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VERTEBRATE PALEOECOLOGY OF THE LATE CAMPANIAN
(CRETACEOUS) FRUITLAND FORMATION, SAN JUAN BASIN, NEW
MEXICO (USA)

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Sediments of the Fruitland Formation in northwestern New Mexico represent a delta plain that prograded northeastward over the retreating strandline of the North American epeiric seaway during the late Campanian. Fruitland fossil vertebrates are fishes, amphibians, lizards, a snake, turtles, crocodillans, dinosaurs (mostly hadrosaurs and ceratopsians) and mammals. Autochthonous fossils in the Fruitland Formation represent organisms of the tropically-complex *Parasaurolophus* community. Differences in diversity, physical stress and life-history strategies within the *Parasaurolophus* community fit well the stability-time hypothesis. Thus, dinosaurs experienced relatively low physical stress whereas fishes, amphibians, small reptiles and mammals experienced greater physical stress. Because of this, dinosaurs were less likely to recover from an environmental catastrophe than were smaller contemporaneous vertebrates. The terminal Cretaceous extinctions selectively eliminated animals that lived in less physically-stressed situations, indicating that the extinctions resulted from an environmental catastrophe.

Key words: Fruitland Formation, New Mexico, delta plain, stability-time hypothesis, Cretaceous extinctions.

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INTRODUCTION

The Fruitland Formation in the west-central San Juan Basin, New Mexico (USA) contains an abundant record of the biota that lived along part of the western shore of the North American epeiric seaway during the late Campanian (Late Cretaceous). Although study of Fruitland paleontology and stratigraphy began over 60 years ago (Bauer 1916; Gilmore 1916), knowledge of Fruitland fossils and sediments has only recently reached a point where a reasonable, albeit general, paleoecological synthesis is possible. This paper presents such a synthesis.

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GEOLOGY OF THE FRUITLAND FORMATION

The Fruitland Formation is exposed in a relatively narrow and discontinuous belt around the central San Juan Basin (fig. 1). Isolated outcrops north of the San Juan Basin in western Colorado also have been assigned to the Fruitland (Dickinson 1965).

Due to uplift on the eastern side of the San Juan Basin during the Laramide Orogeny, the Fruitland Formation is poorly exposed there on the slopes of steeply-dipping hogbacks. On the western edge of the



Fig. 1. Location and distribution of the Fruitland Formation in the San Juan Basin, New Mexico and Colorado (after Fassett and Hinds 1971; pl. 1) and the location of the area from which data used in this paper was derived.

central San Juan Basin, however, nearly flat-lying strata of the Fruitland form extensive and picturesque badlands. Virtually all fossils from the Fruitland have been collected from these western exposures, and the data and interpretations presented here are derived from work in this area (fig. 1).

Thickness and contacts

The exposed strata of the Fruitland Formation in the western-central San Juan Basin range in thickness from 58 to 170 m (Fassett and Hinds 1971). At its base, the Fruitland intertongues with the littoral Pictured Cliffs Sandstone; the Pictured Cliffs is underlain by the deeper marine Lewis Shale. At its top the Fruitland grades into the fluvial Kirtland Shale. Because of this gradation, the Fruitland-Kirtland contact in the western-central San Juan Basin is arbitrarily mapped, either "at the top of the stratigraphically-highest brown sandstone" (Dane 1936: 113) or "at the top of the highest coal bed or carbonaceous shale bed" (Fassett and Hinds 1971: 19). These arbitrarily chosen boundaries are within a few meters of each other.

Lithology and fossil occurrences

The Fruitland Formation is composed of three major lithologies:

(1) *Sandstones*. — Most Fruitland sandstones are fine- to medium-grained, calcite-cemented, submature subarkoses (Fassett and Hinds 1971). Many sand bodies display through cross-stratification, are laterally discontinuous and have scour bases. These sandstones typically decrease in grain size upward. Fossil "log jams" sometimes occur near their bases and carbonized plant matter often follows cross-stratification. Isolated dinosaur bones and turtle shells are common in the sandstones. Dinosaur skeletons are rare in the sandstones, and in the Fruitland as a whole. Accumulations of small-vertebrate remains occur frequently in coarse to gravelly beds at the bases of the sandstones.

(2) *Shales and siltstones*. — Fine-grained clastics of the Fruitland Formation are generally fissile, drab-colored (gray, buff, olive) shales and siltstones. Gray-black shales containing significant amounts of carbonaceous material also are common and locally contain well-preserved fossil leaves. Some dinosaur and turtle remains occur in Fruitland shales, though less frequently than in sandstones. Coquina beds and isolated shells, either of unionids and gastropods, or of oysters, are common in shales of the lower part of the Fruitland. Although individual beds of shale and siltstone are laterally discontinuous within a few tens of meters, shale-siltstone sequences within the Fruitland may continue over one km or more, only intermittently interrupted by sandstones.

(3) *Coal*. — The most laterally continuous beds of the Fruitland Formation are coals; some are over nine m thick and extend laterally for several km.

In general, the thicker coals and sandstones are confined to the lower part of the Fruitland. The upper part of the formation contains more shale and also is more fossiliferous than the lower part.

DEPOSITIONAL ENVIRONMENT OF THE FRUITLAND FORMATION

Deposition of the Fruitland Formation took place along the northwest-southeast trending shoreline of the epeiric seaway that bisected North America during the Late Cretaceous (Fassett and Hinds 1971). Source areas from which Fruitland sediments were derived were primarily to the west of the present San Juan Basin (Hayes 1970; Fassett and Hinds 1971). Erpenbeck and Flores (1979), Fassett and Hinds (1971) and Hunt (1981), among others, have suggested that Fruitland deposition took place on a delta-plain. We agree with this interpretation and identify six environments (fig. 2) in the Lewis Shale-Pictured Cliffs Sandstone-Fruitland Formation-Kirtland Shale sequence that fit well the model of high-constructive deltaic deposition presented by Weimer and Land (1975).

(1) *Neritic environment*. — Gray, fissile, slity shales and clayey siltstones of the Lewis Shale contain rare sand- and silt-filled burrows of deposit feeders (*Planolites*) and sparse fossils of open marine animals such as ammonites, sharks and mosasaurs (Mannhard 1976; Lucas and Reser 1981). They clearly were deposited in deep water below wave base. The great thickness of the Lewis Shale (up to 600 m) suggests abundant mud supply and high sedimentation rates that would have led to low bioturbation rates (Mannhard 1976).

(2) *Prodelta environment*. — Gray, fissile shales and some thin, fine-grained, subparallel-laminated sandstones of the uppermost Lewis Shale infrequently contain fossils of ammonites and pelecypods. They reflect prodeltaic sedimentation in water depths just below effective wave base at the furthest reaches of coarse clastic deposition from the delta front.

(3) *Distal delta front environment*. — Tan, fine-grained, subparallel-laminated sandstones alternating with gray shale layers of the lower part of the Pictured Cliffs Sandstone contain the trace fossils of burrowing crustaceans (*Ophiomorpha*) and rare molds of pelecypod shells. This sequence represents the lower-energy, distal portions of distributary-mouth bars.

(4) *Proximal delta front environment*. — Tan, fine- to medium-grained sandstone, trough-crossbedded in part and with deformed "ball and pillow" structures in places, characterizes the upper part of the Pictured Cliffs Sandstone. *Ophiomorpha* and other fossils are extremely rare in

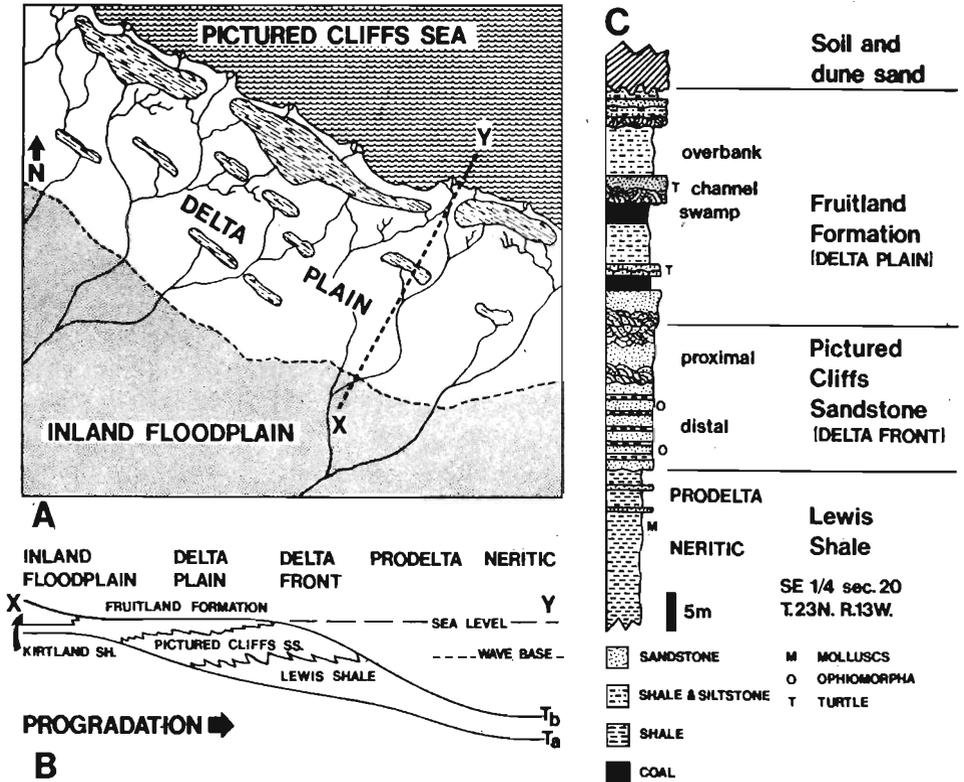


Fig. 2. Depositional environments of the Lewis Shale, Pictured Cliffs Sandstone, Fruitland Formation and lower part of the Kirtland Shale (A), Diagrammatic paleogeographic map of part of northwestern New Mexico during the late Campanian showing the environments of deposition of the rocks that now compose the Lewis Shale, Pictured Cliffs Sandstone, Fruitland Formation and Kirtland Shale (lower part). (B), Diagram showing relationships of the Lewis Shale, Pictured Cliffs Sandstone, Fruitland Formation and Kirtland Shale (lower part) to a deltaic sedimentation model. (C), Measured section of the Lewis Shale (upper part), Pictured Cliffs Sandstone and Fruitland Formation (lower part) at a locality in the western-central San Juan Basin, exemplifying the depositional environments depicted diagrammatically in (A) and (B).

this lithology. A higher-energy environment, typical of the proximal portions of distributary mouth bars is indicated.

(5) *Delta plain environment.* — The Fruitland Formation is a typical deltaplain deposit in which a variety of subenvironments can be identified. Crossbedded sandstones represent fluvial channel and crevasse splay subenvironments; shales and siltstones represent overbank floodplain and pond subenvironments; thick coals represent extensive interdistributary swamp subenvironments and thin coals represent smaller swamp and pond subenvironments. The extensive and thick coals of the Fruitland indicate a densely-vegetated and predominantly subaqueous environment.

(6) *Inland floodplain environment*. — Medium- to coarse-grained sandstones, mudstones and a virtual absence of coal in the Kirtland Shale indicate fluvial deposition on relatively well-drained inland floodplains.

BIOTA OF THE FRUITLAND FORMATION

Plants

Fruitland Formation megafossil plants, represented by leaves and wood, are ferns, conifers and angiosperms. Following the antiquated taxonomy of Knowlton (1916), common angiosperms are *Ficus*, *Magnolia*, *Platanus*, *Carya* and *Sabalites* (Tidwell *et al.* 1981). Most angiosperm leaves are mediumsized, nearly entire- or entire-margined and have "drip tips". This type of leaf shape, combined with the presence of ferns and palms, suggests the presence of a warm and wet (ergo subtropical) climate during Fruitland deposition.

Invertebrates

Invertebrates found in the Fruitland Formation are unionids, gastropods and *Ostrea* (Stanton 1916). A single leaf mine is evidence of the presence of insects (Tidwell *et al.* 1981). Most molluscs in the lower part (35 m) of the Fruitland are brackish-water forms; in the upper part of the Fruitland freshwater forms are more abundant (Hartman 1981).

Vertebrates

The vertebrate fauna of the Fruitland Formation is a taxonomically diverse array of fishes, amphibians, lizards, a snake, turtles, crocodylians, dinosaurs and mammals (Lucas 1981: table 1). Teeth of sharks (Hybodontidae, Isuridae, Orectolobidae) and rays (e.g., *Myledaphus*) are abundant, but bony fishes, except amiids and gars, are rare. Anurans also are poorly known, but salamanders and baenid, dermatemydid and trionyhid turtles are abundant as fossils. Lizards (teiids and anguids), however, are not well represented. Crocodylians include *Brachychampsia*, *Leidyosuchus* and a possible occurrence of *Thoracosaurus*.

Fruitland dinosaurs consist of very rare remains of ankylosaurs, carnosaurs, dromaeosaurs and pachycephalosaurs; infrequent remains of coelurosaurs; and abundant remains of hadrosaurs ("*Kritosaurus*", *Parasaurulophus*) and ceratopsians (*Pentaceratops*, *Monoclonius*?). Mammals from the Fruitland are "typical latest Cretaceous mammals" (Clemens and Archibald 1980), mostly marsupials and ptilodontoid multituberculates and less common eutherians.

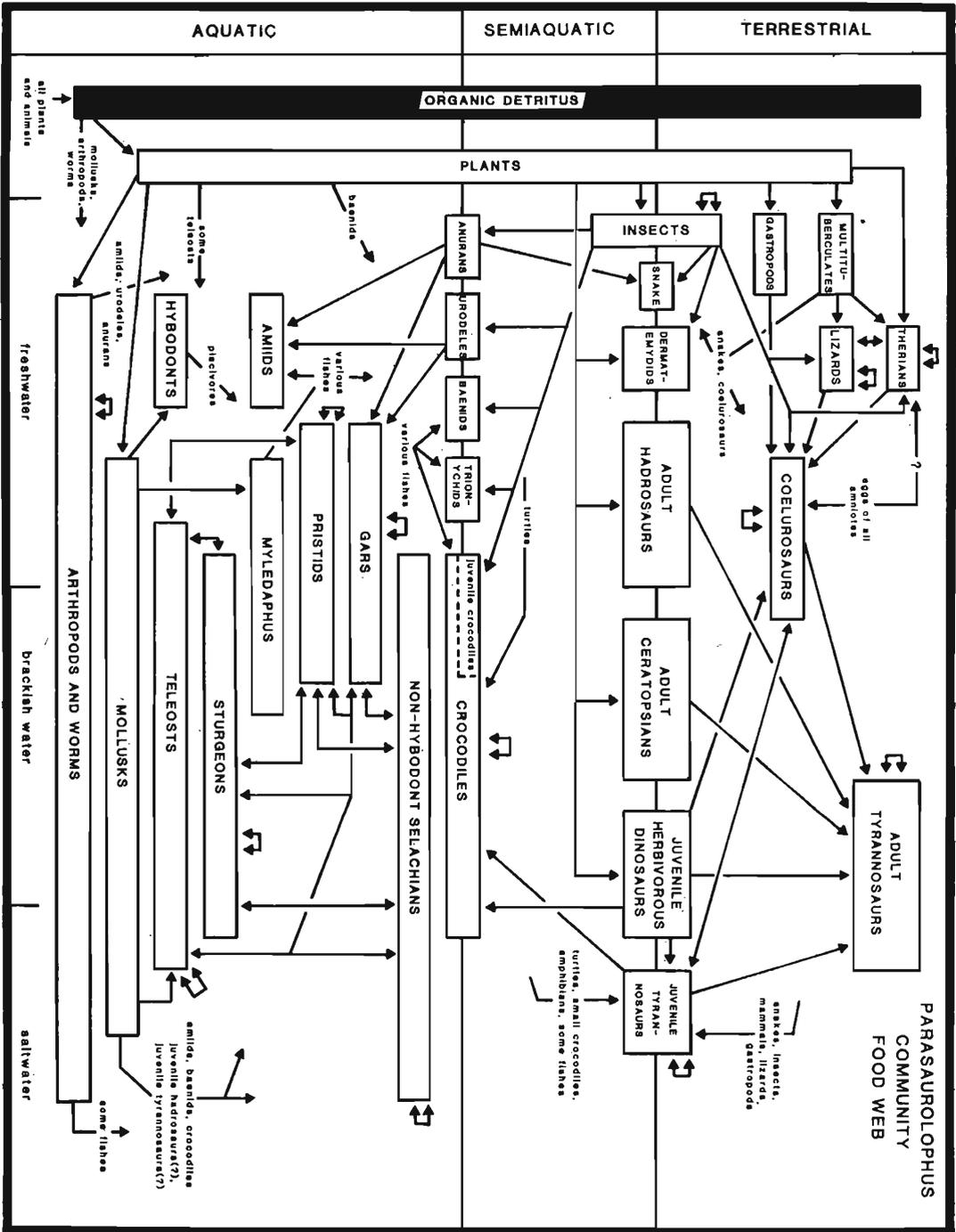


Fig. 3. Hypothesized food web of the *Parasaurolophus* community (from Lucas 1981). Relative size of boxes and names of organisms is of no significance. Arrows indicate inferred direction of flow of trophic energy.

VERTEBRATE PALEOECOLOGY

Trophic analysis

Autochthonous fossils in the Fruitland Formation are assumed to represent organisms that were part of a community that lived on the delta plain in northwestern New Mexico during the Late Campanian. Lucas (1981) named this community the *Parasaurolophus* community and constructed a hypothetical food web (fig. 3) based on autecological assumptions and inferences. Because the fossil assemblage from the Fruitland Formation closely resembles other well-sampled assemblages from Late Cretaceous deltaic sediments elsewhere in western North America, Lucas (1981) suggested that the trophic structure of the *Parasaurolophus* community was typical of Late Cretaceous deltaic communities in North America.

Stability-time hypothesis

The stability-time hypothesis (Sanders 1968; Rollins and Donahue 1975) states that low physiological stresses acting through time produce predominantly biologically-accomodated communities (low taxonomic diversity of stenotopic k-strategists) whereas high physiological stresses produce predominantly physically-accomodated communities (high taxonomic diversity of eurytopic r-strategists). Although Sanders' concept was derived from studies of benthic marine communities, we believe that the animals of the *Parasaurolophus* community can be arranged along a spectrum that has as its end points the two community types specified by the stability-time hypothesis (fig. 4).

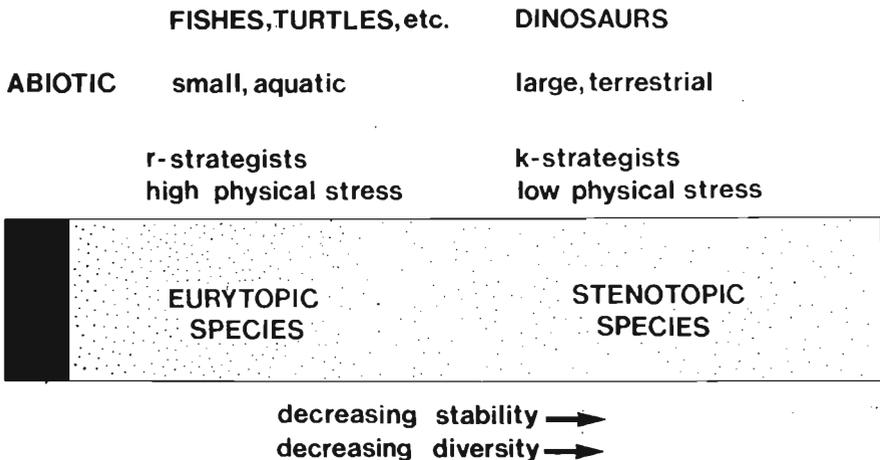


Fig. 4. Schematic representation of Sanders' stability-time hypothesis (modified from Rollins and Donahue 1975) applied to the *Parasaurolophus* community.

In this arrangement, we view the relatively diverse fishes, amphibians and small reptiles of the *Parasaurolophus* community as r-strategists largely living in channels and ponds on the delta plain where physical changes of an unstable, prograding shoreline (e.g., channel switching) placed them in a physically-stressed environment. Because of their small size, mammals would also have been subject to the high physical stress induced by unstable delta substrates and vegetational patterns. We envision dinosaurs, on the other hand, as large terrestrial to semiaquatic k-strategists (relative to their contemporaries) whose large size made them less subject to physical stresses.

Bretsky and Lorenz (1970) demonstrated that animals living in situations of high physical stress are able to recover more rapidly from environmental catastrophes than those that normally experience little physical stress. We believe that it is significant that the terminal Cretaceous extinction eliminated the dinosaurs, here envisioned as animals living in situations of low physical stress, whereas most of the animals here identified as those that lived in situations of high physical stress persisted into the Tertiary (or at least close, ecologically similar, relatives did). These circumstances suggest that the terminal Cretaceous extinction of dinosaurs resulted from an environmental catastrophe. The dinosaurs were unable to cope with this catastrophe, but their smaller, more opportunistic contemporaries, whose Cretaceous world was characterized by relatively high physical stress, survived.

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