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 *Cyathermia* Warén and Bouchet, 1989; *Melanodrymia* Hickman, 1984; *Rhynchopelta* McLean, 1989; *Peltospira* 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 relics (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., vesicomyid, bathymodiolin 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 relics. 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.

ACKNOWLEDGMENTS

Financial support for field work was provided to KAC by a National Research Council Research Associateship, administered through NASA Ames Research Center, Moffett Field, California, and by J. Farmer through NASA's Exobiology Program and the NASA Astrobiology Institute. J. Goedert helped collect specimens and kindly donated comparative fossil material for study. K. Fujikura and T. Okutani generously supplied shell measurements for *Retiskenea diploura* from the Japan Trench. We thank S. Kiel and A. Warén for communications regarding microgastropod taxonomy and for insightful comments on the manuscript. W. Elder and J. Goedert assisted with fossil identifications and accessing collections. E. A. Nesbitt was particularly obliging with comments on technical aspects of taxonomy, and age estimates for Washington formations, that improved an earlier version of the manuscript. At CAS, D. Ubick operated the scanning electron microscope, and J. DeMouthe and A. Grimes offered exceptionally helpful curatorial support. C. Hobbis and B. James assisted with further SEM studies at the University of Auckland. L. Cotterall prepared many of the figures. Special thanks and much appreciation go to the Wilbur Hot Springs Resort, W. Goddard, the Pettyjohns, and Mr. and Mrs. L. Whitlock for access permission to the Wilbur Springs, Rice Valley, Cold Fork of Cottonwood Creek and Paskenta sites in northern California.

REFERENCES

BATHURST, R. G. C. 1975. Carbonate Sediments and their Diagenesis. Developments in Sedimentology 12. Elsevier, Amsterdam, 658 p.

BERKLAND, J. O. 1973. Rice Valley outlier—new sequence of Cretaceous–Paleocene strata in northern Coast Ranges, California. Geological Survey of America Bulletin, 84:2389–2406.

BIRGEL, D., V. THIEL, K.-U. HINRICHS, M. ELVERT, K. A. CAMPBELL, J. REITNER, J. D. FARMER, AND J. PECKMANN. 2006. Lipid biomarker patterns of methane seep microbialites from the Mesozoic convergent margin of California. Organic Geochemistry, 37:1289–1302.

BOUCHET, P. AND J.-P. ROCROI (eds.). 2005. Classification and nomenclature of gastropod families. Malacologia, 47(1–2):1–397.

CALLENDER, W. R. AND E. N. POWELL. 1999. Why did ancient chemosynthetic seep and vent assemblages occur in shallower water than they do today? International Journal of Earth Sciences, 88:377–391.

CAMPBELL, K. A. 1995. Dynamic development of Jurassic–Pliocene cold seeps, convergent margin of western North America. Ph.D. thesis, University of Southern California, Los Angeles, 195 p.

CAMPBELL, K. A. 1996. Gastropods of Mesozoic cold-seep carbonates, California. Geological Society of America Abstracts with Program, 28(7): A298.

CAMPBELL, K. A. 2006. Hydrocarbon seep and hydrothermal vent palaeoenvironments and palaeontology: Past developments and future research directions. Palaeogeography, Palaeoclimatology, Palaeogeography, 232:362–407.

CAMPBELL, K. A. AND D. J. BOTTJER. 1993. Fossil cold seeps (Jurassic–Pliocene) along the convergent margin of western North America. National Geographic Research & Exploration, 9:326–343.

CAMPBELL, K. A. AND D. J. BOTTJER. 1995a. *Peregrinella*: An Early Cretaceous cold-seep-restricted brachiopod. Paleobiology, 21:461–478.

CAMPBELL, K. A. AND D. J. BOTTJER. 1995b. Brachiopods and chemosymbiotic bivalves in Phanerozoic hydrothermal vent and cold-seep environments. Geology, 23:321–324.

CAMPBELL, K. A., C. CARLSON, AND D. J. BOTTJER. 1993. Fossil cold seep limestones and associated chemosymbiotic macroinvertebrate faunas, Jurassic–Cretaceous Great Valley Group, California, p. 37–50. *In* S. Graham and D. Lowe (eds.), Advances in the Sedimentary Geology of the Great Valley Group. Society of Economic Paleontologists and Mineralogists, Pacific Section, 73.

CAMPBELL, K. A., J. D. FARMER, AND D. DES MARAIS. 2002. Ancient hydrocarbon seeps from the Mesozoic convergent margin of California: Carbonate geochemistry, fluids and paleoenvironments. Geofluids, 2:63–94.

CARLSON, C. 1984a. Stratigraphic and structural significance of foliate serpentinite breccias, Wilbur Springs, p. 108–112. *In* C. Carlson (ed.), Depositional Facies of Sedimentary Serpentinite: Selected Examples from the Coast Ranges, California. Society of Economic Paleontologists and Mineralogists, Pacific Section, Tulsa, Oklahoma.

CARLSON, C. 1984b. General geology of the northern Coast Ranges and the Wilbur Springs area, p. 104–107. *In* C. Carlson (ed.), Depositional Facies of Sedimentary Serpentinite: Selected Examples from the Coast Ranges, California. Society of Economic Paleontologists and Mineralogists, Pacific Section, Tulsa, Oklahoma.

CAVAGNA, S., P. CLARI, AND L. MARTIRE. 1999. The role of bacteria in the formation of cold seep carbonates: Geological evidence from Monferrato (Cenozoic, NW Italy). Sedimentary Geology, 126:253–270.

CLARI, P. A. AND L. MARTIRE. 2000. Cold seep carbonates in the Tertiary of northwest Italy: Evidence of bacterial degradation of methane, p. 261–269. *In* R. E. Riding and S. M. Awramik (eds.), Microbial Sediments. Springer-Verlag, Berlin.

FUJIKURA, K., Y. FUJIWARA, S. KOJIMA, AND T. OKUTANI. 2002. Micro-scale distribution of mollusks occurring in deep-sea chemosythesis-based communities in the Japan Trench. Venus, 60:225–236.

GABB, W. M. 1869. Cretaceous and Tertiary Fossils: Palaeontology. Vol. II. Geological Survey of California, Philadelphia, Caxton Press of Sherman & Co., 299 p.

GISCHLER, E., M. R. SANDY, AND J. PECKMAN. 2003. *Ibergirhynchia contraria* (F. A. Roemer, 1850), an Early Carboniferous seep-related rhynchonellide brachiopod from the Harz Mountains, Germany—a possible precursor to *Dzieduszyckia*? Journal of Paleontology, 77:293–303.

GOEDERT, J. L. AND S. R. BENHAM. 1999. A new species of *Depressigyra*? (Gastropoda: Peltospiridae) from cold-seep carbonates in Eocene and Oligocene rocks of western Washington. The Veliger, 42:112–116.

GOEDERT, J. L. AND K. A. CAMPBELL. 1995. An early Oligocene chemosynthetic community from the Makah Formation, northwestern Olympic Peninsula, Washington. The Veliger, 38:22–29.

GOEDERT, J. L. AND K. L. KALER. 1996. A new species of *Abyssochrysos* (Gastropoda: Loxonematoidea) from a middle Eocene cold-seep carbonate in the Humptulips Formation, western Washington. The Veliger, 39:65–70.

GOEDERT, J. L. AND R. L. SQUIRES. 1990. Eocene deep-sea communities in localized limestones formed by subduction-related methane seeps, southwestern Washington. Geology, 18:1182–1185.

GOEDERT, J. L., V. THIEL, O. SCHMALE, W. W. RAU, W. MICHAELIS, AND J. PECKMANN. 2003. The Late Eocene 'Whiskey Creek' methane-seep deposit (western Washington State) Part I: Geology, palaeontology, and molecular geobiology. Facies, 48:223–240.

GRADSTEIN, F. M., J. G. OGG, A. G. SMITH, F. P. AGTERBERG, W. BLEEKER, R. A. COOPER, V. DAVYDOV, P. GIBBARD, L. A. HINNOV, M. R. HOUSE, L. LOURENS, H. P. LUTERBACHER, J. MCARTHUR, M. J. MELCHIN, L. J. ROBB, J. SHERGOLD, M. VILLENEUVE, B. R. WARDLAW, J. ALI, H. BRINKHUIS, F. J. HILGEN, J. HOOKER, R. J. HOWARTH, A. H. KNOLL, J. LASKAR, S. MONECHI, K. A. PLUMB, J. POWELL, I. RAFFI, U. RÖHL, P. SADLER, A. SANFILIPPO, B. SCHMITZ, N. J. SHACKLETON, G. A. SHIELDS, H. STRAUSS, J. VAN DAM, T. VAN KOLFSCHOTEN, J. VEIZER, AND D. WILSON. 2004. A Geologic Time Scale 2004. Cambridge University Press, Cambridge, 589 p.

HASZPRUNAR, G. 1988. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. Journal of Molluscan Studies, 54:367–441.

INGERSOLL, R. V. 1983. Petrofacies and provenance of Late Mesozoic forearc basin, northern and central California. AAPG Bulletin, 67:1125–1142.

JONES, D. L. AND E. H. BAILEY. 1973. Preliminary biostratigraphic map, Colyear Springs Quadrangle, California. U.S. Geological Survey Miscellaneous Field Studies, MF-517.

JONES, D. L., E. H. BAILEY, AND R. W. IMLAY. 1969. Structural and stratigraphic significance of the *Buchia* zones in the Colyear Springs-Paskenta area, California. U.S. Geological Survey Professional Paper, 647-A, 24 p., 5 pl.

KIEL, S. 2004. Shell structures of selected gastropods from hydrothermal vents and seeps. Malacologia, 46:169–183.

KIEL, S. 2006. New records and species of molluscs from Tertiary cold-seep carbonates in Washington State, USA. Journal of Paleontology, 80:121–137.

KIEL, S. AND K. A. CAMPBELL. 2005. *Lithomphalus enderlini* gen. et sp. nov. from cold-seep carbonates in California—a Cretaceous neomphalid gastropod? Palaeogeography, Palaeoclimatology, Palaeoecology, 227:232–241.

KIEL, S. AND C. T. S. LITTLE. 2006. Cold-seep mollusks are older than the general marine mollusk fauna. Science, 313:1429–1431.

LITTLE, C. T. S. 2002. The fossil record of hydrothermal vent communities. Cahiers de Biologie Marine, 43:313–316.

LITTLE, C. T. S. AND R. C. VRIJENHOEK. 2003. Are hydrothermal vent animals living fossils? Trends in Ecology and Evolution, 18:582–588.

LITTLE, C. T. S., K. A. CAMPBELL, AND R. J. HERRINGTON. 2002. Why did ancient chemosynthetic seep and vent assemblages occur in shallower water than they do today? Comment. International Journal of Earth Sciences, 91: 149–153.

LITTLE, C. T. S., R. J. HERRINGTON, R. M. HAYMON, AND T. DANELIAN. 1999. Early Jurassic hydrothermal vent community from the Franciscan complex, San Rafael Mountains, California. Geology, 27:167–170.

MACINTYRE, I. G. 1985. Submarine cements—the peloidal question, p. 109–116. *In* N. Schneidermann and P. M. Harris (eds.), Carbonate Cements. Society of Economic Paleontologists and Mineralogists Special Publication, 36.

MAJIMA, R., T. NOBUHARA, AND T. KITAZAKI. 2005. Review of fossil chemosynthetic assemblages in Japan. Palaeogeography, Palaeoclimatology, Palaeoecology, 227:86–123.

MCARTHUR, A. G. AND B. F. KOOP. 1999. Partial 28s rDNA sequences and the antiquity of hydrothermal vent endemic gastropods. Molecular Phylogenetics and Evolution, 13:255–274.

MCARTHUR, A. G. AND V. TUNNICLIFFE. 1998. Relics and antiquity revisited in the modern vent fauna, p. 271–291. *In* K. Harrison and R. Mills (eds.), Modern Ocean Floor Processes and the Geological Record. Geological Society Special Publication, 148.

MCLEAN, J. H. 1981. The Galapagos rift limpet *Neomphalus*: Relevance to understanding the evolution of a major Paleozoic–Mesozoic radiation. Malacologia, 21:291–336.

MCLEAN, J. H. 1989. New archaeogastropod limpets from hydrothermal vents: New family Peltospiridae, new superfamily Peltospiracea. Zoologica Scripta, 18:49–66.

MCLEAN, J. H. 1990. A new genus and species of neomphalid limpet from the Mariana vents with a review of current understanding of relationships among Neomphalacea and Peltospiracea. The Nautilus, 104:77–86.

MOXON, I. W. 1990. Stratigraphy and structure of Upper Jurassic–Lower Cretaceous strata, Sacramento Valley, p. 5–29. *In* R. V. Ingersoll and T. H. Nilsen (eds.), Sacramento Valley Symposium and Guidebook. Pacific Section SEPM, 65.

OKUTANI, T. AND K. FUJIKURA. 2002. Abyssal gastropods and bivalves collected by *Shinkai 6500* on slope of the Japan Trench. Venus, 60:211–224.

PECKMANN, J. AND V. THIEL. 2004. Carbon cycling at ancient methane-seeps. Chemical Geology, 205:443–467.

PECKMANN, J., J. L. GOEDERT, V. THIEL, W. MICHAELIS, AND J. REITNER. 2002. A comprehensive approach to the study of methane-seep deposits from the Lincoln Creek Formation, western Washington State, USA. Sedimentology, 49:855–873.

PECKMANN, J., V. THIEL, W. MICHAELIS, P. CLARI, C. GAILLARD, K. A. CAMPBELL, O. H. WALLISER, AND J. REITNER. 2001. A growing Paleozoic record of hydrocarbon seep deposits. American Geophysical Union Annual Meeting, December 2000. 81(48) Fall Meeting, Supplement OS61B-05.

PECKMANN, J., V. THIEL, W. MICHAELIS, P. CLARI, C. GAILLARD, L. MARTIRE, AND J. REITNER. 1999. Cold seep deposits of Beauvoisin (Oxfordian, southeastern France) and Marmorito (Miocene, northern Italy): Microbially induced authigenic carbonates. International Journal of Earth Sciences, 88: 60–75.

PONDER, W. F. AND D. R. LINDBERG. 1997. Towards a phylogeny of gastropod mollusks: An analysis using morphological characters. Journal of the Linnean Society, 119:83–265.

SANDY, M. R. AND K. A. CAMPBELL. 1994. A new rhynchonellid brachiopod genus from Tithonian (upper Jurassic) cold-seep deposits of California and its paleoenvironmental setting. Journal of Paleontology, 68:1243–1252.

SIBUET, M. AND K. OLU. 1998. Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. Deep-Sea Research II, 45:517–567.

SQUIRES, R. L. 1995. First fossil species of the chemosynthetic-community gastropod *Provanna*: Localized cold-seep limestones in Upper Eocene and Oligocene rocks, Washington. The Veliger, 38:30–36.

SQUIRES, R. L. AND J. L. GOEDERT. 1991. New Late Eocene mollusks from localized limestone deposits formed by subduction-related methane seeps, southwestern Washington. Journal of Paleontology, 65:412–416.

SQUIRES, R. L. AND J. L. GOEDERT. 1995. An extant species of *Leptochiton* (Mollusca: Polyplacophora) in Eocene and Oligocene cold-seep limestones, Olympic Peninsula, Washington. The Veliger, 38:47–53.

STANTON, T. W. 1895. Contributions to the Cretaceous paleontology of the Pacific coast: The fauna of the Knoxville beds. U.S. Geological Survey Bulletin, 133: 132 p.

SUESS, E., G. BOHRMAN, R. VON HUENE, P. LINKE, K. WALLMAN, S. LAMMERS, AND H. SAHLING. 1998. Fluid venting in the eastern Aleutian subduction zone. Journal of Geophysical Research, 103:2597–2614.

SURPLESS, K. D., S. A. GRAHAM, J. A. COVAULT, AND J. L. WOODEN. 2006. Does the Great Valley Group contain Jurassic strata? Reevaluation of the age and early evolution of a classic forearc basin. Geology, 34:21–24.

THIEL, V., J. PECKMANN, R. SEIFERT, P. WEHRUNG, J. REITNER, AND W. MICHAELIS. 1999. Highly isotopically depleted isoprenoids: Molecular markers for ancient venting. Geochimica et Cosmochimica Acta, 63:3959–3966.

UNITED STATES GEOLOGICAL SURVEY. 1957. Colyear Springs Quadrangle, California—Tehama Co., 15-minute series (topographic). United States Department of the Interior, Geological Survey, Denver, Colorado.

UNITED STATES GEOLOGICAL SURVEY. 1967. Paskenta Quadrangle, California—Tehama Co., 7.5-minute series (topographic). United States Department of the Interior, Geological Survey, Denver, Colorado.

UNITED STATES GEOLOGICAL SURVEY. 1967. Potato Hill Quadrangle, California, 7.5-minute series (topographic). United States Department of the Interior, Geological Survey, Denver, Colorado.

UNITED STATES GEOLOGICAL SURVEY. 1989. Wilbur Springs Quadrangle, California, 7.5-minute series (topographic), provisional edition. United States Department of the Interior, Geological Survey, Denver, Colorado.

UNITED STATES GEOLOGICAL SURVEY, AND CALIFORNIA DIVISION OF MINES AND GEOLOGY. 1966. Geologic Map of California. United States Department of the Interior, Geological Survey, Washington, D.C., Miscellaneous Geological Investigations, Map I-512.

VAN DOVER, C. L. 2000. The Ecology of Deep-Sea Hydrothermal Vents. Princeton University Press, Princeton, New Jersey, 424 p.

WARÉN, A. AND P. BOUCHET. 1989. New gastropods from East Pacific hydrothermal vents. Zoologica Scripta, 18:67–102.

WARÉN, A. AND P. BOUCHET. 1993. New records, species, genera and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. Zoologica Scripta, 22:1–90.

WARÉN, A. AND P. BOUCHET. 2001. Gastropoda and Monoplacophora from hydrothermal vents and seeps; new taxa and records. The Veliger, 44:116–231.

YAMAGUCHI, T., W. A. NEWMAN, AND J. HASHIMOTO. 2004. A cold seep barnacle (Cirripedia:Neolepadinae) from Japan and the age of the vent/seep fauna. Journal of the Marine Biological Association of the United Kingdom, 84:111–120.

ACCEPTED 10 OCTOBER 2006