

# Dimerelloid brachiopod *Dzieduszyckia* from Famennian hydrocarbon seep deposits of Slaven Chert, Nevada, USA, with insights into systematics and paleoecology of the Dimerelloidea

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This study describes an assemblage of *Dzieduszyckia* brachiopods preserved in sedimentary barite deposits from the Famennian, Upper Devonian of Nevada, USA. The brachiopods lived in a methane-seep environment like those described from Sonora, Mexico, and the Western Meseta, Morocco. Although the original carbonate fabrics are not preserved, pockets of limestone within the brachiopod barite are depleted in  $\delta^{13}\text{C}$  values ranging from -31.1 to -27.3‰ VPDB. The fossils are preserved as internal and external molds only but record enough detail to demonstrate key internal features of *Dzieduszyckia* such as a pronounced dorsal septum, septalium, and vertical dental plates. The lack of common bifurcation or trifurcation of the costae as well as larger size of the shells recommends against inclusion within *D. sonora* as previously published. Based on the number of costae per width of shell, it is possible that there are two distinct species in Nevada, like other localities in Morocco, the Urals, and South China. These new data expand the body of knowledge of these earliest dimerelloids and it is hypothesized that this seep-dwelling macrofauna arose from depauperate-successful lineages between the Famennian biotic crises. As nearly all global *Dzieduszyckia* deposits are associated with active tectonic margins, it is also suggested that tectonically-driven methane expulsion in low nutrient waters spurred the evolution of dimerelloids.

Key words: Brachiopoda, Dimerelloidea, hydrocarbon seeps, chemosynthesis-based communities, Devonian, Nevada.

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## Introduction

Methane seep ecosystems are special geobiological targets as the food web is founded on a diverse microbial consortium that links methane oxidation to sulfate reduction primarily in subsurface conditions (Case et al. 2015). The modern dominant macrofauna endemic to these chemically challenging environments have adapted to the low nutrition state by evolving symbiotic relationships with sulfide and/or methane oxidizing bacteria (e.g., Levin et al. 2010; Pereira et al. 2021). Paradoxically, most of the time interval for seeps, the Late Devonian through Early Cretaceous, approximately 240 million years, was macroscopically dominated by one superfamily of brachiopods, the Dimerelloidea (Campbell and Bottjer 1995a, b; Sandy 2010; Kiel et al. 2014; Kiel and

Peckmann 2019; Baliński et al. 2022). This challenges conventional ecological wisdom as no modern brachiopods host symbionts, brachiopods at modern seeps are suspension feeders, and the bauplan of most brachiopods is not advantageous for hosting symbionts (Kiel and Peckmann 2019; however, see Angiolini et al. 2019 for a discussion of large brachiopods). Furthermore, it is important to note that bivalves likely analogous to extant chemosymbiotic forms are found locally in abundance in older late Silurian and Middle Devonian seeps in Morocco (see review in Jakubowicz et al. 2022).

Currently there is no geochemical evidence to unambiguously argue for symbiosis with methane or sulfide oxidizers in the rock record. While modern symbiotic mollusks have adapted their soft parts to maximize symbiosis and tissues record highly  $^{13}\text{C}$  depleted sources, those clues are

not transferred to the fossil record (Ferrier-Pagès and Leal 2018). The shells themselves record no influence of methane or other hydrocarbons, with isotopic ratios of carbon recording sea water (e.g., Peckmann et al. 2007). Biomarkers of symbiotic bacteria cannot be isolated from forms free-living at the seep site.

Instead, paleontologists rely on general and yet unique characteristics of the skeletal record of the macrofauna. It has been long recognized that the macrofauna of seeps and hydrothermal vents tends to be dominated by high abundance and low diversity, typically monospecific assemblages (Campbell and Bottjer 1995a, b). These taxa often (at least with hydrothermal vents) show gigantism relative to other members of their clade (Van Dover et al. 2002). There are no current skeletal features that define obligate symbioses. Instead, researchers use a systematic approaching, linking fossil taxa to modern, seep or vent-obligate groupings. Lineages, such as the bivalve families Lucinidae and Vesicomidae and gastropod subfamily Alviniconchinae, tend to be symbiotic and are frequently found at seeps or vents (see summaries in Amano et al. 2022; Kaim 2022). There may be other characteristics such as buffering from effects of background and mass extinctions (e.g., Danise and Higgs 2015) but more work is necessary to substantiate these claims.

Therein lies the paradox. One extinct lineage of brachiopods, the Dimerelloidea, (however, see discussion on Cryptoporidae below) dominated seeps from the Late Devonian through Early Cretaceous, are nearly always found at seeps (and one hydrothermal vent system), and are among the largest Mesozoic brachiopods. However, no modern brachiopods have symbionts to demonstrate this evolved lifestyle (Kiel and Peckmann 2019; Baliński et al. 2022). One group of putative dimerelloids, the Cryptoporidae, are not found at seeps but are likely not related to other dimerelloids (see fuller discussion below).

The purpose of this study is to provide new information on the *Dzieduszyckia*, the oldest dimerelloid, from massive barite deposits of Nevada, USA. While the new details on paleoecology, taxonomy, and taphonomy may not solve the challenge of recognizing symbiosis in the rock record, it is hoped the information may fuel future research and spur new avenues of inquiry.

*Institutional abbreviations.*—USNM, Smithsonian Institute National Museum of Natural History, Washington, D.C., USA.

## Historical background

The Dimerellidae, at the rank of family, were defined by Buckman (1918) for a group of “Rhynchonellacea” brachiopods with small to absent deltidial plates, triangular foramen, dorsal medial septa, or largely developed crura. He further noted that each genus likely possessed some of the

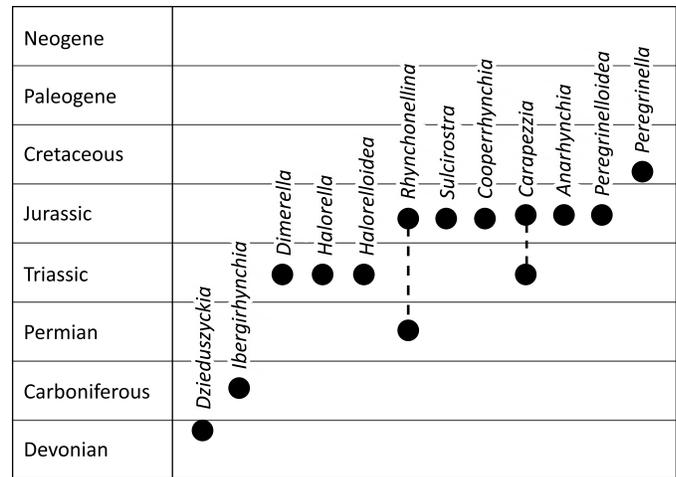


Fig. 1. Stratigraphic occurrences of dimerelloid brachiopod genera belonging to superfamily Dimerelloidea (Buckman, 1918). Note that this arrangement is based solely on first appearance and does not imply evolutionary lineages. The Permian age of *Rhynchonellina* is based on Diener (1903) and Reed (1944).

key characteristics but not all. The group was named after *Dimerella* Zittel, 1870, and originally included one other genus, *Rhynchonellina* Gemmellaro, 1871, and two potential genera. The family Dimerellidae was raised in rank to the superfamily Dimerelloidea in Savage (1996: 257, 260) and is the currently accepted grouping (e.g., Williams et al. 2000; Manceñido 2000; Manceñido and Owen 2001; Manceñido et al. 2002). Currently, the Dimerelloidea are included within the Order Rhynchonellida Kuhn, 1949 (Savage 1996; Savage et al. 2002).

As of this study, the Dimerelloidea range from the Late Devonian to the Early Cretaceous and are composed of twelve short-lived genera (e.g., Ager 1968; Sandy and Campbell 1994; Campbell and Bottjer 1995a, b; Gischler et al. 2003; Kiel and Peckmann 2008; Sulser and Furrer 2008; Peckmann et al. 2011, 2013; Kiel et al. 2014, 2021; Sandy and Peckmann 2016; Palfy et al. 2017), though perhaps the grouping is paraphyletic (Kiel et al. 2021; Guo et al. 2022) (Fig. 1). There are conflicting taxonomic organizational schemes in the literature, but most researchers define at least two branches: a more basal branch containing the family Peregrinellidae (Ager, 1965), and the more derived families Dimerellidae (Buckman, 1918) and Halorellidae (Ager, 1965). Manceñido and Owen (1996, 2001) included the family Cryptoporidae into the superfamily, suggesting the largely Cenozoic group is derived from the dimerelloid stock. They note that Buckman (1918) also recommended this inclusion. This inclusion is significant to the present paper as there are no known cryptoporids from seep or vent settings and nearly all of the other dimerelloids are exclusive to seeps and, in the case of *Anarhynchia*, a hydrothermal vent (Little et al. 2004).

However, in contradiction to the morphological assignment of taxonomic groups, Cohen and Bitner (2013) performed a phylogenetic analyses of small subunit (SSU/18S)

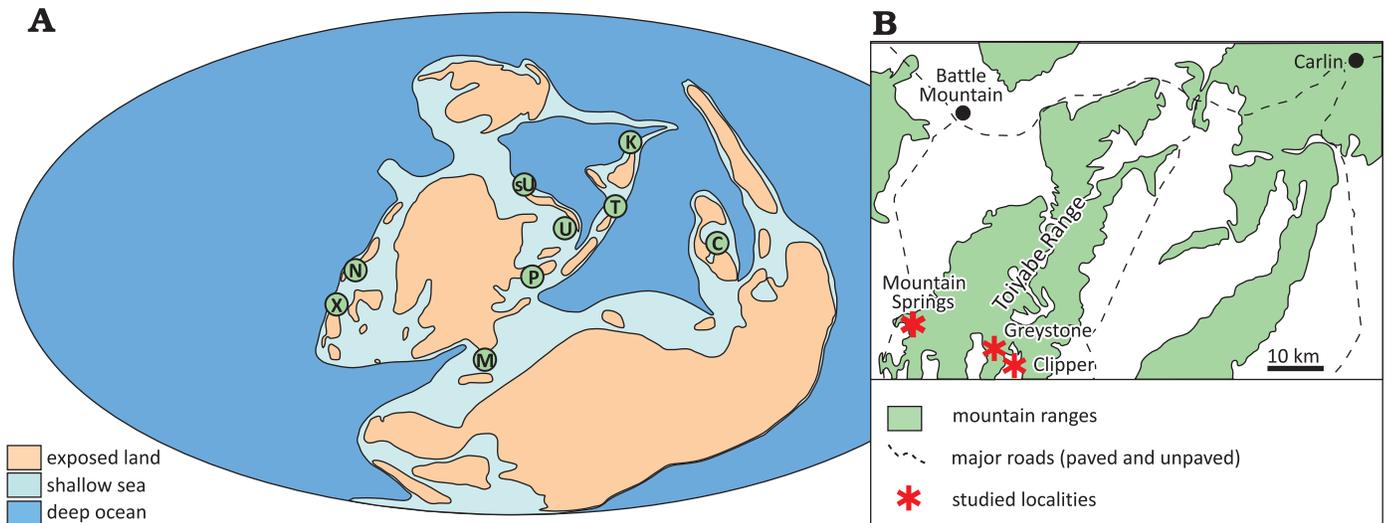


Fig. 2. **A.** Global distribution of dimerelloid brachiopod *Dzieduszyckia* in a reconstruction of Late Devonian paleogeography. **B.** Map showing studied Famennian localities in Nevada, USA. Abbreviations: C, China; K, Kazakhstan; M, Morocco; N, Nevada; P, Poland; sU, Subpolar Urals; U, Urals; T, Tajikistan; X, Mexico. Inset shows localities noted in the text. Image based on data and concept in Baliński and Biernat (2003: fig. 1) who used the reconstruction of Golonka et al. (1994). The position of Tajikistan is not well constrained.

and large subunit (LSU/28S) ribosomal DNA (rDNA) sequences from twelve rhynchonellide species, representing four extant superfamilies. *Cryptopora gnomon*, an extant cryptoporid and, thus, a dimerelloid sensu Manceñido and Owen (1996, 2001), was included in the study. The results defined three distinct clades in addition to the terebratulid and “inarticulate” outgroups. *Cryptopora gnomon* belongs to their Clade A1 which also includes species of Pugnacoidea, Hemithiridoidea, and Norelloidea. In fact, Cohen and Bitner’s (2013) study shows that genomic assessment of rhynchonellides is strongly incongruent with the morphological rankings, though a similar treatment of non-rhynchonellide brachiopods show quite good general agreement at higher taxonomic levels. Specifically, they draw attention to the Cryptoporidae as being controversial (Cohen and Bitner 2013: 215). Therefore, it is my opinion that the non-Cryptoporidae dimerelloids should be treated as a distinct, if paraphyletic grouping, of mostly hydrocarbon seep-obligate brachiopods.

The oldest genus of the dimerelloids is *Dzieduszyckia*. First noted by Georg G. Pusch in 1825 from the Kadzielnia quarry in Kielce, Góry Świętokrzyskie (Holy Cross Mountains) of Poland (Pusch 1833), the fossils were assigned to *Terebratula amphitoma* (Bronn, 1832) by Buch (1834). Unfortunately, in this publication, Buch included an unrelated Carboniferous specimen possessing a spiral brachidium. Roemer (1866: 671) recognized that the specimens figured by Buch (1834) were not *T. amphitoma* and reassigned the lot to a new species, *Terebratula (?) kielcensis*.

The species was formally redefined and named *Dzieduszyckia* by Siemiradzki (1909). Siemiradzki’s publication included the unrelated specimen, confounding taxonomists until the careful sleuthing of Biernat (1967) who detailed the error. In that critical manuscript, Biernat (1967) gave a thorough diagnosis as well as a comparison of all known

occurrences up to 1967. The emended and current diagnosis for *Dzieduszyckia* focuses on the large biconvex shell with both valves sulcate; variably transverse form; anterior zig-zag commissure; asymmetrical shell; radial costae, simple or dichotomous; prominent ventral beak, slightly incurved; small teeth with thin dental plates; dorsal septum; and thin, well-developed crura. The Late Devonian genus has a global yet spotty distribution including Poland, Morocco, Russia (North and South Urals), Kazakhstan, south China, Tajikistan, Mexico, and the USA (Fig. 2).

*Dzieduszyckia* is found in high abundance, low diversity populations. Most dimerelloids, such as *Halorella* and *Anarhynchia*, comprise 99–100% of the macrofossil record in monospecific assemblages (e.g., Gischler et al. 2003; Peckmann et al. 2011; Palfy et al. 2017). At the same time, in seeps from Silurian to the Early Cretaceous, mollusks are common and diverse at some seep deposits, and they may or may not co-occur with some dimerelloid brachiopods (see taxonomic review list and references in Hryniewicz 2022).

In this regard, *Dzieduszyckia* is unique in that it has been found in samples with multiple species and more diverse fauna. At Sidi Amar, Western Meseta, Morocco, *Dzieduszyckia* is found as four species based on shell morphology (Termier and Termier 1948), emended to three species by Baliński and Biernat (2003). Analysis by subsequent authors have upheld the taxonomic splitting, though only two species, *Dzieduszyckia crassicostata* and *Dzieduszyckia tenuicostata*, are clearly distinct and common (e.g., Peckmann et al. 2007). The original taxonomic paper from South China also defined four species (Xian and Jiang 1978) though further analysis by Nie et al. (2016) argued for morphologic plasticity and narrowed the collections to one species. Biernat (1967) in her invaluable critical review of *Dzieduszyckia* noted similar variation in the Polish specimens from the Ruda Strawczyńska borehole but argued for environmental

plasticity over taxonomic splitting. Additional details are provided below in the Systematic palaeontology section. Regardless, the data show that the variation between specimens of *Dzieduszyckia* at the outcrop scale exceeds those of other dimerelloids (e.g., Termier and Termier 1948; Nie et al. 2016). Also, it is common for *Dzieduszyckia* to be found amongst other Late Devonian fauna such as cephalopods, crinoids, and trilobites (e.g., Peckmann et al. 2007)

*Summary of occurrences.*—*Poland: Dzieduszyckia kielcensis* was first erected as the type species by Siemiradzki (1909) from material from a ca. 1825 collection by Pusch from the Kadzielnia quarry in Kielce, Holy Cross Mountains, in Poland (Pusch 1833; Roemer 1866; Biernat 1967). The original horizon has never since been relocated. Biernat (1967) was able to access material from a borehole at Ruda Strawczyńska near Kielce. The boring intersected a highly fossiliferous layer, similar to the original quarry, though other details are lacking. Unfortunately, there are no additional details on the facies, petrofabrics, or geochemistry beyond noting the brachiopods were from a layer of crystalline limestone with subordinate marl and clay (Pawłowska and Pawłowski 1978).

The general geology of the region of the Kadzielniański Range (the Holy Cross Mountains) is well understood. Devonian deposits comprise belts starting with intrashelf carbonate facies on the east and west separated by shallow water carbonates around Kielce.

*Russia (Urals):* The occurrence of *Dzieduszyckia* from the Ural Mountains has been noted for over a hundred years. The first mention was of the naming of *Leiorhynchus bashkiricus* Tschernyschew, 1887. Nalivkin (1947) noted *L. bashkiricus* from the western slopes of the Southern Urals and Rozman (1962) transferred the species to the genus *Dzieduszyckia*. Markovsky (1937) had listed the brachiopod as *Nudirostra bashkirica*, found with *Leiorhynchus ursus* in the Marzakayev (also transliterated at Murzakaev and Murzakayev) beds of the Southern Urals (reported in Rozman 1960; see Sartenaer 1959). Two additional species, *Dzieduszyckia prima* Mizens, 2008, and *Dzieduszyckia cordiformis* Mizens, 2006, have also been recognized in the Southern Urals alongside *Dzieduszyckia bashkirica*.

*Dzieduszyckia bashkirica* (also erroneously listed as *D. baschkirica* or *D. baschkiricus*) has been used as a rare but valuable correlative fossil along with *L. ursus* for the “Famennian III” interval which equates to the *Prolobites* Ammonoid Zone (e.g., Baranov and Sartenaer 1996). The distribution of *Dzieduszyckia* in the Dzerzhinka section of the eastern slope of the Southern Urals was recently summarized in Gatovsky et al. (2017), noting that both *D. bashkirica* and *D. cordiformis* are confined to the upper half of the Murzakaevian (lower Trachytera Zone, upper Famennian). Mizens et al. (2003) noted *Dzieduszyckia* from the western slopes in the Zilair Synclinorium, west of Magnitogorsk in the Chelyabinsk Oblast. Additional locality details were recently summarized in Zhuravlev and Sokiran (2020) who also listed *D. bashkirica* in the Tchernyshev Swell along

the eastern part of the Pechora Platform (Bolshaya Synya River, Sher-Nyadelta River) and Subpolar Urals (Kozhym River, Syvyu River) (Yudina 1997; Yudina et al. 2002; Tsyganko 2011). The authors also drew the connection to the Murzakaevian regional horizon of the western slope of the Southern Urals (e.g., Tagarieva 2012). Mizens and Mizens (2017) in their article on brachiopod distributions expanded the range of *Dzieduszyckia* downward into the Makarovian (lower to lower–middle Famennian) horizon in the west but restrained to the Murzakaevian on the eastern slope.

In general, the Famennian formations of the Western Urals (e.g., Zilair Synclinorium) are organic-rich and immature mudstones that were deposited in tectonically active back-arc rift and other basins (Gorozhanina et al. 2010). These deposits show intensive folding and overthrusting as a result of late Famennian tectonic collision (Ivanov and Puchkov 2020). The Eastern Urals at Dzherzhinka also record deep water deposition as a series of carbonate turbidites, perhaps on a deep-water ramp (Gatovsky et al. 2017). Similarly, Yudina et al. (2002) summarized the sequence in the Subpolar Urals as comprising gray to dark-gray, thin- to thick-bedded limestone, marls, and marly shales. There are also siliceous limestone with black chert nodules and lens-like nodular limestones. In general, the Subpolar Urals may be reconstructed as a series of isolated carbonate platforms rimmed by tectonically-driven subsidence basins (Gruzdev 2021).

*Kazakhstan:* The main record of *Dzieduszyckia bashkirica* comes from the Mugodzhar (= Mugudzhary) Hills in Kazakhstan (Rozman 1962) as well as the Zajsan-Irtysh region, but no additional details are provided for the latter. Rozman (1960) noted that *Nudirostra (Dzieduszyckia) bashkirica* is found in the Bakay Trough (north-northwest of Berchogur) within the cephalopod limestones of the *Prolobites* Zone.

The Famennian deposits are found in the Berchogur syncline along the western margin, overlying the Frasnian deposits (Rozman 1960). The entire sequence starts off with volcanic-rich Lower Devonian units and ends with nearly a kilometer of fine siliciclastic and carbonate beds (Nikolaeva et al. 2022). Rozman (1960) placed the brachiopods within “sandy limestone” equivalent to the Murzakaevian of the Urals. In many reconstructions, the units of the Mugodzhar Hills were formed on the edge of a microcontinent. Not long after deposition or perhaps concurrent, the region was deformed by major subduction or obduction as recorded in the eastern Mugodzhar zone (Golionko and Ryazantsev 2021).

*Tajikistan: Dzieduszyckia bashkirica* was reported by Menakova (1991) from the Shishkat section of the northern Zeravshan Range (Tien Shan) in central Tajikistan, near the border with Uzbekistan. This section has been well studied for nearly 100 years for its excellent and continuous middle Paleozoic sequence (Markovsky 1937; Sabirov 2019). The stratigraphic position was not noted by Menakova (1991), but in general, the Frasnian–Famennian of Shishkat is composed of deep water turbidites, chert, and lime mudstone. Based solely on an assumed Famennian age and using

the detailed stratigraphic summaries of Bardashev et al. (2006), it is likely the brachiopods were recovered from the Kulyali Formation which is composed of thin to medium bedded limestone clastic sediments deposited as distal turbidites. Local brachiopod coquinas were noted by the authors though no faunal lists were provided. The overlying Surkhobi Formation, which ranges into the Carboniferous, is also primarily composed of deep-water debris flow deposits (Bardashev et al. 2006).

Reconstructing the paleotectonic setting of the region has been a significant challenge with often contradictory results. Based on the broader tectonic picture, it is likely that the Tien Shan and other regional blocks represent independent island arcs and microcontinental slivers that amalgamated between the Cambrian and Devonian before being sutured onto the leading edge of “Kazakhstania” and ultimately connecting to the Uralian suture (Domeier and Torvick et al. 2014). It is also likely that tectonism was still active in this region during the Famennian though active arc volcanics are older (Middle Devonian) and younger (Early Carboniferous).

**Morocco:** Rhynchonellide brachiopods from isolated limestone lenses were first described by Termier (1936, 1938) and Termier and Termier (1948, 1949). The field context and age of the *Dzieduszyckia* deposits were further described by Hollard et al. (1970) and Hollard and Morin (1973). Additional critical papers on the brachiopods were presented by Ager (1968), Ager et al. (1976), Baliński and Biernat (2003), and Peckmann et al. (2007). A recent review by Jakubowicz et al. (2022) provides an excellent summary of the Moroccan localities.

All of the known *Dzieduszyckia* collections are from the eastern border of the Western Meseta. Most localities, including the Sidi Amar locality of Peckmann et al. (2007), are from unnamed Devonian limestone blocks found as olistoliths within deep water sandstone and shale of Carboniferous (late Viséan) age (Ager et al. 1976). The Sidi Amar blocks are found along a low ridge that strikes parallel to the larger Tabainout mountain ridge to the west. The blocks were emplaced into the tectonic basin during the Variscan Orogeny (Walliser et al. 2000; Hoepffner et al. 2005). Therefore, the stratigraphic context is missing though the age is constrained (Peckmann et al. 2007). However, detailed petrologic and geochemical analysis of the limestone blocks clearly established a methane seep origin (Peckmann et al. 2007; Jakubowicz et al. 2022). A locality north of Khenifra along the southeastern slopes of the Gara de M'rirt contains rare, small, isolated blocks embedded within early Carboniferous strata and overlain by nodular griotte limestone (Ager et al. 1976; Becker et al. 2020). This area is referred to as the “Bou-Ounebdou section” in the older literature (e.g., Termier and Termier 1948; Ager et al. 1976). In all cases, brachiopods are generally found as dense coquinas of articulated shells. Coarse cements are rare except for spar within the interiors of articulated shells. It is noteworthy that at least two distinct species are found together at the Sidi Amar locality (Termier and Termier 1948; Peckmann et al. 2007; RSS personal ob-



Fig. 3. Field photograph showing two clearly distinguished dimerelloid brachiopod species, *Dzieduszyckia tenuicostata* (left) and *Dzieduszyckia crassicostata* (right), together in an allochthonous limestone boulder. Famennian (Upper Devonian), Sidi Amar, Western Meseta, Morocco.

servation; Fig. 3). In addition to these allochthonous deposits, *Dzieduszyckia* coquinas are found in situ within Famennian deposits west of the Carboniferous basin (Hollard and Morin 1973; El Hassani and Benfrika 2000).

**South China:** Xian and Jiang (1978) defined four species from Guizhou: *Dzieduszyckia oblonga* Xian in Xian and Jiang, 1978, *Dzieduszyckia elongata* Xian in Xian and Jiang, 1978, *Dzieduszyckia xiasiensis* Jiang in Xian and Jiang, 1978, and *Dzieduszyckia acutiplicata* Xian in Xian and Jiang, 1978, based on variations in shell shape, depth of the sulcus, and costae density. Further evaluation by Nie et al. (2016) on hundreds of specimens from a broader area concluded that the diversity was related to plasticity and driven by environmental conditions, thus only one species, *D. oblonga*, was valid.

Deposits of *Dzieduszyckia* in South China are unique as the fossils are found in outer platform oolite as well as intraplatform basinal limestone (Nie et al. 2016). Originally described from near Guiyang, Guizhou Province from deep water deposits (Xian and Jiang 1978; Xian et al. 1980), the distribution was expanded to include shallower, offshore platform turbidite deposits (Nie et al. 2016; Tong et al. 2021). The fossils comprise dense accumulations of largely articulated shells although one deep water locality at Changtang is noteworthy for transported disarticulated shells (Nie et al. 2016). Tong et al. (2021) performed a detailed sedimentological and stratigraphic analysis and concluded that the shells of the intraplatform basins were transported.

**Mexico:** Silicified molds of *Dzieduszyckia* were reported from Devonian massive barite deposits of Mazatán, east of Hermosillo, Sonora, Mexico by Noll et al. (1984). The fossils are found in two localities from both barite and reddish siltstone pockets within the barite of the Los Pozos Formation. Overall, the stratigraphy of the Guayacan Group is dominated by argillite and siliceous shales (Noll 1981). Boucot et al. (2008) reported conodonts of the late Marginifera

Zone for the deposit at Rancho Los Chinos. The geology of the area is structurally quite complex (Noll et al. 1984). The authors note that the brachiopods are found in dense clusters within monospecific coquinas and that individuals are mostly articulated. The detailed paleoenvironment is not well known but a shelf-margin or upper slope deposit was proposed. Based on the co-occurrence of *Nereites*-facies trace fossils, thin-bedded argillite, siltite, chert, barite, and rare limestone, Boucot et al. (2008) narrowed the environment to bathyal depths in a continental rise environment. Further details restricted the setting to an accretionary tectonic margin beneath a highly productive water column (Canet et al. 2014). Canet et al. (2014) firmly established a methane seep ecosystem based primarily on significantly  $^{13}\text{C}$  depleted carbonates,  $^{34}\text{S}$  enriched barites showing sulfate reduction coupled to the anaerobic oxidation of methane, and gas-rich fluid inclusions within the barite.

**USA:** Occurrences of *Dzieduszyckia* in Laurussia were first confirmed by Cloud and Boucot (1971) from massive barite deposits of the Slaven Chert in Nevada. The Nevada fossils were originally misidentified as *Halorella* though the U.S. Geological Survey stratigraphers felt the barite beds should be older than Triassic. Following the clarification of Biernat (1967), Cloud and Boucot (1971) correctly recognized the genus and the Late Devonian age. Though no fossils have been formally presented, Boucot et al. (2008) noted that the Slaven Chert *Dzieduszyckia* were associated with conodonts of the lower and possibly upper Marginifera Zone in the northern Shoshone Range.

The Nevada brachiopods come from several open-pit barite mines in the northern Shoshone Range. Cloud and Boucot (1971) relied on U.S. Geological Survey collections from the Greystone, Hilltop and Mound Spring Mine (both of the latter are now part of the current Mountain Springs Mine). Additional fossils collected and described in the present paper come from the Clipper Mine. All the fossils are found in massive to coarsely laminated barite beds that are replacive after limestone and chert. The original depositional setting was a deep water outer continental slope or fringing island arc bathyal setting (e.g., Dubé 1988; Madrid et al. 1992). More details are provided below in the Geological setting section. These units may be considered syntectonic with the early stages of the Antler Orogeny in which deep marine units were obducted or overthrust onto shelfal limestones (Koski and Hein 2003).

It is interesting to note that while there are no other *Dzieduszyckia* deposits described from the United States, there is a mention of “Leiorhynchoidea-like” brachiopods in spiculitic lime mudstone with interbedded black mudstone and siltstone from a restricted, low-energy marine Famennian settings of Utah (Silberling et al. 1995), several hundred kilometers east of the *Dzieduszyckia* beds. This environment would have been a foreland basin during the early stages of the Antler Orogeny.

**Stratigraphy of occurrences.**—All published dates of *Dzieduszyckia* place the genus as a Famennian fossil and the ge-

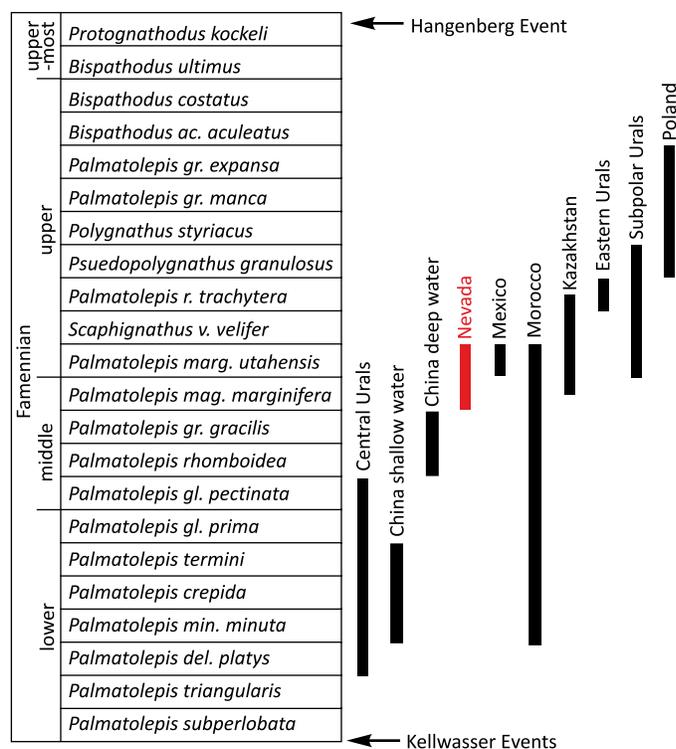


Fig. 4. Stratigraphic distribution of dimerelloid brachiopod *Dzieduszyckia* within the Famennian (Upper Devonian) based on conodonts and ammonoids. Biozones based on the divisions of Spalletta et al. (2017), retaining the divisions on lower, middle, upper, and uppermost Famennian. See text for age references.

nus has been used to correlate deposits in the Ural Mountains (e.g., Mizens and Mizens 2017). A graphic compilation (Fig. 4), described below, converts the published zonations to the recent schematic of Spalletta et al. (2017). In the most robust study, Nie et al. (2016) provided strong evidence from conodonts that platform deposits of *Dzieduszyckia* in South China date to the Upper Triangularis Zone and are found through the Lower and Middle Crepida zones. Deeper water deposits in South China are slightly younger and range up through the Rhomboidea Zone. Thus, the South China fossils are constrained to the lower Famennian.

Polish fossils were reported as potentially as old as Upper Trachytera to Lower Expansa zones (Biernat 1988). Peckmann et al. (2007) recorded the Sidi Amar deposit of Morocco as Upper Triangularis to Upper Marginifera zones, confirming the broader Famennian assignment of Hollard and Morin (1973) based on conodonts and goniatites. In contrast, Menakova (1991) recorded *Dzieduszyckia* in the Frasnian of Tajikistan but details on the specific fossils and stratigraphy are lacking. Boucot et al. (2008) noted that the Mexican *Dzieduszyckia* is from the Upper Marginifera Zone and the Nevada deposits had conodonts of the Lower and possibly Upper Marginifera zones but did not provide details.

Rozman (1960) noted that Lipina (1955) recorded *Leiorhynchus* (*Dzieduszyckia*) *bashkiricus* in the Prolobites Ammonoid Zone of the Western Urals and drew the equivalence to the Murzekayev Beds of Kazakhstan. This is also referred to

as “Famennian III” in older literature. The *Prolobites* Zone approximately is coincident with the current Middle Marginifera to Middle Trachytera conodont zones. In the Central Urals, Mizens (2012) presented evidence that *Dzieduszyckia prima* was clearly assigned to the lower Makarov Horizon (Middle Triangularis–Trepida zones), here interpreted to be restricted to the Platys through Pectinata zones of Spalletta et al. (2017). In the Southeastern Urals, both species of *Dzieduszyckia* are noted from the upper Murzakaevian regional substage, equivalent to the Trachytera Conodont Zone (Gatovsky et al. 2017). Finally, in the northern or Subpolar Urals, *Dzieduszyckia* is recorded from the Utahensis through Granulosis zones (Zhuravlev and Sokiran 2020). While the data presented are not refined enough to draw a concrete picture of origination and expansion, it is clear that *Dzieduszyckia* is restrained to the Famennian, between the major extinction intervals (or biotic crises) of the Lower and Upper Kellwasser and the Hangenberg events.

**Taxonomy:** Thus far, there have been twelve species of *Dzieduszyckia* recognized from the Upper Devonian (Tables 1 and 2). However, there is still discussion on the validity of differentiating species versus intraspecific morphological plasticity as the genus is noted for its broad variability (e.g., Nalivkin 1947; Biernat 1967; Baliński and Biernat 2003; Nie et al. 2016).

The various species are largely distinguished based on the overall shape of the external shell and the variation of size, shape, and diversity of the costae. Unfortunately, the critical analysis of the interior elements such as the septalium, crural bases, and crura, needs to be expanded upon for many species (Baliński and Biernat 2003).

Regardless, the following sections summarize the differences thus far reported. The type species, *D. kielcensis*, was distinguished by Biernat (1967) for its large, subrounded to pentagonal biconvex shell, subtransverse to transverse elongation, sulci in opposing valves, and variably sized costae. She noted that the interior of the shell demonstrated hinge plates, short dental plates and small teeth, a distinct septalium, and a dorsal septum that reaches halfway down the length of the shell. Both Nalivkin (1947) and Rozman (1962) described *D. bashkirica* as having variable shell morpholo-

gies but typified by a roundly triangular to transversely oval shell. Later, Menakova (1991) described *D. bashkirica* as distinctive from *D. kielcensis* due to its rounded triangular shape and smaller number of costae. Like *D. kielcensis*, the costae vary in their origination point on the shell relative to the umbo and thickness. The two species may be conspecific though *D. bashkirica* may be unique due to its thickened and incurved ventral umbo.

In the Middle and Eastern Urals, Mizens (2006, 2008) described two new species of *Dzieduszyckia* that were distinctive from *D. bashkirica*. *Dzieduszyckia cordiformis* from the section at Dzerzhinka is noteworthy for its fine costae and biconvex heart-shaped shell with opposing sulci. In addition, the costae are strongly dichotomous and triangular in cross-section. Mizens (2006) notes the similarity to *D. tenuicostata* from Morocco (below) but argued that the species was distinct due to the narrower shell and a shorter hinge. In a later paper, Mizens (2008) described *D. prima* from the Middle Urals. This species is like *D. bashkirica* but distinguished by its flatter profile, smaller size, deeper sulcus in both valves, and coarser and sparser costae.

The Moroccan species were originally described by Termier (1936) and Termier and Termier (1948) and later carefully re-evaluated by Baliński and Biernat (2003). Like the earlier review of Biernat (1967), they were challenged by defining the differences between *D. crassicostata* and *D. intermedia*. Both species possess a high dorsal septum that thickens posteriorly and terminates midway along the shell. The crura are ciliform, similar to *D. kielcensis*. The crural bases are closely set and near the ventral surface of the hinge plates and fused with the top of the median septum. In contrast, the authors agreed that *D. tenuicostata* is distinct largely due to its triangular to fusiform shell with many fine costae. Occasional faint and wide irregular plicae were noted on larger *D. tenuicostata* shells. The crura of *D. tenuicostata* widen anteriorly and twist from horizontal to vertical. Finally, the median septum is low though still extends half of the shell width.

Xian and Jiang (1978) distinguished four species of *Dzieduszyckia* from South China. *Dzieduszyckia oblonga* was noted for the transversely quadrate shell outline with

Table 1. Species of dimerelloid brachiopod *Dzieduszyckia* with locations and key references.

Species	Location	Key references
<i>Dzieduszyckia kielcensis</i>	Poland	Siemiradzki 1909; Biernat 1967
<i>Dzieduszyckia bashkirica</i>	Urals, Kazakhstan, Tajikistan	Nalivkin 1947; Rozman 1960, 1962; Menakova 1991
<i>Dzieduszyckia prima</i>	Middle Urals	Mizens 2008
<i>Dzieduszyckia cordiformis</i>	Eastern Urals	Mizens 2006
<i>Dzieduszyckia sonora</i>	Mexico, USA	Noll et al. 1986
<i>Dzieduszyckia crassicostata</i>	Morocco	Termier and Termier 1948
<i>Dzieduszyckia intermedia</i>	Morocco	Termier 1936
<i>Dzieduszyckia tenuicostata</i>	Morocco	Termier 1936
<i>Dzieduszyckia oblonga</i>	China	Xian and Jiang 1978
<i>Dzieduszyckia elongata</i>	China	Xian and Jiang 1978
<i>Dzieduszyckia xiasensis</i>	China	Xian and Jiang 1978
<i>Dzieduszyckia acutiplicata</i>	China	Xian and Jiang 1978

Table 2. Key distinguishing features of species of dimerelloid brachiopod *Dzieduszyckia*. NA, not available.

Species	Shell margin	Costae	Additional key feature
<i>Dzieduszyckia kielcensis</i>	subrounded to pentagonal, subtransverse to transverse elongation	variable	NA
<i>Dzieduszyckia bashkiricus</i>	transversely oval to roundly triangular	variable but generally few and thick	thickened and incurved ventral umbo
<i>Dzieduszyckia prima</i>	flatter profile, deep sulcus in both valves	coarse and sparse	smaller than <i>D. bashkirica</i>
<i>Dzieduszyckia cordiformis</i>	biconvex and heart-shaped	fine and bifurcating	NA
<i>Dzieduszyckia sonora</i>	subtriangular to subovate	bifurcating and rarely trifurcating	median size is smaller than European or Moroccan species
<i>Dzieduszyckia crassicostata</i>	wide, heart-shaped, and globulose	thick, angular to rounded	high dorsal septum that thickens posteriorly
<i>Dzieduszyckia intermedia</i>	asymmetric elongation	weak radial ornamentation	high dorsal septum that thickens posteriorly
<i>Dzieduszyckia tenuicostata</i>	triangular to fusiform shell	many fine costae; faint and wide irregular plicae	crura widen anteriorly and twist from horizontal to vertical.
<i>Dzieduszyckia oblonga</i>	transversely quadrate shell outline	simple, angular in cross-section	weak ventral sulcus
<i>Dzieduszyckia elongata</i>	rounded triangular shell with distinct geniculation	low and round costae, disappear posteriorly	no sulcus
<i>Dzieduszyckia xianensis</i>	transversally oval outline	simple, restricted to anterior of shell	bisulcate
<i>Dzieduszyckia acutiplicata</i>	small, subrectangular	abundant thin costae, many branching	weakly bisulcate

simple costae and a weak ventral sulcus. The costae are more pronounced anteriorly than posteriorly. *Dzieduszyckia elongata* has a relatively larger and rounded triangular shell with distinct geniculation in the lateral and anterior commissures, and no fold or sulcus. *Dzieduszyckia xiansiensis* was distinguished by the transversally oval outline and biconvex shell with distinct sulcus in both valves. Finally, *Dzieduszyckia acutiplicata* was distinguished for having a smaller shell, though biconvex and weakly bisulcate and more and finer costae. However, a review by Nie et al. (2016) that included more specimens and additional localities concluded that the forms were all variations of a single species (*D. oblonga*; Yuanlin Sun, personal communication, 2022), though there are some patterns defined by facies (platform or intraplatform basin) and locality. The most recent study of Tong et al. (2021) included more specimens and additional localities but there was no further discussion of distinguishing separate species.

*Dzieduszyckia sonora* was described by Noll et al. (1984) from silicified molds preserved in barite in the Hermosillo region of Mexico. Although more poorly preserved and lacking some internal details, they felt a new species was justified due to the commonly bifurcating and rarely trifurcating costae. The biconvex shell varies greatly from subtriangular to subovate and possesses a gently incurved beak. The internal molds demonstrate short, widespread dental plates, a small septalium, and a prominent septum extending halfway along the shell. The authors also drew attention to the fact that the median size of *D. sonora* is smaller than European or Moroccan specimens. No details were provided on the crura or crural bases.

It should be noted that historically, many of these brachiopods were originally referred to the genus *Leiorhynchus*

(or *Nudirostra*), a small costate rhynchonellide used as a biostratigraphic marker within the Devonian. In Xian and Jiang (1978), several fossils referred to as new species of *Leiorhynchus* may actually be *Dzieduszyckia* (Yuanlin Sun, personal communication 2022). Additional comments on the connection with *Leiorhynchus* are discussed below. Other incorrect generic assignments include *Eoperegrinella* from Morocco and China as well as the Triassic *Halorella* in Nevada (USA) and Morocco.

## Geological setting

The brachiopod deposits described in this paper are found in rare, isolated lenses within the Upper Devonian Slaven Chert in the Shoshone and Toquima ranges, northcentral Nevada (USA). The exact stratigraphic position is difficult to establish as the Slaven Chert is highly faulted and folded with poor surface exposures. Nevertheless, some general comments on the stratigraphy and geologic setting may be deduced.

Originally described by Gilluly and Gates (1965) in Slaven Canyon near Mount Lewis in the Shoshone Range, the Slaven Chert is found throughout northcentral Nevada where it is a unit within the lower plates of one or several major low angle faults (Speed and Sleep 1982; Miller et al. 1984; Burchfiel and Royden 1991; Holm-Denoma et al. 2011, 2017). The older literature refers to this tectonic package as the “Roberts Mountains Allochthon” or “Western Facies Assemblage” (Ketner 2013) (Fig. 5). This package of units ranges from the Cambrian to uppermost Devonian and represents primarily low-energy, deep water deposition. Proximal and distal turbidites, debris-flow deposits, and hemipelagic deposits indicate submarine slope-fan-ba-

sin floor environments (Poole 1974). Although the lower Cambrian–Silurian formations contain terrigenous detrital grains, the younger Slaven Chert is relatively clean suggesting a distal or isolated depocenter.

The majority of the Slaven Chert is composed of dark radiolarian and spicular chert with lesser amounts of barite, phosphate, siltstone and sandstone, rare limestone and very rare greenstone (Gilluly and Gates 1965; Koski and Hein 2003; Donkervoort et al. 2022). Beds are typically less than 10 centimeters thick though rare limestone layers in the Cortez Mountains reach over 5 meters in thickness (Gilluly and Masursky 1965) (Fig. 6). The total thickness is unknown but likely exceeds several hundreds of meters. Fossils are rare but include ostracods, tentaculitids, corals, bryozoans, and crinoid columnals (Gilluly and Masursky 1965).

There are multiple models on the depositional setting of the Slaven Chert though they all agree on a deep marine setting. Earlier models purport the Slaven Chert and the rest of the western facies assemblage to have been deposited along the slope of an island arc that collided with North America (Speed and Sleep 1982). Burchfiel and Royden (1991) presented evidence that the deformation and sedimentation more likely supported deposition in a back-arc extensional basin. An alternative model suggests that deposition happened in rift basins developed on Laurentian continental crust (Madrid et al. 1992; Finney et al. 1993).

The age of the Slaven Chert is taken as Famennian based on radiolarians and conodonts (Holdsworth 1980; Holdsworth and Jones 1980; Dubé 1988). However, Boundy-

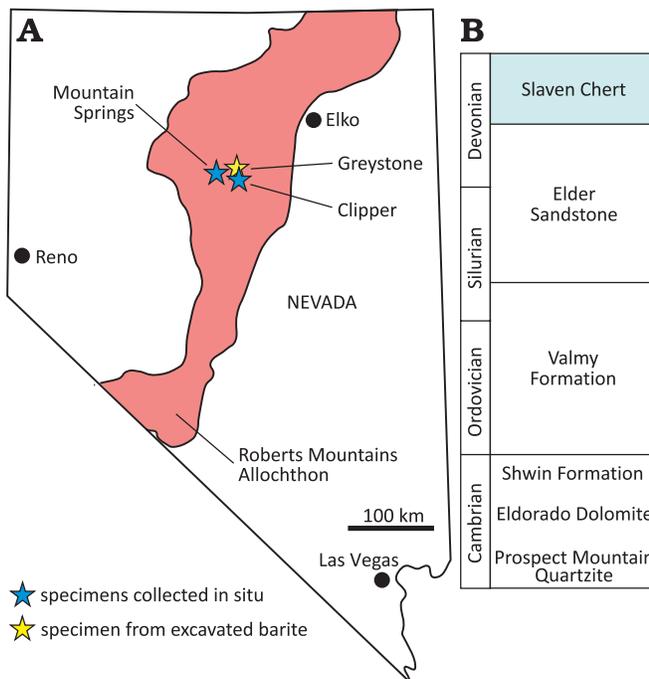


Fig. 5. **A.** The distribution of the Roberts Mountains Allochthon with key mines cited in this study. **B.** Stratigraphy of the Roberts Mountains Allochthon. Note exact position of *Dzieduszyckia* within the Slaven Chert is unknown due to intense faulting within the allochthon. Base map modified from Holm-Denoma et al. (2017). Stratigraphic chart based on Ketner (2013).

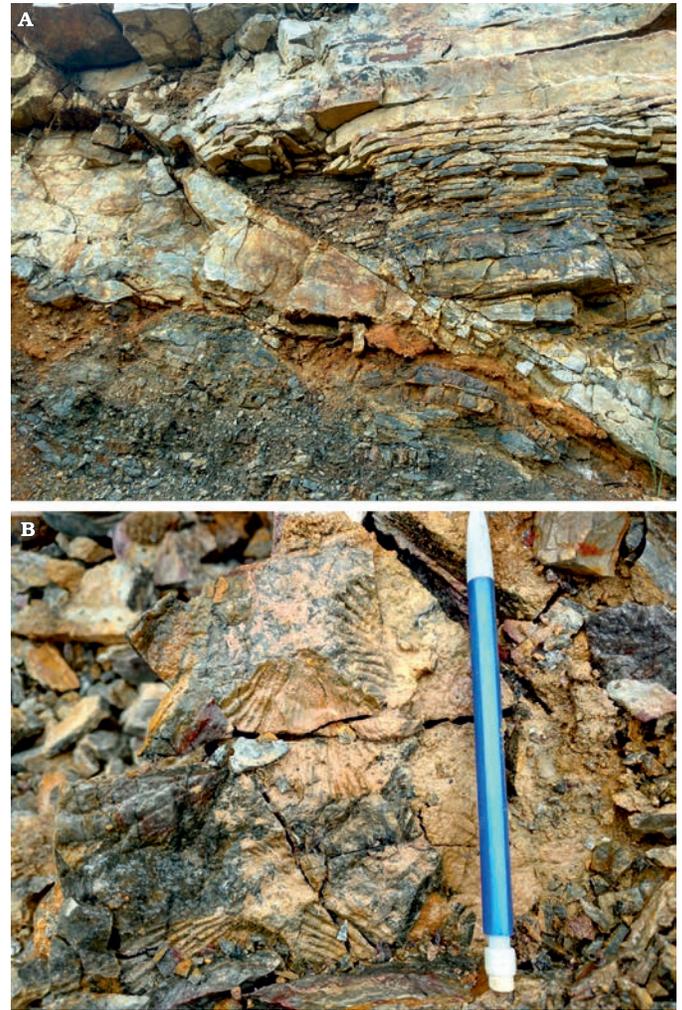


Fig. 6. A typical Slaven Chert exposed in open pit mines from Famennian, Nevada. **A.** Interbedded dark chert and light grey barite. Beds above fault approximately 10 cm thick. **B.** Exposure of in situ brachiopod molds in floor of Mountain Springs Mine (Pit A).

Sanders et al. (1999) reported a suite of conodonts, radiolarians, and sponge spicules from the type section at Slaven Canyon that pushed the maximum age to the Frasnian (late Rhenana stratigraphic Zone) (Ziegler and Sandberg 1990). It is of note that the authors also draw the connection to the Sonora district near Hermosillo, Mexico. As noted above, Boucot et al. (2008) specified that the Nevada *Dzieduszyckia* collections were associated with conodonts of the early and possibly late Marginifera zones.

## Material and methods

Specimens for the present study were collected during surveys of active and closed open-pit barite mining operations in the northern Shoshone Range, Nevada between 2016 and 2020. Specifically, fossils were collected in situ from a bench floor of the Mountain Springs Mine (Pit A) and pit wall of the closed Clipper Mine. Additional specimens were

collected from barite stockpiles at the Mountain Springs and Clipper Mines as well as the Greystone Mine (see localities in Fig. 5 and Table 3). In total, over fifty rock samples were collected and many of these provided multiple brachiopod specimens. All specimens are preserved as external or internal molds within barite. A few specimens from the Clipper Mine stockpile are preserved as calcite within coarsely recrystallized calcite. In total, over 100 individual fossils were recovered from the barite or barite-limestone samples.

Petrographic analysis was carried out on standard thin sections of 30  $\mu\text{m}$  thickness on an Olympus BX-51 petrographic microscope at California State University, Chico. Polished samples of primarily limestone were also observed for cathodoluminescence with a Reliotron CL scope mounted on a Nikon Optiphot microscope with a 10 $\times$  objective. The Reliotron was run with the vacuum at  $\sim 42$  mTorr and an operating voltage of 7.8 kV and power at  $\sim 0.032$  DCmA.

Samples were prepared for taxonomy with the use of air-hammers, focusing mainly on external molds. For photography and measurements, casts using modeling clay were utilized for some samples. Because of the incomplete nature of the preservation, standard taxonomic techniques could not be employed. Instead, brachiopod internal and external molds were measured for minimum width and numbers of costae. If the sulcus was present, the minimum “half-width” of the shell was also recorded (Fig. 7). Beaks were very rarely preserved so the length of the shells recorded are a minimum and are not statistically significant. In total, 93 individual shells were measured. Samples with less than six costae preserved were not included but were used for detailed description and/or thin-section petrography.

Stable carbon isotope analyses were performed on rare pockets of calcite within barite from the stockpile at Clipper Mine. Powders were recovered using a handheld rotary drill. Carbonate  $\delta^{13}\text{C}$  values were determined using a Picarro CRDS (G2131-i) coupled to Picarro Liaison interface and a modified AutoMate autosampler in the Will Berelson lab at the Department of Earth Sciences, University of Southern California. The powdered carbonate was weighed and placed in an AutoMate vial and sealed with a rubber septum screw-cap. The AutoMate acidified these samples on-line using 10% phosphoric acid, and the resulting  $\text{CO}_2$  was carried in a nitrogen stream, through a Nafion desolvating line, to the Picarro Liaison sampling bags. The flow of gas from the AutoMate into the Picarro Liaison’s discrete sample bag was mass flow controlled such that every bag had precisely

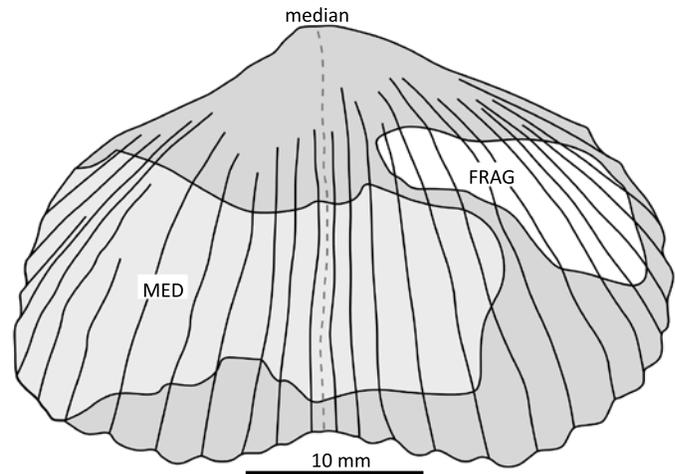


Fig. 7. Measurements of shell features. FRAG, measured fossil is a fragment of a valve. MED, fragment of valve that retains the margin and sulcus and can be used to estimate minimum width.

the same mass of  $\text{N}_2 + \text{CO}_2$ . Each bag was then introduced to the Picarro CRDS for continuous analysis over an 8 minute interval. Drift over the course of a run ( $<10$  h) was almost never above a few tenths of a permil and resulting Picarro standards (in house  $\text{CaCO}_3$  standard calibrated against VPDB) typically had a standard deviation of under 0.1%.

## Results

**Petrology.**—Nearly all the brachiopods are preserved within massive to banded barite beds preserved as crystal mosaics (Fig. 8A). Barite crystals vary in size and are randomly distributed. Most crystals are monocrystalline, others are fragments of radiating fans. Crystals are anhedral with “zigzag” irregular margins. Poikilotopic fabrics are common. In all cases, the crystal margins show no preferred orientation to the voids left by brachiopod valves, suggesting a later stage of diagenetic replacement.

At Clipper Mine, small (millimeter-scale) irregular pockets of calcite are rarely found with the brachiopods (Fig. 8B). The calcite crystals range in size from 28.3 to 256.6  $\mu\text{m}$  with a skewed median of 93.1  $\mu\text{m}$  ( $n = 218$ ). Most crystals show strong cleavage lines and twinning is common. The crystals are anhedral with jagged margins and enfacial junctions. The smaller crystals could be construed as “microspar” but there is no clear connection to common limestone fabrics

Table 3. Nevada localities of dimerelloid brachiopod *Dzieduszyckia* noted in this paper. Note that Mountain Springs and Greystone are privately owned mines and Clipper is now on federally-managed (Bureau of Land Management) lands. Coordinates are in the WGS84 datum.

Mine	Latitude, longitude	Description	Figured specimens
Mountain Springs	40.32045, -117.04322	in situ brachiopods collected from barite beds in Pit A	none
Mountain Springs	40.31555, -117.04208	loose specimens collected from Pit C	USMN PAL 794578
Clipper	40.25089, -116.83484	in situ brachiopods collected from faulted massive barite in mine wall	USMN PAL 794576, 794577, 794582–794586
Clipper	40.24946, -116.83063	loose specimens recovered from high-grade barite stockpile	USMN PAL 794579–794581
Greystone	40.27160, -116.86859	singular loose specimen collected from excavated high-grade barite	none

such as cements, micrite, or peloids. Very rare brachiopod valves are preserved in the limestone displaying remnants of the fibrous layer though the primary columnar layer is recrystallized into large, twinned calcite crystals (Fig. 8C).

One relatively large sample (~90×30 mm) of nearly pure limestone was recovered from the high-grade stockpile at Clipper. The hand specimen is dark grey-black like the barite but the low specific gravity and reaction to dilute hydrochloric acid provided field confirmation as limestone. In thin-section, the calcite crystals are similar to those found as pockets within the barite. While the polished hand specimen shows coarse wavy and parallel banding, there are no clearly defined petrofabrics in the calcite crystals. Under cathodoluminescence, the entire sample glows bright orange with no distinguishing zonation.

*Taphonomy.*—Except for rare potential preservation as replacement coarse calcite shells within irregularly-sized calcite, nearly all of the brachiopods are preserved as internal and external molds (Fig. 9). No complete shells were recognized; however, it is believed the shells were buried complete and many were articulated and the diagenetic replacement with barite led to the shell destruction. Multiple samples preserve evidence of both shells. Internal details of the hinge area including septalia and the dorsal septa are preserved on internal molds. Unfortunately, no crura or crural bases were observed in any specimen.

Details of the external shell preserve evidence of shell healing and fine details such as concentric growth lines. Based on comparison with samples collected in Morocco, it is believed there was minimal compaction or other deformation of the shells as the overall morphology is similar to *Dzieduszyckia crassicostata* and *D. tenuicostata* in preserving rounded biconvex and bisulcate shells.

Shells are commonly found in dense accumulations (Fig. 9B). Most shells are subparallel to each other suggesting preservation along bedding surfaces. Shell size, based on costae width as well as shell dimensions, varies throughout the surface suggesting mixed populations preserved in each sample. Unfortunately, the mode of preservation does not allow for recognition of fragmented shells.

In situ deposits at the Mountain Springs Mine record the brachiopods in beds of pure barite ranging from 50–100 mm thick. The beds are either massive or show subparallel bedding planes at the centimeter scale. As noted above from loose blocks, the fossils are generally subparallel to bedding. The presence of articulated shells suggests burial in place though the preservation is not sufficient for more detailed paleoecological interpretation. Comparison of samples between the three mines did not show any unique, locality-specific patterns.

*Carbon isotopes.*—Comparing the Slaven Chert limestones to other fossil hydrocarbon seeps is hampered by the pervasive diagenesis. Crucially, one cannot differentiate distinct microfabrics with diverse isotopic signatures common at seeps (e.g., micrite, botryoidal cement, isopachous rim ce-

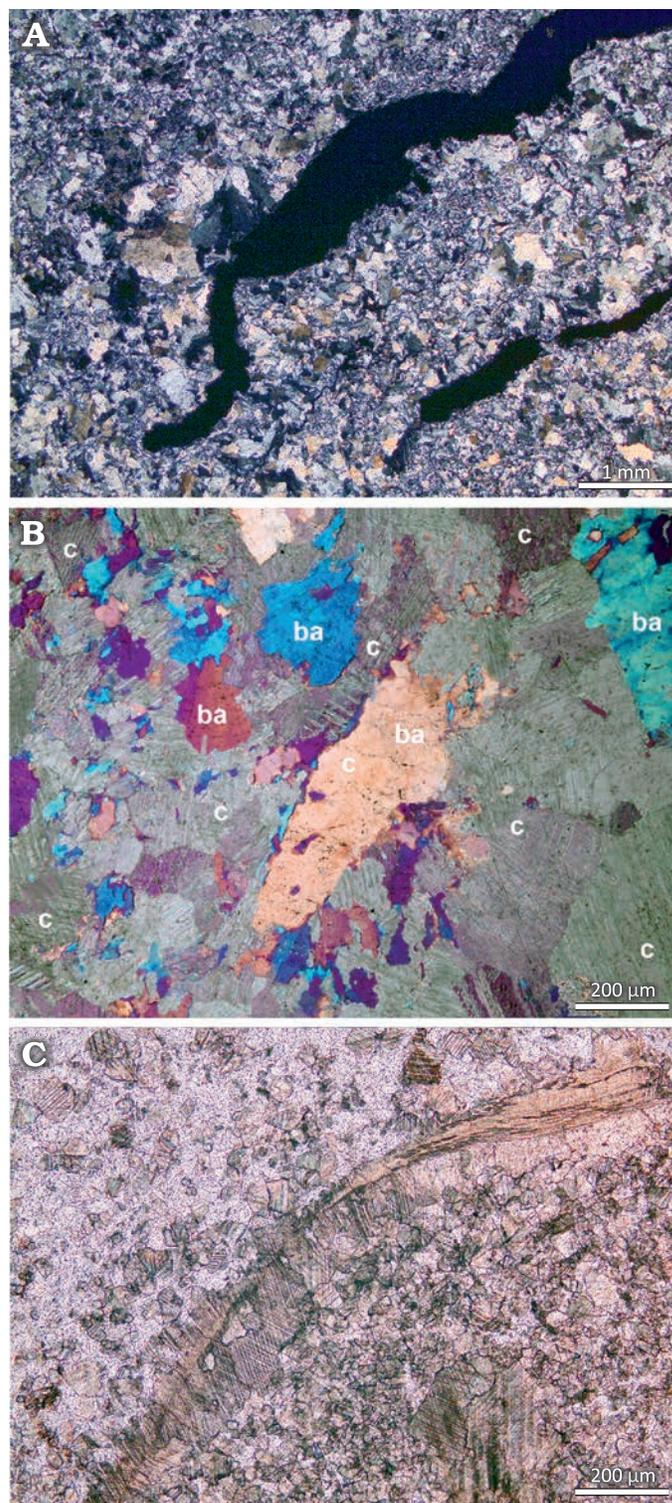


Fig. 8. Slaven brachiopod sediments in thin-section from Famennian, Nevada. **A.** Void of brachiopod shells surrounded by poikilotopic barite. Note that the barite has no preferred orientation to the shells. **B.** Intergrowth of coarse twinned calcite and subhedral barite. Use of retardation plate causes barite (ba) to show as bright colors against the calcite (c). **C.** Poor preservation of layered brachiopod shells within coarse calcite.

ment). Analysis for biomarkers was not undertaken due to the levels of alteration.

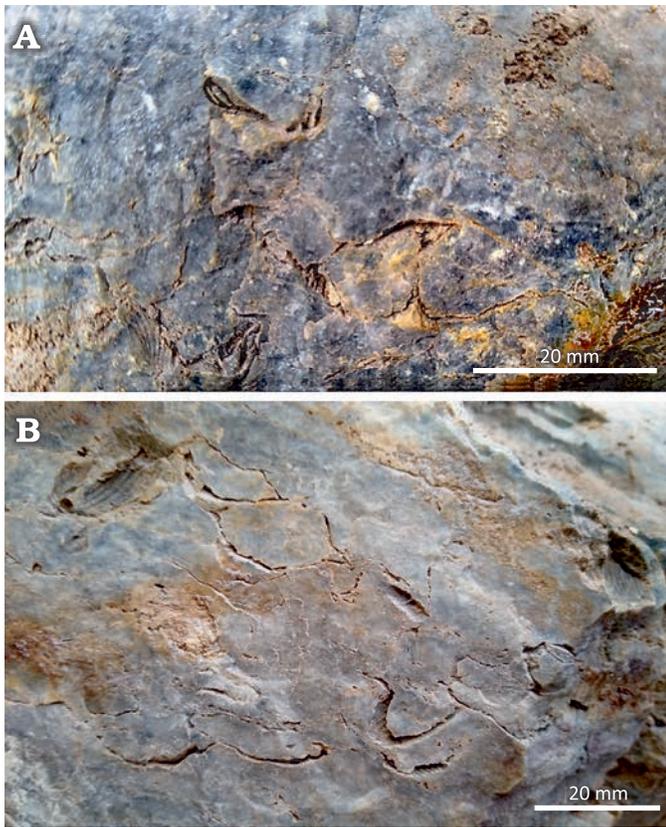


Fig. 9. Preservation (in situ) of brachiopods within massive to bedded barite blocks at Clipper Mine (Famennian, Nevada). **A.** Details of preservation showing costae and internal features such as the septalium and septum in sample above the scale bar. **B.** Typical block with dense, subparallel accumulation as seen by molds.

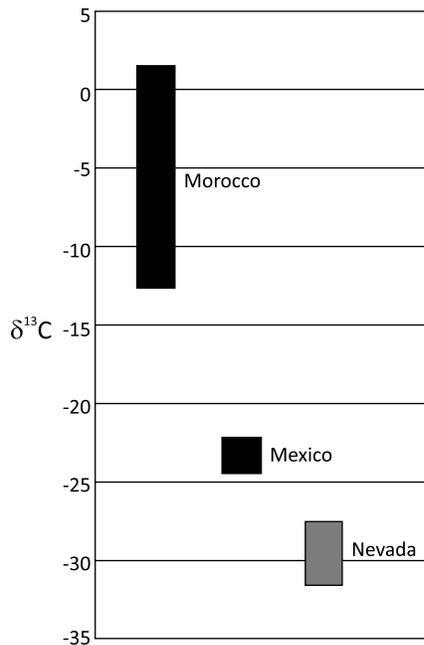


Fig. 10. δ<sup>13</sup>C isotopic ratios of limestone from Clipper Mine, Nevada compared to Mexico and Morocco (Famennian). Data from Batther 2020 and this study (Nevada); Canet et al. 2014 (Mexico); Peckmann et al. 2007 (Morocco).

Table 4. Carbon isotope data from limestones associated with dimereloid brachiopod *Dzieduszyckia* in Nevada and Mexico. Values are relative to the Vienne Pee Dee Belemnite (VPDB) standard.

Location	δ <sup>13</sup> C	Reference	
Los Pozos, Sonora, Mexico	-21.2	Canet et al. 2014	
	-20.0		
	-23.5		
	-22.3		
	-24.3		
Clipper, Nevada, USA	-28.6	Batther 2020	
	-31.1		
	-30.9		
	-29.9		
	-31.7		
	-30.2		
	-30.4		
	-30.4		
	-29.7		
	-31.4		
	-31.2		
	-27.3		
	-30.8		
	-29.7		this study
	-30.2		
	-30.5		
	-30.5		
-30.1			
-30.2			
-29.7			
-29.0			
-30.5			
-30.0			
-29.8			
-30.3			
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-30.3			
-30.5			
-30.1			
-30.8			
-30.3			
-30.6			
-30.5			
-30.3			
-30.1			
-30.6			
-30.8			
-30.5			
-30.3			
-30.3			

The 43 measured samples from Nevada show a strongly <sup>13</sup>C depleted carbonate signature (average δ<sup>13</sup>C = -30.24‰ VPDB), ranging from -31.1 to -27.3‰ VPDB (Batther 2020

and this study) (Fig. 10 and Table 4). Canet et al. (2014) presented five values from equivalent units in Sonora, Mexico, ranging from -24.3 to -20‰ VPDB (Fig. 10 and Table 4). The overall variation, ~4‰, is not as broad as at many seeps in the geological record. Whether this is a function of diagenetic homogenization or reflects an original signature is still under investigation. However, deep subsurface alteration would more likely increase rather than decrease the ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$ . This shows that Nevada sites do show a geochemical signal for primary oxidation of methane as one of the inorganic carbon sources.

## Systematic palaeontology

Phylum Brachiopoda Duméril, 1805

Subphylum Rhynchonelliformea Williams et al., 1996

Class Rhynchonellata Williams et al., 1996

Order Rhynchonellida Kuhn, 1949

Superfamily Dimerelloidea Buckman, 1918

Family Halorellidae Ager, 1965

Subfamily *Dzieduszyckiinae* Savage, 1996

Genus *Dzieduszyckia* Siemiradzki, 1909

*Type species: Terebratula (?) kielcensis* Roemer, 1866; Upper Devonian, Kadzielnia, Poland.

*Dzieduszyckia* spp.

Figs. 11, 12.

1971 *Dzieduszyckia* sp.; Cloud and Boucot 1971: 175–180, pl. 1: 6–17.

*Material*.—Over one hundred specimens (including ten figured specimens USNM PAL 794576–794586 and materials of Cloud and Boucot 1971, Table 5: 160184–160193, 337301–337325) preserved as internal and external molds in diagenetic barite and rare crystalline limestone from the Clipper, Mountain Springs, and Greystone Mines, northern Toiyabe Range, Nevada, USA (see Table 3 for locality details). Note that the following discussion is based on new collections and the author did not review the collections at the USNM due to restrictions enacted during the coronavirus epidemic (Table 5).

*Description*.—No complete shells were observed in this study but many external and internal molds preserved enough details for general comment on external form and internal details. Overall shell outlines include both rounded triangular and transverse biconvex shells though most fossils are preserved as incomplete fragments that do not define the margin (Fig. 11). Where a midline was preserved, shells have a median sulcus on both valves. As noted, no complete shells were recovered but the largest individual fragment is 73 mm wide. By using the presence of the sulcus, the largest half-width measured is 43 mm, yielding a minimum total width of 86 mm. Along the lateral and anterior margins,

many shells are rounded to rectilinear. The ventral umbo is distinct and strongly recurved. In rare examples, fine growth rings and plicae were observed.

Costae are well-preserved and show variability from sharp rectangular to rounded and triangular cross-sections. Many shells show complete costation; in others the costae on the external surface start approximately one third of the distance from the umbo. Bifurcation of costae is very rare (only two samples out of over 100 noted) and no trifurcation was observed.

While no crura were observed in this study, a number of critical internal features are preserved on internal molds (Fig. 12). A dorsal median septum is pronounced and preserved in multiple specimens. The septum is relatively thick in smaller shells but does not thicken with the increase in shell size. No complete shell was observed but based on the dimensions it is likely the septum extends to approximately one half of the shell length. Small dental sockets can be observed. The septalium is distinct and thicker than the septum. However, internal skeletal growth sequences are not preserved. Additionally, several fortuitous samples preserve the impressions of dental plates.

*Discussion*.—Noll et al. (1984) provided detailed descriptions of the external morphology of *Dzieduszyckia* from silicified fossils in barite from Sonora but did not undertake serial sectioning to show the crura shapes and bases. However, the authors argued for the erection of a new species, *D. sonora*, based primarily on bifurcation and trifurcation of costae in the mature shells and secondarily on the generally smaller size. They also stated that the Nevada fossils were the same species. In their table of twenty specimens, 18 show bifurcation and/or trifurcation (Noll et al. 1984: 1419, table 1). Only two of the over 100 brachiopods collected for the present study and only one of the specimens figured by Cloud and Boucot (1971: pl. 1: 15) shows any bifurcation. In each of those cases, only one or two costae were bifurcated. Noll et al. (1984: fig. 6) also relied on the size variation to connect the Mexican and Nevada specimens. They show a figure with the measured ratios of width to length of type specimens as well as means for *D. sonora*, *D. kielcensis*, *D. crassicosata*, and *D. bashkirica*. The Mexican species has a smaller width and length average (~30 mm for each dimension). Noll et al. (1984) did not provide the measurements of the Nevada specimens but lumped them with the Mexican samples. Using the minimum widths of Nevada shell fragments, the average minimum width is 43 mm, more in line with *D. kielcensis* and *D. crassicosata*. The data provided herein support distinguishing a separate species from *D. sonora*. Specifically, the lack of common bifurcation (and no trifurcation) of the costae, a relatively thin dorsal septum, and larger size are contradictory to the Mexican species diagnosis.

Ninety-three specimens were measured for number of costae relative to the width of the fossil fragment. However, the line of cross-section was random and not along the commissure due to the limited material. The results are plot-

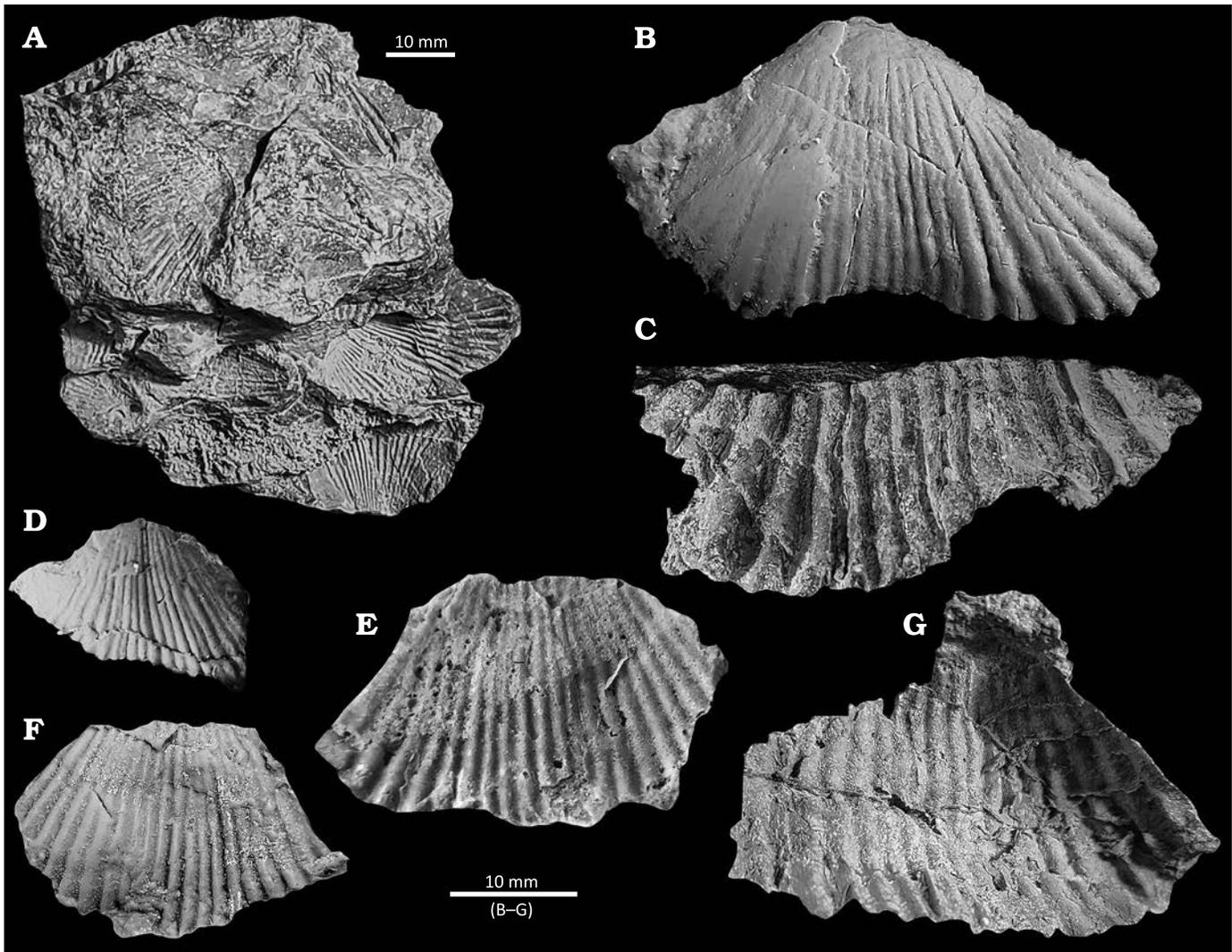


Fig. 11. External molds of dimerelloid brachiopod *Dzieduszyckia* spp., Famennian, Nevada, USA. **A.** USNM PAL 794576, block showing dense concentration of shells from in situ deposit, Mountain Springs Mine. **B.** USNM PAL 794577, cast showing typical triangular outline and deep sulcus. **C.** USNM PAL 794578, shell fragment showing relatively large costae and sulcus. **D.** USNM PAL 794579, specimen showing thinner costae and asymmetry about the midline. Note the rare bifurcation to left of midline. **E.** USNM PAL 794580, fragment of a more rounded shell with rounded costae. **F.** USNM PAL 794581, portion of shell showing radially divergent costae. **G.** USNM PAL 794582, external mold emphasizing strong biconvexity of shell.

ted as a histogram with bins set to 0.10 costae/mm width (Fig. 13A).

The histogram may be interpreted in two ways. In the first, the observations represent variance within a single species, in which costae frequency width skews toward lower values. A scatter plot (Fig. 13B) shows the observed fragment width and observed costae have a significant ( $p = 7.751 \times 10^{-5}$ ), if middling, positive correlation (Pearson's  $\rho = 0.41$ ).

Alternatively, the data may represent two distinct species of brachiopods, with low (ca. 0.5 costae/mm) and high (ca. 1.0 costae/mm) median costae frequencies, respectively. In this interpretation, the lack of observed specimens with 0.8–0.9 costae/mm (Fig. 13A) coincides with each species distribution's upper and lower tails, respectively. When the data are cut at this threshold, the tallied costae correspond more closely to fragment size. As shown in Fig. 13C, spec-

imens with higher costa frequency (costa/width  $>0.8$ ) have a strong, significant correlation between costae tally and fragment size (Pearson's  $\rho = 0.91$ ;  $p = 4.69 \times 10^{-10}$ ), while specimens with lower costa frequency (costae/width  $<0.8$ ; red{?}) retain a strong significant association (Pearson's  $\rho = 0.69$ ;  $p = 1.19 \times 10^{-10}$ ). Based solely on these values, it may be possible to draw out two separate species. The low numbers of recovered specimens as well as the use of fragments of shells must be considered. Coupled with the lack of details of the crura, there is a hesitation to erect two distinct species. This relationship of two species of *Dzieduszyckia* inhabiting the same environment is similar to Morocco, where two dominant species—*D. crassicostata* and *D. tenuicostata*—are easily defined by density of costae relative to the shell (Termier and Termier 1948). Baliński and Biernat (2003) also noted that the crura of *D. tenuicostata* widen anteriorly and twist from horizontal to

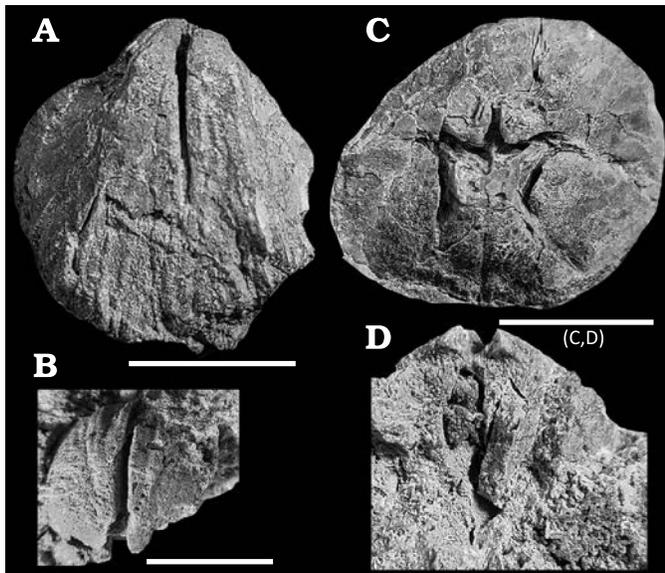


Fig. 12. Internal features of dimerelloid brachiopod *Dzeduszyckia* sp., Famennian, Nevada, USA. A. USNM PAL 794583, dorsal valve showing pronounced septum. B. USNM PAL 794584, internal mold of small shell showing deep septum and biconvex shell. C. USNM PAL 794585, view of hinge displaying septalium in upper, dorsal shell and vertical dental plates in lower, ventral shell. D. USNM PAL 794586, internal mold preserving relatively tall septalium. Scale bars 10 mm.

vertical, a comparison thus far not tested in Nevada. A similar situation is found in the Southern Urals where Mizens (2006) defined *D. cordiformis* as a distinct species from *D. bashkirica* and *D. prima* in part by its fine costae. Finally, a similar conclusion was drawn by Xian and Jiang (1978) in China, erecting *D. acutiplicata* based on its fine costae.

## Discussion

Understanding the role of *Dzeduszyckia*, the oldest dimerelloid, in hydrocarbon seeps is the most critical question about this large Devonian genus. The carbon isotopic data from Nevada very strongly supports the connection to an original methane seep system even though the diagenetic alteration to barite destroys primary petrofabrics. Similar deposits in the Los Pozos Formation, Mexico, also show a geochemical record of hydrocarbon seepage. Indeed, Torres et al. (2003) expanded this connection to say that large scale bedded barite deposits are related to methane seepage; however, Bather (2020) provides convincing evidence that the methane seepage is coincidental to the barite deposits.

Expanding globally, the only other *Dzeduszyckia* deposit specifically analyzed for a connection to hydrocarbon seeps is the Sidi Amar locality in Morocco. Baliński and Biernat (2003) argued against a seep setting based on seawater stable carbon isotope ratios in shell material but Peckmann et al. (2007) performed a study using multiple fabrics and showed carbon isotope depletion relative to seawater. The values of Peckmann et al. (2007) were confirmed

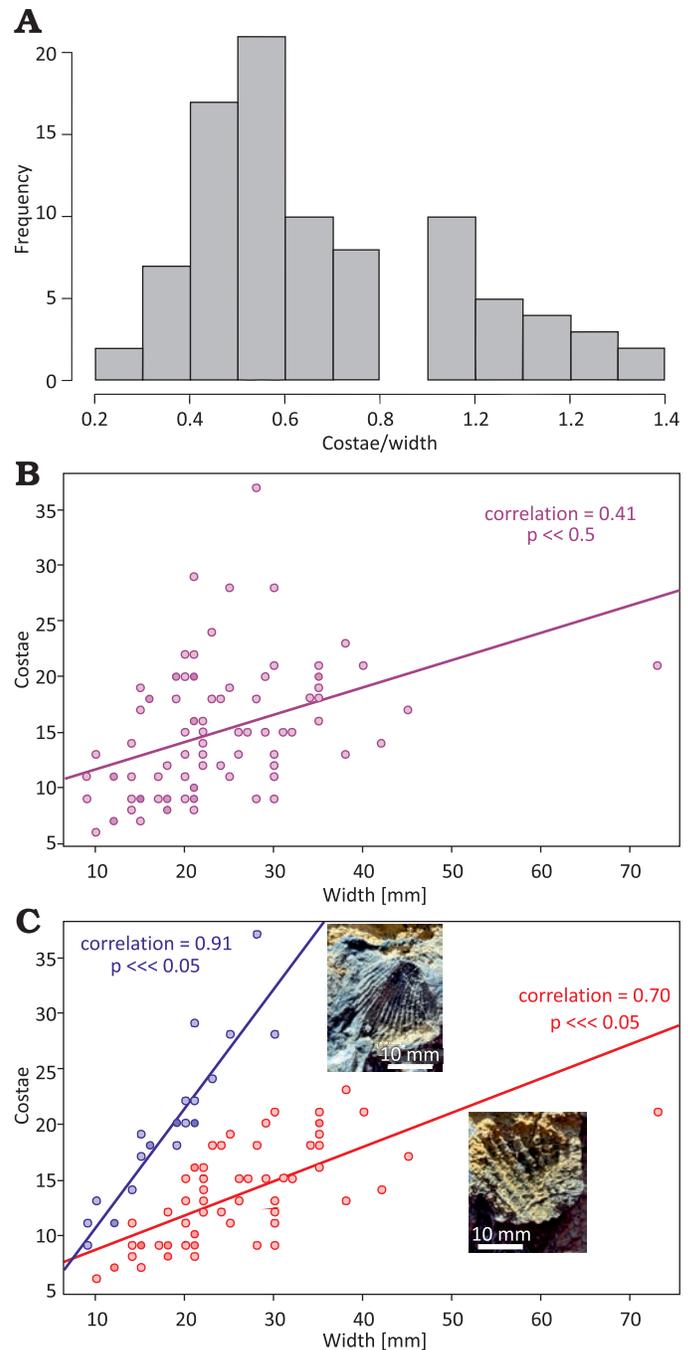


Fig. 13. Number of costae per width in centimeters of fragments in *Dzeduszyckia* sp. from Nevada. A. Histogram of data from all measured specimens. B. Best fit regression line assuming variance within a single species, in which costae frequency width skews toward lower values. C. Separation into two distinct species of brachiopods, with low (ca. 0.5 costa/mm) and high (ca. 1.0 costa/mm) median costae frequencies with best fit regression lines. Photos show one field sample with a representative of each group.

by the author using material also collected at Sidi Amar. Furthermore, Jakubowicz et al. (2022) argued that these values showed significant depletion compared to contemporaneously high Famennian sea water values though this is contradictory to the Nevada values not available to those authors.

Table 5. Specimens of *Dzieduszyckia* sp. in the collections of the USNM.

USNM catalog number	Scientific name (as filed)	Reference	Date collected	Province/State	Site/Station Number
337301	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337302	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337303	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337304	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337305	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337306	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337307	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337308	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337309	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337310	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337311	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337312	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337313	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337314	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337315	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337316	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337317	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337318	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337319	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337320	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10453
337321	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10452
337322	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10452
337323	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10452
337324	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10452
337325	<i>Dzieduszyckia sonora</i> Noll et al.	Noll et al. 1984	1980	Sonora, Mexico	10452
160184	<i>Dzieduszyckia</i> sp. of Cloud & Boucot	Cloud and Boucot 1971	1957	Nevada, USA	USGS GREEN LOC M134
160185	<i>Dzieduszyckia</i> sp. of Cloud & Boucot	Cloud and Boucot 1971	1957	Nevada, USA	USGS GREEN LOC M134
160186	<i>Dzieduszyckia</i> sp. of Cloud & Boucot	Cloud and Boucot 1971	1957	Nevada, USA	USGS GREEN LOC M134
160187	<i>Dzieduszyckia</i> sp. of Cloud & Boucot	Cloud and Boucot 1971	unknown	Nevada, USA	unrecorded
160188	<i>Dzieduszyckia</i> sp. of Cloud & Boucot	Cloud and Boucot 1971	1957	Nevada, USA	USGS GREEN LOC M134
160189	<i>Dzieduszyckia</i> sp. of Cloud & Boucot	Cloud and Boucot 1971	1957	Nevada, USA	USGS GREEN LOC M134
160190	<i>Dzieduszyckia</i> sp. of Cloud & Boucot	Cloud and Boucot 1971	1950	Nevada, USA	USGS GREEN LOC 25453
160191	<i>Dzieduszyckia</i> sp. of Cloud & Boucot	Cloud and Boucot 1971	1957	Nevada, USA	USGS GREEN LOC M134
160192	<i>Dzieduszyckia</i> sp. of Cloud & Boucot	Cloud and Boucot 1971	1957	Nevada, USA	USGS GREEN LOC M134
160193	<i>Dzieduszyckia</i> sp. of Cloud & Boucot	Cloud and Boucot 1971	1957	Nevada, USA	USGS GREEN LOC M134

In contrast, the diverse localities in South China have been argued not to be seep settings. This is largely based on the paleogeographic setting (outer carbonate platform as well as intrabasinal deep water deposits) and stratigraphy. While no geochemical data have thus far been published, preliminary data on 13 different petrofabrics provided to the author strongly argue for normal ocean carbonate  $\delta^{13}\text{C}$  values without hydrocarbon input (Yuanlin Sun, personal communication 2022). However, in the same communication it is noted that hydrocarbons are found as pockets in the limestone.

Broadening the discussion to a global scale, nearly all the other occurrences of *Dzieduszyckia* are from deeper water, organic-rich and likely low oxygen settings that are also connected with either active tectonism or slightly pre-dating major orogenic episodes. It should be re-emphasized that the distribution is global and across diverse ocean basins. Deep water slope and basin settings along active tectonic margins

are among the most common regions for hydrocarbon seeps throughout the geological record (e.g., Sandy et al. 2012; Peckmann et al. 2013; Hryniewicz 2022).

Additionally, it is important to note that the dimerelloids got their start in the narrow window of two major extinction intervals: the Frasnian–Famennian Kellwasser Events and the end-Famennian Hangenberg Biotic Crisis. The analysis of this interval is beyond the scope of this paper but in general, the modern consensus is that these biotic crises were related to high productivity and concomitant oxygen depletion (Reershemius and Planavsky 2021) as well as eustatic transgressions that constrained vicariance-driven evolutionary diversity throughout the Famennian (Stigall 2012). It is possible that the Famennian biotic crises removed mollusks from seeps, allowing dimerelloids to access these environments (Baliński et al. 2022). Baliński et al. (2022) proposed that the dimerelloids evolved out of a lineage of brachiopods

that were already adapted to dysoxic and low nutrient deep-water settings (e.g., Boyer and Droser 2007) and thus were generalists in depauperate conditions. I agree and would add that this environmental plasticity enabled *Dzieduszyckia* to be primed for the transgressions of the Famennian. There is still work to be done to develop this hypothesis but it is interesting how the leiorhynchids are found in similar deep water settings in the Frasnian and Famennian. In fact, the generic name *Leiorhynchus* has been used for species of *Dzieduszyckia* as well as the Carboniferous dimerelloid, *Ibergirhynchia* (Gischler et al. 2003). Potentially, both dimerelloids and leiorhynchids are related through the same ancestral rhynchonellide. Regardless of the origin, in this hypothesis, some localized populations found themselves coincidentally at sites of hydrocarbon seepage and adapted to this environment. This is why *Dzieduszyckia*, more so than other dimerelloids, is found at both seep and non-seep settings. Eventually, the populations that successfully inhabited seeps gave rise to the dimerelloid descendants such as *Ibergirhynchia*, *Halorella*, and *Anarhynchia*. Other subpopulations not found at seeps or vents became evolutionary dead-ends; however, see important discussion of non-seep dimerelloids in Kiel et al. (2021).

This conjectural model explains a few of the intriguing features about *Dzieduszyckia*. First, of all the dimerelloids, the genus shows the most diversity including the strong likelihood of multiple species cohabitating. This diversity is a representation of the morphological plasticity afforded during a protracted time of intense environmental perturbation. Post-Devonian seeps are monospecific with regards to brachiopods, perhaps alluding to a time when only derived seep-obligate forms were successful. Secondly, nearly all dimerelloids are only found in seep or vent settings, with the exception of some extraordinary *Halorella* and *Sulcirostra* deposits (Kiel et al. 2021). As the first dimerelloid, *Dzieduszyckia* evolved during a time of experimentation thus is found at both seep (Nevada, Mexico, Morocco) and non-seep settings (China and possibly Poland).

## Conclusions

*Dzieduszyckia* brachiopods preserved in diagenetic barite and rare coarse limestone record a methane seep system from the Famennian (Late Devonian) time period. Preserved as internal and external molds, there is not enough internal structure preserved to allow for species diagnosis; however, the fossils are not equivalent to the diagnosis of *D. sonora* (Noll et al. 1984). Based on nearly 100 partial shell impressions, it may be possible to distinguish two separate species based on the coarseness and density of the costae, similar to situations in Morocco (Baliński and Biernat 2003; Peckman et al. 2007), the Urals (Mizens 2006), and South China (Xian and Jiang 1978). However, the recognition of one or two distinct species is not currently supported by the available material and will remain for future studies. The origina-

tion and global distribution of *Dzieduszyckia* in the dysoxic and nutrient-poor oceans of the Famennian, suggests that the Dimerelloidea may have evolved from the same ancestral stock as the leiorhynchids, another rhynchonellide from similar settings. *Dzieduszyckia*-bearing deposits are also connected in time to the interval between the Kellwasser and Hangenberg biotic crises. While *Dzieduszyckia* may have lived in both seep and non-seep settings, younger dimerelloids are obligate to seeps or hydrothermal vents with rare exceptions. *Dzieduszyckia* represents an initial experimental phase in the dimerelloid lineage with subsequent genera volumetrically dominating hydrocarbon seeps for 230 million years.

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