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Jurassic and Cretaceous gastropods from hydrocarbon seeps in forearc basin and accretionary prism settings, California

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Fourteen gastropod species from 16 Mesozoic hydrocarbon seep carbonate deposits of the Great Valley Group and Franciscan Complex in California are described. Two genera are new: *Bathypurpurinopsis* has a fusiform shell with a siphonal fold, and variable *Paskentana* has turbiniform or littoriniform shells with spiral and/or scaly sculpture and convex or shouldered whorls. Due to the lack of data on shell microstructure and protoconch morphology, many of our taxonomic assignments have to remain tentative at present. Species that are described as new include: *Hokkaidoconcha bilirata*, *H. morenoensis*, *H. tehamaensis* (Hokkaidoconchidae), *Abyssochrysis? giganteum* (Abyssochrysidae?), *Paskentana globosa*, *P. berryessaensis*, and *Bathypurpurinopsis stantoni* (Abyssochrysoidea, family uncertain). The total fauna represents a mixed bag of taxa that were: (i) widely distributed during the late Mesozoic (*Amberleya*); (ii) restricted to late Mesozoic seep carbonates in California (*Atresius*, *Bathypurpurinopsis*, *Paskentana*); and (iii) members of seep/deep-sea groups with a long stratigraphic range (abyssochrysid, hokkaidoconchids).

Key words: Gastropoda, hydrocarbon seeps, deep-water, Great Valley Group, Franciscan Complex, California.

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Introduction

A diverse Mesozoic gastropod fauna in western California has been considered noteworthy since Stanton (1895) first named 10 species of *Turbo*, *Amberleya*, *Atresius*, *Hypsipleura?*, and *Cerithium* from isolated “white limestones” of the so-called Knoxville Beds, a thick sequence of fine-grained sandstone and mudstone of the lower Great Valley Group. The Knoxville Beds contain a low diversity megafauna dominated by buchiid bivalves and scattered ammonites typical of continental margin turbidites of the Mesozoic Pacific Ocean (Jones et al. 1969). In contrast, gastropods in the volumetrically minor “white limestones” within the Knoxville Beds are associated with an unusual, recurring assemblage of rhynchonellide brachiopods, lucinid and solemyid bivalves, worm tubes, and microbial fossils that are now recognized as hydrocarbon-seep related (Campbell et al. 1993; Sandy and Campbell 1994; Campbell and Bottjer 1995; Campbell 1996; Campbell et al. 2002; Birgel et al. 2006). A gastropod species from these car-

bonates, *Lithomphalus enderlini* Kiel and Campbell, 2005, not recognized by earlier studies, was recently identified as a possible member of the Neomphalidae, a family that is confined to deep-sea, chemosynthesis-based environments (Kiel and Campbell 2005). In addition, two new species of a seep-related, neomphalid microgastropod attributed to *Retiskeneia?* have been recognized and described recently from several of these Californian Mesozoic carbonates (Campbell et al. 2008).

Based on abundant newly collected material and surveys of collections in several U.S. institutions, we now can evaluate this unusual Jurassic and Cretaceous gastropod fauna from 16 sites (Fig. 1), and describe herein two new genera and seven new species. We also discuss the overall fauna of 14 species in an evolutionary context with respect to other gastropods from Mesozoic, Cenozoic, and Recent hydrothermal vents and hydrocarbon seeps.

Institutional abbreviations.—CAS, California Academy of Sciences, San Francisco, USA; LACMIP, Los Angeles County Museum of Natural History, Invertebrate Paleontol-

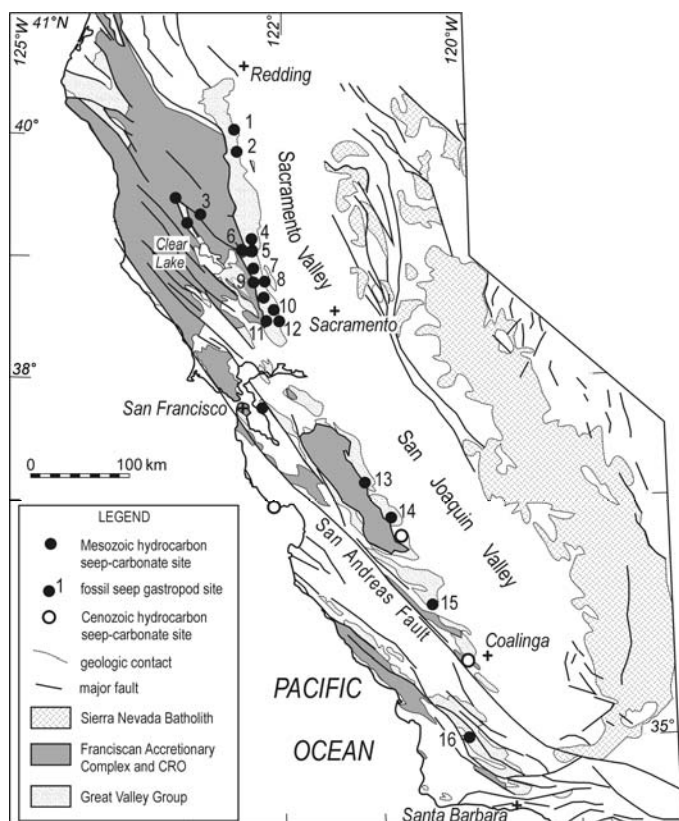


Fig. 1. Mesozoic (solid circles) and Cenozoic (open circles) seep carbonate occurrences, California, showing their broad geologic setting and overall geographic extent over ~130 m.y. and >600 km along the continental margin. Numbered sites indicate the 16 fossil gastropod-bearing deposits of this study. Relevant geologic features of the north-south trending, Mesozoic–Paleogene convergent margin include: belts of mélangé, broken formation and ophiolites (Franciscan Accretionary Complex and Coast Range Ophiolite, CRO); siliciclastic forearc turbidites (Great Valley Group); and present-day root of the volcanic arc (Sierra Nevada Batholith). Geology simplified from the 1:2,500,000 Geologic Map of California (1966, U.S. Geological Survey and California Division of Mines and Geology). Appendix 1 lists locality data, ages and fossil lists for each of the 16 sites. 1, Cold Fork of Cottonwood Creek; 2, Paskenta; 3, Rice Valley; 4, Bear Creek; 5, Wilbur Springs; 6, Little Indian Valley; 7, Rocky Creek; 8, Foley Canyon; 9, Knoxville; 10, NW Berryessa; 11, W Berryessa; 12, E Berryessa; 13, Romero Creek; 14, Moreno Gulch; 15, Gravelly Flat; 16, Charlie Valley.

ogy section, Los Angeles, USA; UCB, University of California, Berkeley, USA; UCMP, University of California Museum of Paleontology, Berkeley, USA; USGS M, United States Geological Survey Mesozoic collections, Menlo Park branch, California, USA, now housed at UCMP; USNM, Smithsonian National Museum of Natural History, Paleobiology collection, Washington D.C., USA.

Geologic setting and stratigraphy

To date, at least 20 Upper Jurassic to Upper Cretaceous hydrocarbon seep carbonate occurrences have been recognized in Great Valley and Franciscan strata, and their equivalents,

in northern and central California (Campbell 2006). These strata have long been considered to represent the overriding plate of a Mesozoic convergent system in western California, as recognized in the early years of plate tectonic reconstructions of continental margin geology (Hamilton 1969; Ernst 1970; Dickinson 1971). Petrofacies and tectono-chronologic links have since been identified among the forearc basin (Great Valley Group), accretionary wedge (Franciscan Complex), and Sierra Nevadan magmatic arc (Ingersoll 1983). The roughly parallel regional belts of Franciscan and Great Valley rocks have had a complicated tectonic history. There has long been evidence for northward migration of the Franciscan Complex terranes (see papers in Blake 1984); hence, these coeval belts were not necessarily adjacent at the time of deposition. However, Great Valley forearc strata were traditionally considered to have formed in situ along the western North American continental margin, from the Late Jurassic and into the Paleogene (Ingersoll and Dickinson 1981). Recently, an alternative tectonic model for the Great Valley forearc has been proposed. Wright and Wyld (2007) have suggested hundreds of kilometers of northward translation of the forearc “sliver”, owing to inferred oblique rather than orthogonal convergence during its 80 m.y. history.

Lithologically the Great Valley Group consists of >15 km of interbedded mudstone and sandstone turbidites, conglomerate and other minor rock types, including isolated carbonate lenses (Ingersoll and Dickinson 1981). These strata have been difficult to subdivide into mappable lithostratigraphic units because of lateral changes in lithofacies (Ingersoll 1990), and/or known or previously unrecognized structural complexities (cf. Kiel and Campbell 2005). Some local divisions have been erected (e.g., Lawton 1956, for the Morgan Valley area). Detailed sandstone point-count and conglomerate clast analyses in some areas have provided compositional differentiation, allowing for somewhat more regional lithologic correlations (e.g., Dickinson and Rich 1972; Bertucci and Ingersoll 1983; Ingersoll 1983; Seiders 1988; Seiders and Blome 1988; Short and Ingersoll 1990). In this paper, we follow Ingersoll’s (1983) petrostratigraphy for the Sacramento and San Joaquin valleys (Fig. 2). Recently Surpless et al. (2006) have claimed that few to no upper Jurassic rocks occur in the Great Valley Group, based on zircon dates of seven presumed Tithonian samples collected between Wilbur Springs and Corning. This scenario is currently being tested at a location with simple structure and abundant marker fossils (Dean A. Enderlin and Bob J. McLaughlin, personal communication 2007).

A biostratigraphy of the Great Valley Group in northern California (Upper Jurassic–Upper Cretaceous) has been established using bivalves, scattered ammonites, radiolarians, and calcareous nannofossils (e.g., Jones et al. 1969; Imlay and Jones 1970; Bralower 1990). In particular, a *Buchia* zonation is in common field usage to divide Tithonian through Valanginian stages (Fig. 2), based on Jones et al. (1969) as modified by Bralower (1990). Historically some older, informal divisions have been applied regionally, such

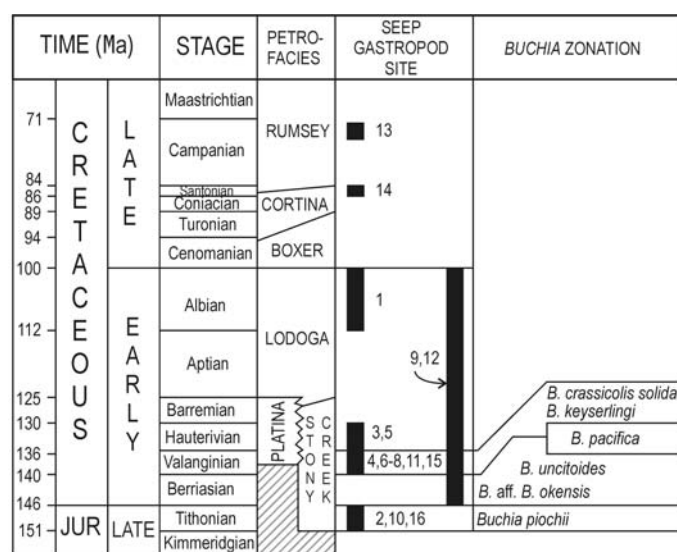


Fig. 2. Stratigraphic distribution of the 16 fossil-bearing, seep carbonate deposits of this study (Fig. 1), correlated with petrofacies (Ingersoll, 1983, for Sacramento Valley), and a *Buchia* bivalve biostratigraphy (Tithonian through Valanginian stages; Jones et al., 1969, as modified by Bralower, 1990). Geologic time divisions (Gradstein et al. 2004) for each stage are shown to the nearest 1 m.y. Ages of these seep carbonate deposits are relatively poorly known, with most sites resolved to stage level only. A few others are even more poorly known, e.g., probable Early Cretaceous age, and one is more finely resolved to sub-stage level (i.e., Late Campanian). Tithonian and Valanginian sites comprise the majority of the gastropod-rich deposits, with relative ages constrained by a six species *Buchia* zonation. Hauterivian sites contain the seep-restricted brachiopod, *Peregrinella whitneyi* (see Campbell and Bottjer, 1995, for discussion of caveats with respect to using this genus to establish relative ages). Albion and younger Cretaceous sites are dated based on ammonite occurrences. See Appendix for complete fossil lists. Most deposits occur within forearc mudstone of the Great Valley Group, except for two sites (3, 5) associated with serpentinite (diapir) deposits. A further two (6, 16) are enclosed in accretionary prism rocks of the Franciscan Complex, and one (3) is in a Great Valley outlier within Franciscan rocks. Similar seep fossil assemblages and associated buchiids allow relative age correlations for these Franciscan-related deposits.

as the “Knoxville series” equated with Upper Jurassic strata, the “Shasta series” and “Horsetown” and “Paskenta beds” assigned to the Lower Cretaceous (cf. Anderson 1938, 1945), and the “Chico series” attributed to the Upper Cretaceous (cf. Murphy 1956). However, these terms originally were erected only for local reference (reviewed in Popenoe et al. 1960). Some were later extended inappropriately to formation status (e.g., Knoxville Formation) despite being defined on fossil content (discussed in Ingersoll 1990).

Most gastropod-bearing carbonates of this study are located in Great Valley forearc strata of the western Sacramento and San Joaquin valleys (Fig. 1). A few such deposits also are situated in Great Valley-equivalent outliers (Fig. 1) (e.g., Rice Valley of Berkland 1973), or in strata associated with the Franciscan Complex (e.g., Little Indian Valley terrane of McLaughlin et al. 1990), which structurally underlies the forearc rocks (Fig. 1). Unlike the Great Valley Group, Franciscan rocks are compositionally heterogeneous and structurally

deformed into mélanges (Ingersoll and Dickinson 1981). Franciscan biostratigraphy is based on its deep oceanic condensed sections, in particular its radiolarian cherts and foraminifera in seamount-associated pelagic carbonates (e.g., Murchey 1984; Murchey and Jones 1984; Sliter 1984; Sliter 1999). Scattered fossils in Franciscan mélanges, including buchiids and other invertebrates, may be problematic as age indicators, as some originally may have been derived from distal Great Valley sediments that were subsequently incorporated tectonically into the Franciscan Complex (Bob J. McLaughlin, personal communication 2007). However, the Little Indian Valley terrane, from which some gastropods were evaluated in this study, is an exception in that it is a relatively intact package of strata within the Franciscan Complex (McLaughlin et al. 1990). Where possible in this study, age diagnostic fossils were identified from museum and/or field collections for each seep carbonate, or from the literature, and are plotted in a stratigraphic range chart (Fig. 2) and cited in the faunal list for a given site (Appendix 1).

The hydrocarbon cold-seep interpretation of the 16 geographically and stratigraphically isolated “white limestones” (Stanton 1895) of this study is based on several criteria (cf. Campbell et al. 1993). Specifically the deposits (e.g., Fig. 3) exude a strong petroliferous odor when struck with a hammer. They are lensoidal in geometry, with nodular micritic carbonate extending a short distance into the surrounding mudstone, as is typical of other ancient seep deposits elsewhere (e.g., Gaillard et al. 1992). Several deposits have been studied in detail for their textural, petrographic, stable isotopic and geochemical attributes (i.e., Paskenta, Wilbur Springs and Cold Fork of Cottonwood Creek sites), and show clear methane-derived components (Campbell et al. 2002; Birgel et al. 2006; Campbell 2006). Other sites are inferred herein as seep-related, as yet without detailed geochemical assessment (e.g., Kiel and Campbell 2005), but they also display similar stratigraphic, sedimentologic, petrographic and macrofossil character, consistent with confirmed seep deposits in the region. The faunas of these Mesozoic seep carbonates have not previously been studied in depth taxonomically; early works by Gabb (1869) and Stanton (1895) recorded some of the biota, and individual taxa have been treated in a few recent papers (Sandy and Campbell 1994; Kiel and Campbell 2005; Campbell et al. 2008). Stanton (1895), in particular, noted the diverse fossil gastropods present, which we have found to be in places so abundant as to be coquinoïd in their preservation state (Fig. 3). Herein, we update the systematic paleontology of these early studies and, for the first time, evaluate collectively the extensive field and museum collections of the gastropod macrofauna from these distinctive deposits.

Systematic paleontology

We have tried to illustrate as many of Stanton’s type specimens as possible, to supplement Stanton’s drawings (Stanton 1895).

Class Gastropoda Cuvier, 1797

Subclass Vetigastropoda Salvini-Plawen, 1980

Family Eucyclidae Koken, 1897

Genus *Amberleya* Morris and Lycett, 1850

Type species: *Amberleya bathonica* Cox and Arkell, 1950; Bathonian (Middle Jurassic), England.

Discussion.—Although our two species agree with the diagnosis of *Amberleya*, we find it difficult to distinguish them from modern *Bathybembix*. Our species also are similar to several Jurassic species that were recently assigned to *Eucycloscala* Cossmann, 1895 (see Gründel 2003; Kaim 2004), and they resemble to some extent the type species of *Eucyclus* Eudes-Deslongchamps, 1860 as figured by Wenz (1938–44, figs. 544, 545). Warén and Bouchet (1993) noted that the Jurassic–Cretaceous eucyclid *Oolitica* Cossmann, 1894 resembles the modern hydrothermal vent genus *Ifremeria* Bouchet and Warén, 1991 (Provannidae). Some characteristics like the broadly littoriniform shell and the nodular spiral sculpture are indeed somewhat similar, but Eucyclidae and Provannidae can easily be distinguished based on their shell microstructure: eucyclids have nacre (Hickman and McLean 1990) whereas provannids have crossed lamellar structure (Kiel 2004). However, the shell microstructure of *Oolitica*'s type species has most likely never been investigated. Due to the strong variability observed within the Californian species we prefer to use a conservative approach and assign them to *Amberleya*.

Amberleya dilleri Stanton, 1895

Fig. 4A–C.

1895 *Amberleya dilleri* sp. nov.; Stanton 1895: 68, pl. 12: 7–9.

Material.—The three specimens figured by Stanton (USNM 23074) from Paskenta (site 2); one specimen each from LACMIP loc. 15912 (Paskenta float blocks) and LACMIP loc. 15922 (Paskenta field number PS1-2; in Campbell 1995). Stanton's (1895) specimen with the intact aperture (our Fig. 4C) is herein designated as lectotype.

Description.—High-spined turbiniform shell of at least four or five whorls with incised suture and slightly oblique growth lines; whorls with broad and smooth subsutural ramp and prominent, tuberculate keel at center of whorl, which marks its widest point, about 15 tubercles per whorl; basal margin gently convex, marked by tuberculate spiral cord; at least four additional, finely beaded spiral cords on base, which decrease in strength and spacing towards columella; aperture almost round except for its pointed apical end.

Discussion.—Stanton (1895) emphasized similarities between his specimens and those assigned by d'Orbigny (1850–60) to *Purpurina* d'Orbigny, 1850. It was subsequently shown that *Amberleya* has nacreous shell and therefore belongs to the Trochoidea (Hickman and McLean 1990); whereas *Purpurina* is a cenogastropod due to its orthostrophic, multiwhorled protoconch (Kaim 2004). One of Stanton's specimens (Fig. 4C) shows that the aperture has a rounded base typical of juvenile eucyclins. In contrast, *Purpurina* has at least a small aper-

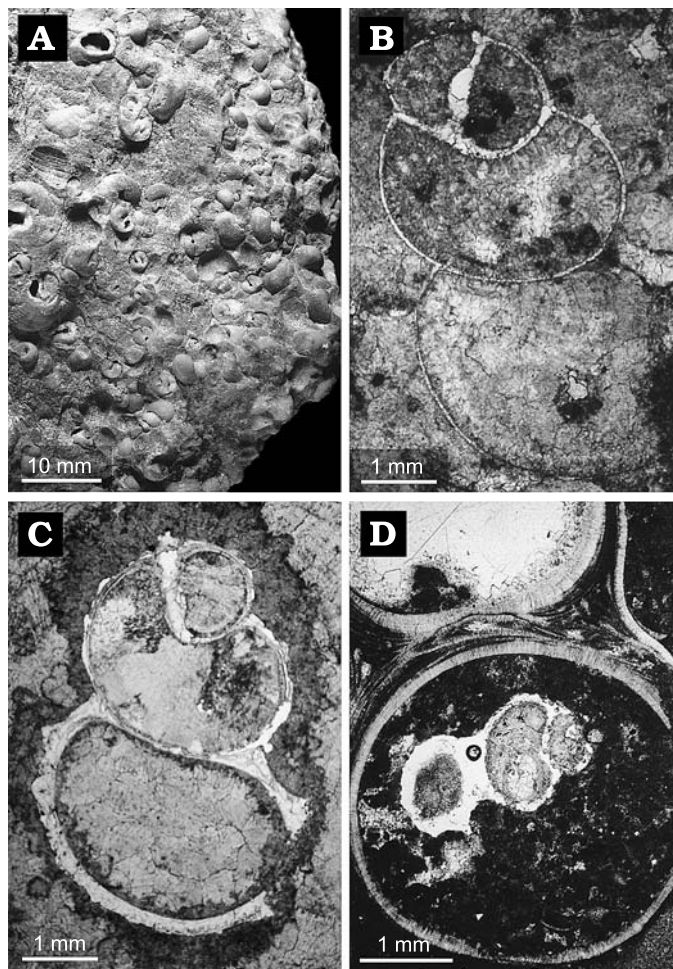


Fig. 3. Hand sample and petrographic thin section (plane polarized light) occurrences of selected Mesozoic seep gastropod fossils, California, USA. A. Fossil coquina of *Paskentana paskentensis* from Bear Creek (site 4) carbonates pod. B. Thin section photomicrograph of *Bathypurpurinopsis stantoni* in clotted micrite with pore-filling fibrous cement, from Cold Fork of Cottonwood Creek (site 1). C. Longitudinal section through *Paskentana paskentensis* encased in early diagenetic (seafloor) anhedral yellow calcite cement (dark; cf. Campbell et al. 2002), with pores filled by lighter-colored fibrous cement, from Paskenta (site 2). D. Small individual of *Paskentana paskentensis* preserved in clotted micrite within serpulid worm tube; Bear Creek site (site 4).

tural notch. Thus, Stanton's (1895) assignment of this species to *Amberleya* seems most appropriate. Two very similar species from the Great Oolite of southern England are *A. pagodiformis* (Hudleston 1887–1896: pl. 22: 9), which differs from *A. dilleri* only by the presence of a fine tuberculate row below the suture, and *A. orbignyana* (Hudleston 1887–1896: pl. 22: 7), which has slightly higher whorls, allowing an additional tuberculate row just above the lower suture. Observation by the senior author on *Amberleya* spp. from these English outcrops stored in the British Natural History Museum in London suggest that these species generally have a more distinctive spiral sculpture than the Californian ones concerned here.

Amberleya dilleri and *A. cf. dilleri* both differ from the Early Cretaceous (Valanginian) species *A. morganensis* from Rocky Creek (site 7) by lacking a tuberculate subsutural cord.

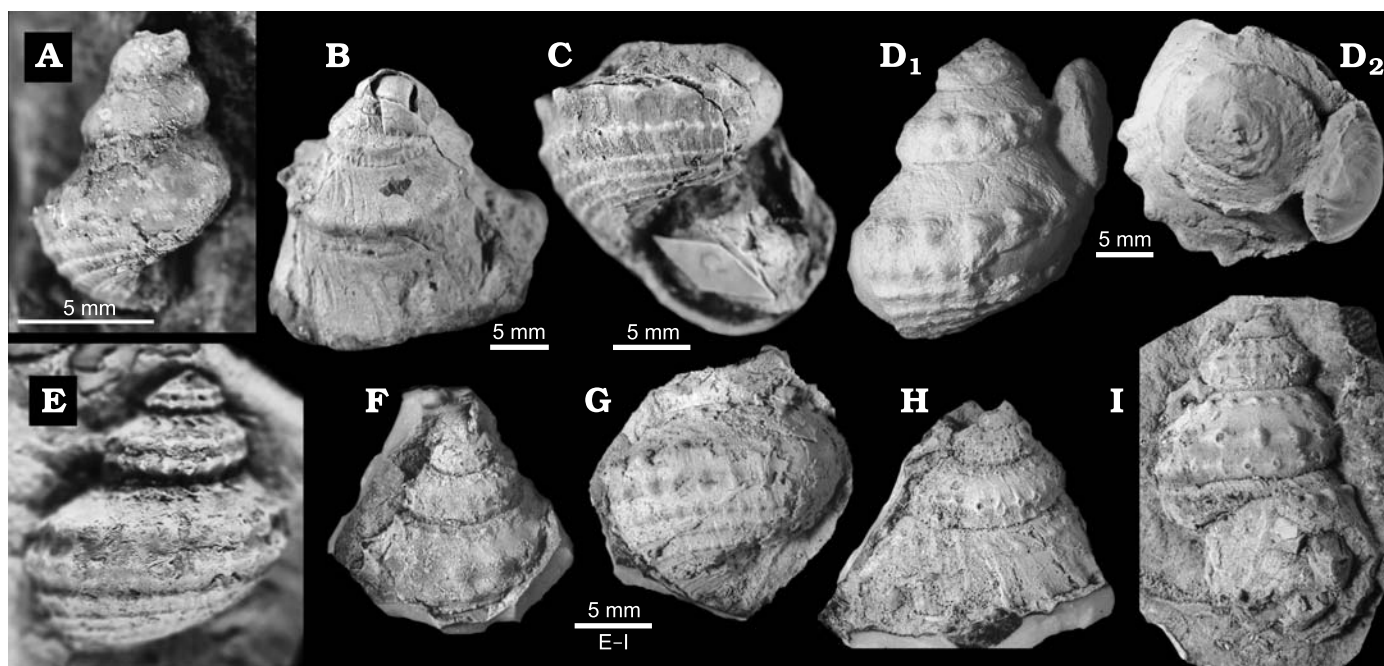


Fig. 4. Late Jurassic and Early Cretaceous eucyclid *Amberleya* spp. from seep carbonates in California, USA. **A–C.** *Amberleya dilleri* Stanton, 1895, type specimens from Paskenta (site 2). **A.** Spire of juvenile specimen (USNM23074a). **B.** Spire of large specimen (USNM 23074b). **C.** Lectotype (USNM 23074c) showing the aperture. **D.** *Amberleya* cf. *dilleri* (UCMP 555090) from NW Berryessa (site 10). **E–I.** *Amberleya morganensis* (Stanton, 1895) from Rocky Creek (site 7). **E.** Lectotype (USNM 23071). **F.** Spire (CAS 70386) with two tuberculate spiral cords. **G.** View on flank and basal margin (CAS 70387). **H.** Spire (CAS 70388) with lower tuberculate spiral largely concealed by succeeding whorl. **I.** Specimen (CAS 70389) with narrow apical angle. **F–I.** rubber casts.

Amberleya dilleri also differs from *A. morganensis* by being higher spired and having a weaker spiral cord below the main spiral cord that forms the whorl's shoulder.

Stratigraphic and geographic range.—Tithonian (Upper Jurassic) at Paskenta (site 2), Great Valley Group, California, USA.

Amberleya cf. *dilleri* Stanton, 1895

Fig. 4D.

Material.—One specimen from NW Berryessa (site 10; UCMP 555090), and two fragments from the Franciscan Little Indian Valley terrane (site 6).

Discussion.—These specimens have a stronger second tuberculate cord below the main one compared to Stanton's (1895) type specimens of *A. dilleri*, and lacks the nodular subsutural cord of *A. morganensis*. Because the specimens are rather poorly preserved, we only hesitantly assign them to *A. dilleri*.

Stratigraphic and geographic range.—Tithonian (Upper Jurassic) to Valanginian (Lower Cretaceous), restricted to seep carbonates at NW Berryessa of the Great Valley Group and Little Indian Valley terrane, Franciscan Complex; California, USA.

Amberleya morganensis (Stanton, 1895)

Fig. 3E–I.

1895 *Turbo morganensis* sp. nov.; Stanton 1895: 66–67, pl. 12: 13.

Material.—Stanton's (1895) type material (USNM 23071

and 23074) from the Rocky Creek site in Morgan Valley (site 7) and specimens collected from the same site by Dean A. Enderlin, James L. Goedert, and KAC. Most specimens examined were steinkerns, along with several external rubber molds extracted from the same indurated carbonates. Because Stanton (1895) did not designate a holotype, the specimen illustrated on Fig. 4E is here designated as lectotype of “*Turbo*” *morganensis*.

Description.—Shell moderately high-spired, turbiniform, with angulate whorls; medium sized, up to 30 mm in height, with at least 4–5 teleoconch whorls; sutures incised to grooved. Whorls sculptured with three nodular spiral cords, first cord below suture, either directly adjacent to suture or up to the cords' widths away from suture; two lower cords variable in strength and position, they may be equally strong and greatest width of the whorls are at the lower cord, or the upper cord is stronger and also marks the greatest width of the whorl; number and position of tubercles in these three cords are not aligned, central row has slightly fewer tubercles per whorl than the other two. Succeeding whorl attached at or below lower cord. Basal margin convex, base sculptured by 5–7 tuberculate cords that decrease in strength and increase in number of finer nodes towards columella. Spiral cords not crossed by axial ribs, nodes remain distinct and separate between successive spiral ribs. Aperture subovate to subquadrate; prosocline to prosoclyt growth lines visible in some specimens.

Discussion.—The specimen illustrated by Stanton (1895) is a “gutta-percha cast of a natural mold” which actually has a

deeper suture than shown on his illustration. Subsequently collected specimens often differ from Stanton's by having less angular whorls resulting from a steeper subsutural ramp, and by having a strong middle spiral and a weak lower spiral, whereas in Stanton's specimen the two spirals are almost equally strong. However, there is sufficient morphological flexibility in these characters among the examined material that we consider this as intra-specific variation.

Stanton (1895: 67) noted from his total collection of 4 internal molds and 2 external molds that *Amberleya morganensis* was somewhat similar to "Turbo" *colusaensis* (see *Paskentana paskentaensis* below), "which has the same general form and style of sculpture." Our inspection of type material in the USNM and additional material from our own collection shows that the sculpture of *A. morganensis* and "Turbo" *colusaensis* is not at all similar. It is possible that confusion arose because many specimens are preserved as internal molds, which are generally moderately to coarsely cancellate in appearance. *Amberleya morganensis* is actually much more similar to *Amberleya dilleri* than to "Turbo" *colusaensis*.

Stratigraphic and geographic range.—Valanginian (Lower Cretaceous), Great Valley Group, in seep carbonates of Rocky Creek, Morgan Valley (site 7), California, USA.

Subclass Caenogastropoda Cox, 1959

Superfamily Abysochrysoidea Tomlin, 1927

Family Hokkaidoconchidae Kaim, Jenkins, and Warén, 2008

Genus *Hokkaidoconcha* Kaim, Jenkins, and Warén, 2008

Type species: *Hokkaidoconcha tanabei* Kaim, Jenkins, and Warén, 2008, Cenomanian (Upper Cretaceous), Yezo Group, Kanajirisawa Creek, Hokkaido, Japan.

Discussion.—Small, elongate gastropods with mainly axial ornament like those described here as *Hokkaidoconcha* are common in late Mesozoic shallow water deposits and they belong to different taxonomic groups including zygopleurids, cerithiopsoids, and cerithioids. Gastropods with similar adult shells found at ancient vents and seeps were either placed in these groups (Stanton 1895; Little et al. 1999; Gill et al. 2005), or were considered as provannids (Little and Vrijenhoek 2003; Campbell 2006), a gastropod group restricted to reducing deep-sea habitats with adult shells similar to those of zygopleurids or cerithioids. However, placing these gastropods in any of these families without knowledge of their larval shells is guesswork at best. Recently, Kaim et al. (2008) showed that Cretaceous seep-restricted gastropods with cerithioid teleoconch shape have provannid or provannid-like (i.e., hokkaidoconchid) larval shells, which nicely documented that provannids and other abyssochrysoids have a history at seeps that goes back at least into the Late Cretaceous.

Hokkaidoconcha occidentalis (Stanton, 1895), *H. bilirata* sp. nov., *H. morenoensis* sp. nov., and *H. tehamaensis* sp. nov.

are placed here in *Hokkaidoconcha* based on their similarity in teleoconch shape to *H. tanabei*, but evidence from larval shells is lacking. These four species share the more-or-less opisthocline ribs that are tuberculate to various degrees below the suture and tend to fade on the lower half of the whorl; and the increased strength of the spiral sculpture at the basal margin. The main differences are in the convexity or straightness of the whorls' flanks and the development of the spiral sculpture. In the Californian species, their intra-specific variability made it somewhat difficult to distinguish among these species, and they are here referred to as the *Hokkaidoconcha occidentalis*-group. The principal species was originally placed in the zygopleurid genus *Hypsipleura* Koken, 1892 with some hesitation (Stanton 1895). However, *Hypsipleura* has higher whorls with a steep and angulated shoulder (Kittl 1891; Wenz 1938–44).

The zygopleurid genus *Ampezzopleura* is very similar regarding shell shape and sculpture, especially as spiral sculpture was documented for the type species (Nützel 1998). Very similar opisthocline ribs can, for example, be seen in *Ampezzopleura hybridopsis* Nützel, 1998. Nützel (1998) introduced the new genus *Striazyga* for species that are similar to *Ampezzopleura* but also have spiral sculpture. However, in that same paper he described and figured "weak spiral sculpture" for the type species of *Ampezzopleura*, *A. tenuis*, which sheds doubt on the validity of the genus *Striazyga*.

Similar shell characters can also be found in several procerithiid or cryptaulaxid species, although usually the axial ribs are straight in these groups. For example, the juvenile whorls of holotype of *Procerithium quinquegranosum* Cossmann, 1902, type species of *Procerithium*, figured by Gründel (1997: pl. 5: 1, 2) are very similar to those of *Hokkaidoconcha occidentalis*. *Procerithium russiense* d'Orbigny, 1945 as figured by Guzhov (2004: pl. 5: 4–10), has similar axial ribs with strong knobs on the anterior side of its very early whorls. However, that species develops the typical cancellate procerithiid sculpture on its later whorls, which is not seen in *Hokkaidoconcha occidentalis*. Also some *Cryptaulax* Tate, 1869 species have similar straight-sided or slightly convex whorls with strong axial ribs, but intersections with spiral cords are usually spiny (Gründel 1999), as in most procerithiids and cryptaulaxids.

Other groups with slender turriculate shells and subsutural nodes or spines like *Hokkaidoconcha occidentalis* are certain campanilids or possibly related taxa. *Campanile*, although usually much larger, has similar subsutural nodes, and also has similar opisthocline growth lines (Houbrick 1981; Houbrick 1989; Kiel et al. 2000). The Early Cretaceous *Diatrypesis kurushini* Kaim, 2004, which has a campaniloid protoconch (cf. Kiel 2006a), has subsutural nodes and growth lines that are opisthoclyt at the base.

Hokkaidoconcha occidentalis (Stanton, 1895)

Fig. 5A–C.

1895 *Hypsipleura*? *occidentalis* sp. nov.; Stanton: 70, pl. 13: 3, 4.

Material.—Stanton's specimens (USNM 23077), two specimens from NW Berryessa (site 10; figured specimen: UCMP

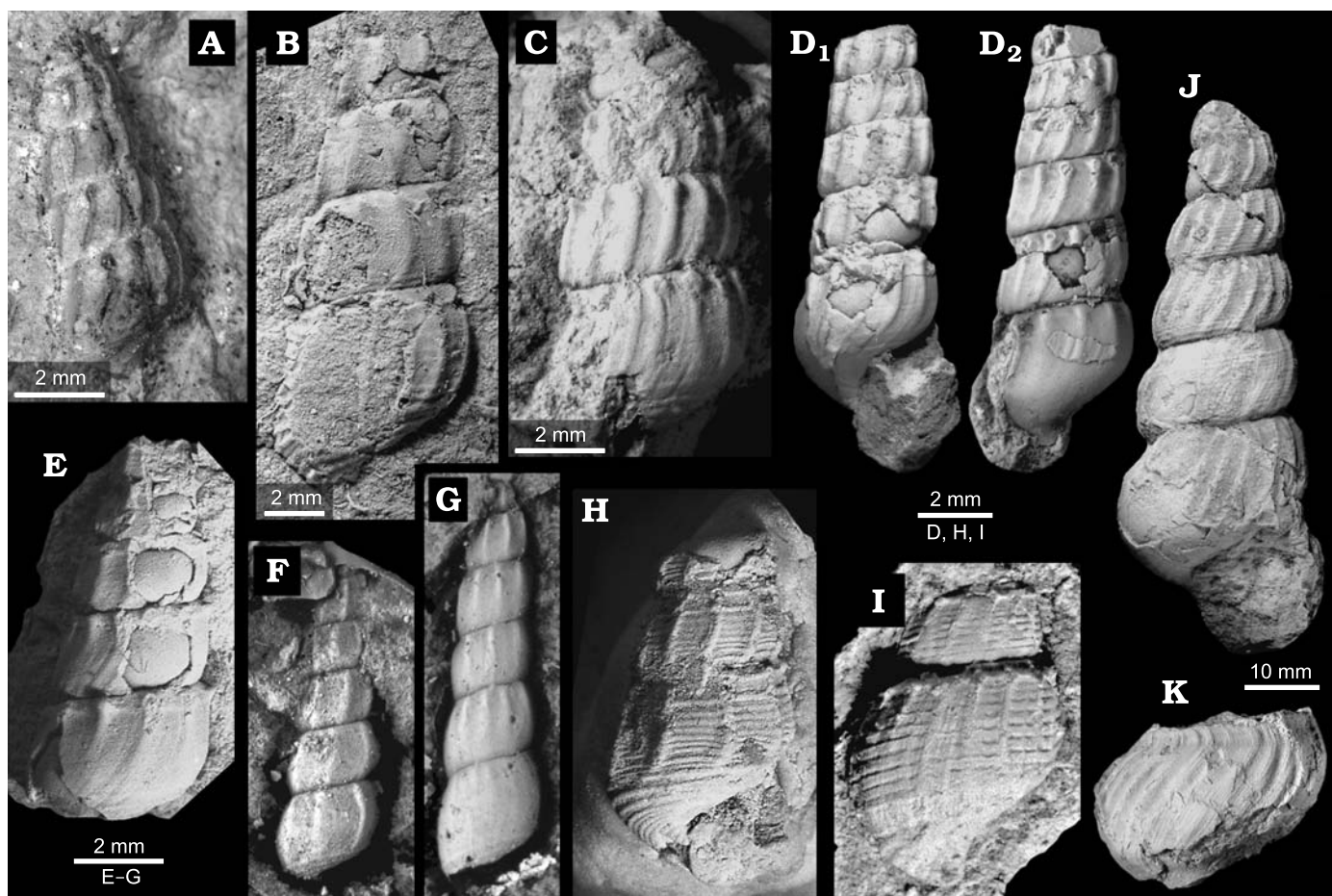


Fig. 5. Late Jurassic and Early Cretaceous abyssochrysoids *Hokkaidoconcha* spp. and *Abyssochrysos? giganteum* sp. nov. from seep carbonates in California, USA. **A–C.** *Hokkaidoconcha occidentalis* (Stanton, 1895). **A.** Lectotype (USNM 23077) from Paskenta (Tithonian; site 2). **B.** Specimen (CAS 70391) with well-developed spiral sculpture from Wilbur Springs (Hauterivian; site 5). **C.** Specimen (UCMP 555091) with poorly developed spiral sculpture from NW Berryessa (Tithonian; site 10). **D, E.** *Hokkaidoconcha tehamaensis* sp. nov. from Paskenta (Tithonian; site 10). **D.** Holotype (UCMP 555092); apertural (**D₁**) and lateral (**D₂**) views. **E.** Paratype (CAS 70390), note fading axial ribs on flank. **F, G.** *Hokkaidoconcha morenoensis* sp. nov. from Moreno Gulch (Santonian; site 14) **F.** Holotype (LACMIP 13483) with well-developed axial ribs and spiral sculpture on base. **G.** Paratype (LACMIP 13484) with fading axial ribs on later whorls. **H.** *Hokkaidoconcha bilirata* sp. nov., holotype (UCMP 555093) from Wilbur Springs (Hauterivian; site 5). **I.** *Hokkaidoconcha* sp. (UCMP 555094) from NW Berryessa (Tithonian; site 10). **J, K.** *Abyssochrysos? giganteum* sp. nov. from E Berryessa (Lower Cretaceous; site 12). **J.** Holotype (UCMP 555095). **K.** Paratype (UCMP 555096).

555091), three specimens from Paskenta (site 2), and two specimens from Wilbur Springs (site 5). Stanton (1895) did not designate a holotype. His material consists of a gutta-pertcha cast with many specimens, one of which is indicated by an arrow scratched into the cast, and fits his illustration of *Hypsipleura? occidentalis*. This specimen is here designated as lectotype of *Hypsipleura? occidentalis* and figured on Fig. 5A.

Description.—Small, slender cerithiform shell with at least five slightly convex whorls and fine, incised suture. Ribs varix-like and opisthocyrt to various degrees; additional sculpture of 6–8 fine spiral threads that are pronounced between axial ribs but almost invisible on ribs; these threads are equally spaced except for the uppermost, subsutural spiral, which is a bit set apart from those below, this subsutural spiral often forms tubercles at the intersection with the axial ribs. Basal margin convex, marked by fading of axial ribs,

and onset of strong spiral cords; aperture oval-lenticular. The lectotype is 9 mm high and 3 mm wide.

Discussion.—From Eocene to Miocene cold seep carbonates in Barbados, Gill et al. (2005) described a quite similar species as “zygopleurid sp. A”. In contrast to *Hokkaidoconcha occidentalis*, that species has a sharply delimited basal edge, a feature that is common in modern epitoniids but occurs only occasionally in Mesozoic zygopleurids.

Stratigraphic and geographic range.—Tithonian (Upper Jurassic) to Hauterivian (Lower Cretaceous), seep carbonates in the Great Valley Group at Paskenta, NW Berryessa, and Wilbur Springs.

Hokkaidoconcha tehamaensis sp. nov.

Fig. 5D, E.

Etymology: After Tehama County, California, USA, county of the type locality.

Type material: Holotype: UCMP 555092, specimen with the aperture and five whorls preserved; paratype: CAS 70390, specimen with fading axial ribs.

Type locality: Paskenta (site 2), California, USA.

Type horizon: Tithonian (Upper Jurassic) seep carbonates, Stony Creek Formation, Great Valley Group.

Material.—Type material and four additional specimens from the type locality.

Diagnosis.—Shell slender turriculate, whorls straight-sided, with about 12 opisthocline, axial ribs that are usually tuberculate or spiny below suture; fine spiral threads vary from moderately well developed to absent; basal margin marked by thin spiral cords.

Description.—Teleoconch with at least five whorls and incised sutures; axial ribs are tuberculate and strongest on upper part of whorl, and may or may not disappear completely on lower half; growth lines strongly prosoclyt on basal margin and base, and end perpendicular to the margin of the aperture. Holotype 13 mm high and 4.5 mm wide.

Discussion.—This new species differs from the other *Hokkaidoconcha* species described here in having straight rather than convex sides, and the axial ribs are more tuberculate or spiny below the suture.

Stratigraphic and geographic range.—Type area only.

Hokkaidoconcha morenoensis sp. nov.

Fig. 5F, G.

Etymology: After the type locality at Moreno Gulch, California, USA.

Type material: Holotype: LACMIP 13483. Specimen with five whorls showing axial ribs across the entire height of the whorls and spiral sculpture on the base; paratype: LACMIP 13484, from the type locality.

Type locality: Moreno Gulch, California, USA.

Type horizon: Santonian (Upper Cretaceous) seep carbonates at Moreno Gulch, Great Valley Group.

Material.—Type specimens and several specimens from the type locality and from Romero Creek (site 13).

Diagnosis.—Slender turriculate shell with slightly convex whorls; ribs widely spaced, variably opisthoclyt to opisthocline, on entire whorl or restricted to upper part; base with fine spiral cords.

Description.—Teleoconch with eight or more whorls, suture incised; whorls sculptured by eight to ten varix-like ribs per whorl, interspaces between ribs two to four times the width of the ribs; ribs variably developed on the entire height of the whorl to completely obsolete; aperture unknown. Holotype with five whorls 8 mm high and 3 mm wide, tallest specimen with eight whorls 16 mm high and 4 mm wide.

Discussion.—*Hokkaidoconcha morenoensis* is most similar to *H. tehamaensis* but differs in having whorls that are more convex and in lacking the spiral sculpture present on whorl flanks of *H. tehamaensis*, *H. occidentalis*, and *H. bilirata*.

Stratigraphic and geographic range.—Santonian–Campanian (Upper Cretaceous) seep carbonates, Great Valley Group, California, USA.

Hokkaidoconcha bilirata sp. nov.

Fig. 5H.

Etymology: After its two prominent subsutural spiral cords.

Type material: Holotype: UCMP 555093, specimen with the two last whorls preserved.

Type locality: Wilbur Springs (site 5), California, USA.

Type horizon: Hauterivian (Lower Cretaceous) seep carbonates, Great Valley Group.

Material.—Three specimens from Cold Fork of Cottonwood Creek (site 1), Albion.

Diagnosis.—Slender, high spired shell with straight to slightly convex whorls, sculpture of oblique to opisthocline ribs and spiral cords, of which the upper two are the strongest; basal margin gently convex, marked by disappearance of axial ribs and two or three strong spiral cords that give way to up to ten finer spirals on base. Aperture oval, inner lip smooth.

Description.—High spired shell with numerous whorls and an incised to grooved suture; 9–12 oblique to opisthocline ribs per whorl, and about 10 spiral cords, of which the apical two are strongest, more widely spaced than those below, and form tubercles at intersection with ribs; lower spirals subequal in strength and spacing, more strongly developed between axial ribs than on top of them; the basal margin is gently convex and marked by the disappearance of the axial ribs. Holotype with 2.5 whorls 11 mm high, largest specimen with 3.5 whorls 14.5 mm high.

Discussion.—*Hokkaidoconcha bilirata* differs from *H. occidentalis* by always having the two uppermost spiral cords well developed, whereas in *H. occidentalis* only the uppermost tubercle-forming spiral is well-developed.

Stratigraphic and geographic range.—Hauterivian–Albion (Lower Cretaceous) seep carbonates in the Great Valley Group, California, USA.

Hokkaidoconcha sp.

Fig. 5I.

Material.—Two specimens from NW Berryessa (site 10; figured specimen: UCMP 555094).

Description.—Broad cerithioid shell with three or more whorls and deeply incised suture; whorls variably convex, sculptured by widely spaced and sometimes with very strongly opisthoclyt ribs, and broad, almost flat-topped spiral cords, nine such spirals per whorl; these cords are separated by narrow interspaces, numerous fine and opisthoclyt growth lines give spiral cords and their interspaces an undulating appearance; subsutural spiral is most strongly developed and also axial ribs are strongest near the suture, producing tubercles at their intersections; base appears to have only spiral ornament.

Discussion.—This species is listed here among *Hokkaidoconcha* solely because it shares the strong subsutural tuberculate cord with the *Hokkaidoconcha* species described above. But it differs markedly from them by having a broader apical angle, the whorls are more convex, the ribs are opisthoclyt

rather than opisthocline, and the spiral cords are broad and flat-topped in contrast to the fine spiral threads of *Hokkaidoconcha*. Aperture and protoconch morphology are unknown, which makes it currently impossible to confidently place this species in any gastropod family.

Stratigraphic and geographic range.—Tithonian (Upper Jurassic) seep carbonates at NW Berryessa in the Great Valley Group, California, USA.

Family Abysochrysidae? Tomlin, 1927

Genus *Abysochrysos*? Tomlin, 1927

Type species: *Abysochrysos melanioides* Tomlin, 1927; Recent, South Africa.

Abysochrysos? *giganteum* sp. nov.

Fig. 5J, K.

2006 Large, high-spired abysochrysid; Campbell 2006: 382, fig. 6B.

Etymology: After its extremely large size compared to other abysochrysid.

Type material: Holotype: UCMP 555095, large specimen with five-and-a-half sculptured whorls preserved; paratypes: one specimen from East Berryessa (site 12; UCMP 555096).

Type locality: East Berryessa, Napa County, California, USA (site 12).

Type horizon.—Seep carbonates, Lower Cretaceous, Great Valley Group.

Diagnosis.—Large, high-spired cerithiform shell with at least five-and-a-half evenly convex whorls; juvenile sculpture of strong ribs and densely spaced spiral cords; spiral sculpture fades on later whorls and a subsutural constriction may develop. Basal margin well rounded, aperture simple, round, siphonal notch not apparent.

Description.—Largest available fragment has five-and-a-half whorls and incised suture; early whorls sculptured by 14–16 strong opisthocline ribs crossed by 18 densely spaced spiral cords of variable strength, spirals crossed by numerous fine growth increments, giving them a plaited appearance; on later whorls spiral sculpture becomes weaker or disappears. Last whorl up to 30 mm wide, largest specimen at least 73 mm high.

Discussion.—As with many of the gastropods described here, the lack of protoconch data makes it difficult to place this species. On the basis of teleoconch characters alone this species is indistinguishable from *Abysochrysos*. It has the same type of spiral and axial ornament that is often reduced on late whorls, the same opisthocline growth lines, and a similar base and simple aperture (Houbrick 1979; Bouchet 1991; Killeen and Oliver 2000). However, extant species of *Abysochrysos* are only up to 40 mm high and 10 mm wide, whereas *Abysochrysos*? *giganteum* sp. nov. reached at least three times that size. Therefore our new species is only tentatively assigned to *Abysochrysos*.

In size and whorl profile *Abysochrysos*? *giganteum* resembles the presumed zygopleurid *Zebalia suciaensis* (Packard, 1922) from Late Cretaceous sediments of western North America (Squires and Saul 2003), but in that species the ribs are blade-like near the upper suture, a feature not

seen in *Abysochrysos*? *giganteum* or other *Abysochrysos* species. Remarkable are the similarities between *Abysochrysos*? *giganteum* and some extant potamidids (hyper-saline and brackish-water cerithioideans) such as some large species of *Cerithidea* Swainson, 1840 in respect to ornament, or *Telescopium* Montfort, 1810 regarding the opisthocline growth line (Houbrick 1991). Superficially similar is a species that was originally described as *Abysochrysos raii* Goeder and Kaler, 1996 from a seep carbonate in the middle Eocene Humptulips Formation in Washington State, USA (Goedert and Kaler 1996). Subsequent collection of better preserved material by James L. Goedert and the senior author at the type locality showed that this species has two very deep sinuses in the outer lip of its aperture, a feature that is not found in extant *Abysochrysos*; the species belongs to the new genus *Humptulipsia* (Kiel 2008).

Stratigraphic and geographic range.—Early Cretaceous, restricted to seep carbonates in the Great Valley Group, California, USA.

Family uncertain

Genus *Paskentana* nov.

Etymology: After the type locality near Paskenta in California, USA.

Type species: *Turbo paskentaensis* Stanton, 1895; Upper Jurassic to Lower Cretaceous, Paskenta, California, USA.

Diagnosis.—Adult shell littoriniform, of moderate size, very thin-shelled, whorls convex or shouldered, bearing mainly spiral sculpture with minor axial elements on whorl's shoulder; spirals smooth, tuberculate, or spinose; juvenile whorls with mostly smooth spiral sculpture only; aperture oval, apical side somewhat pointed; inner lip smooth and may have callus; growth lines mostly straight but may be somewhat sinuous on shoulder.

Discussion.—At the Bear Creek site (site 4) we found a fragment of a single isolated larval shell (Fig. 6E) consisting of one whorl that is 350 µm wide and is sculptured by collabral ribs and spiral cords. Larval shells of this size and sculpture are known from provannids, abysochrysid and the recently established hokkaidoconchids (Warén and Bouchet 1993; Kaim et al. 2008). *Paskentana paskentaensis* occurs in rock-forming masses at the Bear Creek site (see Fig. 3A) and thus we find it most likely that this isolated larval shell belongs to this gastropod species. Kaim et al. (2008) considered the “decollate” protoconch of provannids as the distinguishing feature to hokkaidoconchids: juvenile provannids apparently seal the base of their protoconch with a plug of calcium carbonate, above which the shell typically is not preserved (Kaim et al. 2008). Thus our isolated larval shell is insufficient to distinguish between the two groups. Hokkaidoconchids and abysochrysid both have very elongate, high-spired shells (Houbrick 1979; Kaim et al. 2008), whereas certain provannids have rather globular shells, namely the genera *Alviniconcha* Okutani and Ohta, 1988 and *Ifremeria* (Okutani and Ohta 1988; Bouchet and Warén 1991). In addition, provannids have similar sculpture on the early whorls.

Among the provannid genera, *Provanna* and *Desbruyeresia* Warén and Bouchet, 1993 differ from *Paskentana* by having fewer spiral cords per whorl, and by being not as strongly shouldered as some of the *Paskentana* specimens. *Alviniconcha* Okutani and Ohta, 1988 is quite close to *Paskentana* regarding shell shape; the sculpture on the first whorls of *Alviniconcha* tends to be more tuberculate than in the juvenile shell of *Paskentana paskentaensis*; the suture is less distinct in *Alviniconcha* and the whorl is also not shouldered, as are whorls of some specimens of *Paskentana*. Adult *Ifremeria* develop a notch in the adapical part of the aperture that results in a scaly subsutural ridge on the whorls, which is not seen in *Paskentana*. Early whorls of *Ifremeria* are more angular and have stronger spirals with stronger tubercles (Warén and Bouchet 1986; Warén and Ponder 1991; Warén and Bouchet 1993). In sum, we place *Paskentana* in the superfamily Abysochrysoidea. Better preserved material is needed to clarify its position at the family level.

One genus and species that is potentially related to *Paskentana* is *Elmira cornuarterietis* Cooke, 1919 from a presumably Oligocene seep deposit in Cuba (Cooke 1919; Kiel and Peckmann 2007). It resembles *Paskentana* in its general shell shape but is more lower spired than even the globular *Paskentana globosa* sp. nov., and has coarse, undulating spiral sculpture which we have not seen in any of our *Paskentana* species.

Several gastropod groups build adult shells similar to those of *Paskentana*, for example certain Purpurinidae or Eucyclidae. Juvenile eucyclids have a very broad apical angle and evenly convex whorls that are sculptured by distinct axial ribs (see Kiel and Bandel 2001; Kaim 2004). Thus, they are quite unlike the juvenile shell of *Paskentana*, which has an angulation in the lower half of the whorl and shows spiral ornament only. Juveniles of *Purpurina* have strongly angulate whorls with the angulation in the upper half of the whorl, and strong axial sculpture with only minor spirals (Kaim 2004). Therefore the juvenile shell of *Purpurina* also is very different from that of *Paskentana*. In addition to this, the missing tip of the *Paskentana paskentaensis* specimen shown on Fig. 5F is 600 µm wide. This would be wide enough to accommodate a eucyclid (or vetigastropod) protoconch, which usually does not exceed 400 µm in width (Bandel 1982). Purpurinid larval shells, however, are 1000 to 1500 µm in diameter (Kaim 2004) and thus too wide to fit onto the missing tip, although lecithotrophic protoconchs might have been smaller. Similar shells are also known from members of the intertidal caenogastropod families Planaxidae Gray, 1850, and Littorinidae Gray, 1840, and from the deep-water family Provannidae Warén and Ponder, 1991. Planaxids and littorinids have ornamentation on the early teleoconch that is very similar to that seen in *P. paskentaensis*, and their protoconchs do not exceed 300 µm in width and would thus fit onto the missing tip of *P. paskentaensis* (Houbrick 1987; Reid 1996; Reid 2004).

Stratigraphic and geographic range.—Tithonian (Upper Jurassic) to Hauterivian (Lower Cretaceous), Great Valley Group and Franciscan Accretionary Complex, California, USA.

Paskentana paskentaensis (Stanton, 1895)

Fig. 6.

1895 *Turbo paskentaensis* sp. nov.; Stanton 1895: 64–65, pl. 12: 5–6.
 1895 *Turbo wilburensis* sp. nov.; Stanton 1895: 65, pl. 12: 15.
 1895 *Turbo trilineatus* sp. nov.; Stanton 1895: 65–66, pl. 12: 12.
 1895 *Turbo colusaensis* sp. nov.; Stanton 1895: 66, pl. 12: 14.
 1895 *Turbo? humerosus* sp. nov.; Stanton 1895: 67, pl. 12: 10, 11.
 2006 Thin-shelled possible provannid; Campbell 2006: 382, fig. 6A.

Material.—Stanton's (1895) type material [USNM 23067 (= *T. paskentaensis*), USNM 23068 (= *T. wilburgensis*), USNM 23069 (= *T. trilineatus*), USNM 23070 (= *T. colusaensis*), USNM 23072 and 23073 (= *T.? humerosus*)], and 163 specimens from subsequent collections. Stanton's (1895) specimen of *Turbo paskentaensis* from Paskenta (site 2) illustrated here on Fig 6I is designated as lectotype.

Description.—Shell ovate fusiform, moderately high-spired, apical angle 58–60°, four to five teleoconch whorls, with globose last whorl; suture distinct, incised; whorls strongly convex, and vary from evenly rounded to angulate, resulting from straight subsutural ramp that ends with distinct angulation at whorl's periphery; if present, up to two spiral cords on the ramp; number of spiral cords on periphery varies between five and ten, up to ten spiral cords present on the base; spiral cords either of equal strength, or show alternating pattern of strong and weak ones, or strength decreases towards base; interspaces either of same width as spirals or slightly wider, in rare cases up to three times as wide; growth lines vary in strength and cause fine crenulations, nodes, or strong, half-tube-like spines or scales when they cross spiral cords; this pattern is usually strongest on periphery below ramp, where it can form a spiny or tuberculate shoulder, and tends to become slightly weaker towards the base; aperture sub-ovate to lenticular, columella convex and smooth.

Discussion.—This species shows great morphologic plasticity, ranging from individuals having well-rounded whorls with beaded spiral ornament, to individuals having strongly shouldered whorls and ornament where the intersections of axial growth lines with spiral cords form small scaly spines. Similar scaly ornament can also be seen on specimens with well-rounded whorls, whereas other individuals have a strong shoulder but almost smooth spiral cords. This plasticity may have led Stanton (1895) to erect five different species, although he noted that they are rather closely related. We have examined Stanton's material, as well as other museum collections and new field collections, and have found a continuum in these characters. Therefore we synonymize *Turbo wilburensis*, *Turbo trilineatus*, and *Turbo colusaensis* with *Paskentana paskentaensis* as this was the first among the species that Stanton (1895) described.

Also a synonym of *Paskentana paskentaensis* is *Turbo? humerosus* Stanton, 1895. Stanton's material includes three specimens, of which he illustrated two, and he provided two USNM numbers (23072 and 23073). However, he did not specify which specimen had which number, and all specimens are in the same box along with a label stating both num-

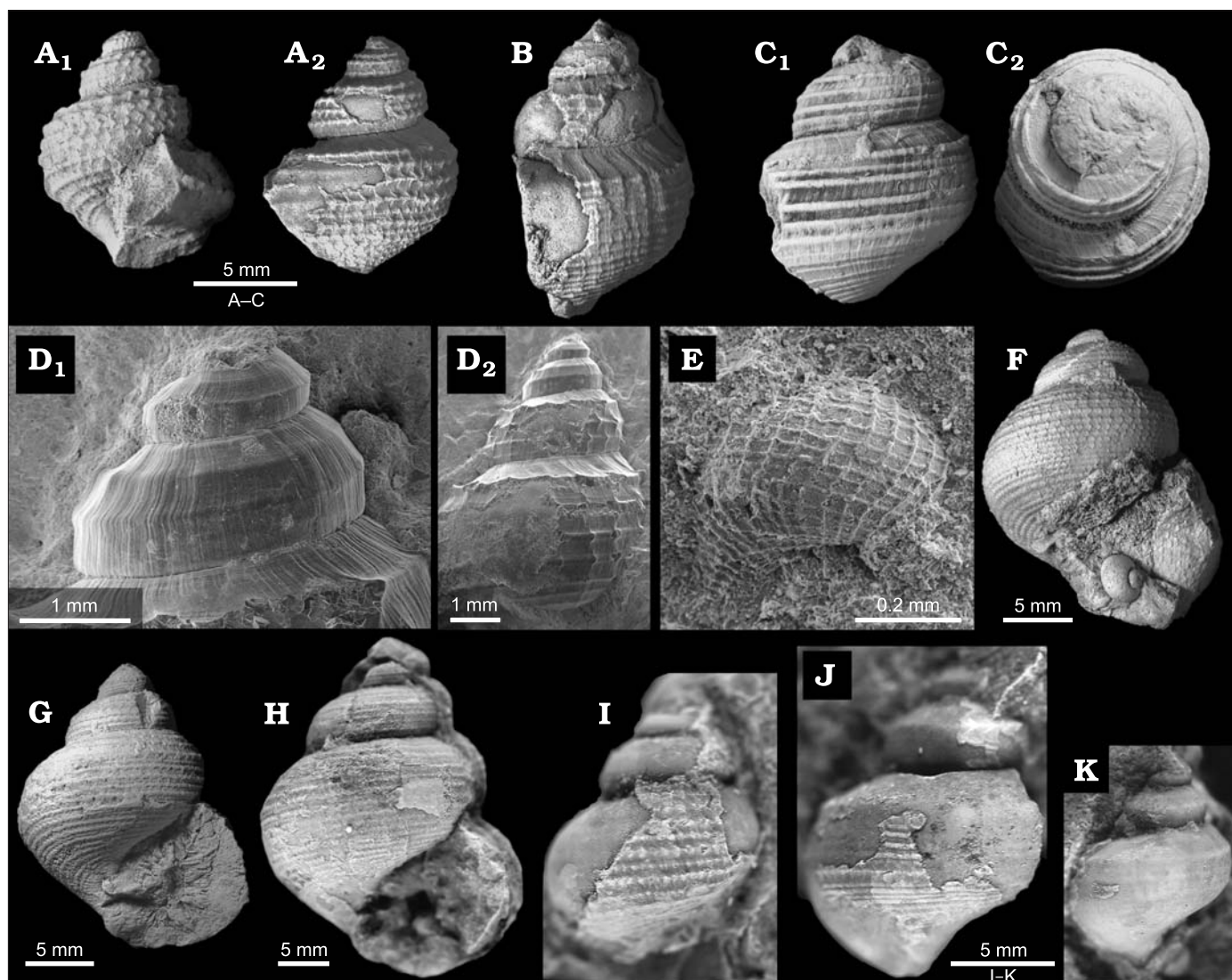


Fig. 6. Abyssochrysid gastropod *Paskentana paskentaensis* (Stanton, 1895) from Late Jurassic and Early Cretaceous seep carbonates in California, USA. **A**. Small specimen (CAS 70392) with strong scaly sculpture from Bear Creek (Valanginian; site 4); apertural (**A₁**) and lateral (**A₂**) views. **B**. Specimen (CAS 70393) with broad shoulder from Bear Creek (Valanginian; site 4). **C**. Specimen (UCMP 555097) with broad shoulder and almost smooth spiral sculpture, from Little Indian Valley (Valanginian?; site 6). **D**. Juvenile specimen (UCMP 555104) from Bear Creek (Valanginian; site 4), close-up on first whorls (**D₁**) and entire specimen (**D₂**). **E**. Isolated partial larval shell (UCMP 555105) from Bear Creek (Valanginian; site 4) that most likely belongs to *Paskentana paskentaensis*. **F**. Specimen (UCMP 154113) without shoulder and fine scaly sculpture, from Rice Valley (Hauterivian?; site 3). **G**. Specimen (UCMP 13701) without shoulder, from Wilbur Springs (Hauterivian; site 5). **H**. “*Turbo*” *wilburensis* Stanton, 1895 (pl. 12: 15), lectotype (USNM 23068) from Wilbur Springs (Hauterivian; site 5). **I**. “*Turbo*” *paskentaensis* Stanton, 1895 (pl. 12: 6), lectotype (USNM 23067) from Paskenta (Tithonian; site 2). **J**, **K**. “*Turbo*” *humerosus* Stanton, 1895 from Wilbur Springs (Hauterivian; site 5). **J**. Lectotype (USNM 23072). **K**. Paralectotype (specimen illustrated by Stanton 1895: pl. 12: 10).

bers. Two of his specimens are steinkerns, only one has a moderate amount of shell material preserved. This latter specimen (Stanton’s fig. 11, our Fig. 5M) is here designated as the lectotype of *Turbo*? *humerosus* Stanton, 1895, and given the USNM number 23072. Our new material shows that *T.*? *humerosus* falls within the broad morphologic range of *Paskentana paskentaensis*, and therefore *T.*? *humerosus* is synonymized with *Paskentana paskentaensis*.

Superficially similar to *Paskentana paskentaensis* is the “epitoniid gastropod from Memi” from a vent community in the Turonian (Late Cretaceous) Troodos ophiolite on Cyprus (Little et al. 1999: fig. 2I) because it has a similar sculp-

ture as some specimens of *Paskentana paskentaensis* (e.g., Fig. 6A, F). But the Troodos species is higher spired and has fine spiral microornament that we have not seen on any of our *Paskentana* species.

Stratigraphic and geographic range.—Tithonian (Upper Jurassic) to Lower Cretaceous, restricted to seep carbonates in the Great Valley Group and Franciscan Accretionary Complex, California, USA. This species is widespread and occurs at the following localities: Paskenta, site 2, and NW Berryessa, site 10 (Tithonian), Little Indian Valley, site 6, and Bear Creek, site 4 (Valanginian?), Foley Canyon, site 8 (Valanginian–Hauterivian), Wilbur Springs, site 5 (Hauterivian),

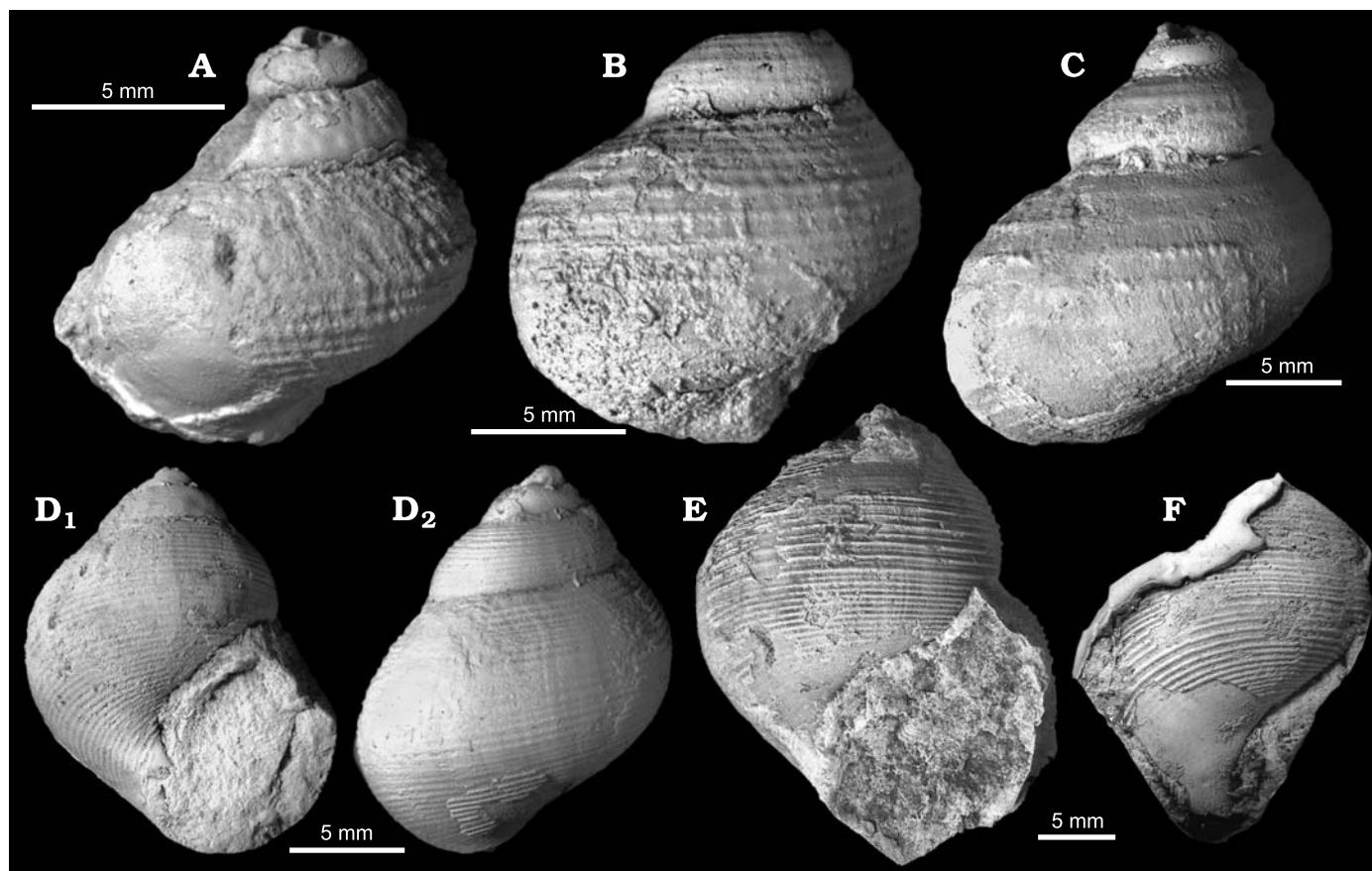


Fig. 7. Abyssochrysoïd gastropod *Paskentana* spp. from Late Jurassic and Early Cretaceous seep carbonates in California, USA. **A–C.** *Paskentana berryessaensis* sp. nov. **A.** Holotype (UCMP 555098), small specimen with nodular sculpture from NW Berryessa (Tithonian; site 10). **B.** Paratype (UCMP 555099), specimen with beaded spiral cords from NW Berryessa (Tithonian; site 10). **C.** Paratype (UCMP 555100) from Bear Creek (Valanginian; site 4), specimen with spiral sculpture and fine axial growth increments. **D–F.** *Paskentana globosa* sp. nov. **D.** Paratype (UCMP 555101) from Little Indian Valley (Valanginian?; site 6). **E.** Holotype (CAS 70394), large specimen from Knoxville (Early Cretaceous?, site 9). **F.** Rubber cast of a last whorl, from Knoxville.

Rice Valley, site 3 (Lower Cretaceous), Gravelly Flat, site 15, and E and W Berryessa, sites 12 and 11 (possibly Lower Cretaceous).

Paskentana berryessaensis sp. nov.

Fig. 7A–C.

Etymology: After the type locality at Berryessa Lake, California, USA.

Type material: Holotype: UCMP 555098, small specimen with nodular sculpture. Paratypes: UCMP 555099 from the type locality; UCMP 555100 from Bear Creek (site 4), California, USA.

Type locality: NW Berryessa, Napa County, California, USA (site 10).

Type horizon: Seep carbonate in the Tithonian (Upper Jurassic) of the Great Valley Group.

Material.—The type material and three additional specimen from Bear Creek (site 4).

Diagnosis.—Shell broad turbiniform, last whorl globose, apical angle 65°; whorls strongly convex, rounded or slightly angular; increasing number of nodular spiral cords through ontogeny; growth lines fine and prosocline; same sculpture on base but less strong.

Description.—Moderately high-spired shell with at least three teleoconch whorls; suture distinct, incised; number of

spiral cords per whorl increases from 3 on early whorls to 6 on later ones, new spirals appear gradually between existing ones; spirals nodular at intersections with fine prosocline growth lines. The holotype is 36 mm high.

Discussion.—These specimens have the general shape and sculpture of *P. paskentaensis* but differ from “typical” *P. paskentaensis* by being much broader (having a wider apical angle). *P. paskentaensis* is generally highly variable regarding shell sculpture and whorl profile, but it appears to be relatively constant with regard to its apical angle.

Stratigraphic and geographic range.—Tithonian (Upper Jurassic) to Valanginian (Lower Cretaceous), seep carbonates at the NW Berryessa and Bear Creek localities of the Great Valley Group, California, USA.

Paskentana globosa sp. nov.

Fig. 7D–G.

Etymology: The species is named for its globose shell shape.

Type material: Holotype: CAS 70394, large specimen with last whorl and most of the aperture preserved; paratype: UCMP 555101 from Little Indian Valley (site 6), California, USA.

Type locality: Knoxville, Napa County, California, USA.

Type horizon.—Specific horizon in Great Valley Group unknown.

Material.—Type material and four specimens from Knoxville (site 9).

Diagnosis.—Delicate shell with inflated last whorl; whorls convex, numerous spiral cords on periphery and base; growth lines with slight opisthocyrt sinus on apical part of whorl and straight to slightly prosocline below; aperture roundish, slightly pointed apically, columella smooth and concave with respect to aperture.

Description.—Medium sized littoriniform shell, suture shallow but distinct; sculpture of numerous (45–50 on last whorl) spiral cords that are slightly more widely spaced on periphery than near suture, this sculpture continues uninterrupted across well-rounded basal margin onto base; base of aperture and possible siphonal feature unknown. Height of holotype 40 mm.

Discussion.—*Paskentana globosa* sp. nov. differs from *P. paskentaensis* by its more globose shell, the less incised suture, and by the more regular ornament of numerous thin spiral cords. *Paskentana berryessaensis* sp. nov. has coarser sculpture and a larger whorl expansion rate.

Stratigraphic and geographic range.—Early Cretaceous (?), in seep carbonates in the Great Valley Group (Knoxville, site 9) and Franciscan Group (Valanginian, Little Indian Valley, site 6), California, USA.

Superfamily and family uncertain

Genus *Atresius* Gabb, 1869

Type species: *Atresius liratus* Gabb, 1869; Early Cretaceous, Great Valley Group, Wilbur Springs (site 5), California, USA.

Original diagnosis.—“Shell elongate, spire elevated; whorls rounded, aperture ovate, slightly produced in front, outer lip entire, thin; columella not incrustated, imperforate; surface marked by revolving ribs.” (Gabb 1869: 168).

Emended diagnosis.—High-spined, littoriniform shell with five or more whorls and deeply incised suture; shell thin; whorls almost straight-sided, weakly convex, or with steep shoulder; sculpture of several spiral cords of subequal strength, interspaces mostly wider than spirals; basal margin rounded to strongly angular and keeled; spirals on base similar to those on whorl's flank but finer and more narrowly spaced; umbilical slit may be present; growth lines opisthocyrt, fine, and numerous, occasionally clumped into ribs; aperture rhomboid, inner lip apparently smooth and without folds, short siphonal notch.

Discussion.—Gabb's (1869) original diagnosis obviously applies to a broad range of gastropods, therefore an emended diagnosis is provided here, based on more material than was available to Gabb (1869). The taxonomic position of *Atresius* is doubtful. Suggestions include littorinids (Gabb 1869; Stanton 1895), turbinids (Stanton 1895), or trichotropids (Cossmann 1906; Wenz 1938–44). Gabb (1869: 169) suggested that *Atresius* should be placed near *Tuba* Lea, 1833 and *Spironema* Meek, 1876, two genera that Wenz (1938–44) placed in the

heterobranch family Mathildidae Dall, 1889. A family of cenogastropods that also builds similar shells is the Planaxidae Gray, 1850, which today is largely found in the intertidal zone. This wide range of placements reflects the difficulties in classifying this genus if no additional information on shell microstructure and/or protoconch is available. We find it unlikely that *Atresius* belongs to the Turbinidae Rafinesque, 1815 because most members of this family are not as high-spined as *Atresius*, and have a round aperture, rather than a strongly angulate one like *Atresius*. Regarding sculpture and growth lines, *Atresius* also resembles *Paskentana*. Based on currently available evidence, we consider *Atresius* to be a cenogastropod which could have affinities to the littorinids, cerithioids, provannids, and/or *Paskentana*.

Several species have been assigned to *Atresius* over the years, but none of them can be confirmed. Diller and Stanton (1894: 442) reported “*Atresius liratus* Gabb (?)” from a carbonate block in shales in CFCC that also contained the seep-restricted “*Modiola*” *major* Gabb, 1868. A year later Stanton (1895: 69) mentioned that “*Atresius liratus* Gabb (?)” belonged “to a distinct, undescribed species”. The species in question was not figured and the material could not be tracked down, thus it remains uncertain whether this is *A. liratus* or a new species. Cossmann (1906) placed several European species in *Atresius*, including *Cerithium cornuelianum* d'Orbigny, 1842, for which Wood (1910) pointed out that it bears little resemblance to the type of *Atresius*; *Cerithium lallierianum* d'Orbigny, 1842, which Kollmann (2005) convincingly classified as *Cirsocerithium*; and “*Cerithium*” *cenomanense* d'Orbigny, 1843, which is the only species from Cossmann's list that does indeed resemble *Atresius liratus* to some extent, and was re-illustrated and marked as “*species incertae sedis*” by Kollmann (2005: 171–172, pl. 18: 1a, b). Casey (1961: 557) reported “*Atresius fittoni* (d'Orbigny)” of Casey (1961) from the Sandgate Beds in Sussex, England, which is in fact *Cerithium lallierianum* (i.e., Kollmann, 2005: 160). Five further species which Cossmann (1906) considered as belonging to *Atresius* were reported by Holzapfel (1888) from the Vaals greensands but they resemble Cretaceous cerithiids, epitoniids, and nysitellids rather than *Atresius*. In sum, *Atresius* appears to be monospecific and restricted to Early Cretaceous seep carbonates in the Great Valley Group in California, USA.

Atresius liratus Gabb, 1869

Fig. 8A–F.

- 1869 *Atresius liratus* sp. nov.; Gabb 1869: 169, pl. 28: 50.
- 1894 ?*Atresius liratus* Gabb (?); Diller and Stanton 1894: 442.
- 1895 *Atresius liratus* Gabb; Stanton 1895: 68–69, pl. 11 : 6.
- 1906 *Atresius liratus* Gabb; Cossmann 1906: 193, fig. 19.
- 1927 *Atresius liratus* Gabb; Stewart 1927: 426, pl. 23 : 3.
- 1938 *Atresius liratus* Gabb; Wenz 1938: 893, fig. 2627.
- 2006 *Atresius liratus* of Stanton, 1895; Campbell 2006: 382, fig. 6F.

Material.—Two specimens (USNM 23075a, b) figured by Stanton (1895) from Wilbur Springs (site 5) and numerous specimens from Rocky Creek (site 7).

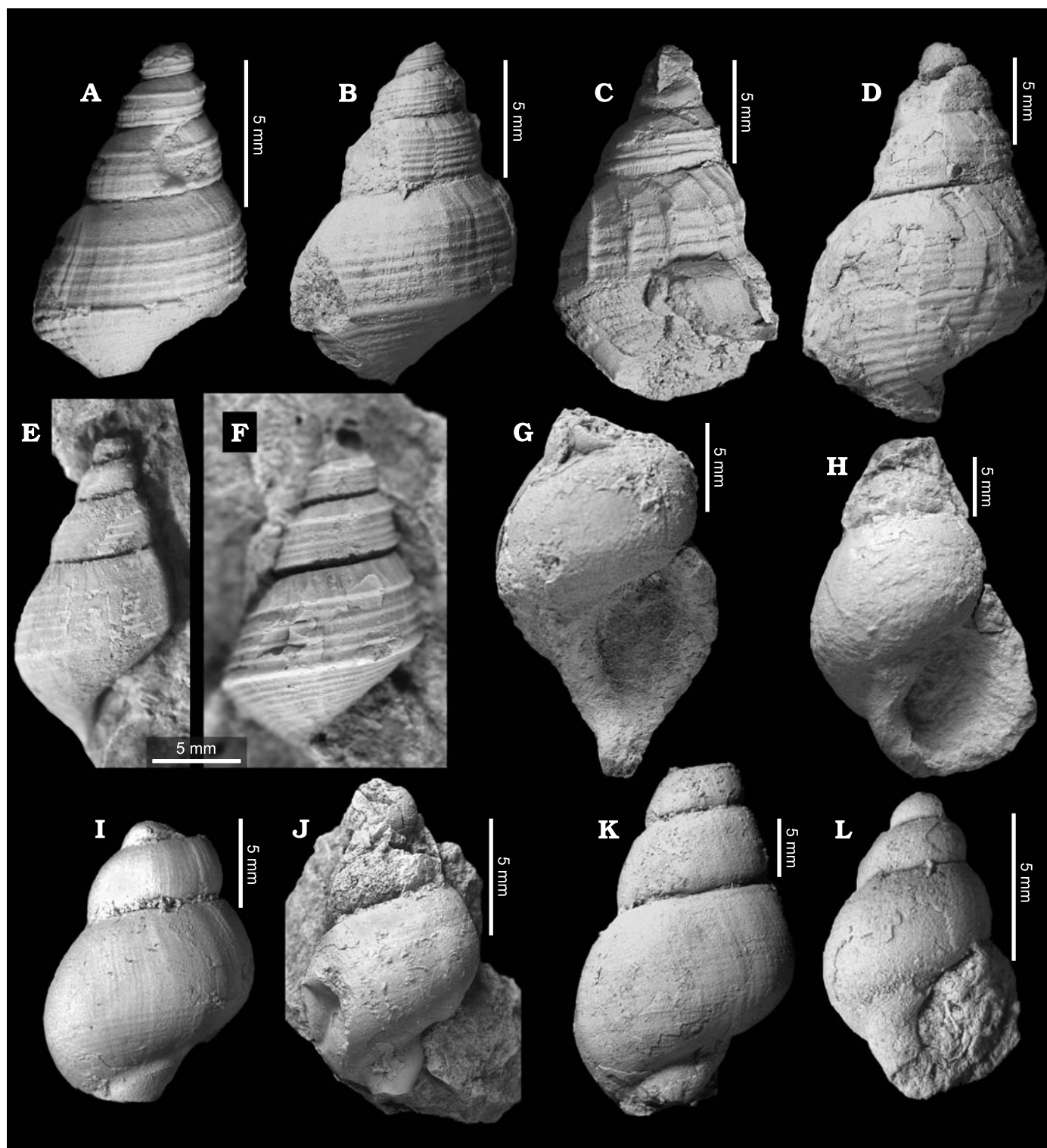


Fig. 8. Gastropods of uncertain taxonomic position, *Atresius liratus* Gabb, 1869 and *Bathypurpurinopsis stantoni* sp. nov., from Early Cretaceous seep carbonates in California, USA. **A–F.** *Atresius liratus*. **A.** Specimen (CAS 70395) with broad shoulder, from Rocky Creek (Valanginian; site 7). **B.** Specimen (CAS 70396) from Rocky Creek, note fine spiral sculpture on shoulder. **C.** Specimen (CAS 70397) with strong axial ribs, from Rocky Creek. **D.** Large specimen (CAS 70398) with rounded basal margin, from Rocky Creek. **E.** Specimen (USNM 23075a) illustrated by Stanton (1895: pl. 11: 6). **F.** Another specimen (USNM 23075b) from Stanton's lot with fewer but stronger spirals, and a more angular basal margin. **G–L.** *Bathypurpurinopsis stantoni*, from Cold Fork of Cottonwood Creek (Albian; site 1). **G.** Specimen (CAS 70399) with thin apertural fold and preserved siphonal column. **H.** Specimen (CAS 70400) with excavated aperture. **I.** Specimen (UCMP 555102) showing fine spiral sculpture and sinuous growth lines. **J.** Specimen (CAS 70401) with well-developed apertural fold, note the indented shell on the left. **K.** Holotype (CAS 70402). **L.** Smooth specimen (UCMP 555103) with excavated aperture.

Description.—Protoconch unknown. Teleoconch fusiform, moderately high spired, up to five whorls, apical angle 35–40°; suture distinct, deeply incised; whorls almost flat-sided, slightly convex, or angular, often with steep shoulder, basal margin strongly angular to rounded; sculpture consists of four to eight spiral cords, uppermost one at edge of shoulder, lowermost at basal margin, these two are usually strongest, interspaces between cords two to three times as wide as cords; spirals are crossed by dense, opisthocyrt growth lines of variable strength, in few specimens growth lines develop into axial ribs of same strength as spiral cords; base with seven to ten spirals of various strength, sometimes with alternating strong and weak cords, interspaces as wide as cords or narrower; aperture angular lenticular, apical side pointed; columellar features unknown.

Discussion.—The high variability of the whorl profile in this species, ranging from rounded to bicarinate to almost flat-sided was noted by Stanton (1895). Stewart (1927) suggested that Stanton's (1895) species may be distinct from Gabb's (1869) holotype because growth lines and spiral cords were different. However, our material shows all transitions between the morphologies documented by Gabb (1869) and Stanton (1895), and we have no doubt that they belong to one and the same species. In addition, we document that this species was also variable regarding the strength of its growth lines, which develop into strong axial ribs in some specimens.

Stratigraphic and geographic range.—Valanginian to Hauterivian (Lower Cretaceous), in the seep carbonates at Wilbur Springs and Rocky Creek, Great Valley Group, California, USA.

Genus *Bathypurpurinopsis* nov.

Etymology: A *Purpurina*-like gastropod from bathyal depth.

Type species: *Bathypurpurinopsis stantoni* sp. nov. Great Valley Group, Early Cretaceous, Cold Fork of Cottonwood Creek, Tehama County, California, USA.

Diagnosis.—Moderately high-spired fusiform to littoriniform shell with several evenly convex whorls and incised suture, sculpture may consist of fine spiral threads crossed by slightly sinuous growth lines. Aperture broadly lenticular, with siphonal notch and short and pointed siphonal column, columella with prominent siphonal fold.

Discussion.—Protoconch and shell microstructure are unknown. This new genus has an interesting combination of characters for Early Cretaceous gastropods. The spire resembles that of modern Littorinidae or Mesozoic Ampullinidae Cossmann, 1918 (Ampullospiridae Cox, 1930 of some authors), for example *Pictavia* Cossmann, 1925. These taxa, however, differ markedly from *Bathypurpurinopsis* gen. nov. in their apertural features. The siphonal notch and the prominent siphonal fold of the aperture are very similar to those seen in modern neogastropods, especially among muricids, buccinids, and cancellariids.

Some members of the Mesozoic Purpurinidae have columellar and siphonal features like *Bathypurpurinopsis* includ-

ing a fold and corresponding notch (e.g., the Cretaceous *Purpuroidea* Lycett, 1848). Most purpurinids, however, have a strongly angular shoulder, and axial and tuberculate sculpture. An exception to this is the Middle Jurassic genus *Ochetochilus* Cossmann, 1899, which, like *Bathypurpurinopsis*, has only fine spiral sculpture, mainly convex whorls, a rather long siphonal canal, but lacks a siphonal fold. However, that genus is only poorly known and even its position within the Purpurinidae is uncertain.

The siphonal fold suggests neogastropod or cassoidean affinities, but Early Cretaceous members of these groups have quite different shell shapes (Taylor et al. 1983). Thus *Bathypurpurinopsis* gen. nov. might either represent a very early radiation of neogastropods into the seep environment, or a rather late member of the mainly Triassic and Jurassic Purpurinidae.

Stratigraphic and geographic range.—Early Cretaceous cold-seep carbonates in the Great Valley Group of California, USA.

Bathypurpurinopsis stantoni sp. nov.

Fig. 8G–L.

Etymology: After Timothy William Stanton (1860–1953) who pioneered detailed taxonomic studies of invertebrate fossils from the Great Valley “white limestones”.

Type material: Holotype: CAS 70402, large specimen with three whorls and a distinctive basal fold; paratypes: two specimens from the type locality (UCMP 555102, 555103) and four additional specimens from the type locality.

Type locality: Cold Fork of Cottonwood Creek, Tehama County, California, USA (site 1).

Type horizon: Albian (Lower Cretaceous) seep carbonates, Lodoga Formation, Great Valley Group.

Diagnosis.—As for genus.

Description.—Shell moderately high spired, fusiform to littoriniform, with at least three whorls and incised suture, apical angle 38°; whorls convex, sculptured by fine, equally sized spiral threads, interspaces slightly wider than threads; growth lines fine, sinuous, slightly prosocyrty in upper half of whorl, slightly opisthocyrt in lower half; basal margin strongly constricted with a prominent siphonal fold below, growth lines on fold very strongly opisthocyrt, suggestive of deep siphonal notch; aperture broadly oval.

Stratigraphic and geographic range.—Known only from the type locality, Lodoga Formation, Great Valley Group; Albian (Lower Cretaceous).

Species of uncertain affinity

“*Cerithium*” sp.

Fig. 9A.

1895 *Cerithium* sp.; Stanton 1895: 71.

Material.—The specimen described by Stanton (USNM 23081) from Cold Fork of Cottonwood Creek (site 1).

Description.—Two or three straight-sided whorls preserved, sculpture of nodular subsutural cord, another cord with two rows of tubercles near base; basal margin sharp, base flat, columellar and parietal lip of aperture smooth and strongly convex, suggestive of round aperture. Height 3.5 mm.

Discussion.—The described characters can be found in the Cretaceous campanilid *Metacerithium* (cf. Kiel 2006a) and in modern cerithiopsids (cf. Marshall 1978). The specimen is figured here because it was collected from presumed seep carbonates at Cold Fork of Cottonwood Creek (Stanton 1895) and because Stanton did not figure it.

Stratigraphic and geographic range.—Albian (Lower Cretaceous), seep carbonates at Cold Fork of Cottonwood Creek, Lodoga Formation, Great Valley Group, California, USA.

Fusiform gastropod

Fig. 9B.

Material.—One specimen from Rocky Creek (site 7).

Description.—Fusiform shell with two whorls preserved; suture incised, deep; whorls slightly convex, first whorl apparently smooth, on last whorl sinuous growth lines thickened to form sinuous, axial ribs; conspicuous ridge below suture that becomes tuberculate on last whorl where it is crossed by axial ribs; nine to ten spiral cords develop on lower third of last whorl, these cords are subequally spaced, interspaces as wide as cords, and with rounded crests; growth lines sinuous; opisthocyrt notch below suture, almost straight on whorl's flanks, gently sloping backwards on lower third of whorl. The shell is 9 mm high.

Discussion.—At first glance, this specimen resembles some neogastropods from the Upper Cretaceous Ripley Formation of the US Gulf Coast plains, especially *Ornopsis* or *Bellifusus* (see Sohl 1964). However, the basal part of the specimen is not preserved or visible, hence the presence of a siphon is uncertain. The specimen may actually have just a siphonal notch in its aperture like cerithioids or littorinids. It could also be a *Paskentana*.

Stratigraphic and geographic range.—Known only from the Rocky Creek site, Valanginian (Lower Cretaceous), Crack Canyon formation, Great Valley Group, California, USA.

High spired gastropod

Fig. 9C.

Material.—Two specimens from W Berryessa (site 11).

Description.—Two-and-a-half whorls preserved; shell slender, high spired, whorls convex, suture finely incised; last whorl with nine spiral ribs that frequently show short, forward-pointing, hollow spines, ribs with rounded crests and subequally spaced, with interspaces about one to two times the width of ribs; growth lines narrowly spaced and strongly opisthocyrt.

Remarks.—This type of spiral sculpture without any obvious axial elements is quite unusual for cerithiiform gastropods of

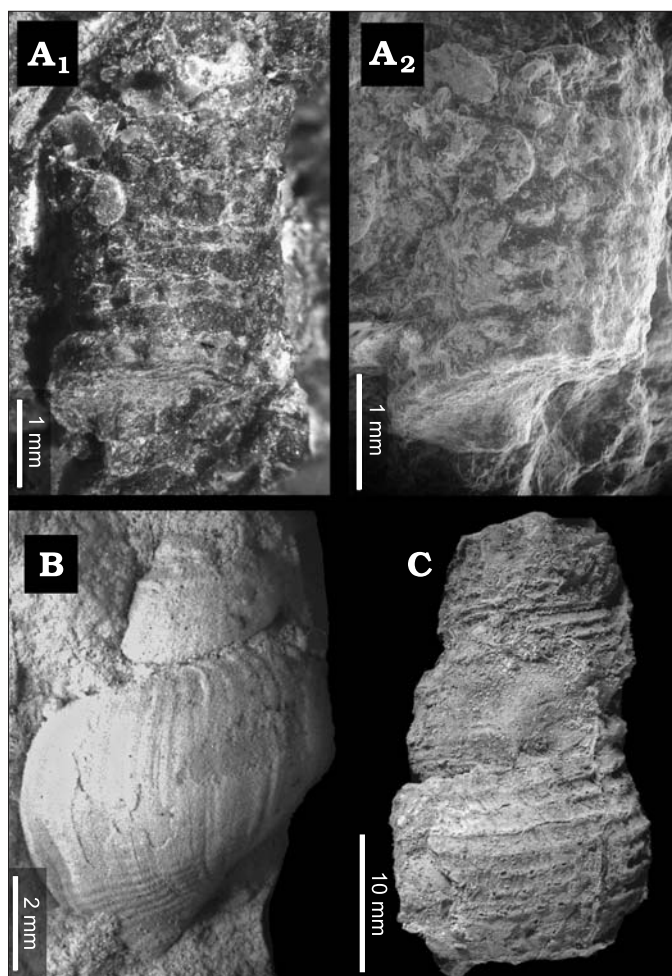


Fig. 9. Gastropods of uncertain affinities from Early Cretaceous seep carbonates in California, USA. **A.** Stanton's (1895) "*Cerithium*" sp. (USNM 23081) from Cold Fork of Cottonwood Creek (Albian; site 1), image taken with light microscope (**A₁**) and with SEM (specimen uncoated, **A₂**). **B.** Fusiform gastropod (CAS 70403) from Rocky Creek (Valanginian; site 7). **C.** High-spired gastropod (CAS 70404) from W Berryessa (probably Valanginian; site 11).

this age. The poor preservation precludes a more precise classification of this species.

Stratigraphic and geographic range.—Known only from the W Berryessa, Early Cretaceous (probably Valanginian), Great Valley Group, California, USA.

Discussion

Faunal composition.—The Californian Jurassic and Cretaceous seep fauna described herein consists of a mixed bag of species that belong to (i) a well-known and widely distributed genus of that age, (ii) a modern deep-water genus, and (iii) a number of probably seep-restricted groups.

(i) The well-known genus is the eucyclid *Amberleya*, which is widely distributed especially in Jurassic shallow-water sediments (Hudleston 1887–1896; Hickman and McLean 1990; Kaim et al. 2004).

(ii) The potential abyssochrysid *Abyssochrysos? giganteum* described herein is much larger than the extant members of this deep-sea genus. Most potential abyssochrysid seep sites in the geologic past were larger than their extant, non-seep relatives (Goedert and Kaler 1996; Gill et al. 2005; Kiel 2008), but the identity of all these taxa needs confirmation.

(iii) Among the taxa that appear restricted to the seep environment are the new genera *Bathypurpurinopsis* and *Paskentana*, the recently established *Hokkaidoconcha*, and the long-known genus *Atresius*. Despite the fact that *Atresius* was described more than 130 years ago, it has never been convincingly reported from localities other than the isolated “white limestones” in Morgan Valley of California.

Relationships to other fossil seep gastropods.—The only gastropod genus shared between the Californian seep fauna described here and the Late Cretaceous seep fauna of Japan is the abyssochrysid *Hokkaidoconcha* (Kaim et al. 2008). The small, globular vetigastropods that are common at Japanese sites (Hikida et al. 2003; Jenkins et al. 2007a, b) were not seen in the Californian sites. The hokkaidoconchids also provide links to younger seeps: Kaim et al. (2008) indicated that certain zygopleurids and abyssochrysid seeps might belong to the Hokkaidoconchidae. Two further Caribbean abyssochrysid seeps are *Hemisinus bituminifer* Cooke, 1919 and *Hemisinus costatus* Cooke, 1919 from a presumably Oligocene seep site on Cuba, which were recently re-allocated to *Abyssochrysos* (Cooke 1919; Kiel and Peckmann 2007). The large “*Abyssochrysos raii*” Goedert and Kaler, 1996 from middle Eocene seep sites in western Washington resembles in size and sculpture the Californian *Abyssochrysos? giganteum*, but the Washington species shows unique apertural features and the new genus *Humptulipsia* Kiel, 2008 has recently been established for it (Kiel 2008). Whereas Kiel (2008) considered it an abyssochrysid, Kaim et al. (2008) suggested that it might belong to the hokkaidoconchids.

The only genus that is potentially shared among the late Mesozoic Californian sites, the Paleogene seep sites in Washington State, and Recent seeps is the neomphalid *Retiskenea*. It is described from the late Mesozoic Californian sites in a separate paper (Campbell et al. 2008), and is known from Eocene–Oligocene sites in Washington and from Recent seeps off Oregon, the Aleutian trench, and Japan (Warén and Bouchet 2001; Sasaki et al. 2005; Kiel 2006b). The remainder of the taxa described herein appear to be restricted to late Mesozoic seeps in California. Although this fauna and the modern seep fauna share only a few taxa, they resemble each other in that both are a mixed bag of long-ranging taxa, deep-sea taxa, and seep-restricted taxa (cf. McArthur and Tunnicliffe 1998; Warén and Bouchet 2001). This finding supports the view that new taxa adapted continuously to the seep environment through earth history (Warén and Bouchet 2001; Kiel and Little 2006).

Evolutionary patterns among the Eucyclidae.—The two species assigned here to *Amberleya* do not fit into the tradi-

tional ecologic concept of *Amberleya* as being a shallow water inhabitant (Hickman and McLean 1990). In their revision of trochoidean systematics, Hickman and McLean (1990) separated the tribes Eucyclini and Calliotropini within the subfamily Eucyclinae mainly on ecologic grounds. Accordingly, eucyclinids (including *Amberleya*) occurred in warm shallow environments in the Mesozoic, whereas calliotropinids (including *Bathybembix*) occur in cool deep-water environments from the Eocene onwards. Among the shell characters cited to distinguish the two tribes were the thickness of the shell wall and an ontogenetic change in apertural characters. Kiel and Bandel (2001) and Kaim (2004) expressed doubts about the separation of these two tribes, and here we provide evidence that also the ecologic and temporal distinction of the two tribes could be an artifact resulting from the poor record of fossils from deep-marine environments. *Amberleya* and other eucyclinids are indeed well-represented in later Mesozoic shallow water sediments, but we show here that they also occurred in deep water. Furthermore, Kaim (2004) also showed that *Calliotropis*, the name-giving genus of the Calliotropini, occurred in Late Jurassic deep basinal sediments.

Hickman (1984) correlated the appearance and radiation of the Calliotropini in the Eocene with an abrupt cooling event 40 Million years ago. This was based on the sudden appearance of *Bathybembix* communities in Washington and Oregon. However, this “abrupt” appearance could well be an artifact resulting from the lack of Late Cretaceous to Paleocene deep-water sediments in the U.S. Pacific Northwest and the abrupt beginning of the uplift of deep-water sediments in the Eocene (Brandon and Calderwood 1990; Brandon and Vance 1992; Batt et al. 2001; Stewart and Brandon 2004). We believe that Eucyclini and Calliotropini represent a single clade, as suggested earlier (McLean 1981; McLean 1982; Kiel and Bandel 2001; Kaim 2004), and show that members of the Eucyclinae have been present in bathyal depth at least since the Late Jurassic. We propose that members of the Eucyclinae have repeatedly moved offshore during their evolutionary history.

Folding of thin-shelled individuals.—Some individual gastropod shells from the Mesozoic seep study collection were folded rather than crushed upon compaction, specifically *Bathypurpurinopsis stantoni* (Fig. 8J), *Atresius liratus*, and *Paskentana paskentaensis* (Fig. 10). The shells are quite thin (<1 mm, e.g., Fig. 3B). The bivalve *Pinna* has a high proportion of organic matter in its shell which makes it flexible (Coan et al. 2000: 199). Also some of the small modern vent- and seep-inhabiting gastropods have a high amount of organic matter in their shells (Kiel 2004). It may thus be speculated that the above mentioned thin shelled species also may have had flexible shells due to a high content of organic matter. However, neither their shell microstructure, nor its potential organic content are known. Some modern vent-related gastropods also possess thin shells, such as provannid *Alviniconcha hessleri* Okutani and Ohta, 1988, buccinid *Bayerius*

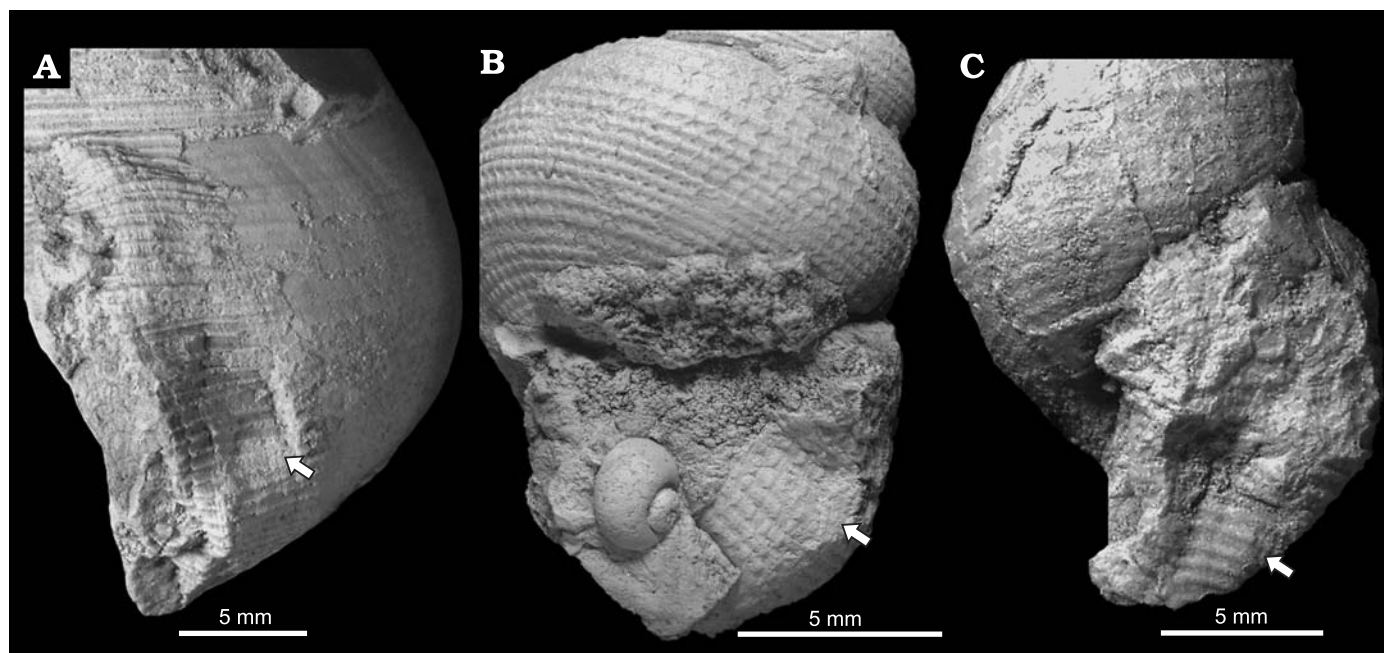


Fig. 10. Examples of “folded” rather than crushed shells. **A.** *Paskentana globosa* sp. nov. (CAS 70394) from Knoxville (Lower Cretaceous; site 9). **B.** *Paskentana paskentaensis* (Stanton, 1895) (UCMP 154113) from Rice Valley (Hauterivian?; site 3). **C.** *Atresius liratus* (CAS 70405) from Rocky Creek (Valanginian; site 7).

peruvianus Warén and Bouchet, 2001, and turrid *Bathybela papyracea* (Warén and Bouchet 1993, 2001). Whether thin shells in some species are an adaptation to the vent-seep environment or a deep-water characteristic of some groups is unknown.

Morphological plasticity.—Of the 14 gastropod species described in this study, two show a high degree of morphological variation. One of these, *Paskentana paskentaensis*, is a Mesozoic Californian seep endemic and also occurs at ten geographically widespread seep sites over a significant time span (Late Jurassic–Early Cretaceous). A similarly great morphologic and geographic variability also has been reported for some *Provanna* species, such as *Provanna antiqua* Squires 1995 in Upper Eocene to Upper Oligocene seep carbonates of western Washington, USA (Squires 1995), and *Provanna variabilis* Warén and Bouchet 1986 from vents and seeps of the northeast Pacific (Warén and Bouchet 1986, 1993, 2001). In *P. variabilis*, the range in morphological characters, including within individual specimens, does not seem to follow any obvious pattern (e.g., in relation to size; cf. Warén and Bouchet 1986). The wide geographic distribution of many living vent/seep provannids has been attributed to good dispersal capability (Warén and Bouchet 2001), a character not commonly attributed to taxa with lecithotrophic larvae such as these. The second morphologically plastic gastropod of this study, *Atresius liratus*, is also apparently a seep-endemic taxon from the Mesozoic of California, but seems to have been more geographically restricted (2 seep sites). It shows great variation in shell sculpture and apertural shape. The remaining fossil gastropod species described herein appear to have been more geo-

graphically restricted, a pattern typical of many modern vent and seep gastropods, which perhaps in some cases may be an artifact reflecting limited sampling among isolated sites (cf. Warén and Bouchet 1986, 1993, 2001).

Several modern mollusks from non-vent/seep settings also display morphological plasticity within populations and/or individuals, driven by environmental cues such as predation intensity, population density, wave climate, degree of exposure to desiccation, substrate type/orientation, and water temperature (e.g., Trussell 2000; Trussell and Smith 2000; Urabe 2000; Yeap et al. 2001). Evolutionary ecologists are interested in deciphering the relative roles of genetics vs. environmental influences on phenotypic plasticity, and how the phenomenon arises in the first place (Trussell 2000 and references therein). Some studies have inferred that wide dispersal of certain living and fossil mollusks with planktotrophic larvae may have caused genetic homogenization, while at the same time exposing species to different environmental pressures, ultimately inducing eco-phenotypic change (Parsons 1997; Parsons 1998; Crampton and Gale 2005).

It is difficult to assess larval feeding mode in the fossil gastropods of this study without protoconch details. As several of our taxa are from historical museum collections, new field studies are warranted to increase the potential to obtain more complete individuals and also to assess the paleogeographic extent of these fossil species. This information would allow a better evaluation of whether widespread dispersal might have enhanced morphological plasticity among taxa in this abundant and diverse suite of seep-related gastropods from the Mesozoic of California.

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Note added in proof

A species belonging to *Paskentana* has been described from an Hauterivian seep site on the Crimean peninsula (Kiel and Peckmann 2008). It closely resembles *P. paskentaensis* from California and shows that *Paskentana* had a wide geographic distribution during the Early Cretaceous.

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Appendix 1

Localities (stratigraphy and fossil content)

1. Cold Fork of Cottonwood Creek

Description.—USGS M2676, USGS M1070, LACMIP loc. 16818, UCMP 36215; Tehama County, California, USA. 20 km W Red Bluff. 1.6 km up Cold Fork of Cottonwood Creek from Pettyjohn ranch house, northeast of Stevenson Peak and due west of Wilcox Flat, section 29, T. 27 N., R. 7 W., U.S. Geological Survey, 15 minute, Colyear Springs Quadrangle. 260 m long lens along hillside (N36W/35NE), with concretions in mudstone in adjacent salt box hollow and to several tens of meters northwestward over top of hill.

Stratigraphy.—Lodoga Formation, Great Valley Group; Albian (Lower Cretaceous), based on the ammonite *Leconteites* cf. *deansi*.

Fauna.—Worm tubes (abundant, two sizes); Bivalvia: lucinids, *Aucellina* sp., “*Modiola*” *major*; Gastropoda: *Bathypurpurinopsis stantoni*, ?*Atresius liratus*, “*Cerithium* sp.” and patelliform gastropods of Stanton, 1895, *Retiskenea*? *kieli* Campbell, Peterson, and Alfaro, 2008; Cephalopoda: *Leconteites* cf. *deansi* (Stanton 1895; Jones and Bailey 1973; Campbell et al. 2008; herein).

2. Paskenta

Description.—USNM 23051, 23205, 23245, USGS M5515, 1096, LACMIP locs. 15912 and 15922, UCMP A-2930, 36213. Tehama County, California, USA, also known as “Keyserling’s gate” locality. 4.8 km northwest of Paskenta by Thomes Camp Road, on knoll between road and Digger Creek, southeast ¼ of section 25, T. 24 N., R. 7 W., U.S. Geological Survey, 7.5 minute, Paskenta Quadrangle. Two low-relief, light-gray carbonate lenses (to 3.5 m thick, 30 m long) separated by 2 oak trees (formerly marking Keyserling’s gate), striking parallel (N-S) to enclosing thin-bedded turbidites.

Stratigraphy.—Great Valley Group, turbidites of the lower middle portion of the Stony Creek Formation (cf. Ingersoll 1978; Bertucci 1983; Bertucci and Ingersoll 1983; Ingersoll 1983). Common *Buchia piochii* and rare *Buchia fischeriana* (reported as “*Aucella*” *piochii* and “*A.*” *piochii* var. *ovata* in Stanton, 1895), indicate Middle–Upper Tithonian (cf. Jones et al. 1969).

Fauna.—Worm tubes (moderately abundant, thin); Bivalvia: *Buchia piochii* and *Buchia fischeriana*, *Cardinopsis*, *Corbula*, “*Lucina*”, *Nucula*, and *Solemya*; Gastropoda: *Amberlaya dilleri*, *Hokkaidoconcha occidentalis*, *Paskentana paskentaensis*, patelliform gastropods; Cephalopoda: *Phylloceras knoxvillensis* and belemnite fragments; Brachiopoda: *Cooperhynchia schucherti* (common) (Stanton 1895; Sandy and Campbell 1994; herein).

3. Rice Valley

Description.—USGS M6010; “Fossil Rock”—M6395, M6396, M6986. Rice Valley, Lake County, California, USA. Small, isolated carbonates along the “walls” of Rice Valley. 1950’ N, 1600’ west of southeast corner of section 10, T. 17 N., R. 9 W., U.S. Geological Survey, 7.5 minute, Potato Hill Quadrangle.

Stratigraphy.—Great Valley Group; Lower Cretaceous, possibly Hauterivian (but see Campbell and Bottjer 1995) based on the occurrence of *Peregrinella whitneyi*.

Fauna.—Worm tubes (rare); Bivalvia: *Pecten complexicosta*, “*Modiola*” *major*; Gastropoda: *Paskentana paskentaensis*, *Retiskenea*? *tuberculata* Campbell, Peterson, and Alfaro, 2008; Brachiopoda: *Peregrinella whitneyi* (Berkland 1973; Campbell et al. 2008; herein).

4. Bear Creek

Description.—UCMP A-7308, D-2725, CAS loc. 1350, Colusa County, California, USA, ~170 m E of benchmark 1243, NW ¼ of NW ¼ of section 22, T14 N, R5 W, Wilbur Springs Quadrangle, 7.5’ series (1989 provisional edition, U.S. Geological Survey). Due E of Bear Valley Road, at the mouth of Hamilton Canyon, a W-draining tributary of the N-S-trending Bear Creek. The locality data herein update incorrect site details recorded in the University of California locality register for UCMP A-7308. Two specimens were examined from this fossil collection, which was made by a UCB geology class in the summer of 1951, in a steep E-W cliff situated on the N side of the tributary, at approximately 470 m elevation MSL. Fossil-rich carbonate float blocks also are abundant in the tributary at the base of the cliff. This locality was visited by KAC in 1996 and comprises in situ carbonate pods (0.1–1.5 m diameter) with nodular boundaries within thin-bedded siltstone turbidites.

Stratigraphy.—Great Valley Group, Grizzly Canyon member of Crack Canyon formation (cf. Lawton, 1956: 78; = unit 1C of Rich 1971). The buchiids are probably *B. crassicolis solida*, indicative of a Valanginian age (cf. Jones et al. 1969).

Fauna.—Serpulid worm tubes; Bivalvia: “*Modiola*” *major* some exceeding 15 cm in length, *Buchia crassicolis solida*?, solemyids and possibly arcoids; Gastropoda: *Lithomphalus enderlini*, *Paskentana paskentaensis*, fissurellid limpet; Scaphopoda: *Dentalium*? (collections of KAC and a UCB lot of fossils [UCMP D-2725] collected in 1942 by the geologist N.L. Taliaferro from the same location).

5. Wilbur Springs

Description.—USGS M7012, Colusa County, California, USA. On hill 1.5 km S/SE of Wilbur Hot Springs Resort, above Sulphur Creek, Lat 39° N, long. 122° W, 1000 ft. [304 m] north, 300 ft. [91 m] east of southwest corner of section 28, T. 14 N., R. 5 W., U.S. Geological Survey, 7.5 minute, Wilbur Springs Quadrangle. $\delta^{13}\text{C}$ values of fibrous cements and micrite from these carbonates range from -19.25 to -23.95‰ relative to PBD standard (Campbell and Bottjer 1995).

Stratigraphy.—Great Valley Group; Hauterivian (Lower Cretaceous, cf. Campbell and Bottjer 1995).

Fauna.—Scattered thin worm tubes; Bivalvia: “*Modiola*” *major*, *Solemya stantoni*, “*Lucina*” *colusaensis*, *Pecten complexicosta*; Gastropoda: *Paskentana paskentaensis*, *Retiskenea*? *tuberculata*; Brachiopoda: *Peregrinella whitneyi* (Stanton 1895; Campbell et al. 2008; herein).

6. Little Indian Valley

Description.—USGS M7183, UCMP 36214. Lake County, California, on jeep trail north of North Fork of Cache Creek, 400’ S, 900’ E of NE corner sec. 12 (in unsurveyed area), T. 14 N., R. 7 W., U.S. Geological Survey, 7.5 minute, Benmore Canyon Quadrangle. Map location #26 of McLaughlin et al. (1990), field number MG79-142, collected by Rob J. McLaughlin. Field notes (Bob J. McLaughlin, personal communication 1996) describe: “a fossiliferous ‘reef-like’ limestone concretion weathering out of gritty graywacke and slaty argillite, and associated with carbonate-cemented, tuffaceous basalt pod. Fossil assemblage includes abundant trochospiral ornamented gastropods...”

Stratigraphy.—Franciscan Complex; Lower Cretaceous (Valanginian?), based on possible occurrence of *Buchia keyserlingi*. Occurs in Little Indian Valley Terrane (McLaughlin and Ohlin 1984; McLaughlin et al. 1990).

Fauna.—Worm tubes?; Bivalvia: *Solemya*, large *Buchia* fragment, possibly *B. keyserlingi*; Gastropoda: *Amberleya dilleri*, *Paskentana paskentaensis*, *Paskentana globosa* (McLaughlin and Ohlin 1984; McLaughlin et al. 1990; herein).

7. Rocky Creek

Description.—USNM 23266, CAS loc. 69275, Morgan Valley, Lake County, California, USA, NE ¼ of SW ¼ of section 12, T. 12 N., R. 6 W., Wilson Valley Quadrangle, 7.5' series (1993 revised edition, U.S. Geological Survey). The site was originally referred to as isolated white carbonates "1 mile NW of Palmer's" ranch (Gabb 1869; Stanton 1895). Fossils were collected from carbonate boulders at a creek crossing on a small tributary to Rocky Creek, and from a carbonate outcrop ~100 m west of the creek crossing. See locality description in Kiel and Campbell (2005) for details.

Stratigraphy.—This area has been mapped as Valanginian (Lower Cretaceous) as part of the Blue Ridge member, comprising the lower member of the Crack Canyon formation (informal name of Lawton 1956), Great Valley Group. However, the extent and complexity of the bedding-plane faults in this area, with the resulting unconformities, was not fully appreciated in Lawton's time, and many of the age assignments are based on inferences that require further structural and stratigraphic evaluation (Dean A. Enderlin, personal communication, 2004). The *Aucella* (= *Buchia*) may be *B. pacifica*, or possibly *B. crassicolis* (Stanton, 1895: 58), either of which support a Valanginian age assignment (Jones et al. 1969).

Fauna.—Bivalvia: *Pecten complexicosta*, *Astarte trapezoidealis*, and "Aucellas which are more inflated than *Aucella piochii* but not as large as *Aucella crassicolis*" (Lawton 1956: 87), on-going research suggests that the scallop may be seep-related, owing to its widespread distribution solely in other Mesozoic seep carbonates of California (KAC, unpublished data); Gastropoda: *Atresius liratus*, *Amberleya morganensis*, *Lithomphalus enderlini* (Stanton 1895; Lawton 1956; Kiel and Campbell 2005).

8. Foley Canyon

Description.—CAS loc. 69393. Foley Canyon in Morgan Valley, E of Knoxville, Napa County, California, USA. Quarried carbonate, with float blocks scattered in ravine to the SW. Site is in N half of the SE ¼ of Sec. 5, T. 11 N., R. 4 W., Mount Diablo Base and Meridian. Two parallel lenses of fault-bounded carbonate lie near or in a lens of detrital serpentine that extends southeastward along strike from the larger serpentinite body at Little Blue Ridge (Dean A. Enderlin, personal communication 2007).

Stratigraphy.—Eastern lens is bounded on both sides by Crack Canyon Formation, Great Valley Group; Valanginian–Hauterivian (Lower Cretaceous, cf. Lawton 1956), age based on associated inflated *Buchia*).

Fauna.—Bivalvia: "*Modiola*" *major*, inflated *Buchia*, *Pecten complexicosta*; Gastropoda: *Paskentana paskentaensis*; Brachiopoda: *Peregrinella whitneyi*.

9. Knoxville

Description.—CAS loc. 6778.01; originally designated CAS 14549. No detailed information available. Gastropods are preserved in carbonate rock typical of other "white limestones" in this study. Specimen card reads: "three miles east of Morgan Valley, on the

road to Knoxville, Napa County, California." Collector: California State Mining Bureau, May 21, 1895. Dean A. Enderlin (personal communication 2007) noted "there was once a county road that connected Reiff Road and Knoxville [township now deserted] through [Morgan] valley that is now Davis Creek Reservoir. The road was abandoned in the mid-20th Century by the counties, but it still exists as a ranch road through the McLaughlin Reserve." We postulate that this site could possibly be the Foley Canyon seep deposit, although *Paskentana globosa* has not been found in more recent collections there. It is more likely that the material represents another seep carbonate, perhaps a small outcrop or one now submerged beneath the reservoir.

Stratigraphy.—Great Valley Group; probably Lower Cretaceous.

Fauna.—Gastropoda: *Paskentana globosa*.

10. NW Berryessa

Description.—UCMP A-4312, A-4489, A-4500. NW Berryessa, also known as "Christensen's Ranch". Center of Sec. 27, T. 9 N., R. 4 W., Walter Springs 7.5 min quadrangle, Napa County, California, USA. 38°41' N, 122°17' 20" W. Locality data from Paleo 103 class (UCB), 1947 describes an "impure limestone just past the gate into Mr. Christianson's property on the southwest side of the road." Angel (1947: 18) reported that interbedded with shales of the upper Knoxville beds are "many lenses and nodules of impure limestone, which weather to a dirty white and on a fresh surface are grey-black. These lenses range from six inches to a foot in thickness, and several fossiliferous horizons were found."

Stratigraphy.—Great Valley Group; probably Tithonian (Upper Jurassic) based on presence of *Buchia* aff. *piochii* (Angel 1947; Angel and Conrey 1947).

Fauna.—Bivalvia: "*Lucina*" *ovalis*, *Buchia* aff. *piochii*; *Tivela*?; Gastropoda: *Amberleya* cf. *dilleri*, *Hokkaidoconcha occidentalis*, *Paskentana paskentaensis*, *Paskentana berryessaensis*, *Fissurella*?; Cephalopoda: belemnite phragmocone; Brachiopoda: a species closely similar to *Cooperrhynchia schucherti* (Stanton 1895; Angel 1947; Angel and Conrey 1947; Klosterman et al. 2001; herein).

11. West Berryessa

Description.—CAS locs. 1351, 28493, 33529. W Berryessa, Napa County, California, USA. CAS 1351 only gives generalized locality data as: "West border of Berryessa Valley, 3 miles west of Monticello. Frank M. Anderson collector, 1928." A visit to the area by KAC in 1996 did not turn up the outcrop, but boulders of white, strongly recrystallized carbonate bearing very large "*Modiola*" *major* (to 25 cm long) were found bordering a road at Oak Shores regional park (Lake Berryessa 7.5 minute quadrangle, revised 1993 edition). CAS 28493 noted gastropods and pelecypods from "limestone outcrops located approximately near center NE ¼ sec. 7, T. 8 N., R. 3 W. of St. Helena 15 minute quadrangle (1945 edition). Local residents suggested to KAC that the carbonate "reef" is situated just offshore in present-day Lake Berryessa, with a hazards buoy posted on it to warn boaters of shallowly submerged rocks. Pieces of the outcrop were bulldozed during park construction and now line the roadside.

Stratigraphy.—Great Valley Group; probably Valanginian (Lower Cretaceous) based on inflated buchiids in CAS collections. However, C.F. Tolman of Stanford University sent samples to J.P. Smith in 1923, who mentioned *Aucella* [= *Buchia*] *piochii* in early collections (recounted in Griffiths 1970). Other taxa noted in a historical account of private collections (but not verified) include: *Phylloceras*, *Ammonite* [sic!] *crioceras*, *Belemnites tehamaeveris*, *Molioluss* [sic!] *ma-*

for, and *Turbo passquentaensis* [sic!] (Griffiths 1970). Smith (as relayed by a copy of a letter to the local Griffiths family by Tolman dated October 3, 1923) conveyed that this collection indicates that the fossils “belong to the Lower Knoxville formation, probably the lowest horizon of the Knoxville of which we have any knowledge” (Griffiths 1970: 3).

Fauna.—Worm tubes; Bivalvia: “*Modiola*” *major*, *Astarte trapezoidalis*, *Buchia* cf. *crassicolis solida*(?); Gastropoda: *Paskentana paskentaensis*.

12. East Berryessa

Description.—UCMP A-7281, A-7280. E Berryessa, Napa County, California, USA, Lake Berryessa 7.5 minute quadrangle (1959 edition). Both localities contain the same fauna and were collected by UC Berkeley students (Geology 118) in Summer 1951. Locality details for A-7280 are: 6094 ft. [1857 m] N. 88.0° E of B.M. 310 which is located at State Highway Bridge over Putah Creek about 1 1/3 miles [2 km] S. of Monticello. Elevation approximately 410 ft. [125 m] “Large pelecypods and gastropods from recrystallized, light gray carbonate reef with maximum thickness of about 500 ft. [152 m]. Dip appears to be about 15–25° towards W.” Locality A-7281 was collected from the same carbonate, south along strike, at an elevation of approximately 390 ft. [118 m]. The carbonate is currently underwater in Lake Berryessa, and the bridge and town of Monticello also were submerged to make way for the dam project.

Stratigraphy.—Great Valley Group; possibly Lower Cretaceous.

Fauna.—Bivalvia: large “*Modiola*” *major*; Gastropoda: *Paskentana paskentaensis*, *Abyssochrysis*? *giganteum*.

13. Romero Creek

Description.—USGS M6991, M8766. Romero Creek, Merced County, California, USA. Near San Luis Dam, East Diablo Range. North side of mouth of Romero Creek at south end of small point, about 244 m east of center of section 26, T. 9 S., R. 8 E., U.S. Geological Survey, 7.5 minute, San Luis Dam Quadrangle; Most recent collection by Elder and Miller (1993), map no. 160, M8766: On slope 200 m W of California Aqueduct, 400 m N of Romero Creek SW center of NE ¼ of section 26, T. 9 S., R. 8 E.

Stratigraphy.—Near base of Mustang Shale member, Moreno Formation, Great Valley Group; Upper Campanian (Upper Cretaceous).

Fauna.—Bivalvia: *Idonearca*?, *Thyasira cretacea*, large solemyid, heterodonts indet., inoceramid indet.; Gastropoda: *Hokkaidoconcha morenoensis* sp. nov.; Cephalopoda: *Metaplacenticeras* cf. *pacificum*, tetragonitid ammonite (Elder and Miller 1993; herein).

14. Moreno Gulch

Description.—LACMIP loc. 10912. Two carbonate localities in Moreno Gulch, Panoche Valley 15 minute quadrangle, Fresno County, California, USA. 10912: In small depression just SW of ridge saddle, approximately 600 ft. [183 m] N, 1450' E of SW corner of sec. 9, T. 14 S., R. 11 E. Gully leading west from a branch of Moreno Gulch, 350' S, 2000' E of NW corner of sec. 16, T. 14 S., R. 11 E.

Stratigraphy.—Santonian (Late Cretaceous).

Fauna.—Bivalvia: *Anomia*; Gastropoda: *Hokkaidoconcha occidentalis*; Cephalopoda: *Baculites capensis*.

15. Gravelly Flat

Description.—Gravelly Flat in Priest Valley, Coalinga Springs, Fresno County, California, USA. Formerly (1940s–60s) a Stanford University undergraduate geology mapping area. Less than 2 miles W-SW of Coalinga Mineral Springs, in the Priest Valley 15 minute quadrangle (1944 edition). Site not yet specifically relocated.

Stratigraphy.—Upper part of Gravelly Flat Formation (~300 m below top of formation), Great Valley Group; Lower Cretaceous.

Fauna.—Bivalvia: *Buchia crassicolis*, “*Modiola*” *major*; Gastropoda: *Paskentana paskentaensis*; Brachiopoda: *Peregrinella whitneyi* (Rose and Colburn 1963).

16. Charlie Valley

Description.—USGS 24662, LACMIP loc. 5952; also locality #1 of Easton and Imlay (1955: 2339). Franciscan carbonate boulder on a shale slope 5 feet below top of small knoll, 200' E and 150' N of SW corner of sec. 36, T. 12 N., R. 32 W. Chimney Canyon 7.5 minute quadrangle (1967 edition), San Luis Obispo County, California, USA. Easton and Imlay (1955) noted the affinity of this fossil assemblage to Stanton's (1895) Paskenta locality.

Stratigraphy.—Franciscan Group; Tithonian (Upper Jurassic).

Fauna.—Bivalvia: *Nucula gabbi*, *Solemya stantoni*, *Buchia piochii*, “*Lucina*” cf. *colusaensis*, *Cardiniopsis* cf. *unioides*, *Arcomya*?, mytilid?; Gastropoda: *Amberleya*? *dilleri*; Cephalopoda: *Aulacosphinctes*?