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NONMARINE BIVALVES FROM THE LOWER PERMIAN (WOLFCAMPIAN) OF THE CHAMA BASIN, NEW MEXICO

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ABSTRACT.—The Welles quarry is an Early Permian (Wolfcampian) vertebrate fossil locality developed in a pond deposit in the El Cobre Canyon Formation of the Cutler Group near Arroyo del Agua, Rio Arriba County, New Mexico. We describe an extensive assemblage of thin-shelled, freshwater bivalves from the quarry preserved as external and (rarely) internal casts. Typical preservation is with the paired valves wide open (~180°), the hinge intact, and exterior surfaces facing upward. The clams are equivalent, inequilateral, and elongate oval in shape. Ligaments are external and opistodetic, hinges are straight and edentate, and adductor muscle scars are absent or not preserved. Length ranges from ~1 to ~23 mm. Umbones are slightly inflated and located at ~0.25 of length from the anterior end. Ornamentation consists only of concentric growth ridges. Two variants, one with a rounded posterior end, and the other more blunt, may represent sexual dimorphs. Allometric height-to-length ratio (~0.45) and overall morphology are essentially identical to the Late Permian anthracosiid Palaeanodonta parallela (Amalitzky), known from South Africa and Russia. However, due to the large temporal and geographic range differences between P. parallela and the Welles quarry specimens, we provisionally assign them to P. cf. P. parallela. This is the first report of Palaeanodonta from the Permian of North America, a substantial extension of its stratigraphic range from the Middle Permian to nearly the base of the Permian and suggests that too little is known of late Paleozoic nonmarine bivalves for them to be of great biostratigraphic utility.

INTRODUCTION

In 1877, David Baldwin discovered fossil vertebrates in Lower Permian strata of the Cutler Group near Arroyo del Agua, Rio Arriba County, New Mexico. Subsequent collecting in the early part of the 20th Century, especially by field parties from the University of California at Berkeley, revealed numerous bonebeds southeast of Arroyo del Agua that are now among the classic Early Permian vertebrate fossil localities in North America (Langston, 1953; Romer, 1960; Berman, 1993). One of these localities is the Welles quarry (Fig. 1), a pond deposit that has produced fossils of fish (Xenacanthus and Progyrolepis), amphibians (Chenoprosopus, Eryops, Zatrachys and Platyzostrix) and stem reptiles and pelycosaurs (Diadectes, Sphenacodon and Ophiacodon). Sporic coprolites are common in the quarry and probably pertain to xenacanth chondrichthyans. The Welles quarry also yields an extensive assemblage of bivalves described here. In this article, NMMNH = New Mexico Museum of Natural History and Science, Albuquerque.

DESCRIPTION AND IDENTIFICATION

During the summer of 2002, we collected several hundred bivalves from the Welles quarry (NMMNH locality 4825). The clams are preserved as high-quality impressions and casts and are cataloged in the NMMNH collections (P-38771 through P-38790). The fossils frequently occur as isolated individuals but more often in clusters (Fig. 2A). Generally, the valves are attached at the external hinge and are wide open. A few individuals are preserved in dorsal view (Fig. 2C). Internal casts (steinkerns) have been prepared out of a few individuals that were preserved with their valves closed (Fig. 2D).

Shell fragments are rare, and when they do occur they are thin and poorly preserved. Internal shell characteristics such as the crossed lamellar structure seen in the Palaeomutelidae can be important diagnostic features (Silantiev, 1998) but are not available for examination in our sample. Considerable lateral compression of the fossils is evident and probably occurred during compaction of the muddy shale matrix. Many of the impressions show evidence of crushing before the dissolution of the shells (Fig. 2D). We believe that the width of the specimens has been artificially reduced, so we do not include it in the morphometrics. Two morphological variants are present. One morph shows a relatively blunt posterior (Fig. 2F) and probably represents the female form. The other more rounded-posterior morph (Fig. 2G) may represent the males, as in Recent freshwater clams (Johnson, 1947).

The Welles quarry bivalves correspond to the description, diagnoses and illustrations of Palaeanodonta parallela (Amalitzky) in the literature. Thus, they are equivalent, inequilateral and elongated, and they have parallel postero-dorsal and ventral margins, a vertical to slightly obliquely truncated posterior end, are unornamented, have umbones at ~0.25 of length, lack ornamentation except growth rings and have a hinge structure that is straight, edentate and opistodetic, with external ligament (cf. Amalitzky,
FIGURE 2. Selected specimens of *Palaeanodonta* cf. *P. parallela* from the Welles quarry. All scale bars are in mm. **A**, NMMNH P-38772, high density cluster of shells. **B**, NMMNH P-3878B, an individual bivalve in typical preservation aspect (approximately same scale as **F**). **C**, NMMNH P-38787, an individual preserved in dorsal view. **D**, NMMNH P-38789, an internal cast (steinkern). **E**, NMMNH P-38778, a rare internal mold showing the edentate hinge structure. **F**, NMMNH P-38785, an individual with the “blunt posterior” morphology, possibly the female form. **G**, NMMNH P-38781, an individual with the “rounded posterior” morphology, possibly the male form.
GROWTH

Growth of the Welles quarry clams was assessed by two methods: growth ring measurement, and statistical analysis by probability plotting (Fig. 4). Growth ring measurements of an individual are shown by the open squares in Figure 4A. These data form a straight line and do not show the approach to the growth asymptote because the individual was not large enough. On larger specimens, however, the small growth rings near the umbones are difficult to distinguish. So, we used a probability plotting method to resolve the size classes (~ yearly age groups) of the clam population.

In the probability plot (Fig. 4B) the lengths of 36 individuals are plotted against a Normal (Gaussian) cumulative probability scale. The filled circles (all data) show a multi-modal distribution of lengths as indicated by numerous concave-up-to-concave-down inflections (King, 1971; Peck, 1987). The component modes of this multi-modal distribution are resolved by separating the data at the inflection points and replotting them as distinct distributions (modes 1 through 8 in the plot). Straight line fits to these components show that they are normally distributed and that the modes have been correctly resolved.

The mean values of the resolved modes were then overplotted on the growth ring measurement curve (Fig. 4A). The probability plotting method agreed remarkably well with the growth ring data and retrieved two additional size classes that show the approach to the growth asymptote. The age of the largest individual (assumed to be at or near the asymptote) is somewhat arbitrarily assigned to 10 years, but could be higher.

Growth in the bivalves appears to fit the standard von Bertalanffy (1938) equation,

\[ L(t) = A_e \cdot (1 - e^{-kt}) \]

where \( L(t) \) is length as a function of time, \( A_e \) is the growth asymptote, \( k \) is the growth constant, and \( t \) is time in years. The small number of larger specimens leads to difficulty in accurate curve fitting, but at the level of confidence that we can achieve, we approximate \( A_e = 25 \text{ mm} \) and \( k \approx 0.1 \) to 0.15.

DISCUSSION

The order Unionoida, which encompasses most of the nonmarine bivalves, originated in the Devonian and persists today (Cox, 1969). Bivalves are long-lived and ecologically important elements of freshwater biological systems (Anthony and Downing, 1999). They compete with fish for food resources; they frequently constitute the bulk of biomass in streams and ponds, and are important prey species. Evidence exists that their current growth rates, production, and ecological position have been in place since at least the Triassic (Rinehart et al., 2002).

Late Paleozoic nonmarine bivalves, including the anthracosids, palaeomutelids, and some myalinids (brackish water) had a worldwide distribution. Examples include (but are not limited to): the Middle-Upper Permian Karoo Supergroup of southern Africa.
ACKNOWLEDGMENTS

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Gusev, A. K., 1990, Nomenclature of the Upper Permian (Tatarian) strata of the Oka-Volga River Basin of Russia: Gusev, 1990; Silantiev, 1998; and the Upper Carboniferous Coal Measures of northern France, England, and Ireland (Davies and Trueman, 1927; Eager, 1962). Additional assemblages are known from southern Asia (Rossouw, 1970) and South America (Simoes et al., 1998). The genus Palaeanodononta is known from the Middle or Late Permian of Antarctica, South Africa, Kenya, Russia, Burma and Siberia, among other places (Amalitzky, 1895; Bradshaw, 1984; Gusev, 1990). These are all records of Tatarian age, which is to say they are Capitanian to Changshingian on the marine timescale (Lucas, 2004) and thus much younger than the Welles quarry.

The Welles quarry bivalves are the first occurrence of Palaeanodononta in the North American Permian and they extend the temporal range of this genus back to the Early Permian. This substantial range extension suggests to us that the true distributions in time and space of all late Paleozoic freshwater bivalves are not well known. This should make us very cautious in using them for biostratigraphy.
population of Revueltean (Upper Triassic: Early-mid Norian) unionids from West Texas: Geological Society of America, Abstracts with Programs, v. 34, no. 6, p. 354.


