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Authors: Jenkins, Robert G., Kaim, Andrzej, Little, Crispin T.S., Iba, Yasuhiro, Tanabe, Kazushige, et al.

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Worldwide distribution of the modiomorphid bivalve genus *Caspiconcha* in late Mesozoic hydrocarbon seeps

ROBERT G. JENKINS, ANDRZEJ KAIM, CRISPIN T.S. LITTLE, YASUHIRO IBA, KAZUSHIGE TANABE, and KATHLEEN A. CAMPBELL



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Exceptionally well preserved specimens of the bivalve mollusc *Modiola major* were collected from a Lower Cretaceous (Barremian) hydrocarbon seep deposit in northern California. This material, together with the type series of *M. major*, and various other specimens from Upper Jurassic to Lower Cretaceous seep localities in California, is redescribed and referred to the hydrocarbon seep-restricted modiomorphid genus *Caspiconcha*. We include also a description of *Myoconcha americana* because some previous reports have incorrectly synonymized *Myoconcha americana* with *Caspiconcha major*. In addition, we report *Caspiconcha* sp. from a Lower Cretaceous (Albian) hydrocarbon seep from Hokkaido, Japan, and we review all currently described species of *Caspiconcha*, and other species that probably belong to this genus. We demonstrate that *Caspiconcha* had a widespread distribution in Late Jurassic to Early Cretaceous hydrocarbon seeps, but became rare thereafter, with the last representative occurring in Upper Cretaceous strata of Japan. This macroevolutionary pattern is similar to that observed in the seep-restricted brachiopods. After the decline of *Caspiconcha* at the end of the Early Cretaceous and its last occurrence in the Campanian, the ecological niche of epifaunal to semi-infaunal seep endemic bivalves was largely vacant and not reoccupied until the Eocene with the appearance of the vesicomyid and bathymodiolin bivalves. The formal placement of *M. major* into the genus *Caspiconcha* restricts the fossil record of mytilids at seeps to post-Mesozoic times, and thus there is less discrepancy between the fossil record of chemosynthetic mytilids and their divergence age estimates from molecular data.

Key words: Bivalvia, Modiomorphidae, Kalenteridae, chemosynthesis-based ecosystem, cold seeps, Mesozoic, California, Japan.

Robert G. Jenkins [robertgj@staff.kanazawa-u.ac.jp], School of Natural System, College of Science and Engineering, Kanazawa University, 920-1192, Japan;
Andrzej Kaim [kaim@twarda.pan.pl], Institute of Paleobiology, Polish Academy of Sciences, PL-00-818 Warszawa, ul. Twarda 51/55, Poland and Bayerische Staatssammlung für Paläontologie und Geologie, 80333 München, Germany;
Crispin T. S. Little [C.T.S.Little@earth.leeds.ac.uk], School of Earth and Environment, University of Leeds, Leeds LS2 9JT, United Kingdom;
Yasuhiro Iba [iba@mail.sci.hokudai.ac.jp], Department of Natural History Sciences, Hokkaido University, Sapporo 060-0810, Japan;
Kazushige Tanabe [tanabe@um.u-tokyo.ac.jp], University Museum, University of Tokyo, Tokyo 113-0033, Japan;
Kathleen A. Campbell [ka.campbell@auckland.ac.nz], School of Environment, The University of Auckland, Auckland 1142, New Zealand.

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Introduction

Bivalve and gastropod molluscs are both abundant and diverse in marine chemosynthesis-based ecosystems (hydrocarbon seeps, hydrothermal vents, sunken wood, and vertebrate bones), and a number of dominant species possess symbiotic bacteria that obtain energy from the oxidation of hydrogen sulphide and/or methane. These chemosynthetic environments are also characterized by a high level of endemism in the bivalves and gastropods, with many taxa not known from more typical marine environments. The fossil record of molluscs from chemosynthetic environments has been traced back to the Silurian (Little et al. 1997; Campbell 2006), but the abundance and diversity of bivalves and gastropods in chemosynthesis-based communities increased significantly during the Jurassic and Cretaceous (Campbell and Bottjer 1995a; Little and Vrijenhoek 2003; Kiel 2010). The earliest occurrences of many modern seep- and vent-restricted bivalve and gastro-

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pod genera was in the late Mesozoic (Little and Vrijenhoek 2003; Campbell 2006; Kiel and Little 2006; Kaim et al. 2008a, 2009; Kiel 2010), a pattern also seen in sunken wood and vertebrate bone environments (Kaim et al. 2008b, 2011; Kiel et al. 2009). Although Upper Cretaceous chemosynthesis-based communities have been relatively well studied recently (e.g., Amano et al. 2007; Jenkins et al. 2007a, b, 2008; Kaim et al. 2008a, b, 2009, 2010; Kiel et al. 2008b), their Jurassic to Lower Cretaceous counterparts remain less well known (e.g., Sandy and Campbell 1994; Kiel and Campbell 2005; Campbell et al. 2008; Kiel et al. 2008a, 2010; Hammer et al. 2011; Kaim 2011). A better knowledge of fossil seep communities from this time period is therefore important in order to elucidate the pattern of bivalve and gastropod migration into this unusual environment.

Of particular importance in the ecology of Cenozoic hydrocarbon seeps are the large bivalves that host symbiotic bacteria in their gills belonging to the family Vesicomyidae (e.g., *Calyptogena*) and the mytilid subfamily Bathymodiolinae (e.g., *Bathymodiolus*), both of which appeared in the Eocene (Kiel and Little 2006; Amano and Kiel 2007). It is likely that during the Late Jurassic to Early Cretaceous their place was occupied ecologically by species of the extinct modiomorphid bivalve genus *Caspiconcha*, although it is not known if this bivalve possessed chemosymbionts. The type species of *Caspiconcha* (*C. whithami*) was first described from seep carbonates of East Greenland (Kelly et al. 2000) and another species (*C. rubani*) was subsequently proposed based on material from the Ukraine (Kiel and Peckmann 2008; Kiel et al. 2010). Kiel and Peckmann (2008) and Kiel et al. (2010) suggested that the large modioliform bivalve *Modiola major* Gabb 1869, widely distributed in Upper Jurassic to Lower Cretaceous hydrocarbon seeps in California, USA (Campbell et al. 1993), may also belong to *Caspiconcha*. Furthermore, Kiel et al. (2010) used the name *Caspiconcha major* for the species, although without proper systematic treatment. Due to poor preservation of the type series of *M. major*, up until now it has proved difficult to establish whether this species indeed belongs to *Caspiconcha* (or to the genus *Myoconcha*, as suggested in 1930 by Stewart). In 2005 and 2006 we collected new specimens of a *Caspiconcha*-like bivalve from the Eagle Creek seep locality of California (Fig. 1), two of which were extraordinarily well-preserved, including having original shell mineralogy. We compared this new material with Gabb's (1869) original type material of *M. major*, historical specimens of the species from Stanton (1895), and several other newly collected *M. major*-like specimens from various Californian seep sites, including the type locality (Table 1). This work allowed us to conclude that the Eagle Creek specimens are conspecific with *M. major*, and moreover that *M. major* is indeed a species of *Caspiconcha*. We use the new material to emend the diagnosis of *Caspiconcha major* (Gabb, 1869) herein. We also checked the type material of *Myoconcha americana* Stanton, 1895, which was considered as a juvenile specimen of *Caspiconcha major* by Stewart (1930: 104) and Kiel et al. (2010: 37), but conclude herein that this is a separate species which probably does not belong to *Caspiconcha*. We also report a new occurrence of *Caspiconcha* from a Lower Cretaceous (Albian) seep deposit from Hokkaido, Japan. These data show that *Caspiconcha* had a wide geographical distribution in seeps in the late Mesozoic, particularly during the Early Cretaceous, and was thus an important faunal element within these communities.

Institutional abbreviations.—BSPG, Bayerische Staatsammlung für Paläontologie und Geologie, München, Germany; CAS, California Academy of Sciences, San Francisco, USA; MCZ, Museum of Comparative Zoology at Harvard University, Cambridge, USA; NMNS, National Museum of Nature and Science, Tokyo, Japan; SMUC, Sedgwick Museum, University of Cambridge, Cambridge, UK; UCMP, Museum of Paleontology, University of California, Berkeley, USA; USGS, United States Geological Survey, Reston, USA; USNM, National Museum of Natural History in the Smithsonian Institution, Washington, USA; YNU, Yokohama National University, Yokohama, Japan; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Material and methods

The material described in this paper comes from a number of Upper Jurassic to Lower Cretaceous hydrocarbon seep deposits in California and Hokkaido (Fig. 1, Table 1). Newly collected specimens from California and Hokkaido were first prepared in the laboratory by means of mechanical preparation and some were then cast using silicone rubber. The resulting specimens were photographed either by the authors or in the photo-labs of BSPG and ZPAL. The shell microstructure of the Eagle Creek specimen (CAS 72527-9) was observed using a Phillips XL20 SEM at ZPAL. XRD analysis on the same specimen was performed at the YNU using Rigaku Rint 2500 equipment. In addition to the specimens listed in Table 1 we examined the type specimens of *Caspiconcha whithami* Kelly, 2000, which are now stored at the SMUC. All figured specimens are stored at the MCZ, CAS, USNM, UCMP, NMNS or SMUC.

Two of the localities with newly discovered specimens of *Caspiconcha*, at Eagle Creek, California, and at Utagoesawa Creek, Hokkaido, are still pending detailed description that will be published elsewhere. However, in Appendix 1 we provide preliminary information about these sites pertinent to our study.

Systematic palaeontology

Class Bivalvia Linnaeus, 1758

Subclass Autobranchia Grobben, 1894

Superorder Heteroconchia Gray, 1854

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Table 1. List of figured *Caspiconcha* and *Myoconcha* specimens treated in this paper.

Register number	Species	Locality	References	Remarks	Figure no.
MCZ 10539	*Caspiconcha major* (Gabb, 1869)	East of Knoxville	Gabb 1869; Stewart 1930	lectotype	Fig. 5
MCZ 108540	*Caspiconcha major* (Gabb, 1869)	East of Knoxville	Gabb 1869	paralectotype	Fig. 6A
MCZ 108538A	*Caspiconcha major* (Gabb, 1869)	Wilbur Springs	Gabb 1869	paralectotype	Fig. 6B
MCZ 108538B	*Caspiconcha major* (Gabb, 1869)	Wilbur Springs	Gabb 1869	paralectotype	Fig. 6C
MCZ 108538C	*Caspiconcha major* (Gabb, 1869)	Wilbur Springs	Gabb 1869	paralectotype	Fig. 6D
USNM 23041	*Caspiconcha major* (Gabb, 1869)	Cold Fork of Cottonwood Creek	Stanton 1885		Fig. 7
CAS 72527-9	*Caspiconcha major* (Gabb, 1869)	Eagle Creek	this paper		Fig. 3
CAS 72530	*Caspiconcha major* (Gabb, 1869)	Eagle Creek	this paper		Fig. 8A
CAS 72531.1	*Caspiconcha major* (Gabb, 1869)	Eagle Creek	this paper		Fig. 8B
CAS 72531.2	*Caspiconcha major* (Gabb, 1869)	Eagle Creek	this paper	counter part of CAS 72531.1	listed
UCMP 10225	*Caspiconcha major* (Gabb, 1869)	Cold Fork of Cottonwood Creek	this paper		Figs. 9A, 10E
UCMP 10226	*Caspiconcha major* (Gabb, 1869)	Cold Fork of Cottonwood Creek	this paper		Fig. 10B
UCMP 152077	*Caspiconcha major* (Gabb, 1869)	Cold Fork of Cottonwood Creek	this paper		Fig. 9B
CAS 72532	*Caspiconcha major* (Gabb, 1869)	Cold Fork of Cottonwood Creek	this paper		listed
CAS 72533	*Caspiconcha major* (Gabb, 1869)	Cold Fork of Cottonwood Creek	this paper		listed
CAS 72534	*Caspiconcha major* (Gabb, 1869)	Bear Creek	this paper		Fig. 9J
CAS 72535	*Caspiconcha major* (Gabb, 1869)	Lake Berryessa	this paper		Fig. 10A
CAS 72548	*Caspiconcha major* (Gabb, 1869)	Lake Berryessa	this paper		Fig. 9H
CAS 72536	*Caspiconcha major* (Gabb, 1869)	East of Berryessa	this paper		Figs. 9I, 10D
CAS 71880	*Caspiconcha major* (Gabb, 1869)	Wilbur Springs	this paper		Fig. 9C
CAS 71882	*Caspiconcha major* (Gabb, 1869)	Wilbur Springs	this paper		Fig. 9D
CAS 71881	*Caspiconcha major* (Gabb, 1869)	Wilbur Springs	this paper		Fig. 9E
CAS 72537	*Caspiconcha major* (Gabb, 1869)	Wilbur Springs	this paper		Figs. 9G, 10C
CAS 71883	*Caspiconcha major* (Gabb, 1869)	Wilbur Springs	this paper		Fig. 9F
NMNS PM25523	*Caspiconcha* sp.	Utagoesawa Creek	this paper		Fig. 11A
NMNS PM25524	*Caspiconcha* sp.	Utagoesawa Creek	this paper		Fig. 11B
NMNS PM25525	*Caspiconcha* sp.	Utagoesawa Creek	this paper		Fig. 11C
USNM 23042	*Myoconcha americana* Stanton, 1895	Cold Fork of Cottonwood Creek	Stanton 1885; Kiel et al. 2010		Fig. 12

Order Modiomorphoida Newell, 1969

Remarks.—The order Modiomorphoida was originally proposed by Newell (1969) for extinct Paleozoic marine bivalves. The group was treated thereafter under the Pholadomyoida (e.g., Fang and Morris 1997; Kelly et al. 2000, Griffin and Pastorino 2006) or Carditoida (e.g., Chavan 1954, 1969; Newell 1957; Nevesskaja 2009). Bouchet et al. (2010) placed the superfamily Modiomorphoidea under "order uncertain", but following Bailey (1983) we here place the superfamilies Modiomorphoidea and Kalenteroidea in the order Modiomorphoida, pending further investigations. As here considered, the order Modiomorphoida was diverse in the Paleozoic, but decreased in importance through the Mesozoic, with the last representatives reported from the Neogene (Kelly et al. 2000; Griffin and Pastorino 2006).

Superfamily Kalenteroidea Marwick, 1953

Family Kalenteridae Marwick, 1953

Remarks.—Originally classified as a modiomorphid bivalve in the subfamily Myoconchinae (Kelly et al. 2000), *Caspiconcha* indeed shares many features with *Myoconcha*, including the deeply set anterior adductor muscle scars with myophoric buttress, modioliform shape, and extreme reduction of the shell anterior (Fig. 2). Therefore, following Kelly et al. (2000), we place *Caspiconcha* into the family Kalenteridae (an older synonym of Myoconchidae; see e.g., Bouchet et al. 2010). We also compare *Caspiconcha* to *Myoconcha americana* because of previous incorrect placements of the latter species within the former genus (Stewart 1930; Kiel et al. 2010).

Genus *Caspiconcha* Kelly in Kelly et al., 2000

Type species: *Caspiconcha whithami* Kelly in Kelly et al., 2000; Upper Barremian (Lower Cretaceous), NE Greenland.

Emended diagnosis.—Shell subtrapezoidal to cuneiform, or even modioliform in shape with extreme reduction of its anterior margin; triangular depression running from the umbonal area widening towards the mid flank; umbones located anteriorly but not reaching the anterior end; exterior ornament smooth apart from commarginal growth lines; edentulous hinge structure; anterior adductor muscle scar deeply set

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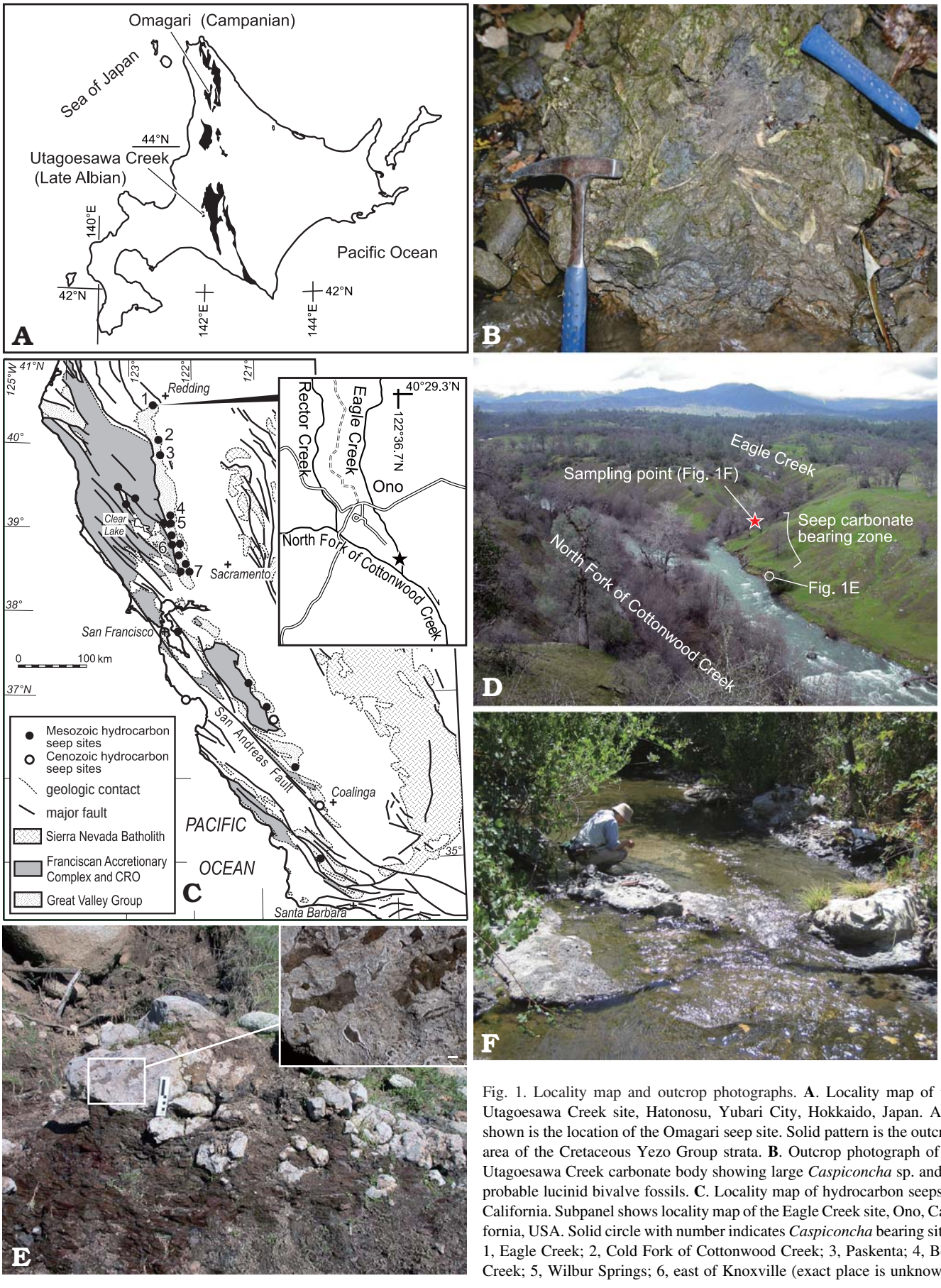


Fig. 1. Locality map and outcrop photographs. **A**. Locality map of the Utagoesawa Creek site, Hatonosu, Yubari City, Hokkaido, Japan. Also shown is the location of the Omagari seep site. Solid pattern is the outcrop area of the Cretaceous Yezo Group strata. **B**. Outcrop photograph of an Utagoesawa Creek carbonate body showing large *Caspiconcha* sp. and/or probable lucinid bivalve fossils. **C**. Locality map of hydrocarbon seeps in California. Subpanel shows locality map of the Eagle Creek site, Ono, California, USA. Solid circle with number indicates *Caspiconcha* bearing sites. 1, Eagle Creek; 2, Cold Fork of Cottonwood Creek; 3, Paskenta; 4, Bear Creek; 5, Wilbur Springs; 6, east of Knoxville (exact place is unknown); →

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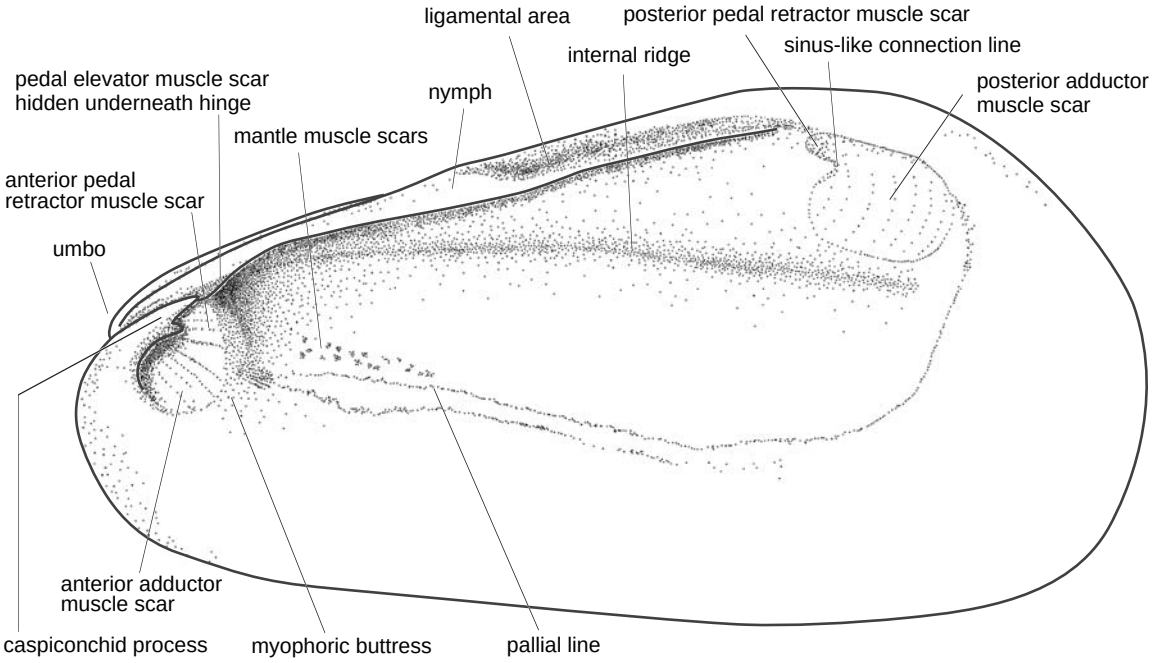


Fig. 2. Schematic illustration of the right valve internal features of *Caspiconcha major* (Gabb, 1869).

within myophoric buttress; caspiconchid process present, partially covering anterior adductor muscle scar; entire shell aragonitic.

Species included.—*Caspiconcha whitmani* Kelly, 2000 from the Barremian of Greenland (Kelly et al. 2000), *C. rubani* Kiel, Campbell, and Gaillard, 2010 from the Hauterivian of the Crimean Peninsula, Ukraine (Kiel and Peckmann 2008; Kiel et al. 2010), and *C. major* (Gabb, 1869) of northern California. These Californian localities largely constitute seep carbonates within the *Buchia* bivalve-bearing mudstone of the "Knoxville Beds", lower Great Valley Group, which is Late Jurassic to Early Cretaceous in age. They include Tithonian (Paskenta), Valanginian (Bear Creek), Hauterivian (Wilbur Springs), Albian (Cold Fork of Cottonwood Creek), and some poorly dated, probably Lower Cretaceous, sites (East of Knoxville, East Berryessa) (Gabb 1869; Stanton 1895; Sandy and Campbell 1994; Kiel et al. 2008a). In addition, the newly recognized Barremian (Eagle Creek) seep deposit near Ono, northern California, also contains *C. major*, many lucinid bivalves, but no buchiids.

We also include in *Caspiconcha* a probable new species, reported below, from the Albian Utagoesawa Creek, Yubari area, central Hokkaido, and a single specimen that is probably a different species from the Campanian Omagari seep, northern Hokkaido. *Myoconcha* aff. *transatlantica* (Ascher 1906) from Lower Cretaceous (Hauterivian) strata of the Czech Carpathians could also be a *Caspiconcha* species, and Kelly et al. (2000) suggested that an undescribed bivalve from the Cretaceous of New Zealand also might be related to *Caspiconcha* (Kelly et al. 2000). The age of the latter is Late Albian to mid-Cenomanian (Kiel et al. in press). *Caspiconcha* sp. has been also reported recently from the Late Albian Ispaster seep carbonates in northern Spain (Agirrezabala et al. in press). All occurrences listed above are from confirmed or likely hydrocarbon seep deposits, apart from Ascher's (1906) locality, which seems to be no longer accessible (Vašíček and Skupien 2004). *Caspiconcha* and *Caspiconcha*-like species are listed in Table 2.

Remarks.—*Caspiconcha* shares a number of characters with *Myoconcha* (see above), but lacks the external radial ornament of that genus and, unlike it, possesses an edentulous hinge. The shell of the type species (*C. whithami* Kelly, 2000) was interpreted by Kelly et al. (2000) to be composed of aragonite. We can confirm this feature for the genus in specimens of *C. major* (Gabb, 1869) from the Eagle Creek locality. Kelly (in Kelly et al. 2000: 242) suggested that the original inner shell layer of *C. whithami* was nacreous, although in all Greenland specimens the original shell had been entirely replaced by silica. The Eagle Creek *C. major* specimens (Fig. 3) clearly show that in this species the shell layers are not nacreous, but have cross-lamellar and homogenous microstructures (Fig. 4). According to Morris et al. (1991: 273), the shell of *Myoconcha* is composed entirely of homogeneous structure, although Carter (1990: 271) argued that further SEM observations are necessary to fully clarify the microstructural composition of *Myoconcha* shells. The differing shell microstructure of *Myoconcha* and *Caspicon-*

7, East Berryessa. CRO: Coast Range Ophiolite. The map is modified from Kiel et al. (2008a). **D**. Overview photograph of the Eagle Creek site. The hydrocarbon-seep carbonates crop out near the junction between Eagle Creek and North Fork of Cottonwood Creek. **E**. Photograph of typical seep carbonate bodies at the Eagle Creek site. Right-top inset shows detail of carbonate cements with stromatolite-like laminae. **F**. Photograph of strata at the Eagle Creek locality yielding *Caspiconcha* specimens.

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Table 2. Species list of *Caspiconcha* and *Caspiconcha*-like bivalves with locality information.

Locality	Area	Age	Stratigraphic unit	Species	Reference
Capas con *Pecten bodenbenderi*, Neuquén	Argentina	Early Jurassic	Piedra Pintada Formation	*Myoconcha neuquena*, *Myoconcha neuquena* var. *torulosa*	Leanza 1940; Griffin and Pastorino 2006
Paskenta	Tehama County, California, USA	Tithonian, Late Jurassic	Stony Creek Formation, Great Valley Group	*Caspiconcha major*	Campbell and Bottjer 1993a; Kiel et al. 2008
Bear Creek	Colusa County, California, USA	Valanginian, Early Cretaceous	Grizzly Canyon Member, Crack Canyon Formation, Great Vally Group	*Caspiconcha major*	Kiel and Campbell 2005; Kiel et al. 2008; this paper
Lake Berryessa	Napa County, California, USA	probably Valanginian?, Early Cretaceous	Great Valley Group	*Caspiconcha major*	Kiel et al. 2008a; this paper
Koniakauer Schloss (Hradiště)	Carpathians, Czech Republic	Hauterivian, Early Cretaceous	Tesin-Hradiště Formation	*Myoconcha* aff. *transatlantica*	Ascher 1906
Planerskoje	Crimean Peninsula, southern Ukraine	Hauterivian, Early Cretaceous	Planerskoje section	*Caspiconcha rubani*	Kiel and Peckmann 2008; Kiel et al. 2010
Wilbur Springs (= Simmon's Spring according to Durham 1998)	Colusa County, California, USA	Hauterivian, Early Cretaceous	Great Valley Group	*Caspiconcha major*	Campbell et al. 2002; this paper
Eagle Creek	Ono, Shasta County, California, USA	Late Barremian, Early Cretaceous	Lower Chickabally Mudstone Member, Budden Canyon Formation, Great Valley Group	*Caspiconcha major*	Stanton 1895; this paper
Kuhnpasset	Wollaston Forland, Northeast Greenland	Late Barremian, Early Cretaceous	Kuhnpasset Beds	*Caspiconcha whitmani*	Kelly et al. 2000
Cold Fork of Cottonwood Creek	Tehama County, California, USA	Aptian–Albian, Early Cretaceous	Lodoga Formation, Great Valley Group	*Caspiconcha major*	Campbell and Bottjer 1993; Kiel et al. 2008; this paper
Utagoesawa Creek	Hatonosu, Yubari City, Hokkaido, Japan	Albian, Early Cretaceous	Hikagenosawa Formation in Takashima et al. (2004); Main part Formation in Matsumoto and Harada (1964), Yezo Group	*Caspiconcha* sp.	Ogihara 2005; this paper
Ispaster	Basque-Cantabrian Basin, Spain	Late Albian, Early Cretaceous	Black Flysch Group	*Caspiconcha* sp.	Agirrezabala et al. in press
Port Awanui	New Zealand	Late Albian–mid-Cenomanian, Cretaceous	Tikihore Formation	*Caspiconcha* sp.	Kiel et al. in press
East of Knoxville	Napa County, California, USA	Early Cretaceous	Great Valley Group	*Caspiconcha major*	Gabb 1869; this paper
Omagari	Nakagawa Town, Hokkaido, Japan	Campanian, Early Cretaceous	Omagari Formation, Yezo Group	*Caspiconcha* sp.	Hikida et al. 2003; Jenkins et al. 2007a; Kiel et al. 2008; Kaim et al. 2008; Kaim et al. 2009

cha does not necessarily mean that they cannot be closely related, because Morris et al. (1991: 53) inferred that an evolutionary sequence from nacreous through homogenous to cross-lamellar microstructure is commonly observed in bivalves. Therefore, the shell microstructure of *Caspiconcha* could be interpreted as an end-member of a similar shell macroevolutionary sequence in the family Kalenteridae.

Kelly et al. (2000) incorporated *Caspiconcha* into the subfamily Myoconchinae, identifying numerous characters of that genus in common with *Myoconcha*. He also classified the Myoconchinae as a subfamily of the Modiomorphidae within the superfamily Modiomorphoidea. The Modiomorphidae was considered by Morris (1978), Fang and Morris (1997) and Carter et al. (2000) as a family of Anomalodesmata. However, many other ideas for its placement have developed since then (see recent discussion in Griffin and Pastorino 2006). The entirely aragonitic shell of *C. major* supports placement of the Modiomorphidae among the anomalodesmatans, which have wholly aragonitic shells (Carter 1990), rather than with the Mytilidae, the majority of genera of which possess both calcitic and aragonitic shell layers (Carter 1990).

Stratigraphic and geographic range.—Tithonian (Upper Jurassic) to Campanian (Upper Cretaceous). Barremian of NE Greenland, Tithonian to Albian of California, Hauterivian of Crimea and possibly Czech Republic, Albian–Cenomanian of New Zealand, Albian of Spain, and Albian and Campanian of Hokkaido.

Caspiconcha major (Gabb, 1869)

Figs. 2–10.

1869 *Modiola major* sp. nov.; Gabb, 1869: 191–192, 246, pl. 31: 88.

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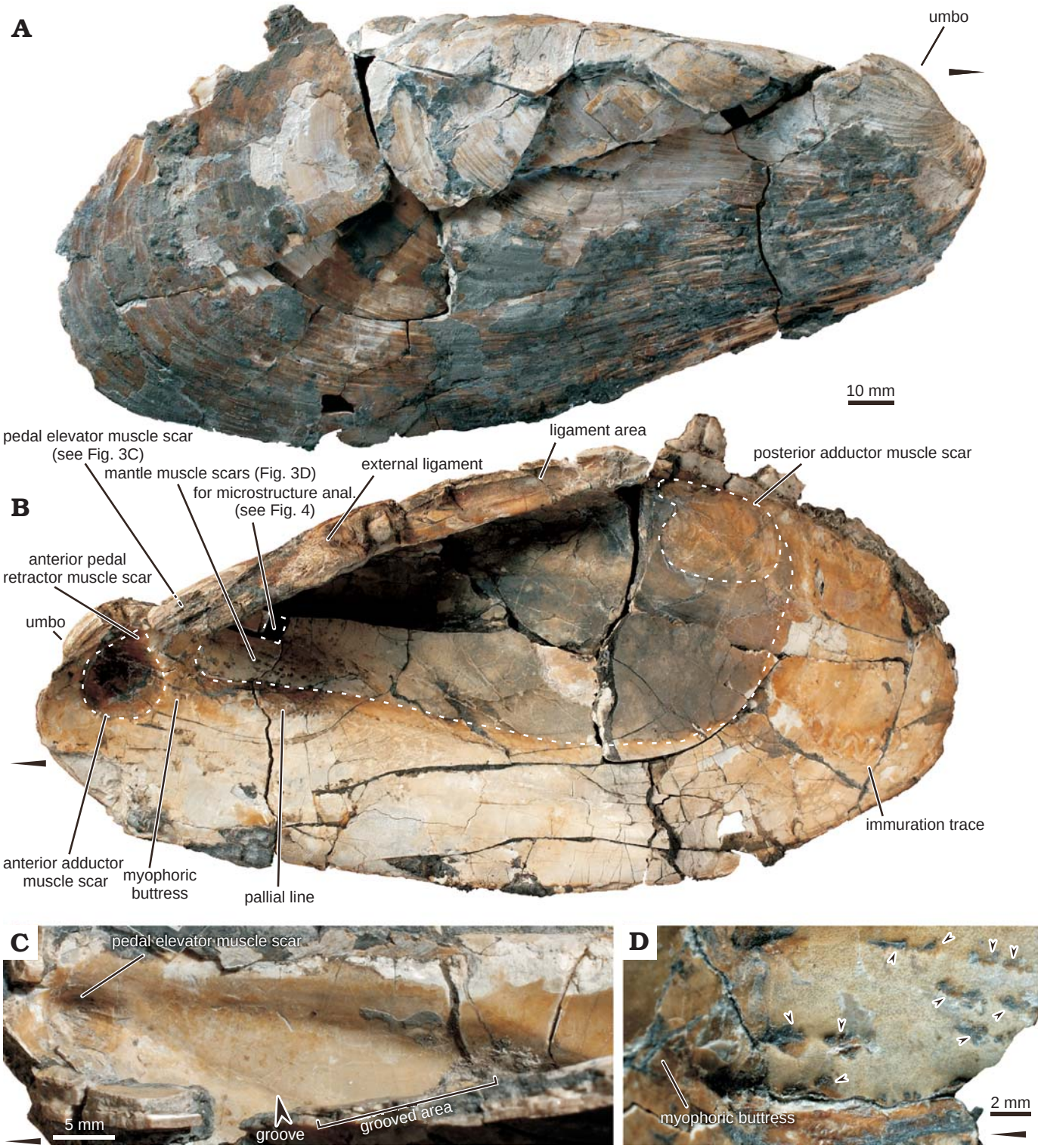


Fig. 3. Modiomorphid bivalve *Caspiconcha major* (Gabb, 1869) CAS 72527-9 from Eagle Creek, California, USA, Upper Barremian (Lower Cretaceous). Right valve. **A**. External view. **B**. Internal view. Details of pedal elevator muscle scar (**C**) and mantle muscle scars indicated by small arrowheads (**D**). Location of shell microstructure analysis (Fig. 4) is marked with a dotted white line. Black arrowheads point to the anterior.

1876 *Modiola major* Gabb, 1869; Whiteaves 1876: 74.
1894 *Modiola major* Gabb, 1869; Stanton (in Diller and Stanton 1894): 442.
1885 *Modiola major* Gabb, 1869; White 1885: 20.
1895 *Modiola major* Gabb, 1869; Stanton 1895: 48, pl. 3: 1.
1897 *Modiola major* Gabb, 1869; Cooper 1897: 84.
1902 *Modiola major* Gabb, 1869; Anderson 1902: 45.
1907 *Modiola major* Gabb, 1869; Crandall 1907: 34.
1909 *Modiola major* Gabb, 1869; Grabau and Shimer 1909: 521, fig. 701.
1914 *Modiola major* Gabb, 1869; Dickerson 1914: 128.

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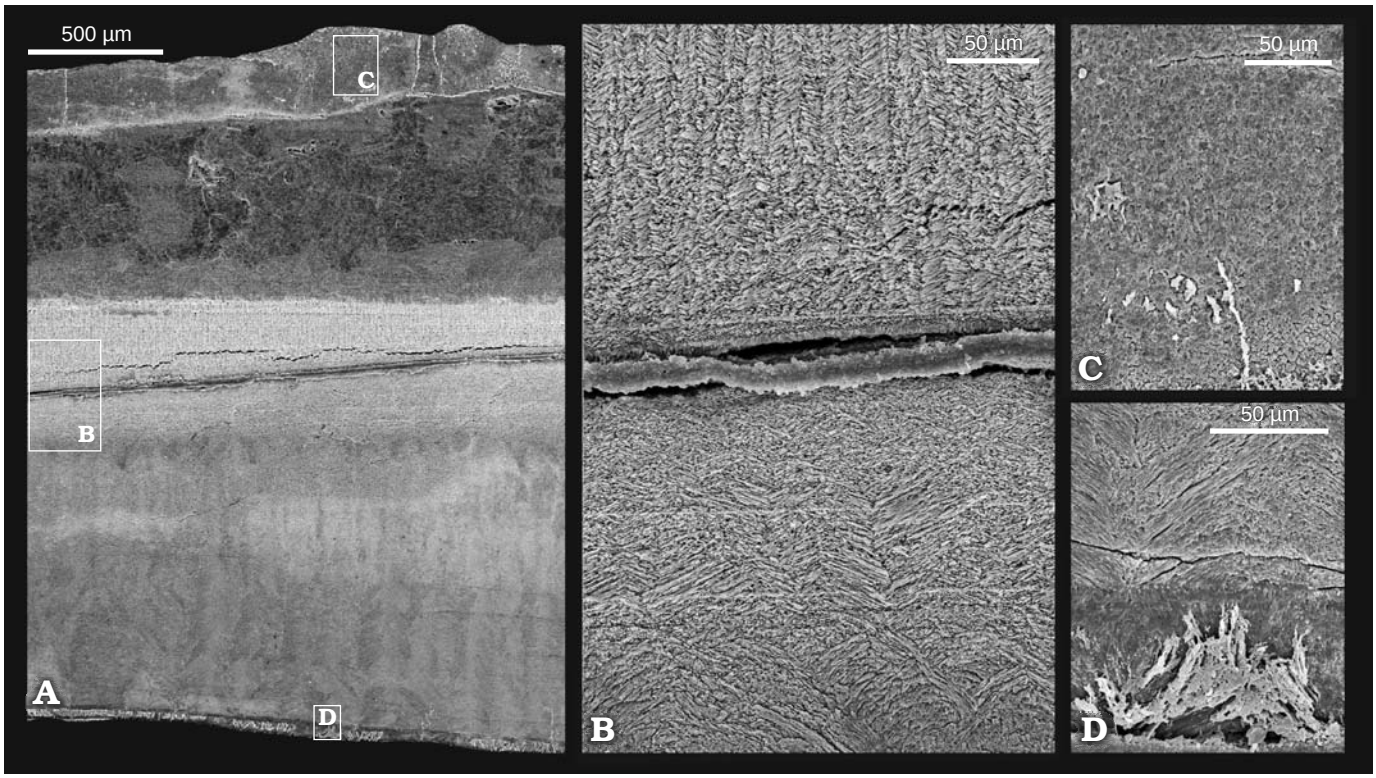


Fig. 4. Shell microstructure of modiomorphid bivalve *Caspiconcha major* (Gabb, 1869) CAS 72527-9 from Eagle Creek, California, USA, Upper Barremian (Lower Cretaceous). External shell surface upwards in all figures. **A**.Vertical cross section through shell in the pallial region; see Fig. 3B for location. **B**. Demarcation between middle (cross lamellar) and inner (complex cross lamellar) layers. **C**. Outer layer homogeneous structure. **D**. Lower part of inner layer, note diagenetic alteration at base.

1914 *Modiola major* Gabb, 1869; Lawson 1914: 8.
1930 *Myoconcha major* (Gabb, 1869); Stewart 1930: 104, pl. 4: 1.
1993 *Modiola major* Gabb, 1869; Campbell et al. 1993: 39, 42–44, fig. 2.
1993 *Modiola major* Gabb, 1869; Campbell and Bottjer 1993: 334, table 1.
1995 *Modiola major* Gabb, 1869; Campbell and Bottjer 1995b: 470, 474, fig. 5.
2006 *Modiola major* Gabb, 1869; Campbell 2006: 394, Table 1.
2006 "*Modiolus*" *major* Gabb, 1869; Squires and Saul 2006: 121.
2008 *Modiola major* Gabb, 1869; Kiel and Peckmann 2008: 757.
2010 *Caspiconcha major* (Gabb, 1869); Kiel et al. 2010: 37, 43.

Type material: Gabb (1869) did not designate a holotype in his original description. Here we designate the single specimen (MCZ 108539) figured by Gabb (1869: pl. 31: 88) to be the lectotype. Thus the four remaining syntypes are paralectotypes. Lectotype: MCZ 108539, Fig. 5. Almost complete large articulated specimen. Poorly preserved, with the umbonal part of the right valve missing. The specimen label states, "East of Knoxville, Lake County" as the collection locality, the site details of which are further assessed in Kiel et al. 2008a. Paralectotypes: MCZ 108538 and 108540, Fig. 6. The MCZ 108538 includes three specimens, which we designate as MCZ 108538A, B and C, from Wilbur Springs, Colusa County, California. MCZ 108540 is from "East of Knoxville, Lake County".

Type locality: East of Knoxville in Napa County, California, USA.

Type horizon: "Knoxville Beds", lower Great Valley Group.

Emended diagnosis.—Shell strongly elongated cuneiform with nearly straight dorsal and ventral margins; umbo above hinge line; weak internal ridge running from anterior pedal elevator muscle scar towards ventral margin of the posterior adductor muscle scar; rounded anterior adductor muscle scar deeply set; posterior adductor muscle scar rounded with dorsally located narrow posterior pedal retractor muscle scar projected anteriorly; well rounded connected line between ventral part of posterior pedal retractor muscle scar and posterior adductor muscle scar; shell entirely aragonite.

Description.—The description as follows is a composite of features seen in Gabb's (1869) type material, Stanton's (1895) material, three new specimens from the Eagle Creek locality, and some other specimens collected from various Cretaceous hydrocarbon seep sites in California (Table 1). Because of the highly intraspecific and ontogenetic variability of the species we also include detailed descriptions of these specimens separately in Appendix 2, in part to avoid future confusion. A schematic drawing of the species is presented in Fig. 2 showing the most important shell characters.

The shell is large (lectotype 131 mm long, 60 mm high, 34 mm wide) and strongly elongated cuneiform in shape with nearly straight dorsal and ventral margins. The valves are equivalved and strongly inequilateral, and the anterior margins are moderately inflated near the umbones. The umbones are close to the anterior end of the shell and are situated slightly above or almost at the same height as the hinge line. The shell thickness is variable, and is thickest at the myophoric buttress where the anterior muscle scar area is located.

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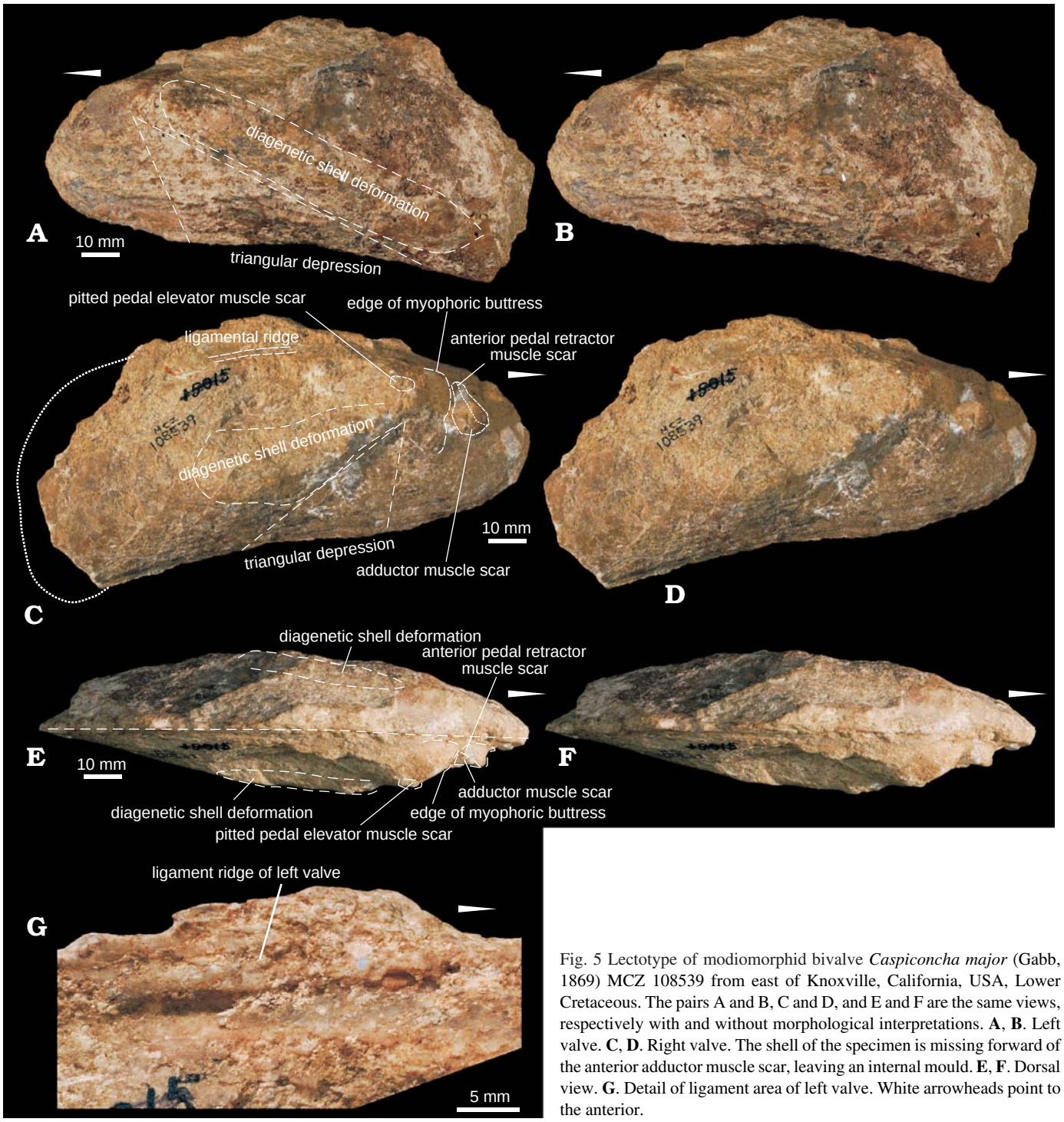


Fig. 5 Lectotype of modiomorphid bivalve *Caspiconcha major* (Gabb, 1869) MCZ 108539 from east of Knoxville, California, USA, Lower Cretaceous. The pairs A and B, C and D, and E and F are the same views, respectively with and without morphological interpretations. **A**, **B**. Left valve. **C**, **D**. Right valve. The shell of the specimen is missing forward of the anterior adductor muscle scar, leaving an internal mould. **E**, **F**. Dorsal view. **G**. Detail of ligament area of left valve. White arrowheads point to the anterior.

The shell is relatively thick in the antero-dorsal to antero-ventral area, thinning conspicuously in the posterior-ventral to mid-flank of the ventral area.

The dorsal margin is straight in lateral profile for the full extent of the nymph and ligament area and is then curved ventrally at the postero-dorsal area. The posterior margin is well rounded. The ventral margin is almost straight and is feebly indented at the mid-flank. The anterior margin is short and rounded. The shell is moderately inflated in dorsal aspect, with a wedge shape in both the anterior and posterior margins. A triangular depression runs from the umbonal area, widening towards the mid flank. There is an external ornament of commarginal growth lines, which are more pronounced on the shell anterior.

The shell interior is smooth apart from muscle scars and the pallial line. The pallial line runs commarginally from the anterior adductor muscle scar towards the posterior and then turns dorsally towards the posterior of the posterior adductor muscle scar without a pallial sinus. The anterior adductor muscle scar is rounded with pedal retractor muscle scars lo-

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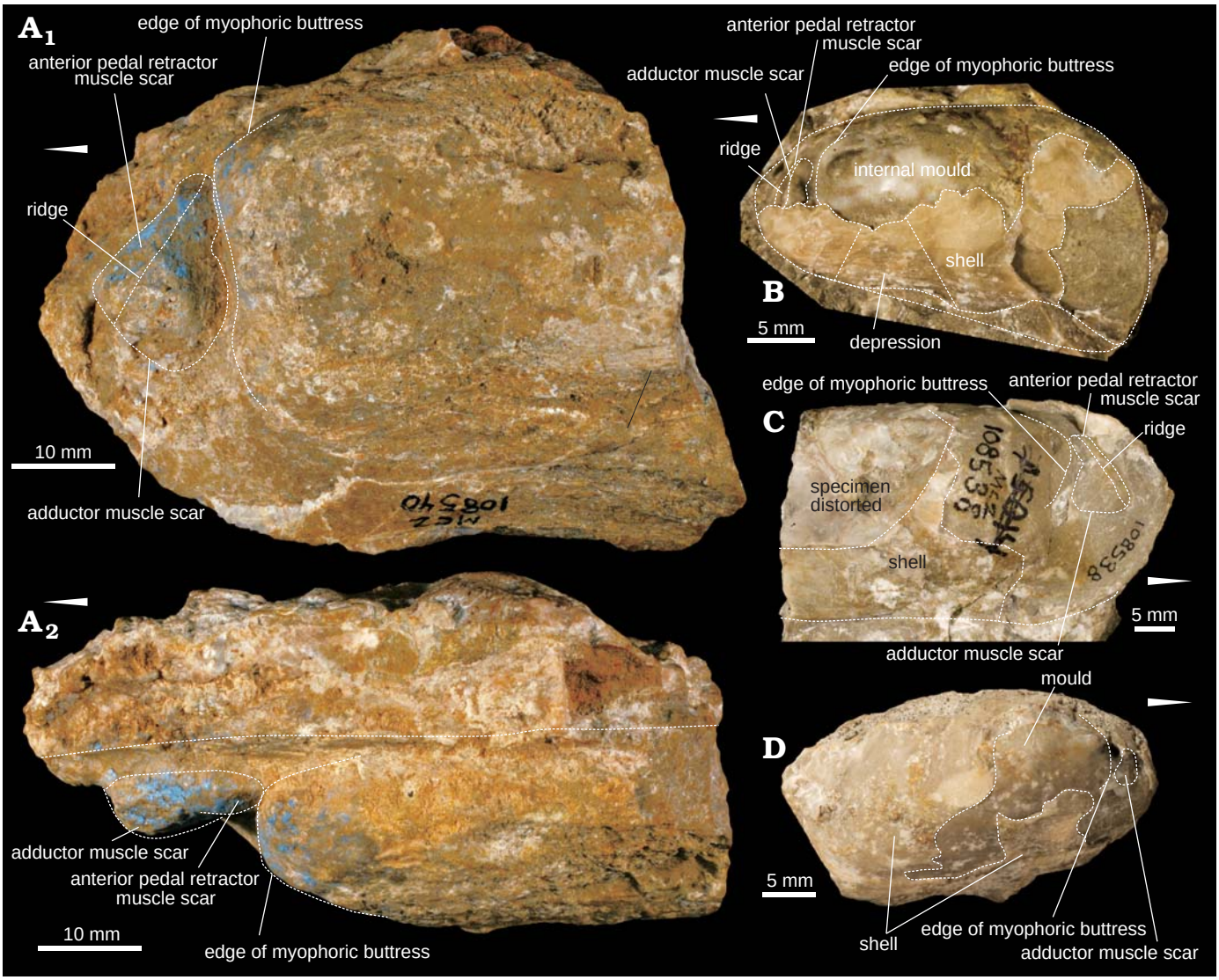


Fig. 6. Paralectotypes of modiomorphid bivalve *Caspiconcha major* (Gabb, 1869). **A**. MCZ108540 from east of Knoxville, California, USA, Lower Cretaceous. Internal mould of left valve (A_1), dorsal view (A_2). **B**–**D**. Three specimens of *Caspiconcha major* (Gabb, 1869) from Wilbur Springs, California, USA, Hauterivian (Lower Cretaceous). **B**. Left valve of MCZ 108538A. **C**. Internal mould of right valve of MCZ 108538B. **D**. Right valve of MCZ 108538C. White arrowheads point to the anterior.

cated dorsally. The posterior adductor muscle scar is rounded with an antero-dorsally located narrow posterior pedal retractor muscle scar, which projects towards the anterior. The ventral connection between the posterior pedal retractor muscle scar and posterior adductor muscle scar is depressed posteriorly with well rounded line. A weak internal ridge runs from anterior pedal elevator muscle scar towards the ventral margin of the posterior adductor muscle scar, paralleled by an oblique groove on its ventral side.

The myophoric buttress is moderately steep but varies in shape among individuals. The hinge is stout and edentulous. The nymph and ligament groove is very long and straight. The external ligament is sturdy and triangular in cross-section, with a well-mineralized C-spring-type aragonite fibrous sublayer.

There are at least three shell layers. The outermost layer is homogeneous, the middle layer is of cross lamellar structure, and the innermost layer is of complex cross lamellar structure. The shell is composed entirely of aragonite.

Ontogenetic variation.—The shell anterior thickens significantly as the individual grows and occurs mostly by growth in the inner surface of the shell. As a result the pedal elevator muscle scar becomes much deeper and stronger during growth, although we observed some variation in this character, with some juvenile specimens having deep and some adults having shallow pedal elevator muscle scars.

Remarks.—*Caspiconcha major* was first described as *Modiola major* by Gabb (1869) based on poorly preserved specimens. The species was later transferred to *Myoconcha* by Stewart (1930) who stated that its shell is "… heavily buttressed and with a long posterior lateral [tooth]" (Stewart 1930: 104). He most likely confused the lateral [tooth] with the ligamental groove, and, notwithstanding, his nomencla-

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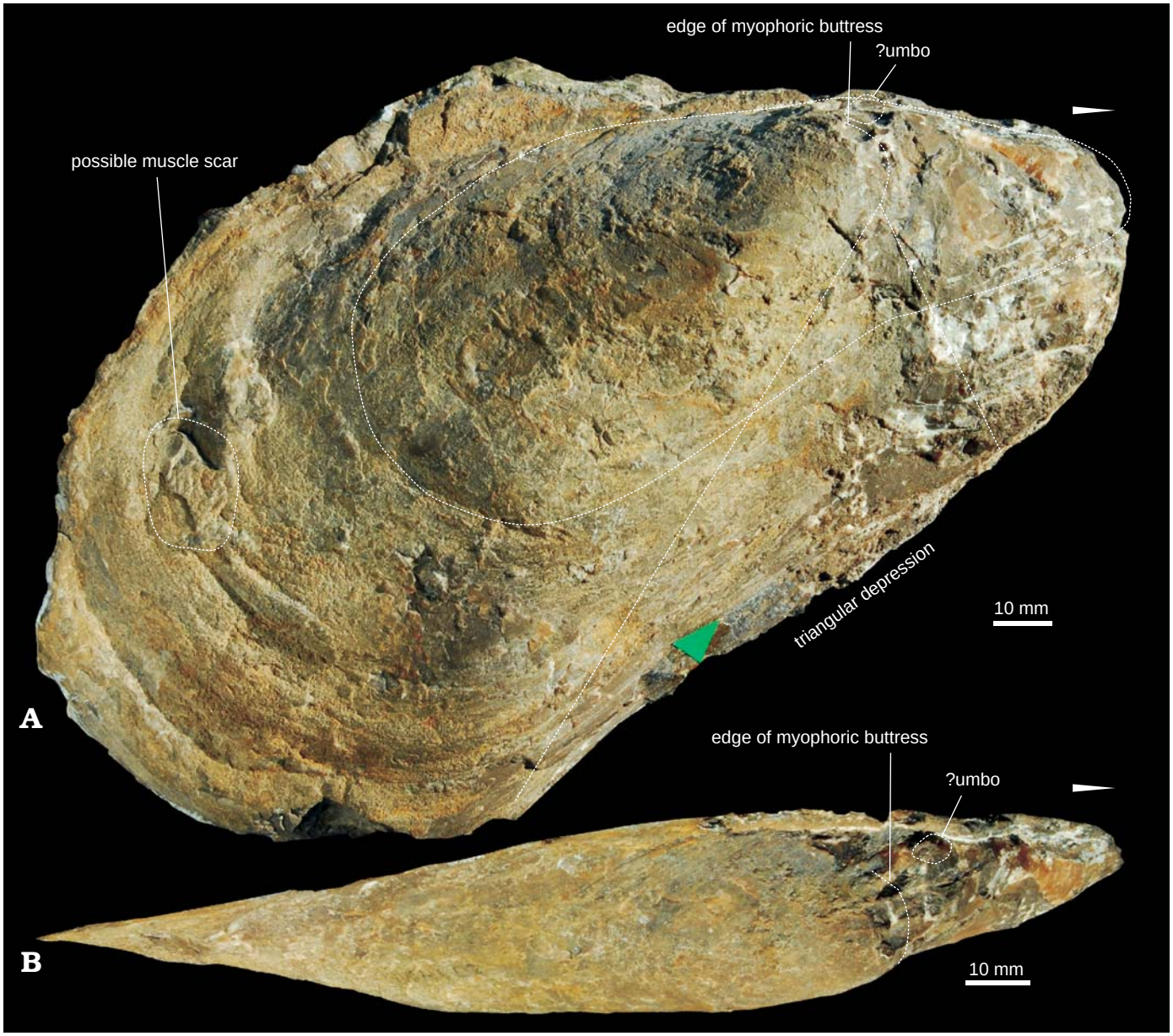


Fig. 7. Modiomorphid bivalve *Caspiconcha major* (Gabb, 1869) USMM 23041 from Cold Fork of Cottonwood Creek, California, USA, Albian (Lower Cretaceous), figured in Stanton (1895). **A**. Right valve. **B**. Dorsal view. White arrowheads point to the anterior.

tural change for *Modiola major* was not followed by later authors (e.g., Campbell 2006) exclusive of Squires and Saul (2006) who referred to this species as "*Modiolus*" *major*.

The shell shape of the lectotype is apparently much more cuneiform than the shape of the Eagle Creek specimens. However, the elongation of the lectotype is apparently due to the diagenetic deformation of the specimen.

Caspiconcha major differs from *C. whithami* in general shell shape that is cuneiform rather than subtrapezoidal, and possesses a much thinner shell, particularly in the posterior area. The anterior adductor muscle scar of *C. major* is rounded rather than elongated, and much smaller than that of *C. whithami*. The caspiconchid process is short and narrow and possesses a small process-like undulation protruding in-between the two anterior pedal retractor muscle scars. The resilifer of *C. major* is short and narrow in contrast to that of *C. whithami*, which is long and wide. The umbo of *C. major* projects well above the hinge line, while in *C. whithami* it lies below or at least level with the hinge line.

Kiel et al. (2010) stated that *C. rubani* can easily be distinguished from *C. major* by the presence of a strong internal ridge in the former species which, according to Kiel et al. (2010), is absent in *C. major*. However, the shells of *C. major* from Eagle and Bear Creeks display a weak, but clearly visible internal ridge. Thus, *C. major* differs from *C. rubani* by its much weaker internal ridge and general shell shape that is more cuneiform in *C. major* rather than subtrapezoidal as in *C. rubani*. Furthermore, according to Kiel et al. (2010: fig.

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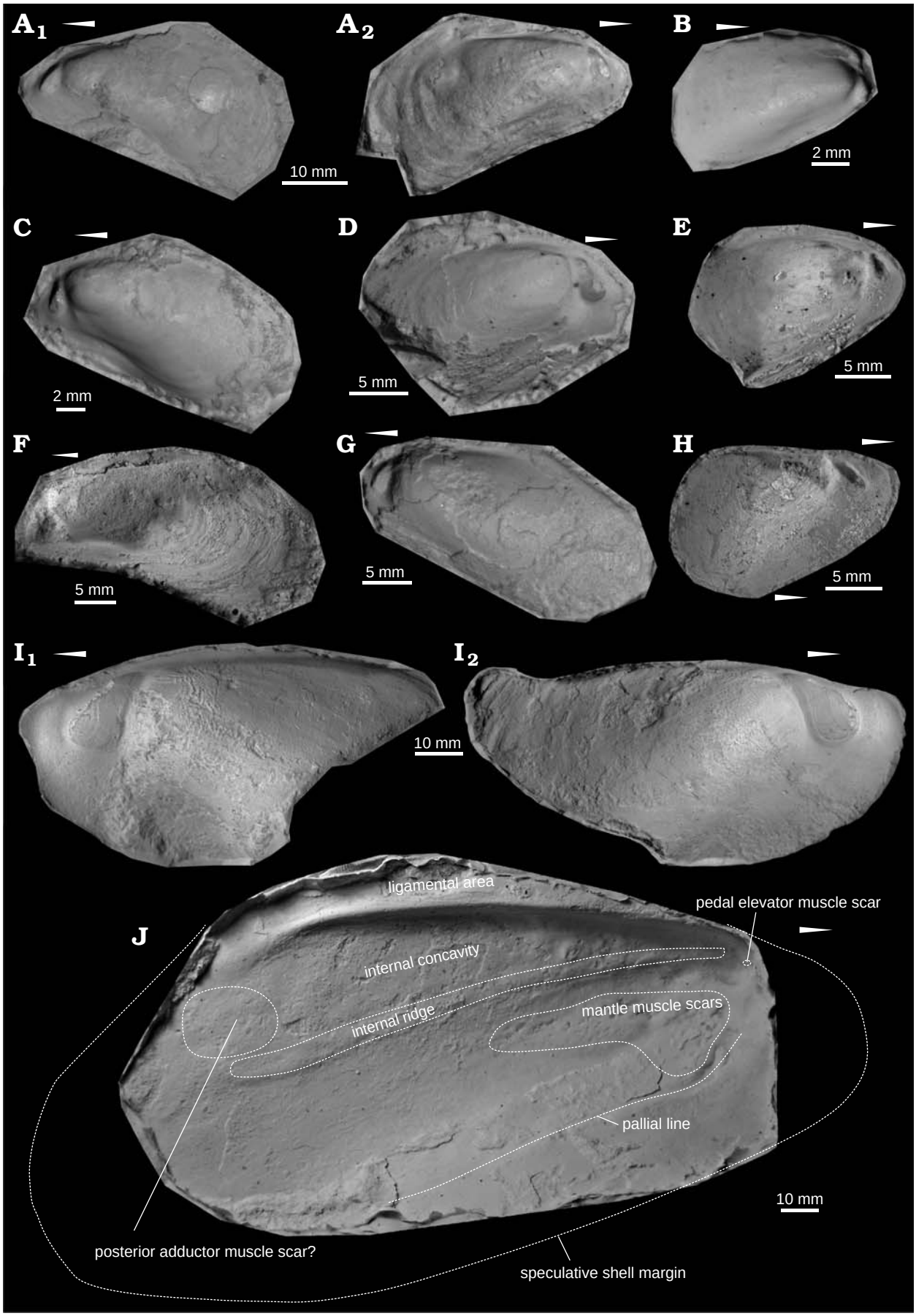
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Fig. 8. Modiomorphid bivalve *Caspiconcha major* (Gabb, 1869) from Eagle Creek, California, USA, Upper Barremian (Lower Cretaceous). **A**. CAS 72530, left (A_1) and right (A_2) valves. **B**. CAS 72531.1, left (B_1) and right (B_2) valves, dorsal view (B_3). White arrowheads point to the anterior.

Fig. 9. Silicone rubber casts of modiomorphid bivalve *Caspiconcha major* (Gabb, 1869) from Cold Fork of Cottonwood Creek (A), Wilbur Springs (B–G), East Berryessa (H, I) and Bear Creek (J), all California, USA. **A**. Internal surface of articulated small specimen UCMP 10225, right valve (A_1), left valve (A_2). **B**. Internal surface of left valve of small specimen UCMP 152077. **C**. Internal surface of right valve of small specimen CAS 71880. **D**. Internal surface of left valve of small specimen with some shell remains along the ventral margin CAS 71882. **E**. Internal surface of left valve of small specimen CAS 71881. **F**. Internal surface of right valve of small specimen CAS 71883. **G**. Internal surface of right valve of small specimen with some shell remains in posterior area CAS 72537. **H**. Internal surface of left valve of small specimen CAS 72548. **I**. Internal surfaces of articulated specimen CAS 72536 with missing posterior margin, right valve (I_1), left valve (I_2). **J**. Internal surface of left valve of partial large specimen with internal shell details highlighted with dotted white lines CAS 72534. White arrowheads point to the anterior. →

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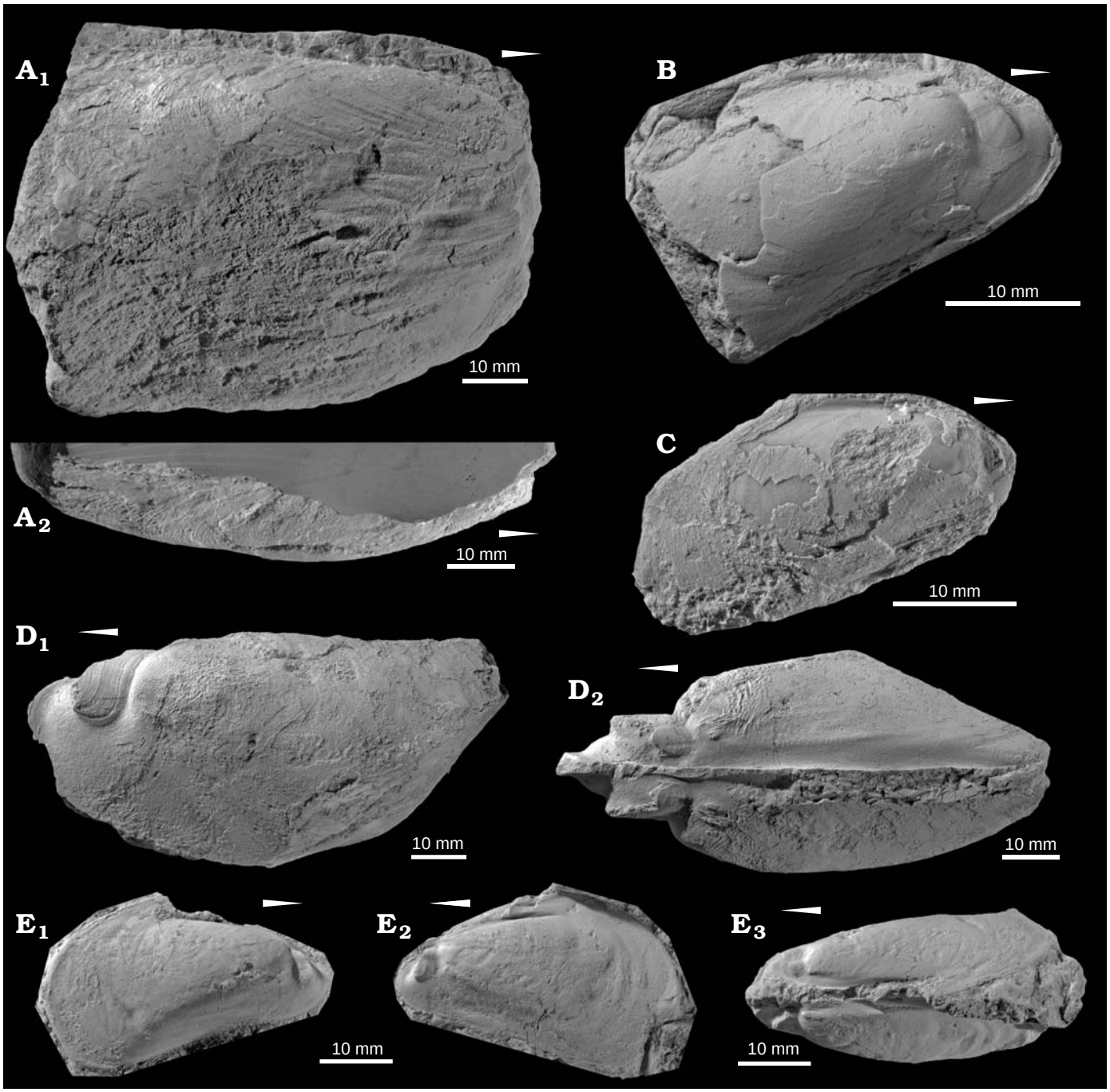


Fig. 10. Modiomorphid bivalve *Caspiconcha major* (Gabb, 1869) from east of Berryessa (A and D), Cold Fork of Cottonwood Creek (B and E), and Wilbur Springs (C), all California, USA. **A**. Right valve of large specimen CAS 72535 with missing posterior area, right valve (A_1), dorsal view (A_2). **B**. Right valve of small specimen UCMP 10226. **C**. Internal mould of right valve of small specimen CAS 72537; see Fig. 9G for cast. **D**. Articulated specimen internal mould with missing posterior margin CAS 72536, left valve (D_1), dorsal view (D_2). See Fig. 9I for casts. **E**. Articulated small specimen internal mould UCMP 10225, right (E_1) and left (E_2) valves, dorsal view (E_3). See Fig. 9A for cast. White arrowheads point to the anterior.

7F), the pallial line of *C. rubani* converges with the ventral edge in its posterior part. In contrast, the pallial line of *C. major* is almost parallel to the ventral edge.

Stratigraphic and geographic range.—Upper Jurassic (Tithonian) to Lower Cretaceous (Albian) of California. The ca. 50 myr range of *C. major* matches some other seep-restricted molluscs, e.g., *Conchocele bisecta* (Conrad, 1849), which ranges from the Eocene to the Recent (e.g., Goedert et al. 2003; Amano and Jenkins 2007). However, further investigations of the morphology and ontogeny of additional *C. major* specimens may reveal that the characters now considered to be of an interspecific variation actually reflect a presence of different species.

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Fig. 11. Modiomorphid bivalve *Caspiconcha* sp. from Utagoesawa Creek, Hokkaido, Japan. **A**. NMNS PM25523, articulated large specimen, right (A_1) and left (A_2) valves. **B**. NMNS PM25524, right valve anterior-ventral fragment, external (B_1) and internal (B_2) views. **C**. NMNS PM25525, articulated small specimen, anterior area missing. White arrowheads point to the anterior.

Caspiconcha sp.

Fig. 11.

Material.—NMNS PM25523 (Fig. 11A): One incomplete adult shell with two articulated valves lacking the posterior

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part and much of the ventral part of the right valve; NMNS PM25524 (Fig. 11B) partially preserved anterior part of the left valve of large specimen; NMNS PM25525 (Fig. 11C) juvenile mould of a shell with two articulated valves in butterfly position preserving some shell material in the umbonal areas of both valves. All specimens from the Utagoesawa Creek locality, Yubari City, Hokkaido, seep carbonate in Main Part Formation, Upper Albian, Lower Cretaceous.

Description.—The shell is large (the largest specimen NMNS PM25523 is 247 mm long) and elongated, subtrapezoidal in lateral aspect, with strong inflation in the dorsal part of the central flank running obliquely towards posterior part of the ventral margin. The valves are equivalve and strongly inequilateral. The umbones are close to the anterior end, situated at, or slightly below, the hinge line. The shell is thick, especially in the anterior part where the growth lines become more densely packed. A triangular depression runs from the umbonal area widening towards the mid flank. The dorsal margin is slightly curved around its whole extent. The posterior margin in the adult shells is not preserved, while in the juvenile it is rounded, but strongly curved at the junction with ventral margin which, in turn, becomes slightly rounded starting from this point. The exterior ornament consists of commarginal growth lines, more pronounced on the shell anterior.

The shell interior is well preserved only in NMNS PM25524 and represented by a generally smooth surface with a large and elongated anterior adductor muscle scar bordered posteriorly by a stout myophoric buttress. Oblique grooves are visible on the mould surface of the juvenile NMNS PM25525 corresponding to the oblique ridge of the shell. The hinge is stout with very long ligamental groove. The other features of the hinge are obscured by diagenesis.

Remarks.—The specimens are partially silicified including some parts of adjoining sediment what hampered appropriate preparation. We could not observe the internal surface of the most completely preserved specimen (NMNS PM25523); thus, we decided to leave this species in open nomenclature. The species is similar to *C. whithami* in having a very thick shell, subtrapezoidal shape, and elongated anterior adductor muscle scar, but differs in having a curved hinge line and strong inflation of the lateral flanks. It differs from *C. major* in having very thick subtrapezoidal shell, with strongly inflated lateral flanks and elongated anterior adductor muscle scar. The Utagoesawa *Caspiconcha* is probably a new species, but we feel this needs confirmation from better preserved material.

Genus *Myoconcha* Sowerby 1824

Type species: *Myoconcha crassa* Sowerby, 1824; Bajocian (Middle Jurassic), near Bristol, United Kingdom.

Myoconcha americana Stanton, 1895

Fig. 12.

1895 *Myoconcha americana* sp. nov.; Stanton 1895: 48, pls. 2–11.
1930 *Myoconcha americana*; Stewart 1930: 104.
2010 *Myoconcha americana*; Kiel et al. 2010: 37.

Holotype: USNM 23042, moderatly preserved almost complete right valve.

Type locality: Stephenson's, Cold Fork of Cottonwood Creek, Tehama County, California, USA. <1 km northeast of Stevenson Peak, and ~1.5 km due west of Woodyard Flat (Jones and Bailey 1973). Detailed map can be found in Campbell et al. (2002).

Type horizon: Lower Cretaceous Knoxville Beds, Albian according to Kiel et al. (2008a).

Dimensions.—The holotype is 40.4 mm long, 21.2 mm high, and 4.7 mm wide.

Description.—The specimen is a right valve only and is preserved in a dark grey mudstone with abundant skeletal detritus, including crinoid brachials, echinoid spines and some other unidentified shell fragments. The right valve is almost complete apart from the most anterior part that is partially broken. It is slender cuneiform in shape with fine, regularly increasing growth lines. The hinge is almost straight and extends over 28 mm. The umbonal part is ornamented by faint radial and commarginal ribs. The commarginal ribs are slightly angulated at the crossing with the radial ribs (Fig. 12D), a pattern typical for *Myoconcha*. Unfortunately the specimen surface is covered by some kind of glue that prevents further observations. The internal surface is covered by sediment apart from the most anterior part where a small and elongated lateral tooth is visible on the anterodorsal margin (Fig. 12C).

Remarks.—Observations of the holotype of *Myoconcha americana* confirms that it belongs to the genus *Myoconcha* rather than to *Caspiconcha*. Most diagnostic features are the umbonal ornament and presence of a probable tooth. We are not sure, however, whether the presence/absence of the tooth is a stable character during ontogeny, or a feature of juvenile individuals. Stewart (1930) and Kiel et al. (2010) interpreted *Myoconcha americana* as a juvenile of *C. major* and synonymized this species with the latter. Here we recommend a return to the original concept of Stanton (1895), retaining the species in *Myoconcha*.

Discussion

Vermiform grooves in *Caspiconcha*

In the description of *Caspiconcha whithami*, Kelly (in Kelly et al. 2000: 243) noted that "the interior surface of the type specimen shows evidence of irregular vermiform grooves, ca. 1.5 mm wide and up to 51 mm long, and with a semi-lunular cross-section". We examined the type material of *C. whithami* at SMUC and we found that apart from the holotype (K8318) these grooves also are present in one of the paratypes (K8433). The healed hole in the mid-ventral area of the holotype (K8318) of *C. whithami* seems to be the end of an abandoned trace. This hole displays deflection of the growth lines, strongly suggesting syn-vivo interaction between bivalve and the bioeroder. Similar grooves occur in the shells of *C. major* specimens from Eagle Creek, although they have a more

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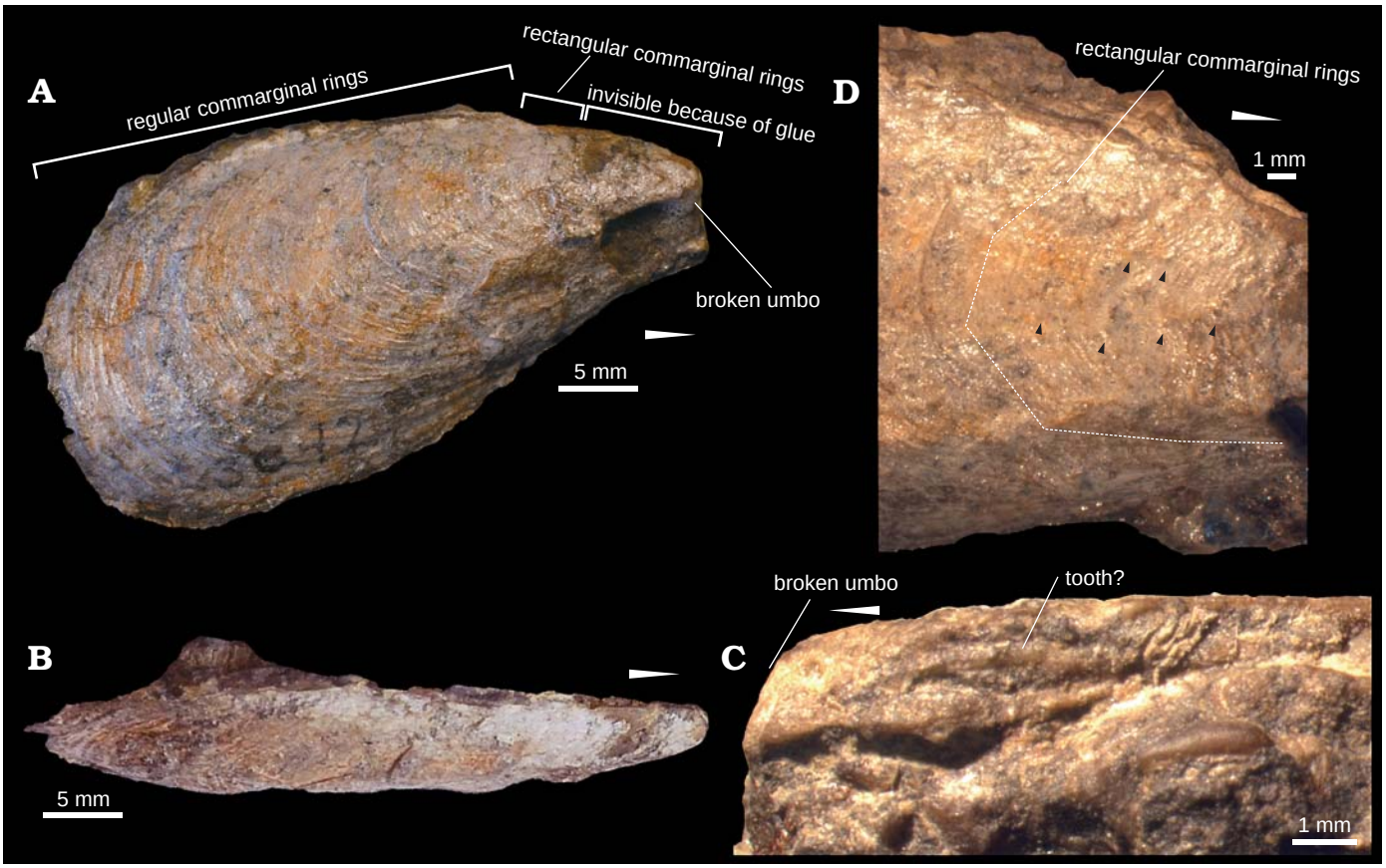


Fig. 12. Modiomorphid bivalve *Myoconcha americana* Stanton, 1895 (USNM 23042), right valve. **A**. External view. **B**. Dorsal view. **C**. Detail of the hinge area showing a possible tooth. **D**. Detail of shell surface ornamentation. Growth lines show rectoangular shape of shell. Black arrowheads point to faint radiaxial ribs mostly obscured by the glue in this image. White arrowheads point to the anterior.

strongly meandering morphology than those in *C. whithami* shells. These grooves in the Eagle Creek *C. major* shells are located both in the pallial region and the shell periphery, and they generally extend from inside the shell towards its periphery, and end at the shell margin (Fig. 3B). Similar trace fossils are also known from internal shell surfaces of juvenile *C. rubani* specimens from Ukraine (Kiel and Peckmann 2008: fig. 6C), and the probable *Caspiconcha* specimen from the Omagari seep site, Japan (Hikida et al. 2003: fig. 9-3).

We suspect that all these *Caspiconcha* specimens were settled by the same type of animal and we consider this to be most likely a polychaete worm. Many Recent seep bivalves (e.g., *Adula*, *Calyptogena*, *Acharax*, *Bathymodiolus*, *Conchocele*, *Lucina*, *Solemya*, and *Thyasira*) are known to be infested by parasitic polychaetes from the family Nautiliniellidae (Miura and Laubier 1989, 1990; Miura and Hashimoto 1996), and an arabellid polychaete has been reported by Dean (1992) as infesting wood-boring pholadid bivalves. Although Miura and Laubier (1989, 1990) and Miura and Hashimoto (1996) reported several nautiliniellids living in bivalve mantle cavities, there is no indication that they may have caused any traces. Nevertheless, several polychaetes do produce such traces in the skeletons of other marine invertebrates (e.g., Korringa 1952; Voigt 1965; Bromley and D'Alessandro 1987; Rodrigues et al. 2008), although these are usually U-shaped and are attributed to polydorids or spionids. The *Caspiconcha* inhabiting worm apparently lived in the space between mantle and shell interior surface while the host bivalve was alive, inhibiting its shell growth. Based on the principle of actualism, we hypothesize that the possible polychaete worm was a parasite on the fossil bivalve. The infestation could have happened to *Caspiconcha* at any time because of its sessile ecology (see below). The presence of traces in most *Caspiconcha* species known so far might indicate that the *Caspiconcha*/worm interaction had a worldwide distribution.

Palaeoecology of *Caspiconcha*

A common feature of chemosynthesis-based ecosystems is the occurrence of abundant specimens of large bivalves. For example, *Calyptogena magnifica* living at hydrothermal vents on the Galápagos Rift reaches 241 mm in length (Boss and Turner 1980), and *Calyptogena* sp. from Late Pliocene seeps of the Boso Peninsula, Japan grew as long as 234.5 mm (Majima et al. 1992). Large sized shells also are found in other bivalve groups inhabiting these ecosystems, e.g., lucinids (Bouchet and von Cosel 2004; Taylor and Glover 2009) and solemyids (Kanie et al. 1999). This gigantism results

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from the abundance of nutrition available to the bivalves via their chemosymbiotic bacteria, and is similar to that seen in the photosymbiotic giant clams (tridacnids). Some bivalve clades possessing both symbiotic and non-symbiotic taxa, e.g., thyasirids, display clear correlation between body size and the presence of symbiotic bacteria (Dufour 2005). The large body size in *Caspiconcha* strongly suggests the animals also hosted chemosymbiotic bacteria.

The presence of a gape at the anterior ventral shell margin of *C. whithami* suggests that this species was equipped with a byssus (Kelly et al. 2000). A similar gape can be also observed in *C. major* and the Utagoesawa *Caspiconcha* sp. The gape indicates that *Caspiconcha* was a sessile animal using its byssus for attachment, as suggested by Kelly et al. (2000). *C. whithami* occurs in densely-packed clusters of shells in the core of carbonate mounds (Kelly et al. 2000: 236). This type of occurrence is known also from *C. major* specimens from the Cold Fork of Cottonwood Creek and Wilbur Springs localities (Campbell et al. 1993, 2002). In addition, specimens of *C. whithami* and *C. rubani* are frequently found at angle of 30° relative to the bedding plane (Kelly et al. 2000; Kiel and Peckmann 2008). Based on these lines of evidence, we suggest that *Caspiconcha*, like modern bathymodiolin mussels, could live both attached onto hard substrates and also semi-infaunally, partially buried in sediment.

Palaeogeography and evolutionary history

Table 2 lists the occurrences of *Caspiconcha* and *Caspiconcha*-like bivalves. The Jurassic species *Myoconcha neuquena* Leanza, 1940 from Argentina could be an ancestor of *Caspiconcha*, based on its shared characters with *Caspiconcha*, e.g., edentulous hinge with probable caspiconchid process (Leanza 1940: pl. 1A; Griffin and Pastorino 2006: figs. 4-1, 4-2), although this species needs further study. *Caspiconcha* itself ranged from the Jurassic to Late Cretaceous and had a worldwide distribution (Figs. 13, 14). Most occurrences of *Caspiconcha* are from Lower Cretaceous strata, indicating that this genus was characteristic of Early Cretaceous hydrocarbon seep environments. By the Late Cretaceous, however, *Caspiconcha* is found only in the Campanian Omagari hydrocarbon seep locality (Hikida et al. 2003: fig. 9-3). Kelly et al. (2000) suggested that a much younger (Maastrichtian) species of modiomorphid might be present in New Zealand. This species, identified as *Caspiconcha* sp. is actually of Late Albian–mid-Cenomanian age (Kiel et al. in press).

Caspiconcha and the macroevolutionary history of chemosynthetic communities

Seep palaeoecology.—*Caspiconcha* grew to over 300 mm in length (Kelly et al. 2000) and apparently was the largest bivalve genus inhabiting Early Cretaceous chemosynthesis-based ecosystems. The only other bivalves comparable in size to *Caspiconcha* in the Cretaceous are the lucinid *Nipponothracia* from the Albian Ponbetsu and Cenomanian Kanajirisawa seep localities, both from Hokkaido (Kanie et al. 1993, Kanie and Kuramochi 1996; Kiel et al. 2008b), and unidentified lucinid bivalves from the Albian Utagoesawa seep locality (RGJ and AK, unpublished data). After the rapid decrease of *Caspiconcha* occurrences at the end of Early Cretaceous, large-sized bivalves in chemosynthesis-based ecosystems were rare for the rest of the Mesozoic, with the exception of the lcunids from Kanajirisawa (middle Cenomanian; Kanie and Kuramochi 1996) and New Zealand (Campanian; Kiel et al. in press), and the Campanian *Caspiconcha* sp. from Omagari. Bivalves larger than 10 cm were excessively rare in seep sites until the early Miocene and the occurrence of large vesicomyids clams and bathymodiolin mussels (e.g., Amano and Kiel 2007), although a large lucinid bivalve has been reported from an Eocene non-seep environment in Jamaica

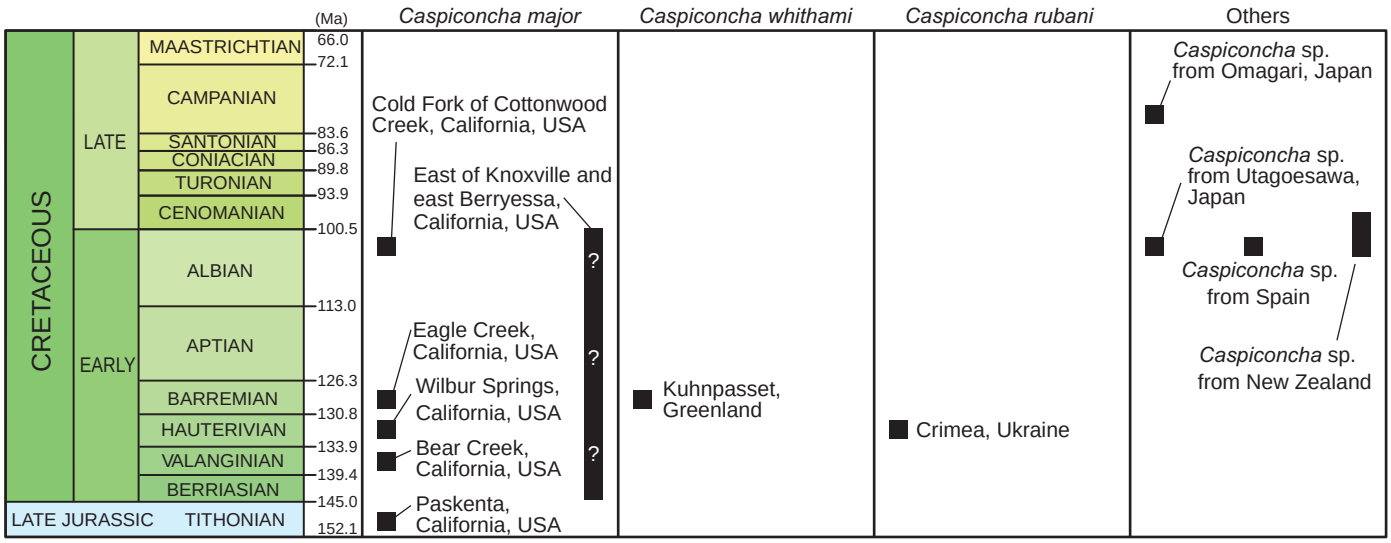


Fig. 13. Stratigraphical range of *Caspiconcha* and *Caspiconcha*-like species. See text and Tables 1 and 2 for details of species and localities.

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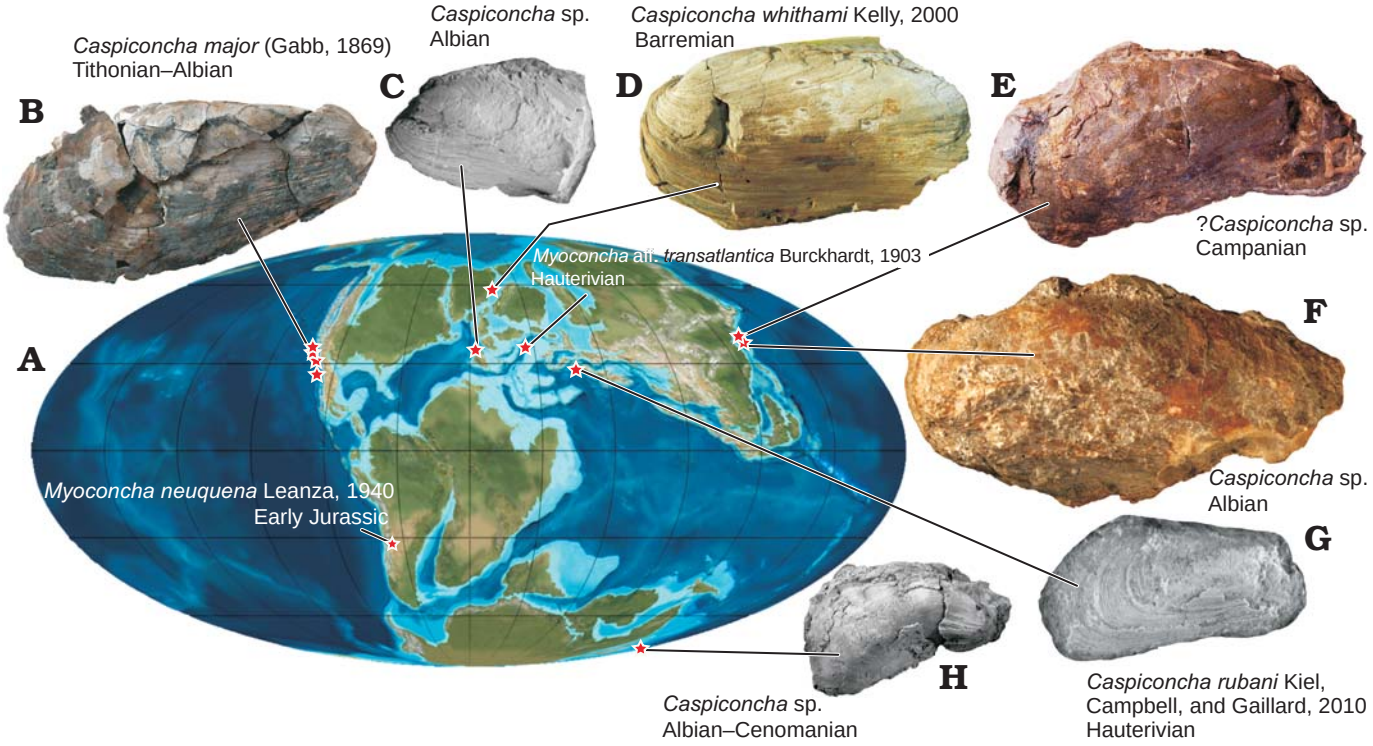


Fig. 14. Palaeobiogeographical distribution of *Caspiconcha* and *Caspiconcha*-like species in the late Mesozoic world's oceans. **A**. Palaeomap at 120 Ma from http://jan.ucc.nau.edu/~rcb7/index.html. **B**. *Caspiconcha major* (Gabb, 1869), Late Jurassic (Tithonian) to Early Cretaceous (Albian) from California, USA. The specimen is from the Eagle Creek site. **C**. *Caspiconcha* sp., Lower Cretaceous (Albian) of Basque, Spain (image from Agirrezabala et al. in press). **D**. *Caspiconcha whithami* Kelly, 2000, Lower Cretaceous (Barremian) of Greenland (SMUC K 8318, holotype). **E**. Possible *Caspiconcha*, described as *Calyptogena* sp. in Hikida et al. (2003) from the Upper Cretaceous (Campanian) Omagari site, Hokkaido, Japan. **F**. *Caspiconcha* sp., Lower Cretaceous (Albian), Utagoesawa Creek, Hokkaido, Japan. **G**. *C. rubani* Kiel et al. (2010), Lower Cretaceous (Hauterivian) of Ukraine (image from Kiel et al. 2010). **H**. *Caspiconcha* sp., Lower Cretaceous to Upper Cretaceous (Upper Albian to middle Cenomanian) of New Zealand (image from Kiel et al. in press).

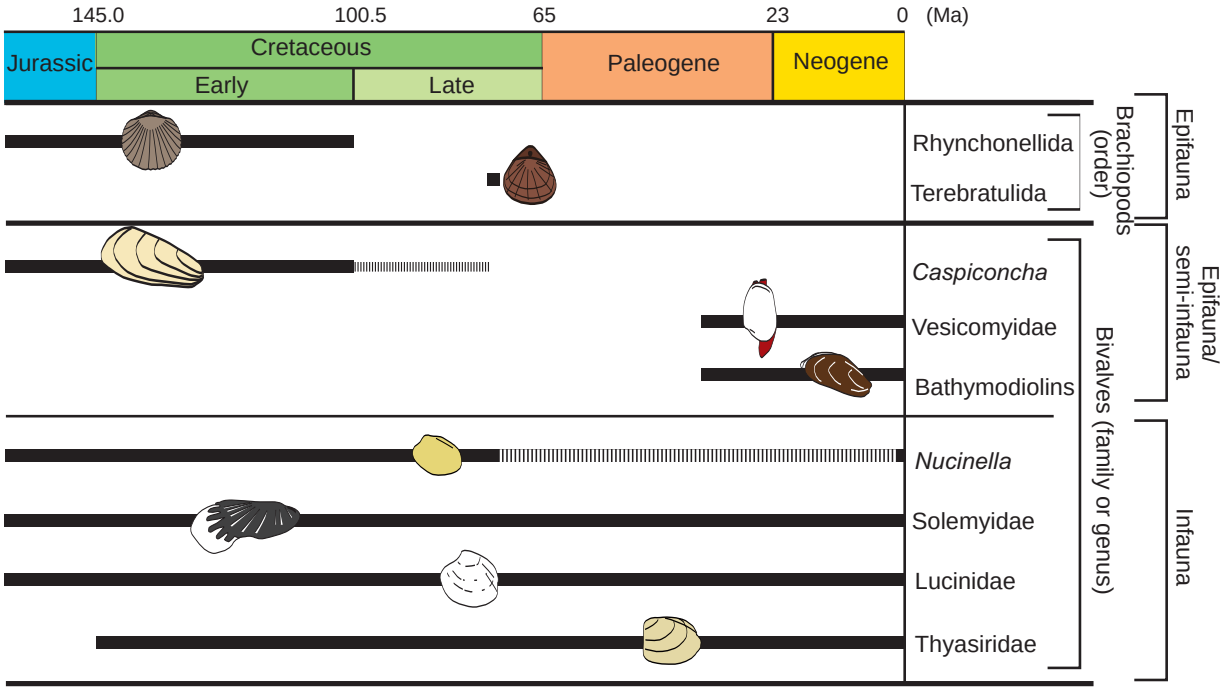


Fig. 15. Ranges and palaeoecological interpretations of major group of chemosynthetic bivalves and brachiopods from Late Jurassic to Recent hydrocarbon seeps. The epifauna and semi-infauna almost vanished at the end of Early Cretaceous and did flourish again from the Eocene with the appearance of vesicomyids and bathymodiolins. *Caspiconcha* was common until the end of the Early Cretaceous after which there was only one occurrence in the Late Cretaceous. In contrast, infaunal bivalves were present continuously from the late Mesozoic to the Recent.

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(Taylor and Glover 2009). We shall stress, however, that this larger seep bivalve occurrence gap could be an artefact resulting from the general paucity of Maastrichtian and Paleocene seep deposits known to date.

Substantial faunal changes in chemosynthesis-based communities took place during the late Mesozoic to early Paleogene time period (Campbell and Bottjer 1995a). Brachiopods dominated Palaeozoic to Jurassic chemosynthesis-based communities (Campbell and Bottjer 1995b; Sandy 1995, 2010; Kaim et al. 2010; Peckmann et al. 2011) and then started to decrease in importance through to the Late Cretaceous, although the rhynchonellide brachiopod *Peregrinella* was extremely abundant in Early Cretaceous hydrocarbon seep communities (Campbell and Bottjer 1995a, b; Kiel and Peckmann 2008). The abyssochrysoid gastropod genus *Paskentana* had a similar pattern of occurrence as *Caspiconcha* and *Peregrinella*, being widely present in seeps of the Early Cretaceous, but becoming extinct at the end of this time period (Kiel and Peckmann 2008). From the late Mesozoic to the Paleogene, bivalve-dominated chemosynthesis-based communities increased in number (Campbell and Bottjer 1995a), and many modern-type chemosynthetic molluscs appeared, e.g. vesicomyid and bathymodiolin bivalves and provannid gastropods.

Having a semi-infaunal and/or epifaunal ecology, *Caspiconcha* may have been a competitor to rhynchonellide brachiopods in seep environments during the time period they co-existed, although the sessile rhynchonellide brachiopods had less mobility than the bivalves, which, although byssate, would have been able to move if conditions became sub-optimal. The seep-restricted rhynchonellide brachiopods became extinct at the end of Early Cretaceous (Kiel and Peckmann 2008), while *Caspiconcha* survived to the Late Cretaceous in Japan (Hikida et al. 2003; Kiel et al. 2010), although known so far from a single specimen at a single locality. After their extinction the niche for epifaunal and semi-infaunal organisms in hydrocarbon seeps was apparently unoccupied from the Late Cretaceous until the appearance of bathymodiolin bivalves in the Eocene (Fig. 14), the reasons for which are presently unclear.

***Caspiconcha major* is not a mytilid**.—Because *Caspiconcha major* was originally considered a mytilid bivalve there was an apparent temporal conflict between the fossil record of seep restricted mytilid bivalves and the estimated age of divergence of the subfamily Bathymodiolinae based on molecular analyses, with the oldest "mytilid" (i.e., *C. major*) specimens being Tithonian (~150 Ma) and the divergence age estimate being 22–94 Ma (Little and Vrijenhoek 2003). Now, however, with the taxonomic shift of *M. major* into the genus *Caspiconcha*, seep restricted mytilids no longer range into the Mesozoic fossil record. Thus the oldest seep restricted mytilid bivalve is *Bathymodiolus willapaensis* (Squires and Goedert, 1991) from lower Middle Eocene to Oligocene strata in Washington State (Kiel 2006). As a result the fossil record of this group becomes much more compatible with the estimated molecular divergence age of the chemosynthetic mytilids.

Conclusions

Detailed study of Gabb's (1869) type series of *Modiola major* Gabb, 1869, other *Modiola major* specimens from several localities in California, and new exceptionally well-preserved specimens from the Eagle Creek locality, allowed us to formally transfer this species to the genus *Caspiconcha* and family Kalenteridae. Species of this genus had a worldwide distribution in hydrocarbon seeps of Jurassic to Early Cretaceous age, but thereafter were rare, with the last occurrence from an Upper Cretaceous hydrocarbon seep locality in Japan. A similar pattern is seen in the seep-restricted brachiopods. It remains unclear why these two major epifaunal/semi-infaunal groups disappeared in the Early to Late Cretaceous while the infaunal bivalves were unaffected. The niche for epifauna/semi-infauna in seeps was then unoccupied until appearance of bathymodiolin and vesicomyid bivalves in the Eocene.

Note added in proof

In a recently published paper Kaim and Schneider (2012) investigated juvenile specimens of *Myoconcha crassa* (the type species of *Myoconcha*) from Middle Bathonian (Middle Jurassic) clays of southern Poland. Very well preserved shells of this species displayed original microstructure comprising two layers: inner complex cross-lamellar and outer simple cross-lamellar. These microstructure types are the same as the inner and middle layers of *Caspiconcha major* investigated herein. Kaim and Schneider (2012) use this information to argue that both *Myoconcha* and *Caspiconcha* , and by inference the family Kalenteridae, belong to the order Carditida, as earlier suggested by e.g., Chavan (1954, 1969); Newell (1957, 1969) and Nevesskaja (2009), rather than the Pholadomyoida or Palaeoheterodonta (see also discussion in Damborenea 2004).

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References

Agirrezabala, L.M., Kiel, S., Blumenberg, M., Schäfer, and N., Reitner, J. (in press). Outcrop analogues of pockmarks and associated methane-seep carbonates: A case study from the Lower Cretaceous (Albian) of the Basque-Cantabrian Basin, western Pyrenees. *Palaeogeography, Palaeoclimatology, Palaeoecology*.

Amano, K. and Jenkins, R. 2007. Eocene drill holes in cold-seep bivalves of Hokkaido, northern Japan. *Marine Ecology—an Evolutionary Perspective* 28: 108–114.

Amano, K. and Kiel, S. 2007. Fossil vesicomyid bivalves from the North Pacific region. *Veliger* 49: 270–293.

Amano, K., Jenkins, R.G., and Hikida, Y. 2007. A new gigantic *Nucinella* (Bivalvia: Solemyoida) from the Cretaceous cold-seep deposit in Hokkaido, northern Japan. *Veliger* 49: 84–90.

Anderson, F.M. 1902. Cretaceous deposits of the Pacific coast. *Proceedings of the California Academy of Sciences, Third Series* 2 (1): 3–155.

Ascher, E. 1906. Die Gastropoden, Bivalven und Brachiopoden der Grodischter Schichten. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* 19: 135–167.

Bailey, J.B. 1983. Middle Devonian Bivalvia from the Solsville Member (Marcellus Formation), central New York State. *Bulletin of the American Museum of Natural History* 174: 196–325.

Bouchet, P. and von Cosel, R. 2004. The world's largest lucinid is an undescribed species from Taiwan (Mollusca: Bivalvia). *Zoological Studies* 43: 704–711.

Bouchet, P., Rocroi, J.P., Bieler, R., Carter, J.G., and Coan, E.V. 2010. Nomenclator of bivalve families with a classification of bivalve families. *Malacologia* 52: 4–172.

Boss, K.J. and Turner, R.D. 1980. The giant white clam from the Galapagos Rift, *Calyptogena magnifica* species novum. *Malacologia* 20: 161–194.

Bromley, R. and D'Alessandro, A. 1987. Bioerosion of the Plio-Pleistocene transgression of southern Italy. *Rivista Italiana di Paleontologia e Stratigrafia* 93: 379–442.

Campbell, K.A. 2006. Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: Past developments and future research directions. *Palaeogeography Palaeoclimatology Palaeoecology* 232: 362–407.

Campbell, K.A. and Bottjer, D.J. 1993. Fossil cold seeps. *National Geographic Research & Exploration* 9: 326–343.

Campbell, K.A. and Bottjer, D.J. 1995a. Brachiopods and chemosymbiotic bivalves in Phanerozoic hydrothermal vent and cold seep environments. *Geology* 23: 321–324.

Campbell, K.A. and Bottjer, D.J. 1995b. *Peregrinella*: an Early Cretaceous cold-seep-restricted brachiopod. *Paleobiology* 21: 461–478.

Campbell, K.A., Carlson, C., and Bottjer, D.J. 1993. Fossil cold seep limestone and associated chemosynthetic macroinvertebrate faunas, Jurassic–Cretaceous Great Valley Group, California. *In*: S.A. Graham, and D.R. Lowe (eds.), *Advances in the Sedimentary Geology of the Great Valley Group, Sacramento Valley, California*, 37–50. Society of Economic Paleontologists and Mineralogists, Pacific Section, Los Angeles.

Campbell, K.A., Farmer, J.D., and Des Marais, D. 2002. Ancient hydrocarbon seeps from the Mesozoic convergent margin of California: carbonate geochemistry, fluids and palaeoenvironments. *Geofluids* 2: 63–94.

Campbell, K.A., Peterson, D.E., and Alfaro, A.C. 2008. Two new species of *Retiskenea*? (Gastropoda: Neomphalidae) from Lower Cretaceous hydrocarbon-seep carbonates of northern California. *Journal of Paleontology* 82: 140–153.

Carter, J.G. 1990. Evolutionary significance of shell microstructure in the Palaeotaxodonta, Pteriomorphia and Isofilibranchia (Bivalvia: Mollusca). *In*: J.G. Carter (ed.), *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends*,135–296. Van Nostrand Reinhold, New York.

Carter, J.G., Campbell, D.C., and Campbell, M.R. 2000. Cladistic perspectives on early bivalve evolution. *Geological Society, London, Special Publications* 177: 47–79.

Chavan, A. 1954. Les *Pleurophorus* et genres voisins. *Cahiers Géologiques Seyssel* 22: 200.

Chavan, A. 1969. Family Mactromyidae, Superfamily Carditacea. Part N, Mollusca 6. *In*: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology*, N511–513, N543–548. Geological Society of America and University of Kansas Press, Lawrence.

Cooper, J.G. 1897. List of fossils. *In*: M.E. Watts (ed.), Oil and Gas Yielding Formations of Los Angeles, Ventura, and Santa Barbara Counties. *California. State Mining Bureau. Bulletin* 11: 79–87.

Crandall, R. 1907. The Cretaceous stratigraphy of the Santa Clara Valley region in California. *American Journal of Science, Fourth Series* 24: 33–54.

Damborenea, S.E. 2004. Early Jurassic *Kalentera* (Bivalvia) from Argentina and its palaeobiogeographical significance. *Ameghiniana* 41: 185–198.

Dean, H.K. 1992. A new arabellid polychaete living in the mantle cavity of deep-sea boring bivalves (Family Pholadidae). *Proceedings of the Biological Society of Washington* 105: 224–232.

Dickerson, R.E. 1914. Fauna of Martinez Eocene of California. *University of California Publications, Bulletin of the Department of Geology* 8 (6): 61–180.

Diller, J.S. and Stanton, T.W. 1894. The Shasta-Chico series. *Bulletin of the Geological Society of America* 5: 435–464.

Dufour, S.C. 2005. Gill anatomy and the evolution of symbiosis in the bivalve family Thyasiridae. *Biological Bulletin* 208: 200–212.

Durham, D.L. 1998. *California's Geographic Names: A Gazetteer of Historic and Modern Names of the State*. 1658 pp. Word Dancer Press, California.

Fang, Z.-J. and Morris, N.J. 1997. The genus *Pseudosanguinolites* and some modioliform bivalves (mainly Paleozoic). *Palaeoworld* 7: 49–74.

Fernando, A.G.S., Nishi, H., Tanabe, K., Moriya, K., Iba, Y., Kodama, K., Murphy, M.A., and Okada, H. 2011. Calcareous nannofossil biostratigraphic study of forearc basin sediments: the Lower to Upper Cretaceous Budden Canyon Formation (Great Valley Sequence), northern California. *Island Arc* 20: 346–370.

Futakami, M. 1982. Cretaceous stratigraphy and ammonite assemblages of the Hatonosu area, central Hokkaido. *Journal of Geological Society of Japan* 88: 101–120.

Gabb, W. 1869. Cretaceous Fossils. *Palaeontology of California* 2 (section 2, part 1): 125–205.

Goedert, J.L., Thiel, V., Schmale, O., Rau, W.W., Michaelis, W., and Peckmann, J. 2003. The Late Eocene "Whiskey Creek" methane-seep deposit (Western Washington State) Part I: Geology, Palaeontology, and Molecular Geobiology. *Facies* 48: 223–240.

Grabau, A. and Shimer, H. 1909. *North American Index Fossils, Invertebrates*. 853 pp. A.G. Seiler and Company, New York.

Griffin, M. and Pastorino, G. 2006. *Madrynomya brunerin* gen. and sp. (Bivalvia: ?Modiomorphidae): A Mesozoic survivor in the Tertiary of Patagonia? *Journal of Paleontology* 80: 272–282.

Hammer, Ø., Nakrem, H.A., Little, C.T.S., Hryniewicz, K., Sandy, M.R., Hurum, J.R., Druckenmiller, P., Knutsen, E.M., and Høyberget, M. 2011. Hydrocarbon seeps from close to the Jurassic–Cretaceous boundary, Svalbard. *Palaeogeography, Palaeoclimatology, Palaeoecology* 306: 15–26.

Hikida, Y., Suzuki, S., Togo, Y., and Ijiri, A. 2003. An exceptionally well-preserved fossil seep community from the Cretaceous Yezo Group in the Nakagawa area, Hokkaido. *Paleontological Research* 7: 329–342.

Jenkins, R.G., Kaim, A., and Hikida, Y. 2007a. Antiquity of substrate choice among acmaeid limpets from the Late Cretaceous chemosynthesis-based communities. *Acta Palaeontologica Polonica* 52: 369–373.

Jenkins, R.G., Kaim, A., Hikida, Y., and Tanabe, K. 2007b. Methane-flux-dependent lateral faunal changes in a Late Cretaceous chemosymbiotic assemblage from the Nakagawa area of Hokkaido, Japan. *Geobiology* 5: 127–139.

Jenkins, R.G., Hikida, Y., Chikaraishi, Y., Ohkouchi, N., and Tanabe, K.

http://dx.doi.org/10.4202/app.2011.0026

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2008. Microbially induced formation of ooid-like coated grains in the Late Cretaceous methane-seep deposits of the Nakagawa area, Hokkaido, northern Japan. *Island Arc* 17: 261–269.

Jones, D.L. and Bailey, E.H. 1973. Preliminary biostratigraphic map, Colyear Springs quadrangle, California. *U.S. Geological Survey Miscellaneous Field Studies* Map 517.

Kaim, A. 2011. Non-actualistic wood-fall associations from Middle Jurassic of Poland. *Lethaia* 34: 109–124.

Kaim, A. and Schneider, S. 2012. A conch with a collar: Early ontogeny of the enigmatic fossil bivalve *Myoconcha*. *Journal of Paleontology* 86: 652–658.

Kaim, A., Jenkins, R.G., and Warén, A. 2008a. Provannid and provannid-like gastropods from the Late Cretaceous cold seeps of Hokkaido (Japan) and the fossil record of the Provannidae (Gastropoda: Abyssochrysoidea). *Zoological Journal of the Linnean Society* 154: 421–436.

Kaim, A., Kobayashi, Y., Echizenya, H., Jenkins, R.G., and Tanabe, K. 2008b. Chemosynthesis-based associations on Cretaceous plesiosaurid carcasses. *Acta Palaeontologica Polonica* 53: 97–104.

Kaim, A., Jenkins, R.G., and Hikida, Y. 2009. Gastropods from Late Cretaceous Omagari and Yasukawa hydrocarbon seep deposits in the Nakagawa area, Hokkaido, Japan. *Acta Palaeontologica Polonica* 54: 463–490.

Kaim, A., Bitner, M.A., Jenkins, R.G., and Hikida, Y. 2010. A monospecific assemblage of terebratulide brachiopods in the Upper Cretaceous seep deposits of Omagari, Hokkaido, Japan. *Acta Palaeontologica Polonica* 55: 73–84.

Kanie, Y. and Kuramochi, T. 1996. Description of possibly chemosynthetic bivalves from the Cretaceous deposits of the Obira-cho, northwestern Hokkaido. *Science Report of the Yokosuka City Museum* 44: 63–68.

Kanie, Y., Yoshikawa, Y., Sakai, T., and Takahashi, T. 1993. The Cretaceous chemosynthetic cold water-dependent molluscan community discovered from Mikasa City, central Hokkaido. *Science Report of the Yokosuka City Museum* 41: 31–36.

Kanie, Y., Kuramochi, T., Kanno, S., Mizota, C., Shimizu, M., and Takakuwa, Y. 1999. New occurrence and the shell form of the Middle Miocene *Acharax gigas* (Bivalvia: Solemyidae) in Gunma Prefecture. *Bulletin of Gunma Museum of Natural History* 3: 17–23.

Kelly, S.R.A., Blanc, E., Price, S.P., and Whitham, A.G. 2000. Early Cretaceous giant bivalves from seep-related limestone mounds, Wollaston Forland, Northeast Greenland. *In*: E.M. Harper, J.D. Taylor, and J.A. Crame (eds.), *The Evolutionary Biology of the Bivalvia*, 227–246. Geological Society, London.

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

Kiel, S. 2010. The fossil record of vent and seep mollusks: Aspects from Microbes to Ecosystems. *In*: S. Kiel (ed.), *The Vent and Seep Biota*, 255–277. Springer-Verlag, Dordrecht.

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

Kiel, S. and Little, C.T.S. 2006. Cold-seep mollusks are older than the general marine mollusk fauna. *Science* 313: 1429–1431.

Kiel, S. and Peckmann, J. 2008. Paleoecology and evolutionary significance of an Early Cretaceous *Peregrinella*-dominated hydrocarbon-seep deposit on the Crimean Peninsula. *Palaios* 23: 751–759.

Kiel, S., Amano, K., and Jenkins, R.G. 2008b. Bivalves from Cretaceous cold-seep deposits on Hokkaido, Japan. *Acta Palaeontologica Polonica* 53: 525–537.

Kiel, S., Amano, K., Hikida, Y., and Jenkins, R.G. 2009. Wood-fall associations from Late Cretaceous deep-water sediments of Hokkaido, Japan. *Lethaia* 42: 74–82.

Kiel, S., Birgel, D., Campbell, K.A., Crampton, J.S., Schiøler, P., and Peckmann, J. (in press). Cretaceous methane-seep deposits from New Zealand and their fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology*.

Kiel, S., Campbell, K.A., Elder, W.P., and Little, C.T.S. 2008a. Jurassic and Cretaceous gastropods from hydrocarbon-seeps in forearc basin and accretionary prism settings, California. *Acta Palaeontologica Polonica* 53: 1214–1216.

Kiel, S., Campbell, K., and Gaillard, C. 2010. New and little known mollusks from ancient chemosynthetic environments. *Zootaxa* 2390: 26–48.

Korringa, P. 1952. Recent advances in oyster biology. *Quarterly Review of Biology* 27: 266–308.

Lawson, A.C. 1914. San Francisco Folio. *U.S. Geological Survey Folio* 193: 1–24.

Leanza, A. 1940. *Myoconcha neuquena* n. sp. del Lias de Piedra Pintada en El Neuquén. *Paleontologia* 22: 123–131.

Little, C.T.S., Herrington, R.J., Maslennikov, V.V., Morris, N.J., and Zaykov, V.V. 1997. Silurian hydrothermal-vent community from the southern Urals, Russia. *Nature* 385: 146–148.

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

Majima, R., Tanase, S., Uchimura, R., and Honme, T. 1992. Finding of *Calyptogena* sp. (Bivalvia) from the Neogene of the southern end Boso Peninsula, central Japan. *Journal of Geological Society of Japan* 98: 373–376.

Matsumoto, T. and Harada, M. 1964. Cretaceous stratigraphy of the Yubari Dome, Hokkaido. *Memoirs of the Faculty of Science, Kyushu University, Series D, Geology* 15: 79–115.

Miura, T. and Laubier, L. 1989. *Nautilina calyptogenicola*, a new genus and species of parasitic polychaete on a vesicomyid bivalve from the Japan Trench, representative of a new family Nautilinidae. *Zoological Science* 6: 387–390.

Miura, T. and Laubier, L. 1990. Nautiliniellid polychates collected from the Hatsushima cold-seep site in Sagami Bay, with descriptions of new genera and species. *Zoological Science* 7: 319–325.

Miura, T. and Hashimoto, J. 1996. Nautiliniellid polychaetes living in the mantle cavity of bivalves from cold seeps and hydrothermal vents around Japan. *Publications of the Seto Marine Biological Laboratory* 37: 257–274.

Morris, N.J. 1978. The infaunal descendants of the Cycloconchidae: an outline of the evolutionary history and taxonomy of the Heteroconchia, superfamilies Cycloconchacea to Chamacea [and discussion by Eagar and Morris]. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 284: 259–275.

Morris, N., Dickins, J., and Astafieva-Urbaitis, K. 1991. Upper Palaeozoic anomalodesmatan Bivalvia. *Bulletin of the British Museum, Natural History. Geology* 47: 51–98.

Murphy, M.A. 1956. Lower Cretaceous stratigraphic units of northern California. *Bulletin of the American Association of Petroleum Geologists* 40: 2098–2119.

Murphy, M.A. 1975. Paleontology and stratigraphy of the Lower Chickaball Mudstone Barremian–Aptian in the Ono quadrangle northern California, USA. *University of California Publications in Geological Sciences* 113: 1–52.

Murphy, M.A., Rodda, P.J., and Morton, D.M. 1969. Geology of the Ono quadrangle, Shasta and Tehama counties, California. *California Division of Mine and Geology Bulletin* 192: 1–28.

Nevesskaja, L. 2009. Principles of systematics and the system of bivalves. *Paleontological Journal* 43: 1–11.

Newell, N.D. 1957. Notes on certain primitive heterodont pelecypods. *American Museum Novitates* 1857: 1–14.

Newell, N.D. 1969. Classification of the Bivalvia. *In*: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology*, N205–224. Geological Society of America and University of Kansas Press, Lawrence.

Ogihara, S. 2005. The evolution of chemosynthetic biological community at the site of cold-seep carbonate precipitation [in Japanese with English abstract]. *Fossils* 78: 40–46.

Peckmann, J., Kiel, S., Sandy, M.R., Taylor, D.G., and Goedert, J.L. 2011. Mass occurrences of the brachiopod *Halorella* in Late Triassic methane-seep deposits, eastern Oregon. *The Journal of Geology* 119: 207–220.

Rodrigues, S., Sims, M., Kowalewski, M., Petti, M., Nonato, E., Martinez, S., and Del Rio, C. 2008. Biotic interaction between spionid polychaetes and

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bouchardiid brachiopods: Paleoecological, taphonomic and evolutionary implications. *Acta Palaeontologica Polonica* 53: 657–668.

Sandy, M.R. 1995. A review of some Palaeozoic and Mesozoic brachiopods as members of cold seep chemosynthetic communities: "unusual" palaeoecology and anomalous palaeobiogeographic patterns explained. *Földtani Közlöny* 125: 241–258.

Sandy, M.R. 2010. Brachiopods from ancient hydrocarbon seeps and hydrothermal vents. *In*: S. Kiel (ed.), *The Vent and Seep Biota*, 279–314. Springer, Dordrecht.

Sandy, M.R., and Campbell, K.A. 1994. New rhynchonellid brachiopod genus from Tithonian (Upper Jurassic) cold seep deposits of California and its paleoenvironmental setting. *Journal of Paleontology* 68: 1243–1252.

Stanton, T. 1895. Contributions to the Cretaceous paleontology of the Pacific coast: the fauna of the Knoxville beds. *Bulletin of the United States Geological Survey* 133: 11–132.

Stewart, R.B. 1930. Gabb's California Cretaceous and Tertiary type lamellibranchs. *The Academy of Natural Sciences of Philadelphia, Special Publication* 3: 1–314.

Squires, R.L. and Saul, L.R. 2006. New Late Cretaceous mytilid and tellinoidean bivalves from California. *Veliger*. 48: 121–135.

Takashima, R., Kawabe, F., Nishi, H., Moriya, K., Wani, R., and Ando, H. 2004. Geology and stratigraphy of forearc basin sediments in Hokkaido, Japan: Cretaceous environmental events on the north-west Pacific margin. *Cretaceous Research* 25: 365–390.

Taylor, J. and Glover, E. 2009. A giant lucinid bivalve from the Eocene of Jamaica-systematics, life habits and chemosymbiosis (Mollusca: Bivalvia: Lucinidae). *Palaeontology* 52: 95–109.

Vašíček, Z. and Skupien, P. 2004. Historie geologických a paleontologických výzkumů svrchnojurských a spodnokřídových sedimentů na Štramberku. *Sborník vědeckých prací Vysoké školy báňské – Technické univerzity Ostrava Řada hornicko-geologická* 50: 83–102.

Voigt, E. 1965. Über parasitische Polychaeten in Kreide-Austern sowie einige andere in Muschelschalen bohrende Würmer. *Paläontologische Zeitschrift* 39: 193–211.

White, C.A. 1885. Mesozoic and Cenozoic paleontology of California. *Bulletins of the United States Geological Survey* 3 (15): 7–33.

Whiteaves, J. 1876. Part 1. On some invertebrates from the coal-bearing rocks of the Queen Charlotte Island. *In: Mesozoic Fossils*, 1–92. Geological Survey of Canada, Montreal.

Wright, J.E. and Wyld, S.J. 2007. Alternative tectonic model for the Late Jurassic thorugh Early Cretaceous evolution of the Great Valley Group, California. *Geological Society of America Special Paper* 419: 1–15.

http://dx.doi.org/10.4202/app.2011.0026

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Appendix 1

Geographical and geological setting of new *Caspiconcha* localities in California and Japan.

Eagle Creek, California (Late Barremian).—The locality with *Caspiconcha* is exposed along Eagle Creek approximately 10 metres upstream from its confluence with the North Fork of Cottonwood Creek near Ono village, Shasta County, California (Fig. 1C–F) (GPS coordinates: N 40°27'55.3", W 122°36'41.1"). The locality exposes the upper part of the Lower Chickabally Mudstone Member, Budden Canyon Formation, Great Valley Group. The age of the Lower Chickabally Mudstone Member is assigned to the Late Barremian, indicated by the ammonites *Eulytoceras phestum*, *Ancyloceras elephas*, *Heteroceras jeletzkyi*, *Shasticrioceras poniente* (Murphy 1956, 1975; Murphy et al. 1969). This age determination is also confirmed by recent investigations using nannoplankton fossils (Fernando et al. 2011). The locality was mentioned by Stanton (1895: 48), but has until now not been recognized as a hydrocarbon seep deposit.

Approximately 1-m-sized in diameter carbonate bodies are scattered along 40 metres of Eagle Creek and the North Fork of Cottonwood Creek (Fig. 1D). The carbonate rocks display several textures typical of hydrocarbon seep deposits, i.e., isopachous fibrous rim cements with stromatolite-like laminae and clotted micrite. The carbonates and surrounding mudstone contain specimens of *Caspiconcha major*, solemyid and lucinid bivalves, unidentified gastropods and numerous decapod crustaceans. The carbon isotopic compositions of the carbonates display negative values as low as -46‰ VPDB (RGJ, AK, YI, and KT unpublished data). Both the textures and the carbon isotope composition show the carbonates were formed under the influence of the anaerobic oxidation of methane, a biogeochemical process typical of hydrocarbon seep activity (Campbell et al. 2002; Campbell 2006). This site is the northernmost Mesozoic seep deposit recognized in the Franciscan-Great Valley subduction system (Fig. 1c). The Great Valley Group in this northernmost region laps onto the Klamath Mountains terrane rather than upon Coast Range Ophiolite basement. Wright and Wyld (2007) have suggested a different tectonic history for these northern Great Valley strata.

Utagoesawa, Japan (Late Albian).—The Utagoesawa site is located along Utagoesawa Creek in the Hatonosu area of Yubari City, Hokkaido (Fig. 1A, B)(GPS coordinates: N 43°04'88.8" and E 141°55'80.1"). The strata exposed here belong to the Yezo Group, part of the post-Aptian fore-arc basin deposits distributed along the central axis of Hokkaido, and extending towards Sakhalin (Takashima et al. 2004). In the Hatonosu area, the Yezo Group is represented by relatively well exposed Upper Albian to Lower Santonian (Cretaceous) deposits (Matsumoto and Harada 1964; Futakami 1982).

Our specimens (Table 1) come from an accumulation of carbonate bodies (ca. 1 m in diameter each), distributed along approximately 10 metres of the southern bank of Utagoesawa Creek (Fig. 1A, B). The carbonates are surrounded by Upper Albian (Lower Cretaceous) Yezo Group sediments and, in addition to *Caspiconcha* sp., contain numerous specimens of large lucinid and solemyid bivalves, and provannid-like gastropods (Fig. 1B; RGJ and AK unpublished data). The Utagoesawa Creek carbonates display textures typical of hydrocarbon seeps, i.e., isopachous fibrous rim cements, clotted micrite, and numerous peloids. The carbonates also are characterised by depleted carbon isotopic compositions to -47‰ VPDB (RGJ and AK unpublished data). Biomarker analysis performed by Ogihara (2005) on carbonate samples from this locality revealed crocetane and pentamethylicosane (PMI) with highly depleted in ^{13}C carbon isotopic compositions as low as -121.7‰ VPDB, indicative of the presence of anaerobic methane oxidizing archaea. These lines of evidence strongly suggest that the Utagoesawa Creek carbonate deposits were also formed by the anaerobic oxidation of methane in a hydrocarbon seep setting.

Appendix 2

Detailed descriptions of specimens of *Caspiconcha major* (Gabb 1869)

Gabb's (1869) type series. Lectotype MCZ 108539 (Fig. 5).—The specimen was collected from East of Knoxville, Lake County, California (Loc. #1063; according to a label with the specimen), in the "Knoxville beds" of the lower Great Valley Group, Lower Cretaceous, and figured by Gabb (1869: pl. 31: 80) and Stewart (1930: pl. 4). The shell is elongated cuneiform to mytiliform in shape. The left valve retains original shell; the right valve is mostly an internal mould apart from the most posterior portion and ventral parts where shell material is preserved. The left valve contains a deep triangular depression extending from umbonal region to the mid-ventral part. The shell is strongly inflated in the area immediately posterior to the triangular depression. However, this might be diagenetically enhanced as the shell appears to be slightly compressed in the vertical plane. Regular commarginal growth lines are visible on the anterior part. There is a shallow indentation in the shell outline in the middle part of the ventral margin, which also could result from vertical diagenetic compression of the shell.

The myophoric buttress is deep. The anterior adductor muscle scar is small and deep, seemingly slightly delimited from the anterior pedal retractor muscle scar, although this feature might be obscured by excessive preparation. The imprint of a caspiconchid process is clearly visible anterior to the adductor muscle scar. The hinge is straight and extends over 51.3 mm dorsal to the umbonal area. Posterior to the hinge there is a long groove visible parallel to the dorsal shell margin, which apparently is an imprint of the ligamental ridge (thickened shell margin). This structure was apparently interpreted by Stewart (1930) as a "long posterior lateral" and consequently cited by Griffin and Pastorino (2006) as a lateral tooth. The shell is 131.1 mm long, 59.7 mm high, and 33.9 mm wide.

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Gabb's (1869) type series. Paralectotype MCZ 108540 (Fig. 6A). —This specimen was collected from East of Knoxville, Lake County, California (Loc. #1063; according to a label with the specimen), in the "Knoxville Beds" of the lower Great Valley Group, Lower Cretaceous. The anterior part of the shell is composed of original shell (poorly preserved) of the right valve and an internal mould of the left valve. The left valve displays characters of the internal shell morphology. The myophoric buttress is deep and steep. The adductor muscle scar is deep and delicately separated from the anterior pedal retractor muscle scar. A pitted pedal elevator muscle scar is well expressed immediately below the dorso-anterior end of myophoric buttress. The hinge and umbonal area poorly preserved.

Gabb's (1869) type series. Paralectotype MCZ 108538 (Fig. 6B–D).—Three juvenile specimens A, B, C (A and B on a single piece of rock) were collected from Wilbur Springs, Colusa County, California (Loc. #1046), Great Valley Group, Hauterivian (Lower Cretaceous). Specimen MCZ 108538A (Fig. 6B) is an almost complete juvenile left valve. It is an internal mould with shell material remaining in the anterior and middle of ventral part and dorso-posterior part. The shell is associated with a brachiopod coquina (*Peregrinella whitneyi*). The shell is cuneiform and the myophoric buttress is deep. The anterior adductor muscle scar is deep and the hinge line is straight. There is a concavity in the mid-part of ventral shell region. Specimen MCZ 108538B (Fig. 6C) comprises an internal mould of a juvenile (but larger than MCZ 108538A) right valve with anterior part preserved. The myophoric buttress is deep but not steep. The anterior adductor muscle scar is deep and somewhat separated from anterior pedal retractor muscle scar. The umbonal and hinge area is poorly preserved but the hinge line apparently straight and an impression of the ligamental ridge is partially preserved. Specimen MCZ 108538C (Fig. 6D) constitutes a right valve internal mould, with shell material still present in the posterior and mid-ventral parts. The myophoric buttress is deep but not steep. The anterior adductor muscle scar is deep but the tip of its mould is broken.

Stanton's (1885: pl. 3: 1) *Caspiconcha major* (Gabb, 1869). USNM 23041 (Fig. 7).—The specimen was collected from Cold Fork of Cottonwood Creek, Tehama County, California. Lodoga Formation, Great Valley Group, of Aptian–Albian (Early Cretaceous) age. It is an internal mould of a right valve with very few remnants of recrystallised shell material in the anterior part. In several places the shell is not completely eroded so the internal features of the shell are obscured. The most anterior part of the shell is broken. The left valve appears to be present in the matrix. A cross-section of the most posterior part of the left valve is visible. The matrix is a solid beige coloured carbonate with some admixture of broken bivalve and gastropod shells, including a few other small specimens of *Caspiconcha*. These specimens would need further preparation in order to be described adequately.

The shell is wide cuneiform in shape and strongly inflated in the anterior part. It becomes much flatter in the posterior and dorsal parts that comprise the adult portion of the shell. The triangular depression running from the umbonal area and widening towards the mid flank is well-developed. The myophoric buttress is poorly preserved, but it seems to be rather shallow (similar to the specimen CAS 72527-9 from Eagle Creek). The anterior muscle scar is not clearly visible due to the poor state of preservation. The posterior muscle scar is not preserved, or very faint (Fig. 7). The caspiconchid process is invisible under the overlying shell material. The hinge is almost straight and extends over the 74.5 mm of the dorsal margin of the shell. No hinge characters are preserved. The growth lines accumulate gradually, apart from the most ventral part where the growth lines occur more densely. The shell is 201 mm long, 112.7 mm high, and 32.5 mm wide.

***Caspiconcha major* (Gabb, 1869) from Eagle Creek**.—Specimen CAS 72527-9 (Fig. 3) is an almost complete adult shell lacking the posterior part of the left valve. Specimen CAS 72530 (Fig. 8A) is an adult shell with articulated valves imperfectly preserved, and a large part of dorsal margin missing. Specimen CAS 72531.1 (Fig. 8B) is an almost complete juvenile shell with articulated valves. The anteriormost part of the shell is broken; the right valve shell material has peeled off; and the counterpart of the shell preserved as a separate specimen CAS 72531.2.

The best preserved shell CAS 72527-9 (Fig. 3) is large and strongly elongated. In lateral aspect it changes during ontogeny from subtrapezoidal to cuneiform–modioliform shape, with moderate inflation in the anterior near the umbo. The valves are equivalve and strongly inequilateral. The umbones are close to anterior end and are slightly elevated above the hinge line. The shell thickness is variable, being thickest at the myophoric buttress (anterior adductor muscle scar area), relatively thick in the antero-dorsal to antero-ventral area, and thinning conspicuously in the posterior-ventral to mid-flank of the ventral area. In the antero-dorsal to ventral area the shell thickens, and the lateral shell growth is limited in comparison to the posterior part. A triangular depression runs from the umbonal area widening towards the mid flank. The dorsal margin is straight in lateral profile for the extent of the nymph and ligament area, and then curved ventrally at the postero-dorsal area. The posterior margin is well rounded. The ventral margin is almost straight, and feebly indented at the mid-flank, probably for a byssal attachment. The anterior margin is short and rounded. The shell is moderately inflated in dorsal aspect, with a wedge shape in both anterior and posterior margin. The exterior ornament is commarginal, and enhanced in the shell anterior. At least four shell layers are preserved, with the outermost and innermost layers composed of brown coloured diagenetic calcite. The two inner layers are aragonite and whitish.

The shell interior is smooth apart from a pitted mantle muscle scar area in the anterior part of the pallial region. The pallial line is well expressed running comarginally from the anterior adductor muscle scar towards the posterior, and then turns upward to the posterior of the posterior adductor muscle scar, with no pallial sinus. An internal ridge runs from the anterior pedal elevator muscle scar towards the ventral margin of the posterior adductor muscle scar, paralleled by an oblique groove on its ventral side. the anterior adductor muscle scar is rounded with two pedal retractor muscle scars located dorsally and subdivided by a narrow but conspicuous undulation of the caspiconchid process. This process is narrow and weakly expressed, with the posterior tip broken in the available specimens. The myophoric buttress is moderately steep. The posterior adductor muscle scar is rounded, with a dorsally located narrow posterior pedal retractor muscle scar projected anteriorly. The hinge is stout and edentulous. The nymph and ligament groove are very long and straight. The resilifer is very narrow and elongated. It is sharply pointed both to the anterior and posterior, and widest in its mid-part immediately after the end of the anterior adductor muscle

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scar. The external ligament is sturdy and triangular in cross-section, with a well-mineralized C-spring-type aragonite fibrous sublayer.

The small, presumably juvenile, specimen CAS 72531 is 25 mm long, 16 mm high, and 8 mm wide. The shell is water-drop shaped and is very thin and generally much less elongated than the adult shells. The hinge is narrow and long extending at least up to the 2/3 of the dorsal shell margin, and covered along the whole extent by a corresponding long and narrow exterior ligament. The inner surface of the hinge is visible on the counterpart (CAS 72531.1), including a circular anterior adductor muscle scar with no myophoric buttress developed.

Shell mineralogy and microstructure have been observed from specimen CAS 72527-9 (Fig. 4). The shell can be divided into three sublayers (Fig. 4A). The outermost layer is homogeneous (Fig. 4C). The middle layer displays cross lamellar structure (Fig. 4A, B) while the inner layer is complex cross lamellar (Fig. 4A, B). XRD analysis shows that the original shells are composed entirely of aragonite. The ligament is also biomineralized by aragonite. Some parts of the shell underwent partial recrystallisation to calcite (see dark spots on Fig. 4A).

***Caspiconcha major* (Gabb, 1869) from Cold Fork of Cottonwood Creek**.—Specimen UCMP 10225 (Figs. 9A, 10E) is the internal mould of a small articulated shell. Specimen UCMP 10226 (Fig. 10B) is an internal mould of a small right valve. Specimen CAS 72532 is an internal mould of an articulated adult shell (shell material partially preserved with the posterior half missing). Specimen CAS 72533 comprises an internal mould of a left valve, with its hinge and anteriormost parts broken.

The shells from Cold Fork of Cottonwood Creek are strongly elongated, cuneiform to modioliform in both young and adult stages, with a moderate inflation in the anterior near umbonal area. The shells are equivalve and strongly inequilateral; the umbones are close to the anterior end and slightly elevated above, or equal to, the hinge line. The shell thickness is uncertain. A triangular depression runs from the umbonal area and widens towards the mid flank. The dorsal margin is straight in lateral profile for the extent of the ligamental area and is then curved ventrally at the postero-dorsal area. The posterior margin is well rounded while the ventral margin is almost straight, and feebly indented at the mid-flank. The anterior margin is short and rounded. The shells are moderately inflated in dorsal aspect, with a wedge shape in both anterior and posterior margin.

The shell interior is smooth with no internal ridge visible. The anterior adductor muscle scar is rounded with the pedal retractor muscle scars located dorsally. The myophoric buttress is moderately steep. The ligament groove is very long and straight.

***Caspiconcha major* (Gabb, 1869) from Bear Creek** (CAS 72534; Fig. 9J).—The specimen is an articulated internal mould of a large specimen with the anteriormost and posteriormost parts missing. The shell is large and strongly elongated. Being an internal mould the shell thickness is unknown. The shell interior is smooth apart from pitted mantle muscle scar area in the anterior part of the pallial region. The pedal elevator muscle scar is well visible. The pallial line is well expressed, running comarginally from the myophoric buttress towards the posterior. An internal ridge runs from anterior pedal elevator muscle scar towards ventral margin of the posterior adductor muscle scar, parallel to the pallial line. The anterior adductor muscle scar and caspiconchid process are not preserved. The myophoric buttress is moderately steep. The probable posterior adductor muscle scar is oval to rounded. The nymph and ligament groove is very long and straight.

***Caspiconcha major* (Gabb, 1869) from East Berryessa**.—Specimen (CAS 72535; Fig. 10A) is a right valve with anteriormost and posterior parts missing. The shell is almost entirely preserved. Specimen CAS 72548 (Fig. 9H) is an internal mould of a young left valve. Specimen CAS 72536 (Figs. 9I, 10D) is an internal mould of the anterior half of an articulated shell.

The shell is moderate to small in size, elongated modioliform, with moderate to strong inflation in the anterior near umbonal part. The valves are strongly inequilateral. The dorsal margin is straight in lateral profile for the extent of the ligament area and then curved ventrally in the postero-dorsal area. The posterior margin is well rounded, while the ventral margin is almost straight. The anterior margin is short and rounded. The shell is moderately inflated in dorsal aspect with a wedge-shaped anterior margin. The shell interior is smooth. The pallial line and internal ridge are not seen. The anterior adductor muscle scar is rounded with two pedal retractor muscle scars located dorsally. The myophoric buttress is moderately steep for CAS 72535 and 08, and is steep for CAS 72536. The pedal elevator muscle scars are well visible on CAS72536. The posterior adductor muscle scar is not seen. The hinge is stout and edentulous. The ligament groove is very long and straight. The shell is very thick in its anterior part while it is much thinner in the posterior part.

***Caspiconcha major* (Gabb, 1869) from Wilbur Springs**.—Specimen CAS 71880 (Fig. 9C) is a right valve. Specimen CAS 71882 (Fig. 9D) is an internal mould of left valve. Specimen CAS 71881(Fig. 9E) is internal mould of left valve. CAS 72537 (Fig. 9G, 10C) is an articulated specimen. Specimen CAS 71883 (Fig. 9F) is an internal mould of a right valve. Specimen UCMP 152077 (Fig. 9B) is an internal mould of a minute left valve.

The shells are small and elongated, cuneiform to modioliform, and moderately inflated in the anterior (adjacent to umbonal) part. The valves are equivalve and strongly inequilateral. The umbones are located close to the shell anterior. A triangular depression runs from the umbonal area, widening towards the mid flank. The dorsal margin is straight in lateral profile for the extent of the nymph and ligament area, and then curved ventrally in the postero-dorsal area. The posterior margin is well rounded while the ventral margin is almost straight, feebly indented at the mid-flank. The anterior margin is short and rounded. The shell is moderately inflated in its dorsal aspect and wedge-shaped at both anterior and posterior margins. The exterior ornament consists of commarginal growth lines. The shell interior is smooth. The pallial line is poorly seen. An internal ridge is not present. The anterior adductor muscle scar is rounded with two pedal elevator muscle scars located dorsally. The myophoric buttress is moderately steep. The hinge is stout and edentulous. The nymph and ligament groove are very long and straight.

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