

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 diplooura* 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. *diplooura* 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

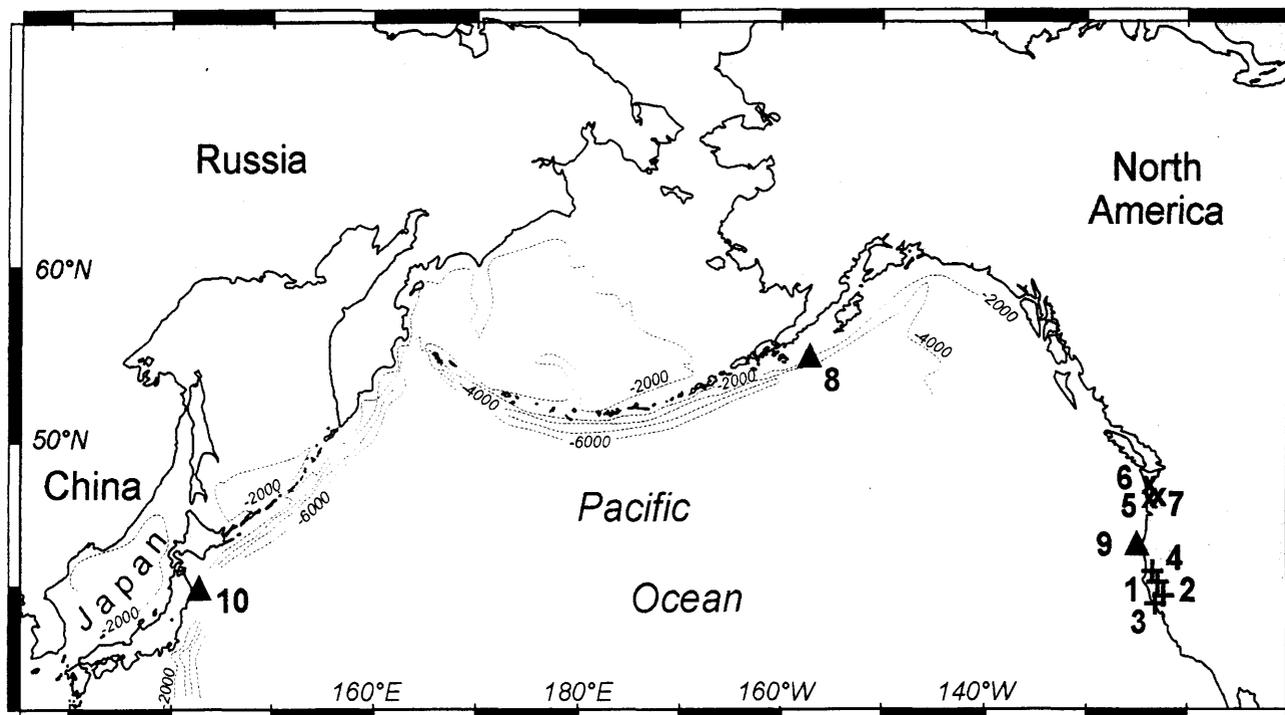


FIGURE 1—Geographic distribution map of occurrences of neomphalids with affinities to or ascribed to *Retiskenea* in hydrocarbon-seep settings of the Pacific Rim, ~148 Ma to present. From oldest to youngest: 1, Indeterminate coiled neomphalid microgastropod, Upper Jurassic (Tithonian, ~148 m.y.) Great 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 RETISKENEIA 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

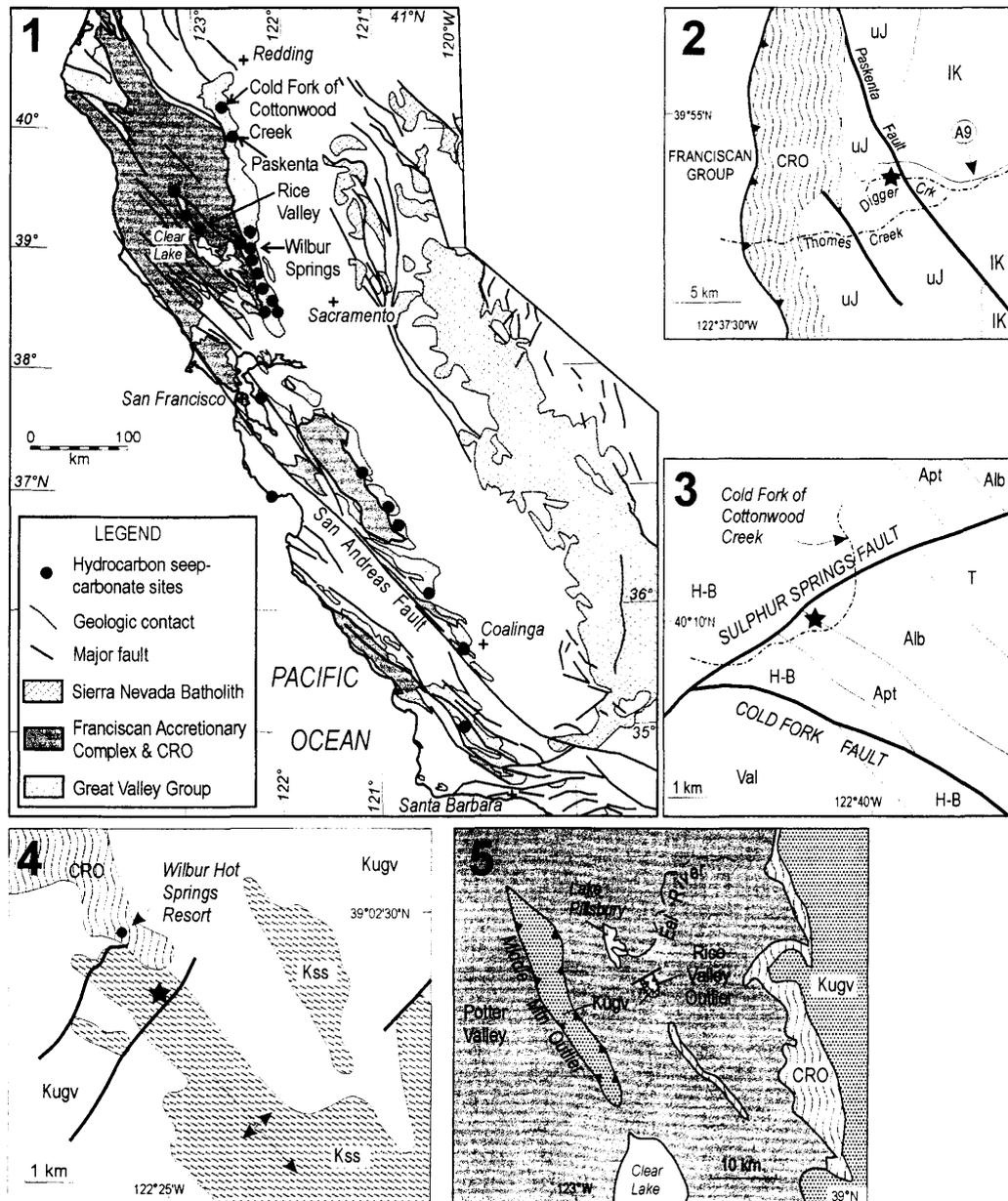


FIGURE 2—Geologic and location maps of sites of this study. 1. Simplified geology of the north-south-trending Mesozoic convergent margin system includes, from west to east: undifferentiated Franciscan Accretionary Complex (Jurassic to Cretaceous)—belts of mélangé, broken formation—and Coast Range Ophiolite (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 syndimentary 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 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.