Disclaimer/Publisher's Note: The statements, opinions, and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions, or products referred to in the content.

Luning Formation (Nevada, USA) Paleobathymetry 2 3 4 MARK A. S. MCMENAMIN 5 Department of Geology and Geography 6 Mount Holyoke College 7 South Hadley, Massachusetts, USA 01075 8 mmcmenam@mtholyoke.edu 9 10 11 Abstract: A silicified, thick-shelled, smooth-surfaced nuculanoid bivalve has been recovered by acid 12 maceration of the Late Triassic (Carnian-Norian) strata of the Luning Formation, Nevada. Comparable modern nuculanoid clams inhabit water depths from 525-2,562 meters, and the living clam (an 13 undescribed species of Pseudoneilonella from Caleta Sierra, Coquimbo, Chile) most similar to the 14 fossil lives at 878-933 m. The Triassic nuculanoid clam (possibly a neilonellid) is inferred here to have 15 16 inhabited marine waters at approximately 1000 m deep during deposition of the Shaly Limestone 17 Member of the Luning Formation. This new fossil discovery falsifies hypotheses that the ichthyosaurs (Shonisaurus popularis) of Berlin-Ichthyosaur State Park, Nevada, USA, were deposited, respectively, 18 19 in either shoreline deposits or in strata that accumulated above storm wave base. 20 21 Keywords: taxodont bivalves; Nuculanoidea; Neilonellidae; Triassic; Nevada; Luning Formation; 22 paleobathymetry, Berlin-Ichthyosaur State Park 23

1. Introduction

The Triassic (Carnian-Norian, *ca.* 225-235 Ma) Luning Formation of west-central Nevada has been the focus of spirited debate [1-5] regarding its depositional environment and paleoecology (Figs. 1-2). Repeated attempts have been made to determine the paleobathymetry of the Shaly Limestone Member of the Luning Formation of Berlin-Ichthyosaur State Park (BISP), central Nevada, USA. Further analysis is required to help ascertain the cause of death, and reasons for postmortem emplacement in virtually the same spot, of seven to nine large carcasses, representing full grown adults, of the ichthyosaur *Shonisaurus popularis*. Camp [6-7] originally suggested death by stranding on a Panthalassic shoreline. Holger [1] challenged this hypothesis by showing that the rock matrix in question was deposited in deep water, thus falsifying the ichthyosaur mass stranding hypothesis. The ichthyosaurs occur in the Shaly Limestone Member of the Luning Formation, close to the peak transgressive phase of marine sediment deposition in the region (Figure 2). The cause of death of the shonisaurs remains unresolved, and their emplacement in a deep water site constitutes a major paleontological anomaly.

In a recent study of the Luning Formation at Berlin-Ichthyosaur State Park, the Pyenson Lab [8] argued that there was no evidence for significant environmental perturbation that could be blamed for the deaths of the ichthyosaurs. Kelley et al. [8] further maintained that the ichthyosaurs at BISP were deposited between fair-weather wave base and above maximum storm wave base, in other words, between approximately 15-90 meters depth. This relatively shallow depth estimate incidentally helped support the hypothesis that the adult shonisaurs died in as part of a philopatric grouping engaging in reproductive behavior [8]. Unfortunately, the Pyenson Lab scenario provides

neither a killing mechanism for the ichthyosaurs, nor a method for sequentially transporting their bodies to virtually the same spot on the seafloor—a problem that is magnified if BISP indeed represents a deep water site. As shown by evidence presented below, the Kelley et al. [8] depth estimate is too shallow by at least a factor of ten, making it highly unlikely that the ichthyosaurs perished as part of a group engaged in geographically localized reproductive behavior.

2. Methods

Bivalves and other mollusks are common in the Shaly Limestone Member of the Luning Formation, but are usually preserved as steinkerns that lack both taxonomically diagnostic surface ornamentation and detailed hinge structure morphology. Due to this limited mode of preservation, there are significant gaps in our knowledge of the Late Triassic bivalve, gastropod and cephalopod faunas of the Shaly Limestone Member of the Luning Formation.

Mount Holyoke College paleontological field expeditions in 2013-2014 recovered limestone samples from the Shaly Limestone Member of the Luning Formation from sites near BISP. Acetic acid maceration (in November 2022) of field sample 12 of 5/23/14 produced a single specimen of a right nuculanoid valve, preserved by silicification (Figs. 3-5). This is a rare mode of preservation in the Shaly Limestone Member (most of its clam fossils are preserved as steinkerns). The fossil (IGM 5010) is taxonomically significant considering that both its valve interior and exterior, as well as its hinge teeth series, are preserved. The same acid maceration produced fossil fish teeth, silicified malacostracan chelae [4], and other fossils. The rock material and associated fossils were collected

under the rubric of the United States Department of the Interior, Bureau of Land Management,
 Paleontological Resources (Use Permit N-92224).

3. Results

The discovery of this nuculanoid clam fossil provides support for a deep marine interpretation of the depositional environment of the Shaly Limestone Member of the Luning Formation [1]. By comparison with similar living nuculanoids, the fossil nuculanoid allows a depth estimate to be made for the Shaly Limestone Member depositional environment. *Neilonella mexicana*, *N. corpulenta* and *N. brunnea* are modern nuculanoids that inhabit depths of 1207 m [9], 525 m [10], and 2,562 m [11], respectively. *Pseudoneilonella* species A (Caleta Sierra, Coquimbo, Chile [12]), very similar to the fossil described here, lives at 878-933 m. The water depth of the habitat of the Triassic nuculanoid is estimated here at approximately 1000 m water depth, based on comparisons with the most similar living species (*Pseudoneilonella* species A [12]).

4. Conclusions

A thick-shelled, smooth-surfaced nuculanoid (possibly neilonellid) bivalve from the Late Triassic of Luning Formation, Nevada, provides support for the deep marine interpretation of the depositional environment of the Shaly Limestone Member of the Luning Formation. As such, it supports Holger's [1] deep water interpretation over both Camp's [6-7] strandline interpretation and the Pyenson Lab's [8] hypothesis of deposition above storm wave base. The closest living relatives of the Triassic nuculanoid clam inhabit marine water depths from 500-2500+ m, with the most similar modern clam

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occurring at 878-933 m. The Luning Formation fossil clam is thus estimated here to have lived at approximately 1000 m water depth. 5. Systematic Paleontology Repository Data: IGM, Institute of Geology Museum, Departmento de Paleontología, Cuidad Universitaria, Delegacíon de Coyoacán, 04510, México. 98 Class Bivalvia Subclass Protobranchia Order Nuculanida Superfamily Nuculanoidea Remarks: Within the Nuculanoidea, members of the Neilonellidae have thick shells, are subovate/subtrigonal/subquadrate, are not rostrate, have siphons, and have teeth with a noticeable gap under their umbos [12]. Nuculanoid clam Figs. 3-5 Material: One specimen, silicified right valve (IGM 5010), recovered by acetic acid maceration of field sample 12 of 5/23/2014. The specimen was collected under permit from the United States

Department of the Interior, Bureau of Land Management, Paleontological Resources Use Permit N-92224 issued to Mark McMenamin.

Description: A thick-shelled nuculanoid (possibly neilonellid) bivalve with an ovate outline that is slightly elongated posteriorly. The outer surface of the valve is smooth and lacking in ornamentation or growth lines. Hinge amphidetic; resilifer absent. The umbo is broad and relatively large. Anterodorsal margin is slightly concave and relatively short. Postero-dorsal margin is long and gently convex. Hinge plate is wide, with robust teeth in an anterior and posterior series (8 hinge teeth are present on the antero-dorsal margin, and 13-14 teeth are visible on the postero-dorsal margin), separated by an apparently edentulous gap. Hinge teeth at the antero-dorsal margin are generally straight but may be inclined to slightly curved. Both the antero-dorsal and postero-dorsal margins slightly overhang

Remarks: The fact that there is only a single valve currently available for this taxon precludes establishment of a new genus and species. It is likely that the specimen in question represents an undescribed genus and species. The Triassic fossil certainly belongs to Superfamily Nuculanoidea, and could very well be a member of Family Neilonellidae due to the fact that it lacks a resilifer [12]. More thorough taxonomic assessment must await additional material.

the hinge plate, forming a thin shelf. Adductor scars and pallial line/sinus unknown.

Eight hinge teeth are present on the antero-dorsal margin, and 13-14 teeth are visible on the postero-dorsal margin. Teeth vary in width and robustness. Living species (or undescribed living species) similar to the Triassic fossil are *Neilonella mexicana*, *Neilonella corpulenta*, *Neilonella brunnea*, *Pseudoneilonella* sp. A [12] and *Malletia* species A [12]. *Pseudoneilonella* sp. A is the most

similar to the Triassic fossil, as its teeth vary in width and robustness and it also has a very wide hinge plate. The Triassic clam differs from *Neilonella mexicana*, *Neilonella corpulenta*, *Neilonella brunnea* by lacking both outer surface ornamentation and by lacking chevron-shaped hinge teeth.

Locality: Field sample 12 of 5/23/2014, Late Triassic, Norian Stage (*Tropites welleri-Mojsisovicsites kerri* zones), Shaly Limestone Member of the Luning Formation, Nye County, Nevada, float sample probably belonging to Biofacies 2 [1]. This facies is thought to have been deposited in a relatively deep water, 'stagnant outer shelf" basin [1]. The bivalve *Septocardia* sp., a widespread and morphologically variable form, occurs in Biofaces 2 but is more abundant in Holger's [1] Biofaces 1.

The petrology of the Shaly Limestone Member of the Luning Formation limestone sample (12 of 5/23/2014) is as follows. The limestone is a grey, almost bluish grey, slightly muddy-looking wackestone-packstone. Acetic acid maceration of this sample, in addition to producing the nuculanoid clam, also produced silicified bivalve and gastropod fragments. In thin section, the rock shows a fabric of weathered-looking allochem grains (?peloids) and small fossils, with the fabric crossed by thin white calcite veins and occasional stylolites. Microlaminations occur in places.

Patches of silicification occur in the larger shell fragments. Fossils seen in thin section include fossil and whole bivalve valves (petrographic thin section 12 of 5/23/2014B, near thickest vein), gastropods (petrographic thin section 12 of 5/23/2014B, near crossing white veins), and rare echinoderm fragments (stereom lattice, petrographic thin section 12 of 5/23/2014A near big 'bullseye' fossil [possibly *Isocrinus* sp.]).

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160 161 The author wishes to thank D. Fleury, L. Orr, D. Orr, N. Hodge, N. Malchus, J.M. McMenamin, 162 C. Pless and J. Sullivan for assistance with this research. 163 **Conflicts of Interest** 164 165 The author declares no conflict of interest. 166 167 168 References 169 170 1. Holger, J.A. Taphonomy and paleoecology of *Shonisaurus popularis* (Reptilia: Ichthyosauria). Palaios, 1992, 7, 108-117. 171 172 2. McMenamin, M.A.S.; Zapata, L.P.; Hussey, M.C. A Triassic giant amphipod from Nevada, USA. 173 Journal of Crustacean Biology, 2013, 33, 751-759. 174 3. Balini, M.; Jenks, J.F.; Martin, R.; McRoberts, C.A.; Orchard, M.J.; Silberling, N.J. The Carnian/Norian boundary succession at Berlin-Ichthyosaur State Park (Upper Triassic, central 175 Nevada, USA). Paläontologische Zeitschrift, 2014, 89, 399-433. 176 177 4. Starr, H.W.; Hegna, T.A.; McMenamin, M.A.S. Epilogue to the tale of the Triassic amphipod: 178 Rosagammarus McMenamin, Zapata and Hussey, 2013 is a decapod tail (Luning Formation, Nevada, USA). Journal of Crustacean Biology, 2016, 36, 525-529. 179 180 5. Zapata, L.P.; Hussey, M.C.; McMenamin, M.A.S. Multina isp. From the Late Triassic Luning 181 Formation, Nevada. Ichnos, 2017, 24, 64-71.

- 182 6. Camp, C.L. Large ichthyosaurs from the Upper Triassic of Nevada. *Palaeontographica*,
 183 *Abteilung A*, 1980, *170*, 139-200.
- 7. Camp, C.L. Child of the Rocks—The Story of Berlin-Ichthyosaur State Park. Nevada Bureau of
 Mines and Geology, Special Publication, 1981, 5, 1-33.
 - 8. Kelley, N.P.; Irmis, R.B.; dePolo, P.E.; Noble, P.J.; Montague-Judd, D.; Little, H.; Blundell, J.; Rasmussen, C.; Percival, L.; Mather, T.A.; Pyenson, N.D. Grouping behavior in a Triassic Marine apex predator. *Current Biology*, **2022**, *32*, 1-8.
 - 9. Dall, W.H. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer "Albatross," during 1891, Lieut.-Commander Z.L. Tanner, U.S.N., commanding. XXXVII. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross," from October, 1904 to March, 1905, Lieut.-Commander L.M. Garrett, U.S.N., commanding. XIV. The Mollusca and Brachiopoda. *Bulletin of the Museum of Comparative Zoology*, 1908, 43, 205-487.
 - 10. La Perna, R. Taxonomy of the Family Neilonellidae (Bivalvia, Protobranchia): Miocene and Plio-Pleistocene species of *Pseudoneilonella* Laghi, 1986 from Italy. *The Veliger*, **2007**, *49*, 196-208.
 - 11. Huber, M. Compendium of Bivalves; ConchBooks: Hackenheim, Germany, 2010.
- 12. Valentich-Scott, P.; Coan, E.V.; Zelaya, D.G. *Bivalve Seashells of Western South America*; Santa
 Barbara Museum of Natural History: Santa Barbara, California, 2020.

Figure Captions

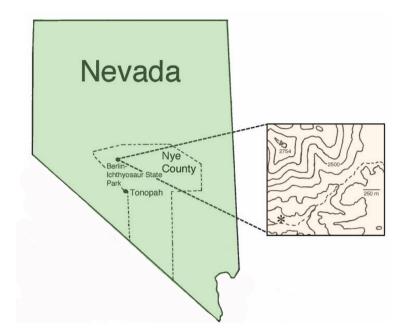


Figure 1. Field locality map, Union Canyon, Shoshone Range, Nevada. The asterisk on the inset map
denotes the nuculanoid fossil bivalve locality. The dashed line on the inset map is the West Union
Canyon jeep trail (National Forest District Road 24), and the 2754 m peak is Buffalo Mountain.

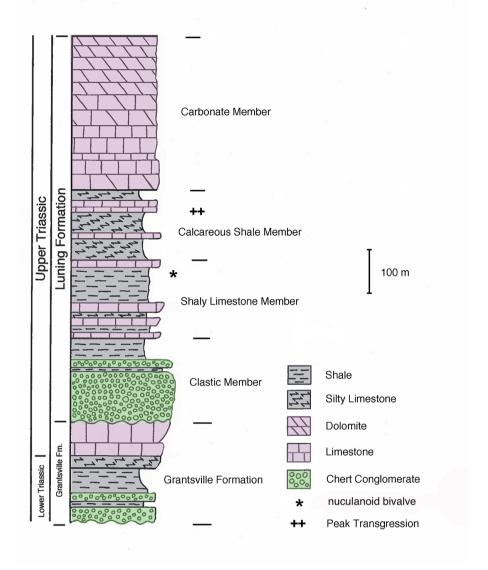


Figure 2. Stratigraphy of the Luning and Grantsville Formations, west central Nevada. Double plus sign (++) represents the point of maximum transgression during the deposition of the Luning Formation; asterisk indicates the fossil horizon. Strata in the formation deposited above this point are part of a shoaling upward interval; strata deposited below this point are part of a deepening upward interval.



216 Figure 3. Nuculanoid clam fossil (IGM 5010). Exterior view of subtrigonal right valve, preserved by

silicification. Scale bar = 1 mm.

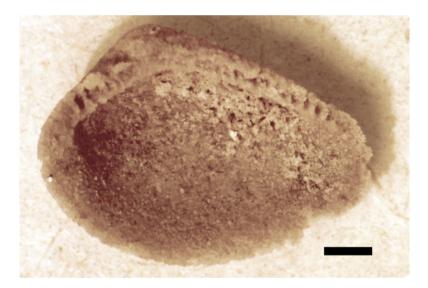
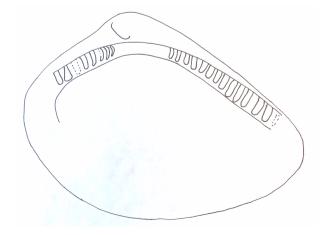


Figure 4. Nuculanoid clam fossil (IGM 5010). Interior view of right valve, showing taxodont dentition.

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- Figure 5. Nuculanoid clam fossil (IGM 5010). Line art sketch of interior view of right valve, showing
- wide hinge plate and taxodont dentition.