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Internal anatomy of a brachyuran crab from a Late Cretaceous methane seep and an overview of internal soft tissues in fossil decapod crustaceans

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ABSTRACT

Cretaceous-aged methane seep carbonates in the Western Interior Seaway, USA, have yielded a relatively high diversity and concentration of fossils, including decapod crustaceans, compared to their surrounding, contemporaneous sediments. With technological advances in non-destructive imaging techniques, the internal anatomy of decapods can be studied in remarkable detail. Here, we present a brachyuran crab specimen from an upper Campanian methane seep carbonate in South Dakota, USA. While the external morphology of the crab is insufficient for species identification (*Secretanella* sp.), remarkable details of the internal morphology are preserved including soft tissues. Four phyllobranchiate gills are visible due to a broken cuticle. A µCT-scan revealed parts of the digestive tract including the esophagus and the cardiac stomach (foregut), and possible anterior gastric muscles. An esophagus has not been reported previously in a fossil decapod. We also found mandibles and their apodemes. Because of soft tissue preservation, the South Dakotan locality may be a candidate Konservat-Lagerstätte. To our knowledge, the studied crab contains the first preserved animal soft tissue reported from an ancient methane seep. Our new overview of internal soft tissues preserved in fossil decapod crustaceans shows that, besides muscles reported previously, gills and remains of the digestive tract are most often reported (8 and 13 occurrences, respectively). Reproductive organs, nerve chords, and the heart are only known from one or two occurrences. Although reports of soft internal anatomy preservation remain relatively rare, continued application of µCT-scans to fossil decapods has the potential to illuminate our knowledge of the evolution of internal decapod anatomy.

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INTRODUCTION

The internal anatomy of fossil arthropods has been increasingly studied over the last decades, leading to new insights about their biology and evolutionary relationships. Some previous studies have relied on exposed internal anatomy of specimens, i.e., through erosion, or mechanical preparation, including destructive sampling (e.g., Secrétan, 1985; Butterfield, 2002; Siveter et al., 2013; Zacaï et al., 2016; Jauvion et al., 2020a; Ortega-Hernández et al., 2022). Technological advances in the last decade have made it possible to non-destructively scan and illustrate the external and internal anatomy of arthropod fossils in great detail, including, among others, eurypterids (Lamsdell et al., 2020), ostracods (Wang et al., 2020), euarthropods (Liu et al., 2020; Laville et al., 2023), spiders (Downen and Selden, 2021), wasps (Szabó et al., 2022), and scorpions (de Carvalho et al., 2022). Decapod crustaceans, major contributors to marine ecosystems since the Mesozoic Decapod Revolution (Klompmaker et al., 2013, 2015; Schweitzer and Feldmann, 2015), have also been studied using newer techniques such as microCT (µCT) to uncover soft tissues (Jauvion et al., 2016, 2020b; Xing et al., 2021; Luque et al., 2021). Specimens with preserved soft tissue are generally derived from classic Konservat-Lagerstätten, from which exceptional preservation is well-known across multiple taxa. Here we report on a Late Cretaceous brachyuran crab from South Dakota, USA, from a deposit that has not been associated with exceptional preservation previously. While the external morphology of the crab is not very well preserved, we reveal a part of the internal anatomy.

GEOLOGICAL SETTING

Upper Cretaceous carbonates associated with cold seeps such as methane seeps in the Western Interior Seaway of the USA have received increased attention over the last decade (e.g., Landman et al., 2022). They range in age from the middle Campanian to the earliest Maastrichtian and are found in Montana, Wyoming, South Dakota, Nebraska, Colorado, and Kansas thus far (Landman et al., 2022). Seep carbonates vary in size and shape and can form mounds. Jointly, these carbonates contain a diverse fauna of invertebrates, vertebrates, and trace fossils (e.g., Bishop and Williams, 2000; Landman et al., 2012, 2022; Hunter et al., 2016; Rowe et al., 2020; Klompmaker and Landman, 2021; Brezina et al., 2022) at a higher concentration than in the adjacent, contemporaneous rocks. These hotspots of diversity in the Western Interior Seaway may have acted as refuges during times of ash fall and as sources for repopulating other parts of the seaway (Brophy et al., 2022).

The crab specimen studied herein was found by Jamie Brezina between 2012–2018 at the American Museum of Natural History Invertebrate Paleontology (AMNH IP) locality 3529 on the eastern edge of the Black Hills in Pennington County, South Dakota, USA (43.9061°, -102.9075°), which used to be part of the Western Interior Seaway (Figure 1). This seep is within the upper Campanian *Didymoceras cheyennense* ammonite Zone in the Pierre Shale, 74.67±0.15 m.y.a. (Landman et al., 2018a, 2022). The fauna recently reported from this locality includes ammonites, bivalves, gastropods, sea stars, crinoids, decapod crustaceans, bryozoans, corals, serpulid annelids, and fish remains (Cochran et al., 2015; Blake et al., 2018; Brezina et al., 2022; Klompmaker et al., 2022; Landman et al., 2022). Decapod crustaceans found here, but not scanned for internal anatomy, include *Protocallianassa? cheyennensis* (Rathbun, 1930), *Latheticocarcinus punctatus* (Rathbun, 1917), *Dakoticancer overanus* (Rathbun, 1917), *Bournelyreidus oaheensis* (Bishop, 1978), and *Secretanella spinosa* (Bishop, 1991) (see also Klompmaker et al., 2022, table 5.1). The specimen herein was discovered as surface float on the southern side of the seep hill, down slope rather than strictly in situ. Based on the carbonate mineralogy of the crab specimen, the specimen must have been derived from the *in situ* carbonates making up the hill.

MATERIALS AND METHODS

High-resolution X-ray computed tomography (µCT) scans of specimen ALMNH:Paleo:6522 were obtained at the Berkeley Preclinical Imaging Facility (UC Berkeley, California, USA) in July 2019 using a GE Healthcare eXplore Locus Micro CT Scanner. The specimen was scanned using a conebeam energy of 80 kV, a current of 450 µA, 2,000 ms exposure time, and no filter, resulting in a voxel resolution of 20.523 µm. Visualization and three-dimensional reconstruction of the resulting µCT data were performed using the open-source software 3D Slicer v.4.13.0 (Fedorov et al., 2012). The µCT-scan data, stored as a 1.28 GB stack of DICOM images, and an .stl 3D-model of the outer surface of the crab are available at Zenodo [https://doi.org/10.5281/zenodo.7686211, https://doi.org/10.5281/zenodo.7686121].

A standard procedure to evaluate whether anaerobic oxidation of methane took place at suspected methane seep deposits, such as AMNH IP loc. 3529, is to analyze the carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopes of the seep carbonates (e.g., Landman et al., 2012). The specimen studied herein (ALMNH:Paleo:6522) did not have sufficient sedimentary or concretionary matrix surrounding the specimen, so the matrix attached to two other decapods from the same locality and carbonate deposit, both benthic decapods (ALMNH:Paleo:20359, *Bournelyreidus oaheensis*; ALMNH:Paleo:20360a, *Protocallianassa cheyennensis*), were analyzed at the UC Santa Cruz Stable Isotope Laboratory (California, USA) using the Thermo Fisher Scientific Kiel IV-MAT 253 device. The methodology is described in detail in Landman et al. (2018b).

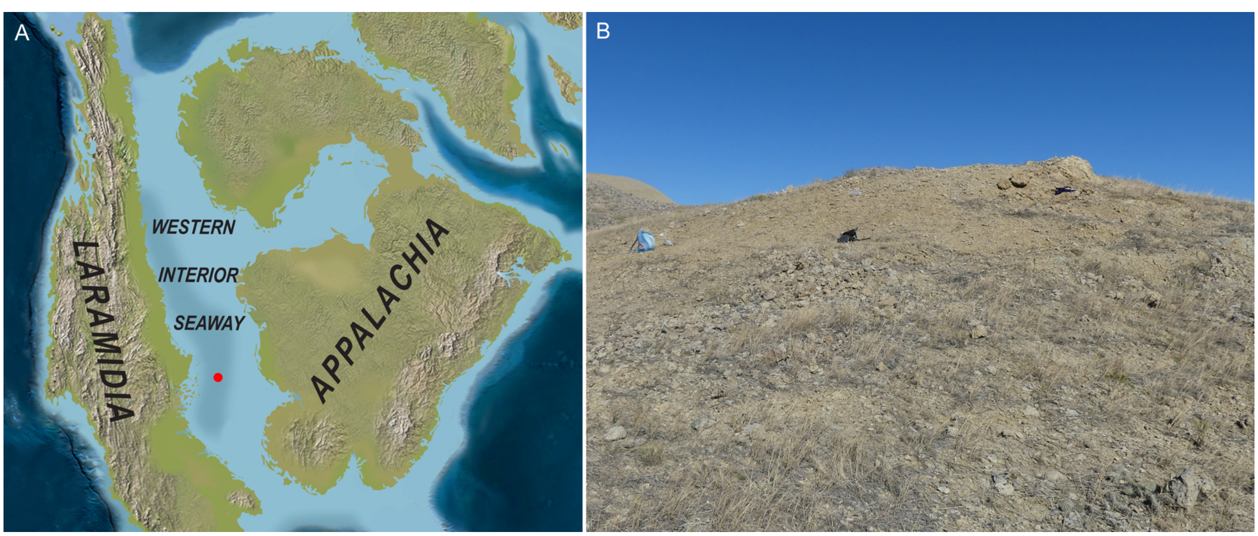

FIGURE 1. Location of study area in South Dakota. **A,** paleobiogeographic map of most of North America during the Late Cretaceous (late Campanian) with the locality indicated by a red dot (modified from Sampson et al., 2010, figure 1). **B,** photo of the locality in Pennington County, South Dakota, USA, where the studied crab specimen was discovered. A massive limestone from the upper Campanian *Didymoceras cheyennense* ammonite Zone is located at the top of the hill on the right and many limestone pieces are found downslope.

The cited specimens are reposited in the Alabama Museum of Natural History paleontology collection, University of Alabama, Tuscaloosa, Alabama, USA (ALMNH:Paleo). The locality is abbreviated by an American Museum of Natural History, New York, New York, USA, invertebrate paleontology number (AMNH IP).

RESULTS

Taxon Identification

Specimen ALMNH:Paleo:6522 represents a female individual given the wide abdomen and is identified as *Secretanella* sp. Two species of *Secretanella* Guinot and Tavares, 2001, are known from the Pierre Shale: (1) *S. occidentalis* (Bishop, 1985) from the lower Campanian Gammon Ferruginous Member within the *Baculites* sp. smooth Zone above the Groat Sandstone and below bentonite H in Butte County, South Dakota (see Landman et al., 2014), and (2) *S. spinosa* from the upper Campanian *Baculites cuneatus* Zone of Grand County, Colorado, and from the same locality that ALMNH:Paleo:6522 originates from in South Dakota (Klompmaker et al., 2022). Key carapace features of ALMNH:Paleo:6522 used to distinguish between these species such as the course of the cervical groove, the degree of ornamentation, and the number of spines on the anterolateral margin (Bishop, 1991; Schweitzer et al., 2012) are poorly preserved in this 21 mm wide specimen to the point that species identification is not feasible. Moreover, possible ontogenetic changes in carapace morphology for these two species are insufficiently known due to the low number of available specimens.

Carbon and Oxygen Isotopes

Isotope analyses of carbonate matrix surrounding a specimen of *Bournelyreidus oaheensis* (ALMNH:Paleo:20359) yielded a $\delta^{13}C$ value of -26.03‰ VPDB and a $\delta^{18}O$ value of -4.97‰ VPDB. Matrix around a specimen of *Protocallianassa? cheyennensis* (ALMNH:Paleo:20360a) resulted in a $\delta^{13}C$ value of -26.66‰ VPDB and a $\delta^{18}O$ value of -5.58‰ VPDB. Similar values were reported by Gao et al. (2021) for this site: a $\delta^{13}C$ value of -23.36±0.01‰ and a $\delta^{18}O$ value of -5.37±0.09‰. These low $\delta^{13}C$ values alone are insufficient to support that AMNH IP loc. 3529 is a methane seep, but the abundant presence of carbonates in the shale in conjunction with typical seep fauna such as lucinid bivalves at this site, in accordance with Landman et al. (2022) support a methane seep hypothesis.

Internal Anatomy

A part of the outside of the replaced carapace cuticle is missing and reveals clear three-dimensionally preserved gill structures including four visible phyllobranchiate gills (Figures 2, 3). We interpret that the fourth partly overlays the third gill. The individual branchial lamellae are visible as dark, vertical bands with calcium carbonate layers in between them (Figures 2, 3). A possible partial afferent vessel may be preserved in the second gill (Figure 3). Despite the incomplete preservation, the individual gills appear similar in overall structure to those in fossil and extant brachyurans (e.g., Robin et al., 2018; Luque et al., 2021). More gills may be present, but they are not exposed. Comparison with gills from extant representatives within the same group (Etyoida) is not possible because all species of this clade are extinct. The subsequent µCT-scan we carried out did not reveal additional gills, but it uncovered other structures not visible to the naked eye. These structures include the esophagus (≤ 1 mm in cross section), cardiac stomach (foregut) (~2.5 mm wide), the mandibles and apodemes (~7 mm wide), and possible anterior gastric muscles (~1.5 mm wide for each) (Figures 4, 5; Appendix 1, Figures S1–S4). The esophagus is positioned below the cardiac stomach to which it connects, which is known from various extant decapods such as brachyurans, anomurans, dendrobranchiatans, and astacideans (e.g., McLaughlin, 1980; Keiler et al., 2016; Castejón et al., 2018; Smolowitz, 2021). The esophageal walls in conjunction with muscles help transport the ingested food into the cardiac stomach for further processing (Davie et al., 2015; Castejón et al., 2018). The apodemes and in particular the attached mandibles are very close to the ventrally located opening of the esophagus. The remaining portions of the digestive tract, gills, and other internal anatomy could not be resolved by µCT-scanning.

DISCUSSION

Konservat-Lagerstätte and Preservation

According to its original definition, the presence of fossilized soft parts is what defines a Konservat-Lagerstätte (Seilacher, 1970). Given the recognition of soft parts within a single crab, AMNH IP loc. 3529 may be considered a candidate Konservat-Lagerstätte. Additional fossils with soft tis-

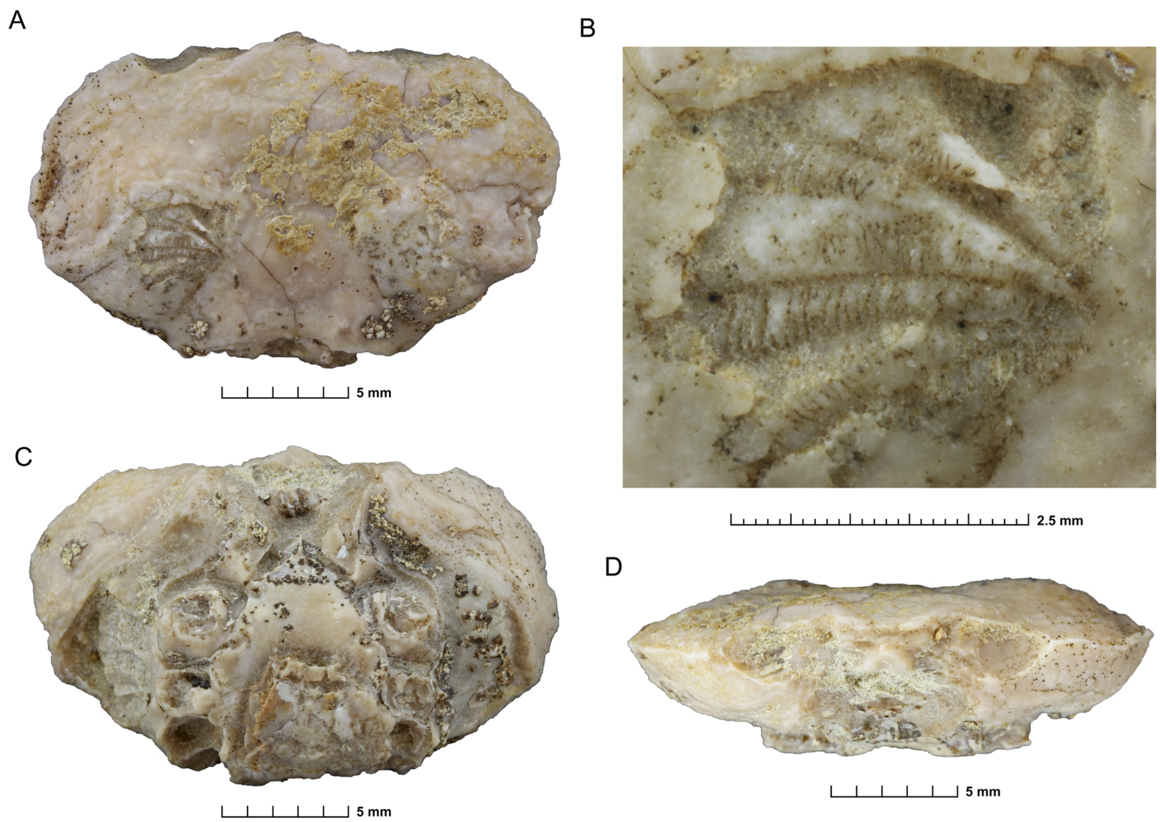

FIGURE 2. The crab *Secretanella* sp. (ALMNH:Paleo:6522) from an upper Campanian methane seep limestone in Pennington County, South Dakota. **A,** carapace in dorsal view. **B,** closeups of the preserved gills in left branchial chamber. **C,** carapace in ventral view. **D,** carapace in frontal view.

sue preservation from this site would strengthen the case to refer to this site as a Konservat-Lagerstätte, because it is generally understood that multiple species with soft tissue preservation at a site constitute a Konservat-Lagerstätte (e.g., Allison and Briggs, 1993; Muscente et al., 2017). The development of imaging methods within the context of fossil specimens has aided the identification of preserved fine morphological details, and has facilitated the recognition of originally soft parts from localities where soft tissue preservation would be less likely to be recognized without these techniques. As a result, many more Konservat-Lagerstätten and perhaps more types of Konservat-Lagerstätten may be reported in the future, but the proportion of sites with exceptional preservation of mineralized soft tissues among all fossil sites is likely to remain low.

The cause for the preservation of these crab soft tissues may differ from classic Konservat-Lagerstätten because of its probable link to methane seep carbonate formation. It is likely that the specimen did not live exclusively in this seep environment (see Mode of life), but methane seepage leading to elevated levels of poisonous hydrogen sulfide could have been the reason for the crab's death (cf. Rowe et al., 2020, for ammonites). Experiments have shown that decapod soft tissues decay relatively quickly (Plotnick, 1986; Krause et al., 2011; Klompmaker et al., 2017) and, therefore, a preservation process would be required to geologically stabilize the soft tissues. At this site, microbially-induced carbonate precipitation and sulfate reduction may have occurred (Peckmann and Thiel, 2004; Pierre and Fouquet, 2007; Case et al., 2015). Microbial methanogenesis and sulfate reduction are linked to seep carbonate precipitation (Beauchamp et al., 1989; Capozzi et al., 2012). The combination of such physio-chemical conditions and microbial activity seems very favorable for rapid mineralization of soft tissue (Jauvion et al., 2020a, and references therein). Rapid mineralization of echinoid muscular soft tissue by amorphous calcium carbonate precipitation was shown experimentally in a marine brine seep setting, sug-

FIGURE 3. Exposed gills of the crab *Secretanella* sp. (ALMNH:Paleo:6522) from an upper Campanian methane seep limestone in Pennington County, South Dakota and an interpretative drawing. 1-4: inferred number of gills; ?af: possible afferent vessel.

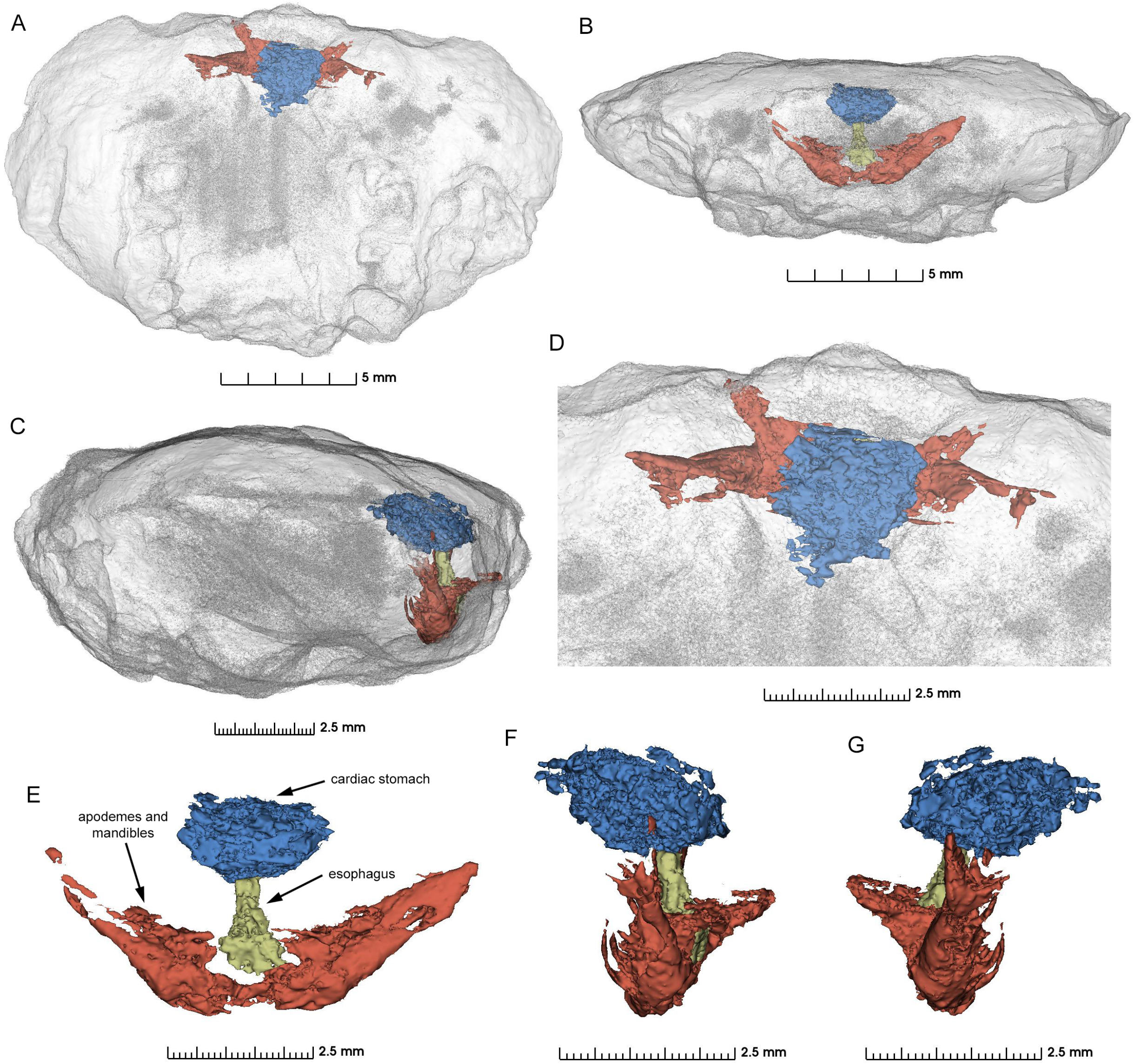

FIGURE 4. MicroCT (μCT) scan results of the crab *Secretanella* sp. (ALMNH:Paleo:6522) from an upper Campanian methane seep limestone in Pennington County, South Dakota. The external surface of the crab is translucent to show the position of the preserved internal structures that the scan detected. Blue: cardiac stomach; yellow: esophagus; red: apodemes and mandibles. **A,** dorsal view. **B,** frontal view. **C,** right lateral view. **D,** closeup of dorsal view. **E,** closeup of frontal view. **F,** closeup of right lateral view. **G,** closeup of left lateral view.

gested to have been aided by sulphide-oxidizing bacteria (Deline and Parsons-Hubbard, 2013).

Several factors may have played a role in the preservation of decapods in seeps including the rate of carbonate precipitation and where crabs were located relative to the highest concentration of seepage. Some seeps may not produce enough carbonate near the surface to allow rapid precipitation of carbonates to preserve soft parts. If crabs are directly on top of the seep field, then carbonate precipitation might have rapidly encased them. If specimens were living on the outer perimeter of the seep, then carbonate precipitation might have been slower or non-existent, allowing predators and scavengers to feed upon animals not rapidly buried. For this particular crab, carbonate precipitation occurred rapidly, and it is likely the crab was at or very near the highest concentration of seepage upon its death. The same scenario may apply to some articulated sea stars (Blake et al., 2018) and a fish with many 3D-preserved, articulated scales (J. B., pers. obs.) from the same site.

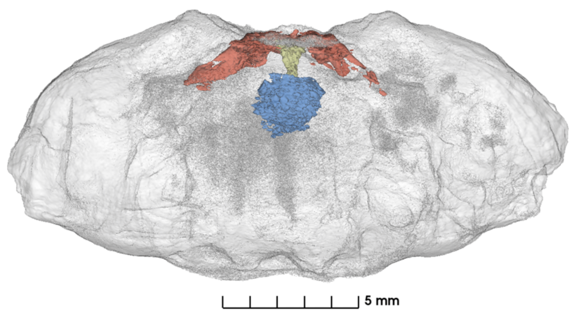

FIGURE 5. Rotating illustration (spin around the dorsal and ventral sides) of the microCT (μCT) scan results of the crab *Secretanella* sp. (ALMNH:Paleo:6522) from an upper Campanian methane seep limestone in Pennington County, South Dakota. Blue: cardiac stomach; yellow: esophagus; red: apodemes and mandibles. See online version for rotation (https://palaeo-electronica.org/content/2023/3973-soft-tissues-in-fossil-crab).

Although the gills are visible from the outside of the specimen, they were not visible in the μCT-scan. It was also the case for the two reconstructed polychelidan lobsters from La Voulte-sur-Rhône (Jauvion et al., 2016, 2020a), whereas thylacocephalans (Secrétan, 1985; Wilby et al., 1996; Jauvion et al., 2020b) and dendrobranchiate shrimps (Jauvion, 2020) from the same locality display exquisite gill preservation when cut and prepared as thin sections. Decapod and thylacocephalan specimens from La Voulte preserved within carbonate concretions display an identical mineralogical composition (Jauvion, 2020). The lack of X-ray contrast of the fossilized gills compared to the fossil matrix might explain why they do not render well with μCT-scans despite their presence. Other internal organs are missing, which may be due to several factors: insufficient μCT-scan resolution, insufficient density contrast compared to the fossil matrix, decay prior to mineralization (e.g., Clements et al., 2022), or, simply, absence of mineral replication of the structures.

Mode of Life

Although only the carapace of this specimen is preserved, we suggest this specimen was capable of swimming because of the relatively low carapace length/width ratio of approximately 0.6, relatively low height (~25% of width), and the flattened morphology of the dorsal carapace (e.g., Hartnoll, 1971; Bishop, 1991; Fraaye, 1996). The mode of life allowed this crab to visit seeps as a migrant rather than being an obligatory inhabitant of seeps. In support of this hypothesis, other specimens of this genus have also been found in non-seep sites in the Pierre Shale (Bishop, 1985, 1991).

Internal Soft Tissue in Fossil Decapod Crustaceans

Although soft tissue preservation in decapod crustaceans remains a rare phenomenon in general, an increasing number of specimens with such preservation are being reported. Muscle tissues in decapod crustaceans have been reported in over 30 species from primarily classic Jurassic and Cretaceous Konservat-Lagerstätten (Klompmaker et al., 2019: table 1) out of well over 3,650 fossil decapod species (Schweitzer and Feldmann, 2016). Other internal structures are even rarer and are also mostly reported from the Jurassic and Cretaceous. Herein (Table 1), we show that gills are known for only eight fossil species, and at least part of the digestive tract has been mentioned for 13 species. Other internal soft tissues interpreted to be preserved in fossil decapods include ovaries, nerve chords, and a heart (Table 1). The specimen reported here is unique in that an esophagus is reported for the first time in a fossil decapod and it is the first decapod from an ancient methane seep reported to preserve soft tissues.

As more finds become available, a more thorough assessment of the evolution of soft tissues within and across decapod clades may become possible. Specimens that do not show soft tissues externally may also contain soft tissues, however, and as imaging techniques become more widely available and cheaper, scanning of fossil decapod specimens will allow the proportion of specimens with soft tissue preserved across deposits and across decapod clades to be evaluated. Our find from a methane seep may serve as a reminder that soft tissue preservation is not restricted to classic Konservat-Lagerstätten but can be encountered at any place where the geochemical conditions are suitable for early diagenetic mineralization.

To our knowledge, no mineralized soft tissue has ever been found in any organismal group from ancient methane seeps until this paper, but fossils from these deposits typically have not been investigated using CT-scanning. Thus, to what extent soft tissue is preserved among seep animals is unknown. Non-soft tissue organic material has been reported from organic-walled fossil elasmobranch egg capsules from ancient seeps (Kiel et al., 2013; Treude, 2022) and fossil organic-walled annelids from fossil seeps and hydrothermal vents (Georgieva et al., 2019; Georgieva and Little, 2022). True soft tissue remains of the digestive

TABLE 1. Adult fossil decapod crustacean with internal soft tissues preserved except muscles for which we refer to Klompmaker et al. (2019: table 1).

Internal structure(s)	Higher taxon	Species	Age	Locality	Reference
Gills	Brachyura	*Archaeoplax signifera* Stimpson, 1863	Miocene	Gay Head, Massachusetts, USA	Cushman (1905)
Gills	Brachyura	*Romaleon franciscae* Robin et al., 2018	Miocene	Kerguelen Islands	Robin et al. (2018)
Gills	Caridea	*Bechleja brevirostris* de Mazancourt et al., 2022	Eocene (Lutetian)	Messel, Germany	de Mazancourt et al. (2022)
Gills	Brachyura	*Secretanella* sp.	Late Cretaceous (late Campanian)	Pennington County, South Dakota, USA	herein
Gills	Dendrobranchiata	*Palaeobenthesicymus libanensis* (Brocchi, 1875)	Late Cretaceous (late Santonian)	Sahel Alma, Lebanon	Audo and Charbonnier (2013)
Gills	Brachyura	*Cretapsara athanata* Luque et al., 2021	Late Cretaceous (early Cenomanian)	Angbamo, Myanmar	Luque et al. (2021)
Gills	Brachyura	*Marylyreidus punctatus* Rathbun, 1935	Early Cretaceous (Albian)	Fort Worth, Texas, USA	Franţescu et al. (2016)
Gills	Dendrobranchiata?	indet.	Middle Jurassic (Callovian)	La Voulte-sur-Rhône, France	Wilby et al. (1996)
Digestive tract (stomach and intestine)	Caridea	*Bechleja brevirostris* de Mazancourt et al., 2022	Eocene (Lutetian)	Messel, Germany	de Mazancourt et al. (2022)
Digestive tract (intestine)	Astacidea	*Aenigmastacus crandalli* Feldmann et al., 2011	Eocene (Ypresian)	McAbee, British Columbia, Canada	Feldmann et al. (2011)
Digestive tract (esophagus and cardiac stomach)	Brachyura	*Secretanella* sp.	Late Cretaceous (late Campanian)	Pennington County, South Dakota, USA	herein
Digestive tract (intestine)	Dendrobranchiata	*Palaeobenthesicymus libanensis* (Brocchi, 1875)	Late Cretaceous (late Santonian)	Sahel Alma, Lebanon	Audo and Charbonnier (2013)
Digestive tract (?stomach)	Dendrobranchiata	*Cretapenaeus berberus* Garassino et al., 2006	Late Cretaceous (Cenomanian)	Djebel Oum Tkout, Morocco	Gueriau et al. (2014)
Digestive tract (intestine)	Paguroidea	*Striadiogenes frigerioi* Garassino et al., 2009	Late Cretaceous (Cenomanian)	Hadjula, Lebanon	Garassino et al. (2009)
Digestive tract (intestine)	Axiidea	*Cretacalliax levantina* Pasini et al., 2020	Late Cretaceous (Cenomanian)	Hadjula, Lebanon	Pasini et al. (2020)
Digestive tract (stomach)	Dendrobranchiata	*Xiaopenaeus electrinus* Xing et al., 2021	Late Cretaceous (early Cenomanian)	Angbamo, Myanmar	Xing et al. (2021)
Digestive tract (intestine)	Glypheidea	?*Mecochirus* sp.	Late Jurassic (early Tithonian)	Causse Méjean, France	Moreau et al. (2022)
Digestive tract (stomach)	Dendrobranchiata?	indet.	Middle Jurassic (Callovian)	La Voulte-sur-Rhône, France	Wilby et al. (1996)

TABLE 1 (continued).

Internal structure(s)	Higher taxon	Species	Age	Locality	Reference
Digestive tract (cardiac and pyloric stomachs, intestine)	Polychelida	*Voulteryon parvulus* Audo et al., 2014	Middle Jurassic (Callovian)	La Voulte-sur-Rhône, France	Jauvion et al. (2016)
Digestive tract (cardiac and pyloric stomachs, hepatopancreas)	Polychelida	*Palaeopolycheles nantosueltae* Jauvion et al., 2020b	Middle Jurassic (Callovian)	La Voulte-sur-Rhône, France	Jauvion et al. (2020b)
Digestive tract (indet.)	Polychelida	*Willemoesiocaris ovalis* (Van Straelen, 1923)	Middle Jurassic (Callovian)	La Voulte-sur-Rhône, France	Audo et al. (2014)
Reproductive organs (ovaries)	Caridea	*Bechleja brevirostris* de Mazancourt et al., 2022	Eocene (Lutetian)	Messel, Germany	de Mazancourt et al. (2022)
Reproductive organs (ovary)	Polychelida	*Voulteryon parvulus* Audo et al., 2014	Middle Jurassic (Callovian)	La Voulte-sur-Rhône, France	Jauvion et al. (2016)
Nerve chords	Dendrobranchiata	*Xiaopenaeus electrinus* Xing et al., 2021	Late Cretaceous (early Cenomanian)	Angbamo, Myanmar	Xing et al. (2021)
Nerve chord (ventral)	Dendrobranchiata?	indet.	Middle Jurassic (Callovian)	La Voulte-sur-Rhône, France	Wilby et al. (1996)
Heart	Dendrobranchiata?	indet.	Middle Jurassic (Callovian)	La Voulte-sur-Rhône, France	Wilby et al. (1996)

tract of pholadoidean bivalves were reported from another ancient chemosynthetic community, a late Oligocene–early Miocene wood fall from Washington State, USA (Kiel et al., 2012).

CONCLUSIONS

The crab (*Secretanella* sp.) we studied from a Campanian methane seep in South Dakota, USA, shows four phyllobranchiate gills in the left branchial chamber. These gills are visible because the carapace cuticle is broken there. A µCT-scan of this crab reveals more details of its internal anatomy, including the esophagus, cardiac stomach (foregut), and possible anterior gastric muscles. The mandibles and their apodemes were also identified. The esophagus is reported for the first time in fossil decapod crustaceans. This crab represents the first animal from a fossil methane seep to have fossil soft tissues identified. Hence, the site can be considered a candidate for a Konservat-Lagerstätte.

Our new overview of internal soft tissues preserved in fossil decapods shows that, besides muscles reported on previously, gills and remains of the digestive tract are most often reported. Despite an increase in reports on fossil decapods with internal soft tissues preserved over the last decade, soft internal anatomy preservation remains relatively rare.

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APPENDIX 1.

Supplementary figures to manuscript.

FIGURE S1. MicroCT (μCT) scan results of the crab *Secretanella* sp. (ALMNH:Paleo:6522) from an upper Campanian methane seep limestone in Pennington County, South Dakota. The external surface of the crab is translucent to show the position of the preserved internal structures that the scan detected. Blue: cardiac stomach; yellow: esophagus; red: apodemes and mandibles; purple-pink: possible anterior gastric muscles. **A,** dorsal view. **B,** frontal view. **C,** right lateral view. **D,** closeup of dorsal view. **E,** closeup of frontal view. **F,** closeup of right lateral view. **G,** closeup of left lateral view.

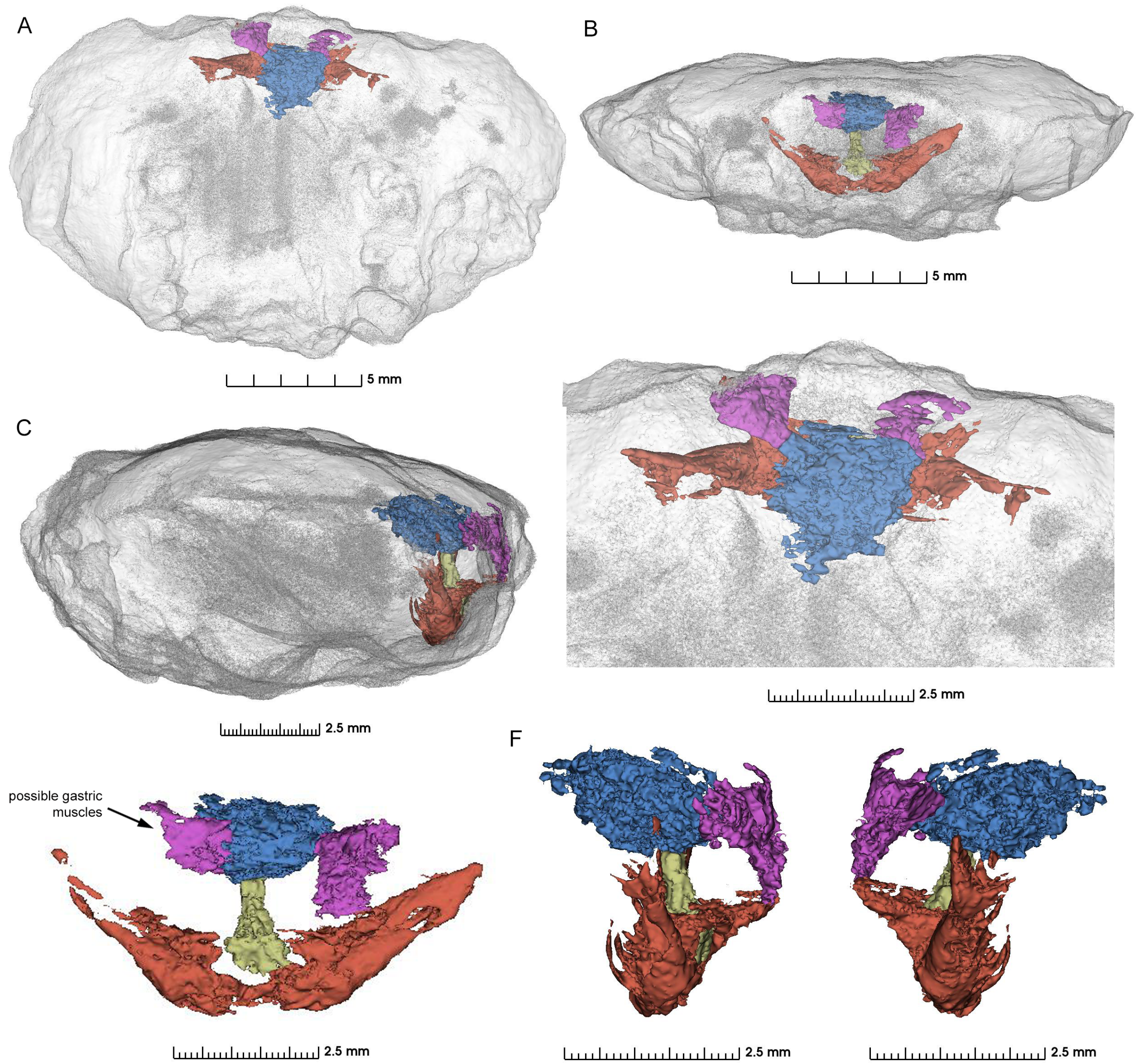

FIGURE S2. Rotating illustration (spin around the lateral sides) of the microCT (µCT) scan results of the crab *Secretanella* sp. (ALMNH:Paleo:6522) from an upper Campanian methane seep limestone in Pennington County, South Dakota. Blue: cardiac stomach; yellow: esophagus; red: apodemes and mandibles. See online version for rotation (https://palaeo-electronica.org/content/2023/3973-soft-tissues-in-fossil-crab).

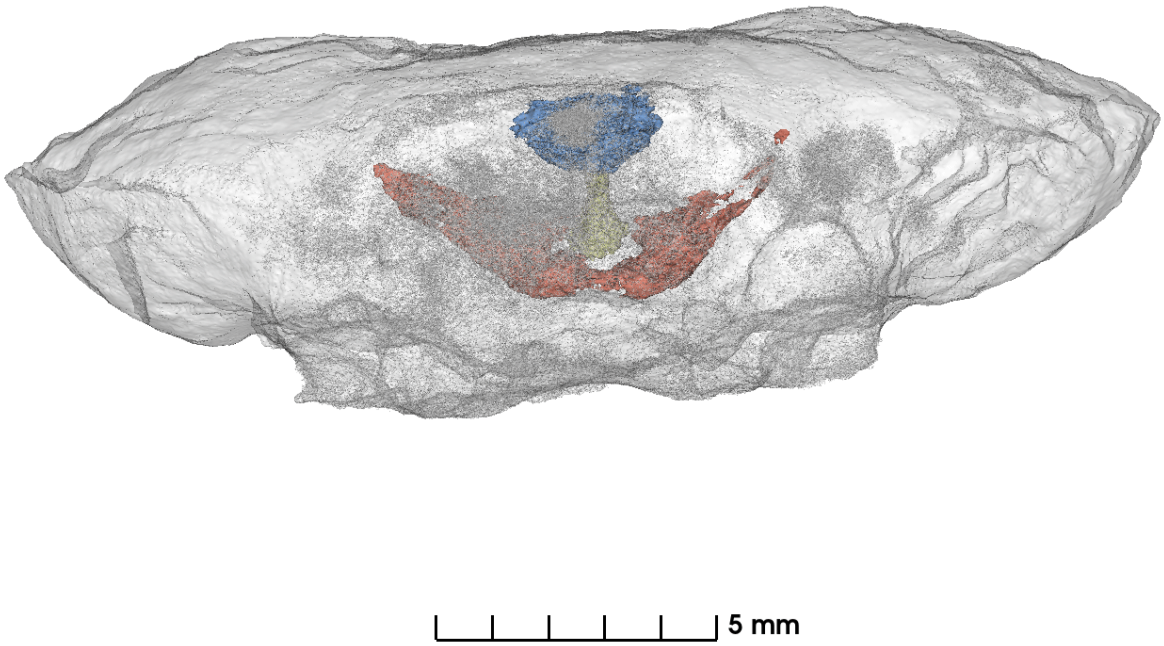

FIGURE S3. Rotating illustration of the microCT (µCT) scan results of the crab *Secretanella* sp. (ALMNH:Paleo:6522) from an upper Campanian methane seep limestone in Pennington County, South Dakota. Blue: cardiac stomach; yellow: esophagus; red: apodemes and mandibles; purple-pink: possible anterior gastric muscles. See online version for rotation (https://palaeo-electronica.org/content/2023/3973-soft-tissues-in-fossil-crab).

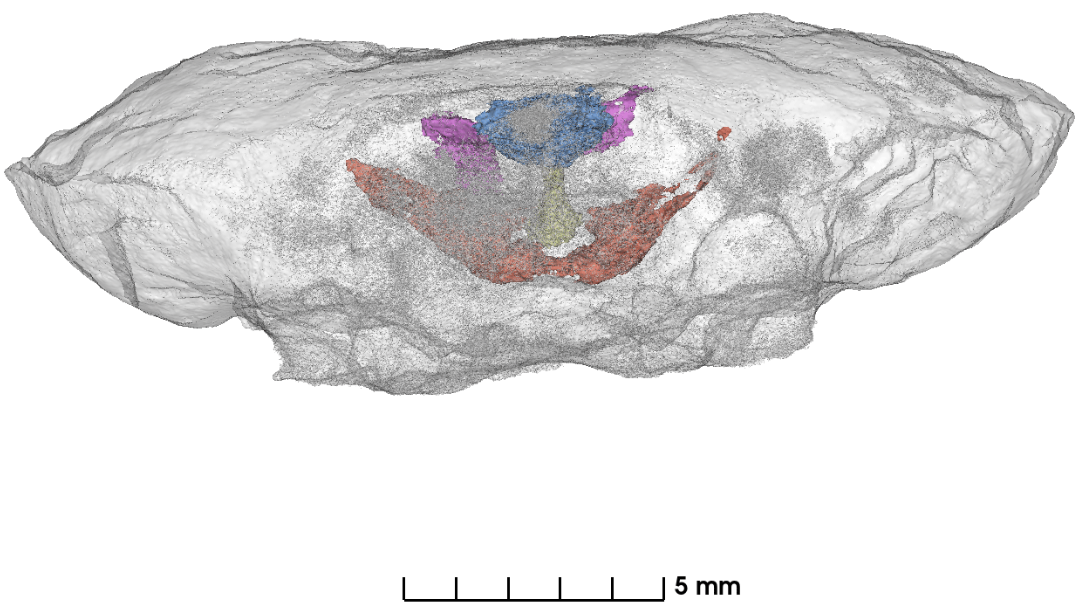

FIGURE S4. Rotating illustration of the microCT (μCT) scan results of the crab *Secretanella* sp. (ALMNH:Paleo:6522) from an upper Campanian methane seep limestone in Pennington County, South Dakota. Blue: cardiac stomach; yellow: esophagus; red: apodemes and mandibles; purple-pink: possible anterior gastric muscles; maroon: unidentified structures near interior most portion of the gill region. See online version for rotation (https://palaeo-electronica.org/content/2023/3973-soft-tissues-in-fossil-crab).