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Journal

PaleoBios, 41(1)

ISSN

0031-0298

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Publication Date

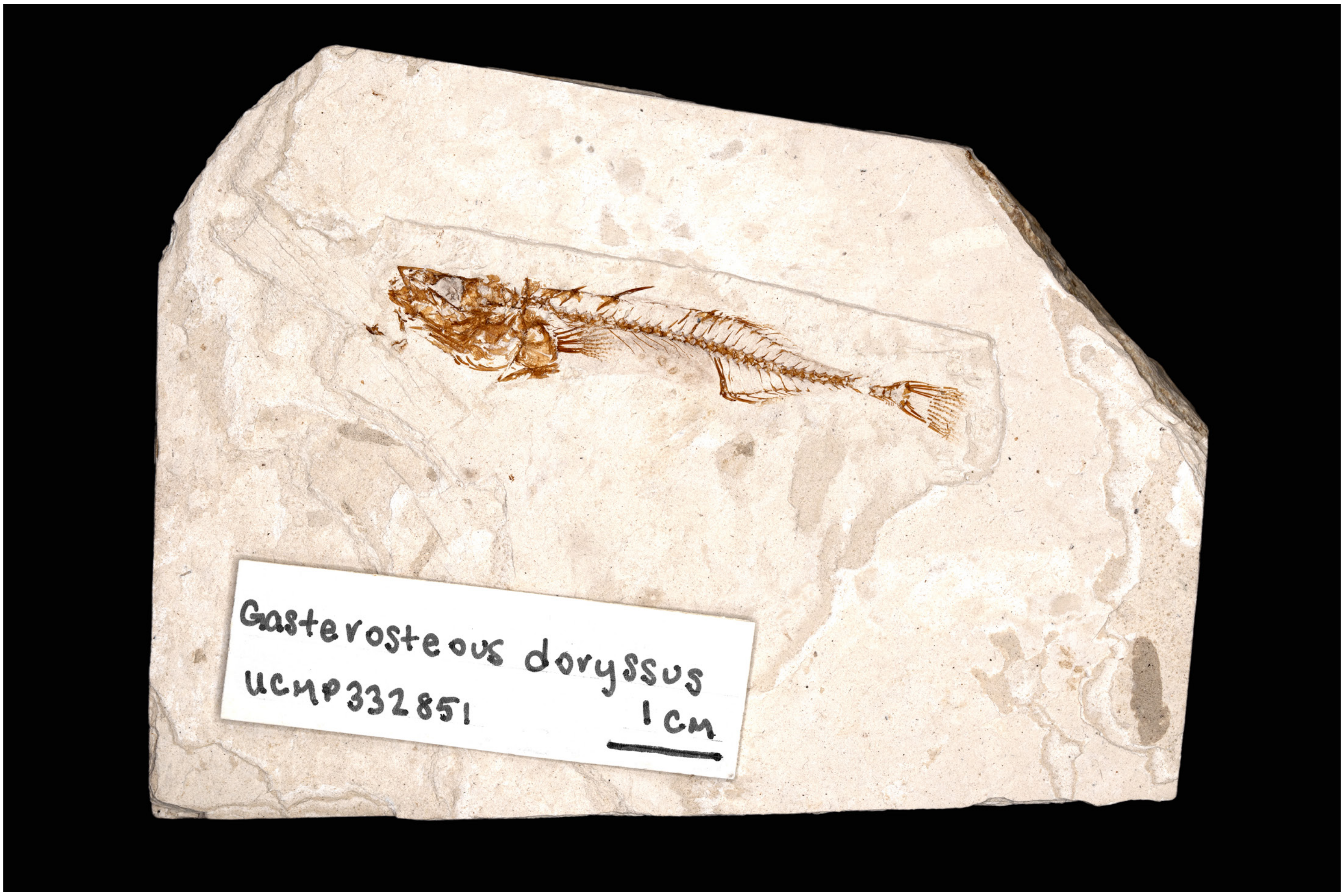
2024

DOI

10.5070/P941161500

PaleoBios

OFFICIAL PUBLICATION OF THE UNIVERSITY OF CALIFORNIA MUSEUM OF PALEONTOLOGY



Jacopo N. CERASONI, Michael A. BELL and Yoel E. STUART (2024).

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Cover: UCMP 332851, one of the thousands of Miocene *Gasterosteus doryssus* preserved in extraordinary detail in the diatomite deposits of the Truckee Formation

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DOI: https://doi.org/10.5070/P941161500

Geology, microstratigraphy, and paleontology of Truckee Formation lacustrine diatomite deposits near Hazen, Nevada, USA, with emphasis on fossil stickleback fish

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Varved lacustrine diatomite deposits of the Truckee Formation near Hazen, Nevada, are of Miocene age (*ca.* 10.3 million years old). They are exposed in several commercial mines and have been a productive source of stickleback fish fossils (*Gasterosteus doryssus*) spanning over 100,000 years of deposition. The evolutionary sequence of *G. doryssus* has revealed stasis, rapid morphological change, genetic evolution, and local extinction against a background of changing diatom communities and lake environments. Here, we draw on published geological, paleolimnological, and vertebrate paleontological data to summarize the geographic and paleontological context of the Hazen diatomite deposits. We include a geomorphological map of the study region as well as a stratigraphic section from a key stickleback quarry describing lithology and specimen frequency at 1 mm and 1 cm resolutions, respectively. This paper should help researchers identify patterns in the distribution of fossil sites on the landscape and better understand the geological processes that have shaped the area, spurring new sampling and future research.

Keywords: Miocene, Paleobiology, Geomorphology, Phytoliths, *Gasterosteus, Fundulus*

INTRODUCTION

Diatomite is a sedimentary rock composed mostly of silicious frustules (shells) of aquatic unicellular algae called diatoms (Dodd 1987; Dejardin 2014; Bradley 2015). Diatom shells accumulate on ocean and lake bottoms after death. Diatomite deposits can therefore reveal long, uninterrupted geological records of ancient aquatic ecosystems with high resolution (Schindel 1982). The Hazen diatomite deposits, located in west central Nevada near the towns of Hazen and Fernley, are one such accumulation. They are estimated to be up to 90 m thick and cover an area of approximately 39 km^2 (Houseman 2004). They are located within the Lahontan Basin, which contained both the Miocene Lake Truckee (Krebs et al. 1987; Cousens et al. 2011; Cohen et al. 2013) and the Pleistocene Lake Lahontan.

Diatomite is often composed of continuously deposited, layered couplets (i.e., varves) formed from diatom shells laid down during the growing season alternating with dark silt deposited between growing seasons. In the Hazen deposit described here, these couplets form annual layers that are about 0.3 mm thick, usually undisturbed by burrowing organisms (i.e., bioturbation) or turbulence. Thus, varves allow the conversion of stratigraphic distance to years (Bell et al. 2006a), resolving specimen time of deposition to as fine as single years (Bell et al. 1987, 1989).

Hazen diatomite has been mined since the early 1900s for industrial applications including filter media, insulation, fire retardant, filler, and abrasives (Houseman 2004). The Hazen mines are notable to paleobiologists because commercial diatomite mining in multiple quarries has

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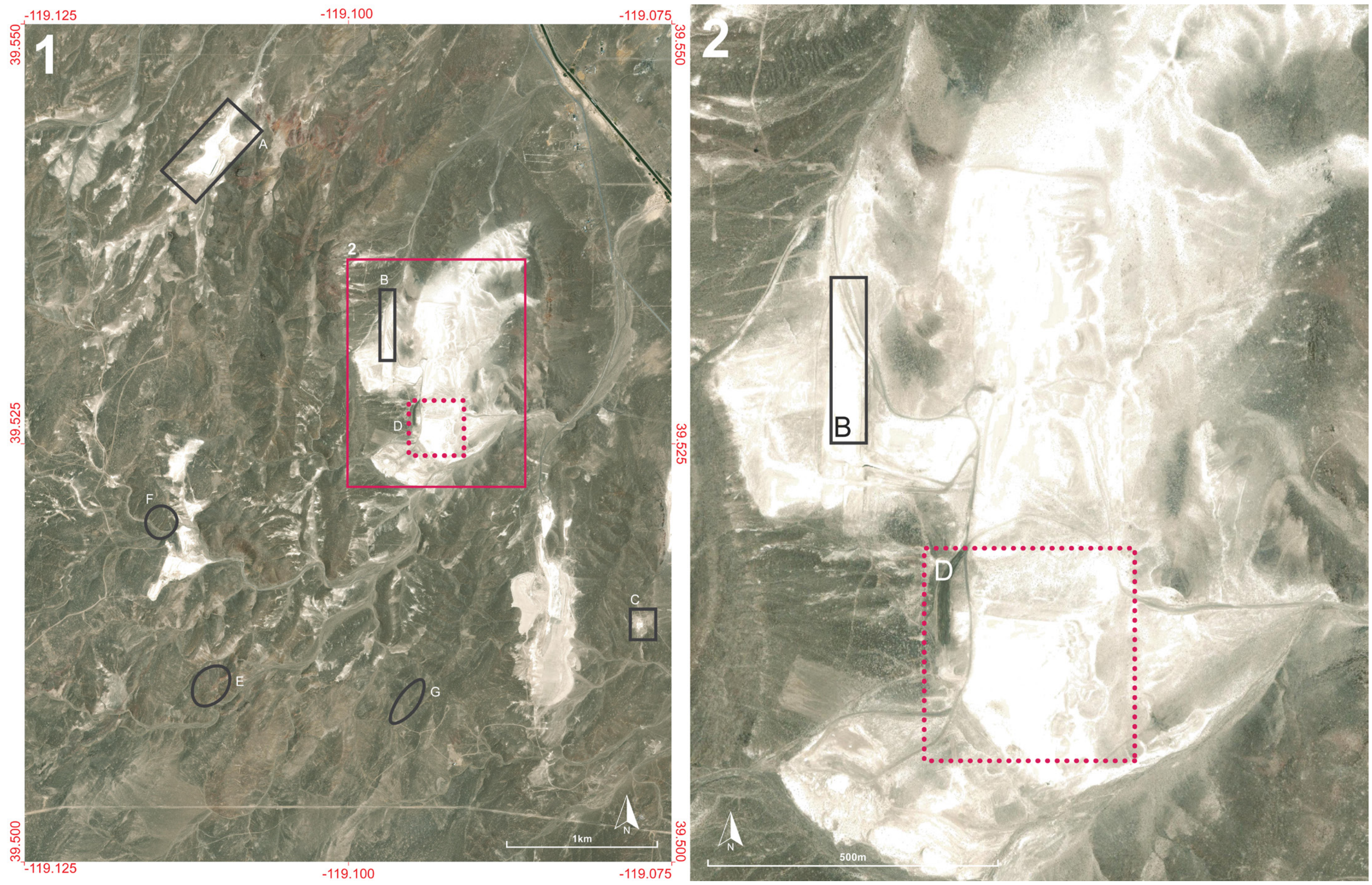

Figure 1. Satellite images of the area southwest of Hazen, Nevada (Imagery from July 2023, Google Earth): Panel 1. Quarries A-G (Table 1 for central coordinates). Note that previously reported coordinates of Quarries A-D were visually confirmed against satellite imagery. Quarries E-G could not be confirmed via satellite imagery and are based solely on Brown (1987). The solid-lined red rectangle shows the coverage of panel two. Panel 2. Enlargement of the area around quarries B (black solid line) and D (red dotted line).

exposed six sections (here called A-F; Table 1) containing well preserved fossil vertebrates, including a sequence of a fossil stickleback fish, *Gasterosteus doryssus* (Table 2). A seventh quarry, G, contains stickleback but was naturally exposed. The stickleback are abundant, well-preserved, and nearly continuously distributed throughout most sections in multiple quarries (Appendix; Table 2). In particular, more than 108,000 years of stickleback deposition is exposed within Quarry D, where stickleback have been studied since 1974 (reviewed in Bell 2009). These works revealed long-term evolutionary stasis and change (Bell et al. 1985), evidence of directional natural selection (Hunt et al. 2008), allometric evolution (Voje et al. 2022), and the genetics of adaptation (Stuart et al. 2020), all within the context of a changing paleoecology (Purnell et al. 2007; Dejardin 2014; Cerasoni et al. 2023). The fossil series is the focus of our ongoing studies on the evolution of reproductive isolation, sexual dimorphism, adaptive walks, ecological change, and the tempo and mode of evolution.

Table 1. Central coordinates for quarries (A-G) at Hazen diatomite deposits derived from reports (Brown 1987; Houseman 2004) and field triangulation using a USGS Two Tips, Nev. 1957 topographic map. All coordinates were recorded using map datum WGS84.

Quarry	Latitude	Longitude
A	39.564	-119.112
B	39.520	-119.100
C	39.515	-119.077
D	39.526	-119.098
E	39.507	-119.115
F	39.514	-119.120
G	39.507	-119.096

In this paper, we present a geomorphological map (Appendix), document the approximate locations and

Figure 2. : Weathered landscape in Quarry D, facing south-southeast. The light surface is entirely weathered diatomite. The dark colored hill is the background is approximately 300 meters distant. Photograph taken by JNC.

relative ages of quarries, and review previous research on fossil vertebrates from the Hazen diatomite quarries within the Middle Member of the Truckee Formation (Axelrod 1957; Houseman 2004) (Figs. 1-4). The main sections of the map are 1) political and topographical information; 2) geology, including geomorphological, paleolimnological, and elevation data, as well as human structures (e.g., roads, canals, etc.); 3) stratigraphy of Pit L in Quarry D, the upper section of Quarry D with the most dynamic stickleback change (Bell et al. 2006a; Hunt et al. 2008) (Figure 5, Figure 6, full map in Appendix). The literature review includes observations on the geographic locations of Quarries D and E, a review of fossils from the quarries, and observations on taphonomic and paleoenvironmental conditions of the stickleback fossil assemblages.

MATERIALS AND METHODS

We compiled information from MAB's field notes and field stratigraphic measurements, as well as geological studies and maps (Brown 1987; Houseman 2004; NBMG Open Data, 2023; OpenStreetMap, 2023; USGS, 2023).

Geomorphological Map

The full map is available in the Appendix and is a combination of the geomorphological map of the local region (Fig. 5) and the stratigraphical section for Pit L in Quarry (Fig. 6).

To produce the geomorphological map we used QGIS 3.22.16 (2023) to generate a low-resolution regional map with data from Nevada Bureau of Mines and Geology (NBMG Open Data 2023) and USGS databases (USGS 2023). Then we built a contour map extrapolated from USGS Eros data (1:250000 scale) with the QGIS contour extraction function. We extrapolated the geolocated boundaries of the quarries from Figure 2 of Houseman (2004) to generate a high-resolution geomorphological map for Quarries A-G (Fig. 5; Appendix).

We exported the map from QGIS as a georeferenced pdf file into Adobe Illustrator 2023. Using the Esri ArcGIS Maps for Adobe Creative Cloud workspace extension (accessed July 2023), we added human structures, political units, and other features (*e.g.*, roads, canals, county boundaries, water bodies) with data from OpenStreetMap (2023). The state-wide and study-area maps were created using ArcGIS Maps for Adobe Creative Cloud on Adobe Illustrator 2023. Esri Natural Earth (accessed July 2023) base vectors were used for both maps.

The photograph of the *Gasterosteus doryssus* specimen in the main map was taken by JNC using a Sony Alpha 7 IV camera and a Sony macro lens FE 90mm f/2.8-22 Macro G OSS (SEL90M28G). The image was post-processed in Adobe Photoshop 2023 using a healing brush tool to remove the sample identification numbers. The image of the fossil was not otherwise modified or manipulated.

Figure 3. Quarry B, facing north-northeast and showing dark layers of volcanic ashes in the upper portion of the stratigraphy. Photograph taken by MAB.

Quarry Coordinate Locations

The geographic locations for quarries A through F were determined during a field survey by MAB and T. R. Haglund in 1978 and reported by Bell et al. (1985, 1987, 1989) and Bell (1994, 2009) based on estimates by Haglund using triangulation with a Brunton Pocket Transit and a paper copy of the USGS Two Tips, Nevada, 1957 topographic map (Haglund, pers. comm. to MAB). Using the same methods F. H. Brown replicated Haglund's estimates and concluded that Haglund erred in coordinates for E and F (Brown, pers. comm. to MAB). Brown reported new coordinates for E and F, as well as coordinates for a new quarry, G (Brown 1987). In 2006, M. D. Shapiro used a GPS device to estimate the location of Pit L in Quarry D, and these coordinates were reported in Bell et al. 2006a and subsequent papers.

We attempted to vet Brown's coordinates by comparing them against satellite imagery to visually confirm that the coordinates were centered in quarries. Inspection of modern satellite imagery (Figure 1) revealed that quarries A through D were indeed close to white areas indicative of open surface mining, and we further confirmed them by reference to the topography, roads, and the shapes of the mined areas. The quarries assigned to A through D in figures 1 and 5 and the appendix as well as the coordinates given in Table 1 are based on this visual confirmation of quarry locations. Quarries E, F, and G could not be verified via satellite, and so locations estimated by Brown (1987) are presented (Table 1).

Quarry D, Pit L Stratigraphy

We used published information and MAB's original field notes and stratigraphic records (Bell et al., 2006a; 2009) to record geographic location and build the stratigraphic section for Pit L in Quarry D (Fig. 6; Appendix). We relied on field measurements tied to field excavated lithological sections to avoid stratigraphical repetition and inversion. These records are available as metadata associated with collections of *Gasterosteus doryssus* in the University of California Museum of Paleontology

Figure 4. A sampling pit in Quarry D (photograph taken by MAB).

(UCMP). The section starts from the upper measured surface (youngest; 0 cm), to the lowest and oldest layer (850 cm). The stratigraphic section includes lithology (rock type), which comprised mostly diatomite interrupted by thin to moderately thick (<3 mm) layers of ashes (crystalline and glassy) and mudstone (Figure 6). The stratigraphic section also includes a histogram with specimen counts for *G. doryssus* at a resolution of 1 mm (~2.9 years/mm based on varve counts). Finally, the star in the stratigraphy indicates the horizon where the low-armored stickleback that had dominated during the first ~93,000 years of quarry D was replaced by a high-armored form (Bell et al. 1985, 2006a; Bell 2009). This is associated with a temporary increase in lake level (Houseman 2004; Bell 2009; Dejardin 2014), with a subsequent water level reduction that was that associated with subsequent reduction in armor (Bell et al. 2006a; Hunt et al. 2008; Stuart et al. 2020).

Institutional abbreviations

LUC–Loyola University Chicago, Illinois; **UNMSM**–University of Nevada, Mackay School of Mines, Reno, Nevada; **UCMP**–University of California Museum of Paleontology, Berkeley, California; **UMMP**–Univesity of Michigan Museum of Paleontology, Ann Arbor, Michigan.

RESULTS

The main map (Appendix) shows the geomorphological context of the seven Hazen quarries (A-G; Figs. 2,4). The quarries are located on the eastern slope of the Virginia Range between about 1340 m and 1400 m elevation on the margin of the Lahontan Basin. The modern

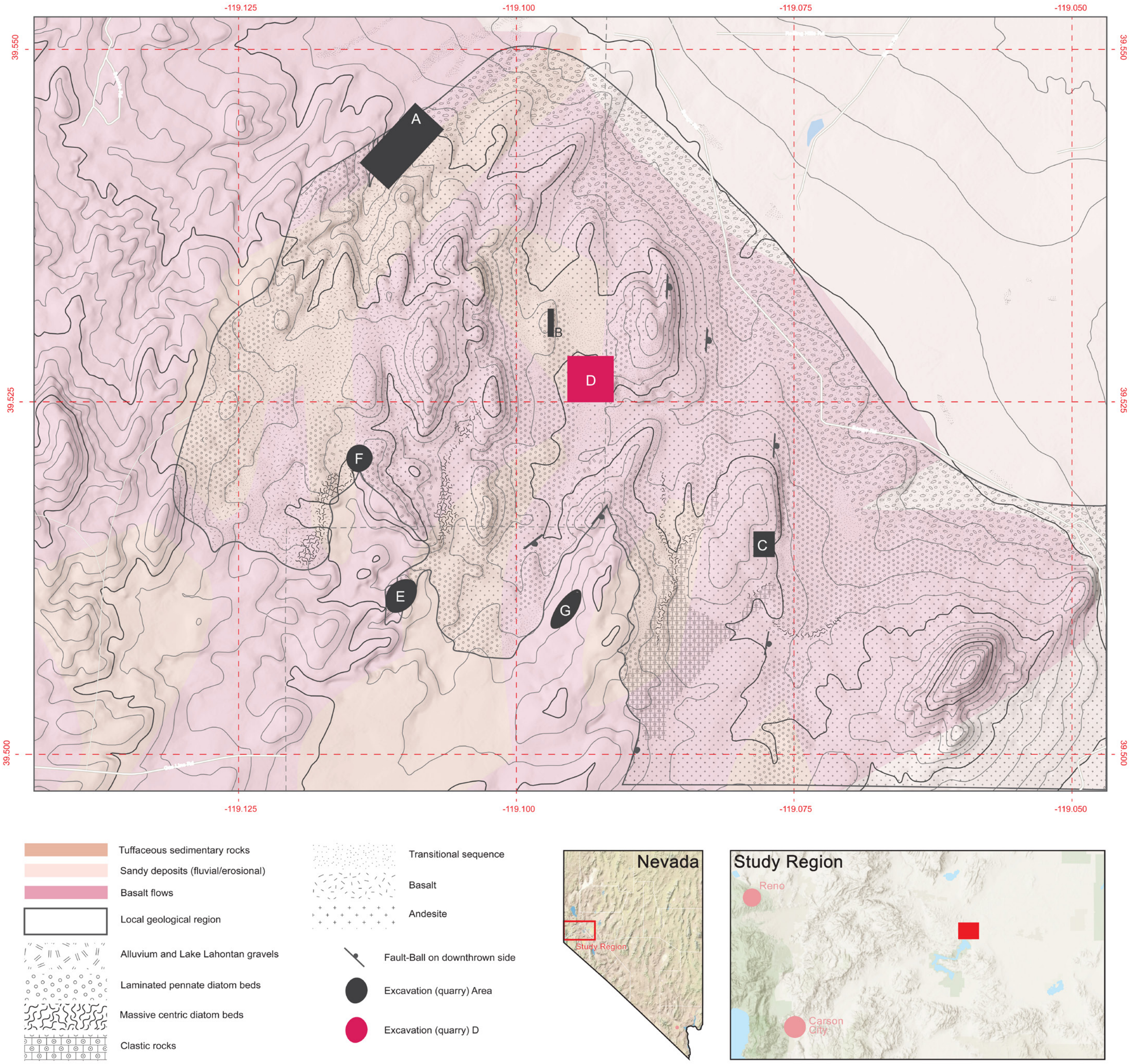

Figure 5. Geomorphological map of the Hazen diatomite deposits. Geomorphological zones were redrawn from from Houseman (2004, fig. 2).

landscape of the Lahontan Basin contains seasonally dry wetlands and deposits of Pleistocene Lake Lahontan (with which the Miocene Lake Truckee has sometimes been confused [La Rivers 1994]). Modern vegetation on the slopes of the Virginia Range is desert scrub (Olson et al. 2001). Riparian woodlands along the Truckee River to the west and the Truckee Canal to the northeast are dominated by cottonwood (*Populus fremonti*) and willows (*Salix* spp.).

Regional geology is characterized by a mix of sedimentary (centric and pennate diatomite, with rare gravels possibly transported into the lake), clastic (of both

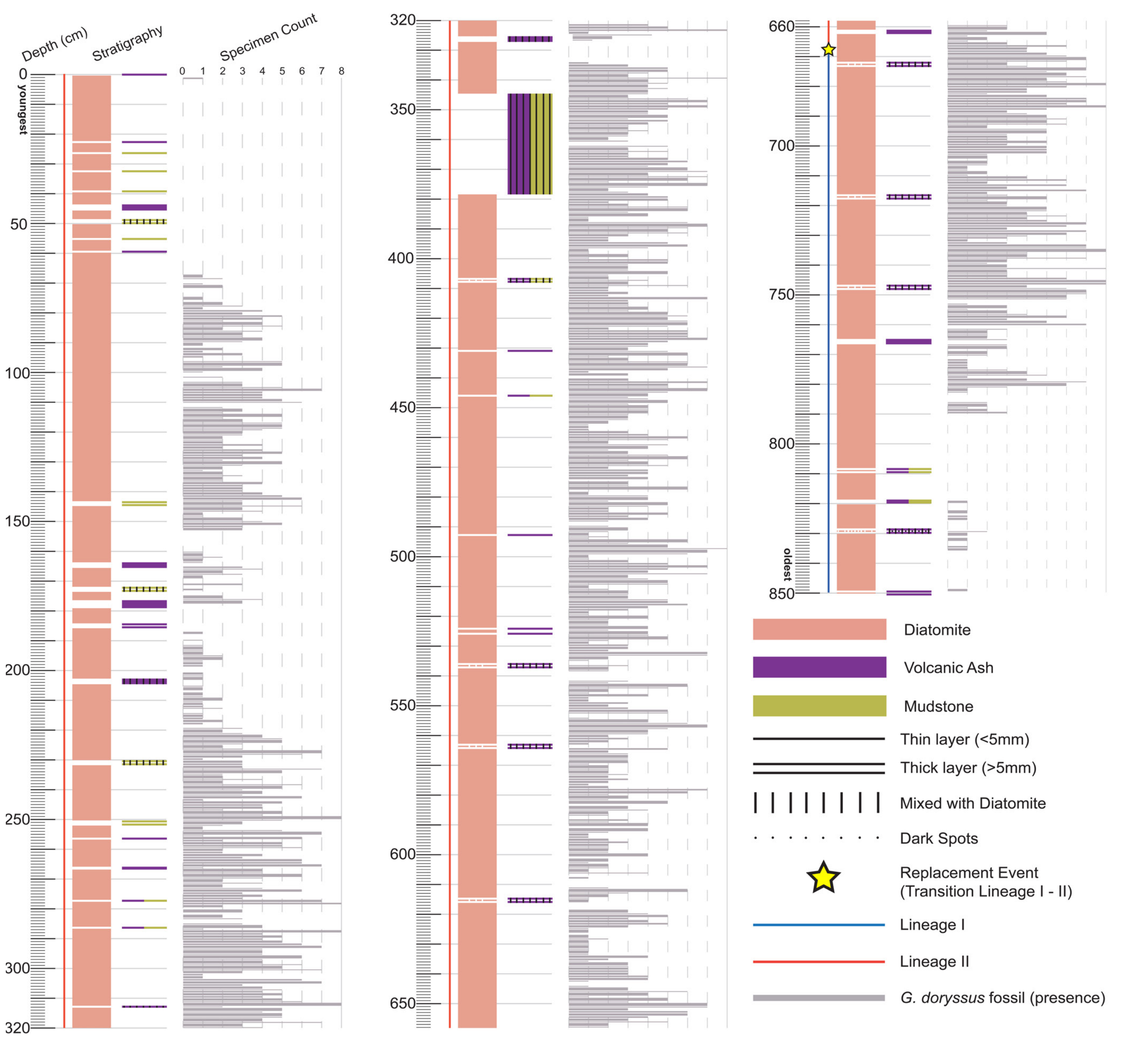

Figure 6: Stratigraphic section of Pit L in Quarry D, spanning 850 cm. Lithological types in the columns to the left are defined in the legend at lower right. Specimen counts of *Gasterosteus doryssus* fossils are shown in grey, with frequency counts at 1mm intervals. Stickleback are missing at the top of the section (~0.5-63cm) because they were replaced by killifish (*Fundulus nevadensis*).

volcanic and sedimentary origin), and volcanic (basalt, andesite) deposits (Stewart and Perkins 1999). The Hazen diatomite deposits are in a topographically complex basaltic setting, probably caused by the site's proximity to several volcanic centers (Stewart 1980; Jayko and Bursik 2011). These centers include the Virginia Range and the Stillwater Range to the east. Both ranges contain lava flows, ash deposits, and tuff. A series of faults formed among Miocene paleolake deposits within this area (Brown 1987; Houseman 2004), and between and within some of the quarries (Fig. 5). The tuffaceous and basaltic deposits shown in the regional map (Appendix) reveal faulting from volcanic activity.

The stratigraphy of Pit L (within Quarry D; Figs. 5 and 6) is consistent with continuous diatom-dominated sedimentation. Quarry D has a composite stratigraphical thickness of over 50 m (Brown 1987). Some of the other quarries contain part of the stratigraphic section present in Quarry D (Quarries A, C, E, and G; Fig. 7; Brown 1987), but differences exist between the fossil assemblages at each quarry. For example, many more fossil plants were retrieved from Quarry E, presumably a near-shore area of the Miocene paleolake Truckee (Bell 2009). The variation observable between quarries suggests that the deposits exposed in quarries A-G are limnetic. Analysis of the layers within Pit L reveals varves representing short chronological formation periods, likely yearly formation following springtime blooms of algal mats (Houseman 2004). These varved diatomite sequences are interrupted by sand-based, mud-based, and volcanic ash-based sediments, or a combination of them. Sometimes sediments are mixed with fossil diatoms.

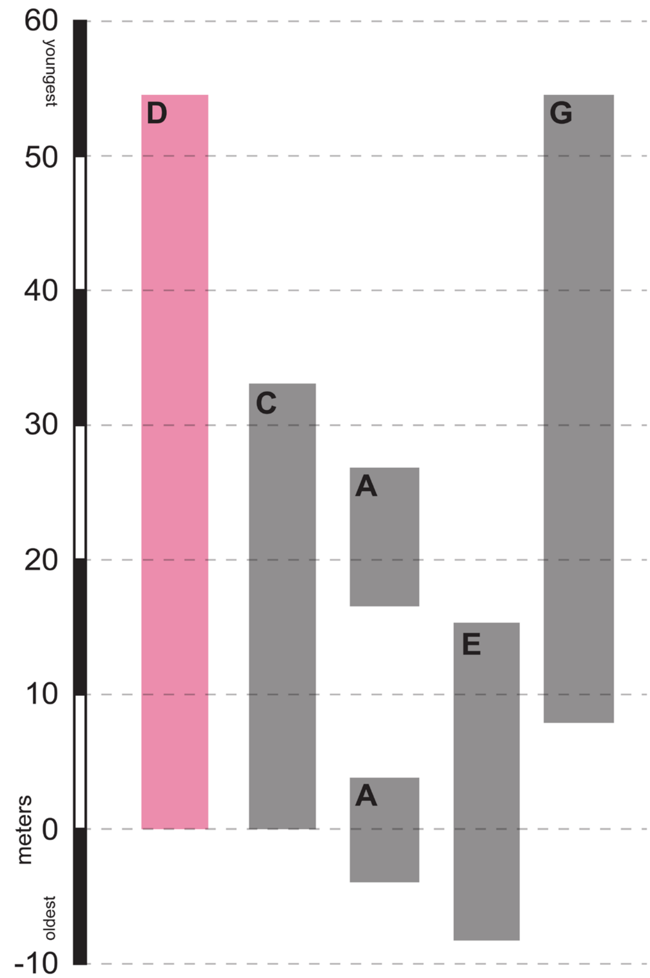

Figure 7: Proposed stratigraphic correlations between sections exposed in the Hazen diatomite quarries, redrawn from Brown (1987, fig. 4). Correlations are based on Brown's (1987, fig. 4) geochemical analyses of crystalline ashes. Note that the stratigraphic correlations of quarries E and G are based on geochemical analyses of crystalline ashes, which conflict with radio isotope dating that suggests that they are younger than Quarries D, C, and D (Brown 1987; Perkins et al. 1998; Houseman 2004).

Corrections and new interpretations for Quarries D and E

<u>Quarry D</u>

The coordinates for Quarry D were incorrectly estimated by T. R. Haglund in 1978 using triangulation. That is, the coordinates reported in Bell and Haglund (1982) were 30.52417 N Latitude and 119.01083 W Longitude. These were taken from MAB's field notes, and "30 N" must have been a typo in Bell and Haglund (1982). This mistake was repeated in Bell et al. (1985) but was subsequently corrected via GPS and reported in Bell et al. (2006a) and subsequent papers.

Coarse red-to-yellow crystalline ashes heterogeneous in particle size are common throughout Quarry D. These ashes are useful for radioisotope dating and stratigraphic correlation. They were probably deposited most often by airfall and then settled through the water column. They were not transported into the quarry by water and therefore should not be called sandstones. Rare grey to brown mudstones were presumably transported from igneous surfaces by streams (Houseman 2004).

<u>Quarry E</u>

The coordinates determined by T. R. Haglund in 1978 for Quarry E were also apparently incorrect (F. H. Brown, pers. comm. to MAB 1988). Haglund used Black Butte and other prominent topographic features and a Brunton Pocket Transit for triangulation and recorded the location of Quarry E on a hard copy of the 1957 USGS 1:62500 scale Two Tips, Nev. topographic map. In 1987, F. H. Brown repeated this procedure to estimate the location of Quarry E and marked his estimate of the location on the original paper map with an arrow from his to Haglund's location (Brown, 1987). We compared this marked map to the current digital map of the same area (USGS Hazen, NV 2014),to locate Quarry E and correct the coordinates (Table 1).

The diatomite in Quarry E is more friable (i.e., more prone to erosion and displacement), and the laminations are thicker than elsewhere. The grey glassy ashes are very thick, indicating nearshore deposition (M. D. Houseman, pers. comm.) because they combine both airfall and ash transported into the depositional environment from the adjacent land. This nearshore interpretation is supported by the presence of abundant plant fossils (Wilson 1980).

Fossil Vertebrates from the Hazen Quarries

Truckee Formation diatomites have produced only eleven vertebrate taxa, with stickleback and killifish being alternatively abundant and having complementary stratigraphic distributions. (Table 2). We know of one other fish taxon, possibly a cyprinid, that is not listed in Table 2 because those specimens have not been acquired from their owners. Six of the rarer taxa were found only from Quarry D, which is probably not due to depositional bias but to greater sampling effort (e.g., Bell and Haglund 1982, Bell et al. 1985; Bell et al. 2006a; Stuart et al. 2020).

Fishes

The stickleback, *Gasterosteus doryssus,* occurs in Quarries A-G and is usually abundant and well preserved (Fig. 8). Stratigraphically, it is almost continuously distributed through the sections in all but Quarry B, facilitating analyses of phenotypic evolution (i.e., Bell and Haglund 1982; Bell et al. 1985, 1987, 1989, 2006a, 2006b; Bell and Legendre 1987; Voje et al. 2022) and inference of ecological shifts (Purnell et al. 2007), natural selection (Hunt et al. 2008), and genetics (Stuart et al. 2020). Several dense samples of *G. doryssus* within single varves (i.e., mass mortality events) are comparable to samples from modern populations, enabling quantification of polymorphism and phenotypic variation within single generations (Bell et al. 1987, 1989). Analysis of phenotypic evolution at a time scale that is intermediate to that observable in typical fossil sequences and from extant populations is feasible (Schindel 1982).

La Rivers (1994) reported that Jordan (1907) incorrectly named the fossils that would come to be recognized as *Gasterosteus doryssus* as a new silverside (Atherinidae) genus and species, *Merriamella doryssa*. Jordan's type specimen came from excavations for the Truckee Canal, near Hazen, and though he dated it accurately, he mistakenly said that it came from Truckee, California, about 105 km to the west. A few weeks later, Hay (1907) described specimens from the same site as *G. williamsoni leptosomus*, a stickleback. From its lack of lateral armor plates, Hay inferred that it was related to the unarmored Threespine Stickleback, the nominal species *G. williamsoni*, from southern California. Jordan (1908) accepted that it was a *Gasterosteus* and properly applied his prior specific name, yielding *Gasterosteus doryssus* (Fig. 8). However, he also accepted Hay's (1907) incorrect inference that the specimen came from late Pleistocene Lahontan beds, which may overlay Truckee Formation deposits near Hazen. Bertin (1925) argued that all phenotypically diverse threespine stickleback species, including *G. williamsoni*, should be synonymized with *G. aculeatus* because differences among them were not heritable. Although his premise that none of their differences were heritable was false, it has become common practice to use *G. aculeatus* for phenotypically diverse populations. *G. doryssus* was

Figure 8. *Gasterosteus doryssus* fossil (UCMP 332916) from Pit L, Quarry D, within its original diatomite matrix. The head is to the left, and the eye is stained grey. Scale is 1 cm. This specimen has three dorsal spines and a full pelvis, structures that are sometimes lost entirely in *G. doryssus.*

already established, however, and the name has continued to be used. Because the pelvic skeleton is often but not always reduced in *G. doryssus* (e.g., Bell 1974, 1987; Bell et al. 1985; 2006a), Mural (1973) proposed that fossil specimens from the Middle Member of the Truckee Formation with a full pelvic skeleton be called *G. doryssus* and those with vestigial or no pelvic skeleton be assigned to a new species, *G. apodus*. Bell (1974) noted that pelvic structure in fossil samples of *G. doryssus* and within several extant populations of *G. aculeatus* (e.g., see Bell 1987; Bell and Ortí 1994) exhibits a wide range of variation from full expression to total absence and thus synonymized *G. apodus* with *G. doryssus*.

Other than *Gasterosteus doryssus,* the extinct Nevada Killifish, *Fundulus nevadensis,* has the greatest potential for evolutionary research because it is abundant and well preserved in long sections from quarries D and B. This species was first discovered near Hazen and described as *Parafundulus nevadensis* by Eastman (1917). Eastman erroneously reported it to be from the Pleistocene Lahontan beds. Subsequent authors have treated it as *Fundulus* (La Rivers 1994; Ghedotti and Davis 2017). In Quarry D, it occurs rarely for the first 115,000 years of the section, where *G. doryssus* is common. However, *G. doryssus* disappears suddenly near the top of the Quarry D section, and *F. nevadensis* simultaneously becomes common (MAB unpubl. data). Of 154 fishes collected by Bell and his collaborators in 1978 in Quarry B, which is apparently up section from Quarry D, only one was a *G. doryssus*, and all the others are *F. nevadensis*. Stickleback persisted but were in other quarries after it disappeared near the top of the section in Quarry D. *F. nevadensis* but not *G. doryssus* was also found during prospecting by MAB in diatomite exposed by a stream cut on the east side of Hazen.

Both *Gasterosteus doryssus* and *Fundulus nevadensis* belong to groups that usually are restricted to coastal lowland regions and are absent from the Great Basin today. The Sierra Nevada range was lower in the late Miocene, and drainages in west-central Nevada drained into the Pacific Ocean when the Truckee Formation was deposited (Axelrod 1957, 1962; Bell 1974). The

Table 2. Fossil vertebrate specimens specimens from the Hazen Quarries, Middle Member of the Truckee Formation. See Figure 2 for quarry locations. Locality and specimen numbers for rare specimens are also included (University of California Museum of Paleontology [UCMP], Loyola University Chicago [LUC], University of Michigan Museum of Paleontology [UMMP], University of Nevada Mackay School of Mines [UNMSM]) for rare specimens..

Taxon	Common Name	Quarry and locality numbers	Specimen number
Gasterosteus doryssus	Threespine Stickleback	A,C,D (UCMP V19019), E	
Fundulus nevadensis	Nevada Killifish	B, D (UCMP V19019)	
Oncorhynchus belli	Cutthroat Trout	D	UMMP V74362
Ameiurus hazenensis	Catfish	E	UMMP V74320
Anura	Frog	D (UCMP V19019)	UCMP 298000
Coluber sp.	Snake	Unknown	UNMSM 0001
Serpentes	Snake	D (UCMP V19019)	UCMP 297999
Sciurus olsoni	Tree Squirrel	A	UMMP 74776
Podicipedidae sp. A	Grebe	D	UMMP 74784
Podicipedidae sp. B	Grebe	D	UMMP 115962
Passeriformes	Perching bird	D	

ancestors of these two fish species probably entered the region from the Pacific coast of North America and went extinct as the Sierra Nevada rose and the Great Basin became drier (Bell 1974). The Lake Truckee basin was also entered by ancestors of *Ameiurus h*azenensis from the Mississippi River basin (see below). However, extant *Gasterosteus* and *Fundulus* species do not occur in the upper reaches of the Mississippi basin (NatureServe 2010) and probably entered from the Pacific.

Two specimens of *Oncorhynchus belli,* a type of Cutthroat Trout (UMMP V74362), were found in the upper part of the Quarry D section (Stearley and Smith 2016). Extant Cutthroat Trout prey on *Gasterosteus aculeatus*, and their predation selects for robust armor (e.g., Hagen and Gilbertson 1972; Reimchen 1994, 1995). However, only two fossil trout were found in Quarry D while thousands of fossil stickleback were collected, and the scales of one of those trout specimens formed intact rows that were displaced from the skeleton, suggesting that the fish was bloated and could have floated a long distance. Trout therefore do not appear to have lived in high abundance in the open water depositional environment of Quarry D or did live in the open water but were much less likely to be preserved for an unknown reason.

Ameiurus hazenensis (Baumgartner 1982; originally described as *Ictalurus hazenensis*) is an extinct bullhead catfish. The holotype was found near Quarry E, apparently a nearshore depositional environment (Bell 2009, see above). Some extant *Ameiurus* species eat fishes (Moyle 2002), and *A. hazenensis* may have consumed *Gasterosteus doryssus*. Stickleback from Quarry E are relatively highly armored compared to *G. doryssus* from the other quarries (e.g., Quarry D) but weakly armored compared to most extant, freshwater *G. aculeatus* populations (e.g., Hagen and Gilbertson 1972; Reimchen 1994).

Occurrence of *Ameiurus hazenensis* in the Truckee Formation has biogeographic implications. The extinct *A. vespertinus* from Oregon and Idaho is the only other bullhead species known from west of the Rocky Mountains. If *A. hazenensis* and *A. vespertinus* are sister species, as Baumgartner (1982) proposed, their common ancestor likely entered the Great Basin by crossing the continental divide north of the present Colorado Plateau, when drainages in Idaho and Nevada were connected, perhaps by the Missouri River system (Spencer et al. 2008).

<u>Amphibians</u>

A large, complete, and previously unreported anuran (UCMP 298000) was collected in the lower third of the section in Quarry D. It has long hind legs, seeming to exclude toads (Bufonidae) and is probably too large to be a treefrog (Hylidae), suggesting that it is a member of the genus *Rana*. The presence of a frog supports inferences from the diatoms that the depositional environment was not very saline (Houseman 2004; Dejardin 2014). Amphibian bones were also identified by D. B. Wake in a bird regurgitation from Quarry D (pers. comm. to MAB).

<u>Reptiles</u>

A snake assigned to the genus *Coluber* was reported from an Eagle Pitcher Mining Company quarry a few kilometers west of Quarry D in Lyon County near its eastern border with Churchill County (Ruben 1971), though its exact quarry is unknown to us. Quarry A is a nearby Eagle Pitcher mine, and it existed when this snake was collected, so perhaps Quarry A is the collection locality. This snake contained three fishes in its esophagus including at least one stickleback (Rubin 1971), indicating that it may have been a garter snake (*Thamnophis sp.*, Colubridae family) that choked on a stickleback. A small snake from Quarry D (UCMP 297999) is complete and well-preserved but has not been studied.

<u>Mammals</u>

The only mammal from these diatomite quarries, a tree squirrel from Quarry A, *Sciurus olsoni* (Emry et al. 2005), lost one front leg, one hind leg, and the tail before deposition. It has complete upper and lower dentition, and several teeth were removed from the skull for study. It was presumably transported into the lake from a forest habitat. It fills a chronological gap in the fossil record of North American tree squirrels between 5 and 15 million years ago. This remarkably long gap might reflect either lack of preservation or extinction of tree squirrels in North America for 10 My and recolonization from Asia. Phylogenetic analysis suggested that this time gap was due to lack of preservation (Mercer and Roth 2003), and occurrence of *S. olsoni* in the middle of the gap is consistent with this phylogenetic inference.

<u>Birds</u>

Bird fossils include nearly complete articulated skeletons, sets of articulated bones, and isolated bones and feathers. Nearly complete skeletons of two undescribed perching birds (Passeriformes) were collected by MAB from Quarry D and a graded area to its north. Two species of grebes (Podicipedidae), a piscivorous group, were described by Ksepka et al. (2013). Bone aggregations are commonly recovered in fossil samples and often contain rounded bones that appear to have been partially dissolved by stomach acid and may be bird regurgitations. These presumptive regurgitations contain stickleback spines. Presumptive regurgitations from samples from horizons with highly armored stickleback sometimes contain those spines, but such spines are absent in presumptive regurgitations from horizons in which intact stickleback have evolved loss of the two large dorsal spines and the two pelvic spines. This association suggests that temporal variation in articulated *Gasterosteus doryssus* represents variation over an area in which grebes foraged during a limited period of time.

Fossil Insects from the Hazen Quarries

Terrestrial insects are often abundant and well preserved in lake deposits (e.g., Wilson 1980; Grande 1984; Meyer and Smith 2008) but insects are nearly absent from Truckee Formation deposits. We have no clear explanation for the lack of insects. Further studies of nearshore deposits are necessary to better understand the observed lack of terrestrial insects at the site.

Fossil Diatoms, Plants and Paleolimnology

The diatomite deposits contain abundant diatoms, many of which are intact and can be identified to study paleolimnology (Houseman 2004; Dejardin 2014; Cerasoni et al. 2023). The composition and abundance of the diatomite community changes through time, indicative of changing atmospheric and environmental conditions. Based on fossil leaves and other flora from Quarry D, Axelrod (1948) inferred that at the time of the *Gasterosteus doryssus* deposition, summers were warm but rarely hot, and winters were mild with only occasional light frosts (Bell 1974). However, presence of very rare pieces of gravel in Quarry D suggests that ice formed near shore and rafted gravel into the lake. Axelrod also inferred that average annual rainfall was 38 to 40 cm, including some summer rain (Bell 1974). Plants are usually rare in Truckee Formation deposits (Fig. 6), though they are relatively abundant in Quarry E. Unusually thick volcanic ash layers at Quarry E may also indicate proximity to shore, as does dominance by planktonic diatom species that are more likely to be held in suspension by shoreline turbulence. Sediments in the other quarries, including D, apparently accumulated far from shore but in shallow water and consist mostly of benthic diatoms (Houseman 2004).

DISCUSSION

The Hazen diatomite quarries captured a rare deposit of tens of thousands of years of stickleback evolution on approximately annual time scales (Anderson and Dean, 1988; Bell et al. 2006a), allowing researchers to observe stasis and adaptation and to infer underlying ecological and genetic processes (Bell et al. 1985; Anderson and Dean 1988; Bell et al. 2006a, 2009; Purnell et al. 2007; Hunt et al. 2008; Dejardin 2014; Stuart et al. 2020; Voje et al. 2022). Why did stickleback preserve so well in this deposit? Benthic diatoms growing seasonally on the lakebed could have formed a thick, sticky, algal mat, protecting dead stickleback from scavengers, organic decomposition, and perturbation (Dodd 1987). Other studies suggest that benthic diatoms like those found in the depositional environment may form a biofilm with antibiotic properties, retarding decay and disarticulation (O'Brien et al. 2008). Potential sedimentological evidence for this phenomenon may include the alternating sediments in the stratigraphy where thick to medium-thick diatom rich deposits alternate with clay- and silt-rich deposits. This could be interpreted as annual recurring springtime bloom events, where thick algal mats formed with little to no incursion of terrestrial sediments.

Fossil stickleback from quarry D often show few signs of post-mortem taphonomic alteration. The most common post-mortem alterations include partial cranial and vertebral disarticulation, arguably caused by generation of gas within the cranial and abdominal cavities. Even during these events, the majority of skeletal remains appear to be undisturbed and close to other skeletal elements. Taphonomic studies are currently underway to better understand preservation of the stickleback in the Hazen diatomite beds. The same chronology used to study stickleback evolution (Bell et al. 1985, 2006; Hunt et al. 2008; Stuart et al. 2020; Voje et al. 2022) has also been used to study paleolimnological changes. Microfossil communities in the diatomite (diatoms, phytoliths, sponge spicules) have been analyzed for changes in richness and abundance (Dejardin 2014; Cerasoni et al. 2023); stable isotope ratios for carbon, nitrogen, and oxygen have also been measured (Dejardin 2014). Together, this evidence can reveal changes in lake level, temperature, salinity, and plankton community ecology on decadal time scales. Detailed palaeoecological studies including high-resolution microbotanical and isotopic reconstructions of the Hazen deposits are currently underway.

The Lahontan Basin can still be explored for more fossil-rich, lacustrine, Truckee Formation deposits. Mines are the easiest sites to sample. They are generally safe, but permission from landowners must be obtained. Transitional sequences between lacustrine diatomites and other lacustrine shales or fluvial deposits may produce other species or stickleback phenotypes. For example, Quarry E appears to be a near-shore deposit and revealed a catfish as well as stickleback that contrast morphologically with those from other sites that apparently formed farther from shore. Brown (1987) used geochemical properties of volcanic ashes to correlate between quarries, and radioisotope dating of some crystalline ashes can be used to estimate the absolute ages of quarries. The high quality, abundance, and frequently continuous stratigraphic occurrence of fossil stickleback, killifish, and diatoms over extended time intervals provide unusual opportunities to observe paleoecological and evolutionary phenomena that require fine temporal resolution but extend over thousands of years. Although the most reliably interesting sampling will involve abundant taxa, further sampling will continue to yield rare but interesting fossil specimens.

ACKNOWLEDGMENTS

We dedicate this paper to Dr. Francis H. Brown, who made major contributions to the quarry dating and stratigraphic correlations published in this paper. This manuscript was funded in part by a National Science Foundation CAREER award to YES (EAR 2145830). No potential conflicts of interest exist for the authors. We thank T. R. Haglund and J. V. Baumgartner for helping MAB sampled all of the quarries (i.e., A to E) that were accessible within a few kilometers of Hazen in 1978. We also thank W. J. Caldecutt for help collecting and preparing lithological samples from the Pit L stratigraphic sequence and N. Tousley for compiling the first draft of the stratigraphic section. We also thank Sidney Ryan for preparing and photographing the fossil used as cover image. Numerous Earthwatch and undergraduate assistants helped collect fossils and counted varves in the lab.

AUTHOR CONTRIBUTIONS

This study was designed by JNC. Cartography and stratigraphy were developed by JNC. MAB contributed field notes and a rough draft of the stratigraphic sequence. The initial draft was written by JNC, and all authors contributed to the writing and revision of the paper.

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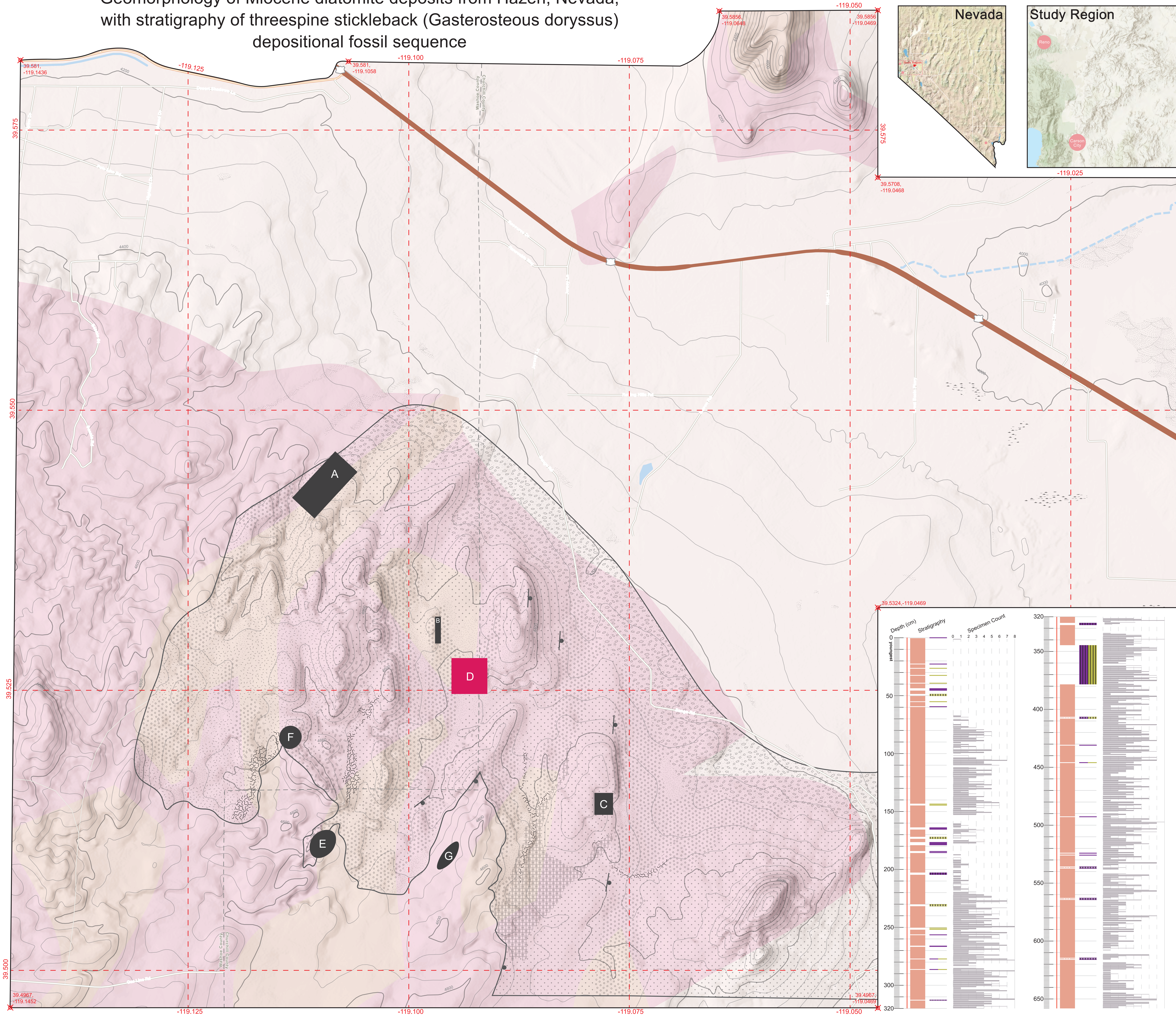
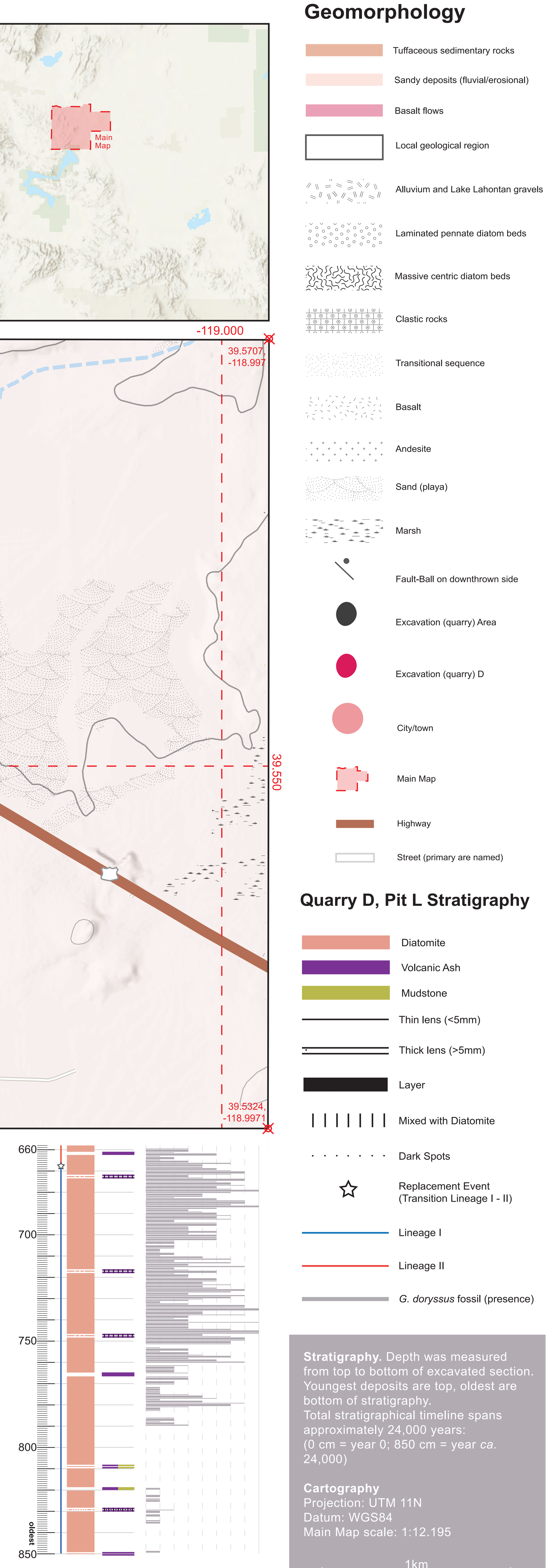
Geomorphology of Miocene diatomite deposits from Hazen, Nevada, with stratigraphy of threespine stickleback (Gasterosteous doryssus) depositional fossil sequence

Gasterosteus doryssus fossil

Example of *G. doryssus* fossil within its original diatomite matrix.

Note: The image was post-processed with ©Adobe Photoshop 2023 (tool - healing brush) to remove sample identification numbers. The fossil was not modified nor manipulated.

Stratigraphy. Depth was measured from top to bottom of excavated section. Youngest deposits are top, oldest are bottom of stratigraphy. Total stratigraphical timeline spans approximately 24,000 years: (0 cm = year 0; 850 cm = year *ca.* 24,000)

Cartography
Projection: UTM 11N
Datum: WGS84
Main Map scale: 1:12.195

1km

N

Appendix to Cerasoni, J. N., Bell, M. A. and Stuart, Y. E. 2024. Geology, microstratigraphy, and paleontology of Truckee Formation lacustrine diatomite deposits near Hazen, Nevada, USA, with emphasis on fossil stickleback fish. PaleoBios 41(1): 1-15.

Funding: National Science Foundation - 'CAREER' Award (ID: 2145830) to Y.E.S.

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