



FIGURE 8—Paleoecological 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,