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2005, pp. 283-287. <https://doi.org/10.56577/FFC-56.283>

in:
Geology of the Chama Basin, Lucas, Spencer G.; Zeigler, Kate E.; Lueth, Virgil W.; Owen, Donald E.; [eds.], New Mexico Geological Society 56th Annual Fall Field Conference Guidebook, 456 p. <https://doi.org/10.56577/FFC-56>

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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 equivalved, inequilateral, and elongate oval in shape. Ligaments are external and opisthodontic, 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 *Palaeonodonta 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 *Palaeonodonta* 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 *Platyhystrix*) and stem reptiles and pelycosaurs (*Diadectes*, *Sphenacodon* and *Ophiacodon*). Spiriferiform 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 avail-

able 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 *Palaeonodonta parallela* (Amalitzky) in the literature. Thus, they are equivalved, 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 opisthodontic, with external ligament (cf. Amalitzky,

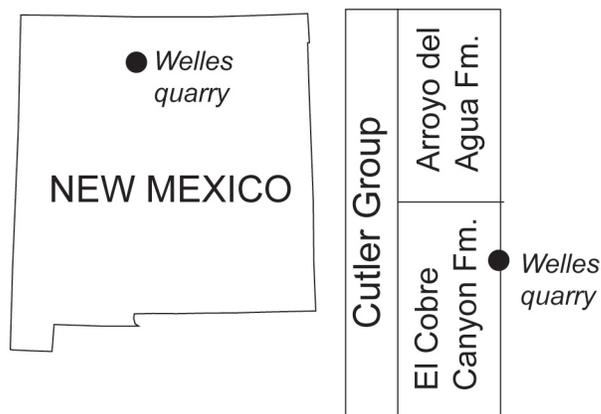


FIGURE 1. Index map and generalized stratigraphy showing location of Welles quarry.

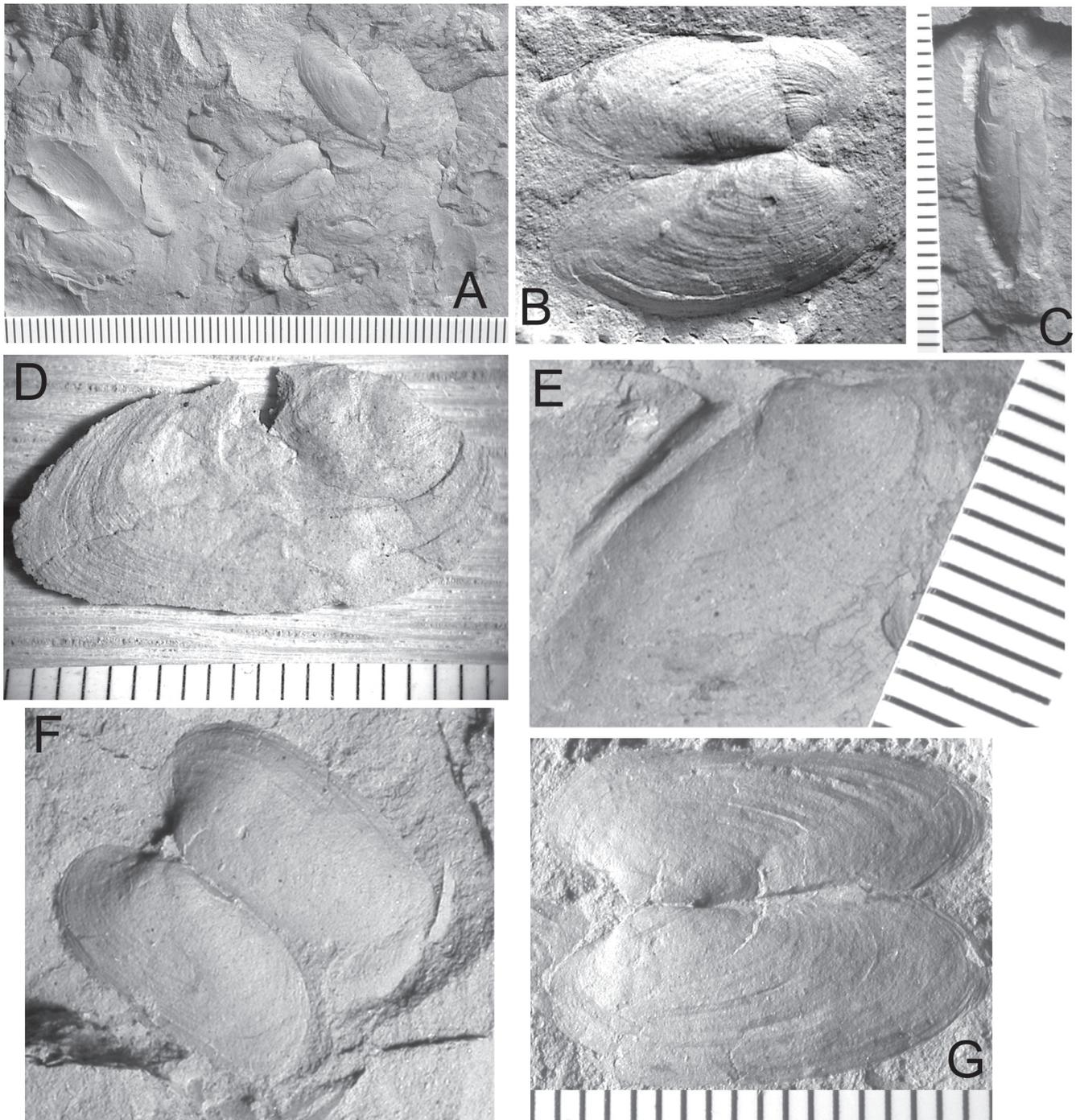


FIGURE 2. Selected specimens of *Palaeonodonta* cf. *P. parallela* from the Welles quarry. All scale bars are in mm. **A**, NMMNH P-38772, high density cluster of shells. **B**, NMMNH P-3878B, an individual bivalve in typical preservation aspect (approximately same scale as F). **C**, NMMNH P-38787, 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.

1895, pl. 13, figs. 5-6b; Cox, 1936, pl. 5, figs. 2-4; Papin and Doroshenko, 1974, fig. 1; Bradshaw, 1984, fig. 3; Gusev, 1990, p. 183, 188, pl. 9, figs. 21-23). The Welles quarry bivalves are readily distinguished from *Anthraconaia*, the genus of late Paleozoic freshwater bivalve most similar to *Palaeanodonta*, by the more pronounced umbones and the not-as-elongate and not-as-prominently rounded anterior lobes (cf. Eagar, 1962, pl. 47; Eagar and Pearce, 1993, fig. 4).

Morphometric analysis also supports assignment of the Welles quarry bivalves to *Palaeanodonta parallela*. Complex morphometric techniques that measure shell curvatures have been proposed for late Paleozoic freshwater bivalves (Papin and Doroshenko, 1974), but few comparative data exist in this format. We apply the height-length (h/l) metric, which is ubiquitous in the literature and, according to Gusev (1990), is the single most significant diagnostic. We thus compare h/l of the most morphologically similar Late Carboniferous and Permian nonmarine bivalves to the Welles quarry specimens in a bivariate plot (Fig. 3). All "P." genera are *Palaeanodonta*, the "A." genus is *Anthraconaia*. In the Welles quarry clams, h/l varies from 0.375 to 0.51 and averages ≈ 0.45 (the slope of the curve fit line). *Palaeanodonta parallela*, *P. oviformis* (Amalitzky) and some others have a similar h/l, but only *P. parallela* is comparable in overall size.

There are caveats to assigning the Welles quarry bivalves to *Palaeanodonta*. Deeply incised adductor scars and anterior lobes that are greater in height than the posterior lobes are characters of *Palaeanodonta*. We have no specimens in which muscle scars are preserved, and some of our specimens show a taller anterior lobe, though others do not. Nonetheless, the Welles quarry bivalves show greater agreement with *Palaeanodonta* than any other late Paleozoic freshwater bivalve genus. Indeed, we cannot distinguish the Welles quarry bivalves from *P. parallela*, but given the great geographic and temporal distance between them and *P. parallela* (Late Permian of Russia and South Africa), and the subtle morphological differences between them, we only assign the Welles quarry bivalves to *P. cf. P. parallela*.

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 (\sim 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,

$$L(t) = A_L \cdot (1 - e^{-kt})$$

where $L(t)$ is length as a function of time, A_L 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 $A_L \approx 25$ 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

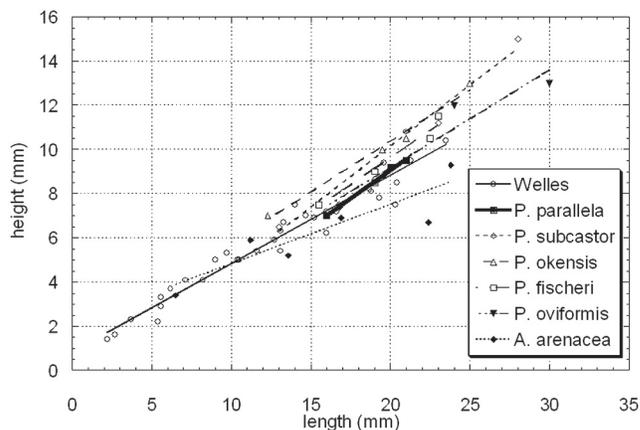


FIGURE 3. Bivariate plot of height versus length for the Welles quarry bivalves and several Permian and Pennsylvanian species of similar gross morphology. The slope of the curve fit is the h/l ratio.

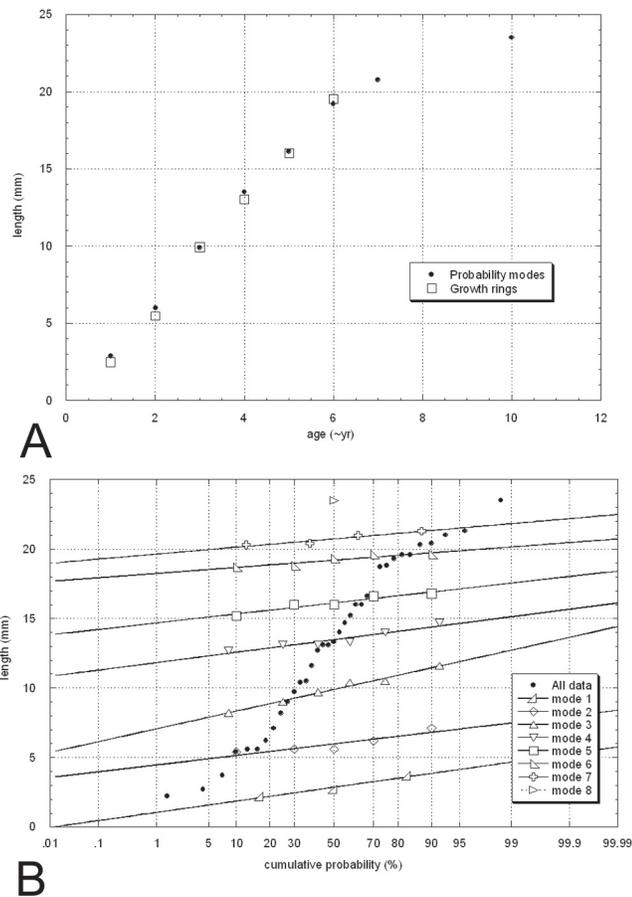


FIGURE 4. A, Growth curve for *Palaeonodonta* cf. *P. parallela* specimens from the Welles quarry generated by growth ring measurements of one individual (squares) and by probability plot method (dots). B, Probability plot of lengths of 36 individuals (dots) and resolved component size classes representing age groups.

and Madagascar (Amalitzky, 1895; Bond, 1954; Cox, 1932, 1936; Rossouw, 1970); the Permian Mount Glossopteris Formation of the Ohio Mountains, Antarctica (Bradshaw, 1984); North America, in the Upper Carboniferous of Nova Scotia (Rogers, 1965) and the Upper Carboniferous-Lower Permian of the eastern United States (e.g., Eagar, 1984); the Upper Permian (Tartarian) 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 *Palaeonodonta* 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 *Palaeonodonta* 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.

ACKNOWLEDGMENTS

The New Mexico State Land Office permitted collecting at the Welles quarry. Several NMMNH volunteers assisted in the field. Andrew Heckert, Joerg Schneider and Kate Zeigler reviewed the manuscript.

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