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RESEARCH PAPER

Mass occurrence of the enigmatic gastropod *Elmira* in the Late Cretaceous Sada Limestone seep deposit in southwestern Shikoku, Japan

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Abstract *Elmira* is a medium-to-large gastropod of uncertain systematic affinity, which has so far been reported only from a presumably Eocene methane-seep deposit in Cuba. This study reports a mass occurrence of *Elmira shimantoensis* Kiel and Nobuhara sp. nov. from a Late Cretaceous hydrocarbon-seep deposit in Shikoku, Japan, called the Sada Limestone. Its paleoecology is reconstructed based on its mode of occurrence, carbonate petrology, and stable carbon isotope analyses. The fauna of the Sada Limestone in general is characterized by an abundance of large chemosymbiotic bivalves of the family Thyasiridae and of "*Serpula*" tubes. The mass occurrence of *Elmira shimantoensis* was found in a lens-shaped carbonate body with a flat top and a concave base, 6.5 m in length and less than 2 m in thickness, consisting of multiple layers of shell accumulations, which were formed by shell-winnowing and the filling of a depression in slope mud. The scarcity of *Elmira shimantoensis* elsewhere in the Sada Limestone suggests that it formed locally from a gregarious population in the vicinity of the depression, possibly on hard ground. The matrix of the mass occurrence is rich in dolomite and ankerite, and is less depleted in ^{13}C ($\delta^{13}C$ values of calcite: −5.3 to −2.4 ‰; of dolomite: −8.3 ‰) than the matrix of the enclosing thyasirid-rich and tube-rich limestones. This suggests that the gastropod mass occurrence was cemented below the sulfate reduction zone and has thus undergone little anaerobic methane oxidation. Therefore, *Elmira shimantoensis* is reconstructed here as a bacteria grazer on a hard substrate such as exposed carbonate mounds rather than as a species that relied on chemosynthetic symbionts for nutrition.

Keywords Cretaceous · Chemosymbiosis · Seep carbonate · *Elmira* · Gastropoda

Kurzfassung *Elmira* ist eine mittelgroße bis große Schnecke ungeklärter systematischer Stellung, die bisher nur aus einem vermutlich eozänen Methanquellen-Karbonat auf Kuba bekannt war. In der vorliegenden Arbeit wird ein Massenvorkommen von *Elmira shimantoensis* sp. nov. im Sada Limestone–Ablagerungen einer oberkretazischen Kohlenwasserstoff-Quelle in Shikoku in Japan–beschrieben und seine Paläoökologie basierend auf der Art des Fossilvorkommens, der Karbonatmikrofazies und der Analyse von stabilen Isotopen rekonstruiert. Die wichtigsten Faunenelemente des Sada Limestone sind Massenvorkommen der großen, chemosymbiontischen Muschel '*Thyasira*' *hataii* und von Röhren von serpuliden Würmern. Das Massenvorkommen von *Elmira shimantoensis* befindet sich in einer etwa 6.5 m langen und fast 2 m

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hohen Kalklinse mit einer flachen Oberseite und einer konkaven Basis, besteht aus mehreren fossilreichen Lagen, und entstand vermutlich durch Ablagerung und Auswaschung der Schalen in einer Vertiefung im Meeresboden. Da *Elmira shimantoensis* außerhalb des Massenvorkommens sehr selten ist, wird vermutet, dass sie gehäuft in der Nähe des Einbettungsortes gelebt hat. Die Matrix des Massenvorkommens ist reich an Dolomit und Ankerit und ist weniger stark an ^{13}C abgereichert ($\delta^{13}C$-Werte des Kalzits: –5.3 bis –2.4 ‰; des Dolomits: –8.3 ‰) als die der umgebenden Thyasiriden- und Wurmröhren-reichen Kalke. Das deutet darauf hin, dass die Zementation des Schnecken-Massenvorkommens unterhalb der Sulfatreduktionszone, und damit nur unter geringem Einfluss anaerober Methanoxidation, stattfand. Wir vermuten, dass *Elmira shimantoensis* Bakterienmatten von Hardgründen abweidete und nicht chemosymbiontisch lebte.

Schlüsselworte Kreide · Chemosymbiose · Methanquellen-Karbonat · *Elmira* · Gastropoda

Introduction

Faunal communities at hydrothermal vents and methane seeps in the deep sea are commonly characterized by mass occurrences of only a few species, most of which rely on chemoautotrophic symbionts for nutrition (Van Dover 2000). The main taxa at modern vents and seeps are vestimentiferan tube worms, bathymodiolin mussels, vesicomyid clams, and various crustaceans such as *Rimicaris* shrimps, and "galatheoid" squat lobsters. At hydrothermal vents, such mass aggregations are occasionally also formed by large gastropods harboring endosymbiotic bacteria, such as the provannids *Alviniconcha* and *Ifremeria* in the West Pacific and Indian Oceans, and peltospirids including the *Chrysomallon* in the Indian and Antarctic Oceans (e.g., Both et al. 1986; Okutani and Ohta 1988; Stein et al. 1988; Van Dover et al. 2001; Nakamura et al. 2012; Rogers et al. 2012; Chen et al. 2015a, b, c). At methane seeps, gastropod mass aggregations are formed by the predatory or scavenging conoideans *Phymorhynchus* and *Oenopota* (Sasaki et al. 2007; Fujikura et al. 2009), but seep communities dominated by chemosymbiotic gastropods have never been reported.

Likewise, fossil vent and seep communities are typically dominated by only a few taxa. The main modern chemosymbiotic bivalve groups at vents and seeps, bathymodiolins and vesicomyids, started to dominate these communities in the mid-Eocene (Amano and Kiel 2007; Kiel and Amano 2013), but the appearance of vestimentiferan tube worms is still debated (Little and Vrijenhoek 2003; Kiel and Dando 2009). In contrast, Mesozoic and Paleozoic vent and seep communities were often characterized by monospecific brachiopod mass occurrences (Campbell and Bottjer 1995). As in the modern ocean, mass occurrences of gastropods at fossil seep deposits are rare. Three Early Cretaceous sites in California at which gastropods probably related to modern provannids were abundant in patches of ca. 50 cm diameter are the Bear Creek site (*Paskentana hamiltonensis*; Kiel et al. 2008, fig. 3A; Kaim et al. 2014) and the Cold Fork of Cottonwood Creek and Rocky Creek sites (*Atresius liratus*; Kiel et al. 2008; SK, own observations). Gastropods that were small in size but also abundant are known from three Upper Cretaceous sites in Hokkaido, and include vetigastropods, limpets, and/or abyssochrysoids. These sites are the Omagari site (*Homaplopoma abeshinaiensis*, *Hikidea omagariensis*, *Bathyacmaea* cf. *subnipponica*, and *Serradonta omagariensis*; Hikida et al. 2003; Kaim et al. 2009, 2014), the Yasukawa site (*Hikidea yasukawaensis*, *Hokkaidoconcha hikidai*; Kaim et al. 2009, 2014) and the Kanajirisawa site (*Desbruyeresia kanajirisawaensis* and *Hokkaidoconcha tanabei*; Kaim et al. 2008).

Here we report a mass occurrence of the enigmatic medium-to-large gastropod *Elmira* in the Late Cretaceous Sada Limestone in southwestern Shikoku, Japan. The Sada Limestone encompasses several limestone boulders enclosed in massive siltstone in the Northern Shimanto Belt. The dominant faunal elements are the large thyasirid bivalve "*Thyasira*" *hataii* (Katto and Hattori 1964) and tubular fossils referred to as "*Serpula*", which occur in great numbers throughout the deposit (Nobuhara et al. 2008). Large thyasirids typically derive their nutrition from symbiotic sulfur-oxidizing symbionts (Dando and Southward 1986; Taylor and Glover 2010), and hence the mass occurrence of the large *"Thyasira" hataii* has been used to suggest a seepage-related origin of the Sada Limestone. Gastropods are generally uncommon in this deposit; only a single lens about 100 × 60 × 60 cm in size yielded a moderate number of specimens of the high-spired gastropod *Humpulipsia nobuharai* (Kaim et al. 2014). The gastropod *Elmira shimantoensis* sp. nov. reported here is found sporadically at various places in the Sada Limestone and occurs in large numbers in a lens that is reported here in detail. *Elmira* has so far been reported only from the Elmira asphalt mine seep site in Cuba (Kiel and Peckmann 2007), which is probably of Eocene age (Kiel and Hansen 2015), and its paleoecology is unknown. The aims of the present study are (1) to systematically describe the new species *Elmira shimantoensis* from the Sada Limestone, (2) to make clear the formation process of the mass occurrence based on its modes of occurrence, detailed mapping of its lithologies, and stable carbon and oxygen isotope analyses, and (3) to discuss the paleoecological significance of this mass occurrence (sedimentary process, habitat condition, and seep influence) based on our findings. All figured specimens are deposited at the University Museum, University of Tokyo, Japan (UMUT).

Geologic setting

The Sada Limestone is a group of Upper Cretaceous seep-carbonate rock bodies found near the village of Sada in southwestern Shikoku, Japan (Nobuhara et al. 2008). Geologically, southwestern Shikoku belongs to the Shimanto Belt, a Cretaceous to Miocene accretionary complex running from the Ryukyu Island Arc in the south along the Pacific side of the Japanese Islands of Kyushu and Shikoku, and reaching the Boso Peninsula in central Honshu in the north. This accretionary complex was formed by the northward subduction of the Kula Plate in the northwest Pacific region. In southwestern Shikoku, the Shimanto Belt is subdivided into two subbelts, the Cretaceous Northern Shimanto Belt and the Paleocene to Miocene Southern Shimanto Belt. Both are characterized by turbidite and mélange facies (Fig. 1). Geographically, the boundary area between the northern and southern subbelts is characterized by the Nakasuji Lowland Belt (with an axis in the E–W direction), which consists of uppermost Cretaceous to Eocene basin-to-slope deposits of the Henai Group (Kano et al. 2003). The mudstones and sandstones of the Henai Group unconformably overlie the Shimanto accretionary complex.

The Sada Limestone occurs within the Upper Cretaceous Nakamura Formation in the southern part of the Northern Shimanto Belt, and is located about 2 km north of the northern boundary of the Nakasuji Lowland Belt. The Nakamura Formation consists mainly of mud-dominated turbidites (Kano et al. 2003) and black shales (Tashiro 1980), but the surroundings of the Sada Limestone seep deposit are composed of gray massive siltstone. The exact stratigraphic age of the Sada Limestone is not well constrained; the surrounding Nakamura Formation includes ammonoids, inoceramids, and radiolarians that indicate a Campanian to Maastrichtian age (Matsumoto 1980; Taira et al. 1980). In addition, Tashiro (1980) reported the laternulid bivalve *Periplomya nagaoi* Ichikawa and Maeda (1958) from the Nakamura Formation, which is considered to be restricted to Maastrichtian strata in Japan (the Izumi, Nemuro, and Hakobuchi Groups). The paleobathymetry of the Nakamura Formation was suggested to be shelf to slope based on mollusks and lithology by Tashiro (1991).

The carbonate rock bodies of the Sada Limestone are exposed in patches in an elliptical area (ca. 400 m in NE–SW direction, ca 250 m in NW–SE direction), as shown by Nobuhara et al. (2008) (Fig. 2). The main taxa that characterize the deposit are a large thyasirid bivalve "*Thyasira*" *hataii* Katto and Hattori, and tubular fossils possibly belonging to the serpulids. The limestones include seep-related lithologies such as inverted stromatactoid structures (Nobuhara et al. 2008). The irregular and gradational contact between the carbonate rock bodies and the surrounding siltstone indicates that the Sada Limestone formed autochthonously in the silt deposits of the Upper Cretaceous Nakamura Formation. The gastropod mass occurrence on which the current study focuses was found at

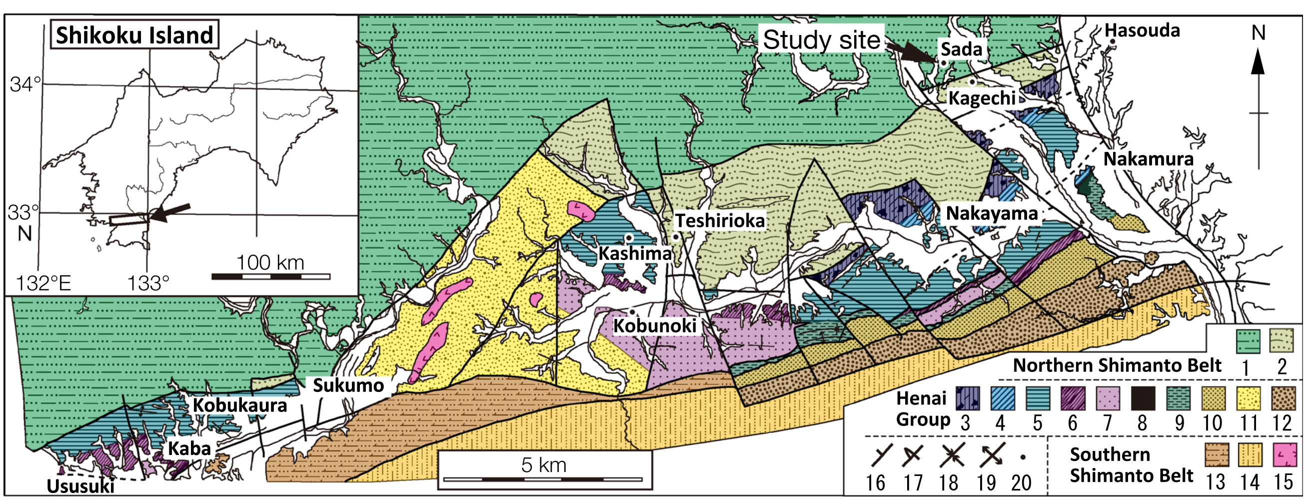


Fig. 1 Geological map of the study area in southwestern Shikoku. Northern Shimanto Belt: *1* Nakamura Formation; *2* Gudo Unit. Henai Group: *3* Kusushima Mudstone Member; *4* Daiyoji Mudstone Member; *5* Marunouchi Mudstone Member; *6* Kaba Mixed Rock Member; *7* Kurokawa Mudstone Member; *8* Iwasaki Mudstone Member; *9* Fuba Shale Member; *10* Uyama Sandstone Member; *11* Hirata Formation; *12* Tanokuchi Formation. Southern Shimanto Belt: *13* Tatsugasako Formation; *14* Hiromi Complex. *15* Neogene intrusive rocks. Symbols: *16* dip and strike of the normal strata; *17* dip and strike of the overturned strata; *18* syncline; *19* anticline; *20* megafossil localities (redrawn from Kano et al. 2003)

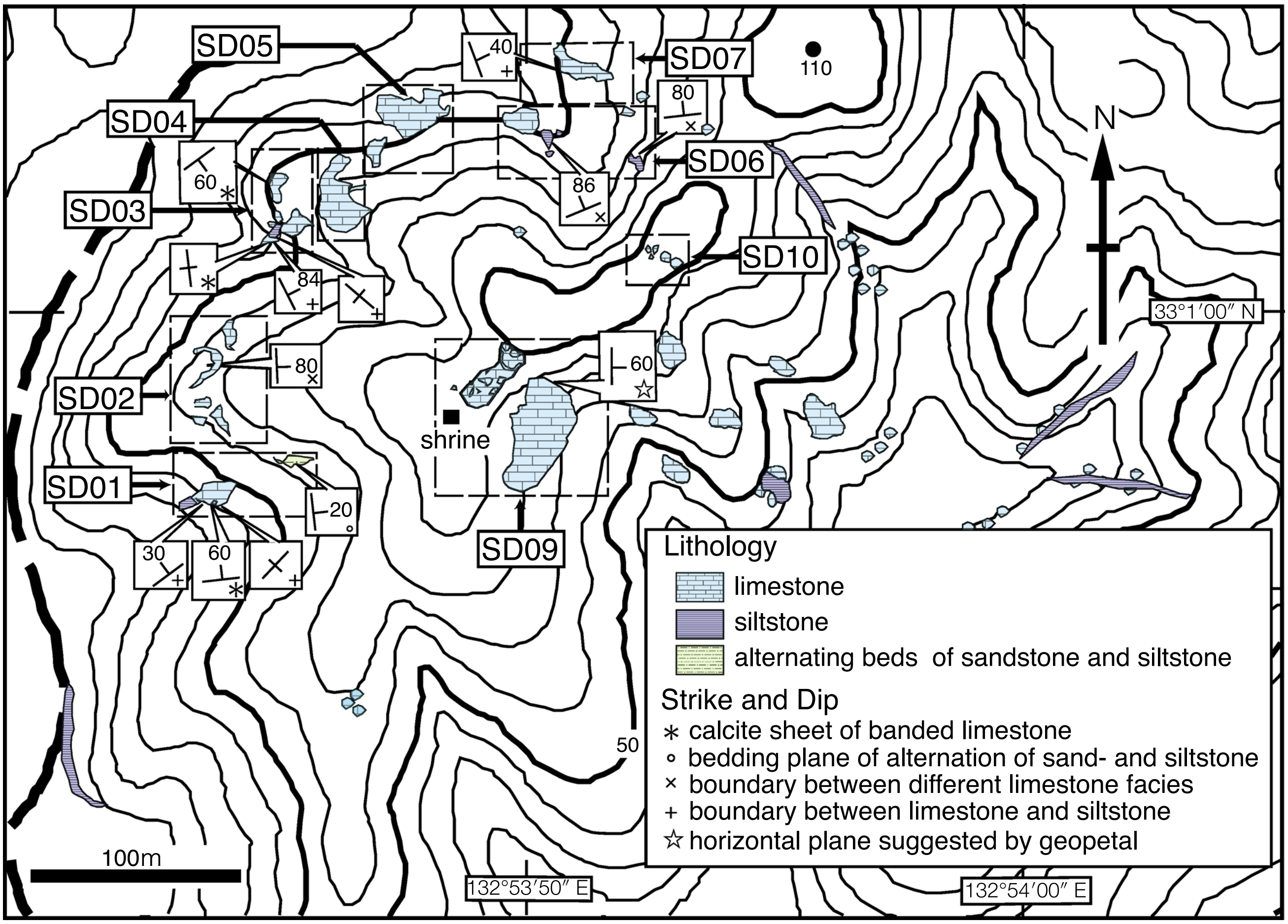


Fig. 2 Distribution of the outcrops of Sada Limestone (after Nobuhara et al. 2008). The gastropod mass occurrence reported here was found in outcrop SD04

the outcrop labeled SD04 in Nobuhara et al. (2008) (Fig. 2), where a large number of carbonate rocks are exposed in Karrenfeld-like conditions on a steep slope over an area of ca. 20 × 40 m spanning and 20 m of altitude (Figs. 3, 4).

Methods

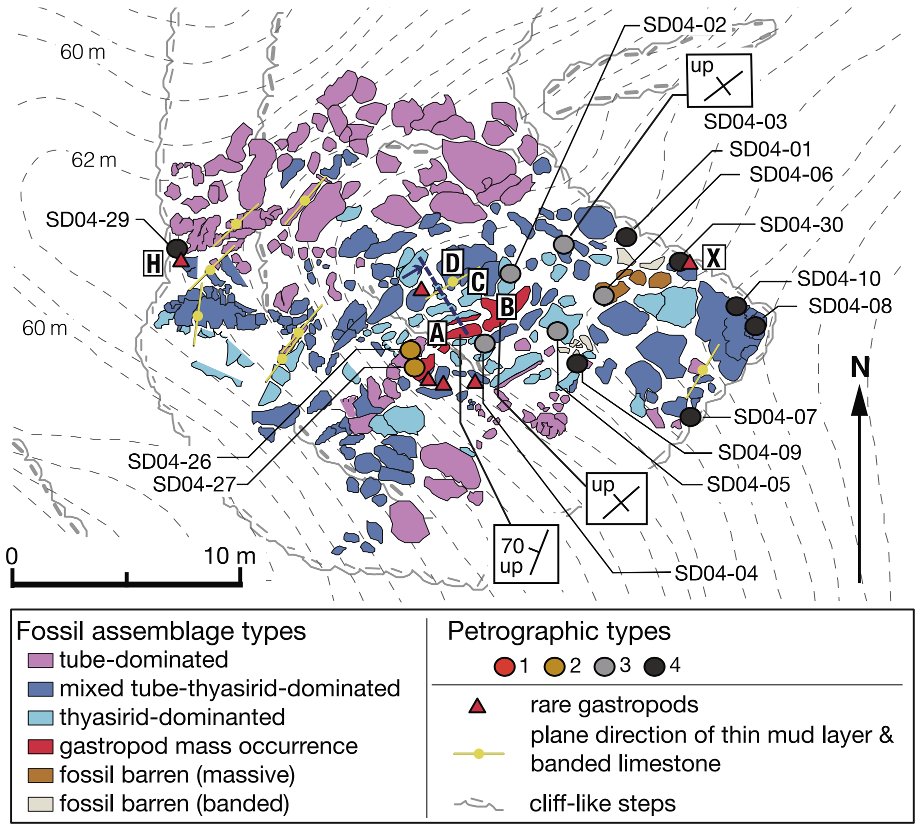
The distribution of sedimentary fabrics and faunal remains at our study site were mapped by covering the rock surfaces with transparent vinyl sheets and marking all relevant features visible to the naked eye using a water-resistant pen. The relevant features included mud clasts and layers, planes of banded zebra-like structure, and faunal remains including geopetal structures. The sheets (4 sheets with a maximum size of 1.2 × 0.8 m) were then photographed and digitized using the software Adobe Illustrator©.

To infer bedding planes of the gastropod-concentrated blocks, we measured trends and plunges of the geopetals (lineation bounding between lower buried mud and upper cement in shells) of two blocks (16 data measurements from block A and 22 measurements from block B), using a digital clinometer. The poles of all lineations were plotted on a Wolf net and hypothetical bedding planes were obtained for all possible pairs of two lineations (120 for block A and 200 for block B). For each block, all poles of hypothetical bedding planes were re-plotted on a Schmidt net to make contour maps of pole distributions. The mode of pole distribution was regarded as the pole of the most plausible bedding plane.

More than 30 rock samples and fossil specimens from the gastropod mass occurrence and the surrounding thyasirid-rich blocks were taken for thin-sectioning, carbon and oxygen isotope analysis, and taxonomic work. Fossil preparation was done either using a pneumatic hammer or by repeated etching of matrix adhering to the fossils with 0.1–0.4 % HCl and removal of the softened matrix by fine needles under a binocular microscope.

In addition to rock samples from the gastropod mass occurrence and its immediate surroundings, supplementary samples from the outcrops SD03, SD07, and SD09 were

Fig. 3 Outcrop sketch of SD04 showing the distribution of fossil assemblages and carbonate types. *Capital letters* (*A*–*D*, *H*, and *X*) indicate rock bodies sampled for fossils and petrographic work. *Blue dotted line* and *arrow* near rocks *A*–*D* indicate the direction and area of the photograph in Fig. 4. *Numbers* with colored circles indicate the locations of the rock samples (numbers 11–25 and 28 are shown in Fig. 4). Strikes, dips, and upward directions are inferred from geopetal lineations (see text for details)



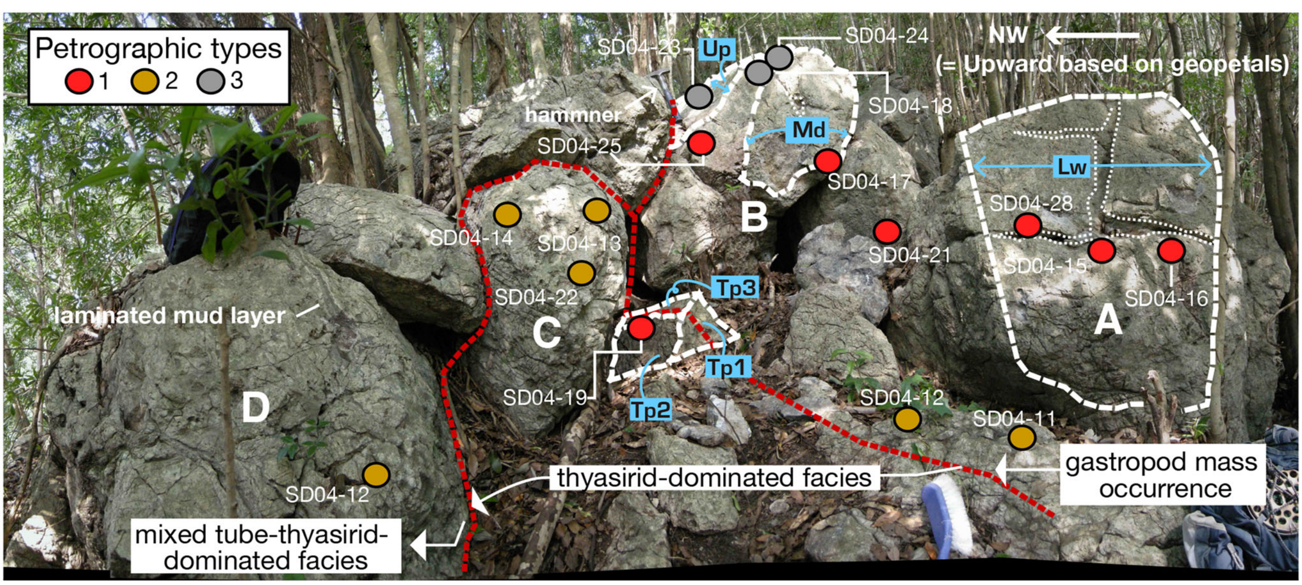


Fig. 4 The outcrop with the gastropod mass occurrence (blocks *A* and *B*) and the neighboring rocks (blocks *C* and *D*); the bedding plane is nearly vertical. Distribution of petrographic types is indicated by *colored circles*; *numbers* indicate sample positions. Areas enclosed by *dashed white lines* (*Lw*, *Md*, *Up*, *Tp1*, *Tp2*, *Tp3*) were investigated for their modes of fossil occurrence (shown in Figs. 12, 13, 14, 15); *dashed red line* indicates boundaries between faunal assemblages. Hammer (length 30 cm) is shown for scale

used for a comparison of the representative lithologies of this deposit (Fig. 2). Polished slab surfaces were observed for all of the samples, and thin sections of representative textures were examined using plane, cross-polarized, and fluorescence microscopy. Thirty-nine powdered samples for X-ray diffraction (XRD) were taken from polished slab surfaces using a hand-held microdrill under a binocular microscope. XRD analyses were carried out using an automated diffractometer (RINT2000 XRD, Rigaku Co. Ltd.) at the Center for Instrumental Analysis at Shizuoka University. Among them, 6 samples from SD04 and 15 supplementary samples from other outcrops of the Sada Limestone were selected for stable carbon and oxygen isotope analyses. Calcite powder samples were analyzed using a continuous-flow isotope ratio mass spectrometry analytical system at Hokkaido University (Ishimura et al. 2004, 2008), which allowed the determination of $\delta^{13}C$ and $\delta^{18}O$ values of as little as 0.2 µg $CaCO_3$ with a long-term external precision of better than ±0.10 ‰ for $\delta^{13}C$ and $\delta^{18}O$. Dolomite powder samples were analyzed following the method of McCrea (1950). Powdered carbonate samples were reacted with 105 % orthophosphoric acid at 25.0 °C under vacuum conditions for 72 h, and the evolved CO_2 gas was transferred into a Finnegan MAT 252 mass spectrometer at Hokkaido University. The analytical precision of the standard sample (calcite) was within ±0.03 ‰ (1 s) for $\delta^{18}O$ and within ±0.02 ‰ (1 s) for $\delta^{13}C$. The $\delta^{18}O$ of the CO_2 extracted from the reaction of phosphoric acid with the carbonate differs from the $\delta^{18}O$ of the initial carbonate. A fractionation factor of 1.01090 between CO_2 and dolomite, and of 1.01025 between CO_2 and calcite, as reported by Sharma and Clayton (1965), was applied for correction. All values are reported relative to the Vienna Pee Dee Belemnite (VPDB) standard.

Fossil assemblages and their distribution

The mass occurrence of the gastropod *Elmira shimantoensis* was discovered in a cluster of several carbonate blocks in the outcrop SD04, mainly blocks A and B in Figs. 3 and 4. This gastropod also occurs sporadically in other blocks in SD04 and in the outcrop SD09, where it is associated with thyasirids or "*Serpula*" tubes, but the mass occurrence seems to be unique to blocks A and B at SD04.

Facies distributions of outcrop SD04 are shown in Fig. 3. The bedding planes inferred from geopetals in the blocks with the gastropod mass occurrence are N28°E, 70°N for block A and N55°E, 90° for block B (Fig. 3). Nearly the same strike and dip (N59°E, 90°) were also observed outside the gastropod mass occurrence (geopetals in two articulated specimens of "*Thyasira*" *hataii* at sampling point 03 in Fig. 3). All the geopetals in these blocks show an upward NW direction. These inferred bedding planes are consistent with the planes of thin intercalated mud layers and zebra-like limestone with inverted-stromatactoid texture whose directions are quite uniform throughout the outcrop SD04 (Fig. 3). Thus, the stratigraphic relation of the rocks appears to have been mostly preserved, despite evidence of shearing of the blocks due to tectonics or topographic movements.

Four types of faunal assemblages are recognized in the outcrop SD04: (1) gastropod mass occurrence, (2) tube-dominated facies, (3) thyasirid-dominated facies, and (4) mixed tube-thyasirid-dominated facies. Facies types 2–4 grade into each other, and were reported as "*Thyasira–Serpula* limestone" by Nobuhara et al. (2008). However, these faunal associations are distinguished here based on the dominance of the respective taxa to facilitate paleoecological discussions. The distribution of the four facies types in the outcrop SD04 is illustrated in Fig. 3. Details of each fossil assemblage are shown below.

Gastropod mass occurrence (Fig. 5a, b)

This assemblage is characterized by the mass occurrence of *Elmira shimantoensis*, typically 20–30 mm in shell diameter (Fig. 6). The carbonate bodies hosting the gastropod mass occurrence show a lens-shaped distribution with a flat top and a concave base, are about 6.5 m in length and less than 2 m in thickness, and are intercalated in the thyasirid-dominated facies (Fig. 3). The gastropod mass occurrence shows multiple layers of shell accumulations enclosed in whitish to pale brown colored muddy matrix, which is in contrast to the dark brown to black matrix seen in the other fossil assemblages. Additional faunal elements include (1) large, articulated specimens of "*Thyasira*" *hataii* (Fig. 7c–e) in random orientations and thus rarely in their living positions, (2) "small elongate bivalves" of unknown taxonomic affinity (their shell outlines indicate that they are not juvenile specimens of "*Thyasira*" *hataii*) reaching 10 mm in length (Fig. 7a, b), and (3) "*Serpula*" tubes with a diameter of less than 10 mm (Fig. 5b).

Tube-dominated facies (Fig. 5f)

Abundant tubular fossils ("*Serpula*") preserved in their presumed upright living positions are enclosed in dark-colored limestone. This is one of the two characteristic fossil assemblages of the Sada Limestone. The tube-dominated facies can be seen in many outcrops of the Sada Limestone, and has for example been illustrated from outcrop SD02 in Nobuhara et al. (2008). In the outcrop SD04, this facies is mainly found in the stratigraphically lower and upper parts, where it changes laterally into mixed tube-thyasirid-dominated facies. The tube-dominated facies also occurs in isolated patches within the

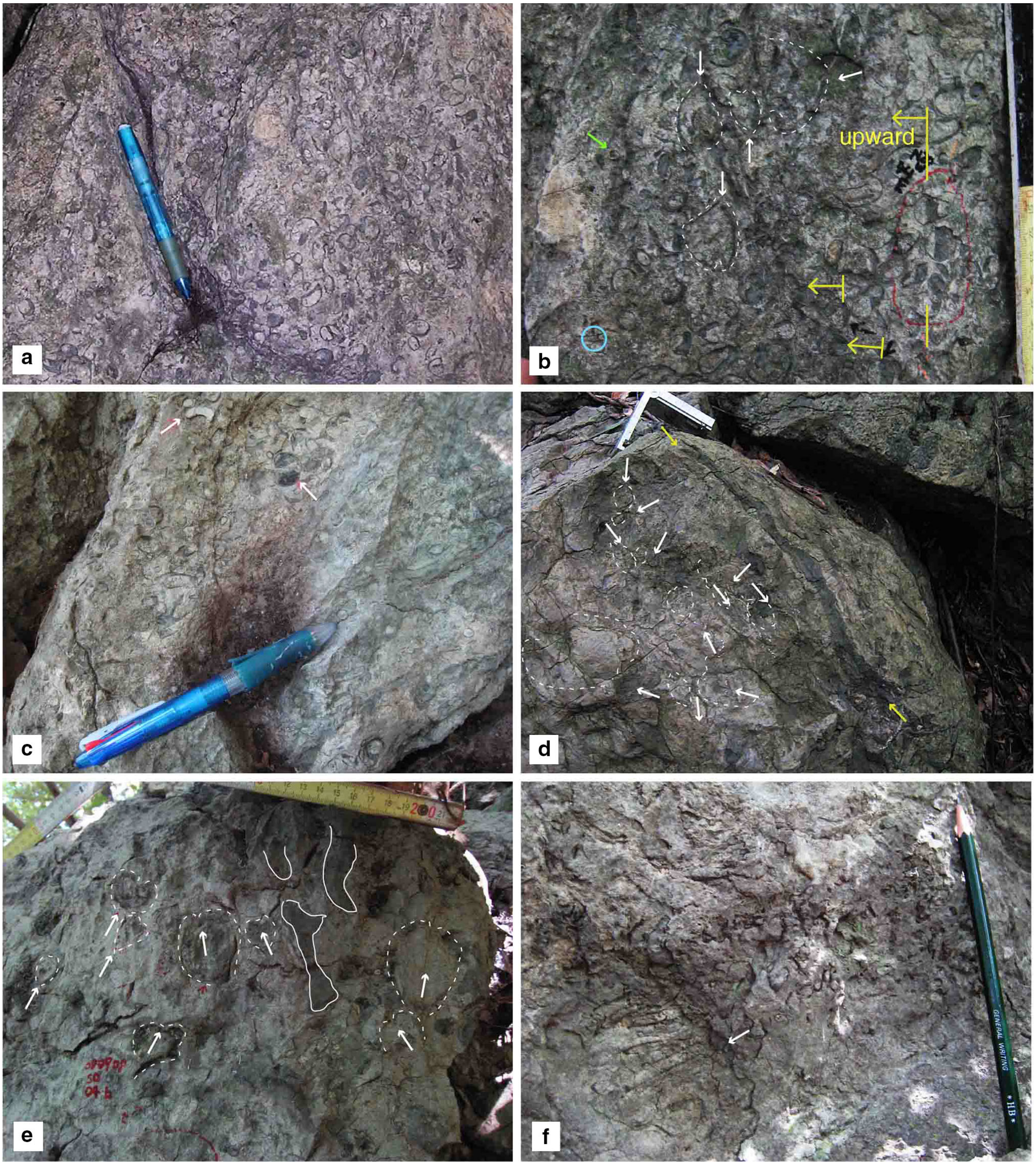
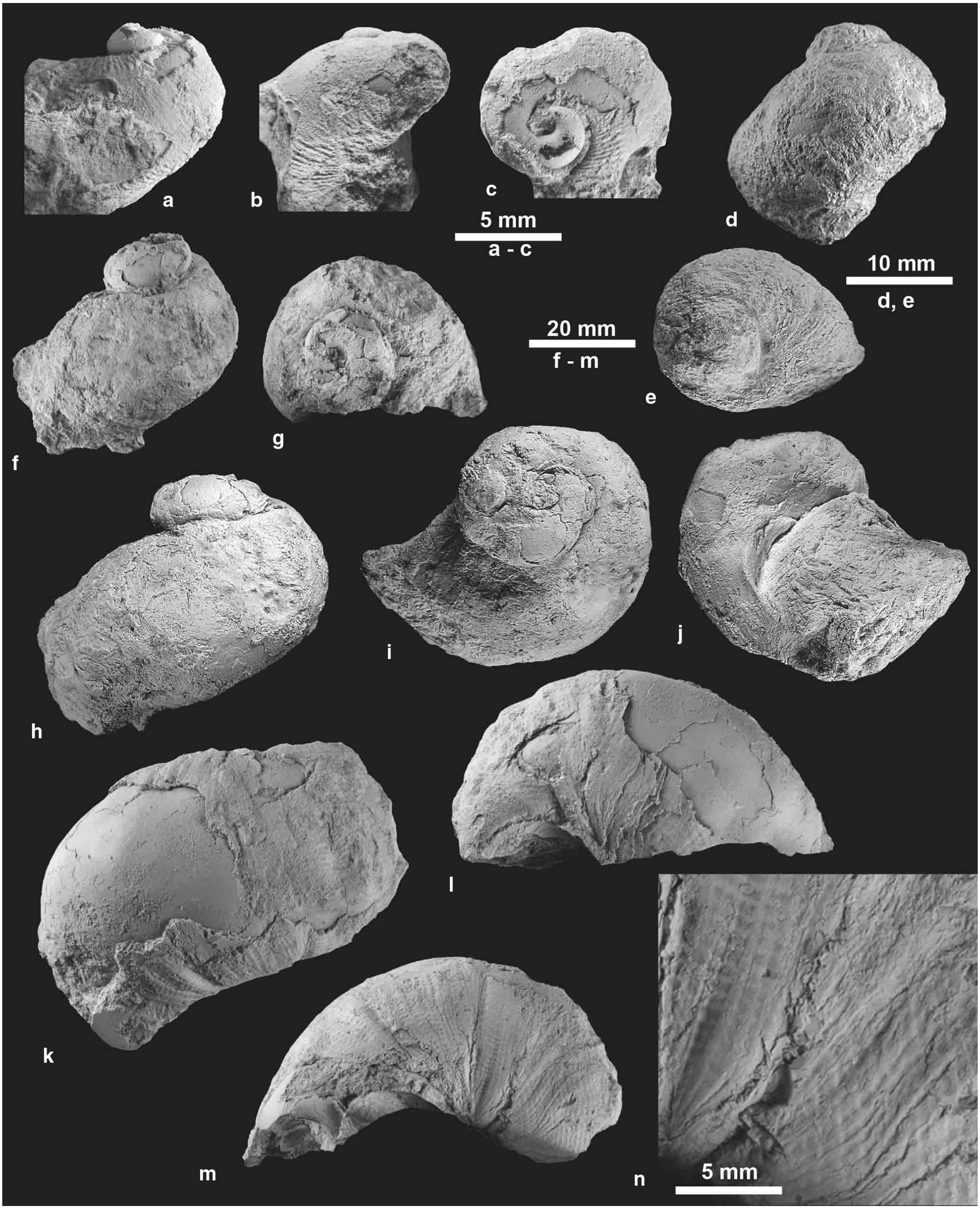


Fig. 5 Field images of outcrop SD04. **a, b** Gastropod mass occurrence: **a** block A; **b** block B, *dotted white lines* indicate articulated thyasirid shells in random orientations (*white arrow* = beak-up direction); worm tubes (*green arrow*) and small bivalves (*inside blue circle*) are rare; *yellow arrows* indicate geopetals. **c, d** Mixed tube-thyasirid-dominated facies; **c** rare occurrences of gastropods (*white arrows*), 2 m below block A; **d** articulated specimen of "*Thyasira*" *hataii* (*dotted lines with white arrows*) in a random orientation compared to the bedding plane of a black mud layer (*yellow arrow*), block D less than 1 m above the top of the gastropod mass occurrence. **e** Thyasirid-dominated facies showing several "*Thyasira*" *hataii* specimens in their living positions (*dotted lines*; *white arrow* = beak-up direction) and burrows (*white lines*), 10 m east of the gastropod mass occurrence. **f** Tube-dominated facies; worm tubes in their living positions (*white arrow*), 10 m laterally away from the gastropod mass occurrence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◀**Fig. 6** *Elmira shimantoensis* Kiel and Nobuhara, a new species from the Late Cretaceous Sada Limestone seep deposit in southwestern Shikoku, Japan. **a–c** Small specimen from SD09 (paratype, UMUT MM 32264). **d, e** Average-sized specimen extracted mechanically from the mass occurrence at SD04 (block A or B; paratype, UMUT MM 32265). **f, g** Large specimen from SD04H showing the general habitus of the species (paratype, UMUT MM 32266). **h–j** Large specimen from SD04H showing the lower and basal part of the inner lip (**j**) (paratype, UMUT MM 32267). **k–n** Holotype UMUT MM 32268, very large specimen from SD09; views of the outer side of the last whorl (**k**), the upper side of the whorl (**l**), the base of the whorl (**m**), and a close-up of the sculpture of the base (**n**)

mixed tube-thyasirid facies in the middle part, for example just to the southwest of the lens with the gastropod mass occurrence (Fig. 3). The maximum observed thickness of this facies exceeds 6 m but may be even greater.

Thyasirid-dominated facies (Fig. 5e)

Large specimens of "*Thyasira*" *hataii* are commonly found in great numbers in dark-colored limestone. This fossil assemblage is common in many outcrops of the Sada Limestone and is the second of its two most characteristic facies. Shells of the infaunal "*Thyasira*" *hataii* are typically articulated, but their orientations indicate two distinct modes of occurrence: (1) in situ burial: in this case almost all of the shells are preserved with the beak oriented upward, indicating their preservation in their living positions, as for example documented at SD09 (fig. 3d in Nobuhara et al. 2008), and (2) reworked through bioturbation or transport for a short distance, as characterized by shells in random orientations. The thyasirid-dominated facies is found in the middle part of outcrop SD04, where it shows a mosaic distribution together with the mixed tube-thyasirid-dominated facies, and reaches a thickness exceeding 7 m.

Mixed tube-thyasirid-dominated facies (Fig. 5c, d)

This is an intermediate type between the tube-dominated and the thyasirid-dominated facies in which both taxa occur in dark-colored limestone in roughly equal

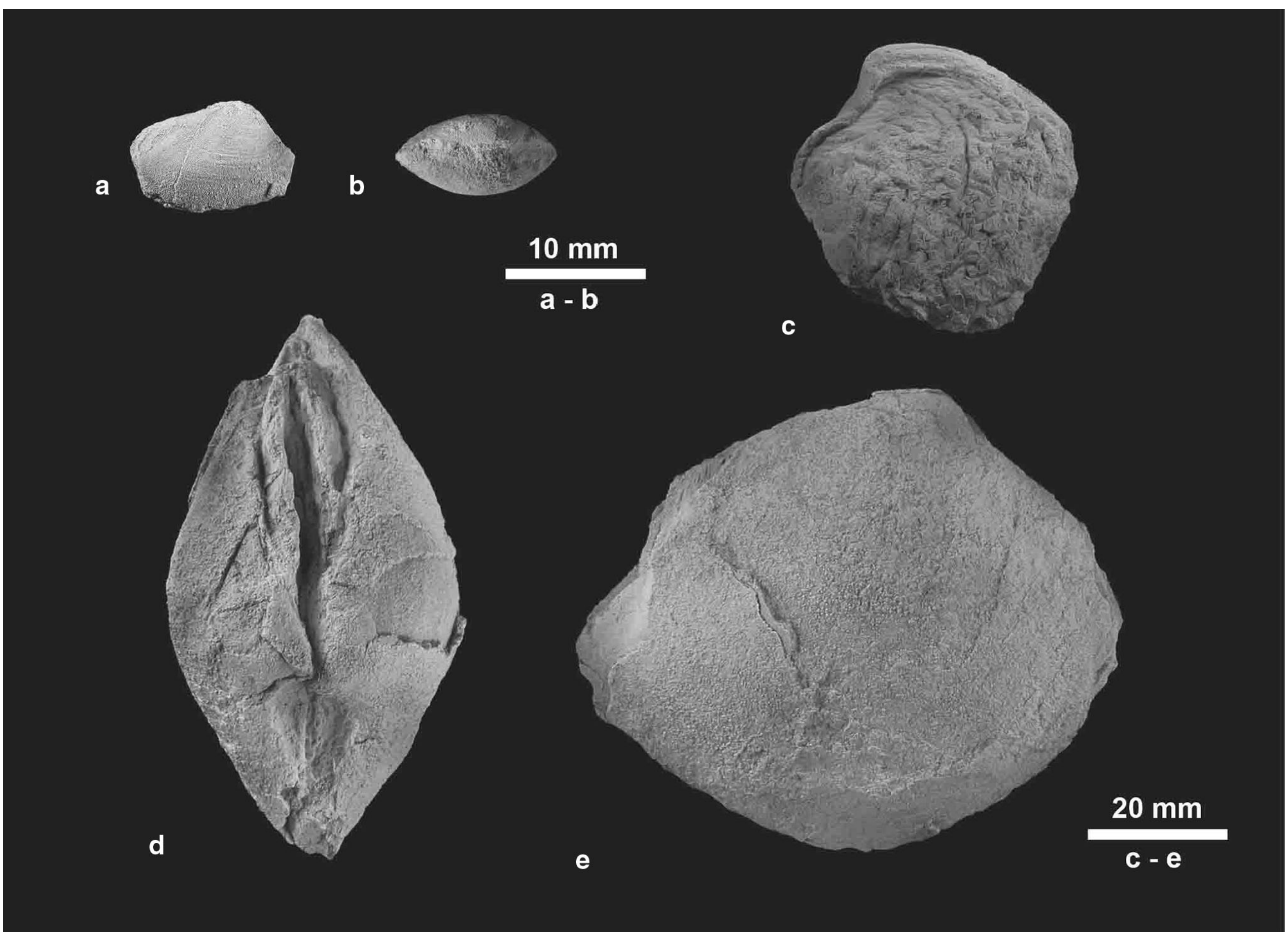

Fig. 7 Fossil bivalves in and around the gastropod mass occurrence from SD04. **a, b** "Small elongate bivalve" from SD04 (block A or B, UMUT MM 32269). **c–e** "*Thyasira*" *hataii* (Katto and Hattori) from SD04H (**c** UMUT MM 32270; **d, e** UMUT MM 32271)

proportions, but less commonly and more patchily than in facies 2 and 3. The thyasirid shells are typically articulated and randomly oriented, and there are occasional gastropod shells (indicated by red triangles in Figs. 3, 5c). This mixed facies dominates the middle part of the outcrop SD04 and also occurs in its lower part, where it laterally grades into the tube-dominated facies. In block B, an approximately 50 cm thick patch of this facies is intercalated in the upper part of the gastropod mass occurrence.

The faunal assemblages show a layered distribution consistent with the bedding planes inferred from geopetals, mud layers, and inverted-stromatacoid textures (Fig. 3). The following approximate temporal variation in fossil biofacies is recognized: dominance of "*Serpula*" tubes with mixed facies at the base; dominance of thyasirid with intercalation of the lens with the gastropod mass occurrence in the middle; and the tube-dominated facies on top.

Petrography

Based on the study of more than 30 polished slabs and thin sections from SD04 and other outcrops of the Sada Limestone, and XRD mineral determinations, we distinguished four petrographically distinct limestone types at SD04. They are described below and representative examples are shown in Fig. 8. These petrographic types are plotted on the outcrop maps (Figs. 3, 4).

Type 1

This petrographic type is characterized by a whitish to pale brown, detritus-rich muddy matrix with large amounts of dolomite and ankerite (bottom in Fig. 8), and its occurrence is restricted to the gastropod mass occurrence (Figs. 3, 4). Neither detritus-poor microsparite nor fissures and voids rimmed by euhedral aragonite or calcite were recognized, except for minute druses lined with euhedral dolomite (Fig. 9b). Enclosed in this muddy dolomicrite are gastropod shells, common plant remains (Fig. 9a), and black muddy clasts a few centimeters in diameter (bottom in Fig. 8). These black muddy clasts as well as the gastropod shells contain large amounts of calcite but no dolomite or ankerite.

Types 2 and 3

These types are characterized by a chaotic mixture of brown and black muddy areas (second and third from the bottom in Fig. 8), and occur in the surroundings of the blocks bearing the gastropod mass occurrence (Figs. 3, 4). Both the brown and black muddy areas consist of micrite containing calcite, dolomite, ankerite, and sometimes aragonite; the black areas are more microsparitic and detritus-poor than the brown areas. The contact between the brown and the black areas is irregular and frequently obscure. The texture of the brown mud on the polished slabs indicates ductile deformation with partial brecciation. The fissures in deformed and broken areas of brown muddy micrite are filled with black detritus-poor micrite. Types 2 and 3 grade into each other but can be distinguished by the dominance of brown over black micrite in type 2, whereas brown and black areas occur in roughly equal proportions in type 3. In addition, type 3 contains small voids infilled by white sparitic calcite, which are not seen in type 2. The distribution of type 2 is restricted to the blocks directly adjacent to the gastropod mass occurrence, whereas type 3 expands more laterally along the horizon of the lens of gastropod mass occurrence (Figs. 3, 4).

Type 4

This type is characterized by the dominance of black microsparite and sparite that encloses gray, mud-rich micrite, and also by abundant white calcitic spar that infills voids of various shapes (top in Fig. 8). It is entirely calcitic; no dolomite or ankerite was detected by XRD. Thin sections indicate that the muddy micrite contains macrosparitic granules (Fig. 9d) and show a chaotic mixture of muddy micrite and microsparite that includes undeformed pelloids (Fig. 9c). When associated with "*Serpula*" tubes, sparite dominates this carbonate type (Fig. 9e, f). Type 4 is the dominant limestone type of the Sada Limestone, as well as at outcrop SD04, but here it is notably absent from the blocks bearing the gastropod mass occurrence (Fig. 3).

Stable isotopic analysis

A cross-plot of $\delta^{13}C$ and $\delta^{18}O$ values of 21 powder samples is shown in Fig. 10: four samples are from the gastropod mass occurrence (limestone type 1); two are from a floatstone in the vicinity of the gastropod mass occurrence (limestone type 3); three are from a tube-dominated rock in outcrop SD03 (limestone type 4); four are from a scarcely fossiliferous massive limestone in outcrop SD03; five are from a banded limestone block in outcrop SD05; and three are from a calcareous siltstone in outcrop SD03. The outcrops SD03 and SD05 are adjacent to outcrop SD04, less than 70 m from it (Fig. 2).

The $\delta^{13}C$ values tend to cluster according to rock type, except for the banded limestone, which shows significant variation in both $\delta^{13}C$ and $\delta^{18}O$. These three clusters include: (1) calcite from in and around the gastropod mass occurrence, with $\delta^{13}C$ values ranging from −5.3 to −2.4 ‰; (2) dolomite in the gastropod mass occurrence, with $\delta^{13}C$ values around −8.3 ‰; and (3) other limestone types, with $\delta^{13}C$ values ranging from −16.4 to −10.5 ‰.

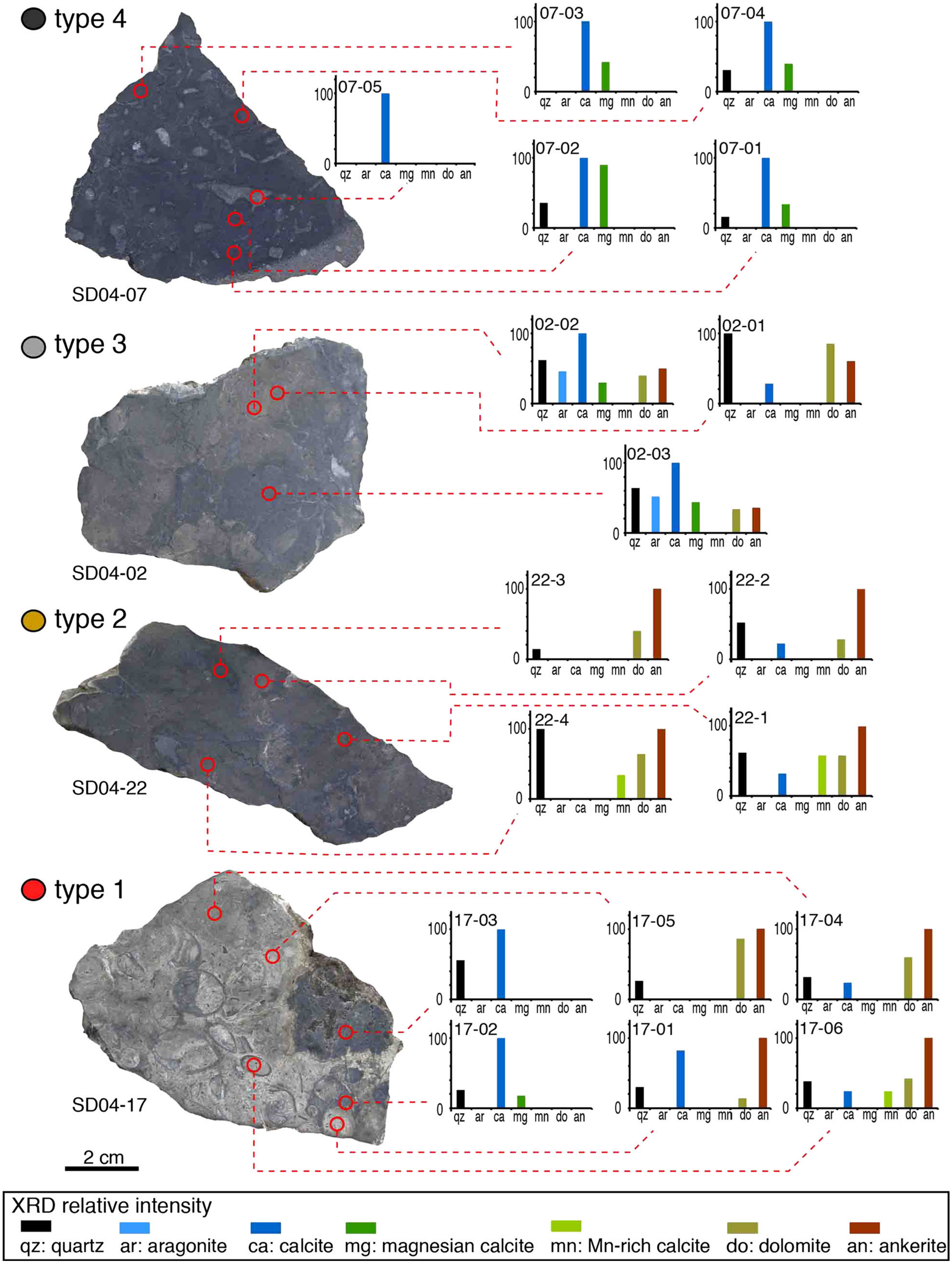

Fig. 8 Textures of polished slabs and mineral phases

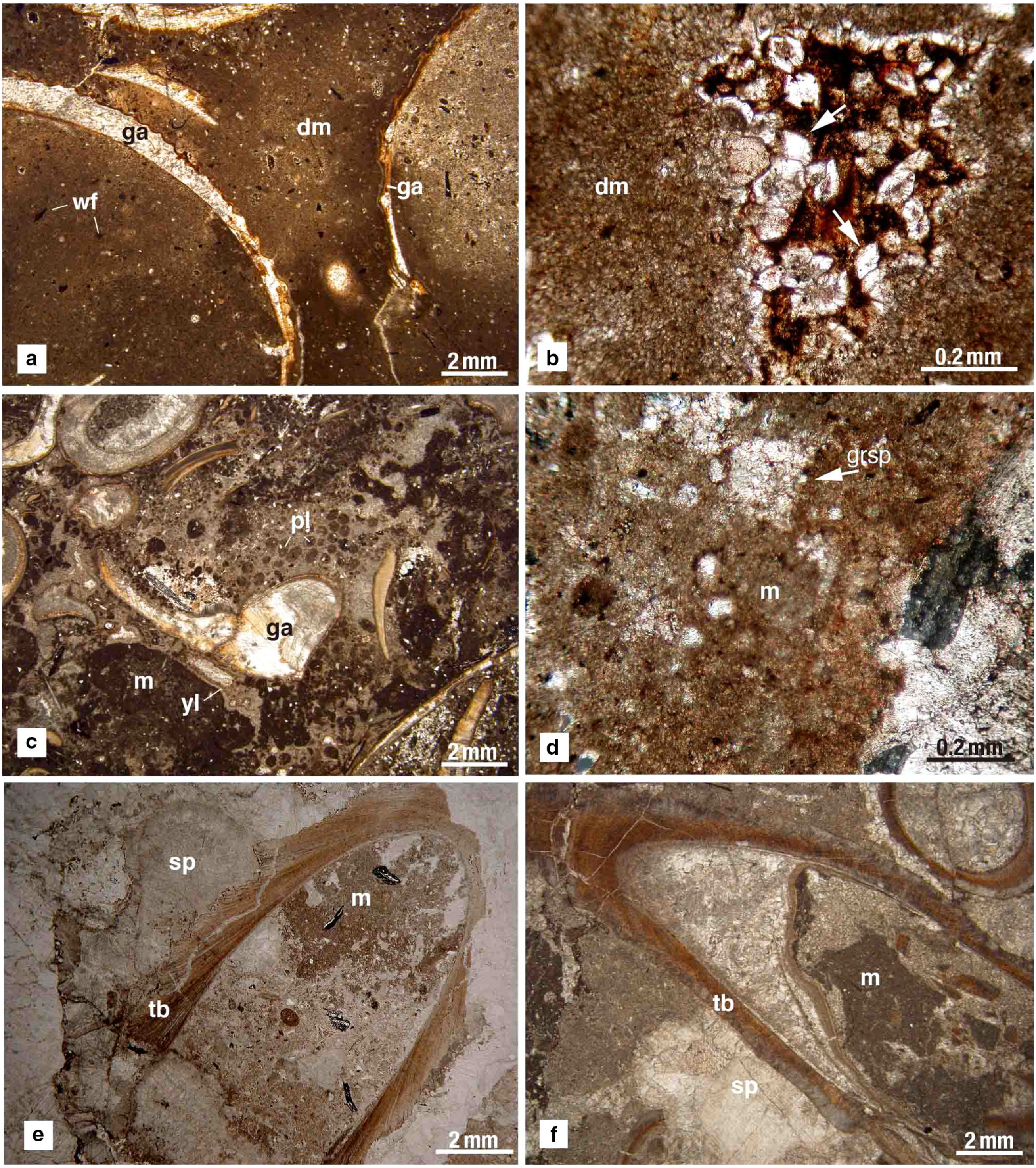

Fig. 9 Thin-section images, obtained in plane-polarized light, of the main facies types described here. **a**, **b** Gastropod mass occurrence. **a** Shells packed in homogeneous dolomicrite (*dm*) with common plant remains (*wf*); outer surface of gastropod shell (*ga*) ornamented by regular undulations; block A. **b** Dolomicrite matrix (*dm*) with minute druse lined with euheral dolomite (*white arrow*); sample 17 in block B. **c**, **d** Mixed tube-thyasirid-dominated facies with a few gastropods (*ga*): **c** muddy micrite (*m*) mixed with detritus-poor micrite enclosing undeformed pelloids (*pl*); void rimmed by yellow calcite (*yl*); block H. **d** Muddy micrite containing microsparitic granules (*grsp*); sample 07. **e**, **f** Tube-dominated facies; note the dominance of sparitic fabrics (*sp*) over muddy micrite (*m*); outer surface of tubes (*tb*) corroded, pelloids rare (**e** = floatstone from SD04, **f** = SD02)

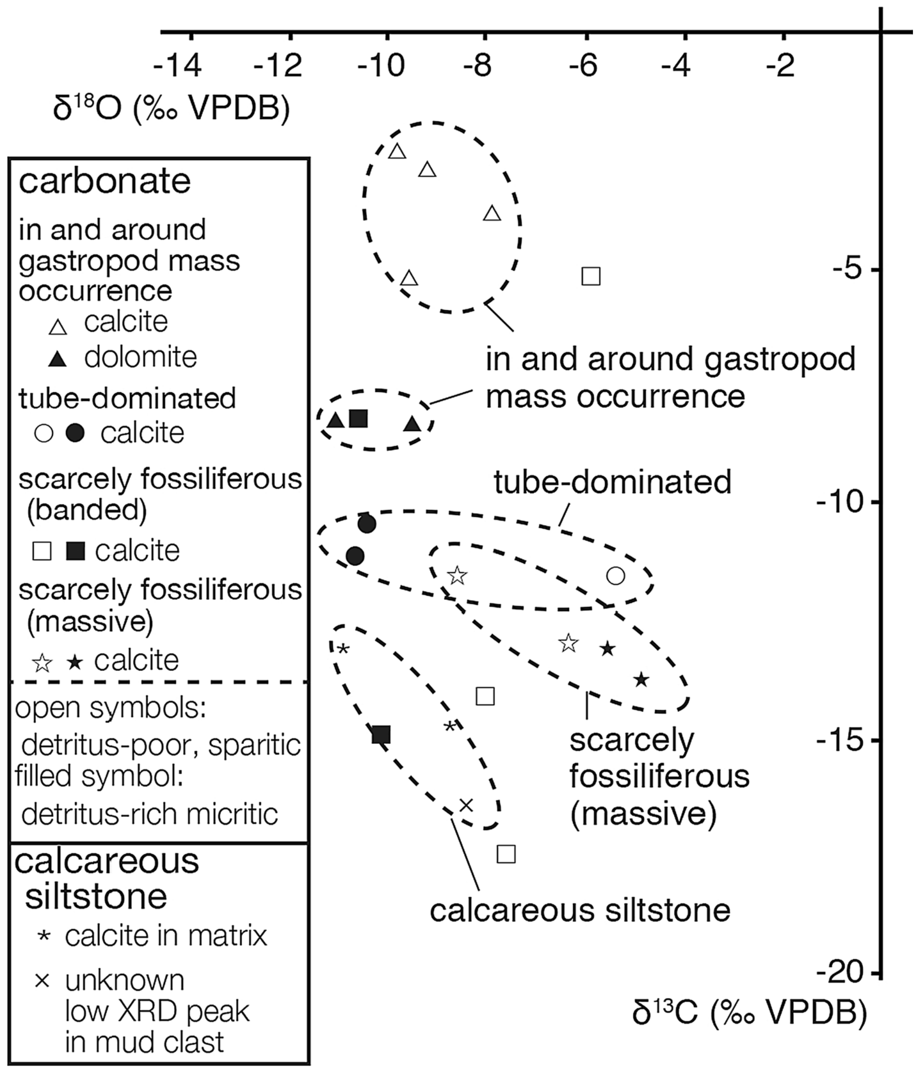

Fig. 10 Cross-plot of stable carbon and oxygen isotope compositions of Sada Limestone

The third cluster shows a trend toward more negative δ^{13}C values from the tube-dominated limestone to the scarcely fossiliferous massive limestone and calcareous siltstone. The δ^{18}O values of the clusters range from −11.0 ‰ (dolomicrite, gastropod mass occurrence) to −4.9 ‰ (micrite, scarcely fossiliferous block), but the values overlap and do not show a clear trend.

Geometry of the gastropod mass occurrence

The succession of faunal assemblages and the geometry of the gastropod mass occurrence of the outcrop SD04 are schematically shown as a columnar section in Fig. 11. The gastropod mass occurrence forms a lens-like body with a flat top, 6.5 m long and 2 m thick, embedded in thyasirid-dominated to mixed tube-thyasirid-dominated facies (Fig. 3). The modes of fossil occurrence and sedimentary structures were mapped on the four main surfaces of the gastropod mass occurrence. These are indicated as Lw (lower), Md (middle), Up (upper), and Tp (top) in Fig. 4, and the results are shown in Figs. 12, 13, 14, and 15. The gastropod mass occurrence is composed of multiple layers of shell accumulations (blue dotted lines in Figs. 12, 13, and 14). These layers are parallel to the bedding planes, as indicated by the geopetals (red line segments in Figs. 12, 13, and 14). In the lower and middle parts of the gastropod mass occurrence, the shell layers are cross-stratified in a low-angle wedge shape (up to 20°; Figs. 12, 13), and are nearly horizontal in the upper part (Fig. 14). Within the upper part there is an approximately 50 cm thick area with the mixed tube-thyasirid facies, again with a gastropod-rich layer on top (Fig. 14). In this uppermost part of the gastropod mass occurrence, articulated specimens of a "small elongate bivalve" (i.e., elongated shells that are clearly not juvenile specimens of "*Thyasira*" *hataii*) occur about as abundantly as the gastropod. Toward the top, the abundance of gastropod shells decreases abruptly and the small elongate bivalve becomes dominant (Fig. 15). This small

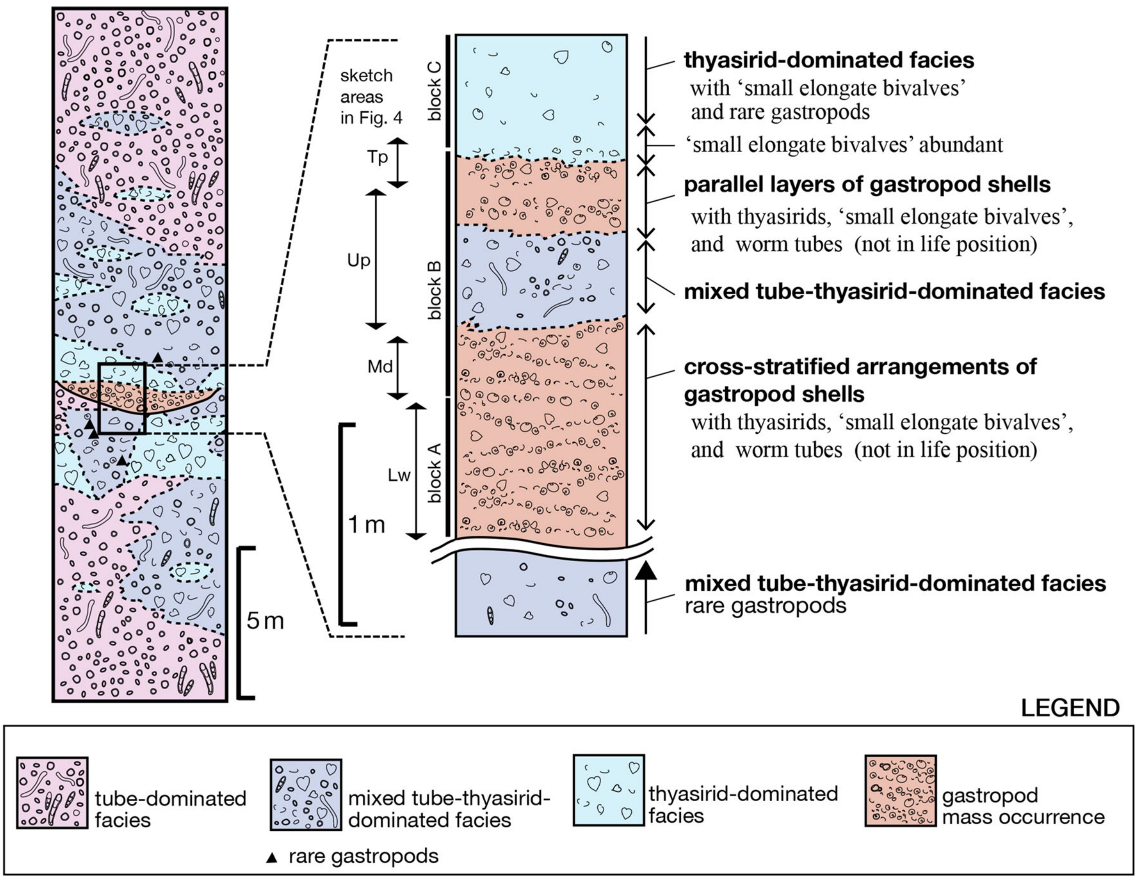

Fig. 11 Schematic columnar section of outcrop SD04

elongate bivalve also occurs sporadically in the thyasirid-dominated facies just above the gastropod mass occurrence (block C in Fig. 4).

The gastropod shells are densely packed and supported by a muddy matrix, partly forming shell-supported clusters. The state of preservation of the shells is rather uniform throughout the deposit, and is a mixture of well-preserved shells and many fragments of shell walls and columellas. They are well sorted for size: most specimens (fragments as well as well-preserved shells) are 20 mm or less in diameter. We have not seen any individuals larger than 30 mm in the mass occurrence, although specimens reaching as large as 70 mm in diameter were collected from other outcrops of the Sada Limestone. The specimens appear to be randomly oriented, although the exact orientation of the globular shells was often difficult to discern. Most fragments of the "*Serpula*" tubes occur in random orientations and are also in the size range 20–30 mm, except for the mixed tube-thyasirid-dominated facies intercalated in the upper part of the gastropod mass occurrence (Fig. 14), where they reach larger sizes (up to 50 mm in length). In addition, small fragments of the true serpulid *Propomatoceros* are scattered throughout the deposit (Vinn et al. 2013).

Many bivalve shells within the gastropod mass occurrence are closed or open-articulated, and some were deformed by the sedimentary load. The proportion of articulated vs. fragmented specimens and the degree of fragmentation cannot be evaluated because bivalve and gastropod fragments are difficult to tell apart on the outcrop surfaces. Most bivalve specimens were found in random orientations (Figs. 5b, 12, 13, 14, and 15). The small elongate bivalves are well sorted for size: almost all are less than about 10 mm in height. In contrast, shells of "*Thyasira*" *hataii* are commonly 40–60 mm in shell height. Smaller "*Thyasira*" *hataii* specimens may be present as well, but in cross-section they are difficult to distinguish from other small bivalve species.

Systematic paleontology

Genus ***Elmira*** Cooke (1919).

Type species. *Elmira cornuartietis* Cooke 1919, from the Eocene of Cuba (Cooke 1919; Kiel and Hansen 2015).

Remarks. The systematic position of *Elmira* is unclear. As noted by Kiel and Peckmann (2007) the "scaly foot snail" *Chrysomallon squamiferum* from hydrothermal vents in the

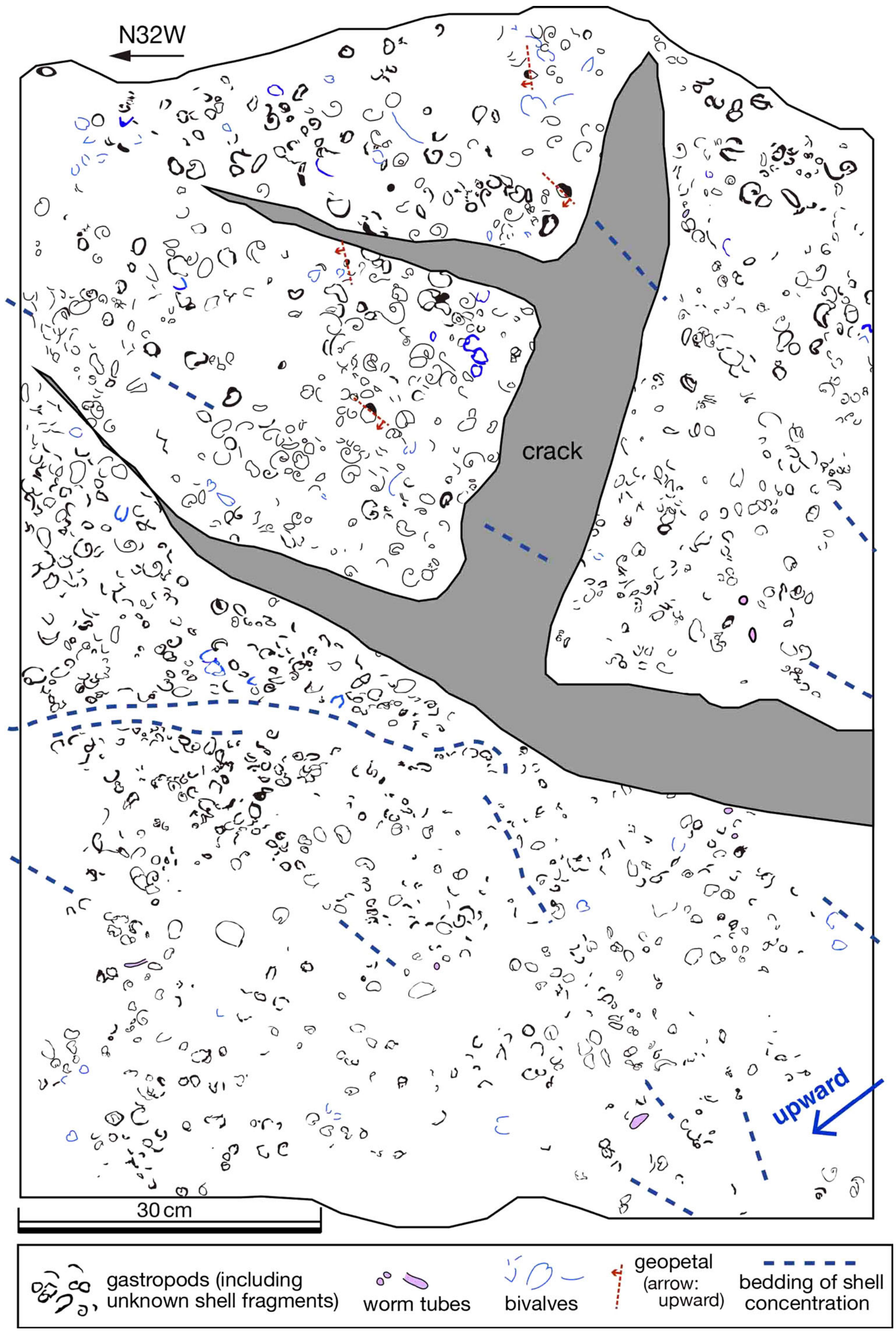

Fig. 12 Distribution of fossils in the lower part of the gastropod mass occurrence (block A, “Lw” in Fig. 4). Outcrop surface (strike of N32°W; dip of 68°W) is near-vertically above the hypothetical bedding shown in Fig. 3

Indian Ocean (Warén et al. 2003; Chen et al. 2015b) is similar to *Elmira* regarding general shell shape. It differs from *Elmira* by having a broader aperture and especially by the much more oblique angle (relative to the spire) of the inner lip of the aperture. Furthermore, the growth lines of *Elmira* are straighter than in *Chrysomallon squamiferum*. Also, the recently reported peltospiroid *Gigantopelta* that inhabits hydrothermal vents on the Scotia Ridge near Antarctica (Rogers et al. 2012; Chen et al. 2015c) has a similar shell. As in the case of *Chrysomallon squamiferum*, the inner lip of the aperture is more oblique than in *Elmira*, and the growth lines of *Gigantopelta* are more oblique than in *Elmira*. Both *Gigantopelta* and *Chrysomallon* belong to the Peltospiridae, a clade characterized by crossed lamellar shell microstructure (Kiel 2004; also confirmed in *Gigantopelta*, SK pers. obs.). Crossed lamellar shell

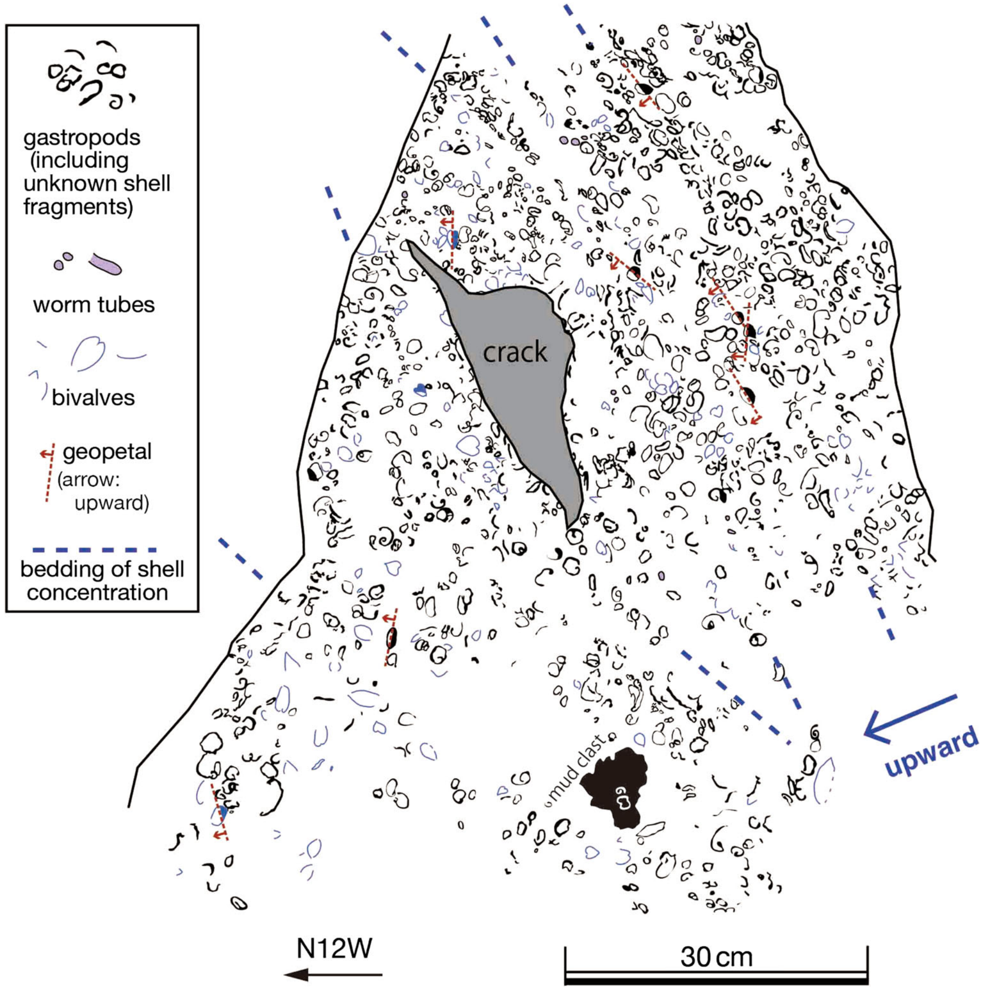

Fig. 13 Distribution of fossils in the middle part of the gastropod mass occurrence (block B, area "Md" in Fig. 4). Outcrop surface (strike of N12°W; dip of 87°W) is near-vertically above the hypothetical bedding shown in Fig. 3

microstructure has also been documented for the type species of *Elmira* (Kiel and Peckmann 2007); taxonomic affinity of *Elmira* to the peltospirids therefore appears possible. While vent-restricted provannids such as the extant *Alviniconcha* (Okutani and Ohta 1988) and the fossil *Kaneconcha knorri* (Kaim et al. 2012) have similar shells and crossed lamellar shell microstructure, the provannids have extremely thin shells, unlike *Elmira* (Kiel 2004; Kiel and Peckmann 2007).

Elmira shimantoensis Kiel and Nobuhara sp. nov.
Figure 6.

Etymology. For the Shimanto River near the type locality.
Holotype. Large specimen with well-preserved surface sculpture from Loc. SD09 (Fig. 6k–n, UMUT MM 32268).

Paratypes. A small specimen from Loc. SD09 (Fig. 6a–c, UMUT MM 32264); a medium-sized specimen from Loc. SD04 (block A or B) (Fig. 6d–e, UMUT MM 32265); two large specimens from Loc. SD04H (Fig. 6f–g, UMUT MM 32266; Fig. 6h–j, UMUT MM 32267).

Studied material. Countless specimens from SD04 (mostly blocks A and B; two specimens from block H), two specimens from SD09.

Locality and horizon. Sites SD04 and SD09 in the Sada Limestone intercalated in the Campanian to Maastrichtian Nakamura Formation, Kochi Prefecture, Shikoku, SW Japan.

Diagnosis. Turbiniform to naticiform shell with rapidly expanding whorls, large for the genus; sculpture consisting of fine spiral threads crossed by irregular, sinuous, opisthocline growth lines; aperture broad and oblique. The largest specimen is 70 mm wide.

Description. Shell turbiniform to naticiform, suture deep, with short ramp below; whorl profile convex, with greatest diameter just below midline; growth lines slightly sinuous, forming broad wrinkles in large specimens; in small specimens (<10 mm) these wrinkles form irregular axial ribs; sculpture in large specimens consisting of indistinct spiral threads forming elongate tubercles at intersections with the sinuous axial wrinkles; aperture broad, with

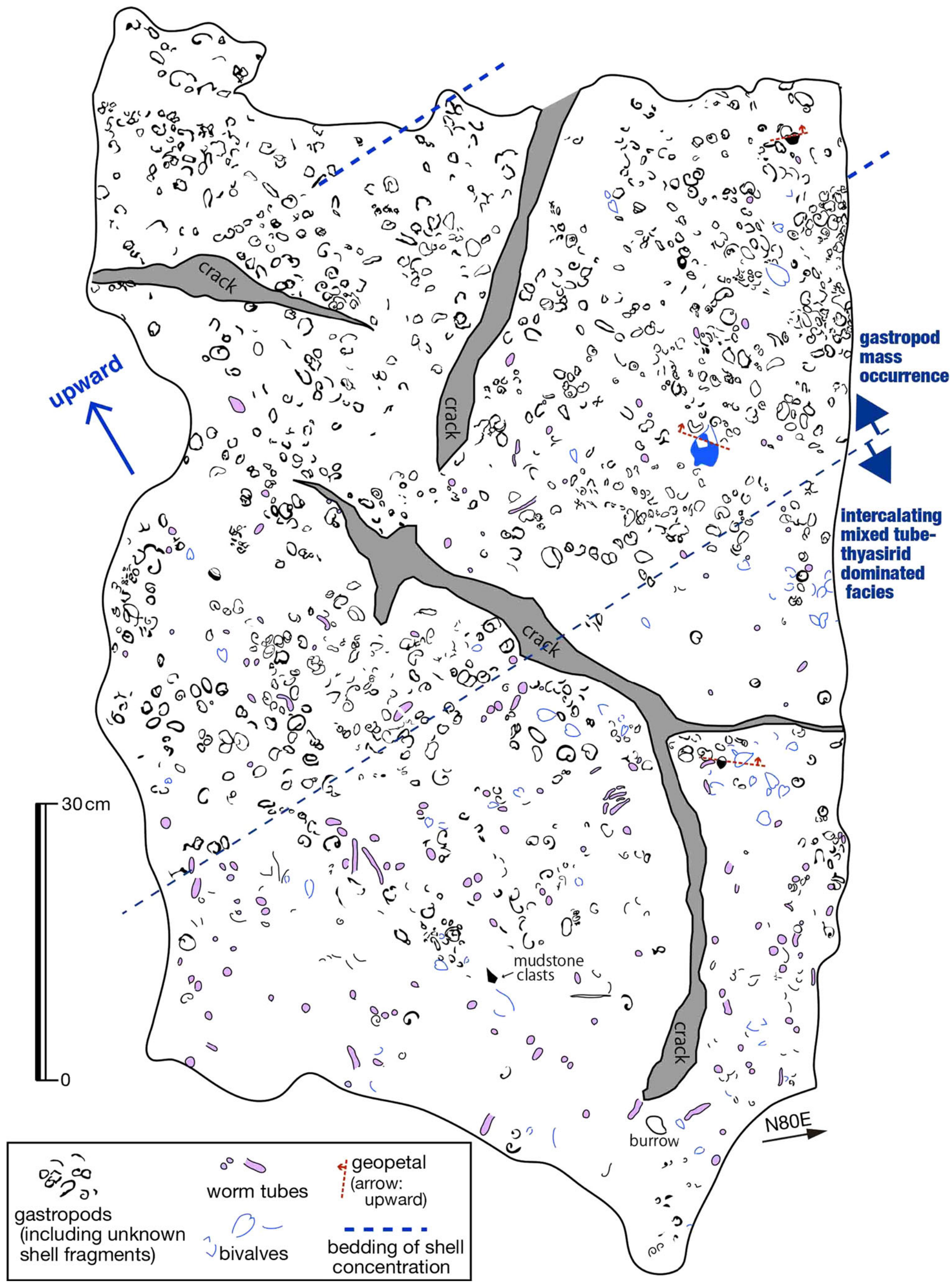

Fig. 14 Distribution of fossils in the upper part of the gastropod mass occurrence (block B, "Up" in Fig. 4). Outcrop surface (strike of N80°E; dip of 40°N) is oblique to the hypothetical bedding shown in Fig. 3

callused, straight, and slightly oblique inner lip, basal part of inner lip with sharp edge; no umbilicus.

Remarks. *Elmira* has so far only been reported from the Eocene of Cuba (Cooke 1919; Kiel and Hansen 2015). *Elmira shimantoensis* differs from the Cuban species by being larger, having a higher spire, and by apparently lacking coarse spiral cords. *Elmira shimantoensis* also resembles *Margarites sasakii* Kaim et al. 2009 from the Upper Cretaceous Omagari seep site in Hokkaido, but that species barely exceeds 1 cm in maximum diameter. If that species does indeed belong to *Margarites*, then it should have a nacreous shell (Hedegaard 1997), in contrast to the crossed lamellar shell structure of *Elmira*.

Discussion

We focus on the formation process and background of this unusual mass occurrence of *Elmira shimantoensis*. Its lens-like shape with the upper boundary showing a gradual

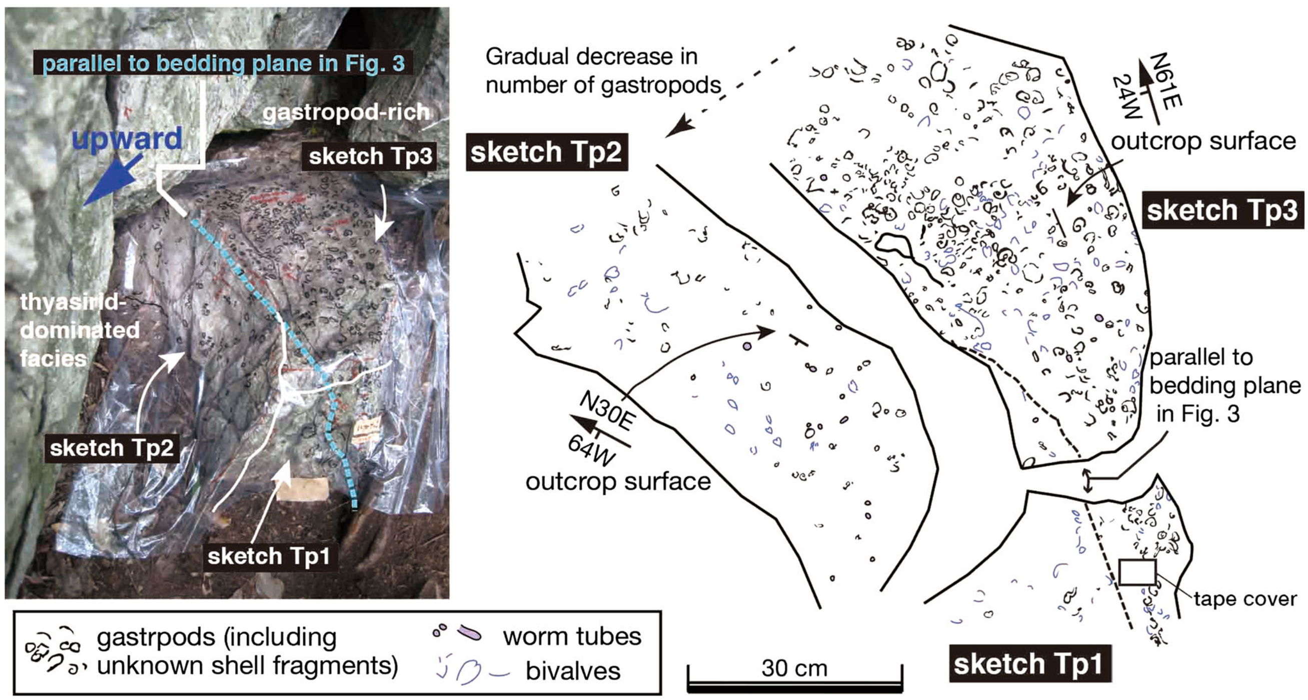

Fig. 15 Field photograph and distribution of fossils at the top of the gastropod mass occurrence (blocks B and C, areas "Tp1," "Tp2," "Tp3" in Fig. 4). *Blue dotted line* indicates the boundary between the gastropod mass occurrence and the area dominated by the "small elongate bivalve" parallel to the bedding plane shown in Fig. 3

transition between faunal assemblages without any lithological discontinuity (Fig. 15) precludes it from being an olistolith, i.e., as an allochthonous rock body transported by submarine sliding. Moreover, *Elmira shimantoensis* is occasionally found in the surrounding mixed tube-thyasirid-dominated facies, but never in the surrounding mudstone, indicating that this species was tied to the environmental conditions representing the facies of the Sada Limestone.

The limestone blocks with the gastropod mass occurrence and the blocks in their immediate surroundings have a peculiar petrography characterized by micrite rich in dolomite and ankerite. In contrast, the widespread "*Serpula*"-dominated facies lacks these minerals and consists instead of calcitic micrite with cavities filled with sparite. Dolomite precipitation is generally inhibited by high sulfate concentrations (Baker and Kastner 1981), so authigenic dolomite is typically associated with pore fluids below the sulfate reduction zone (Greinert et al. 2001). Ankerite and dolomite-rich carbonates may precipitate on the seafloor when Fe-rich fluids seep at high rates, typically in the form of dolomite chimneys (e.g., Jørgensen 1992; Takeuchi et al. 2001; Díaz-del-Río et al. 2003). However, no such chimneys were seen in the Sada Limestone, and we assume that dolomite precipitated below the sulfate reduction zone. Ankerite is generally rare in seep carbonates, and has been interpreted as late diagenetic cement that forms below the sulfate reduction zone (Martin 1999; Peckmann et al. 2001; Díaz-del-Río et al. 2003). Moreover, lithology types 1 and 2, which prevail in the gastropod mass occurrence and its immediate surroundings, lack voids and include shells that show evidence of deformation due to sediment load (Fig. 5d). This suggests a high sediment load before the onset of cementation. In contrast, lithology type 4, which prevails in the widespread "*Serpula*"-dominated facies, is characterized by a chaotic mixture of muddy micrite and microsparite that includes undeformed peloids (Fig. 9c), indicating cementation of the muddy sediments before the onset of compaction due to sedimentary load.

The $\delta^{13}C$ values of the gastropod mass occurrence and its vicinity range from −5.3 to −2.4 ‰ in calcite and are around −8.3 ‰ in the dolomite. These values are thus less negative than in other outcrops around the Sada Limestone, where the $\delta^{13}C$ values of calcite range from −16.4 to −10.5 ‰. Neither of these values are clearly indicative of methane seepage; instead, the less depleted values from the gastropod mass occurrence are consistent with carbonate precipitation—including dolomite and ankerite—below the sulfate reduction zone, and thus with little influence of methane seepage.

Several lines of evidence suggest that the gastropod mass occurrence formed through a combination of repeated transport of shells, sedimentation events, and bioturbation.

Transport of the shells is suggested by the size sorting of the shells: the average size of around 20–30 mm in the mass accumulation suggests that the transporting current could only move shells up to 30 mm in diameter, whereas larger specimens (as found in other parts of the Sada Limestone) were not transported. Furthermore, the fragments of the "*Serpula*" tubes rarely exceed 30 mm in size. The large shells of "*Thyasira*" *hataii* and their random orientations, on the other hand, are interpreted as indicating that they lived in situ and were later redeposited through bioturbation. Repeated sedimentation events are indicated by the multiple layers of shell accumulations (Figs. 12, 13, 14, and 15). The lens-like geometry of the gastropod mass occurrence with a trough-like bottom and a flat top suggests the presence of a depression or scour that experienced repeated inflows of sediment until it was filled.

The extremely large numbers of *Elmira shimantoensis* in the mass accumulation are surprising, considering that this species is very rare elsewhere in the Sada Limestone, which occurs in more than ten large outcrops consisting of the thyasirid-dominated facies (Fig. 2). It seems unlikely that this mass occurrence is explained solely by winnowing; instead, we assume that *Elmira shimantoensis* locally formed highly abundant populations near the depressions in which the shells were accumulated. We speculate that *Elmira shimantoensis* generally preferred hard substrate and only occasionally lived on soft, muddy bottoms, like those inhabited by epifaual "*Serpula*" and infaunal "*Thyasira*" *hataii*. "*Serpula*" attached to tube walls, each other, or to shell fragments, and over half of the tube was buried in the mud. Carbonate rocks are frequently exposed at methane seep sites due to the winnowing of soft sediment on and around the carbonate slabs that formed in the shallow subsurface (Juniper and Sibuet 1987; Greinert et al. 2001; Cordes et al. 2010). Although speculative, this explanation seems feasible because (1) moderately sized trochiform gastropods tend to prefer hard substrate (Beesley et al. 1998), and (2) our hypothesis for the mass accumulation of *Elmira shimantoensis* involves bottom currents that are strong enough to transport moderately sized gastropod shells.

Gastropod mass aggregations are known from a few present-day methane seep sites (Sasaki et al. 2007; Fujikura et al. 2009), and are more common in hydrothermal vent environments (Both et al. 1986; Okutani and Ohta 1988; Stein et al. 1988; Van Dover et al. 2001; Nakamura et al. 2012; Rogers et al. 2012; Chen et al. 2015b). Whereas vents are typically colonized by medium-to-large chemosymbiotic gastropods such as *Alviniconcha, Ifremeria*, and *Chrysomallon*, the mass aggregations at seeps consist of the predatory conoidean *Phymorhynchus* and *Oenopota*. Many "turrid" conoids generally feed on polychaetes (Beesley et al. 1998), which are typically abundant at seeps, and Fujikura et al. (2009) showed that *Phymorhynchus buccinoides* at a seep site in Sagami Bay, Japan, fed on a *Bathymodiolus* colony. In some modern vesicomyid-dominated seeps, small-sized bacteria and detritus grazers such as *Provanna* are also abundant on hard substrates such as shells of living clams (Sasaki et al. 2007).

The feeding strategy of *Elmira* is unknown. We consider *Elmira* to be related to either the provannids or to the peltospirids, two clades which both include grazing deposit feeders as well as chemosymbiotic species (e.g., Fretter 1989; Sasaki et al. 2010; Chen et al. 2015b). Several lines of evidence suggest that the rates of seepage at the Sada Limestone were low (dominance of infaunal chemosymbiotic bivalves and epifaunal suspension feeders such as "*Serpula*"-like tube worms; rather high $\delta^{13}C$ values; and the dominance of micrite over characteristic seep cements, i.e., Peckmann et al. 2009; Kiel et al. 2014; Kiel 2015). Considering that *Elmira* most likely belongs to either of two gastropod families, the provanids and peltospirids, and its occurrence in a lithology (suggesting diffusive seepage), it seems reasonable to speculate that *Elmira* did not host chemosynthetic symbionts but grazed on bacteria.

Conclusions

1. The Late Cretaceous Sada Limestone seep deposit in southern Shikoku, Japan, consists mostly of a thyasirid-rich facies, a worm-tube-rich facies, or a mixture of both. Here we report a mass occurrence of the medium-to-large gastropod *Elmira shimantoensis*, preserved in a lens-shaped body with a flat top and a concave base, 6.5 m long and 2 m thick, embedded in carbonate rich in large thyasirid bivalves. The top of the lens grades into the enclosing thyasirid-dominated facies. *Elmira shimantoensis* also occurs sporadically in the surrounding thyasirid-dominated facies but has never been found in tube-dominated facies, suggesting that *Elmira shimantoensis* lived in the methane-seep sites with the large thyasirid "*Thyasira*" *hataii*.
2. The gastropod mass occurrence is composed of multiple layers of shell accumulations in association with a "small-elongated bivalve," thyasirids, and worm tubes. The shell accumulations consist of a mixture of well-preserved shells and fragments packed in a muddy matrix. The shells are sorted well for size, except for large articulated valves of the thyasirid bivalve. The gastropod mass occurrence was formed through a combination of the repeated transport of shells into a depression or scour on a muddy slope, covering by sedimentation events, and bioturbation. The large articulated thyasirid bivalves may have lived in situ and are preserved in random orientations due to bioturbation.

3. The mass accumulation of *Elmira shimantoensis* cannot be explained by shell-winnowing processes alone because the species is very rare elsewhere in the Sada Limestone. *Elmira shimantoensis* maybe locally formed, highly abundant populations close to the depression where the shells accumulated.
4. The lithology of the gastropod mass occurrence and its immediate surroundings is characterized by detrital micrite rich in dolomite and ankerite, a lack of sparitic phases, and moderately low $\delta^{13}C$ values (calcite, −5.3 to −2.4 ‰; dolomite, −8.3 ‰). This should be compared with the surrounding thyasirid- and tube-dominated facies, which consist of calcitic micrite associated with sparite and more negative $\delta^{13}C$ values (−16.4 to −10.5 ‰). We assume that the gastropod mass occurrence was lithified through carbonate precipitation below the sulfate reduction zone, so there was only a minor contribution of carbonate resulting from the anaerobic oxidation of methane.
5. The feeding strategy of *Elmira shimatoensis* remains unclear, but the low rate of seepages inferred for the habitat of *Elmira shimantoensis* suggests that it did not harbor chemosymbiotic bacteria. Considering that it is presumably related to either of the trochiform gastropod families Provannidae and Peltospiridae, it is more likely that *Elmira shimantoensis* grazed on bacteria, living gregariously on hard substrate such as exposed carbonate mounds.

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