastern Aleutian subduction zone, at diffuse sulfide/methane seeps of the Shumagin site. Various geochemical, sedimentological, and biological hallmarks of fluid venting at this locality were investigated by Suess et al. (1998). The associated, chemosymbiotic mega-invertebrates include *Calyptogena phaseoliformis* Métivier, Okatani and Ohta, 1986, *Acharax* cf. *johnsoni* (Dall, 1891) and tube worms (Suess et al., 1998; Warén and Bouchet, 2001). In addition, Warén and Bouchet (2001) reported a single, decalcified, live specimen (2.4 mm diameter, with apex missing) of *Retiskenea* cf. *diploura* from sulfide/methane seeps along the Oregon convergent margin (600 m water depth at 44°34.235'N, 125°05.8'W). Affiliated chemosymbiotic mega-invertebrates include *Calyptogena* spp. and *Solemya* sp. In the Japan Trench, *R. diploura* was found with the chemosymbiotic bivalve *Calyptogena phaseoliformis* (Fujikura et al., 2002). These modern Pacific Rim, hydrocarbon-seep localities with *Retiskenea diploura* also contain a diverse gastropod fauna, which includes both vent/seep-endemic and more cosmopolitan groups (Warén and Bouchet, 2001, appendix 1, p. 223–224; Fujikura et al., 2002).

Cenozoic *Retiskenea statura* (Goedert and Benham, 1999) was described from localized, methane-derived, authigenic carbonates within bathyal siltstones from three different formations in western Washington (Fig. 1). In particular, *Retiskenea statura* is abundant within the in situ seep deposits, but is uncommon in olistostromal, seep-carbonate blocks of the lower Oligocene Makah

Formation (Goedert and Benham, 1999). Associated mega-invertebrates from these seep occurrences are diverse, and include chemosymbiotic and nonchemosymbiotic bivalves, gastropods, serpulid and vestimentiferan worm tubes, decapod crustaceans, a chiton, and a scaphopod (Goedert and Squires, 1990; Squires and Goedert, 1991, 1995; Goedert and Campbell, 1995).

The Mesozoic *Retiskenea?* from California occur in either fault-turbidite hosted (*R.?* *kieli* n. sp.) or serpentine-diapir associated (*R.?* *tuberculata* n. sp.) geologic settings (Fig. 2), along which hydrocarbon-rich fluids migrated upward to seeps at the seafloor. The structural, stratigraphic, sedimentologic and geochemical signatures for the methane-derived origin of these authigenic carbonates are discussed elsewhere (Berkland, 1973; Carlson, 1984a; Campbell and Bottjer, 1993, 1995b; Campbell et al., 1993, 2002; Campbell, 1995). It is unknown whether the two distinctly different geologic environments (serpentine diapirs versus syndimentary faults) influenced the separate evolution of the two new *Retiskenea?* species, since most Great Valley seep-carbonate localities were already geographically isolated (Fig. 2.1). Campbell (1996; 2006) and Kiel and Campbell (2005) reported gastropods in these and other Californian Mesozoic seep limestones, some of which are so abundant as to constitute gastropod coquinas (e.g., Kiel and Campbell, 2005, fig. 2c; Campbell, 2006, fig. 6). As listed in the systematics section above, the fossil assemblages associated with the two new species of *Retiskenea?* of this study are of low to moderate diversity, and include both vent/seep species and taxa that also occurred outside of seep areas.

In summary, *Retiskenea* and *Retiskenea?* have occurred exclusively in hydrocarbon seep settings of the Pacific Rim for more than 100 million years. They are members of seep (paleo)communities with low to moderate diversity, including chemosymbiotic and other deepsea taxa. Additional discoveries of neomphalid gastropods in other seep deposits are likely, e.g., from Japan (Kaim, personal commun., 2006), such that Pacific Rim distribution patterns eventually may be reconstructed in four dimensions (space and time) for this endemic vent/seep gastropod family.

ORIGINS OF THE NEOMPHALIDS AND *RETISKENEA*

Despite some perceptions to the contrary (cf. McArthur and Tunnicliffe, 1998; Callender and Powell, 1999; McArthur and Koop, 1999; Van Dover, 2000), the fossil record of gastropods in vents and seeps is well-represented in Early Jurassic to Neogene deposits around the Pacific (e.g., Stanton, 1895; Goedert and Squires, 1990; Squires and Goedert, 1991; Goedert and Campbell, 1995; Squires, 1995; Campbell, 1996; Goedert and Kaler, 1996; Goedert and Benham, 1999; Little et al., 1999, 2002; Goedert et al., 2003; Kiel and Campbell, 2005; Majima et al., 2005, and references therein; Kiel, 2006; this study). These data, particularly from fossil seep deposits, confirm that there are few taphonomic losses of small mollusk shells, and that gastropod shells generally preserve many characters, even if recrystallized. Indeed, even a few protoconchs of seep fossils are moderately well preserved (Kiel, 2006; this study). Early diagenetic seafloor cementation by methane-derived carbonates likely enhanced preservation potential in these settings, despite later shell recrystallization to calcite spar (e.g., Fig. 8). Thus, the robust and growing fossil record of seep gastropods around the Pacific allows paleontological testing of phylogenetic hypotheses regarding origination time and place for certain vent/seep gastropod groups (cf. Little and Vrijenhoek, 2003; Kiel and Little, 2006). Such hypotheses generally are based on analyses of morphological characters or molecular sequences of living taxa (e.g., Ponder and Lindberg, 1997; McArthur and Koop, 1999).

Whether the genus *Retiskenea* originated in the eastern Pacific (cf. Fig. 1) is not entirely certain at present. The ubiquitous, long record of seep-carbonates in Japan (Cretaceous to the present,

reviewed in Majima et al., 2005) may potentially yield fossil *Retiskenea* or other neomphalids (Kaim, personal commun., 2006). Nonetheless, the California Mesozoic *Retiskenea?* described in this study may possibly be the oldest known members of the genus, and are among the oldest representatives of the Neomphalidae.

As noted above, all living members of Neomphalidae, except seep-related *Retiskenea diploura*, are endemic to hydrothermal vents (Warén and Bouchet, 2001). Many marine invertebrate families with their main distribution in vents or seeps have undergone considerable evolutionary radiation in these isolated habitats (Warén and Bouchet, 2001; reviewed in Little and Vrijenhoek, 2003). The living vent/seep fauna also has been suggested to represent refugia for some Paleozoic–early Mesozoic taxa, including neomphalid gastropods, and primitive members of several pedunculate and thoracican barnacle groups (reviewed in McArthur and Tunnicliffe, 1998, Warén and Bouchet, 2001, and Yamaguchi et al., 2004). However, few if any of the living vent-endemic lineages implicated as relict have an extensive fossil record (Little and Vrijenhoek, 2003). For example, the primitive barnacles typical of modern hydrothermal vents and hydrocarbon seeps have yet to appear in the fossil record of these paleoenvironments (Little and Vrijenhoek, 2003). As observed by Warén and Bouchet (2001), marine gastropods in general have an excellent fossil record, so that origination ages can be estimated for many major groups (cf. Kiel and Little, 2006). However, convergence of shell features tends to be common among living gastropods, including those from vent and seep settings, such that malacologists typically analyze many soft-part anatomical characters to resolve relationships. As discussed above, this and the sometimes simple shell morphology of some forms also can confound taxonomic analyses among certain gastropod groups, especially for fossils. Nonetheless, the Mesozoic and Cenozoic microgastropods of northeast Pacific seep deposits display a number of characters that may affiliate them with neomphalid *Retiskenea* (cf. Warén and Bouchet, 2001; this study). If so, this vent/seep taxon appears to have been restricted to chemosynthesis-based environments since at least early in the Cretaceous (Hauterivian, ~133 Ma, Wilbur Springs *R.?* *tuberculata*). A second probable neomphalid, *Lithomphalus enderlini* Kiel and Campbell, 2005 occurs in Early Cretaceous seep deposits elsewhere in northern California (Valanginian, ~138 Ma, Bear and Rocky Creek sites; Kiel and Campbell, 2005). In comparison, molecular analysis of living members of Neomphalina (sensu Warén and Bouchet, 1993) suggests a minimum Mesozoic origin of the group, an age estimate derived from a study of members of representative genera *Cyathernia* Warén and Bouchet, 1989; *Melanodrymia* Hickman, 1984; *Rhynchopelta* McLean, 1989; *Peltopspira* McLean, 1989, and *Depressigyra* Warén and Bouchet, 1989 (McArthur and Koop, 1999, table 1, p. 258). As yet, molecular analyses have not been performed on other living taxa within Neomphalina, including *Retiskenea*.

In general, the known modern and fossil distributions of endemic vent/seep biota indicate mosaic origins, with some groups invading these habitats recently and others perhaps evolving in isolation as relicts (McArthur and Tunnicliffe, 1998; Little and Vrijenhoek, 2003). Relatively continuous immigration of taxa into vent/seep settings occurred during the Phanerozoic (Little and Vrijenhoek, 2003; Kiel and Little, 2006). Extinctions have also taken place among some older groups established in seep settings during the Paleozoic (e.g., modiomorphid bivalves, rhynchonellid brachiopods; Campbell and Bottjer, 1995a, 1995b; Little, 2002). Other well-known modern groups appear to have arrived at vents and seeps during the Mesozoic (e.g., vesicomid, bathymodiolid and lucinacean bivalves; Little and Vrijenhoek, 2003). Regardless, many modern vent/seep faunas as yet have only uncertain linkages into the distant geologic past (reviewed in McArthur and Koop, 1999; Warén and Bouchet, 2001, table 2, p. 213; Little and Vrijenhoek, 2003). Thus, it is still a “long step” (Warén and

Bouchet, 2001, p. 213) to explain endemism in vent/seep communities as the product of evolutionary stasis among Paleozoic or Mesozoic relicts. Hence, the Mesozoic occurrences of two new *Retiskenea?* species from several different hydrocarbon-seep sites in California are of significance toward deciphering the origins of gastropods in these geographically isolated extreme environments. Some neomphalids may have originated in northeastern Pacific hydrocarbon-seep settings (i.e., California *Retiskenea?*, *Lithomphalus*), and *Retiskenea?* subsequently may have migrated to and further evolved in other seep habitats. This hypothesis awaits testing by new fossil discoveries of these apparently endemic gastropods among the rich faunas of ancient chemosynthesis-based settings.

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