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

Russell S. Shapiro

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 with δ¹³C 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.

Russell S. Shapiro [rsshapiro@csuchico.edu; ORCID: https://orcid.org/0000-0003-1769-0346], Department of Earth and Environmental Sciences, California State University, Chico, USA.

Received 3 February 2024, accepted 27 February 2024, published online 27 March 2024.

Copyright © 2024 R.S. Shapiro. This is an open-access article distributed under the terms of the Creative Commons Attribution License (for details please see http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

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 ¹³C 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 approach, linking fossil taxa to modern, seep or vent-obligate groupings. Lineages, such as the bivalve families Lucinidae and Vesciomyidae 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 may not 2002). 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 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)
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 (? ) kielicensis.

The species was formally redefined and named Dzieduszyckia by Siemiradzki (1909). Siemiradzki’s publication included the unrelated specimens, 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 zigzag 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 borchole 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 Kадzielnia 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 Straцwczysiska 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 crystal-limestone with subordinate marl and clay (Pawłowska and Pawłowski 1978).

The general geology of the region of the Kadzielniańskie 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 Murzakaevo and Murzakayev) beds of the Southern Urals (reported in Rozman 1960; see Sartenaer 1999). 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, Syvuyu 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 Dzerzhinka 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 Mugodzhär (= 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 Mugodzhär 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 Mugodzhär 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 Torvisk 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:** Rhychonellid 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 and Morin (1973). Additional critical papers on the brachiopods were presented by Ager (1968), Ager et al. (1976), Biłasinska 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 Tabaïnout 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 Khnifisra along the southeastern slopes of the Gara de M’irt 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-

**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 tonic 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 13C depleted carbonates, 34S 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 arch 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 “Leiohynchoidae-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 genus 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 *Leiohynchus (Dzieduszyckia) bashkircus* in the Prolobites Ammonoid Zone of the Western Urals and drew the equivalence to the Murzekayev Beds of Kazakhstan. This is also referred to

---

**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.
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 origin 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 infraspecific 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 septa, 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 septalum, 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 morphologies 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Key references</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dzieduszyckia kielcensis</em></td>
<td>Poland</td>
<td>Siemiradzki 1909; Biernat 1967</td>
</tr>
<tr>
<td><em>Dzieduszyckia bashkirica</em></td>
<td>Urals, Kazakhstan, Tajikistan</td>
<td>Nalivkin 1947; Rozman 1960, 1962; Menakova 1991</td>
</tr>
<tr>
<td><em>Dzieduszyckia prima</em></td>
<td>Middle Urals</td>
<td>Mizens 2008</td>
</tr>
<tr>
<td><em>Dzieduszyckia cordiformis</em></td>
<td>Eastern Urals</td>
<td>Mizens 2006</td>
</tr>
<tr>
<td><em>Dzieduszyckia sonora</em></td>
<td>Mexico, USA</td>
<td>Noll et al. 1986</td>
</tr>
<tr>
<td><em>Dzieduszyckia crassicostata</em></td>
<td>Morocco</td>
<td>Termier and Termier 1948</td>
</tr>
<tr>
<td><em>Dzieduszyckia intermedia</em></td>
<td>Morocco</td>
<td>Termier 1936</td>
</tr>
<tr>
<td><em>Dzieduszyckia tenuicostata</em></td>
<td>Morocco</td>
<td>Termier 1936</td>
</tr>
<tr>
<td><em>Dzieduszyckia oblonga</em></td>
<td>China</td>
<td>Xian and Jiang 1978</td>
</tr>
<tr>
<td><em>Dzieduszyckia elongata</em></td>
<td>China</td>
<td>Xian and Jiang 1978</td>
</tr>
<tr>
<td><em>Dzieduszyckia xiensis</em></td>
<td>China</td>
<td>Xian and Jiang 1978</td>
</tr>
<tr>
<td><em>Dzieduszyckia acutiplicata</em></td>
<td>China</td>
<td>Xian and Jiang 1978</td>
</tr>
</tbody>
</table>
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 xiasiensis* 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 species. 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 rhychnonellide 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 *Halorea* 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-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 µm 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× objective. The Reliotron was run with the vacuum at ~42 mTorr and an operating voltage of 7.8 kV and power at ~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 δ¹³C 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 CO₂ 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 the same mass of N₂ + CO₂. 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 CaCO₃ 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. Polikolitic 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 µm with a skewed median of 93.1 µm (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.

<table>
<thead>
<tr>
<th>Mine</th>
<th>Latitude, longitude</th>
<th>Description</th>
<th>Figured specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mountain Springs</td>
<td>40.32045, -117.04322</td>
<td>in situ brachiopods collected from barite beds in Pit A</td>
<td>none</td>
</tr>
<tr>
<td>Mountain Springs</td>
<td>40.31555, -117.04208</td>
<td>loose specimens collected from Pit C</td>
<td>USMN PAL 794578</td>
</tr>
<tr>
<td>Clipper</td>
<td>40.25089, -116.83484</td>
<td>in situ brachiopods collected from faulted massive barite in mine wall</td>
<td>USMN PAL 794576, 794577, 794582–794586</td>
</tr>
<tr>
<td>Clipper</td>
<td>40.24946, -116.83063</td>
<td>loose specimens recovered from high-grade barite stockpile</td>
<td>USMN PAL 794579–794581</td>
</tr>
<tr>
<td>Greystone</td>
<td>40.27160, -116.86859</td>
<td>singular loose specimen collected from excavated high-grade barite</td>
<td>none</td>
</tr>
</tbody>
</table>
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 replacive 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 cement). Analysis for biomarkers was not undertaken due to the levels of alteration.
The 43 measured samples from Nevada show a strongly 13C depleted carbonate signature (average δ13C = -30.24‰ VPDB), ranging from -31.1 to -27.3‰ VPDB (Batther 2020).

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

<table>
<thead>
<tr>
<th>Location</th>
<th>δ13C</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Los Pozos. Sonora, Mexico</td>
<td>-21.2</td>
<td>Canet et al. 2014</td>
</tr>
<tr>
<td></td>
<td>-20.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-23.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-22.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-24.3</td>
<td></td>
</tr>
<tr>
<td>Clipper. Nevada, USA</td>
<td>-28.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-31.1</td>
<td>Batther 2020</td>
</tr>
<tr>
<td></td>
<td>-30.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-29.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-31.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-29.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-31.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-31.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-27.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-29.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.2</td>
<td>this study</td>
</tr>
<tr>
<td></td>
<td>-29.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-29.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-29.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-29.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-30.3</td>
<td></td>
</tr>
</tbody>
</table>

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. δ13C 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).

The 43 measured samples from Nevada show a strongly 13C depleted carbonate signature (average δ13C = -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 diageneric homogenization or reflects an original signature is still under investigation. However, deep subsurface alteration would more likely increase rather than decrease the ratio of $^{13}$C to $^{12}$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 Rhynchocheliformea Williams et al., 1996  
Class Rhynchoellata Williams et al., 1996  
Order Rhynchoellida Kuhn, 1949  
Family Halorellidae Ager, 1965  
Superfamily Dimerelloidea Buckman, 1918  
Genus *Dzieduszyckia* Siemiradzki, 1909

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

**Dzieduszyckia** spp.

Figs. 11, 12.


*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 placed 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. crassicostata*, 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. crassicostata*. 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-
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, specimens 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...
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 *Dzieduszyckia*, 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, Batther (2020) provides convincing evidence that the methane seepage is coincidental to the barite deposits.

Expanding globally, the only other *Dzieduszyckia* 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 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.
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 $\delta^{13}C$ 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.

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 evolution (Peckmann et al. 2013; Hryniewicz 2022). Baliński et al. (2022) proposed that the Famennian biotic crises removed mollusks related to high productivity and concomitant oxygen depletion. 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 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).
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 genetic 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 rynchonellid. 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 de-}

**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 origination 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 rynchonellid 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.

**Acknowledgements**

The author is grateful to the many years of discussions of seeps with Andrzej Kaim (ZPAL, Institute of Paleobiology Polish Academy of Science, Warsaw, Poland), Jörn Peckmann (Universität Hamburg, Germany), Kathy Campbell (University of Auckland, New Zealand), and Michał Jakubowicz (Adam Mickiewicz University, Poznań, Poland). M-I SWACO, and in particular, Ryan Dockstader, provided access to the private barite mines and encouraged the research. Two graduate students, Harpreet Batther and Brady Derick (California State University, Chico, USA), conducted detailed studies of the barite deposits. Geochemical analysis was graciously provided by Will Berelson (University of Southern California, Los Angeles, USA) and Alex Sessions (California Institute of Technology, Pasadena, USA). Kathleen Ritterbush (University of Utah, Salt Lake City, USA) conducted the statistical analysis presented in Fig. 13. Fieldwork in Morocco was facilitated by Michał Jakubowicz and funded by the California State University. Most critical to this manuscript were the papers provided by Andrzej Kaim, Andrzej Baliński (both ZPAL), Anita Mizens (Institute of Geology and Geochemistry, Ural Branch, Russian Federation), and Yuanlin Sun (Peking University, Beijing, China), the latter translated from the original Chinese. All other translations were by the author who accepts responsibility for inaccuracies. The present manuscript benefited immensely from very thorough and detailed reviews by Miguel Manceño (La Plata Natural Sciences Museum, Argentina), Andrzej Baliński (ZPAL), and two anonymous reviewers, who significantly improved the quality of this paper.

**References**


