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A CHAETETID SPONGE ASSEMBLAGE FROM THE DESMOINESIAN (UPPER MOSCOVIAN) BUCKHORN ASPHALT QUARRY *LAGERSTÄTTE* IN OKLAHOMA, USA

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Abstract. The first detailed study on chaetetids from the Buckhorn Asphalt Quarry Lagerstätte is presented. Among the investigated specimens we found two samples (chaetetid specimens 2 and 6) that are different from all others in the quarry. Thin sections of these display a complex fragmentation of these Buckhorn chaetetids. Additionally, one of these samples contains two chaetetid morphotypes growing side by side, thus, in the same paleoenvironment. These specimens differ in their mode of growth (laminar and domical), which suggests that chaetetid growth was most likely influenced by genetic factors rather than by the paleoenvironment. We observed a feature, not hitherto reported as far as we are aware, on the surface of chaetetids; namely a regular clustering of seven tubules surrounding a central tubule. This feature could have had an exhalant function. Mineralogical analyses of the skeleton indicate primary high magnesian-calcite mineralogy, which is in accordance with reports in the literature. Cements precipitated during diagenesis are either calcite or dolomite and, where associated with microbial mats, they may contain a distinct amount of manganese. The comparison of the chaetetid skeletons from the Buckhorn Asphalt Quarry leads to the impression, that they represent various morphotypes or even species. Because of the lack of unique features, we have refrained however, from describing new species.

Introduction

The Buckhorn Asphalt Quarry is well known as a late Palaeozoic Fossil Lagerstätte. Compared with fossils from other late Palaeozoic Lagerstätten of the American Midcontinent like the Morrowan Kendrick Shale of Kentucky, the Virgilian Holder Formation of New Mexico, and the Virgilian Finis Shale of Texas (e.g., Stehli 1956; Yochelson et al. 1967; Batten 1972; Dickson 1995; Doguzhaeva et al. 1999), preservation of fossil material from the Buckhorn Quarry is commonly much better. This is because the fossil-bearing sediments in the quarry were impregnated by migrating hydrocarbons from the Ordovician Oil Creek Formation during or shortly after deposition, induced by orogenetic activity in Oklahoma during the middle Pennsylvanian (e.g., Ham 1969; Seuss et al. 2009). This early sealing preserved original shell mineralogy (commonly aragonite), skeletal microstructures, and early ontogenetic shells of molluscs (e.g., Stehli 1956; Squires 1973, 1976; Brand 1982, 1987, 1989a, b; Bandel et al. 2002; Seuss et al. 2009). By soaking the sediments, the pore space, and the fossils diagenetic alteration and cementation by circulating pore waters were prevented (e.g., Brand 1989a; Sadd 1991; Wisshak et al. 2008; Seuss et al. 2009, 2012a, b). Thus, Seuss et al. (2009: 609) suggested categorizing the Buckhorn Asphalt deposit and similar deposits as an 'Impregnation Fossil Lagerstätte'. It is one of the very few Paleozoic occurrences of molluscs and other biota with preserved original shell mineralogy (commonly aragonite), skeletal microstructures, and early ontogenetic shells of molluscs (e.g.,

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Fig. 1 - Buckhorn Asphalt Quarry, southern Oklahoma, USA - Geographical position and sampling site.
A) Geographical position of the Buckhorn Asphalt Quarry (dot) and position of the Buckhorn Asphalt Quarry (star symbol).
B) Sample site #2 in the Buckhorn Asphalt Quarry from which the large chaetetid specimens derive.
C) Spoil piles aside the quarry prepared by Mapes, Nützel, and Yancey in 2000 for weathering; single chaetetid remains were found here.

Stehli 1956; Squires 1973, 1976; Brand 1982, 1987, 1989a, b; Bandel et al. 2002; Seuss et al. 2009). The marine biota from this relatively small outcrop is of middle Carboniferous (Desmoinesian/late Moscovian) age. The faunal assemblage is dominated by molluscs, especially by gastropods, cephalopods and bivalves (Seuss et al. 2009). Chaetetid sponges form the only large representatives of the sessile benthos in this community. General characteristics, taxonomy, and the mineralogy of chaetetids from the Buckhorn Asphalt were studied by Squires (1973) in an unpublished PhD thesis. Chaetetids from the quarry were also briefly treated by Seuss et al. (2009). Throughout the past decades, there has been an ongoing discussion about the systematic and phylogenetic relationships of chaetetids. The 'Treatise on Invertebrate Paleontology' (Finks & Rigby 2004) revised the taxonomic position of chaetetids placing them within a group of hypercalcified sponges representing a specific morphotype of the skeleton. West (2011a, b, c; 2012a, b, c) compiled all available information on this problematic assemblage of fossils.

This publication presents a detailed study of the largest benthic organisms from deposits in the Buckhorn Asphalt Quarry. We compare own data with the data of Squires (1973), as well as chaetetids from other localities. The influence of the paleoenvironment on chaetetid growth in the quarry site is studied as well as post mortem processes (e.g. fragmentation, cementation, and diagenesis).

Geography, geology and fauna

The Buckhorn Asphalt Quarry Lagerstätte (GPS NAD84: N 34° 26' 44"; W 96° 57' 41") is situated about 10 km south of Sulphur in southern Oklahoma (Fig. 1A). It is on the northern flank of the Arbuckle Mountains near the Texas state boundary. The Arbuckle Mountains were formed during the collision of Laurasia and Gondwana throughout the Late Carboniferous to Permian (Arbenz 1989). The strata in the vicinity of the Buckhorn Lagerstätte are folded and strata exposed in the quarry dip 20° W and strike 33 to 39° NNE (Squires 1973; Seuss et al. 2009, fig. 3). Today the quarry is about 150 m long, 21 m wide, and 6 m deep and asphalt-stained deposits crop out at the bottom of the pit as well as on both sides.

The Buckhorn Asphalt Quarry exposes deposits of Desmoinesian and Virgilian (uppermost Kasimovian/ Gzehlian) age (e.g., Squires 1973; Cree 1984; Brand 1987; Seuss et al. 2009). The succession of hydrocarbon-impregnated rocks belongs to the Desmoinesian Boggy Formation (Deese Group) and is unconformably overlain by the Virgilian asphalt-free Ada Conglomerate (e.g., Ham 1969; Sadd 1991; Brown & Corrigan 1997; Seuss et al. 2009). The asphaltic deposits in the Buckhorn Asphalt Quarry represent an assemblage of shallow, near-coastal to deeper, open marine environments and are characterized by variable siliciclastic-carbonate composition, grain size, fossil content and amount of asphalt. The coarsest deposits are float- to rudstones (e.g., shell coquinas, conglomerates) and the finest grained facies types are mudstones. Shell beds are frequent and represent mass flow deposits (Seuss et al. 2009). Deposition of the sediments occurred in a tropical setting close to the palaeo-equator (e.g., Brand 1987: 5° S'; Scotese 1998; Algeo et al. 2004) and was periodically influenced by monsoons (Seuss et al. 2012b). During the Pennsylvanian, the North American craton was highly influenced by tectonic movements and frequent sea-level changes caused by the waxing and waning of ice-sheets on Gondwana (e.g., Heckel 1977, 1980, 1986). Sadd (1986) and Seuss et al. (2009) suggested that the strata in the Buckhorn Asphalt Quarry represent a single cycle of transgression and regression.

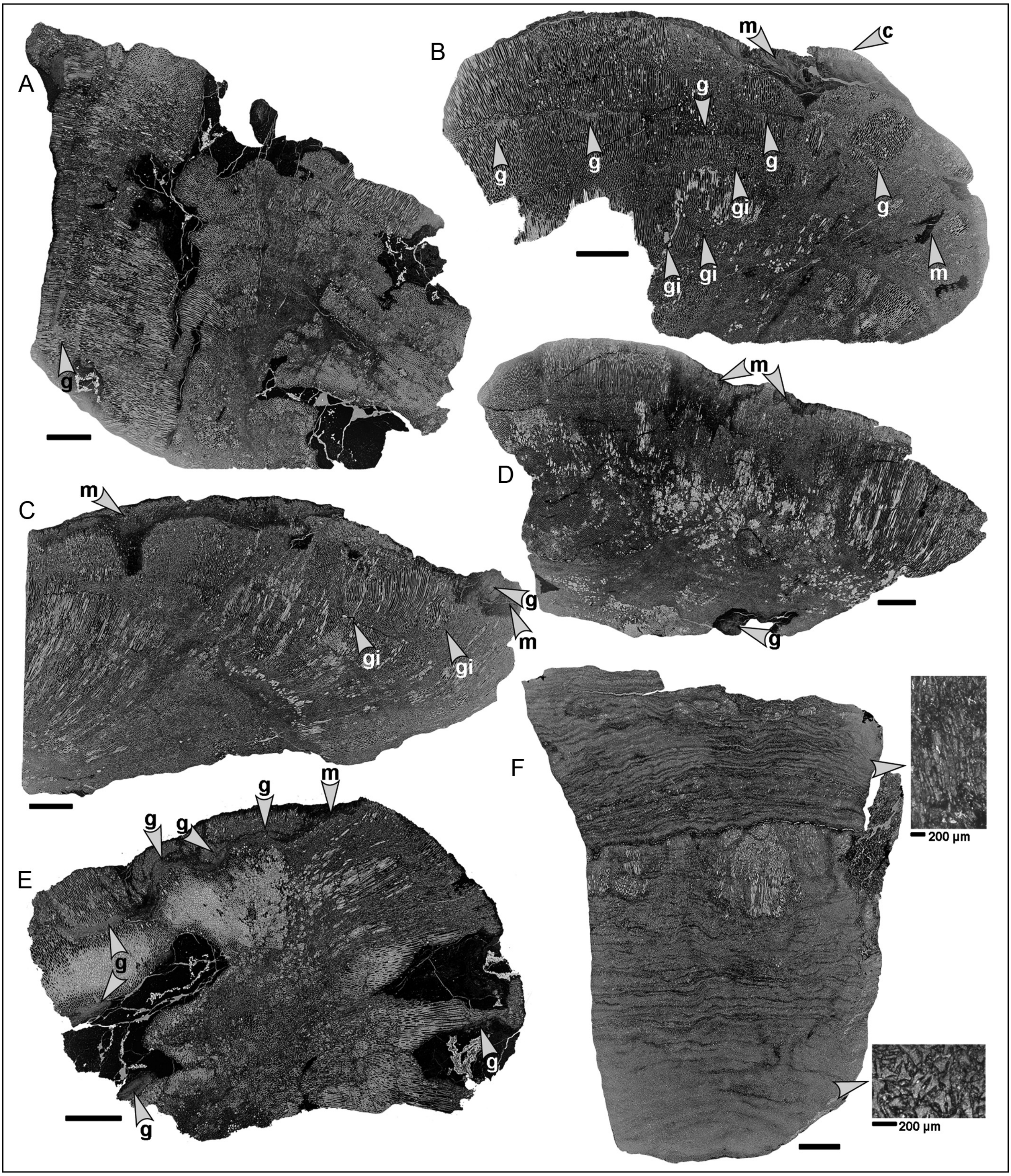

Fig. 2 - Chaetetid thin sections from the Buckhorn Asphalt Quarry Lagerstätte, sample site #2, scale bar: 1 cm.
A) Chaetetid specimen 1 with an irregularly shaped surface and large areas of entrapped asphalt and asphalt stained sediment (BSPG 2011 X 11).
B) Largely overgrown chaetetid specimen 5 with large notch on the left; microbial mats cover the surface and are partly overgrown by a new chaetetid specimen (BSPG 2011 X 15).
C) Chaetetid sponge (specimen 3) overgrown by microbial mats (BSPG 2011 X 13).
D) Thin section of chaetetid specimen 4 illustrating a slightly irregular surface with a large groove filled by microbial mats (BSPG 2011 X 14).
E) Chaetetid specimen 9 containing large hollows filled with asphalt and asphalt stained sediment (BSPG 2011 X 19).
F) Thin section of specimen 2 (BSPG 2011 X 12) consisting of tubule fragments (also compare Figure 12A), centrally a few small intact remains of chaetetid skeletons.
Abbreviations: c, growth of a new chaetetid specimen. g, greyish indistinct structure. gi, growth irregularity. m, microbial mat.

The deeper water deposits in the quarry are dominated by cephalopods and lack a benthic fauna, whereas the shallow-marine deposits (i.e., near-coastal) yield a rich benthic fauna (e.g., gastropods, fusulinids, bivalves), numerous land plant remains and a high amount of terrigenous siliciclastic input. The endolithic ichnocoenosis indicates a deposition of the shallow marine facies in the shallow euphotic zone II – III (Wisshak et al. 2008). The paleo-temperatures of the shallow water deposits range from 28 to 31 °C, while deeper waters had temperatures of only 14 to 15 °C (Seuss et al. 2012b). The fauna found in deposits from the Buckhorn Asphalt Quarry is highly diverse and yields more than 160 species respectively and 125 genera (Seuss et al. 2009, figs 19, 20). Molluscs are the most abundant and diverse phylum and they include more than 60 gastropod species, various bivalves, and numerous cephalopods (coiled and orthoconic nautiloids as well as ammonoids).

Collection and methods

The deposits containing the chaetetids (i.e., sample site #2, Seuss et al. 2009, figs 3, 4; Fig. 1B) comprise a highly diverse marine benthic fauna including gastropods, bivalves, foraminifers, red algae, echinoderms, bryozoans and ostracods. Some chaetetids are overgrown by microbial mats (e.g., Figs 2B-E; 3A, C; 4C-E). Siliciclastic input was high and plant remains are common, while cephalopods are rare. Large remains of chaetetids (i.e., several centimetres up to decimetres in diameter and height) were only found at sample site #2 (Fig. 1B), a shallow marine deposit from a near-coastal setting, while Squires (1973) also discovered remains in the north-eastern area of the quarry in deposits he called 'asphaltic chaetetid mudstone' and in other deposits. However, smaller and weathered (i.e., asphalt-free) chaetetid fragments were found on the spoil piles besides the quarry (Fig. 1C) that were prepared by Mapes, Nützel, and Yancey in 2005 during a field trip. Remains from ten large macroscopically well preserved, asphalt-stained specimens from sample site #2 (Figs 2; 3) and a few chaetetids from the spoil piles (Fig. 5A-C) are integrated in this study.

For a detailed analysis of the chaetetid specimens a series of thin sections was prepared and documented by using a transmitted light scanner (Mikrotek Artix Scan 2020) and a light-optical microscope (Zeiss Axiophot) attached to a digital camera device (AxioCam MRc5). One specimen (BSPG 2011 X 16) was deasphaltized with the organic solvent Methylene chloride (Dichloromethane; CH_2Cl_2) before preparing the thin section (Fig. 3D).

Colouration tests with Feigl-solution and Alizarin red (e.g., Friedman 1959; Kato et al. 2003) were performed to determine the mineralogy. Additionally, the staining method of Choquette & Trussel (1978) was used. Small fragments and blocks (ca. 1 x 1 x 1 cm) (Figs 5; 6) were cut from the chaetetid specimens and prepared for macrophotography and for scanning electron microscope (SEM) and energy dispersive X-ray spectroscopy (EDX) investigation. For SEM-EDX-investigation the logs were deasphaltized before they were affixed to SEM-stubs and sputter-coated. To test whether spicules or spicule pseudomorphs are present, some of the blocks were treated with Titriplex (EDTA/Ethylenediaminetetraacetic acid; $C_{10}H_{16}N_2O_8$) according to the method described by Reitner & Engeser (1987) before the samples were sputter-coated. The SEM-samples were investigated using a VEGA\\xmu (TESCAN) with attached EDX-device (Oxford Instruments). Additionally, X-ray diffraction in combination with a general area diffraction detection system (GADDS) (Bruker AXS) and microprobe (Jeol Superprobe) analyses were performed. All procedures were carried out at the GeoZentrum Nordbayern - FG Paläoumwelt and the GeoZentrum Nordbayern - FG Angewandte Geowissenschaften in Erlangen.

All samples will be housed in the 'Bayerische Staatssammlung für Paläontologie und Geologie' in Munich with the collection numbers BSPG 2011 X 11 to BSPG 2011 X 31 (BSPG 2011 X 11 to BSPG 2011 X 20: thin sections; BSPG 2011 X 21 to BSPG X 31: SEM-samples).

Results

General description of the specimens

Chaetetids are the largest benthic invertebrate remains found in the quarry. The largest specimen is 21 x 14.5 x 8.3 cm in size. The surface of the specimens used for preparing thin sections is either coated with asphalt stained matrix (e.g., Figs 2E; 3C-E), fragmented tubules (e.g., Fig. 3C-E), overgrown by microbial mats (e.g., Figs 2B-E; 3A, C; 4C-E) or the surface is irregularly abraded (e.g., Figs 2A, E; 3B, E). In rare cases, growth of new chaetetid specimens on microbial mats occurs (Figs 2B; 3A). Astrorhizae and other structures on the surface are not present, not preserved, or not visible. Only the surfaces of a few chaetetids collected from the spoil piles could be examined (SEM, macroscopically). A rather regular structure on the surface of a specimen is shown in Figure 5A. It consists of an ordinary pattern of polygonal tubules in transverse view with each tubule surrounded by seven tubules. Such structure has not been reported previously, as far as we are aware. Figure 5D illustrates an etched chaetetid sample studied with the SEM. In some of the chaetetids the walls of the tubules are penetrated by numerous 'interconnections' (Fig. 5E).

The general shape of the specimens is variable and some of the chaetetid thin sections contain more than one specimen (Figs 2B; 3A, D, E). Most of the chaetetids are of more or less domal shape with ragged outlines. The walls of the tubules (Figs 4A; 5-10) consist of microcrystalline low-magnesian-calcite (LMC). The tubule walls are commonly coated with cements (Figs 5E, G; 6C, D; 7D; 8A, D; 9B, D). The walls are smooth to irregular and do not show any beading or distinct structures. The organization of the tubules is variable. An alternation of laterally and longitudinally cut tubules is present in many of the studied thin sections (e.g., Figs 2B; 3A, C, E; 10A). Tabulae (Figs 4A; 5F, G; 6B; 8C, D) are present in all of the specimens except in specimen 2 (BSPG 2011 X 12) in varying amount and distribution. In many thin sections pseudoseptae (Fig. 9C-D) are present. The tubules are polygonal in transverse section (mainly penta- and hexagonal; varying from regular, irregular to rounded outlines) (Figs 5A-D; 6A; 7A, D; 8A; 9B-D; 10B). The internal diameter (Fig. 11) and

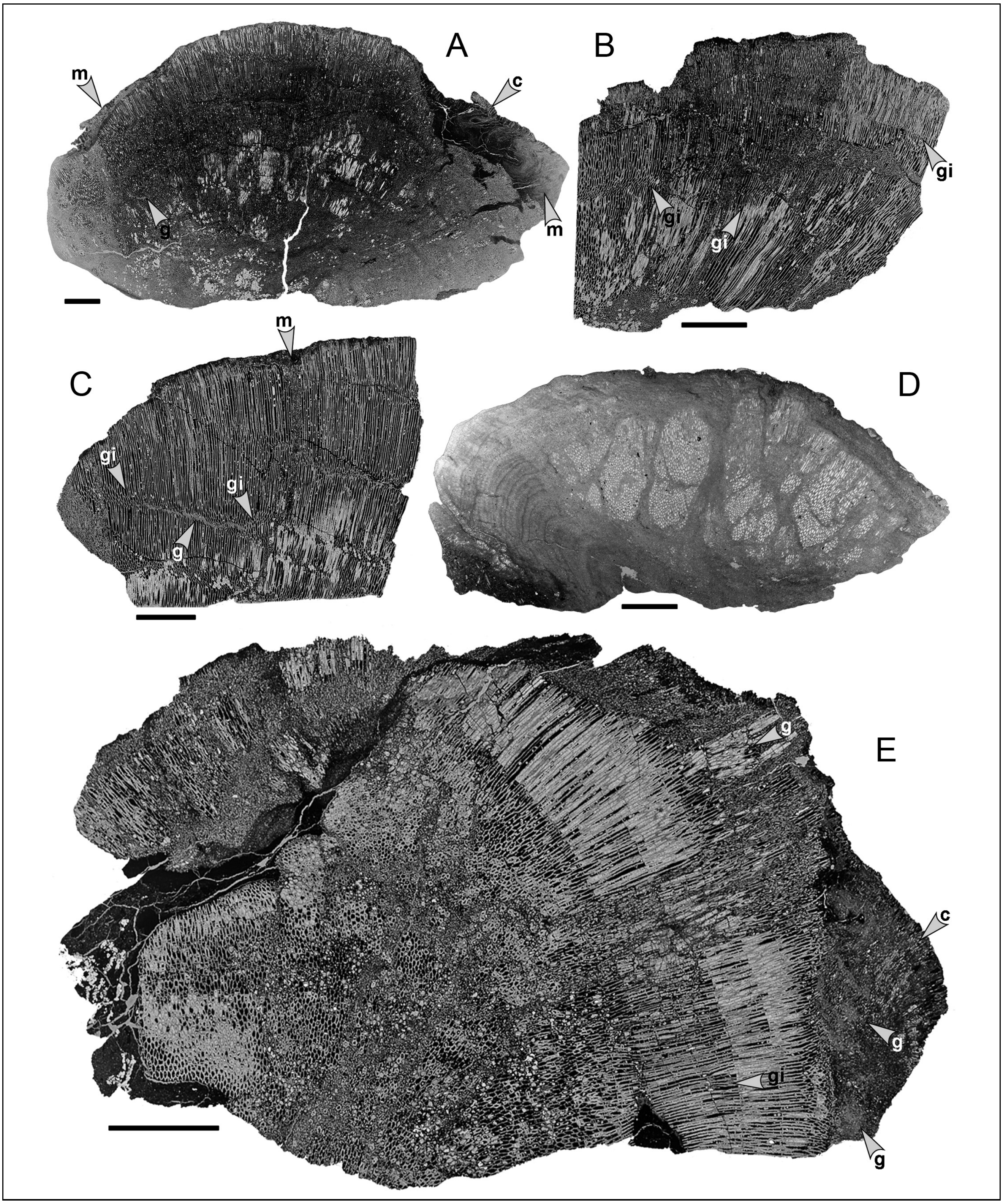

Fig. 3 - Chaetetid thin sections from the Buckhorn Asphalt Quarry Lagerstätte, sample site #2, scale bar: 1 cm.
A) Domal shaped chaetetid sponge (specimen 7) overgrown by microbial mats, on the right a new chaetetid specimen grows on the large microbial aggregation (BSPG 2011 X 17a).
B) Thin section of a chaetetid specimen 8 with lacerated surface (BSPG 2011 X 18a).
C) Chaetetid sponge (specimen 8) with a large crack filled with asphalt and tubule fragments (BSPG 2011 X 18b).
D) Deasphaltized specimen 6, left side illustrates a laminated section that entirely consists of minute tubule fragments, centrally and on the right intact tubules in transverse section separated by skeletal fragments (BSPG 2011 X 16a), also see Figure 12B.
E) Thin section of chaetetid specimen 10 (Seuss et al. 2009, fig. 10c) illustrating a shift in growth direction (center to surface of the specimen) merging from lateral into diagonal cut, and finally longitudinal cut tubules (BSPG 2011 X 20a).
Abbreviations: c, growth of a chaetetid specimen. g, greyish structure. gi, growth irregularity. m, microbial mat.

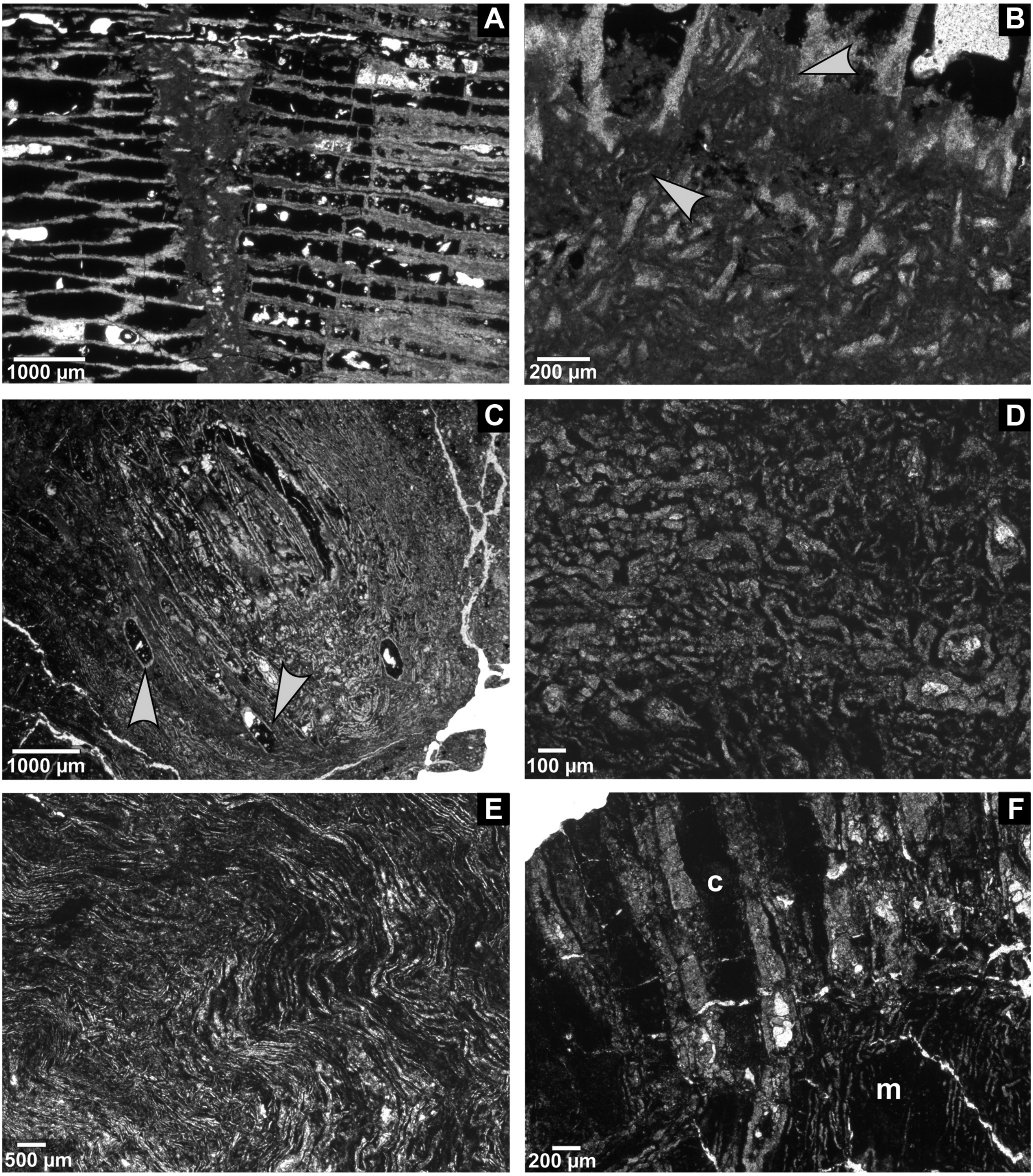

Fig. 4 - Details of various chaetetid specimens from the Buckhorn Asphalt Quarry as seen in thin sections:
A-B) Indistinct greyish structures in the skeleton of chaetetid specimens. A - Greyish structure in specimen 1 (BSPG 2011 X 11) trending rectangular to the tubules on the right. B - Detail of the greyish structure enclosing fragments of tubule in specimen 9 (BSPG 2011 X 19).
C-F) Microbial structures associated with chaetetid specimens from the Buckhorn Asphalt Quarry. C-D - Microbial structures in specimen 3 (BSPG 2011 X 13). C: Microbial and greyish structures surrounded by sediment; structure incorporates greyish structures and tube-like, oval patterns (arrows). D: Microbial structures on the surface of specimen 3 (BSPG 2011 X 13) differing distinctly from those in Figure 4C. E-F - Microbial structures associated with chaetetid specimen 7 (BSPG 2011 X 17a). E: Undulating microbial mats covering the surface of chaetetid specimen 7. F: Microbial structures (m) overgrown by a new chaetetid specimen (c).

length of the tubules are variable. Formation of new tubules (Fig. 9) was noticed in several specimens and expansion of the skeleton by inserting new calicles at the basal margin was recognized. Spicules or pseudomorphs of spicules were not found in any of the specimens. Some of the chaetetids studied display distinct growth disturbances (Figs 2B, C; 3B, C, E; 10C, D) and all studied specimens comprise portions consisting of fragmented walls of tubules (Figs 2; 3; 8A; 10B, D). The base of the skeleton is not preserved in any of the studied specimens. Tubules of the Buckhorn specimens are filled with asphalt (Figs 2A-E; 3A-C; 3E; 4A, F; 7-10), cements (Figs 2; 3; 4A; 5D-G; 6C, D; 7D; 8A; 9B, D; 10B-D), microbial remains (Fig. 2C-E; 3C), tubule fragments, matrix or a combination of these components. Fissures and cracks in the chaetetid skeletons are commonly filled with asphalt. In the following, the results of the geochemical and mineralogical analyses will be outlined.

Mineralogical analyses of the skeleton

Three different staining tests on the asphalt-free thin section of chaetetid specimen 6 (BSPG 2011 X 16) were carried out. Alizarin red stained the thin section red whereas treatment with Feigl solution did not result in any color changes. The Titan yellow test for Mg-calcite (after Choquette & Trussell 1978) turned the thin section red.

Fragments of chaetetids were studied with the SEM to investigate details of the skeleton. The tubules show a homogenous microcrystalline structure. Tabulae exhibit a similar microstructure and merge uniformly with the tubules. An etched chaetetid fragment presents a feature resembling pore-like undulating interconnections between the tubules (Fig. 5D, E). The determination of the mineralogy using EDX was based on the presence or absence of strontium (Sr) and magnesium (Mg) following Sandberg (1983) and Flügel (2004). Sr and Mg were absent in the walls of the tubules in the tested samples. Cements coating the walls partly contain high amounts of Mg.

A polished sample of a chaetetid specimen was analysed with the microprobe. Tubules and tabulae in this specimen are low-Mg-calcite. The cements coating the wall are both, dolomite and low-Mg-calcite.

The analyses of the tubules and tabulae with XRD-GADDS indicate low Mg-calcite for the skeleton. There is no indication for the presence of aragonite. Brownish, concentric cements in microbial structures mainly consist of manganese (Mn) calcitic carbonate and quartz. Pale pink cements filling some of the tubules of those chaetetids growing on microbial mats are also manganese-calcitic with slight amounts of quartz. The exact amount of manganese could not be determined within the precision of the techniques used, but it seems that Mn is present as traces only.

Interpretation and Discussion

Mineralogy and microstructure

Staining the chaetetid skeleton (BSPG 2011 X 16) with Alizarin Red and Feigl solution suggests a calcitic mineralogy for the chaetetid skeleton. The red stain of the chaetetid specimen after treating the skeleton with Choquette & Trussell's method (1978) revealed the presence of a distinct amount of magnesium. According to Choquette & Trussell (1978) the red coloration of the section indicates the presence of at least 5-8 percent $MgCO_3$ and therefore, we conclude that the studied chaetetid specimen had a primary high magnesian calcite (HMC) skeletal mineralogy. This corroborates earlier reports that chaetetid specimens consist of HMC with = 5 % $MgCO_3$ (Squires 1973). High Mg-contents in the calcite of chaetetid skeletons (up to 20 %) were also reported by Wendt (1984). Anyhow, microprobe-, EDX-, and XRD-GADDS-analyses of additional specimens from the Buckhorn Asphalt indicate that their tubules now consist of low Mg-calcite and we found no evidence for the presence of aragonite. The analyses also showed that calcite and dolomite cements cover the walls of the tubules (see also Squires 1973). The magnesium in the dolomite cements likely derives from the HMC skeleton and was released during diagenetic in situ dissolution. This idea is supported by the fact that the walls covered by cements are generally thinner than those without cements (Fig. 11), the former having lost thickness due to dissolution.

Although the microstructure of chaetetid skeletons varies (e.g. West 2011a, 2012a), their composition is primarily aragonite or HMC. This supports suggestions that modern chaetetid sponges are polyphyletic. The modern genera *Merlia* and *Acanthochaetetes* have HMC skeletons, whereas the skeleton of *Ceratoporella* is aragonitic. Fossil chaetetids mainly have HMC skeletons and reports of a primary aragonitic microstructure only comprise occurrences from the Permian and Triassic. Sandberg (1983) proposed a model for the precipitation of non-skeletal carbonate minerals, which included two phases throughout the global history in which precipitation of aragonite would be hindered (i.e., calcite sea) alternating with three phases in which aragonite-precipitation would be facilitated (i.e., aragonite sea). This model was based on changes of the P_{CO2} caused by tectonics. Hardie (1996) showed that such oscillations depend on shifts in the Mg/Ca-ratio of the seawater and mirror spreading rates of mid-ocean ridges. During times where aragonite precipitation is favoured the formation of HMC would also be privi-

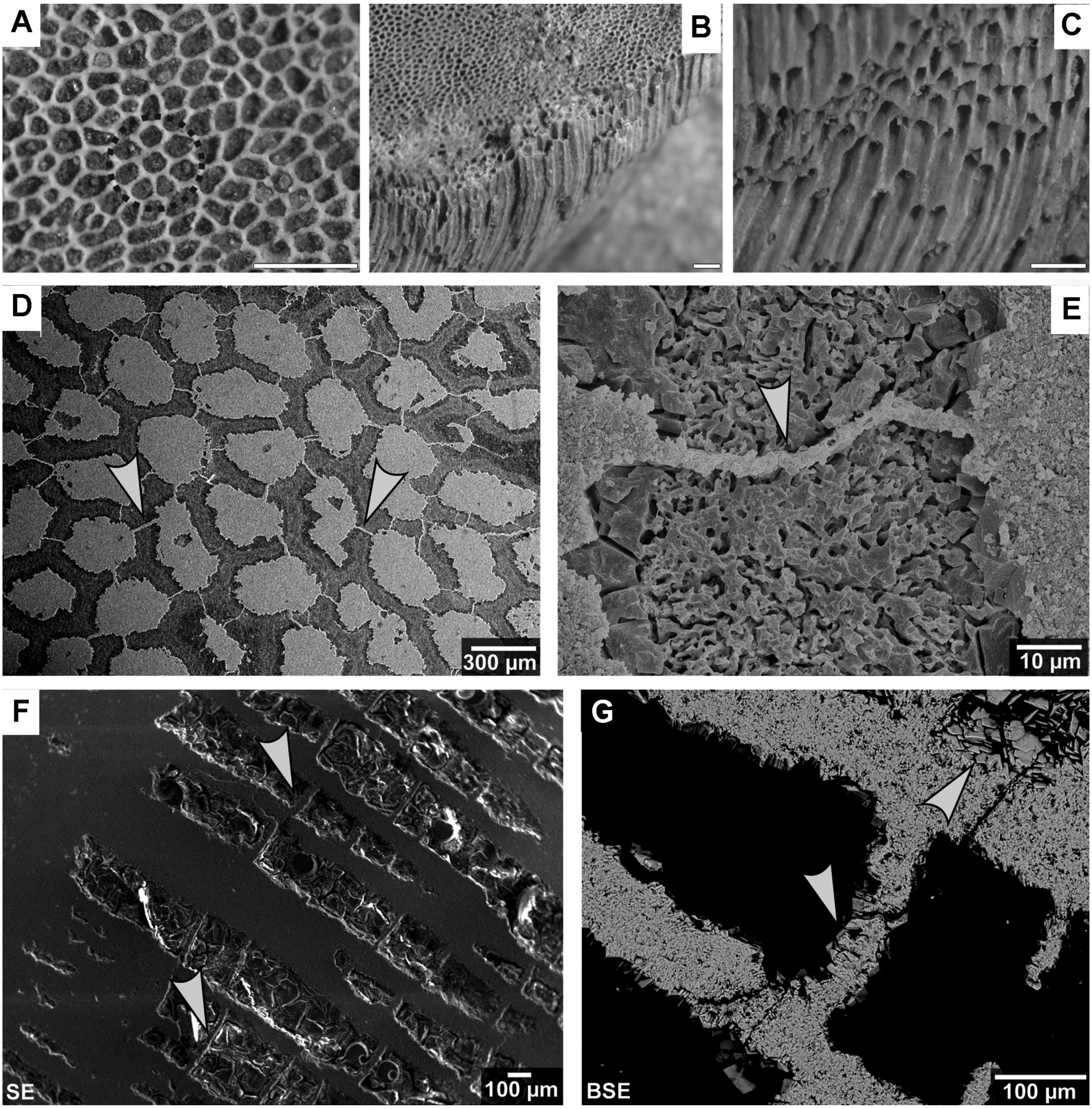

Fig. 5 - Macrophotographs and SEM-pictures of chaetetid specimens from the Buckhorn Asphalt Quarry.
A-C) Macrophotographs of a deasphaltized chaetetid specimen from the spoil piles aside the quarry, scale bar: 5 mm. A - View onto the surface of a chaetetid specimen illustrating the distribution of tubules and their roughly polygonal shape; circled, the regular association of seven tubules surrounding a central tubule. B - Surface of a specimen and lateral view onto the tubules (Seuss et al. 2009, fig. 10d; modified). C - Tubules of a chaetetid specimen, base is broken off.
D-E) SEM-photographs of a log of chaetetid specimen 12 (BSPG 2011 X 22) etched with Titriplex III. D - Surface view, the medium areas represent etched tubules coated by cements (dark grey), light grey structures are synthetic resin filled tubules; note the secondary diagenetic feature (arrows) penetrating the tubule walls and cements. E - Detail of Figure 5.D illustrating a secondary diagenetic feature (arrow) passing through the tubule wall and cements.
F-G) Microprobe photographs of a polished chaetetid log (specimen 14) (BSPG 2011 X 24). F - SEM-photographs (SE) of tubules and tabulae (arrows) of specimen 11 (BSPG 2011 X 21). G - Backscatter electron microscopy (BSE) photograph illustrating the recrystallized wall and tabulae (arrow t), both are coated by cements (e.g. arrow).

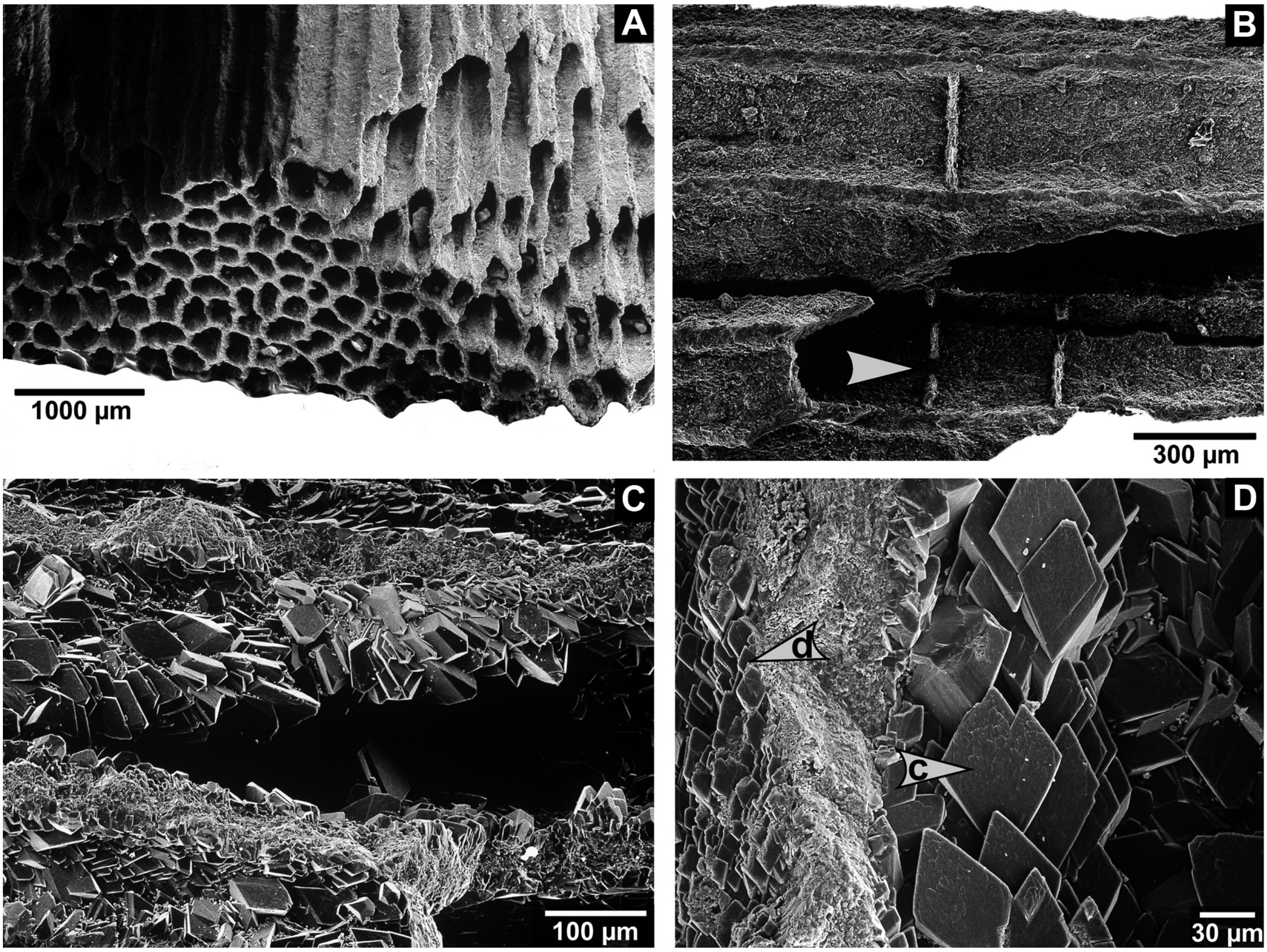

Fig. 6 - SEM-photographs of deasphaltized chaetetid specimens from the Buckhorn Asphalt Quarry.
A) Photograph of a fragment of a chaetetid (specimen 16) illustrating the elongated tubules and their polygonal shape (BSPG 2011 X 26).
B-D) Chaetetid specimen 21 (BSPG 2011 X 31). B - Photograph of tubules of a chaetetid specimen with remains of tabulae, partly broken or perforated (arrow). C - Cements coating the tubules. D - Calcite (arrow c) and dolomite (arrow d) crystals covering the tubule wall (Seuss et al. 2009, fig. 10e; modified).

leged in this model. This is the case in times when the Mg-concentration in the seawater is high (Berner 1997) and the Mg/Ca-ratio is greater than 2 (Morse et al. 1997). More recent calculations depending on the Mg/Ca-ratio by Stanley & Hardie (1998) showed that the general distribution of aragonite and calcite seas proposed by Sandberg (1983) is still valid and only slight corrections on the single ranges were necessary. Stanley (2006), referring to the changes in the seawater chemistry, concluded that many taxa build skeletons and hard parts depending on the Mg/Ca-ratio of the sea. This was based on following observations: 1) Some extant sponges build more robust skeletons when the seawater mineralogy corresponds to their favoured skeletal mineralogy, 2) major reef builders usually correspond to seawater chemistry as it favours rapid growth of the skeleton, and 3) calcifying sponges throughout Earth's history tend to build skeletons corresponding to non-skeletal marine carbonates of the same age (Stanley & Hardie 1998, 1999). During the Carboniferous, the Mississippian was characterized by the calcite sea I and reefs were dominated by calcitic corals. This changed during the mid-Carboniferous when a turnover was recognized and reefs globally became aragonite-dominated (Railsbeck & Anderson 1987) and chaetetid sponges (HMC and aragonite) were exceptionally numerous and widespread. Ota (1977) reported a Carboniferous atoll from Honshu, Japan, with a reef growth that persisted for 45 million years and recorded the transition from calcite sea I to aragonite sea II during the Viséan (middle Mississippian) (i.e., a decrease of rugose corals and the rise of chaetetids) (Stanley 2006). Wendt (1977) reported chaetetids of Permian age (aragonite sea II) in aragonite preservation and Wood (1987) recognized similar patterns in the mineralogy of sponges. She suggested that calcified sponges might have developed repeatedly and built skeletons depending on the seawater chemistry. Regarding the range of aragonite sea II (mid-Mississippian to mid-Jurassic) (Stanley & Hardie 1998; Stanley 2006), the HMC skeletons of the chaetetid sponges from the Buckhorn Asphalt Quarry fit the Aragonite Sea model with aragonite and HMC as preferred skeletal mineralogy. However, there seem to be no reports of chaetetid sponge skeletons primarily consisting of LMC during calcite seas and this could also indicate that chaetetid sponges were more or less independent of the Mg/Ca-ratio in sea water (also see the discussion in West 2012a). Unfortunately, the chaetetids from the Buckhorn Quarry are recrystallized. Thus, their microstructures are unknown and could not be compared with the various microstructures of chaetetids reported by Wendt (1984), Wood (1991), Cuif & Gautret (1993), and Finks & Rigby (2004) and summarized by West (2011a, 2012a).

Growth form and surface

The general growth form of the chaetetid sponges from the Buckhorn Asphalt Quarry is roughly domical with more or less irregular surfaces. Several explanations are possible for such outlines. During its lifetime the tubules of a chaetetid specimen grow synchronously throughout the skeleton. However, it is unlikely that all tubules grew at the same rate and thus, they would produce an uneven, slightly undulating surface. Environmental factors (e.g., local disturbances, sedimentation, influence of sunlight/shady areas) also contributed largely to the formation of irregular surfaces. Disruptions may be caused by destruction of tubules, settlement of organisms, bioerosion, transportation, sedimentation, and disease or death of parts of the tissue. Two of the studied specimens show pronounced disruptions (Fig. 2A, E), a common feature in chaetetids (pers. inf. E. F. Martinez). Both specimens exhibit large deep and irregular incisions on the surface and on the base. An unknown predator or mechanical alteration would be possible explanations for these structures. The surface of some of the studied chaetetids is partly covered by microbial mats (Figs 2B-E; 3A, B). The microbial mats either inhibited tubule growth during lifetime of the sponge or grew post mortem. If growth was during lifetime further expansion of the tubules in covered areas would have been hindered. Those areas of the skeleton that were not overgrown by microbial mats have a rather smooth outline whereas covered areas show more irregular surfaces. This could indicate that microbial growth was only possible where the tissue of the chaetetid was disturbed already or even dead, like after being hit by some solid object or being affected by some predator.

The basal layer is lacking in all of the specimens. Likely, this is due to abrasion during diagenesis. The sediment the chaetetids settled on was unconsolidated. Anyhow, there will have been some solid objects (e.g., shell fragment, pebble) the larvae could settle on, which was removed either during lifetime of the specimen or post mortem (e.g., by waves or by diagenesis). The specimen illustrated in Figure 2B displays a large notch on the left side of the thin section and we suggest that a pebble or some other larger firm substrate had been present to which the chaetetid was attached.

Surface structures were not noticed on any of the specimens used for thin sections because the exterior is either covered by microbial mats, matrix and skeletal fragments or is abraded. Weathered remains from the spoil piles usually display their surface. One of the samples illustrates a regular arrangement of seven ring-forming tubules with a central tubule (Fig. 5A) that has, to our knowledge, not been reported so far. We are not sure about the function of such a structure – it could have been some exhalant function – or of it was functional at all. We found this feature in one of our specimens only and further studies of well preserved, uncovered surfaces are necessary to gather more information on this structure. Possible explanations for such clustering of tubules could also be that they form the base of astrorhizae, mamelons, or other surface structures which were abraded.

Internal features in general

The internal diameter, the length, and the wall thickness of the tubules vary among the specimens and also within a single specimen (Fig. 11). The diameter as well as the thickness of the tubule wall are not useful for a differentiation of taxa (West 1994); this is also true for cross sections of tubules (West 1994, 2011a). West's (1994, 2011a) statement can be supported with the Buckhorn data because of the large variance within the specimens. The tubules are recrystallized and coated and/or filled with cements (i.e., dolomite, calcite, Mn-calcite, and quartz), asphalt, tubule fragments, matrix, and microbial mats. Recrystallization and precipitation of the cements alters/modifies the original mineralogy as well as the thickness of the tubules and thus, negatively influences the available information on the skeleton and on the systematics (an extended discussion is provided by West [2011a: 51-64]). Since the soft tissue of the sponge would have prevented infilling of the tubules during their lifetime, we suggest that most of the fillings occurred post mortem. Due to transportation, erosion, etc., cracks and fractures as well as abrasion are common (West 2011a). As it is for the filling of the tubules of the Buckhorn chaetetids, cracks and fissures (e.g. Fig. 3C, E) filled with asphalt, cements, matrix, and/or microbial remains are post mortem. This is because the tubules above and below these fractures do not represent a new phase of growth of the skeleton based on the comparison of tubules: both ends of the tubules – above and below the cracks – fit together like pieces of a jigsaw and numerous tubules were already coated by cements before they broke apart or were fragmented (Fig. 8A). The longitudinal fractures are due to compaction, while some of the transverse cracks also indicate shifting.

The specimens either display continuous change in growth direction as is indicated by a steady transition of cross-sectioned into longitudinal cuts (or vice versa) without interruption (Fig. 10A) or they show a sudden alternation of cross-sectioned and longitudinal cut tubules (Fig. 10B). An alternation might be caused by external disturbances during growth which forced a change in the growth direction of the tubules or by a higher rate of insertion of tubules in a certain area of the skeleton pushing neighbouring tubules aside. Tabulae are present in all specimens except in specimen 2 (BSPG 2011 X 12) even though the distribution, the amount, their organization, and the thickness vary. Banding with an accumulation of tabulae as reported by Hartman & Goreau (1972) is not present in the studied specimens.

Both, tubules and tabulae are recrystallized and the primary microstructure cannot be determined. Pseudoseptae and splitting of tubules are present in the specimens, but their frequency varies in the studied specimens and also within a single chaetetid specimen. Because of the variance within a single chaetetid skeleton, the taxonomic significance of the density of tabulae is limited. The etched section (Fig. 5D, E) displays the voids of the tubules filled with synthetic resin (light grey). The voids are either surrounded by the medium grey structure (i.e. the skeleton of the chaetetid) or by a darker rim (i.e. the cements coating the inside of the tubules). The arrows in Figure 5D and E point to 'interconnections' which also penetrate the dark cement rim. This is only possible, if the 'interconnections' developed after precipitation of the cements and thus, in our opinion, they cannot represent pores. Pores would have been sealed by the cements and should also show the dark coloration but not the light grey color of the synthetic resin. Therefore, these structures represent a diagenetic feature and no mural pores.

Spicules were not found in the studied specimens and they either were not precipitated or they are not preserved (West 2011a). In modern *Ceratoporella* and its relatives spicules are absorbed as soon as they are entrapped in the skeleton (Hartman & Goreau 1972). *Merlia* and other Pacific tabulate sponges do not enclose their spicules in the skeleton but integrate them in the soft tissue (Hartman & Goreau 1970). Thus, after death of the specimen the tissue will disintegrate and the spicules are lost. Both scenarios as well as diagenetic dissolution of spicules are possible scenarios for the Buckhorn chaetetids.

Growth disturbances

Interruption surfaces are common in chaetetids and accordingly also in the Buckhorn specimens. They provide information on the frequency and severity of disturbances (Miller & West 1997). The periodicity, the rate, and types of sedimentation might also be indicated. Five combinations are proposed by Miller & West (1997). These are in general, breaks in growth with apparent continuity of tubules across the surface, surfaces of rejuvenation or recolonization with reorientation of tubules, sediment-filled tubules or trapped sediment partings, encrusted surfaces, and biocorroded or bored surfaces. Further possible causes resulting in growth disturbances are, for example, transport of the specimen, disease or death of a part of the soft tissue, or physical impact on the skeleton destroying existing tubules by some hard object.

Breaks in growth with subsequent re-growth of the chaetetid skeleton as described by Miller & West (1997) were not observed in the Buckhorn specimens. However, discontinuous growth (e.g., Figs 2B, C; 3B, C; 10C, D) is present in several of the studied specimens by the presence of an exceptional organization of the tubules, a local change of growth direction or a ragged periphery. Possible causes for growth disturbances are injuries of the soft tissue covering the skeleton or death of part of the surface and complete or partial coverage of the skeleton by sediment or overgrowth. As an example, one specimen (Fig. 3B) shows horizontal growth interruptions on the right side of the thin section indicating that only this particular area was affected. Additionally, bioerosion (type 5 of Miller & West 1997) may also cause disturbances in the growth of the tubules.

Some Buckhorn chaetetids display incisions and voids in the skeleton that are filled with asphalt and asphaltic sediment (Fig. 2A-E; 3A, E) and in a few cases with microbial mats (Fig. 2B-E; 3A). It seems that some of these incisions and voids emerged during lifetime of the sponge as they are either incorporated in the skeleton (Fig. 2B; 3A) or they caused an irregular outline of the sponges surface (e.g. Figs 2B; 2C, D; 3A). Incorporation in the skeleton may either be due to settling or boring of some unknown organism or by death/injury of the soft tissue in this area during lifetime of the chaetetid. As soon as the organism had left the site of settlement or boring and after recovery of the soft tissue (this would have also been necessary if some organism bored into the skeleton or settled on the soft tissue) new tubules were formed. We conclude this, because the tubules below the voids are largely intact which, in

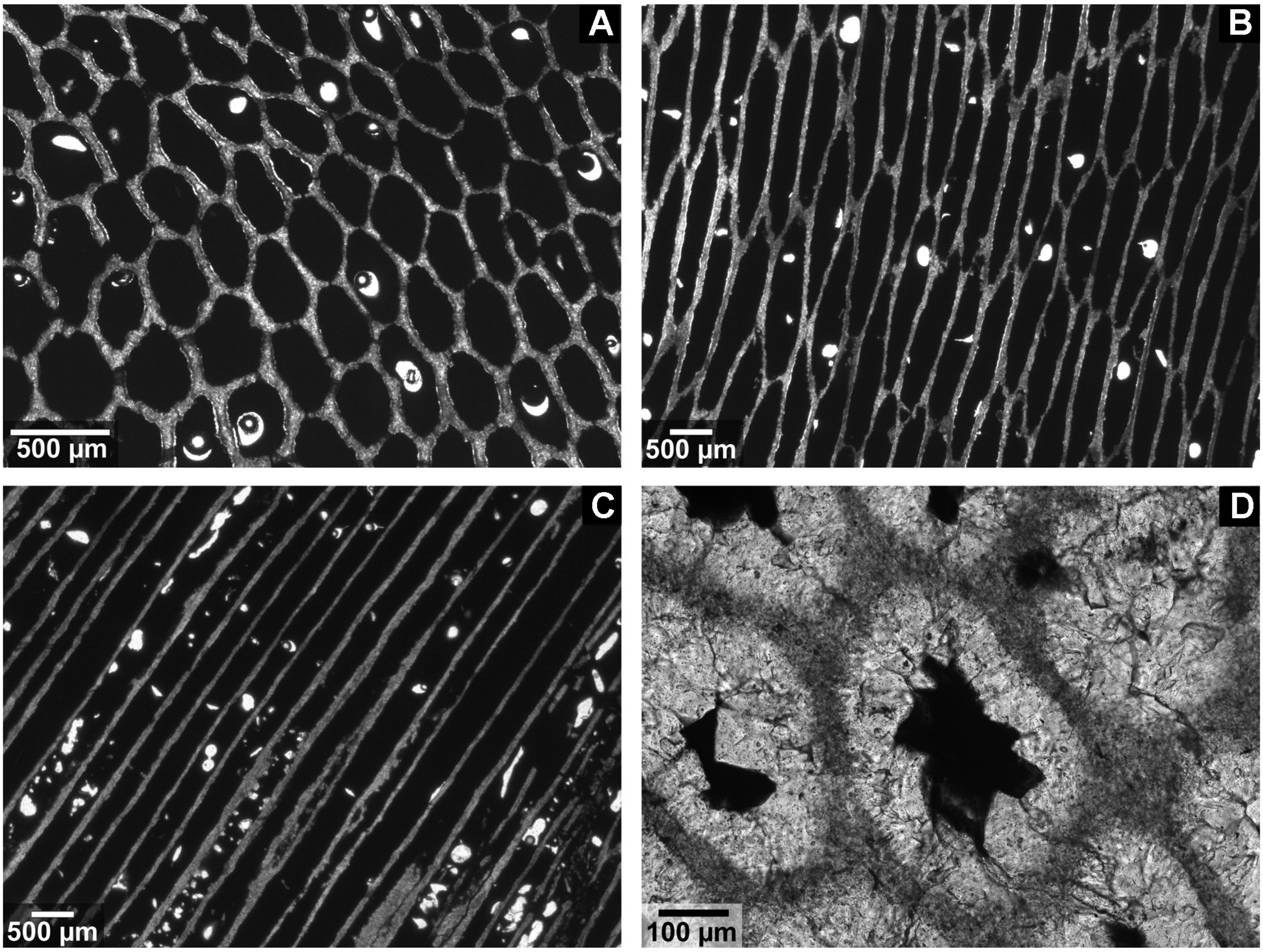

Fig. 7 - Thin sections of chaetetid specimen 8 (BSPG 2011 X 18c) from the Buckhorn Asphalt Quarry.
A-C) Main directions of how tubules are cut in thin sections. A - Lateral cut. B - Diagonal cut. C - Longitudinal cut.
D) Heavily cemented tubules, the remaining space is filled with asphalt; compare differences in color: cements are bright whereas tubule walls appear brownish.

our opinion, excludes physical impact. In other specimens it remains speculative if the incisions and voids emerged during lifetime or post mortem. The specimens illustrated in Figures 2A and E, for example, show deep incisions which could already have evolved during lifetime, causing the irregular surface. On the other hand the specimen could already have been dead and incisions and voids along with the irregular surface are caused by post mortem boring organisms, transport, and/or abrasion.

A sudden change in the growth direction of the tubules (in thin sections a displayed change from transverse to longitudinal sections) could be caused by physical disturbance, by bioturbation, a general instability in growth, and/or instability of the substrate (Miller & West 1997). Physical disturbance by waves and influence during a monsoonal season (Seuss et al. 2012b) resulting in a more suspended water mass could explain changes in growth directions. In this case, the chaetetid specimens would have been partly or completely covered by matrix. If this did not cause death immediately, the covered chaetetid would have been forced to change growth direction of the tubules (type 2 of Miller & West 1997). In some of the specimens (Figs 2A-E; 3A, E) trapped sediment occurs within the skeleton. This could indicate that sediment covered some part of the skeleton and was embedded in the skeleton by overgrowth of tubules (type 3 of Miller & West 1997). In other areas it seems that voids were present in the skeletons that were then filled by sediment ('type 1'/type 3 of Miller & West 1997). The skeleton is intact otherwise and thus we conclude this happened during lifetime of the specimen.

Biocorrosion and bioerosion (type 5 of Miller & West 1997) were not directly recognized. In some of the chaetetids though, some large incisions are present, which could indicate settling or boring of some unknown organism (Figs 2A, E). Overgrowth resulting in a cover by microbial mats is common (Figs 2B-E; 3A, C; 4C-F). Such an overgrowth (type 4 of Miller & West 1997) could hinder expansion of the specimen's

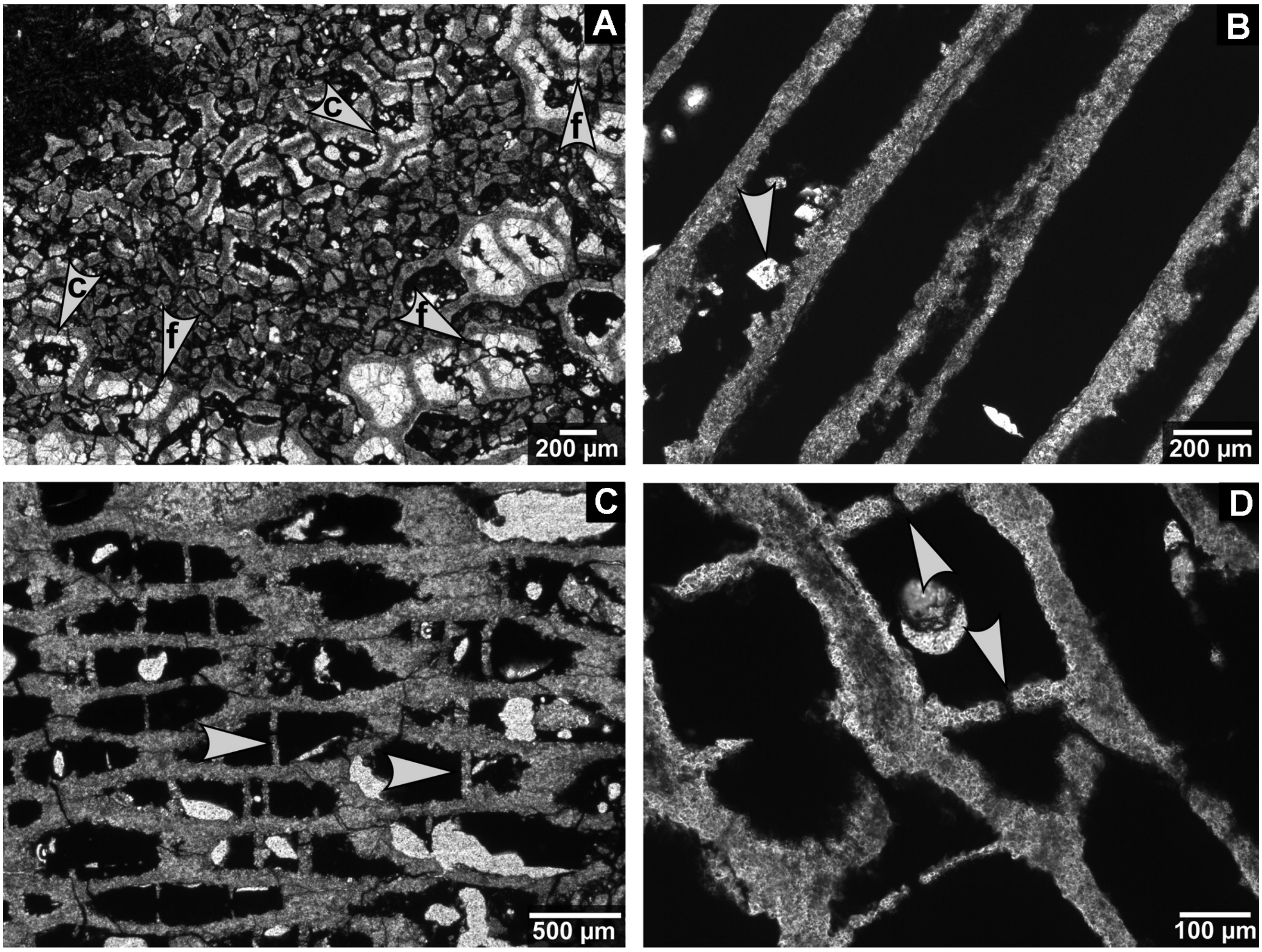

Fig. 8 - Cements and tabulae in chaetetid specimens from the Buckhorn Asphalt Quarry.
A) Heavily fragmented chaetetid skeleton (specimen 4), cement-coating is well visible (arrow c), fragmentation occurred after cementation (arrow f) (BSPG 2011 X 14).
B) Asphalt filled tubules in specimen 7, white rhomboedron (arrow) on the left represents calcite crystal (BSPG 2011 X 17).
C) Transverse cut, numerous tabulae (intact and perforated; arrows) and asphalt filled tubules in specimen 1 (BSPG 2011 X 11).
D) Foramen/pores or incomplete tabulae (arrows) of poorly preserved, asphalt-filled tubules in specimen 10 (BSPG 2011 X 20).

skeleton if the chaetetid sponge was still alive. It could also have caused death of the specimen. In some cases growth of new chaetetids by settling of chaetetid larvae was noticed on the surface of microbial mats (Figs 2B; 4F). These younger specimens differ from the overgrown specimens in wall thickness and tubule diameter and are badly preserved. According to Miller & West (1997) mainly domically shaped or stacked chaetetids are overgrown. This is confirmed by own observations; most specimens from the Buckhorn quarry are of roughly domical shape. Many of the chaetetid sponges from the quarry show incisions (Figs 2A-E; 2A). As discussed above these could derive from some settling or boring organisms. It is also possible that microbial growth in these areas could have inhibited further expansion of the skeleton while surrounding tubules could continue to grow. This could lead to notches and grooves in the surface of the specimens.

Instability due to the growth morphology of the chaetetid specimen or the substrate the sponge was settling on could also contribute to formation of growth disturbances. Specimens from the Buckhorn generally have a more or less domical shape, being wider than high. This should be a rather stable morphology and should prevent toppling to a high degree. Accordingly, we don’t find any evidence of toppling or transportation during lifetime in any of the Buckhorn specimens.

Fragmentation of the skeleton

Fragmentation – i.e. the breakage of the tubules into pieces by transportation, pressure or other physical impact – is present in all of the Buckhorn specimens to various degrees (Figs 2; 3; 8A; 10B, D). It is important to determine if fragmentation was caused before or after death of the chaetetid. The fragments of the chaetetid skeletons are interpreted to be mostly autochthonous. If the chaetetid specimen was alive during fragmentation, an organic tissue strong enough to keep the fragments together was necessary. Anyhow, decay of such a tissue after death would have been rapid and immediate burial without any mobilization of the chaetetid specimen incorporated in the sediment would have been required. Such a scenario is possible, but in our opinion rather unlikely. Even if the sedimentation rate was high enough to encase most of the skeleton and keep marginal fragments in place, such fragments would still be prone to removal and the specimen would disintegrate as such sediment was not consolidated. Additionally, the generally domal shape of the chaetetid sponges suggests rejecting such a hypothesis.

A more plausible explanation for the fragmentation in the Buckhorn chaetetids, in our opinion, is post mortem fragmentation. Many tubules are coated by cements. There are various examples that such cements were precipitated and coated the tubules before the skeleton broke. This can be seen in Figures 8A and 10B which illustrate that not only the tubules, but also the coating cements are broken. To precipitate the cements, the dolomite and the low Mg-calcite, fluid must have been present in the tubules. This, in our opinion, is only possible if the organic tissue covering the skeleton was removed by post mortem decay. After precipitation of the cements and fragmentation the intruding hydrocarbons would then have glued the remains together. This is also the case for the sediments the chaetetids were found in. As soon as the hydrocarbons (i.e. the asphalt) are removed, the sediment disintegrates. Whereas, as an example, *Ceratoporella*'s skeleton is massif with a high bulk density (Hartman & Goreau 1970), it seems that the Buckhorn chaetetids were more prone to breakage as the rate of post mortem fragmentation is high. Fractures are frequent and either filled with skeletal fragments, sediment, and/or with asphalt.

Burial and toppling of chaetetids during their lifetime was reported by West & Kershaw (1991) and West (2011a, b) who recognized that most of the chaetetids continued growth afterwards. Neither burial nor toppling was directly recognized in the chaetetid specimens from the Buckhorn Asphalt Quarry. In most specimens growth was relatively continuous suggesting mainly stable conditions. The largely low domical shape might also indicate fairly stable conditions without the need to escape burial by growing in height, but ragged margins and changes in growth direction of the tubules point to periodical disturbances during growth as is indicated by growth disruptions in the skeletons (Fig. 2B; 3B). An exception is specimen 2 which might have been covered periodically (a discussion is presented later in this manuscript).

Asphalt and cements in the tubules

Asphalt and cements in the skeletons are common. Cements are not present in all of the tubules, but where they coated the tubules this occurred before hydrocarbons intruded (Figs 7D; 8A; 9B, C). EDX and microprobe (mp) analyses show that some of the cements are dolomites (EDX: high Mg-values, mp: dolomite), while others are low Mg-calcitic (EDX: low Mg-values, mp: LMC). We explain the distribution of cements by the primary HMC-mineralogy of the chaetetid skeletons that released Mg-ions during diagenesis. Parts of the skeleton (especially the very central areas) can be interpreted as a closed system in which the Mg-ions were trapped and embedded in the early cements. This is also in accordance with the aragonite sea I (see above). A high concentration of magnesium in the chaetetid skeleton should supply enough Mg-ions to precipitate dolomite. As soon as the magnesium was depleted, low Mg-calcite cements precipitated. Specimens 2 and 6 (BSPG 2011 X 12 and – X 16) display very thin asphalt rims which coat many of the tubules and moreover, they represent two exceptional thin sections differing from all other Buckhorn chaetetids (discussion below). Remaining space in these specimens is filled by blocky calcite indicating diagenesis under freshwater influence.

Manganese calcitic cements

As an example, Tucker & Wright (1990) report the enrichment of low-Mg-calcites in manganese and iron (Fe) during meteoric diagenesis. Nonetheless, diagenesis is not the only explanation for accumulations of manganese and iron in carbonates. Fungi, microorganisms, bacteria, biofilms, or microstromatolites actively form Mn- and Fe-crusts (Ferris 2000; Jones 2000; Reitner et al. 2000; Verrecchia 2000). Polgári et al. (2012) concluded, after a study of the Úrkút manganese deposit in Hungary, that aerobic microbial activity was essential for building this deposit. The Buckhorn Asphalt Quarry is no Mn-carbonate deposit – however, Mn-calcite cements associated with the chaetetids are only present where microbial growth is recognized and thus it is reasonable to suggest that microbial activity or diagenetic impact on the microbial mats induced/supported the formation of the Mn-calcite in the Buckhorn specimens.

'Greyish structures'

Greyish structures in chaetetid skeletons of *Varioparietes geminus* Fenninger, 1969 are reported by Fenninger (1969) from the Valangian in Iran. According to Fenninger (1969) such areas are about 1.5 mm thick and are caused by bending or reduction of the diameter of the tubules, the lack of tabulae, a concentration and undulation of the skeleton, and by a reduction of the microstructure. Some areas appear only as a condensed

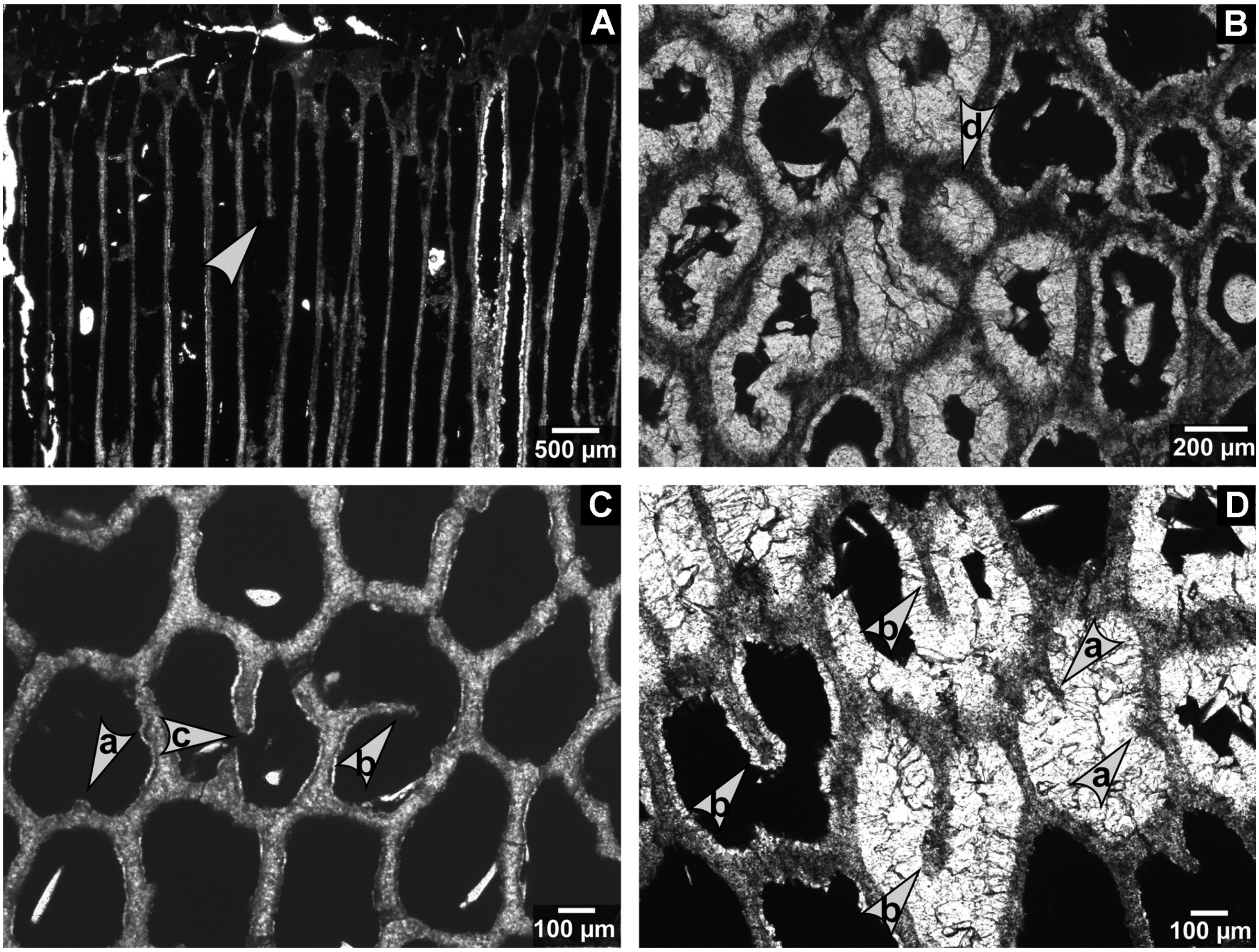

Fig. 9 - Insertion of new tubules in the chaetetid skeleton.
A) Insertion of a tubule wall (arrow) within present tubules in specimen 8 (BSPG 2011 X 18b).
B) Division of a tubule into two tubules (arrow d) in specimen 9 (BSPG 2011 X 19).
C-D) Pseudosepta separating tubules, inition of a pseudoseptum (arrow a), advanced pseudoseptum (arrow b), and two pseudosepta nearly touching and dividing the parental tubule (arrow c). C – Pseudosepta in specimen 4 (BSPG 2011 X 14). D – Pseudosepta in specimen 8 (BSPG 2011 X 18a).

mass of the skeleton. The lower boundary towards the regular zones in the skeleton is sharp whereas the upper boundary is indistinct.

Many of the chaetetid sponges from the Buckhorn Asphalt Quarry contain 'greyish structures' (Figs 2A-E; 3A, C, E; 4A-C). However, they differ from those reported by Fenninger (1969) in terms of general appearance, structure, and arrangement. The 'greyish structures' in the Buckhorn chaetetids are widely distributed in the skeleton and are mostly not arranged in regular levels. Generally, they are associated with fragments of the chaetetid tubules (Fig. 4B). Commonly, but not in all cases, the trend of the 'greyish structures' is more or less parallel to the growth surface of the skeleton (Fig. 4A). Boundaries towards the skeleton are blurry on both sides and an internal structure is lacking. Unidentified filament-like structures are present within some of the 'greyish structures' (Fig. 4B). These are distinctly smaller in size than associated tubule fragments and could have microbial origin. Specimens 8 and 9 (BSPG 22011 X 18 and - X 19) contain areas that are characterized by a distinct amount of hydrocarbons along with such 'filaments'. Figure 4C illustrates 'greyish structures' that follow the organization of circular, more or less layered filaments. Incorporated are oval structures of unknown origin. In specimen 1 (BSPG 2011 X 11) minute round voids are present within the greyish structure and in specimen 9 (BSPG 2011 X 19) asphalt-filled spheres resembling microborings in tubule fragments occur, that are associated with the greyish structure in the specimen. Filament-like structures are not present in all of these 'greyish structures' – this might be due to diagenesis or their primary absence – and therefore, it cannot be clarified if the filaments were crucial components in the development of the 'greyish structures' or not. It appears that the 'greyish structures' primarily develop in areas where a change of growth direction took place. Because of the lack of dis-

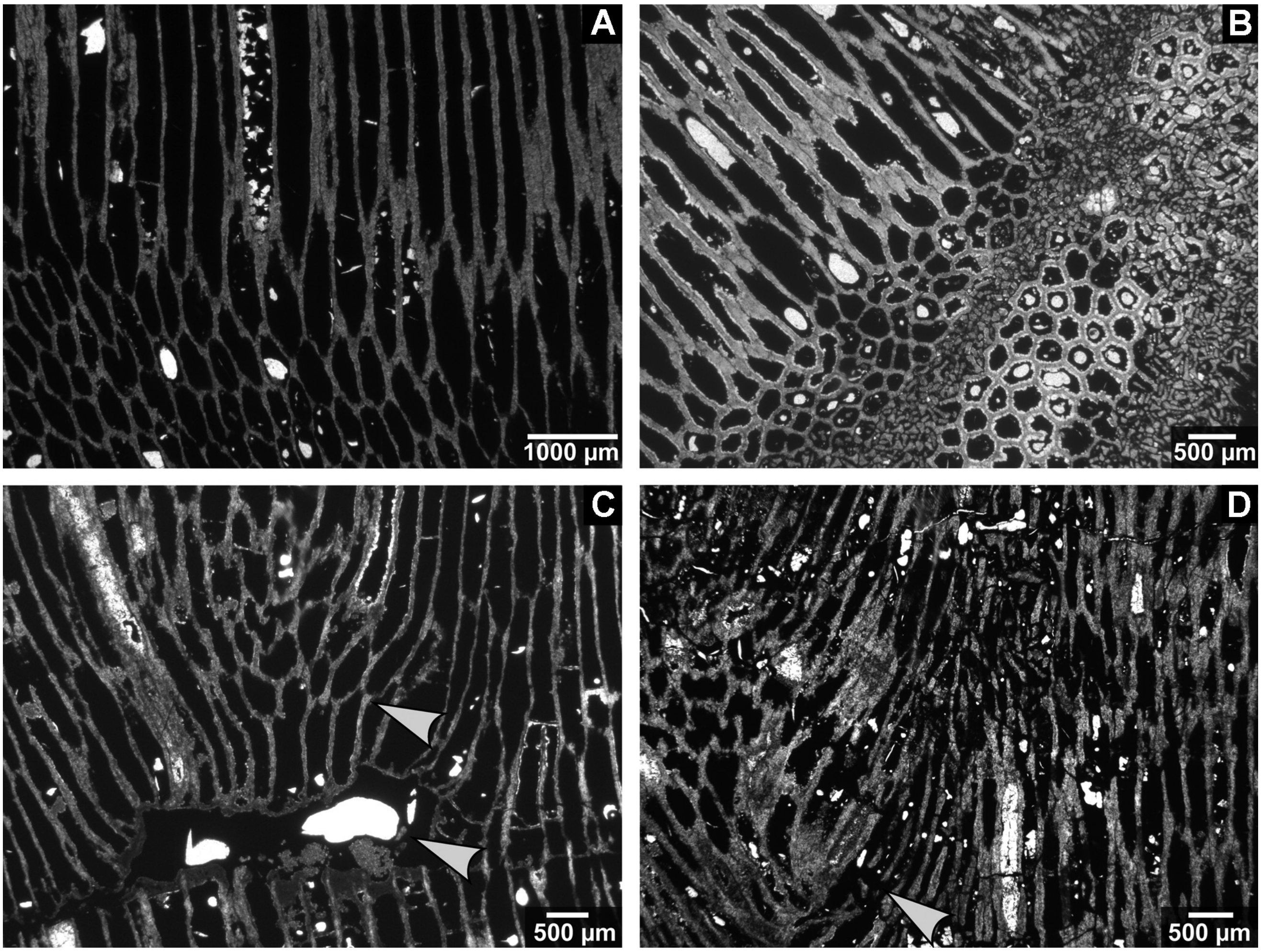

Fig. 10 - Tubules, fragmentation, and growth interruptions in Buckhorn chaetetid sponges.
A) Regular growth in specimen 3 (BSPG 2011 X 13) with constant change in growth direction (lateral to longitudinal), the tubules are filled with asphalt, the tubule in the middle in the upper part of the photograph contains calcite cements.
B) Tubules in specimen 5 (BSPG 2011 X 15), tubules are mostly coated with cements, remaining space is filled with asphalt, on the right an alternation of intact and heavily fragmented tubules is visible.
C-D) Inhomogeneous growth (arrows) in chaetetid specimens. C - Growth interruption in specimen 3 (BSPG 2011 X 13). D - Bending tubules and change in growth direction in specimen 8 (BSPG 2011 X 18c).

tinct characteristics we interpret the 'greyish structures' as a mixed feature, i.e., diagenesis along with skeletal changes (mainly the change of the growth direction) – if any distinct attributes had been present, they are now overprinted.

Facies and paleoenvironment

The large chaetetids used for the thin sections were from sample set #2 which mainly comprises pack- to grainstones as well as floatstones. The matrix of the rocks contains a large amount of asphalt that fills pore space and is characterized by a high amount of well-rounded quartz grains. Micritic clasts and glauconite also occur and shell fragments of the marine benthos are common. In places where asphalt did not fill open space, quartz and calcite cements are present. Other fossils present in sample set #2 are numerous gastropods, foraminifers (mainly fusulinids and palaeotextulariids), echinoderm remains (columnals, spines), bryozoans, ostracods, bivalves, and only few brachiopods. Fusulinids and palaeotextulariids inhabited shallow marine environments as did the gastropods, ostracods, and bryozoans. Shell beds in the succession signify frequent high-energy events (potentially triggered by monsoon, storms). Stanton et al. (1994) and Suchy & West (2001) found an association which is similar to the one in the Buckhorn Asphalt Quarry, and Tischler (1963) reported a relatively similar fauna except that in his association corals and sponges, other than chaetetids occur. In the Buckhorn deposits, sponges other than chaetetids are completely lacking and there are only few reports of a single coral (Webb & Sorauf 2001, 2002; Sorauf & Webb 2003). Remains of algae and land plants also occur in the matrix of the Buckhorn sediments and are relatively frequent. The land plant remains and the presence of high amounts of well-rounded quartz-grains and glauconite indicate a nearshore environment. Algae and the ichnocoenosis reported by Wisshak et al. (2008) point to deposition of the sediments within the photic zone II-III. Seuss et al. (2009) interpreted the sediment succession of sample set #2 as deposits within the regressive sequence of a cyclothem. Miller & West (1997) reported chaetetid specimens from shallowing upward cycles in which the chaetetids are found close to the top. This fits well to own observations. Summing up the facts, it is obvious that the chaetetids from the quarry site inhabited a shallow marine setting, which was well suited to for a diverse benthic fauna.

The deposits were not consolidated at that time (indicated by the asphalt in the pore space), but it seems that the chaetetids in this study did not require such conditions (an extended discussion on substrate is provided by West [2012b: 26-30]). Anyhow, the pack- and grainstones, but also the less frequent floatstones, will at least have provided some hard parts for the chaetetid larvae to settle on. Squires (1973) reported chaetetids from mudstones with large in situ chaetetid specimens. This indicates, on the one hand, fairly quiet conditions and on the other hand also points to the fact that chaetetids did not require a consolidated or lithified substrate for settling as far as any hard part or a solid irregularity was present for chaetetid larvae to settle (West 2012b).

Complex chaetetid specimens 2 and 6

Specimen 2 (BSPG 2011 X 12) (Figs 2F; 12A) differs distinctly if compared with 'regular' chaetetid sponges from the quarry. The upper part of specimen 2 ('Area c') is dominated by longitudinal fragments of the tubules. Towards the base the number of fragments of the points of intersection increases (i.e. the common wall of three or four tubules) ('Area b') and begins to alternate and mix with longitudinal fragments. In the lower third ('Area a') longitudinal fragments are lacking. A few larger remains of chaetetid skeletons are present near the top of the section in 'Area c' and below the prominent fissure separating 'Areas b and c'.

The preservation and internal organization of the sample leaves open questions: 1) Why did the hydrocarbons accumulate in layers and why is the amount of hydrocarbons so little compared to other specimens? 2) The upper section ('Area c') is dominated by longitudinal tubule fragments while 'Area a' contains points of intersection of the tubules only. How can this be explained? 3) How is it possible, that nearly the entire thin section consists of fragments, but in the central area larger fragments of the chaetetids are preserved? 4) Some areas appear poorly preserved (flawy) – why is this?

Answering these open questions remains speculatively. A scenario to explain the formation of the sample is as follows. Initially, in 'Area a', growth of the tubules was in such a direction, that the preserved remains only represent fragments of the point of intersection of the tubules. The tubules thus, were not growing in an upward direction but bent up to 90°, that is in a more or less horizontal plane. In the central area (i.e. 'Area b'), below the distinct fissure, larger remains of chaetetid skeletons are present. Surrounding these, an irregular lamination is visible caused by fragments of the point of intersection, by hydrocarbons, and by the increasing amount of longitudinal fragments. The latter can be explained as a beginning change in the growth direction of the chaetetid skeleton in this area. In the latest phase, represented by 'Area c', the growth of the chaetetid skeleton was laminar and the tubules grew in an upwards direction. This explains the longitudinal fragments in this area. It appears that the chaetetid was periodically covered by a thin micritic sediment layer with subsequent re-growth of the chaetetid or settling of a new laminar growing specimen. Coverage with sediment or rhythmic growth appears to have been more or less cyclic resulting in the relatively regularly laminated appearance. Laminated appearance is produced by hydrocarbons accumulation in layers.

Timing of the fragmentation, the migration of hydrocarbons, and the cementation is a matter of debate. The larger chaetetid fragments in the thin section are only disrupted at their margins and the fragments are not entirely coated by cements. However, space in the intact tubules in the upper part of these structures is filled with cements. Towards the base hydrocarbons intruded first before the remaining space was filled with cements and only a few tubules are entirely filled with asphalt. There is only little asphalt between the fragments of the entire section and where present it is associated with the cements embedding the fragments. Our speculative interpretation is as follows: after death of the individual, the specimen was embedded in sediment and fragmentation occurred due to pressure of the sediment load covering the deposits. The larger specimens, for some reason, were more stable and only the margins were crushed while pressure was too high for the laminated chaetetids ('Area c') and the tubules in 'Area a'. Accordingly, these were completely fragmented. The influx of pore water led to diagenetic precipitation of cements soon after death and burial keeping the fragments in place. It also etched and dissolved skeletal fragments resulting in the flawed appearance of some areas of the thin section. In the domical chaetetids the tubules were partly filled with hydrocarbons before precipitation of cements filled the remaining space. Since cements had already filled most of the open pore space between the fragments only small amounts of hy-

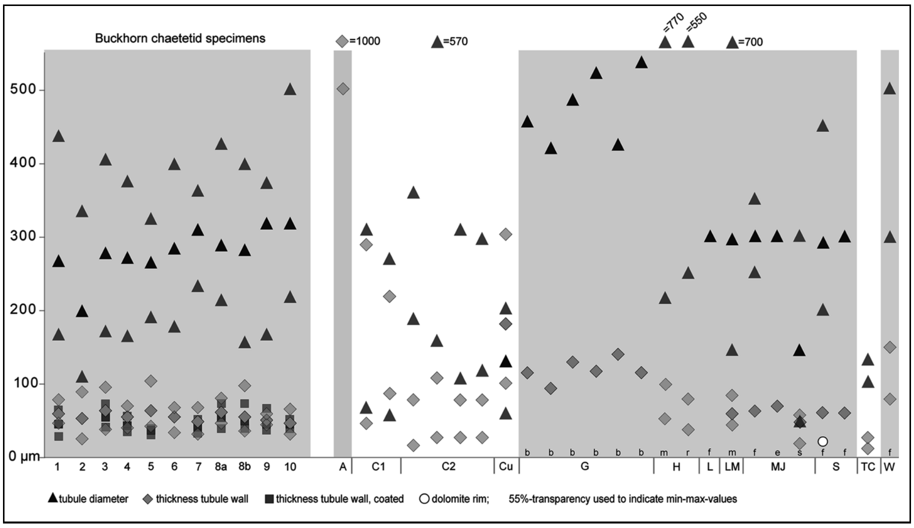

Fig. 11 - Measurements performed on Buckhorn chaetetid specimens combined with published data: three symbols of a kind comprise maximum, mean, and minimum values; two symbols of a kind represent maximum and minimum values. Single symbol represents the mean value only. Buckhorn chaetetid specimens. 1: BSPG 2011 X 11, 2: - X 12, 3: - X 13, 4: - X 14, 5: - X 15, 6: - X 16, 7: - X 17, 8a, b: - X 18a, X 18b, 9: - X 19, 10: - X 20. Data from literature: A: Almazán-Vasquez et al. (2007) - *Chaetetes* sp., Atokan; C1: Cremer (1994) -? *Blastochaetetes astrocanalis* nov. sp., Norian and Genus et sp. indet. Form A, Norian; C2: Cremer (1995) - *Archaeochaetetes alakirensis**, Norian, *Blastochaetetes dolomiticus*, Norian, *Ptychochaetetes* sp., Norian, and ?*Bauneia* sp., Norian; Cu: Cuffey et al. (1979) - *Atrochaetetes alakirensis*, uppermost Jurassic - lower Cretaceous; G: Gray (1980) - six specimens of *Chaetetes* (*Boswellia*) *mortoni*, Mississippian; H: Heritsch (1933) - *Chaetetes milleporaceus* and *Chaetetes radians*, both Carboniferous; L: Lane (1962) - *Chaetetes favosus*, Atokan - early Desmoinesian; LM: Lane and Martin (1966) - *Chaetetes milleporaceous*, Desmoinesian; MJ: Moore and Jeffords (1945) - *Chaetetes favosus*, Morrowan-Atokan, *Chaetetes eximus*, Morrowan, *Chaetetes subtilis*, Morrowan-Atokan; S: Squires (1973) - *Chaetetes* aff. *favosus*, Desmoinesian; TC: Toots and Cutler (1962) - *Chaetetes*?? *demissus*, upper Cretaceous; W: Wilson (1963) - *Chaetetes favosus*, Atokan. * not valid according to West 2012a.

drocarbons could intrude and thus, only little asphalt is present therein. This explains why specimen 2 (BSPG 2011 X 12) contains only little asphalt compared to the other specimens. Because the specimen was embedded and cements precipitated in an early stage, the fragments remained autochthonous.

Specimen 6 (BSPG 2011 X 16) (Figs 3D; 12B) contains two different morphologies. These are a laminated 'Area a' on the left side of the thin section and largely intact chaetetid skeletons surrounded by fragments in the middle and on the right ('Area b'). 'Area a' is characterized by a pronounced, slightly domical lamination of fragments. At the base, fragments of the points of intersection are accumulated. These merge into longitudinal fragments of tubules towards the top. Between the fragments asphalt is nearly absent. In the darker 16 intercalated layers a high amount of micritic sediment mixed with asphalt occurs. The uppermost layer of 'Area a' continues towards the right and partly covers 'Area b'. The left rim of 'Area a' is overgrown by a laminar chaetetid specimen, which seems not only to cover the rim but also, even appearing completely fragmented, the uppermost fragmented layer of 'Area a' continuing to the right and covering about half of 'Area b'.

'Area b' contains numerous large remains of one or more chaetetid specimens. These remains are separated by fragments of tubules, which are distinctly larger than those of 'Area a'. In between the fragments micritic sediment, cements, and a small amount of asphalt are present. The tubule fragments were not coated with cements before breakage. The tubules of the larger remains of the chaetetid(s) are mainly filled with cements. The amount of asphalt is low and the hydrocarbons appear as a thin coating of the tubules. In some cases they also fill the remaining space after precipitation of the cements. On the right, 'Area b' is covered by chaetetid fragments which themselves are covered by a thin sediment layer. The chaetetid fragments resemble those of 'Area a'.

As for specimen 2, questions on the formation of this sample arise. Main questions are: 1) What is the reason that larger chaetetid remains are present centrally and to the right, but not on the left side of the thin section? 2) The size of the fragments differs in both areas, what is the reason for this?

The simplest explanation to answer these questions is the skeleton itself. The tubule thickness in the left section ('Area a') of the sample was smaller than in the centre and the right. We assume that thickness and resistance to breakage are correlated in this case. Consequently, the tubules on the left were more prone to fragmentation and this answers the question why the size of the fragments in 'Areas a and b' differ. The growth form will also contribute to the resistance of a chaetetid skeleton. We suggest that the laminated growth form is more fragile compared to domical growth. Assuming that there are two morphotypes still does not give us an answer to how the lamination on the left side of the thin section occurred. There are 17 bent layers present which are separated by micritic sediment mixed with hydrocarbons and the uppermost layer continues to the right partly covering 'Area b'. This layer is overgrown by a laminar chaetetid which also continues

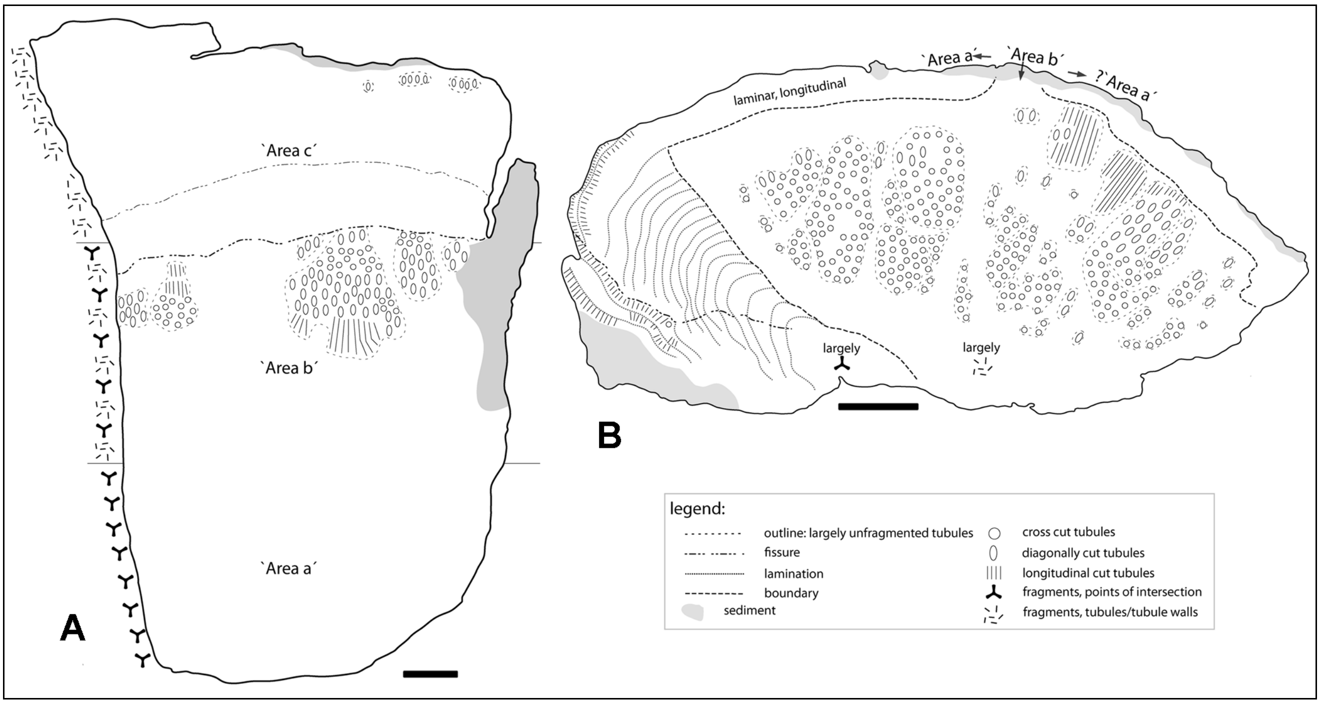

Fig. 12 - Sketches illustrating fragmentation, lamination, distribution of largely intact sections, and other structures within the exceptional thin sections from the Buckhorn Asphalt Quarry site.
A) Specimen 2 (BSPG 2011 X 12a). B) Specimen 6 (BSPG 2011 X 16).
Measure bar: 1 cm.

towards the right. There is no indication that this laminar chaetetid grew on the sediment present in the lower left. The boundary between 'Areas a and b' is indistinct because fragments of both areas immingle.

An interpretation – as for BSPG 2011 X 12 – remains speculative. 'Areas a and b' could represent two morphotypes. Overgrowth of 'Area b' by 'Area a' can be explained either by death of 'Area b' which made settling possible or by a higher rate of growth of 'Area a' facilitating coverage of 'Area b' and resulting in either a stop in growth or in death. Assuming that both areas grew at approximately the same time and side by side, this would have happened at the level of the sixteenth layer of 'Area a'. Anyhow, it is not clear whether both areas started their growth parallel, because the lowermost central part of the thin section appears blended and a definite boundary between these areas is not visible. Because differences in coloration and the distribution of the lowermost layers of 'Areas a and b' it seems, that the specimen of 'Area a' was the first settler but that the specimen of 'Area b' started growth only shortly after. Additionally, because of the growth at an angle of about 30° of the laminated specimen, we conclude that both grew at about the same time hindering expansion to the right respectively left side of the specimen. To explain the lamination of 'Area a' we suggest periodical growth-interruptions as we did for BSPG 2011 X 12. Because of the domical arrangement of the layers and the angle of about 30°, physical factors are excluded by us. It is more likely, that there was a rhythm in growth dependent on the environment (e.g., monsoon season, seasonality) and/or that regular interruptions were triggered by the specimen itself (e.g., reproduction phases). If environmental factors played a major role, 'Area b' was less influenced because of the continuous growth and the general absence of tabulae as indicators of unfavourable conditions. On the other hand 'Area b' could also indicate that conditions were stable and support our impression that growth in 'Area a' was controlled by the specimen itself rather than by the environment. Another difficulty of this sample is to explain the laminar chaetetid in 'Area a' growing along the left side of the larger laminated section. Either this specimen grew upon the sediment or it was directly attached to the laminated section. There is no indication of direct growth on the sediment, but it seems closely attached to the large laminated specimen to its right and follows the shape of the outline. Moreover, it covers the uppermost layer. We suggest that this third specimen grew on the side of the laminated chaetetid of 'Area a' and spread to the right following the outline of 'Area a'. Growth might have been enforced by the initial position of settling from which the chaetetid tried to reach a position which provided more sunlight and thus it overgrew 'Areas a and b'.

Comparison with *Chaetetes favosus* and other Paleozoic chaetetid sponges

Chaetetid sponges from the Buckhorn Asphalt Quarry have been previously studied by Squires (1973) and also discussed by Seuss et al. (2009) briefly. Squires (1973) assigned his specimens to *C.* aff. *favosus* Moore & Jeffords 1945. He classified them as tabulate corals, but noted the possibility that chaetetids could alternatively be members of the coralline sponges. Squires (1973) analyzed the mineralogy of the skeleton and concluded the primary mineralogy of the tubules (Squires called the tubules corallites referring to their coral-affinity) and tabulae was Mg-calcite with about 5 mol per cent $MgCO_3$ or even more in case of the most asphalt-impregnated and thus, likely best preserved specimens. Squires (1973) noticed a thin dolomite cement rim coating the tubules of several specimens. He described the tubules as irregularly shaped polygons with a maximum diameter of 0.30 mm. Wall thickness was about 0.06 mm and the dolomite coating was about 0.02 mm in average. The specimens lack pseudoseptae but tabulae (up to 5 per millimetre chaetetid skeleton) are present, the latter generally concentrated in the middle and basal parts of the specimens. Most of the tubules are filled with asphalt, only few with calcite or quartz cements. Moore & Jeffords (1945) described *C. favosus* from the Marble Falls limestone (Morrowan-Atokan) in Texas as large subcylindrical colonies, which might be rounded at the top. They consist of long, nearly straight prismatic tubules which are slightly bent in order to intersect the surface at right angles. The type specimen is 250 mm in diameter and more than 800 mm in height. The surface allows an investigation of the tubules which display a uniform, fine honeycomb structure and are slightly elongated in one direction. The diameter of the tubules is 0.3 mm on average and the wall 0.06 mm in thickness. A distinct feature is the faint beading of the tubule wall. Pseudoseptae are rare. Complete tabulae are widely spaced and occur in low number only, but are concentrated at some levels. Incomplete tabulae are common. Lane (1962) described chaetetids from the Ely Group (Atokan) in Nevada and assigned them to *C. favosus*. The description of the specimens and the figures he presented resemble those of Moore & Jeffords (1945). According to Lane (1962) the walls are spongy resulting from the wall structure and not from pores. Wilson (1963) reports *C. favosus* from the Ely Limestone (Atokan) in Nevada. According to Wilson (1963) the specimens are 30 cm in height and 20 cm in diameter with irregularly shape polygonal tubules and diameters of 0.3 to 0.5 mm. He reports smooth and beaded walls with thicknesses of 0.08 to 0.15 mm. The general description and measurements of Wilson (1963) disagree with those of Moore & Jeffords (1945) even though there are similarities like features of the tabulae. Thus, the taxonomic interpretation of Wilson (1963) is in doubt in our opinion. Wilson's (1963) specimens also highly differ from the specimens from the Buckhorn Asphalt Quarry and likely represent a different species and/or morphotype.

According to West (1994, 2011a) many features of a chaetetid skeleton are no reliable attributes which could be used for taxonomy. Nevertheless, we want to discuss the available data from the Buckhorn chaetetids here demonstrating the variance within and among chaetetid skeletons. While we agree with the mineralogical results presented by Squires (1973), our own specimens are not assigned to *C. favosus* for the following reasons (also Fig. 11): 1) The mean diameter of the tubules differs, only specimen 7 (BSPG 2011 X 17) has a similar mean diameter. 2) The size range of the diameters of the tubules is larger, only specimen 7 (BSPG 2011 X 17) has a similar range. 3) The thicknesses of the walls of the tubules have different mean values, only specimens 1, 3, 5, and 8 (BSPG 2011 X 11, - X 13, - X 15, - X 18) are similar. 4) The range of the thickness of the walls is highly variable in the Buckhorn specimens, whereas it is relatively uniform in *C. favosus*. 5) The wall from the Buckhorn specimens does not indicate the presence of beads (though they might have been removed by recrystallisation). 6) The distribution of tabulae varies within the Buckhorn specimens. Some chaetetids nearly don't show any tabulae whereas others contain a concentration of tabulae in levels or distinct areas. However the distribution of the tabulae (as well as the size and shape of the skeleton) are interpreted to depend on the environment as well as on gene expression (West & Clark 1984; Stanton et al. 1994). Thus, a comparison seems redundant. 7) The growth form and size differs from the specimens reported by Moore & Jeffords (1945) and Lane (1962). The Buckhorn specimens are wider than high.

Moore & Jeffords (1945) reported two further species of *Chaetetes* namely *C. eximus* Moore & Jeffords 1945 and *C. subtilis* Moore & Jeffords 1945. Both, the mean diameter and the mean wall thickness differ from the Buckhorn specimens. *C. subtilis* additionally is characterized by an irregular arrangement and variable shape of the tubules, which is not the case for the Buckhorn chaetetid sponges. *C. eximus* displays penta- to hexagonally tubules with a moderate amount of pseudoseptae and slightly beaded walls. This generally fits with our findings and the beading might have been lost by diagenesis. Anyhow, *C. eximus* is also characterized by numerous fine, flat, and mostly complete tabulae, which is not the case for the Buckhorn specimens. Gray (1980) describes occurrences of *C.* (*Boswellia*). The specimens highly differ in thickness of the wall, in tubule diameter, in the shape of the tubules, and the organization of the tabulae. Heritsch (1933) described *C. mille-*

poraceus Milne-Edwards & Haime, 1851 with highly variable shape and diameters of the tubules and a heterogenous distribution of tabulae and pseudoseptae. He suggested *C. milleporaceus* could be conspecific to *C. radians* from the Carboniferous of the Russian platform. The assignment to *C. milleporaceus* was doubted by Lane & Martin (1966), who published a re-description of *C. milleporaceus,* based on specimens from the 'de Verneuil collection' at l'Ecole des Mines in Paris. Their measurements of wall thickness and tubule diameter and the morphological descriptions of *C. milleporaceus* show a different construction of the skeleton compared with chaetetids from the Buckhorn Asphalt Quarry. Morgan (1924) describes a new species from the middle Pennsylvanian Homer limestone member of the Holdenville Formation in Oklahoma, namely *Chaetetes schucherti* Morgan 1924. The main criterion not to assign the Buckhorn specimens to *C. schucherti* is based on the absence of the sporadic tubes surrounded by 'corallites' reduced in size reported by Morgan (1924).

Conclusions

Chaetetid sponges form the largest benthic organisms in the deposits at the Buckhorn Asphalt Quarry. They derive from a tropical, shallow marine setting within the photic zone. The sediment during the time of chaetetid settlement was unconsolidated and generally fine grained. There might have been some larger objects for the larvae to settle on. From our analyses, in agreement with Squires (1973), we conclude that only their larvae, but not the growing specimens from the quarry required a solid substrate. The shape of the specimens is roughly domical indicating mainly stable conditions. In any case, monsoons or any periodic events influenced the site of deposition, and accordingly, the growth of the chaetetid sponges. Increased influx of sediment and partial covering of the skeleton caused growth interruptions and sudden change of the growth direction of the tubules. Ragged surfaces of some of the specimens indicate additional disturbances in growth (e.g. due to bioerosion, growth of microbes, or injury of the soft tissue). Mineralogical analyses of the chaetetid sponges from the Buckhorn Asphalt Quarry are in accordance with the results presented by Squires (1973), i.e. the chaetetids had a primary HMC-skeleton. This also fits well to the dolomite cements coating the tubules, the latter providing magnesium for the cements during diagenetic alteration and solution of the tubules.

Two chaetetid samples (BSPG 2011 X 12 and -16) (Figs 2F; 3D; 12A, B) display complex mechanisms of chaetetid growth, fragmentation, and diagenesis. Specimen BSPG 2011 X 16 (Figs 3D; 12B) contains two different morphotypes. They grew at about the same time and thus, derive from the same environment. There is no indication of any kind of protection, e.g. the presence of large boulders which could modify the water energy in a certain area and therefore the environmental conditions for one of the specimens. If chaetetid growth was influenced by the environmental setting mainly, they should display identical morphology. Since this is not the case, we are convinced that genetic factors play a major role in precipitating the skeleton and environmental factors are minor.

Squires (1973) reported *C.* aff. *favosus* from the quarry. We cannot agree with this identification since our own specimens are dissimilar to *C.* aff. *favosus*. Our data and measurements do not fit to any chaetetid species reported in the literature. Thus, a taxonomic identification with published species is not possible. Measurements of tubule thickness, tubule diameter, and the thickness and the distribution of the tabulae show variable values even within a single specimen. Additionally, spicules or their pseudomorphs, which could help identification, were not found and the microstructure of the skeleton is not preserved due to diagenesis. Therefore, following West's statement, that "systematic studies require primary features (spicules, which are commonly absent) and secondary features (the mineralogical composition and microstructure of the calcareous skeleton)" (West 2011a: 61), without spicules/spicule pseudomorphs and preserved microstructure in the Buckhorn chaetetids, we refrain from describing any new species.

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