A REVIEW OF CHAROPHYTES OF THE CLEVELAND-LLOYD DINOSAUR QUARRY AT JURASSIC NATIONAL MONUMENT IN THE UPPER PART OF THE MORRISON FORMATION (LATE JURASSIC), EMERY COUNTY, UTAH, USA

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Cover Photograph of the upper part of the Upper Jurassic Brushy Basin Member of the Morrison Formation from about 45 m south of the Cleveland-Lloyd Dinosaur Quarry. Photograph of Morrison Formation by Jonathan Warnock. Below photograph is the charophyte Aclistochara bransoni from the quarry. Left is apical view, center is lateral view, and right is basal view. See figure 3 more information.

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ABSTRACT

The Cleveland-Lloyd Dinosaur Quarry at Jurassic National Monument in central Utah has been extensively studied for nearly 80 years. During this time, studies have heavily focused on the taphonomy, depositional setting, and potential behavioral inferences of the most dominant vertebrate taxon at the quarry, *Allosaurus fragilis*. However, despite their importance for paleoecological interpretations, microfossils from the quarry, such as charophytes and ostracods, have been conspicuously absent from any detailed discussion in the literature. Here we present a review of the known taxa of charophytes from the Cleveland-Lloyd Dinosaur Quarry and test the variability of abundance and taphonomic conditions throughout the quarry deposit. Our results indicate that significant differences in charophyte abundances exist in the lower and upper parts of the quarry, and a wide variance of taphonomic conditions is present in charophyte gyrogonites in the uppermost contact with the overlying carbonate bed. These results support prior interpretations of the Cleveland-Lloyd Dinosaur Quarry as an ephemeral pond and bring further attention to the importance of microfossils in paleoecological reconstructions.

INTRODUCTION

The Cleveland-Lloyd Dinosaur Quarry (CLDQ) at Jurassic National Monument (JNM) is an Upper Jurassic Morrison Formation fossil locality in central Utah where over 10,000 dinosaur bones have been discovered since the 1920s, including over 70 individuals of 10 different genera of dinosaur (Gates, 2005). More than 70% of the vertebrate fossils discovered are attributed to the Late Jurassic theropod *Allosaurus fragilis* based on left femora, yielding a predator prey ratio of 3:1 (Madsen, 1976; Gates, 2005). Due to the abundance of *Allosaurus* the quarry has been extensively studied in regard to taphonomy and depositional environment (Stokes, 1985; Richmond and Morris, 1996; Bilbey, 1999; Gates, 2005; Hunt and others, 2006; Peterson and others, 2017; Warnock and others, 2018). Whereas the dinosaur remains have been the focus of much research, microfossils such as charophytes (freshwater algae) that are present in the same deposits as dinosaurs have received relatively little attention.

Charophyta, fresh-to-brackish water algae, are com-
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mon microfossils in the Morrison Formation and are regularly found associated with gastropods, ostracods, conchostracans, and dinosaurs. Due to their abundance and taxonomic similarities between extant and fossil taxa, they are of considerable interest for biostratigraphy and paleoecological inferences throughout the fossil record (e.g., Peck, 1937; Wood, 1950; Ross, 1960; Sohn and Peck, 1963; Schudack and others, 1998; Georgescu and Braun, 2006). Whereas charophytes have been found throughout the Morrison Formation, there have been relatively infrequent applications of charophytes in Jurassic paleoecologic studies (Peck, 1957; Bilbey, 1992; Schudack and others, 1998; Turner and Peterson, 2004; Martín-Closas and others, 2008).

Here we present a review of charophytes from the CLDQ at JNM and discuss the taxonomy and taphonomy of charophyte species microstratigraphically throughout the CLDQ bonebed. Two hypotheses are tested in this study: (1) differences exist between the charophyte taxa in the upper and lower parts of the bonebed assemblage, and (2) differences exist between the taphonomic conditions of charophytes within the upper 15 cm of mudstone below the mudstone/limestone contact of the upper CLDQ.

GEOLOGIC SETTING

The CLDQ is located 38 m above the base of the Brushy Basin Member of the Morrison Formation, which was deposited in the Late Jurassic epoch (Tithonian age) (Bilbey, 1992) (figures 1A and 1B). The Brushy Basin Member is characterized by fluvial mudstones, limestones, and channel sandstones (Kirkland and others, 2020) and measures approximately 100 m thick at JNM (Peterson and others, 2017). Furthermore, the climate is interpreted as being strongly seasonal, with monsoons alternated with periods of semi-aridity (e.g., Dodson and others, 1980; Hallam, 1993; Rees and others, 1999; Parrish and others, 2004; Sellwood and Valdes, 2008; Tanner and others, 2014). The bottom part of the quarry is a silty mudstone of variable thickness from several to tens of centimeters that quickly grades upward into a fossiliferous calcareous mudstone, similarly variable in thickness. Above the mudstone is a limestone.

Figure 1. (A) Location of the Cleveland-Lloyd Dinosaur Quarry in Jurassic National Monument, Emery County, Utah, USA, and (B) Stratigraphic placement of the Cleveland-Lloyd Dinosaur Quarry within the Brushy Basin Member of the Morrison Formation.
layer, which is capped with a volcanic ash bed (Bilbey, 1992; Gates, 2005). Microfossils such as charophyte gyrogonites preserve well within the smectite-rich mud and within the limestone unit (Bilbey, 1992).

METHODS

Sampling and Preparation

A total of 110 kg of bulk sediment was collected from the 1-m-thick bonebed. The sediment samples were collected from two sections (upper and lower 50 cm) to explore variation in charophyte floral assemblages throughout the unit.

All collected gyrogonites were obtained by a method of submerged disaggregation with gentle air agitation similar to previously utilized methods (e.g., Mckenna, 1962; Ward, 1981; Peterson and others, 2011, 2017). Sediment samples were placed in 23 x 43 cm (28 cm deep) plastic basins with 1 m of flexible perforated airline tubing coiled at the bottom. The tubing was connected to a double-output aquarium air pump (3.5 watt, 1200 cc air per minute output) placed outside of the basins. The resulting system produced gentle air-powered agitation in the basins to promote sediment disaggregation. Following disaggregation, sediments were rinsed through two 63-micron mesh sieves and left to air dry. Following drying, samples were collected under light microscopy and imaged with a Hitachi S-3000N Environmental Scanning Electron Microscope (SEM) under low vacuum pressure. Only specimens more than 50% complete were tabulated for taxonomic abundance. After tabulation, the results between the upper and lower quarry assemblages of charophytes were tested for statistical significance via the Chi-Square test (p >0.05).

Taphonomic Methods

Charophyte specimens were also analyzed for taphonomic condition in the upper 15 cm transitional zone of the bonebed along the contact of the overlying limestone unit. Samples consisted of a total of 3 kg of mudstone (1 kg from each interval) collected from the uppermost 0 to 5 cm below the limestone, 5 to 10 cm, and 10 to 15 cm below the contact, respectively. Charophyte gyrogonites were extracted, processed, and imaged through the methods outlined above. Specimens were graded based on the completeness of the gyrogonites, degree of fracturing, and degree of abrasion. A complete charophyte gyrogonite showing no discernable fractures or abrasion was scored as a 0, a fractured or weathered charophyte gyrogonite was scored as a 1, and a charophyte gyrogonite displaying both fractures and abrasion was scored as a 2 (figure 2). The tapho-

Figure 2. Taphonomic stages of charophyte gyrogonites. Stage 0 indicates a gyrogonite with no apparent fracture or abrasion, a Stage 1 indicates a gyrogonite displaying fracture or abrasion, and a Stage 2 indicates a gyrogonite displaying both fracture and abrasion.
nomic condition of gyrogonites from the lower 45 cm of the bonebed below the limestone contact was also noted for comparisons with the 15 cm transitional zone.

**RESULTS**

**Systematic Paleontology (Charophytes)**

Three distinct charophyte taxa (*Aclistochara bransoni*, *Latochara concinna*, and *Stellatochara obovata*) (figures 3A through 3I) were identified in the CLDQ mudstone (Bilbey, 1999). Charophytes specimens are housed in the Department of Geology at the University of Wisconsin Oshkosh.

- Phylum Charophyta Migula, 1897
  - Class Charophyceae Smith, 1938
  - Order Charales Lindley and Green, 1836
  - Family Characeae Gray, 1821
  - Subfamily Charoidae Migula, 1897
  - Genus *Aclistochara*
  - *Aclistochara bransoni* Peck, 1937
    (Figures 3A through 3C)

  The general shape of the gyrogonite is ovoid to ellipsoidal with a truncated apex. The spirals are smooth in form, varying from concave to gently convex. The apical opening is closed by the calcified tips of the spiral cells, which differs from charophytes within Porocharaceae where this region is open. The spirals turn on the truncate apex to form its outer rim, then bend down into a central perialpical depression, and finally turn sharply into the center of the summit and expand (Feist and others, 2005).

- Family Porocharaceae (Grambast, 1962)
  - Subfamily Stellatocharoidea (Grambast, 1962)
  - *Latochara concinna* (Peck, 1957)
    (Figures 3D through 3F)

  The general shape of *Latochara* varies from subglobular to ovoid. At the rim of the summit, the spiral cells level off, turn inward, and then turn abruptly upward into an almost vertical position to form a small pyramidal projection in the center of the summit (Feist and others, 2005).

- *Stellatochara obovata* (Peck, 1957)
  (Figures 3G through 3I)

  General shape of *Stellatochara* is usually ovoid, though occasionally ellipsoidal or subglobular. The genus is well characterized by its long apical elongated neck. The spiral cells progressively bend at the rim of the apex forming a wide apical neck that is less than one-third of the total gyrogonite length (Feist and others, 2005).

**Abundance and Taphonomic Analysis**

Over 128 specimens were identified in the upper mudstone, and 59 were identified in the lower (figures 4A through 4I, table 1). An additional 16 gyrogonites from the lower mudstone and 12 from the upper mudstone were collected but were unable to be identified taxonomically due to their fragmentary conditions. The difference in the abundances of gyrogonites between the upper and lower parts of the quarry assemblage was found to be statistically significant ($p < 0.03$).

Comparisons of taphonomic conditions of charophyte gyrogonites in the upper 15 cm of the bonebed along the contact with the overlying limestone revealed a wide variance of taphonomic states (figure 5, table 2). The difference in the variation of taphonomic conditions of gyrogonites in the upper 15 cm of the bonebed was not found to be statistically significant ($p < 0.5$).

**DISCUSSION**

Whereas the three identified taxa are also well known throughout the Morrison Formation, their variable and dynamic abundances have the potential to yield notable paleoecological interpretations. The three identified charophyte genera found in the CLDQ indicate still or slow-moving water with a neutral to sub-alkaline pH; *Aclistochara* and porocharaceans such as *Latochara* and *Stellatochara* suggest fresh-to-brackish and alkaline waters (Peck, 1957; Feist and others, 1991; Turner and Peterson, 2004; Martín-Closas and others, 2008; Benoit and others, 2017). These taxa fit with the
previous interpretation of fresh-to-brackish, sub-alkaline wetlands for the Morrison Formation (Turner and Peterson, 2004; Noto and Grossman, 2010).

The lower mudstone has fewer total charophytes, but a higher proportion are unidentifiable, fragmentary, and abraded gyrogonites relative to the upper mudstone. The relatively higher proportion of abrasion suggests the gyrogonites may represent an allochthonous/parautochthonous assemblage, perhaps introduced during periods of fluctuating water level (Gates, 2005; Peterson and others, 2017; Warnock and others, 2018). Alternatively, the upper mudstone has a considerably higher abundance of well-preserved gyrogonites, representing a more authochthonous assemblage and sug-
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Figure 4. Percent abundance of charophytes in the upper and lower 50 cm of the Cleveland-Lloyd Dinosaur Quarry.

Suggesting that the deposit was becoming a more stable and permanent body of water. The transition to a more permanent body of water is further supported by the freshwater limestone capping the mudstone unit, which also contains charophyte gyrogonites and ostracods. Turner and Peterson (2004) note that brackish, alkali and often ephemeral ponds and wetlands are not conducive to life beyond algae. This, coupled with presence of brackish-tolerant charophytes and the rarity of fish, turtle, and crocodilian fossils found in the Cleveland-Lloyd assemblage, supports the interpretation of the depositional setting as an ephemeral pond (Gates, 2005; Peterson and others, 2017; Warnock and others, 2018).

Furthermore, as with the results of this study, the brackish-tolerant A. bransoni is rarely in high abundance in the Morrison Formation, and Stellatochara and Latochara commonly occur together, but with abundances at odds with one another (Ross, 1960). Relative abundances and associations such as these may be due to taphonomic biases (i.e., transport), sampling biases, or differences in gyrogonites production. However, they may also suggest ecological controls on charophyte distributions, previously suggested by Wood (1950) where extant charophytes demonstrate similar relationships due to seasonal shoreline banding and restrictions to the margins of lakes. Such restriction of charophytes to the margins of lakes may explain the variable abundances of Porocharacean charophytes observed throughout the Cleveland-Lloyd deposit and strengthens interpretations of the deposit as an ephemeral pond (Gates, 2005; Peterson and others, 2017) that fluctuated with water level somewhat regularly with slow-moving waters present during a higher-level stage (Warnock and others, 2018). Furthermore, this result indicates that from a charophyte ecology standpoint, the CLDQ ephemeral pond did not stand out from most other Morrison Formation deposits in the Colorado Plateau. Significantly, this indicates that the environmental conditions important for charophyte ecology (i.e., salinity, pH, stillness of water column) were not different in the CLDQ pond relative to other Morrison Formation environments in the Colorado Plateau.

The variation in taphonomic condition among charophytes in the upper 15 cm of the bonebed is strongly correlated with intramatrix bone fragments observed throughout the quarry deposit (Peterson and others, 2017). The varying degree of abrasions observed in bone fragments has previously been suggested to be the result of fluctuations in water levels during the duration of the deposit accumulation; less-abraded fragments indicate recent breakage of dinosaur bones that had been subaerially exposed before burial in the Jurassic, whereas more abraded fragments represent the remains of bones that had gone through numerous reworking cycles (Peterson and others, 2017). Similarly, the charophyte gyrogonites extracted from the CLDQ show comparable variation in their degree of abrasion, suggesting that the more fractured and abraded specimens indicate periods of subaerial exposure and reworking prior to burial and incorporation into the more stable lacustrine system that is represented by the overlying limestone.

Table 1. Abundance of charophyte gyrogonites from the upper and lower 50 cm of the Cleveland-Lloyd Dinosaur Quarry.

<table>
<thead>
<tr>
<th></th>
<th>Upper (0–50 cm)</th>
<th>Lower (50–100 cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aclistochara bransoni</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Latochara concinna</td>
<td>70</td>
<td>28</td>
</tr>
<tr>
<td>Stellatochara obovata</td>
<td>55</td>
<td>28</td>
</tr>
<tr>
<td>Unidentified gyrogonites</td>
<td>12</td>
<td>16</td>
</tr>
</tbody>
</table>

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CONCLUSION

Microfossils such as charophytes and ostracods play an essential role in extant ecosystems. As such, a more robust understanding of their nature in the Morrison Formation can yield considerable information regarding this important and dynamic ancient ecosystem. Whereas the taxonomic composition of the charophyte assemblages do not significantly change in the upper and lower mudstones, the variability of charophyte abundance and preservation support interpretations of a highly dynamic depositional environment in the latest Jurassic of Utah, corroborating previous results (Peterson and others, 2017; Warnock and others, 2018). These observations help to characterize the depositional environment of the CLDQ, a necessary step for understanding its uniqueness and place in the Morrison ecosystem, while providing an ecological metric for comparison to other Morrison Formation deposits.

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