Geology and paleontology of the Kinney Brick Quarry, Late Pennsylvanian, central New Mexico

Edited by Jiri Zidek

BULLETIN 138 New Mexico Bureau of Mines & Mineral Resources 1992

A DIVISION OF
NEW MEXICO INSTITUTE OF MINING & TECHNOLOGY

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New Mexico Bureau of Mines & Mineral Resources, Socorro, New Mexico 87801

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Published by Authority of State of New Mexico, NMSA 1953 Sec. 63-1-4
Printed by University of New Mexico Printing Services, May 1992

Available from New Mexico Bureau of Mines & Mineral Resources, Socorro, NM 87801

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Contents

Preface

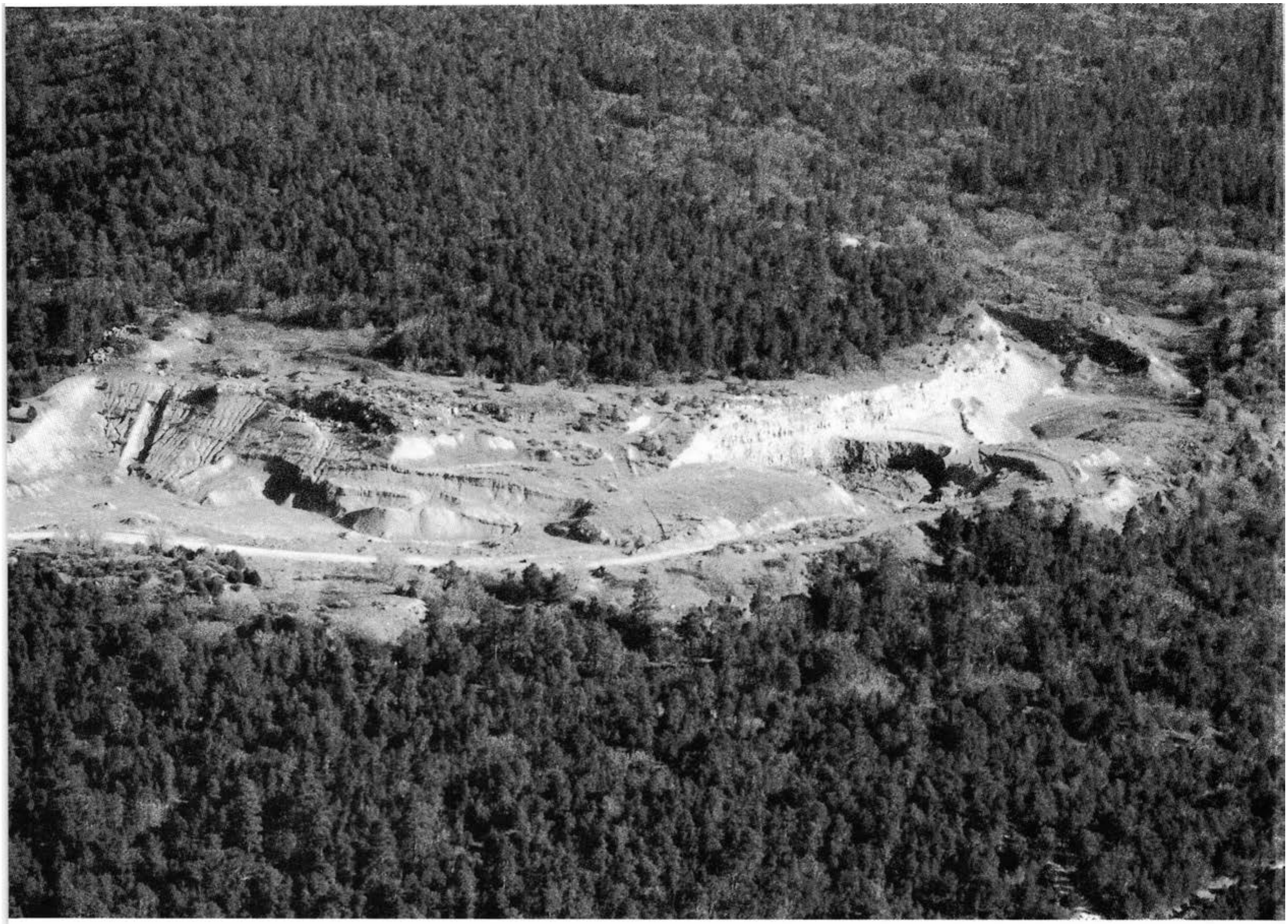
The title of this volume is that of a Geological Society of America/Paleontological Society symposium held on 22 April 1991 at the annual meeting of GSA Rocky Mountain/South-Central Sections in Albuquerque, with the Rocky Mountain Section of the Paleontological Society participating. The idea to organize a symposium on the Kinney Brick Company Quarry came from Phillip Huber sometime in mid-1990, and Spencer Lucas and Robin Burnham of the New Mexico Museum of Natural History (NMMNH) agreed to undertake its organization and co-chair the session. Distribution of fossils to specialists was handled by Phillip Huber (the NMMNH collection), Barry Kues (the University of New Mexico [UNM] collection), and myself (the LaFon collection owned by the Carnegie Museum of Natural History [CM]). Two other major collections of Kinney Quarry material are housed at the National Museum of Natural History (USNM) and the University of Kansas Museum of Natural History (KU), and Sergius Mamay (USNM) and Hans-Peter Schultze (KU) were very helpful in informing other participants about the existence of important specimens in these collections and making them available for study. Abstracts had to be submitted by December 1990, and swift distribution of specimens to the participants thus was essential to the success of the symposium. These efforts resulted in a very well attended and informative session, startlingly high attendance of the field trip, and an evening social hosted by the NMMNH that brought together even more interested parties.

The late Charles Read (U.S. Geological Survey) declared as long ago as 1967 (in a letter to V. C. Kelley of UNM) that the Kinney Quarry is "one of the most remarkable fossil localities in the country," and "if properly developed, it may become one of the classic localities for Upper Paleozoic organisms in the world." Regrettably, it took paleontologists, biostratigraphers, and sedimentologists 23 more years to get together and undertake a multidisciplinary study of the site. Today, 24 years later, it is clear that Read was not exaggerating but, in a sense, actually underestimated the significance of this locality. The diverse floral and faunal assemblages of course are important because they provide much new information, some of it taxonomically, paleoecologically, and biostratigraphically quite surprising, and some of the taxa are so abundant and well preserved that they are very amenable to various paleobiologically oriented studies. Equally important, however, is the abnormally thick clastic section of paralic facies exposed in the quarry, which provides an excellent opportunity for detailed sedimentological analysis. It is the combination of exceptionally well preserved fossil and rock records rather than the fossils alone that makes the site unique.

This volume covers most aspects of geology and paleontology of the Kinney Quarry. It does not include malacostracans and eurypterids because accounts of these groups are available elsewhere (Schram & Schram, 1979, Journal of Paleontology, 53: 169-174, and Kues, 1985, New Mexico Journal of Science, 25: 23-42, respectively), and geochemistry and petrology s.s. because specialists in these disciplines were not available in the required time frame. As Kues & Lucas point out in the concluding remarks of the first, overview article, "the studies of the Kinney Quarry strata and fossils presented in this volume represent only a first step toward complete understanding of the remarkable Late Pennsylvanian record preserved there." One could hardly expect more from a single year's work, but what has been done to date certainly provides a solid foundation for future, more refined studies.

I would like to take this opportunity to thank the authors for their contributions, Bob Jurgena, President of the Kinney Brick Company, for allowing research at the quarry, and the University of New Mexico Printing Services for an outstanding performance in all phases of production of this volume.

jiri Zidek



Aerial photo of the Kinney Brick Company Quarry, looking to the southeast. Photo Elizabeth Lorenz, April 1991.

New Mexico Bureau of Mines & Mineral Resources Bulletin 138, 1992

Overview of Upper Pennsylvanian stratigraphy and paleontology, Kinney Quarry, Manzanita Mountains, New Mexico

Barry S. Kues[1] and Spencer G. Lucas[2]

'Department of Geology, University of New Mexico, Albuquerque, New Mexico 87131-1116;
'New Mexico Museum of Natural History, 1801 Mountain Rd. NW, Albuquerque, New Mexico 87104

Abstract—About 28 m of Upper Pennsylvanian strata exposed in the Kinney Quarry contain varied assemblages of restricted-marine and nonmarine plants, invertebrates, and vertebrates. This biota was discovered in 1961. Since then, isolated elements of the biota, including some plants, insects, malacostracan crustaceans, eurypterids, fish, and amphibians have been studied. Numerous additional aspects of the depositional environments, fauna, and flora were presented at a GSA/Paleontological Society symposium in April 1991, and are discussed at length in this volume. The basal unit of the Kinney sequence is a dark-gray argillaceous limestone containing a restricted-marine fauna dominated by bivalves and *Lingula.* About 0.5 m of overlying fissile shales contains large numbers of plants and fish, and lesser numbers of amphibians, insects, malacostracans, myriapods, and other invertebrates, indicating a brackish environment. Most previous studies of the Kinney biota involved specimens from this interval. Above this, a 2 m thick sequence of laminated to blocky shale contains large numbers of plants and a large species of the pectinacean bivalve *Dunbarella,* but few other animal remains. The laminae may represent varves or tidal rhythmites. The middle part of the sequence comprises about 11 m of silty shales, which are less fossiliferous (mainly plant fragments and small dunbarellas) than the underlying shales. The upper part of the section includes three laminar to trough-crossbedded sandstone units interbedded with thicker brackish to slightly marine, poorly to moderately fossiliferous shale intervals. These units represent overlapping distributary mouth bars and associated sediments, and total about 12 m in thickness. The Kinney section is completed by 2 m of locally trough-crossbedded sandstone and limestone-pebble conglomerate. The entire sequence is largely regressive and reflects progradation of deltaic facies into the area from the northern end of the Pedernal uplift, immediately to the east.

Introduction

A sequence of fossiliferous strata about 28 m thick and probably early Virgilian in age is exposed in the Kinney Quarry southeast of Albuquerque, New Mexico. This sequence contains a restricted-marine fauna at its base, with a variety of nonmarine plants, vertebrates, and invertebrates in the overlying strata. The nonmarine assemblages include numerous plant species, well-preserved remains of several groups of fishes, at least two amphibian taxa, and specimens of insects, crustaceans, conchostracans, eurypterids, myriapods, and brackish-water bivalves, among others. Such assemblages are relatively uncommon compared with normal-marine assemblages in the late Paleozoic, especially in the southwestern United States. The Kinney biota thus provides a rare opportunity to examine the paleontology and paleoecology of Late Pennsylvanian terrestrial, brackish, and possibly fresh-water environments in New Mexico, and to compare the fauna and flora of these nonmarine environments with analogous, more extensively studied biotas in the central and eastern United States.

Some elements of the Kinney biota have been studied previously, and specimens from the quarry are in collections of several institutions, including especially the U.S. National Museum of Natural History (USNM), New Mexico Museum of Natural History (NMMNH), University of New Mexico (UNM), University of Kansas (UK), and the Carnegie Museum of Natural History (CMNH). In general, previous studies have addressed one or two taxa of interest to an investigator, and there has been no general coordinated effort to understand the entire biota and depositional environments of the quarry strata. The present symposium has stimulated revival of interest in these subjects, and has brought together the results of numerous recent studies into a single volume. It thus forms a foundation on which to base future studies, for a number of intriguing aspects of the Kinney biota and stratigraphy remain to be investigated. In this paper, we provide an overview of the stratigraphy and paleontology at the quarry, summarize previous studies, and present some preliminary interpretations of the depositional environments and paleoecology preserved in the exposed strata.

The Kinney Quarry is located along the western side of New Mexico Highway 337 (formerly NM-14 south), about 13 km south of the town of Tijeras, Bernalillo County (Fig. 1). It is privately owned, and permission must be obtained from W. R. Jurgena, President of the Kinney Brick Company, before visiting it. Quarrying operations are intermittent, but obviously take precedence over fossil collecting when they are in progress. Quarrying also effects changes in the quarry; some new outcrops of the stratigraphic sequence are exposed while previously exposed areas are covered. Outcrop photographs included here were taken in 1990. Some quarrying has occurred since that time.

Regional geology and stratigraphy

Pennsylvanian strata in the Manzanita and Manzano Mountains rest unconformably on Precambrian granitic and metamorphic rocks or, locally, on thin erosional remnants of the Mississippian Arroyo Peñasco Group. The thickness of the Pennsylvanian sequence throughout the Manzanita-Manzano uplift, a distance of ca. 75 km, averages about 450 m. These strata are extensively exposed along the crest and gently sloping, dissected eastern flank of the uplift for most of its length (Fig. 1). Pennsylvanian units crop out at elevations ranging from less than 1800 m (6000 ft) to more than 3050 m (10,000 ft) in these mountains, and are typically heavily covered by vegetation. The term Manzano Mountains is often applied to the entire uplift, but the northern

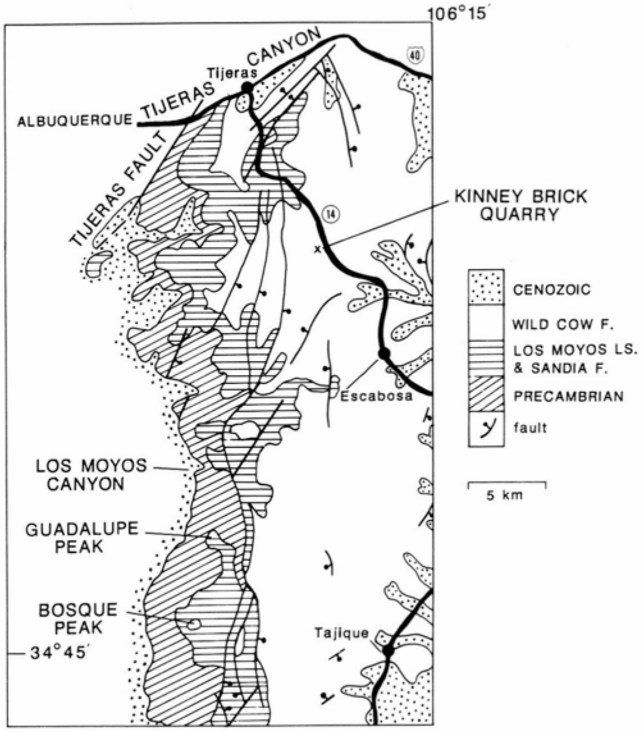


FIGURE 1—Location of Kinney Quarry and general geology of the Manzanita and northern Manzano Mountains, central New Mexico (from Lucas & Huber, 1991).

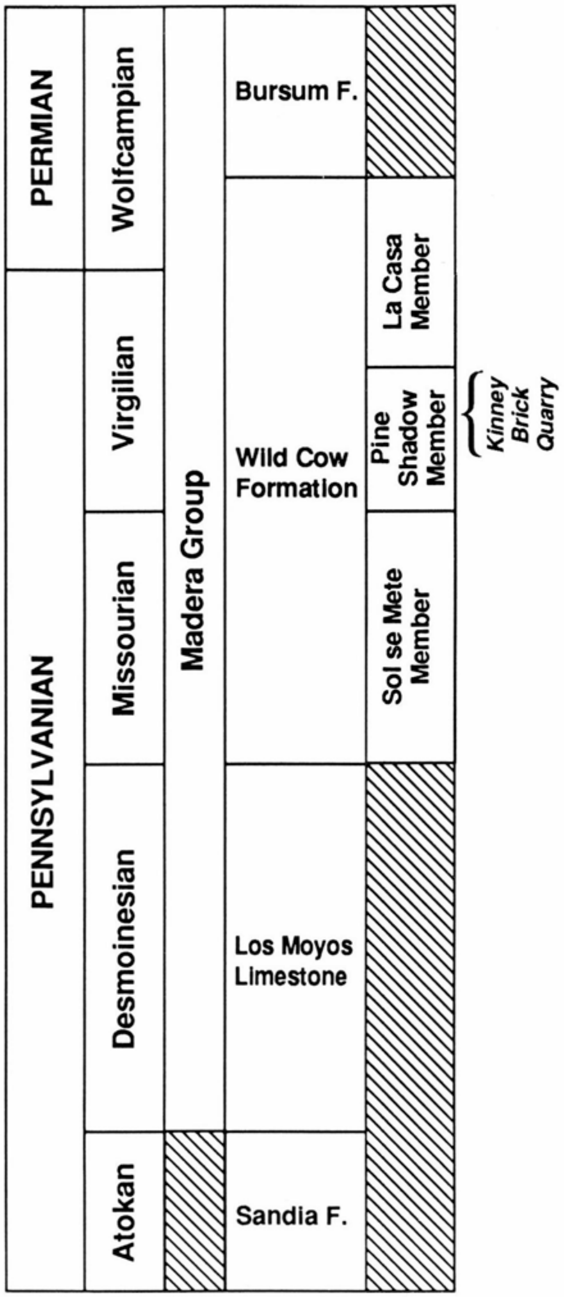


FIGURE 2—Stratigraphic nomenclature of Pennsylvanian and Lower Permian strata in the Manzanita and Manzano Mountains (after Lucas & Huber, 1991).

24 km (immediately south of 1-40 in Tijeras Canyon) is a structurally and topographically distinct portion (Manzanita Mountains) that is lower than the Manzano Mountains sensu stricto to the south (Kelley, 1977). The Manzanita and Manzano Mountains, as well as the Sandia range to the north, are fault-block ranges uplifted along western boundary faults from Miocene time to the present.

The presently accepted stratigraphic division of the Pennsylvanian in the uplift (Fig. 2) is based on the work of Myers (1973). The basal unit (Sandia Formation) is a relatively thin, predominantly sandy siliciclastic unit of Atokan age. It is overlain by the Madera Group, which includes Desmoinesian through earliest Wolfcampian (Permian) strata. The Desmoinesian Los Moyos Limestone consists chiefly of a succession (180 m thick) of massive, cliff-forming, gray, locally cherry limestone beds well exposed in roadcuts along NM-337 from south of the town of Tijeras to about 3 km north of the Kinney Quarry. The Los Moyos Limestone is overlain by the Wild Cow Formation, which is composed of rhythmic sequences of arkosic sandstone, gray, tan, and red shale, and gray marine limestone of Missourian to earliest Wolfcampian age. Myers (1973, 1988) recognized three members of the Wild Cow, in ascending order Sol se Mete, Pine Shadow, and La Casa. In the southern part of the Manzano Mountains, the Wild Cow is overlain by the Bursum Formation, a thin sequence of Wolfcampian red to green shales and sandstones with thin beds of gray marine limestone. This general pattern of thick Middle Pennsylvanian limestone, Upper Pennsylvanian alternation of limestones and marine to nonmarine clastics, and early Wolfcampian red-clastic-dominated strata with minor marine limestone is typical of the Pennsylvanian—earliest Permian sequence throughout central New Mexico (Armstrong et al., 1979). Marine environments in this area ceased with deposition of the Wolfcampian Abo Formation, which is composed of red terrigenous sandstones and shales derived from the north.

About 28 m of the Pine Shadow Member, Wild Cow Formation, are exposed in the Kinney Quarry. The member is ca. 50 to 75 m thick throughout the Manzanita and Manzano Mountains, and consists generally of gray marine limestones alternating with marine or nonmarine shale, sandstone, and conglomerate. Lateral facies changes within the Pine Shadow Member are pronounced (Myers, 1973). The age of the member is reliably established as early Virgilian based on studies of fusulinids at various locations along its outcrop (Myers, 1973, 1988). No fusulinids have been found in the Kinney Quarry, however.

During Pennsylvanian time the geography of New Mexico included several large, north—south-trending landmasses and a few smaller islands separated by wide expanses of ocean (Fig. 3). During this period, variation in rates of tectonic uplift and erosion on the positive areas, and eustatic sea-level changes, combined to produce a mosaic of different terrestrial and marine facies in any one area. Lateral facies changes from area to area within the Pennsyl-

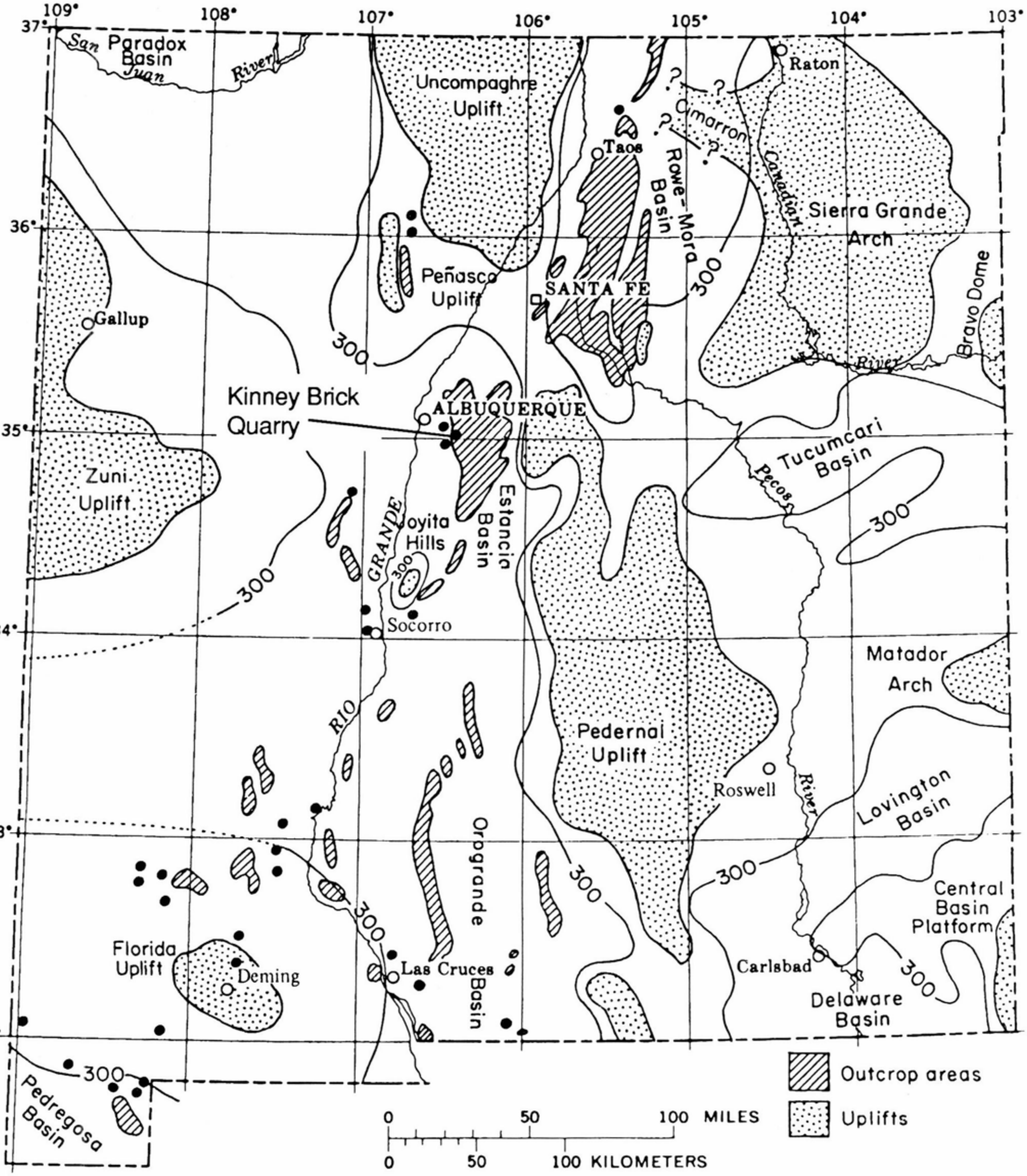


FIGURE 3—New Mexico paleogeography during Pennsylvanian time (after Armstrong et al., 1979).

vanian sequences often have made it difficult to define lithostratigraphic units that could be correlated readily from one area to another. Fusulinids have proven valuable for regional biostratigraphic correlations, but are absent or unstudied in some sequences.

During the time the Kinney strata were deposited, the closest sediment source was the Pedernal uplift to the east and southeast (Fig. 3). This large landmass underwent rejuvenation during Late Pennsylvanian and Early Permian time and shed fairly large volumes of clastic sediments into nearby seas (Kottlowski, 1965; Greenwood et al., 1977). The northwestern margin of the Pedernal landmass was situated within a few kilometers of the Kinney Quarry site (Armstrong et al., 1979: fig. 7) and, therefore, is an obvious source of sediments for the Kinney delta system. If this is true, the major directions of sediment transport away from the Pedernal uplift would have been to the west and southwest. Siemers (1983) attributed most Late Pennsylvanian sedimentation in the area north of Socorro (about 90 km southwest of the Kinney site) to southwesterly transported material eroded from the Pedernal uplift, providing some support for this interpretation. Lorenz et al. (1991), however, reported paleoflow directions to the south based on study of fluvial, crossbedded sandstones near the top of the Kinney sequence. Because the strata exposed in the quarry represent only one local cross section through the lagoonalideltaic sediments, the observed southerly paleoflow indicators could have been associated with one restricted lobe of the delta that was prograding obliquely to the main east-to-west direction of sediment transport (G. Smith, pers. comm. 1991).

Near the beginning of the Permian, locally derived terrigenous sedimentation was overwhelmed by much larger volumes of red and reddish-brown clastic sediments eroded mainly from the Uncompahgre uplift. This mass of nonmarine sediments migrated generally from north to south, initially producing alternating red-bed and marine limestone sequences (e.g. Bursum Formation and equivalent units), followed by thick, completely nonmarine red-bed deposits of the Abo Formation. Abo deposits buried most of the northern Pedernal uplift by the end of Wolfcampian time and extended far into southern New Mexico. There, as in the Sacramento and Robledo Mountains, the Abo thins to become tongues within the marine Hueco Limestone, which was being deposited across the southern part of the eroded Pedernal landmass during late Wolfcampian time.

Previous studies

The presence of terrestrial plant and nonmarine animal fossils in the strata exposed at the Kinney Quarry has been known for nearly 30 years. Kelley & Northrop (1975: 47-48) summarized the reported biota and studies of it through the early 1970's. Here, we amplify the early history a bit, using records in the files of the University of New Mexico (UNM) and the New Mexico Bureau of Mines & Mineral Resources (NMBMMR), and bring the story forward to the present time of renewed interest that culminated in the Kinney Quarry Symposium in April 1991. Additional information relating to collection and study of the plants is presented by Mamay & Mapes (this volume).

The first fossil plants and one insect were apparently discovered by Sidney Ash, C. J. Felix, and G. D. Glover on October 9, 1961 (Kelley & Northrop, 1975; Ash & Tidwell, 1982). These fossils were brought to the attention of the late Charles Read, a paleobotanist with the U.S. Geological Survey (USGS) in Albuquerque. While assisting Read in collecting plants, John R. Bradbury, a UNM graduate student, found the first fossil fish early in 1963. Read sent some fishes to David Dunkle, then at the U.S. National Museum of Natural History (USNM), and Dunkle traveled to the quarry in 1964 to collect additional specimens. At this time both Read and Dunkle believed the plants and fish suggested an Early Permian age, whereas the marine and brackish invertebrates appeared to be Pennsylvanian taxa (Read's letter to Dunkle, May 20, 1963). Sergius Mamay, of the USGS, also learned of the plants from Read, and later (1967 and 1969), with A. D. Watt, made large collections of plants, together with some fishes and invertebrates.

Several UNM students became interested in the quarry biota and stratigraphy in the 1960's. Robert C. Burton, in an unpublished study, reported conodonts from the basal limestone and illustrated specimens belonging to seven genera (Kelley & Northrop, 1975; we have not seen this study). Burton later processed additional samples and reported a total of 16 species and eight genera (letter to Northrop, January 10, 1975). Another graduate student, Paul Stukey, measured a stratigraphic section in and around the quarry as part of a master's thesis on the late Paleozoic stratigraphy in the Manzanita Mountains (Stukey, 1968). His section indicates most of the distinctive beds noted in the section presented here (Figs. 4, 5) and by Lucas & Huber (1991). Undergraduate research papers on Kinney paleontology and stratigraphy were also written by Thomas Lehman in 1977 and Phillip Huber in 1989.

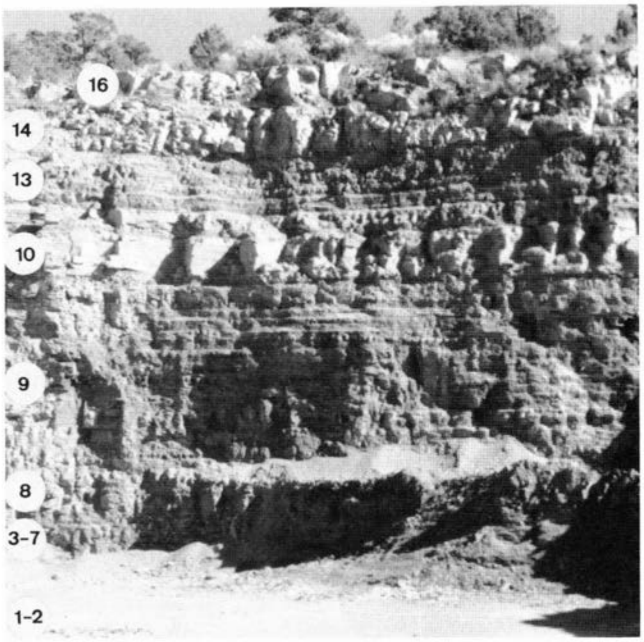
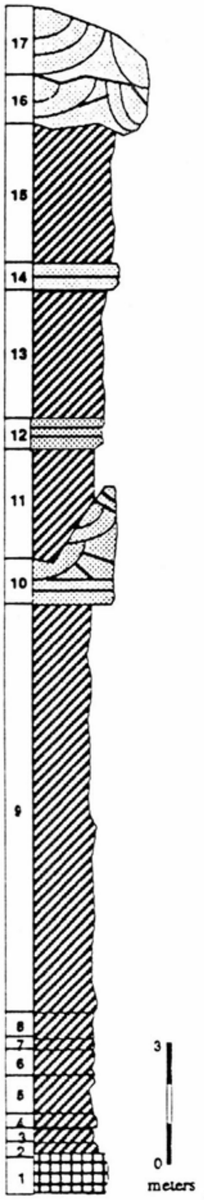


FIGURE 4—View of wall of Kinney Quarry ("lower quarry") showing the stratigraphic sequence. Units 1 and 2 compose the quarry floor; unit 17, a conglomeratic sandstone, is not visible above unit 16 here.

By 1967, Read was proposing a multidisciplinary study of the Kinney biota, with the results to be published as chapters in a USGS professional paper (memo to UNM Department of Geology, June 6, 1967). By then he believed the age of the biota to be Late Pennsylvanian. Another memo (Read to V. C. Kelley, October 30, 1967) referred to a proposal to study the biota that members of the UNM Department of Geology, headed by Stuart Northrop, were planning to submit to the National Science Foundation. Read noted that "this quarry is one of the most remarkable fossil localities in the country, and some people have suggested that, if properly developed, it may become one of the classic localities for Upper Paleozoic organisms in the world." Despite this enthusiastic description, the proposal was either not submitted or not funded, and no concerted or coordinated effort to study the Kinney biota developed.

Mamay's collecting efforts in 1967 and 1969 produced occasional specimens of unusual invertebrates among the plants, including insects, crustaceans, a myriapod, and a eurypterid. These were distributed to specialists for study. The five insects were sent to Frank Carpenter at Harvard, who described (Carpenter, 1970) a paleodictyopteran, *Madera mamayi,* and a calneurodean, *Pseudobiella fasciata,* both new genera and species. The former species was based on a nearly complete specimen, and the latter on wings and part of the body. Carpenter also discussed two specimens of blattoids (cockroaches), illustrating one of them, but did not assign them to genus or species. Jarmila Kukalova-Peck of Carleton University, Ottawa, collected a few insects from the quarry in 1975. At present, the 14 additional insects discovered since Carpenter's work all are indeterminate fragments (Shear et al., 1991, and this volume).

Mamay sent the crustaceans to Frederick Schram, who (Schram & Schram, 1979) described two new species, *Uronectes? kinniensis, a* syncarid, and *Aenigmacaris minima,* a hoplocarid. Schram (1981) noted that these crustaceans were part of a distinctive late Paleozoic lagoonal community also recognized in the Upper Mississippian Heath Shale of Montana. The single Kinney myriapod specimen obtained by Mamay has been augmented by three additional specimens



Unit	Lithology	Thickness (m)
	Wild Cow Formation	
	Pine Shadow Member:	
17	Sandstone and limestone-pebble conglomerate; sandstone is moderate yellowish brown (10 YR 5/4), very fine- to fine-grained, moderately sorted, subangular, calcareous and micaceous; conglomerate has brownish-gray (5 YR 4/1) matrix and clasts are medium gray (N5) to medium dark gray (N4) limestone pebbles 1–5 cm in diameter; trough-crossbedded.	1.0+
16	Sandstone; dark yellowish orange (10 YR 6/6); very fine- to fine-grained; moderately sorted; subangular; calcareous; micaceous; trough-crossbedded and laminar–ripple laminar; forms a ledge.	1.0
15	Shale; olive gray (5 Y 4/1); slightly calcareous; finely laminar to platey; fossiliferous with small *Dunbarella* and *Lingula*.	3.2
14	Sandstone; dark yellowish-orange (10 YR 6/6) and grayish brown (5 YR 3/2); very fine- to fine-grained; moderately sorted; subrounded–subangular; calcareous; feldspathic; laminar–ripple laminar; forms a ledge.	0.5
13	Silty claystone; moderate yellowish brown (10 YR 5/4); plastic; very calcareous; laminar.	3.3
12	Sandstone; same color and lithology as unit 10.	0.8
11	Silty shale; olive gray (5 Y 4/1) and light olive gray (5 Y 5/2); calcareous; contains moderate yellowish-brown (10 YR 5/4) micritic limestone nodules 2–8 cm in diameter.	1.1
10	Sandstone; dark yellowish orange (10 YR 6/6); very fine- to fine-grained; subrounded–subangular; moderately sorted; calcareous; laminar–ripple laminar and trough-crossbedded; unit pinches out over 10 m on strike.	2.8
9	Silty shale; olive gray (5 Y 4/1); calcareous; parts weather blocky; moderately fossiliferous.	9.9
8	Silty shale; greenish gray (5 GY 6/1); slightly calcareous; blocky; forms a ledge.	0.8
7	Shale; dark greenish gray (5 GY 4/1) with moderate yellowish-brown (10 YR 5/4) mottles; plastic; calcareous; highly fossiliferous.	0.2
6	Shale and claystone; shale is olive gray (5 Y 3/2); claystone is dark greenish gray (5 GY 4/1); very calcareous; highly fossiliferous, especially with moderate yellowish-brown (10 YR 5/4) *Dunbarella*.	0.8
5	Shale; olive gray (5 Y 3/2); very calcareous; highly fossiliferous, large *Dunbarella* and plants.	1.0
4	Shale; olive gray (5 Y 4/1); weathers dark yellowish brown (10 YR 4/2); plastic; very calcareous; highly fossiliferous, part of main fish–plant interval.	0.2
3	Shale; olive black (5 Y 2/1); weathers dark yellowish orange (10 YR 6/6); calcareous; highly fossiliferous, part of main fish–plant interval.	0.2
2	Shaly limestone; olive black (5 Y 2/1); mottled and streaked grayish orange (10 YR 7/4); well indurated; highly fossiliferous.	0.1
1	Micritic limestone; dark gray (N3); clayey; laminar to massive; highly fossiliferous; top of unit approximates active quarry floor.	1.0+

FIGURE 5—Diagrammatic stratigraphic section showing units identified in Kinney Quarry (compare with Fig. 4).

collected recently by the NMMNH. The myriapods are discussed by Shear et al. (1991 and this volume).

The eurypterid specimen was originally sent to Leif Stormer in Norway, and apparently passed on to E. Kjellesvig-Waering, but was returned to the USNM following his death in 1980. This specimen, and another discovered by a University of Kansas field party in 1984, were described by Kues (1985). They are conspecific with *Adelophthalmus luceroensis,* originally described by Kues & Kietzke (1981) from earliest Wolfcampian strata in the Lucero area, about 75 km southwest of the Kinney Quarry.

The large number of pectinacean bivalves *(Dunbarella)* that characterize the units immediately above the main fish/plant/crustacean horizon were the subject of an abstract by Clark (1978), and were briefly discussed by Mamay (1981, 1990). They are treated more comprehensively by Kues (this volume). With interest in the Kinney biota directed mainly toward its unusual nonmarine elements, the restricted-marine invertebrate fauna in the basal limestone received little attention. Kues (1990 and this volume) discusses the composition and paleoecology of this fauna, and Mapes (1991) and Mapes & Boardman (this volume) treat the cephalopods.

As noted above, Dunkle and Mamay collected large numbers of fish in the 1960's. Some of these USNM collections, as well as smaller collections at the Carnegie Museum of Natural History, the Oklahoma Museum of Natural History, Norman, and in private hands were studied by Zidek (1975). He described elasmobranch, acanthodian, lungfish, and coelacanth remains, of which *Acanthodes* was the only taxon represented by more than isolated teeth, spines, or scales. In 1984, a University of Kansas field party collected fish from the quarry, including a variety of unusual lower actinopterygians. Gottfried (1987a) described a new, long-snouted palaeonisciform fish, *Tanyrhinichthys mcallisteri*, and reported the first North American occurrence of an aeduellid similar to *Bourbonella* (Gottfried, 1987b). Gottfried (1991 and this volume) also noted the presence of another new taxon, similar to some Triassic subholostean forms. Additional studies of the actinopterygians have been undertaken by Zidek (1991 and this volume), Huber & Lucas (1991), Huber (this volume), and Bardack (this volume). These studies are based on collections at the USNM, UK, NMMNH, and a large private collection recently acquired by the CMNH, Pittsburgh, from Neal LaFon. The quarry's fishes have long been known to amateur collectors and there are undoubtedly specimens in private collections that have not received scientific scrutiny.

In 1971, Neal LaFon and Tom Lehman discovered part o1 the skeleton of a small amphibian. They sent the specimer to Gerard Case of Jersey City, who presented it to the CMNH where it was studied by Berman (1973). He described the specimen *as Lafonius lehmani*, a new trimerorhachid genus and species. Recently three additional amphibian skeletons have been discovered, apparently representing at least a second (new) genus, and these have been studied by Hunt, Lucas, and Berman (Hunt et al., 1989, this volume).

Study of the Kinney plants has proceeded relatively slowly. Kelley & Northrop (1975) stated that Read had identified the basal Permian genus *Callipteris* in the flora, but Mamay's large collections revealed no evidence of that genus. Ash & Tidwell (1982) briefly discussed the Kinney plants, listing the following genera: *Asterophyllites, Calamites, Neuropteris, Pecopteris, Plagiozamites*, and *Walchia*. To date, the only detailed studies have been published by Mamay (1981, 1990). In the first paper he described a new species of the enigmatic genus *Dicranophyllum*, characterized by long, slender, bifurcating leaves. In the second paper he established *Charliea manzanitana*, new genus and species, for parallel-veined, pinnately compound leaves of uncertain affinities. Mamay (1990) also documented the occurrence of *Plagiozamites planchardii* in the Kinney flora. Mamay & Mapes (1991 and this volume) summarize the flora, noting that it contains about 30 species and is dominated by conifers and neuropterid pteridosperms. Willard (1991 and this volume) discusses the palynoflora, which is dominated by cordaite, conifer, and pteridosperm pollen.

Prior to studies undertaken for the present symposium, little work on the stratigraphy and depositional environments of the Kinney sequence had been done. Myers (e.g. 1973, 1988) established the early to middle Virgilian age of the Pine Shadow Member based on fusulinids; the flora within the quarry presents no conflict with that age (Ma-may, 1981). Although studies of the Kinney biota generally have been taxonomic in nature, several authors have suggested a lagoonal environment for the Kinney sequence (e.g. Berman, 1973; Schram & Schram, 1979; Mamay, 1981, 1990; Kues, 1985). Stukey (1968), Gottfried (1987a), Huber et al. (1989), and Lucas & Huber (1991) discussed the stratigraphy of the quarry sequence. More detailed information on the stratigraphy and depositional environments exposed in the quarry is presented below in this paper and in other abstracts and papers prepared for the Kinney symposium.

Stratigraphy and paleontology

The 28 m thick sequence exposed in the Kinney Quarry can be divided into 17 discrete lithologic units, most of which are fossiliferous (Figs. 4, 5, 7; Lucas & Huber, 1991). Here we integrate the paleontology of the Kinney sequence into its general stratigraphic framework, emphasizing where in the sequence the major groups of fossils occur. Fig. 7 displays the stratigraphic occurrence of conspicuous plant and animal groups.

The active quarry floor is developed in a hard, black, splintery limestone having a high clay content (unit 1). No more than the top 40 cm of this unit is exposed (Fig. 6B). It contains a restricted-marine fauna dominated by the inarticulate brachiopod *Lingula* and the bivalves *Solemya* and *Myalina* (Kues, 1990, and this volume). Unomamented ostracodes, conchostracans, *Dunbarella striata*, small ammonoids *(Prothalassoceras*, see Mapes, 1991, and Mapes & Boardman, this volume), and the articulate brachiopod *Chonetinella flemingi* are moderately common subsidiary elements of this fauna. Stenohaline groups such as bryozoans, fusulinids, corals, echinoderms, and most articulate brachiopods are rare or absent, but fragments of plants and fish are not uncommon.

The basal limestone becomes more platy to laminar, and more argillaceous, through an interval of about 10 cm (unit 2). Most major elements of the limestone fauna disappear through this transition zone and are absent from the overlying shale (unit 3). Units 3 and 4 are gray to olive-gray, orange- to brown-weathering shales totaling 30 to 40 cm in thickness (Figs. 4, 6C). Lithological variation within this interval is pronounced. Typically it is finely laminar, relatively compact, and slightly to moderately calcareous, but locally becomes soft and highly fissile, especially in weathered exposures. Nearly all of the published fossils from the Kinney Quarry have been collected from units 3 and 4.

The biota present in these units is characterized by abundant terrestrial plants and fishes. The fishes include elasmobranchs, dipnoans, coelacanths, *Acanthodes*, and actinopterygians, of which the latter group (especially platysomids) is the most abundant. Articulated, complete actinopterygians are common, whereas the dipnoans and coelacanths are represented by isolated scales, teeth, and dermal bones. Complete fish become common in unit 2 (shown as the top of the basal massive limestone by Gottfried, 1987a) and are characteristic elements of the biota in units 3 and 4 as well. Only fragments and isolated skeletal elements have been recovered from unit 1. A partial skeleton of a small, possibly symmoriid shark has been collected from the lower part of unit 3, within 5 cm of its basal contact with unit 2. Four small amphibians, including the specimen described by Berman (1973), have also been obtained from units 3 and 4. Plants consist mainly of pteridosperm and *Walchia* leaves and fronds, but fern, cordaitean, lycopsid, and sphenopsid remains are also present (Mamay & Mapes, 1991, and this volume). Several of the plants are of uncertain affinities (Mamay, 1981, 1990). About 30 species of plants are reported from the Kinney Quarry by Mamay & Mapes (1991 and this volume), mostly collected from units 3 and 4.

A moderately diverse invertebrate fauna is also present in units 3 and 4. Unornamented ostracodes, spirorbid worms, and small *Dunbarella* valves are common throughout this interval. The spirorbids are typically attached to plant remains. Conchostracans continue upward from the basal limestone through unit 2, and are very abundant in the lower 8 to 10 cm of unit 3 where they occur as isolated individuals or in clusters of 10 or more valves. The small malacostracan crustaceans described by Schram & Schram (1979) appear to be restricted to a 4 cm thick zone just above the conchostracan-bearing part of unit 3. A small, high-spired, as yet unidentified gastropod species appears at the top of the basal limestone and is moderately common in units 2 through 4. Insects, myriapods, and possible annelid worms are rare and are not obviously limited to specific horizons in units 3 and 4. Occasional fragments of articulate brachiopods, fenestrate bryozoans, and *Myalina* valves in this interval were reported by Lucas & Huber (1991).

The fauna of units 2 through 4 was designated the fish faunal assemblage by Lucas & Huber (1991). However, more detailed studies of this interval would probably reveal sev-

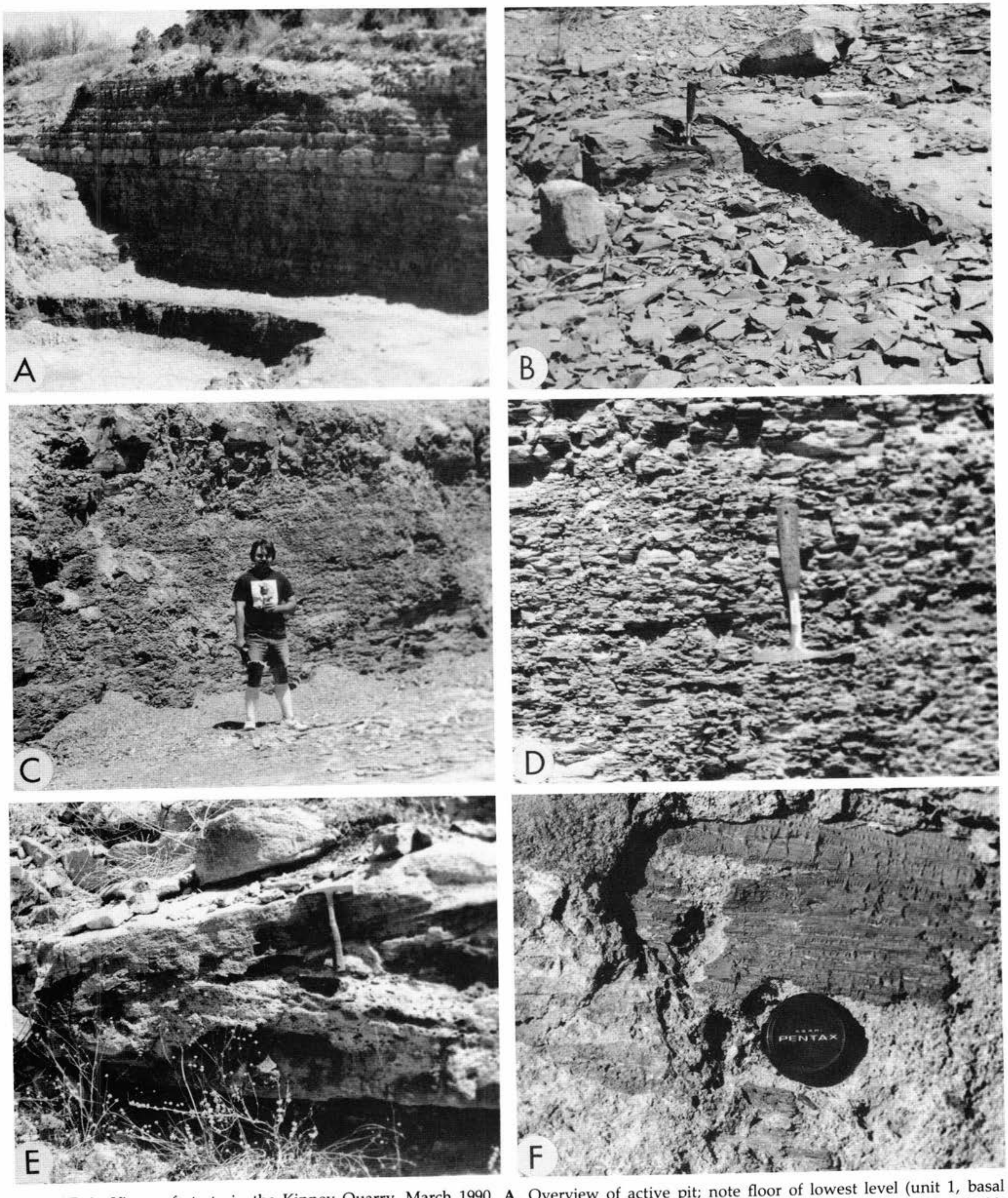


FIGURE 6—Views of strata in the Kinney Quarry, March 1990. **A,** Overview of active pit; note floor of lowest level (unit 1, basal limestone), lower ledge formed on unit 8, and laterally persistent, ledge-forming sandstones near top of quarry face (units 10, 12, 14, 16). **B,** Lowermost limestone (unit 1) at quarry floor. **C,** Lower shale sequence; Phillip Huber is standing on principal fish bed (unit 3), in front of wall composed of units 3 to 7. **D,** Weathered outcrop exposure of shale of unit 5. **E,** Trough-crossbedded fluvial sandstone and conglomerate of unit 17. **F,** Oxidized wood fragment in unit 17.

eral assemblages characterized by subtle differences in biotic composition and relative abundance of the constituent taxa.

Above this lower shale interval are approximately 2 m of generally blockier, thicker-bedded shale composed of laminae ranging from about one to several millimeters in thickness (units 5-7; Figs. 4, 6D). Unit 5 is typically dark gray and slightly to moderately calcareous, whereas unit 6 contains dark greenish-gray claystone intervals. Unit 7 is a thin, mottled greenish-gray and yellowish-brown shale with a thin bed of light-gray plastic clay. Individual laminae in this interval are continuous on strike for at least 10 m. In unit 5 and much of unit 6 the bedding planes at the contact

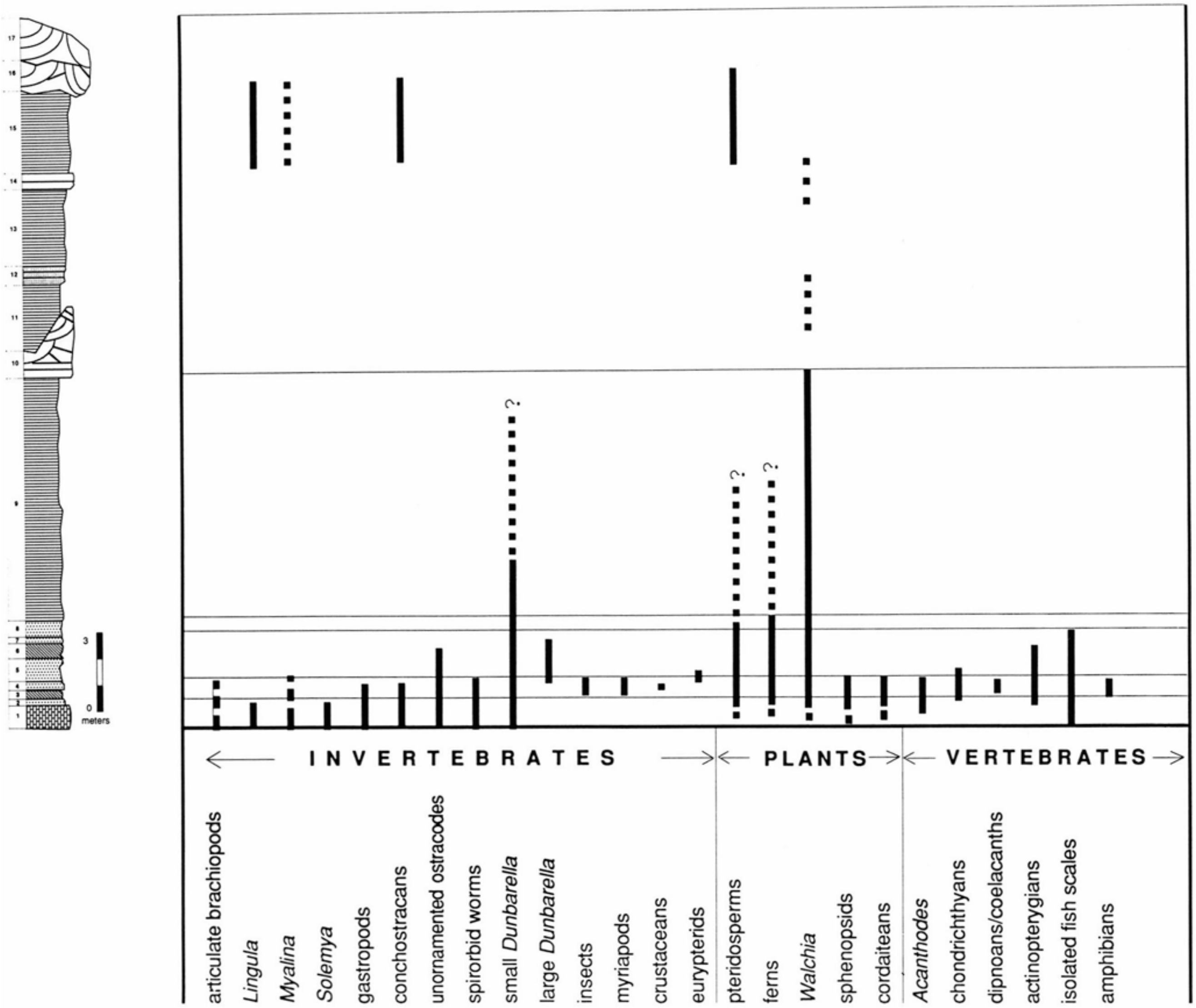


FIGURE 7—Stratigraphic distribution of main groups of animals and plants in the Kinney Quarry section, based mainly on our collections. The main groups of plants may range through more of the section than is indicated here, based on observations of Mamay (written comm. 1991).

between successive laminae are richly fossiliferous. By far the most abundant fossils are leaves and fronds of terrestrial plants (mainly pteridosperms and *Walchia),* and vast numbers of *Dunbarella rectalaterarea* valves. Although *Dunbarella* valves are widely distributed throughout the Kinney sequence, only in unit 5 and part of unit 6 do they attain unusually large sizes. Many of these valves are 35 to 42 mm long, compared with a maximum length of about 15 mm elsewhere in the sequence (see Kues, this volume, for further discussion). These populations of large *Dunbarella* include earlier growth stages as well, down to spat attached to plant fragments (Mamay, 1981, 1990; Kues, this volume). The valves are almost invariably complete and well preserved, although most are disarticulated.

Dunbarella attained nearly complete dominance of the unit 5 and 6 assemblage, comprising in many cases 100% of the preserved animal remains. Other constituents of this assemblage are rare. Unornamented ostracodes and a few actinopterygian fishes are present; the two known Kinney eurypterid specimens probably were collected from unit 5. The low diversity of animals and dominance of large dunbarellas in units 5 and 6 contrast strongly with the more diverse fauna present in units 3 and 4. We have not noticed significant differences in the composition of floras within the two intervals. Lucas & Huber (1991) designated the plants of units 2 through 7 as belonging to a pteridosperm floral assemblage. More detailed paleobotanical studies tied to specific strata may eventually indicate that subtle differences do exist.

Above, and in gradational contact with unit 7, are 10.7 m of greenish- to olive-gray, slightly calcareous, silty shales which coarsen upward slightly (units 8 and 9). This interval represents most of the lower part of the Kinney sequence and extends to the base of the lowest prominent sandstone body (Fig. 4). On outcrop, these units appear blockier and more massive than underlying shale units, with unit 8 forming a minor but persistent ledge around the walls of the quarry (Figs. 4, 6A). Laminae are less distinct and appear to be thicker than lower in the section. Detailed, bed-bybed examination of this thick interval has not been done, but in general it is poorly fossiliferous. Plant fragments (mainly *Walchia)* and small *Dunbarella* valves are sporadically distributed through units 8 and 9 (Lucas & Huber, 1991), and some horizons appear to be unfossiliferous.

The first major sandstone bed (unit 10) in the Kinney sequence is conspicuously exposed about 12 m above the basal limestone. It is a tan, fine- to very-fine-grained lenticular body with laminar and trough-crossbedding, which pinches out after about 100 m of lateral exposure. Above this lowest sandstone is a 10 m thick sequence (units 1116) of relatively thick, olive-gray, silty shale and claystone units interbedded with three thinner, lenticular, ledge-forming, brown to orange sandstone bodies displaying laminar to ripple-laminar structure (Figs. 4, 6A). The lower shale units (11 and 13) are apparently poorly fossiliferous, but have not yet been examined closely. Large pieces of carbonized wood and badly macerated conifer debris were the only fossils reported by Lucas & Huber (1991). Unit 15, the uppermost shale exposed in the quarry, is not lithologically different from units 11 and 13, but a more detailed search for fossils revealed a moderately abundant, low-diversity biota. This biota consists mainly of small *Dunbarella* valves, with a few specimens of *Lingula* and conchostracans, small plant fragments, and one *Myalina* valve. The Kinney Quarry section is completed by a 1 m thick unit of limestone-pebble conglomerate with clasts as much as 8 cm in diameter, and grayish-yellow, trough-crossbedded, subarkosic to sublithic arenite (unit 17; Fig. 6E, F).

Depositional environments

Most workers who have studied specific elements of the Kinney biota (derived mainly from the most fossiliferous lower shale intervals, units 2-5 of our section) briefly speculated on the environmental conditions in which this biota lived. There has been general agreement that the excellent preservation of fragile faunal and floral elements (e.g. complete fish, articulated amphibian skeletons, large plant fronds, little evidence of fragmentation of invertebrate shells) suggests quiet conditions, and that the composition of the lower-shale biota (terrestrial plants, insects, myriapods, amphibians, etc.) indicates brackish or fresh water rather than normal marine salinity. Many workers (e.g. Berman, 1973; Zidek, 1975; Clark, 1978; Schram & Schram, 1979; Mamay, 1981; Kues, 1985) suggested a lagoonal environment for the lower shale beds, although Gottfried (1987a) disagreed, citing the absence of structures and bioturbation that would be expected in a lagoon. The entire Kinney section clearly represents a regressive sequence (e.g. Gottfried, 1987a; Huber et al., 1989; developed in more detail by Lucas & Huber, 1991) probably associated with a prograding-delta system. Studies undertaken for the present symposium by several workers have contributed additional information and a variety of interpretations for some aspects of the depositional environments preserved in the quarry. Here we summarize the progression of paleoenvironments within the Kinney sequence, based on interpretation of the stratigraphy, sedimentology, and paleontology.

The basal limestone (unit 1) represents deposition on a relatively shallow carbonate shelf that was beginning to experience the effects of delta progradation into the area. The water was of normal marine, but possibly somewhat variable, salinity and quiet. The fauna is relatively low in diversity compared to open-marine faunas of similar age in the Manzanita and Manzano Mountains, and is dominated by eurytopic marine organisms *(Lingula, Myalina, Solemya)* that tolerated influx of fresh water, terrestrial siliciclastic sediments, and organic material from nearby land areas. Smaller numbers of stenohaline marine taxa and brackish organisms (e.g. conchostracans, ostracodes) are also present in the fauna; the latter were probably transported from nearer-shore or terrestrial aqueous environments. This fauna and its paleoecology are discussed in detail by Kues (this volume). The biota and lithology of this argillaceous limestone are consistent with deposition in a quiet, sheltered bay or lagoon, relatively close to the edge of a delta, but sufficiently connected with more open marine environments to maintain salinity and carbonate deposition at normal or near-normal levels.

The overlying fish- and plant-dominated shale beds (units 2-4) reflect deposition in conditions of lowered salinity. Most of the restricted-marine taxa from unit 1 disappear through unit 2 and are replaced by a variety of terrestrial and nonmarine aquatic taxa. The uniform fine grain size, fine laminations, lack of bioturbation, dark color, and good preservation of soft-bodied organisms suggest that deposition of units 2 through 4 occurred in quiet, possibly oxygen-poor waters with restricted circulation (Lucas & Huber, 1991; Lehman, 1991). The occurrence of rare, typically fragmented stenohaline groups indicates that connection with normal marine environments persisted.

The observations above are consistent with deposition of units 2 through 4 in a lagoonal or estuarine environment that was closer to the shoreline than the unit 1 sediments and biota. This environment was dominated by the influx of fine-grained clastic sediments and water of low salinity from terrestrial environments, and possibly represents the proximal portions of a deeply indented embayment developed on the delta front. Restriction of this bay by prograding lobes of the delta along its margins may also have been important. Lehman (1991) argued that the depth of this bay or lagoon was at least 15 to 20 m and perhaps as much as 30 to 60 m, and suggested that units 2-4 were deposited from 2 to 30 km away from the shoreline. The presence of occasional marine fossils in these units makes it more likely that the shoreline was a few kilometers rather than tens of kilometers distant. The well-preserved plant fossils in this and overlying shale intervals were derived from vegetation growing along sluggish watercourses emptying into the bay or lagoon (Mamay, 1981).

In units 5 through 7 the estimated volume of terrestrial plants remains high but the fauna changes considerably, becoming much less diverse and dominated by unusually large specimens of *Dunbarella*. The low diversity, virtual absence of marine organisms, and abundance of well-preserved plants suggest greater fresh-water influence and lower salinity than the unit 2-4 environment. A single orthoconic nautiloid and a single *Myalina* valve are the only specimens of marine taxa we have observed in unit 5. Current activity and water agitation were essentially nil. The part of the estuary or lagoon in which units 5-7 were deposited appears to have been a low-salinity, perhaps nearly freshwater environment beyond the tolerance ranges of most brackish groups in units 2-4. Only *Dunbarella* thrived in these conditions, although occasional ostracodes, actinopterygian fishes, and eurypterids were also present.

The strata of units 5-7 are conspicuously laminar. Lamina thickness progressively increases from less than 1 mm in unit 3 to more than 4 mm in unit 5. In unit 5 lamina thickness is variable, ranging from 1.4 to 3.5 mm through one 25 mm thick interval. These laminae clearly represent cyclic packages of sediment. Most of the thickness of each lamina is composed of poorly fossiliferous claystone, with a thin interval between successive laminae that bears high concentrations of plant and *Dunbarella* fossils and disseminated organic material. Each lamina includes five or rnore much finer, dark- and light-colored zones (Archer & Clark, 1991). The major laminae have been interpreted as yearly varves (e.g. Clark, 1978; Mamay, 1990; Lehman, 1991; Anderson, pers. comm. 1990) and as two-week tidal rhythmites (e.g. Feldman et al., 1991; Archer & Clark, 1991; Lorenz et al., 1991; all also in this volume).

Correct assessment of the genesis of these laminae has implications for reconstruction of the paleoenvironments of the lower shale portion of the Kinney sequence. For example, one can visualize the unit 5-7 environment as remote from marine environments and possibly enclosed or nearly enclosed by delta-plain lobes. During the Late Pennsylvanian, New Mexico was situated within about 10° north of the equator, along the west coast of Pangaea (Scotese et al., 1979). Climate models (e.g. Kutzbach & Gallimore, 1989) suggest a summer monsoonal rainy season and relatively arid winter conditions in this area. Seasonal fluctuations in fresh-water and sediment influx into a shallow, nearly enclosed body of water could account for varved sedimentation as well as elevated mortality rates leading to concentration of organic remains in thin zones within each lamina (see Kues, this volume, for additional discussion relevant to *Dunbarella* paleoecology).

Alternatively, if units 5-7 represent proximal sediments within an estuary that was broadly and continuously connected to marine environments several kilometers away, tidal cycles would have been more likely to have left their sedimentary imprint. Feldman et al. (1991 and this volume) and Archer & Clark (1991 and this volume) argue persuasively that the laminae represent two-week tidal cycles, based on comparison with similar modern and inferred late Paleozoic tidally dominated sequences. Tidally dominated sedimentary deposition may be significant at great distances upstream in a fluvial/estuarine system, and amplified in the narrower, proximal portions of an estuary (Feldman & Archer, pers. comm. 1991). Additional study of the stratigraphic variation, detailed fossil distribution, and microsedimentology of these laminae is continuing.

Mudcracks have been reported in the unit 3-6 interval (Berman, 1973; Feldman et al., 1991, and this volume), which would support the idea of deposition in a tidal environment. We have observed mudcrack-like structures in this interval, but believe they represent weathered joint patterns rather than true desiccation structures. Lehman (1991) also noted that this environment was not subject to desiccation.

The thick sequences of overlying silty shales (units 8 and 9) appear to reflect increased sedimentation rates associated with higher levels of fluvial discharge into the Kinney Quarry area. As noted above, biotic remains are relatively sparse—mainly small fragments of *Walchia* and small *Dunbarella* valves—with some intervals apparently unfossiliferous. Details of fossil abundance, distribution, and taxonomic composition in this interval remain to be studied. Tentatively, we interpret the unit 8-9 sequence as representing further sedimentary infilling of the estuary or lagoon, at a faster rate than previously, in environments remote from marine influence. *Walchia* has been considered part of a relatively xerophytic, inland flora (e.g. Ash & Tidwell, 1982). Certainly the genus is common in the slightly younger (Wolfcampian) Abo Formation in central New Mexico, an entirely nonmarine unit for which there is good evidence of deposition in arid climates (Hunt, 1983). The increase in *Walchia* fragments in units 8-9 may reflect closer proximity to inland areas where these conifers were presumably growing in greater abundance. Lorenz et al. (1991 and this volume) interpret this part of the section as prodeltaic; complete absence of marine organisms suggests an interior location possibly close to delta-front or marginal delta-plain environments.

The overlying sequence of three laminar/ripple-laminar to trough-crossbedded sandstone ledges and two interbedded shale/claystone intervals (units 10-14) is interpreted as overlapping distributary mouth bars and associated deposits representing the maximum regressive stage of the Kinney sequence (Lorenz et al., 1991, and this volume; Lucas & Huber, 1991). By analogy with modern deltas (e.g. Gould, 1970), these bar sands developed at the mouths of distributaries at the slope break between the delta plain and delta front. Detailed examination of the shale intervals (units 11, 13) has not yet been completed, so little information regarding their fossil content is available. Only sparse plant debris has been reported (Lucas & Huber, 1991). However, unit 15, which is a similar shale bed above the third sandstone ledge, contains a low-diversity biota consisting mainly of *Dunbarella* but including also *Lingula*, *Myalina*, conchostracans, and small plant leaves and stems. The diversity of this assemblage is much lower than that of the restricted-marine assemblage in unit 1, but the presence of *Lingula* and *Myalina* indicates significant marine influence. Slight migration of the delta plain may have resulted in a transitory transgression of marine waters into the Kinney area. The environment was probably still somewhat brackish, particularly if unit 15 sediments were deposited near a distributary mouth, but the influx of marine waters must have raised the salinity to the lowest levels tolerated by *Lingula* and *Myalina*. Conchostracans were restricted to nonmarine conditions during the late Paleozoic (Calver, 1968; Petzold & Lane, 1988). Therefore, their occurrence in unit 15 may reflect a few individuals living at the upper range of their salinity tolerance, or they may have floated in from slightly more landward, less saline portions of the Kinney bay.

Units 16 and 17, the upper sandstones and limestone-pebble conglomerate of the Kinney sequence, are unfossiliferous except for sparse woody-plant fragments. These units appear to represent another series of distributary mouth bars that were partially eroded by fluvial channels during a subsequent drop in sea level (Lorenz et al., 1991, and this volume).

Concluding remarks

Although much has been learned about the unusual faunas, floras, and depositional environments of the Kinney Quarry in recent years, studies completed by the time of this symposium should not be considered exhaustive. Many of the plants, fishes, and invertebrates remain to be described, and the need for more detailed studies of the stratigraphy and depositional environments on a very fine scale will hopefully beckon future investigators. The quarry strata would be very amenable to a multidisciplinary, lamina-by-lamina study over a relatively broad area, which would no doubt bring to light additional plant and animal taxa as well as provide the means for tracking subtle changes in sedimentation, laminae thickness, and biotic constituents and relationships. Additional field studies outside the confines of the quarry are needed to determine, for example, whether normal, open-marine faunas and environments are present immediately below the basal, restricted-marine limestone assemblages, and whether the regressive sequence exposed in the quarry can be recognized in the Pine Shadow Member outcrops elsewhere in the Manzanita and Manzano Mountains. Thus, the studies of the Kinney Quarry strata and fossils presented in this volume represent only a first step toward complete understanding of the remarkable Late Pennsylvanian record preserved there.

Acknowledgments

We thank Jiri Zidek, New Mexico Bureau of Mines & Mineral Resources, and Sergius Mamay, National Museum of Natural History, for reviewing the manuscript and offering helpful suggestions for its improvement. Both reviewers also supplied historical information relating to the early history of collecting at the Kinney Quarry.

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Sedimentation patterns in Pennsylvanian strata at the Kinney Brick Company Quarry, Bernalillo County, New Mexico

John C. Lorenz[1], Gary A. Smith[2], and Spencer G. Lucas[3]

[1]Division 6253, Sandia National Laboratories, Albuquerque, New Mexico 87185; [2]Department of Geology, University of New Mexico, Albuquerque, New Mexico 87131; [3]New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, New Mexico 87104

Abstract—The Kinney Brick Company Quarry, Bernalillo County, New Mexico, preserves a depositional environment unique within the Pennsylvanian strata of central New Mexico. The quarry floor consists of black, fossiliferous, micritic limestone deposited in a restricted nearshore-marine environment. The overlying 2.5 m of laminated shale were deposited in an estuarine or bay environment, possibly with significant fresh-water influence, as indicated by a well-developed, *Dunbarella*-dominated assemblage that includes conchostracans, ostracodes, amphibians, seed ferns, and other terrestrial organisms. This zone may contain tidal rhythmites. The next 11 m consist of laminated prodelta silty shales that represent an increased sedimentation rate associated with the onset of significant fluvial discharge into the bay. Rapid sedimentation stressed the *Dunbarella* assemblage and the fluvial system introduced an influx of terrestrial conifer debris. The regression culminated in a series of up to three small, overlapping distributary mouth bars (distal bayhead deltas) consisting dominantly of planar-horizontally bedded sandstones. The bars are up to 4 m thick and gradually thin laterally. The package of sandstone bars and interbedded silty shales varies in thickness from 3 to 7 m. Bedding through the sandstones locally offlaps to the south at a very low angle. A brief transgression interrupted sedimentation and was accompanied by the return of the stressed, small *Dunbarella–Lingula* assemblage in a prodelta silty shale 4-5 m thick. Another series of distributary mouth-bar sandstones overlies the siltstones, forming the uppermost strata exposed in the quarry. Fluvial channels containing carbonate ripup clasts and very coarse, crossbedded sandstone were locally eroded into the bars, probably during a fall in sea level. Paleoflow was to the south.

Introduction

This paper provides a context for the richly fossiliferous but relatively thin productive zones found in the Kinney Brick Company Quarry (Fig. 1). By describing and interpreting the entire 28 m thick sedimentary sequence, the depositional system can be reconstructed as it changed through time, and the more specific environments in which the fossiliferous beds were deposited can be better understood. Interpretation of the integrated system, based on building blocks of individual facies, in turn assists in the interpretation of the individual beds. An understanding of the system also allows its placement within the large-scale context of Pennsylvanian paleogeography and transgressive-regressive cycles.

Regional Pennsylvanian paleogeography, tectonics, and eustacy

During Middle Pennsylvanian to Early Permian time, central New Mexico was partitioned into a series of generally north-south-trending, fault-bounded uplifts and basins of the southern ancestral Rocky Mountains. These structures are generally believed to have developed as a very broad, wrench-faulted foreland to the Marathon orogeny (Kluth & Coney, 1981; Grant & Foster, 1989). Present-day outcrops of Pennsylvanian strata are restricted to Laramide (early Tertiary) and Basin-and-Range (late Tertiary) uplifts that also trend largely north-south, providing relatively continuous exposures parallel to the Pennsylvanian depositional strike.

Pennsylvanian rocks in the Sandia-Manzanita-Manzano-Los Pinos Mountains outcrop belt are assigned to the Atokan Sandia Formation and the Desmoinesian-Virgilian Madera Group (formerly Madera Limestone) (Myers, 1973). Clastic and carbonate lithologies are intimately interbedded throughout the section, but clastics are most abundant in Atokan, Missourian, and Virgilian strata (the latter including rocks exposed in the Kinney Quarry; Fig. 2), whereas limestones dominate the Desmoinesian section. Sandstones and conglomerates reflect a largely granitic provenance, presumably the Pedernal uplift 70 km to the east. Pennsylvanian strata in the Sandia, Manzanita, and Manzano Mountains were deposited on a west-sloping shelf or ramp

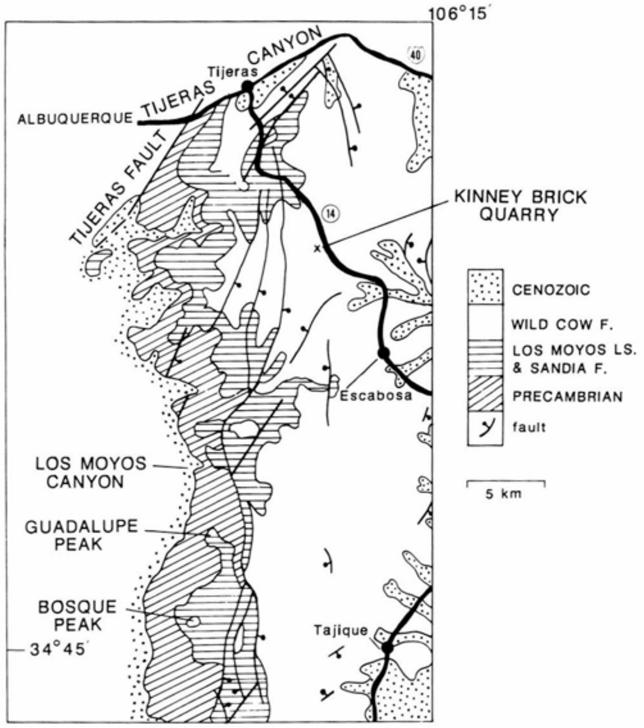

FIGURE 1—Location of Kinney Brick Company Quarry, Bernalillo County, New Mexico (from Lucas & Huber, 1991).

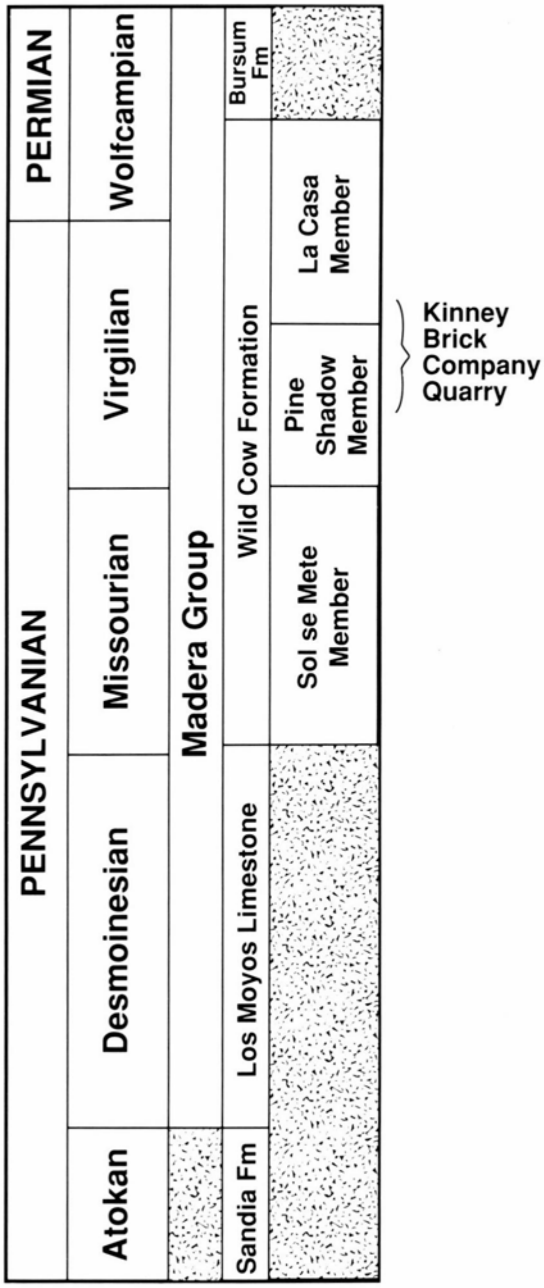

FIGURE 2—Summary stratigraphic chart showing the position of the strata found in the Kinney Brick Company Quarry (after Lucas & Huber, 1991).

separated from the Pedernal uplift by the intervening, 10 km wide Estancia basin, which filled with 1.2 km of Pennsylvanian clastics (Grant & Foster, 1989).

Rhythmic alternations of elastic and carbonate lithologies in central New Mexico are broadly similar to Pennsylvanian cyclic sequences in central North America. Heckel (1986) and Boardman & Heckel (1989) argue that cyclothems of the Midcontinent region formed in response to glacioeustatic sea-level fluctuations driven by expansion and contraction of Gondwana ice sheets. Variations in tectonic subsidence and autogenic processes related to delta pro-gradation may also have influenced cyclicity in the ancestral Rocky Mountain basins, but eustacy was probably the dominant factor in the stratigraphic cyclicity present in central New Mexico.

Madera Group cycles in this region are composed of successive, asymmetric, upward-shoaling sequences. Typical cycles consist of nonmarine elastics that disconformably overlie subtidal limestones (commonly consisting of a thin shoreface grainstone resting erosively on below-wave-base wackestones and mudstones: Smith, 1989a, b; Wiberg & Smith, 1991). The lack of intertidal carbonates, the paucity of shallow-water clastics marking the progradation of delta fronts, and the characteristic occurrence of abundant early meteoric phreatic (and rarely vadose) cements in uppermost regressive grainstones all argue for relative sea-level falls, followed by transgressive flooding, to generate Madera Group cycles (Smith, 1989a, b). Desmoinesian sequences, with reference to the biostratigraphy developed by Myers (1973, 1988), are correlative to inter-regional, fourth-order eustatic sea-level curves developed by Ross & Ross (1987) (Wiberg & Smith, 1991). Rough periodicities of 200 ky to 400 ky are indicated by preserved cycles in the younger strata, similar to dominant glacioeustatic periodicities for the Late Pennsylvanian (Ross & Ross, 1987; Algeo & Wilkinson, 1988). Part of one of these cycles is preserved in exposures at the Kinney Quarry. The sharp upward increase in limestone that marks the stratigraphic base of the Madera Group probably corresponds to the second-order sea-level rise that characterizes the Atokan—Desmoinesian boundary worldwide (Ross & Ross, 1987). The greater abundance of clastics in younger Pennsylvanian strata corresponds to a second-order highstand and a contemporaneous influx of clastics from high-standing ancestral Rocky Mountain uplifts.

Kinney Quarry strata are of Virgilian age and belong mostly to the Pine Shadow Member of the Wild Cow Formation of the Madera Group. The uppermost, coarse-grained sandstone is assigned to the La Casa Member (Myers & McKay, 1976). Myers (1973, 1988) interpreted the basal arkosic sandstone of the La Casa Member to be of regional extent, probably representing deposition following a significant relative sea-level fall. Reconnaissance in the Sandia and Manzano Mountains (Smith, unpubl.; Myers, 1988) and mapping by Myers (1969) and Myers & McKay (1976) show the underlying uppermost Pine Shadow Member to be represented typically by calcareous shales, lime mudstones, and wackestones deposited below wave base. The anomalously clastic-rich section at the Kinney Quarry, therefore, is probably associated with the local progradation of a deltaic headland.

Previous work

Lucas & Huber (1991) summarized studies at the Kinney Quarry prior to the 1991 symposium held at the Geological Society of America Rocky Mountain/South-Central Sections Meeting in Albuquerque, April 1991. Most of the previous studies have focused on describing fossil organisms from the quarry. However, stratigraphic data on the quarry have been presented by Stuckey (1967), Gottfried (1987), and Huber et al. (1989), and they, and many other authors (e.g. Berman, 1973; Zidek, 1975; Clark, 1978; Schram, 1981; Kues, 1985) have commented on the depositional environments of the fossiliferous strata at the quarry. It is important to note that these comments mostly pertain to the lowermost strata at the quarry, for these are the strata from which most fossils have been collected. The present study includes the fossiliferous zones and the overlying exposed strata. In brief, most previous authors have recognized the transition from marine to fresh-water sediments exposed at the quarry. Characterizations of the specific depositional environment of the fossiliferous strata have ranged from nearshore marine to estuarine to lagoonal to deltaic, all probably more or less correct depending on which strata are being discussed.

Strata of the Kinney Brick Company Quarry

The rocks that crop out in the high wall of the Kinney Brick Company Quarry are relatively well exposed (Figs. 3,

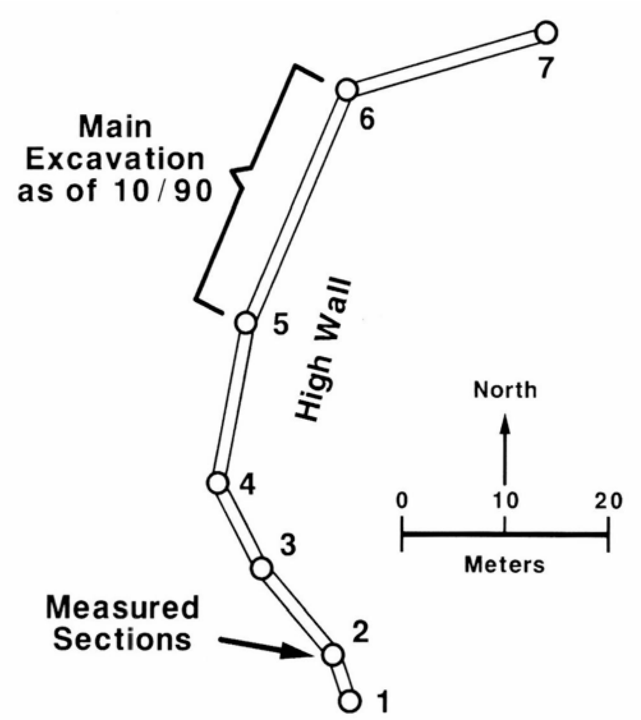

FIGURE 3—Plan view of quarry high wall and location of measured sections.

4) by the quarrying operations, although talus obscures some areas and others are inaccessible due to the steepness of the wall. Photomosaics were used extensively during this study in order to facilitate correlation of beds and to outline the geometry of the sandstones (which is commonly obscured). The exposed strata are about 28 m thick and consist of a generally coarsening-upward sequence, with notable exceptions, beginning with a basal limestone, followed upward by shale, sandstone, and finally a conglomeratic sandstone (Fig. 5).

Limestone

The floor of the quarry consists of an organic-rich, irregularly laminated, clayey micrite of unknown (at least 1 m) thickness (unit 1 of Fig. 5). It contains a marine to brackish-water brachiopod fauna and a terrestrial, primarily coastal-swamp-type floral assemblage that includes calamites, pteridosperms, cordaitaleans, and *Walchia* (conifers). The marine fauna is of relatively low diversity, dominated by eurytopic organisms like the brachiopod *Lingula* and the bivalves *Myalina* and *Solemya* (Kues, 1991). Also common are conchostracans, unornamented ostracodes, the pectinacean bivalve *Dunbarella,* small ammonoids, and the articulate brachiopod *Chonetinella.* Plant fragments and fish debris are also present. This fossil assemblage is much less diverse than the more "normal" marine Madera Group facies. Characteristic marine groups such as fusulinids, echinoderms, corals, and bryozoans are absent and articulate brachiopods are poorly represented.

These data suggest a nearshore, restricted-marine environment with local and/or episodic influxes of fresh water. The limestone is significantly different from the common open-shelf marine limestones of the local Pennsylvanian strata, but it is not dissimilar to other dark-gray micrites of the Madera Group that are probably of subtidal, lagoonal origin. The presence of clay, brackish-water fauna, and terrestrial flora indicate that a not-too-distant source of fresh water and of terrestrial clastics was beginning to encroach on the area. Thus, the lowest strata exposed in the quarry record the first stages of the filling of a restricted-marine environment by terrestrial clastics derived from a fluvial source. The overlying coarsening-upward strata record specific environments associated with a general continuation of this regression.

Calcareous organic shales

The 0.5 m thick interval overlying the limestone consists of an organic- and clay-rich micrite which grades up into a calcareous shale, providing a transition interval between the limestone and the overlying silty shales. This well-laminated zone (units 2-4 of Fig. 5) comprises the main collection horizon for fossil fish.

The 10 cm of platy limestone/calcareous shale immediately above the basal limestone contain a fossil assemblage dominated by fishes and terrestrial plants. The 40 cm of calcareous shale above this bed contain a similar fossil assemblage. Unornamented ostracodes, spirorbid worms, conchostracans, and small *Dunbarella* are also common. The crustaceans, eurypterids, insects, myriapods, and amphibians described from the Kinney Quarry are from this strati-graphic interval, but they are rare or at least limited to abundance on one or a few bedding planes. The fossils from units 2-4, though treated as a single fossil assemblage by Lucas & Huber (1991), represent a complex array of small assemblages dominated by fishes and terrestrial plants. These assemblages contain a significant component of fresh-water and terrestrial organisms and are almost devoid of marine organisms (except for fragmentary and uncommon fenestrate bryozoans, articulate brachiopods, and orthoconic nautiloids).

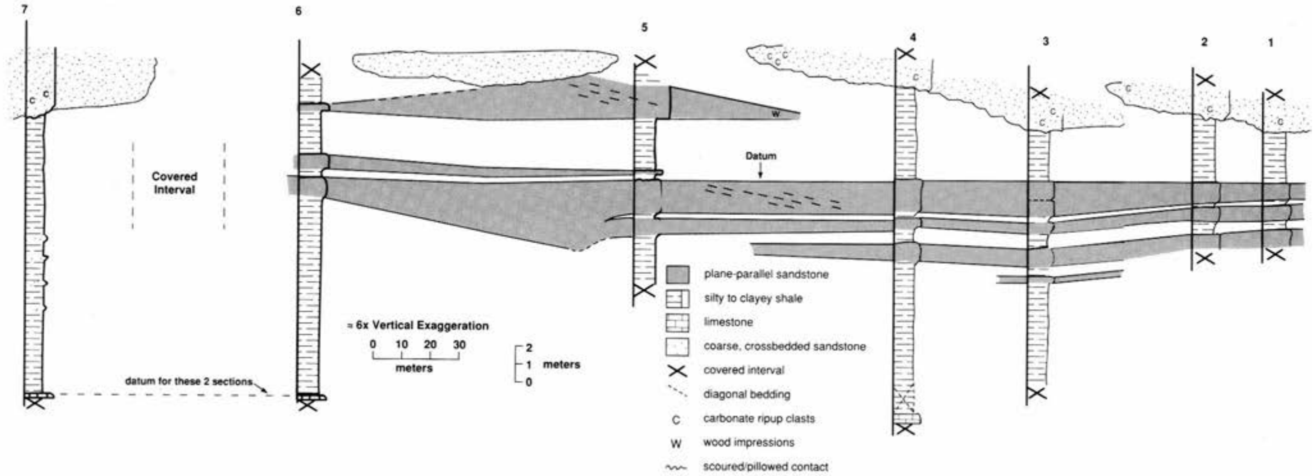

FIGURE 4—Correlated measured sections along high wall of Kinney Brick Company Quarry. Bed A correlates with Fig. 7.

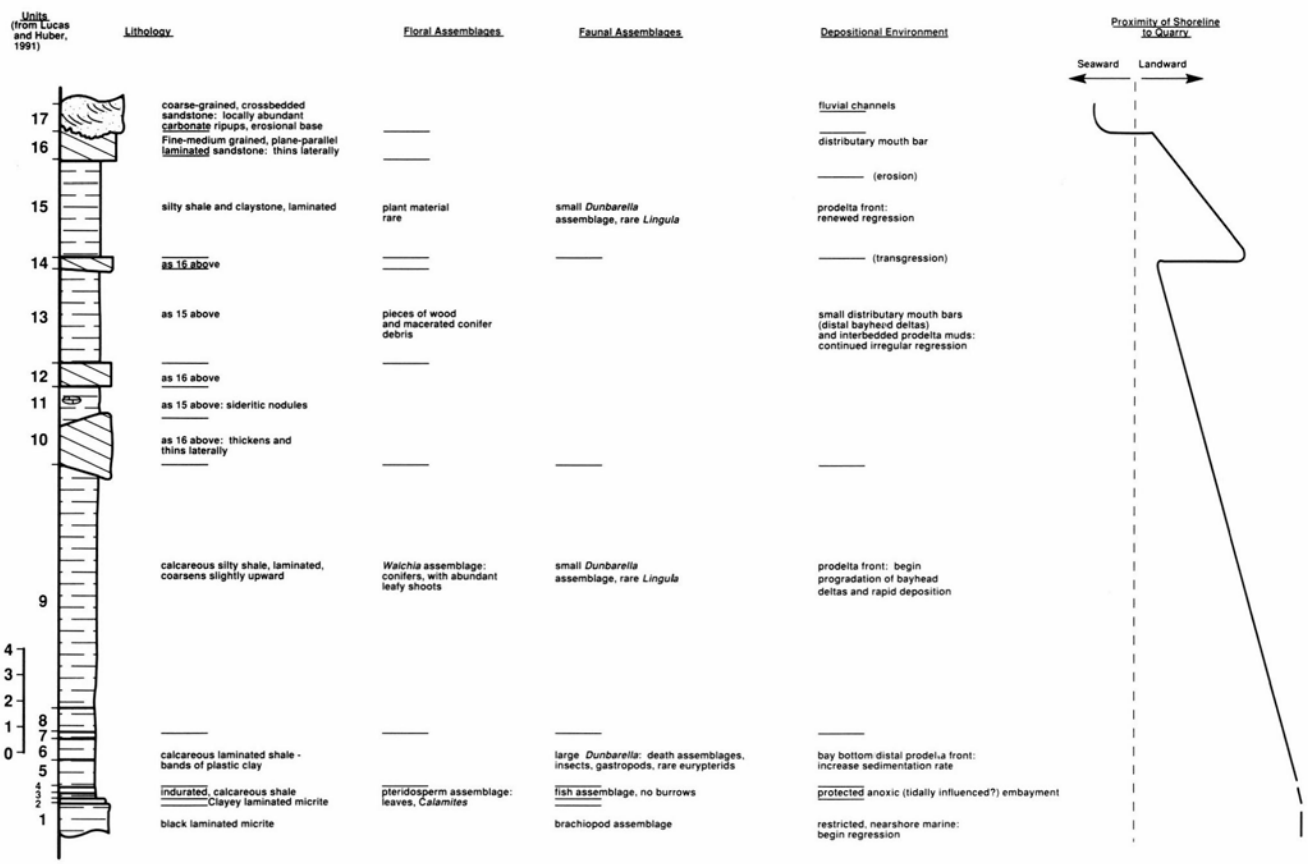

FIGURE 5—Summary chart of type section lithology and fossil assemblages in the Kinney Brick Company Quarry.

Preservation of organic material, soft-bodied organisms, fine laminations, and articulated fish, along with the absence of burrows, suggest an anoxic, very low-energy depositional environment. The fossils also suggest waters of greatly reduced salinity and oxygen content relative to those in which the unit 1 limestone was deposited. The terrestrial pteridosperm floral assemblage is still present, indicating a continued nonmarine source for the associated clays, but this environment was significantly more restricted than that in which the underlying limestone was deposited, and may represent a deep lagoon or bay.

Episodic high-energy (storm?) events in nearby marine environments may be suggested by local fragmentary and disarticulated allochthonous fossil debris (nautiloids, brachiopods, fenestrate bryozoans: Lucas & Huber, 1991). It has also been suggested that the millimeter-scale laminations represent the influence of tidal variations (Kvale, pers. comm. 1990; Feldman et al., 1991) or "varves" (Lehman, 1991). Although it is difficult to reconcile the continually fluctuating currents of a fully developed tidal system with the apparently anoxic, low-energy conditions suggested by the fossil and sedimentary record, these laminations may represent a minimal tidal influence on deposition within a protected embayment. If they are in fact tidal laminations, then this half-meter-thick bed was deposited in about a year. If they are seasonal laminations, however, then a time span of several hundreds of years is suggested. Laminations of this type are also common, however, in the deposits of distal prodelta/ bay environments simply due to the episodic nature of flow in the rivers which transport the clays and silts into the bays, where they settle vertically.

Silty shales

The laminated character of the shales persists upward as they become less organic, less calcareous, and increasingly silty. The 2 m of laminated silty shale (units 5-7 of Fig. 5) that overlie the transitional zone contain a distinctive faunal assemblage dominated by *Dunbarella* and containing insects, fish, and rare eurypterids. The *Dunbarella* shells include all growth stages and are commonly restricted to specific (though numerous) horizons, suggesting mass-mortality assemblages (Archer & Clark, 1991). The transition from the underlying anoxic environment to this slightly coarser-grained depositional setting probably records an increase in the rate of sedimentation on the bottom of the bay, concurrent with the migration of a fluvial system into the bay nearby. This unit may in fact represent a distal prodelta facies. The mass-mortality *Dunbarella* laminae may have resulted from regular seasonal flooding of the river system, producing bay waters that were fresh enough to kill the bivalves, and a lamination of fresh sediment on which to deposit them at the same time.

The laminated silty shales continue upward for another 10 to 11 m (units 8 and 9 of Fig. 5), becoming slightly more silty upward and containing several beds of sandstone up to 20 cm thick in the upper 3 to 4 m. The beds are moderately bioturbated in this interval. Intensive sampling of fossils at the Kinney Quarry has focused on the lowermost strata exposed (units 1-7). Thus, paleontological data from the remainder of the quarry section are somewhat less reliable indicators of environment. The faunal diversity in units 8 and 9 is markedly decreased, being dominated by small *Dunbarella* shells, with less common brackish-water brachiopods. These fossils are consistent with a fresh-water environment, and their sporadic occurrence and largely fragmentary nature may suggest high rates of sedimentation. Moreover, the floral assemblage in this interval consists almost entirely of walchian-conifer shoots (Lucas & Huber, 1991).

The conifer *Wakhia* has traditionally been interpreted as part of a xerophytic, inland flora (Read, 1947; Ash & Tidwell, 1982). If this interpretation is correct, then *Walchia* in units 8 and 9 is entirely allochthonous and must have floated a considerable distance, since no Virgilian rocks at or around the Kinney Quarry, nor in the Manzanita Mountains as a whole, were deposited in a dry, inland environment. One alternative possibility is that some *Walchia,* like some living conifers (e.g. bald cypress) lived in wet, swampy environments. However, the parautochthonous to autochthonous coastal-swamp flora that dominates the basal limestone is virtually absent in these beds, and the *Walchia* debris may indeed represent significant transport from distant inland environments.

In sum, these data suggest that the local sedimentation rate and fresh-water influx had continued to increase as the bayhead delta prograded nearer to the site of the quarry, which was being covered by prodelta shales. The limited size of the *Dunbarella* fauna suggests more frequent and severe flooding, stressing the organisms so that they did not grow, or killing them before reaching maturity.

Sandstone—shale unit

The overlying sandstone and shale sequence (units 1014 of Fig. 5) is generally unfossiliferous except for pieces of carbonized wood and macerated conifer debris. The shales continue to be laminated, but are interrupted by several beds of sandstone. Up to three distinct sandstone beds, as much as 4 m thick, can be measured in any vertical section, but the beds thicken and thin, and split or merge laterally (Fig. 4). The sandstone—shale unit is from 3 to 7 m thick.

Plane-parallel bedding is the overwhelmingly dominant sedimentary structure, with local, isolated units of crossbedding and with obscure low-amplitude ripple bedding at the tops of beds. A few low-angle internal scours are present, and locally the plane-parallel bedding can be shown to offlap to the south at a very low angle. The sandstone beds overlie the laminated silty shales in an uneroded, parallelto-bedding contact that is gradational over several centimeters.

The sandstones are interpreted as small subaqueous distributary mouth bars in front of the distributary channels of a prograding bayhead delta. They represent continued progradation of the delta system across the quarry site. The carbonized wood and macerated conifer debris are consistent with relatively high discharge and high depositional rates. Several distributary mouth bars are present, indicating temporary abandonment and reactivation of the local distributaries (which apparently did not themselves reach this site). Shallowed water across the bars produced laminar flow and resulted in the dominance of plane-parallel lamination in the sand. Abatement of flow during abandonment produced ripple bedding at the tops of the beds. Each bar was probably deposited relatively rapidly, although the local, shallow scour-and-fill structures indicate temporal and/ or spatial variability in flow strength during deposition of individual bars. The interbedded silty shales contain large pieces of carbonized wood that were deposited beyond the bars where the current decreased.

Distributary mouth bars associated with bayhead deltas have been described in other strata elsewhere (e.g. Coleman & Prior, 1982; Horne et al., 1978; Flores et al., 1984; Van Heerden & Roberts, 1988). The principal differences between these descriptions and the bars at Kinney are the much smaller sizes of the Kinney Quarry deposits and their relative paucity of crossbedding. The widths of larger bars are commonly measured in kilometers, whereas the Kinney Quarry bars are a few hundred meters wide. It is this smaller size and associated shallower waters that probably account for the absence of crossbedding. Otherwise, the bar morphologies are similar, thinning in two directions. It is conceivable that these are lateral splays off a larger distributary system, with an associated full-scale distributary mouth bar nearby.

Upper shales and sandstones

A hiatus in deposition of unknown duration apparently followed deposition of the distributary mouth bars, and the overlying shales mark a return of the laminated-shale/prodelta fades and of the small *Dunbarella* faunal assemblage accompanied by a few specimens of *Lingula.* Conchostracans, small leaf and stem fragments, and one specimen of *Myalina* **(B.** S. Kues, written comm. 1991) are also present. *Lingula* and *Myalina* indicate a marine influence. Whether due to sea-level rise, local subsidence, or temporary abandonment of the local fluvial system and compaction of sediment at the quarry site, a transgression had occurred, and 4 to 5 m of prodelta shale were deposited in this area during the ensuing regression. Plant megafossils are relatively rare in this unit, although Willard (1991) reports that it contains a marsh-influenced palynological record. The local culmination of this regression is represented by a single preserved distributary mouth bar that is about 3 m thick and thins in both directions. It also consists of offlapping plane-parallel-bedded sandstone.

Sandstone—conglomerate

The uppermost strata exposed at the quarry (unit 17 of Fig. 5) consist of lenses of medium- to very coarse-grained, crossbedded sandstones up to about 4 m thick, which contain local carbonate ripup-clast zones. Crossbedding indicates that local paleoflow was to the south (Fig. 6). These beds are locally scoured down into the underlying shale or sandstone (Fig. 7). The coarse, crossbedded sandstone at the very northern end of the quarry may have a lateral facies equivalent consisting of the plane-parallel-bedded facies. The only fossils in these strata are oxidized pieces of petrified wood.

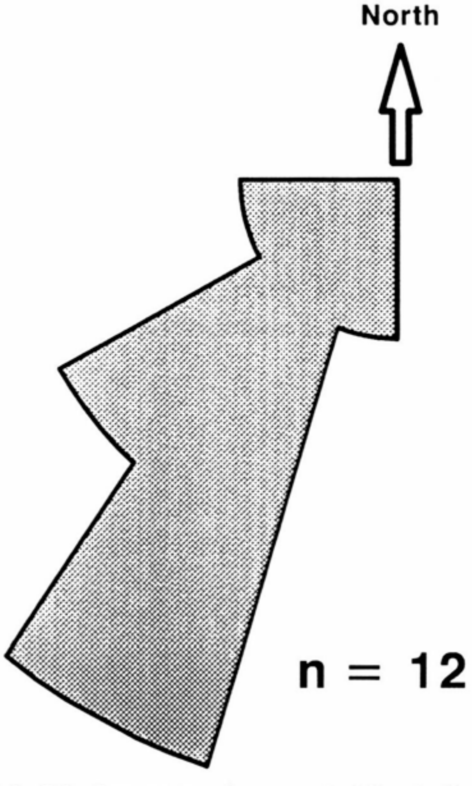

FIGURE 6—Paleoflow vectors from crossbedding in the coarse-grained sandstone facies.

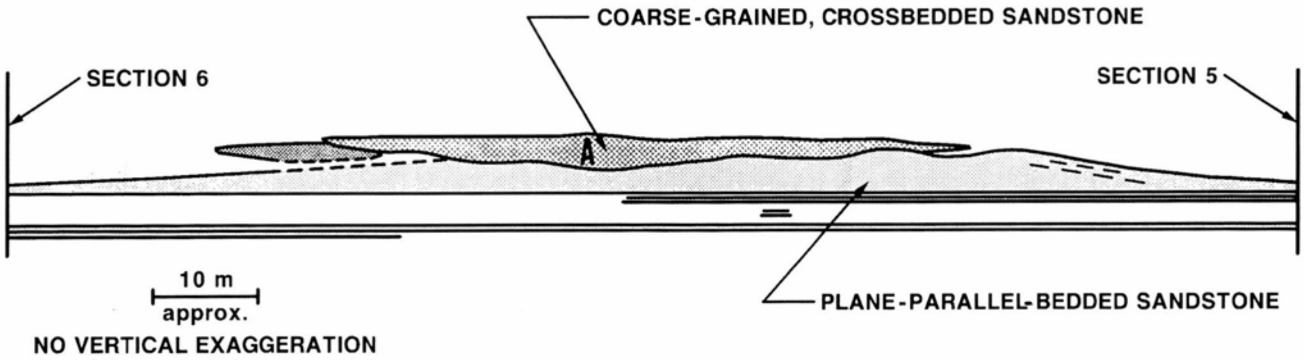

FIGURE 7—Tracing from photomosaic showing a lenticular, coarse-grained, crossbedded sandstone channel incised into a distributary mouth bar. Bed A correlates with Fig. 4.

The coarse-sandstone lenses are inferred to be fluvial channels that were incised during a drop in sea level. As such they are the first deposits at the quarry site to record a nonmarine environment, or one that can be associated with subaerial exposure. The coarse distributary-channel facies was probably never far upstream from the distributary-mouth-bar facies. Local ball-and-pillow structures at the base of the sandstones suggest that the underlying shales were still poorly compacted and that, therefore, the sea-level drop was rapid. The shoreline deposits that would normally be found above the distributary mouth bars and below the fluvial-channel facies were never deposited here, and, as sea level dropped, the fluvial channels prograded rapidly to and beyond the Kinney Quarry site, being incised into the existing subaqueous/marine deposits at the same time. This abrupt facies change corresponds to the transition from the Pine Shadow Member to the overlying La Casa Member of the Wild Cow Formation, and is a regional transition (Myers, 1988) that is probably attributable to a significant relative sea-level fall.

Summary of the local depositional system

The generally coarsening-upward sequence of strata in the Kinney Brick Company Quarry represents the infilling of a restricted-marine bay by a prograding bayhead delta system. The system was similar to, but smaller than, bayhead deltaic systems that have been described in Carboniferous strata of the Appalachian region, in Cretaceous strata of the Rocky Mountain area, and in the modern Atchafalaya basin area (e.g. Horne et al., 1978; Flores et al., 1984; and Van Heerden & Roberts, 1988, respectively).

The basal, clayey, organic-rich limestone represents the initial restriction of the local marine environment, transitional between the clean, fossiliferous open-marine shelf carbonates and the overlying bay fill that is dominated by terrigenous clastics. Once the bay formed, restricted circulation and low energy produced an anoxic environment in which organic compounds and complete fossils were preserved. The silt and clay laminations that form this facies settled out of suspension, probably in a tidally influenced embayment. The excellent preservation allowed by this low-energy, anoxic environment produced the quarry's main fossil-collection horizon.

The beginning of active fluvial discharge into the bay formed a bayhead delta which disrupted the anoxic environments, and is marked by an increase in clay content and decrease in organic content of the strata. It is also signaled by the introduction of the large *Dunbarella* faunal assemblage with its repetitive mass-mortality character. These laminated strata were deposited on the bay bottom in a distal prodelta environment. As the deltaic system encroached on the quarry site, the rate of sedimentation increased and the sediments became siltier. This siltier, still laminated facies is marked by an influx of terrestrial conifer debris and a stressed *Dunbarella* faunal assemblage. Continued progradation brought sandy deposits into the area in the form of small, subaqueous, distributary mouth bars.

This sequence was followed by a temporary transgression (due either to abandonment of the local deltaic system, raised sea level, or subsidence), during which nothing was deposited at the quarry site. The overlying prodelta shales, again containing a stressed *Dunbarella* fauna, record the return to a regressive bay-fill sequence, which is capped by another small distributary mouth bar. Sea level probably dropped rapidly at this time, and the facies prograded rapidly beyond the Kinney Quarry without leaving a record of the shoreline. This progradation caused the coarse-grained fluvial-channel fades of the system to be incised into the existing paralic facies at the site.

Uniqueness of Kinney Quarry strata

The richness and uniqueness of the Kinney Brick Quarry fauna and flora require consideration of why such localities are not more numerous in the Pennsylvanian strata of the region. Coastal-plain or delta-plain lagoons are recorded throughout the Missourian and Virgilian section in the Sandia—Manzanita—Manzano Mountains outcrop belt. These facies, however, are rarely more than 1-2 m thick and their fossil content is generally sparse. Within this outcrop belt, coastal-plain and fluvial sediments commonly rest erosively on subtidal carbonate or, rarely, clastic facies. Strandlines apparently stepped rapidly basinward to the west during sea-level falls, superimposing terrestrial facies directly onto offshore marine facies (Smith, 1989a, b). Aggradation of fluvial channels and of related deltaic lagoonal facies took place in response to subsequent relative sea-level rise and formed generally fining-upward retrogradational sequences. These sequences are truncated abruptly by ravinement and marine-flooding surfaces.

The thick, overall paralic progradational facies at the Kinney Brick Quarry correlate along depositional strike to offshore, below-wave-base limestones (Smith, unpubl.; Myers, 1969, 1988; Myers & McKay, 1976). This suggests that the Kinney Quarry marks the site of progradation of a deltaic headland into relatively deep water, probably during a period of rising sea level. This accounts for the anomalous nature of the local uppermost clastics and for the thickerthan-normal paralic facies of the Kinney Quarry. Accommodation space was created by rising sea level and was nearly balanced by the supply of sediment from the river distributaries. Inequality in sediment supply and sea-level rise may have caused the brief deepening recorded by the upper shales and sandstones. Similar depositional sequences may have been generated during other periods of sea-level rise, but they probably occur in farther downdip positions where fluvial systems extended across the gently sloping shelf or ramp during intervals of sea-level fall. The uppermost sandstone—conglomerate at the quarry represents the westward, basinward overstepping of a fluvial system related to sea-level fall.

Upward-coarsening paralic sequences of modest thickness might also be expected as the product of highstand progradation of coastal-plain sequences. At the longitude of the Manzanita Mountains, however, nearly all periods of sea-level rise created below-wave-base conditions, with highstand shorelines becoming stable in (and eventually prograding from) positions many kilometers to the east. The Kinney Brick Quarry site, therefore, is interpreted to represent the unusual case of a deltaic headland that was well enough supplied with sediment to maintain a local shoreline at an intermediate position on the ramp during sea-level rise.

Acknowledgments

We thank S. Hayden, P. Huber, and B. Kues for assistance and discussions of the paleontology. S. Lucas thanks the New Mexico Museum of Natural History, and G. Smith thanks the Caswell Silver Foundation at the University of New Mexico, for support of this study. J. Lorenz thanks Sandia National Laboratories for ancillary support as Adjunct Curator of Geology at the New Mexico Museum of Natural History.

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The Kinney Brick Company Quarry: Preliminary analysis using an estuarine depositional model

Howard R. Feldman[1], Allen W. Archer[2], Ronald R. West[2], and Christopher G. Maples[1]

[1]Kansas Geological Survey, 1930 Constant Avenue, Lawrence, Kansas 66047; [2]Department of Geology, Kansas State University, Manhattan, Kansas 66056

Abstract—Paleontology and sedimentology of the rocks at the Kinney Brick Company Quarry are comparable to biological and sedimentological patterns within modern estuaries. Modern estuaries are characterized by a complex interaction of marine (mostly tidal) and fluvial processes in an environment where salt and fresh waters mix. Estuaries vary widely in the amount of mixing of fresh and salt water, and the resultant water-circulation patterns. However, a feature common to many estuaries, regardless of circulation pattern, is the presence of a turbidity maximum near the middle of the estuary. Fine-grained sediment can be deposited rapidly from this turbidity maximum in the middle estuary. Coarser sediment may occur in both fluvial and more marine parts of the estuary. However, there is little correlation of sedimentary structures or lithofacies patterns with salinity. There is a strong correlation between biotic composition and salinity, but this may be difficult to apply using Paleozoic fossil assemblages.

The sequence of rocks exposed in the Kinney Quarry can be explained as the progradation of muddy estuarine sediments over a carbonate lagoon. Relative sea level was probably shallow during deposition of the entire sequence. A fish bed occurs at the transition from carbonate lagoon sedimentation to siliciclastic, tidally dominated sedimentation. High sedimentation rates are probably necessary to explain the preservational quality of the fish. Tidal processes are now known to be capable of the high rates of deposition required for such excellent preservation.

Introduction

The Kinney Brick Company Quarry (KBCQ) contains a vertical sequence indicative of coastal sedimentation. We suggest that estuarine deposition can explain not only the vertical sequence, but also details of the fine-scale sedimentology. Of particular interest are conditions within estuaries that can maximize fossil preservation because of the potential for rapid deposition. In addition, high stress from salinity variations and rapid sedimentation can reduce predation and scavenging.

Description of the Kinney site

The study is concerned primarily with the limestone bed at the base of the quarry and the *Dunbarella-rich* beds overlying the limestone, because these beds contain all the fish and most of the other fossils in high concentrations. The stratigraphic units we identify differ slightly from those described by Lucas & Huber (1991) (Fig. 1) and are based on lithology, bedding thickness, and fossil content.

Unit 1 is up to 10 cm thick at the base of the quarry and typically breaks conchoidally. It is a thin-bedded, pelletal, ostracode wackestone. Thin (3-5 mm), finely laminated units alternate with thicker (up to 1 cm) bioturbated units. Some laminae are truncated by burrows (Fig. 2A, B). Animal megafossils include branchiopods, *Solemya, Myalina, Wilkingia?, Lingula, Chonetinella, Composita, Dunbarella,* rare echinoderm plates, cephalopod fragments, and bellerophontid gastropods. Plant fossils such as *Dicranophyllum* and *Annularia* are also common. Many of the bivalves and brachiopods, including *Lingula,* are articulated.

Unit 1 grades upward into unit 2, the fish bed. The thickness of unit 2 ranges from 6 to 14 cm. Unit 2 is similar petrographically to unit 1, except that it is well laminated throughout (Fig. 2B) and breaks readily along these laminations. Laminations are not truncated by burrows. Some laminations are crudely graded from microspar and shell hash at the base to organic-rich micrite at the top. Invertebrate megafossils are rare in unit 2, but include branchiopods, *Dunbarella,* and high-spired gastropods. Plants are also rare. Unit 2 contains the highest concentration of well-preserved, articulated fish.

Unit 3 is 30 cm thick and is composed of laminated gray shale with irregularly spaced layers of light-brown shale to siltstone (Fig. 2C). The most common fossils are large plants, many of which are encrusted with *Spirorbis.* Other common fossils include small *Dunbarella, Myalina,* and small, high-

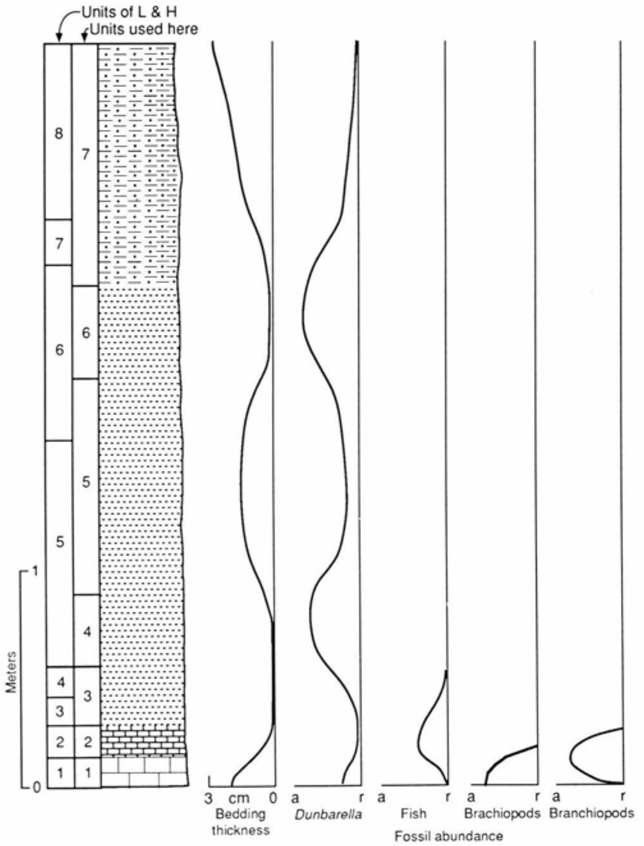

FIGURE 1—General stratigraphy and fossil abundance in the lowets beds, KBCQ. The quarry floor is in unit 1. **L & H,** Lucas & Huber, 1991; **a,** abundant; **r,** rare.

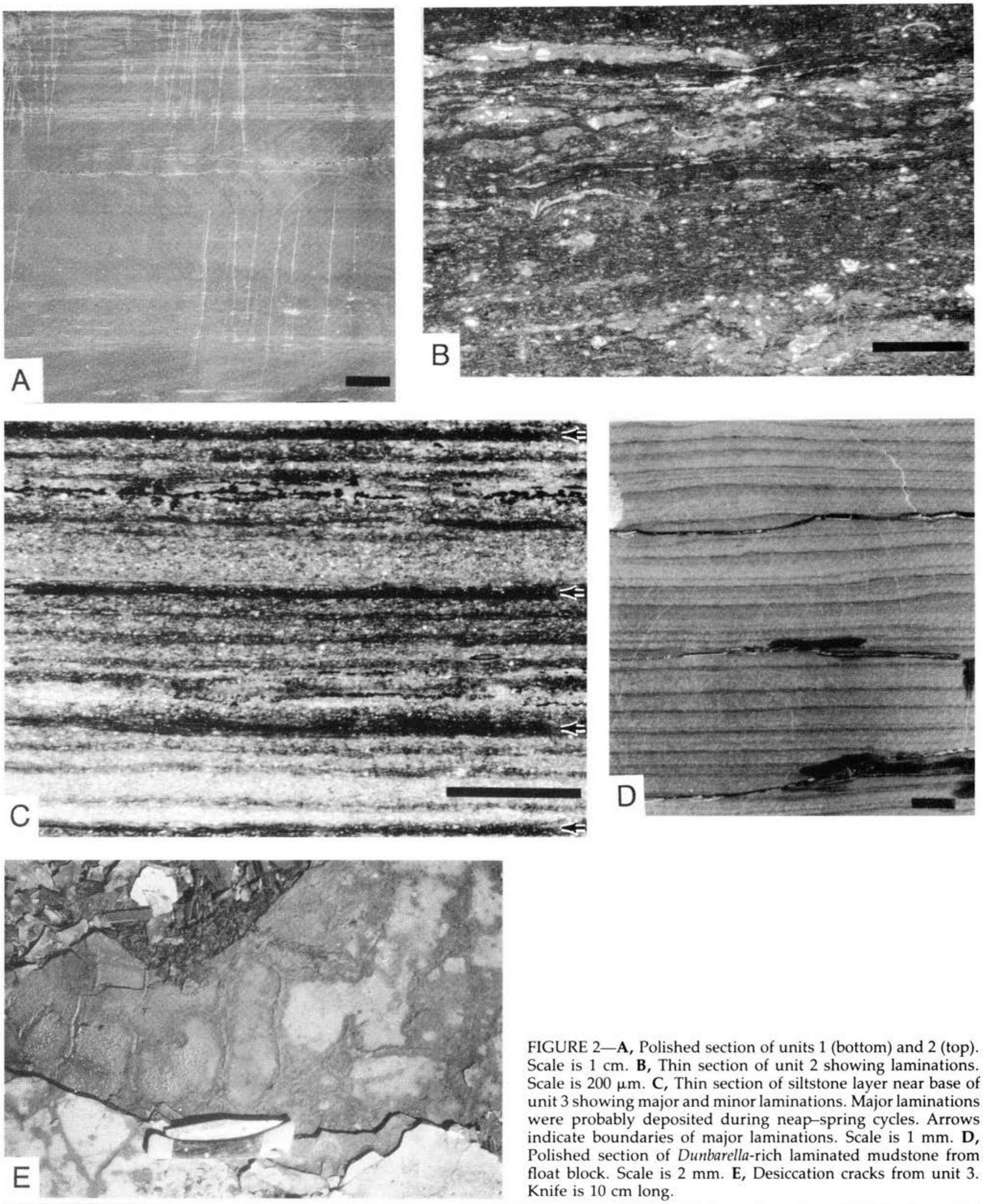

FIGURE 2—**A,** Polished section of units 1 (bottom) and 2 (top). Scale is 1 cm. **B,** Thin section of unit 2 showing laminations. Scale is 200 μm. **C,** Thin section of siltstone layer near base of unit 3 showing major and minor laminations. Major laminations were probably deposited during neap–spring cycles. Arrows indicate boundaries of major laminations. Scale is 1 mm. **D,** Polished section of *Dunbarella*-rich laminated mudstone from float block. Scale is 2 mm. **E,** Desiccation cracks from unit 3. Knife is 10 cm long.

spired gastropods. Unit 3 also contains some articulated fish, mostly platysomids, and all the amphibians and insects recovered from KBCQ to date. In thin section each lamination is a normally graded unit from silt or shale at the base to an organic-rich shale at the top. This is the lowest unit that contains evidence of tidal sedimentation. Some laminations occur in thick—thin couplets and others are grouped into apparent neap—spring cycles with major and minor laminations (Fig. 2C).

Unit 3 and lowest 50 cm of unit 4 contain polygonal structures similar to mud cracks (Fig. 2D). Polygons range from 2 to 20 cm in diameter. The edges of polygons are curled upwards, leaving a gap between adjacent polygons that is filled with mudstone. The cracks do not disturb the immediately underlying major lamination 2 mm below the cracked layer. These structures are similar to mudcracks caused by exposure, but may be a result of desiccation due to salinity changes (Archer & Clark, this volume).

Unit 4 is laminated to thinly bedded shale. Prominent bedding is defined by dark laminae that are spaced from 1 mm to 1 cm apart. Within each of these beds or laminations are 10 or less minor laminae. *Dunbarella* and plant fossils are apparently confined to the dark laminae (see Archer & Clark, this volume). The most common fossil is *Dunbarella*, which occurs in all growth stages, up to 3 cm in hinge length. *Dunbarella* occurs in densities of as many as 700 specimens per square meter. Other animal fossils are rare, but include fish scales and small myalinids. Plant fossils are common and include *Dicranophyllum*, fern and seed-fern foliage, *Walchia*, and sphenopsids.

Unit 5 is thicker-bedded and siltier than unit 4, though the transition is gradual. Bedding thickness averages about 1 cm and ranges up to 3 cm. Unit 5 contains the same fossil assemblage as unit 4, and all fossils are confined to the dark laminae that separate beds. *Dunbarella* are less abundant and generally smaller than in unit 4. Units 6 and 7 are generally similar to units 4 and 5, respectively. Bedding becomes very thick and faint near the top of unit 7, and is indistinct above it.

The entire section at the KBCQ generally coarsens upward to sandstone beds at the top of the high wall. The lowest sandstone beds are horizontally bedded and contain thick—thin couplets suggestive of tidal deposition. The upper sandstone beds are crossbedded and are interpreted as fluvial by Lorenz et al. (this volume).

Interpretation

Unit 1 is the most marine of the rocks exposed at the KBCQ. Presence of marine gastropods, brachiopods, echinoderms, and cephalopods suggests marine or near-marine salinities. The abundance of branchiopods may indicate brackish water, and the abundance of plants indicates a close proximity to land. This unit was probably deposited in a shallow-water, marine environment, possibly a protected lagoon (Kues, 1991).

The abundance of marine invertebrates decreases sharply at the base of unit 2, as the abundance of articulated fish increases. From the base of unit 2 to the lower part of unit 3 bedding becomes thinner, siliciclastic content of the rocks increases, and the size and abundance of plant fossils increases. Also lamination rhythmicity first occurs in the base of unit 3, overlapping with the highest occurrence of articulated fish. All these characteristics can be related to the increasing dominance of rapid siliciclastic deposition in a tidal environment.

Tidal deposits are now widely recognized in Carboniferous fine-grained rocks (Kvale & Archer, 1989; Brown et al., 1990; Keucher et al., 1990) based on rhythmic patterns in lamination thicknesses that are similar to patterns in modern tidal environments. Each tide can potentially deposit a normally graded lamination as suspended sediment settles during waning flow at high or low tide (Dalrymple & Makino, 1989; Smith et al., 1990). The cohesiveness of muddy sediment can prevent subsequent erosion (Wells, 1988) during the next tidal cycle, so there is the potential for deposition and preservation of a new layer of sediment with each tidal cycle. Thickness of the sediment will depend on the height of the water column as well as velocity of the tidal currents. Therefore as tidal height and velocity vary during a neap—spring cycle, so will bed thickness. This results in rhythmic variations in lamination thicknesses (Dalrymple & Makino, 1989; Tessier et al., 1989).

As a result of deposition of a new layer of sediment with each tidal cycle, high depositional rates can be maintained. Rates of deposition of uncompacted sediment in tidal systems range up to 30 cm per neap/spring cycle (Smith et al., 1990; Dalrymple & Zaitlin, 1989; Tessier et al., 1989). Grouping of minor laminae within major laminae in units 4 through 7 is analogous to neap—spring—neap cycles in modern settings (see Archer & Clark, this volume). Major laminations likely represent neap—spring—neap cycles (Fig. 2D). Each minor lamination likely represents a single tidal cycle. Thicker minor laminations near the centers of major laminations were probably deposited during spring tides. Thinner minor laminations near the boundaries between major laminations were probably deposited during neap tides. Current velocities during neap tides are lower, and coarser sediment thus is not kept in suspension. This results in finer-grained laminations. Tidal range is also lower, so each lamination is thinner than those deposited during spring tides.

Biotic diversity in laminated shales is low, which is consistent with a tidal interpretation. *Dunbarella*, the most common fossil in the laminated shales, was likely pseudoplanktonic and lived on algae or floating plant debris (Archer & Clark, this volume). Burrows and benthic fossils were not observed in this sequence. It is not likely that benthic fossils were removed from the laminated shales because there is no evidence of erosion or scouring of the bottom. Whatever lay on the bottom would have been quickly buried and preserved.

The absence of sessile benthos in these shales is somewhat enigmatic. Perhaps the most important factor in restricting assemblages of sessile benthic invertebrates in tidal environments are high depositional rates. Postcompaction thickness of probable neap/spring cycles in the KBCQ ranges up to 3 cm and averages a few millimeters. Larvae of any benthic organism that settled on the bottom would have been quickly covered with mud. Few organisms could have grown faster than the sedimentation rate.

The common benthic invertebrates in Pennsylvanian communities are largely normal-marine fossils such as brachiopods and bryozoans. Both salinity stress and rapid deposition could potentially have similar paleoecologic effects because both would tend to prevent colonization by these organisms. Therefore, absence of a diverse benthos in the laminated muds cannot be used to infer paleosalinity. Also dominantly marine or fresh-water organisms may spend parts of their life cycles in brackish habitats (Day et al., 1989), further complicating salinity interpretations based on fossil assemblages.

High depositional rates associated with tidal environments may also explain the high quality of fish preservation. When fish die they tend to sink to the bottom, particularly if they lack a swim bladder as most late Paleozoic fish. As a carcass rots, decay gases rapidly accumulate causing floating, bloating, and eventual rupture of the organism (Elder, 1985). Cold and deep waters can prevent or delay flotation because decay rates are slower and high pressure keeps the volume of decay gases small (Elder, 1985; Smith & Elder, 1985; Elder & Smith, 1988). In shallow, warm waters rapid burial is generally required to prevent flotation. Anoxia has been cited as a potential explanation of well-preserved fish, but it does not stop decomposition and may not even appreciably retard decomposition (Zangerl & Richardson, 1964; Foree & McCarty, 1970; Allison, 1988a, b; Kidwell & Baumiller, 1989, 1990). Slow deposition in warm, anoxic water will not generally result in well-preserved fish.

Unit 2 is finely laminated and articulated fish are distributed throughout this unit. Therefore, the fish were not killed and buried by a single event but rather by many minor events. Some fish are partially disarticulated with dissociated skeletal elements scattered randomly about, similarly to the results of scavenging described by Elder (1985). There were likely periods of stasis between burial events, during which fish could have been scavenged. The laminations are unlikely to be varves because deposition of varves is much too slow to account for the fish preservation. Storms, turbidites, and tides can all produce laminated sediment and can bury organisms fast enough to account for the fish preservation. Tidal rhythmites are not present in unit 2, but the stratigraphically highest fish specimens and all the terrestrial animals are at the base of unit 3, coincident with the lowest occurrence of tidal rhythmites. The change in lamination patterns and siliciclastic content from the base of unit 2 to the lower part of unit 3 may be the result of increasing tidal influence, increasing depositional rate, and influx of terrigenous detritus. Lack of tidal periodicities in unit 2 may be the result of lack of preservation of each tidal event, perhaps because of insufficient sediment supply.

Shale and mudstone overlying these lower units were not studied in detail by us, but casual observation and data from other studies (Lucas & Huber, 1991; Mamay & Mapes, this volume) indicate that laminated shale with plant fossils and *Dunbarella* occurs sporadically throughout the rest of the fine-grained sequence exposed at KBCQ. This suggests that the upper mudstone beds were deposited in paleoenvironments generally similar to the lower laminated beds (units 4 through 7).

The sequence generally coarsens upward, and the uppermost 15 m of the exposed section contain sandstone beds (Lorenz et al., this volume). The lowest sandstone bed is horizontally bedded and contains numerous thick—thin couplets suggestive of tidal deposition. The uppermost sandstone beds most likely were deposited in fluvial channels (Lorenz et al., this volume).

The sequence of rocks exposed at the KBCQ can be explained as the progradation of an estuary over a carbonate lagoon. Estuaries are sites of complex interactions of marine and fluvial processes and are characterized by brackish or widely fluctuating salinities. Salinity is difficult to determine for ancient systems, so recognition of ancient estuaries is based on similarity of depositional facies. A characteristic common to many estuaries is the deposition of muddy sediment in the center, which results from the establishment of a turbidity maximum (Allen et al., 1980; Reithmüller et al., 1988; Odd, 1988; Dyer, 1988; Gibbs et al., 1989). The turbidity maximum is maintained by circulation patterns that are unique to estuaries. Estuarine circulation patterns are the result of fresh-water discharge, tidal currents, and the interaction of saline and fresh water. In stratified estuaries a well-defined salt wedge intrudes into the estuary along the bottom (Fig. 3A). Upstream of the salt wedge is net transport of fresh water to the sea. Bottom currents in the salt wedge move into the estuary, replacing lost sea water (Fig. 3A). This circulation pattern is based on average current velocities over a complete tidal cycle. At any one time fresh water may move upstream during a flood tide or sea water may move oceanward during ebb tide. There is a point along the bottom where average current velocities are zero, the null point (Fig. 3A). In the area near the null point water moves in a circular pattern as the salt wedge is forced into, and then out of, the estuary during each tidal cycle.

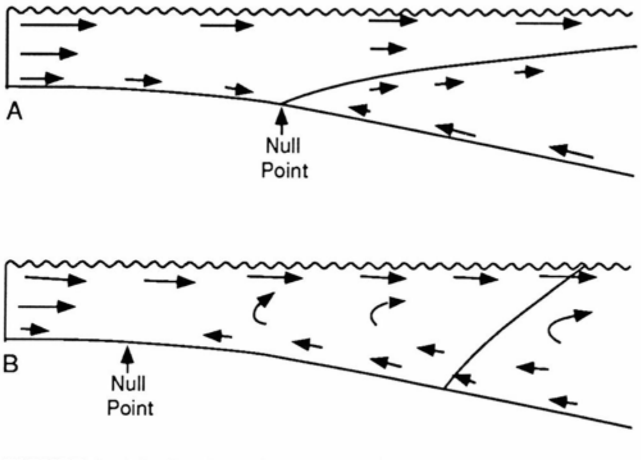

FIGURE 3—Idealized models of circulation in stratified **(A)** and well mixed **(B)** estuaries.

Mud accumulates near the null point. As fresh water mixes with saline water, clay particles tend to flocculate. Flocculation can occur in very low salinities (0.2‰, Gibbs et al., 1989) that are present in the upper estuary far landward from the null point. Flocculated particles are capable of settling much faster than isolated clay particles and can be deposited from suspension within a single tidal cycle (Allen et al., 1980). In stratified estuaries clots of suspended sediment are transported to, and trapped near, the null point, where they form the turbidity maximum and can settle quickly at low current velocities.

In partially or well-mixed estuaries the tidal-current velocities are typically higher than in stratified estuaries, the salt wedge is not well developed, and the difference between surface- and bottom-current velocities is smaller (Fig. 3B). In these systems the turbidity maximum may be maintained primarily by tides. Fine sediment can be alternately eroded, resuspended, and deposited during each semidiurnal tidal cycle (Allen et al., 1980). Because the turbidity maximum is maintained by tides and not by density-driven discharge, it will not necessarily occur near the edge of the salt wedge. In the Gironde estuary during periods of low river flow the turbidity zone can extend up to 40 km landward of the salt wedge to the limit of tidal currents (Allen et al., 1980; Allen, 1972) (Fig. 4). Thus a turbidity maximum will tend to be established in estuaries in any tidal regime, given the presence of sufficient quantities of mud.

As a result of estuarine circulation, bottom velocities decrease from the fluvial environment to the null point. Coarse sand is trapped in the lower reaches of the fluvial channels because currents are no longer powerful enough to transport the coarse bedload. Marine sand (if present) will not be transported into the middle estuary because of a complementary decrease in bottom-current velocities in the salt wedge. These processes can result in a fluvial to marine coarse—fine--coarse pattern of sedimentation (Dyer, 1979; Rahmani, 1989). This pattern of sediment distribution has been observed in the Cobequid Bay—Salmon River estuary, Bay of Fundy (Dalrymple & Zaitlin, 1989), Gironde estuary (Allen, 1972), and the estuary in the Ogeeshe River—Ossabaw Sound (Dörjes & Howard, 1975).

The coarsening-upward sequence at the KBCQ likely corresponds to the change from middle to upper estuary environments and finally into the fluvial environment. The low diversity of faunal assemblages in the laminated shale could be due to salinity stress as well as high depositional rates. Diversity can be strongly correlated with salinity in estuaries. The diversity of benthic communities is typically high at normal-marine and fresh-water salinities and lowest in brackish-water salinity (Fig. 5). Furthermore, migration of the salt wedge during tidal cycles can subject organisms to additional stress. In the mesotidal estuary in Ossabaw Sound (Georgia) the limit of water with a salinity of 20‰ moves as much as 7 km during a single tide and one station in the estuary experienced salinity fluctuations from about 2‰ to 22‰ during a single tidal cycle (Howard et al., 1975).

Relative sea level may not have changed significantly during deposition of the KBCQ sequence. Deposition in a shallow carbonate lagoon was followed by shallow, tidal, estuarine deposition, and the entire sequence was capped by fluvial sandstone. Basin subsidence could account for the lack of change of relative sea level during deposition of the KBCQ sequence.

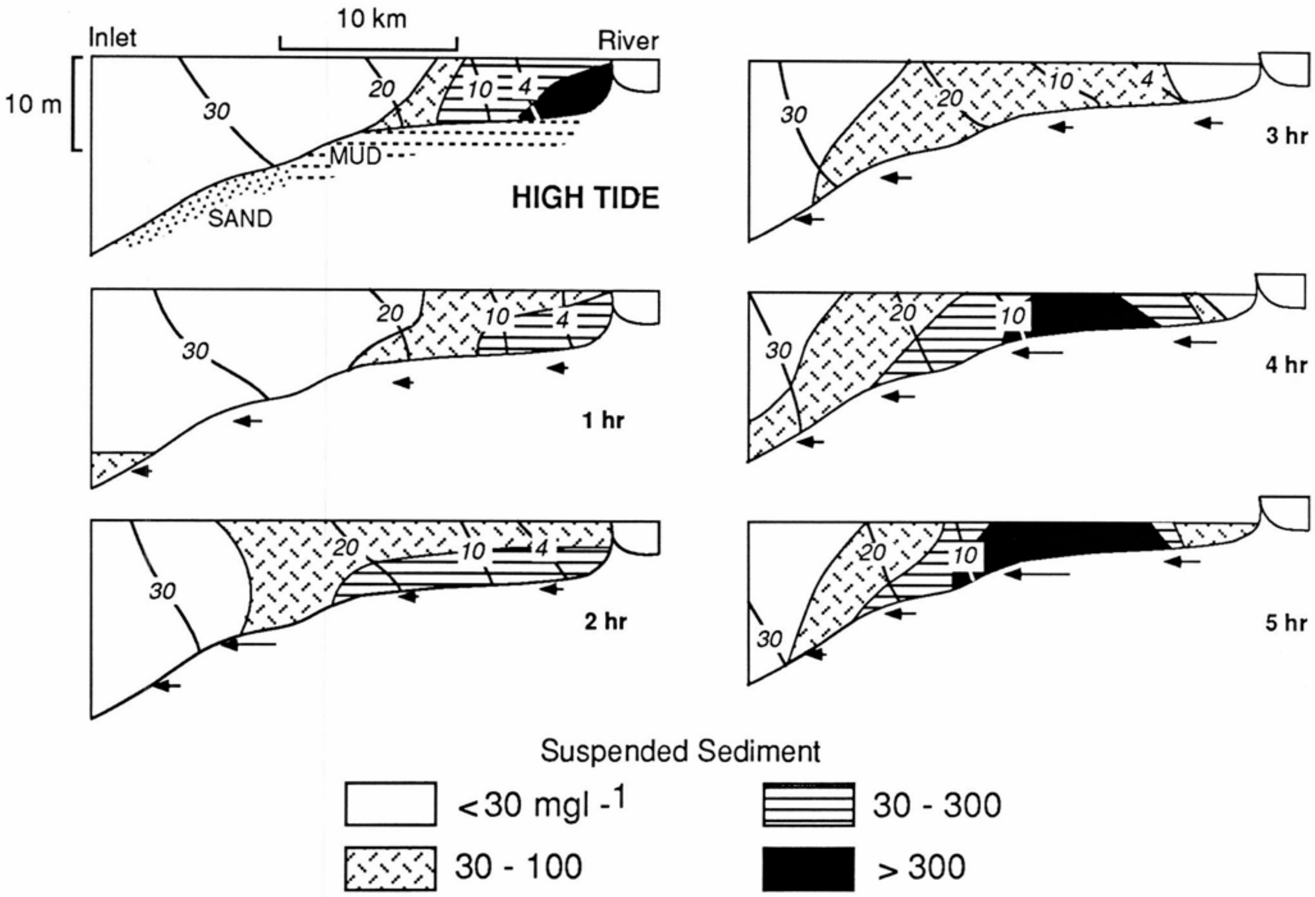

FIGURE 4—The movement and amount of turbidity and salinity during a single, semidiurnal tidal cycle in the Gironde estuary. Note the three-hour period of low current velocities following high tide during which most of the suspended sediment is deposited. Modified from Allen et al. (1980).

Conclusions

The sequence of rocks exposed in the Kinney Quarry can be explained as the progradation of a muddy estuary over a carbonate lagoon. The fish bed occurs at the transition from carbonate lagoon sedimentation to siliciclastic, tidally dominated, estuarine deposition. Good preservation of the fish resulted from rapid sedimentation, possibly associated with tidal processes. The best evidence of tides, however, is in the *Dunbarella-rich* shales immediately overlying the fish bed.

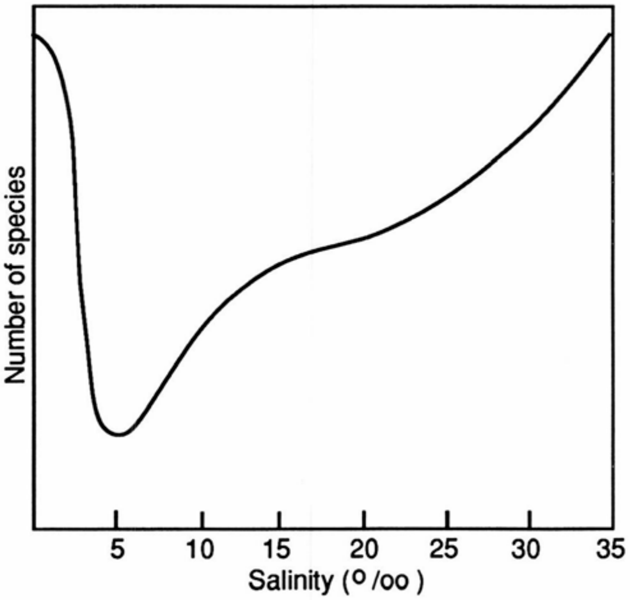

FIGURE 5—Idealized diagram of the diversity of benthic organisms along a salinity gradient. Modified from Remane & Schielper (1971).

Depositional environments of the *Dunbarella-rich* shales and mudstones may be similar to sediments deposited in modern middle-estuarine environments, in which there is commonly a turbidity maximum that results from the estuarine-circulation pattern. Deposition of mud from suspension during slack water at high or low tide can result in generally high rates of deposition. Rates of one or more centimeters of sediment deposited during a single neap—spring cycle have been documented for several modern estuaries. Laminated muds from several Carboniferous sites display rhythmic patterns of thick and thin laminations highly suggestive of rapid deposition by tidal processes.

Salinity is very difficult to interpret from Carboniferous estuarine rocks for several reasons. In modern environments tidal currents can propagate many kilometers beyond the limit of salt water. Thus identification of tide-influenced deposition should not be interpreted as a guide to salinity. Additionally, organisms used as indicators of marine water can be prevented from colonizing substrates by factors other than salinity, including high turbidity and high depositional rates. Other organisms characteristic of marine or freshwater environments may migrate to estuaries for feeding or breeding. Finally, transport of terrestrial elements from the upper, fluvial part of the estuary into the muddly middle estuary, and transport of marine organisms from the lower estuary, can make interpretations of fossil assemblages difficult.

Acknowledgments

We thank Keith Miller for critically reviewing this manuscript. Renate Hensiek drafted the figures. This research was supported by NSF grant EAR-9018079.

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Depositional environment of the *Dunbarella* beds: An exercise in paleoecology and sediment cyclicity

Allen W. Archer and George R. Clark II

Department of Geology, Kansas State University, Manhattan, Kansas 66506

Abstract—The *Dunbarella* beds exposed in the Kinney Quarry (Pine Shadow Member, Wild Cow Formation, Madera Group, lower Virgilian, central New Mexico) display a remarkable combination of laminations, mineralogy, fossils, and shrinkage cracks. Each of these factors places constraints on the interpretation of depositional environment; taken together, they strongly suggest deposition at the bottom of an estuary with strong tides and marshes nearby.

Introduction

The *Dunbarella* beds display a complex pattern of laminae, abundant fossil remains, and probable shrinkage cracks, all undisturbed by bioturbation. This combination of factors presents a rare opportunity for sedimentological and paleoenvironmental analysis, with a good possibility of reconstructing the environment of deposition. This paper presents the preliminary results of such an investigation.

Location and stratigraphy

The *Dunbarella* beds are exposed within a quarry operated by the Kinney Brick Company in the Manzanita Mountains, central New Mexico (Fig. 1). They are part of a complex series of lithofacies, including limestone, silty shales, sandstones, and limestone-clast conglomerates, all in the lower Virgilian Pine Shadow Member of the Wild Cow Formation of the Madera Group (Lucas & Huber, 1991). Details of the vertical sequence are described by Lucas & Huber (1991); in general, the section exhibits a coarsening-upward trend.

As used here, the *Dunbarella* beds refer to the laminated, calcareous gray shales that occur in the lower part of the section (units 5-7 of Lucas & Huber, 1991). Their lower boundary is gradational from the limestone of the quarry floor, and their upper boundary is gradational into a silt-stone. Other shales in the section, some of which contain sporadic concentrations of *Dunbarella*, are not included in this study.

Sedimentology

The shales of the *Dunbarella* beds are shales by virtue of laminations (Fig. 2), not by fissility. They react with dilute HCI, but in general do not completely disintegrate; cements other than calcite must be present. In thin section they can be seen to contain a substantial amount of silt, although not quite enough to call them siltstones. X-ray diffraction patterns show the major mineralogical components to be clay, quartz, calcite, and pyrite (Fig. 3). There is no significant mineralogical difference between light and dark lamellae, so the color is probably due to organic carbon. Examination of thin sections supports this conclusion.

The shales are richly fossiliferous, deriving their informal name from the abundance of the pectinid bivalve *Dunbarella,* whose flat shells impart a specious fissility to the rock (Fig. 2). Other fossils, especially terrestrial-plant remains, are common but not abundant. Some bedding planes, especially those in thinly laminated intervals, exhibit polygonal features that may be shrinkage cracks (Feldman et al., 1991).

Patterns of laminations

Laminations marked by alternating light and dark layers are visible even on fracture surfaces of the shales. Observed combined thickness of these light–dark pairs ranges from 0.6 to 19.9 mm, with the light layers invariably thicker than the dark ones. These were noted by earlier workers and were generally believed to represent seasonal sedimentation patterns, or varves (Clark, 1979, for example).

More recent work involving polished sections and thin sections has found that the light layers are generally subdivided by very narrow, regularly spaced dark bands on an altogether different scale. To distinguish the coarse laminations from the fine ones, we will call the former major

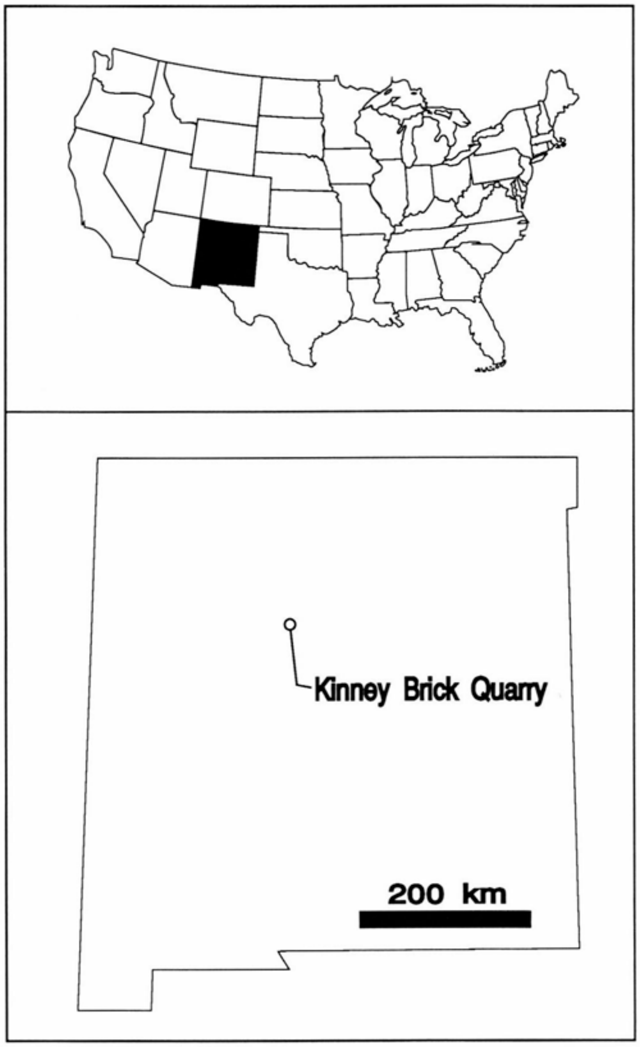

FIGURE 1—Location of Kinney Brick Company Quarry.

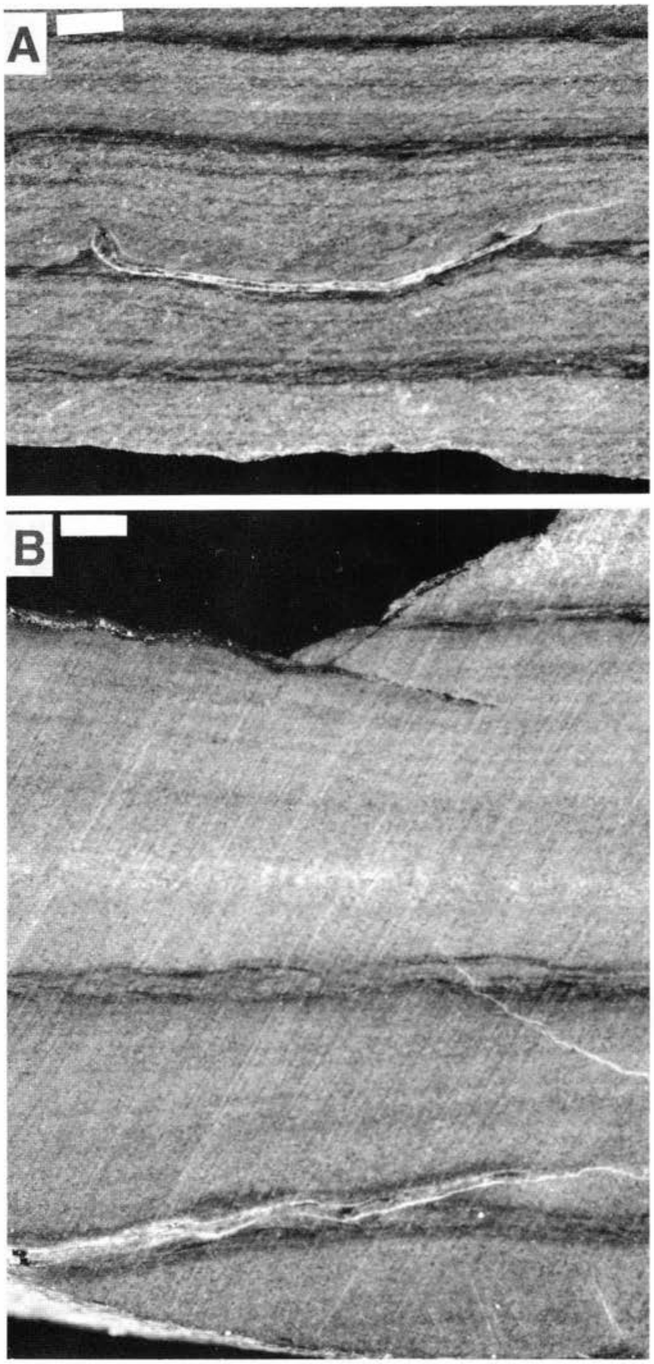

FIGURE 2—Sawed and sanded sections through relatively thin **(A)** and relatively thick **(B)** parts of the *Dunbarella* beds. Scale bars are 1 mm. Note shells of *Dunbarella* in some dark layers; there is soft-sediment deformation associated with the shells, but no sign of erosion or bioturbation.

laminae and the latter minor laminae. The presence of the minor laminae has called into question the earlier interpretation of the major laminae as varves, and provided opportunity for a more rigorous analysis.

Computer-based, optical scanning of the laminae allows quantification of the shades of darkness distinguishing both scales of lamination. By use of an image-analysis system with a CCD-type camera, lamination patterns on photographs or polished sections are converted to a binary format suitable for computerized analyses. The relative coloration of the laminae is converted to 256 scales of gray; these gray levels can then be plotted graphically as "optical density,"

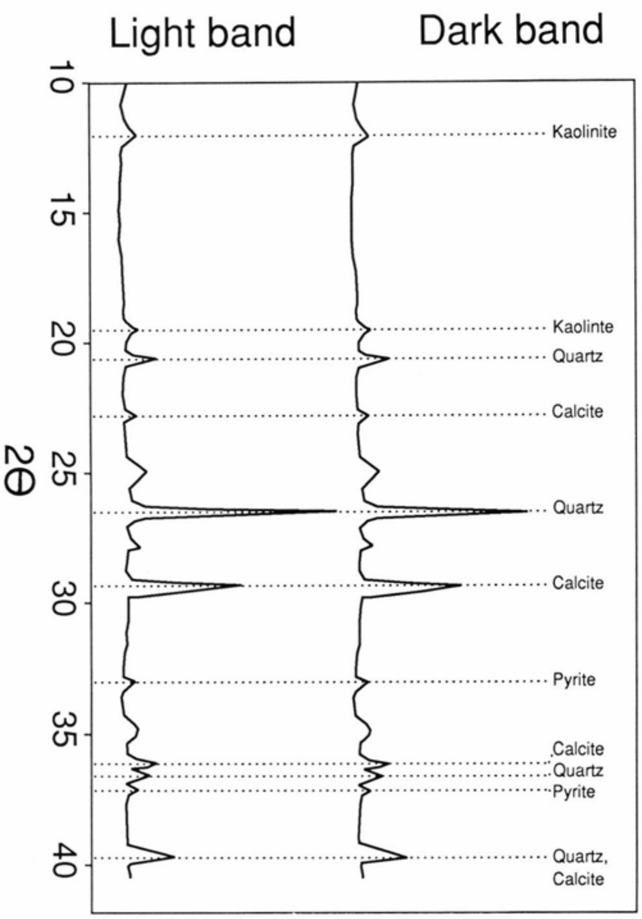

FIGURE 3—Cu K-alpha x-ray diffraction patterns within a dark major lamina **(A)** and a light major lamina **(B).** Other than slightly higher percentages of quartz in the light lamina, there are no significant differences between the mineral compositions of the two.

which can be normalized to range from black (-1) to white (+ 1).

For the preliminary results reported here, shales with relatively thin major laminations were used, and a scanning area ranging from 3 to 4 mm in height was adequate to cover major and minor laminae. Because the laminae are relatively diffuse, an area 2 mm wide was scanned rather than a narrow line, and the gray-scale values were averaged laterally. The laminae are laterally consistent and quite straight, so widening the scan parallel to the laminae was justified.

Fig. 4 illustrates the result of two such scans. These optical-density plots show clearly the differences in optical density between both major laminae, as delineated by the darkest bands (arrows in Fig. 4), and minor laminae, marked by narrower bands of lesser darkness (valleys between numbered peaks in Fig. 4).

There appears to be a general relationship between the thickness of the major laminae and the number of minor laminae that they contain. For example, major laminae that are relatively thin contain about five to six minor laminae (Fig. 4A). Conversely, where the major laminae are thicker (Fig. 4B), there may be as many as 10 minor laminae.

Occurrence of fossils

The most widespread fossil is, of course, *Dunbarella.* This is a thin-shelled, relatively flat, strongly byssate pectinid with a remarkable morphologic similarity to the modern California pectinid *Leptopecten latiauratus.* Much of our speculation about the significance of *Dunbarella* will be based on

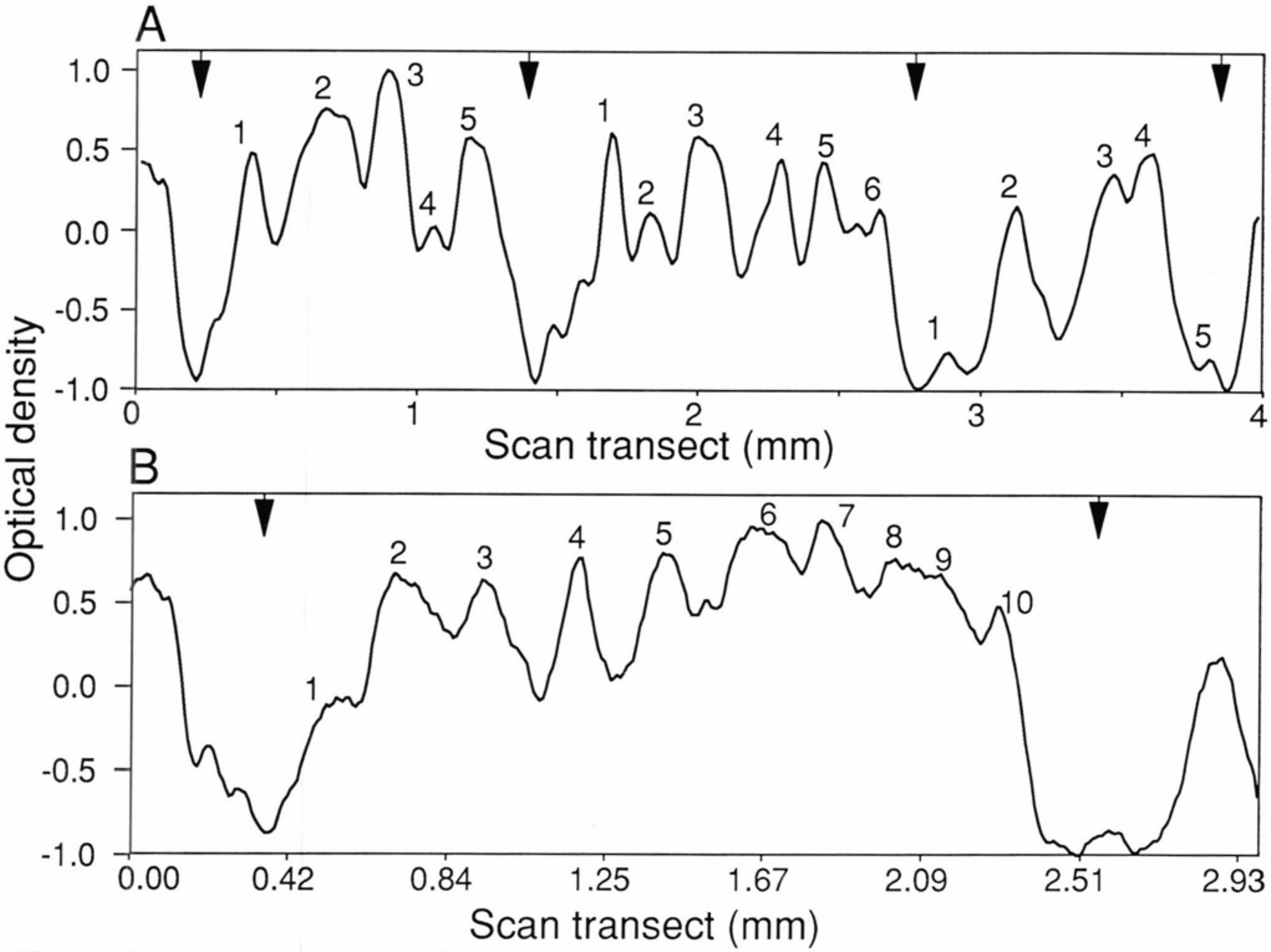

FIGURE 4—Computer-based optical scans of laminated shales. Vertical axis is normalized optical density; low values are darkest. **A,** Thinly laminated shale; **B,** thickly laminated shale. The darkest zones (arrows) separate major laminae, while zones of lesser darkness separate from five to ten minor laminae (numbered) in each.

our understanding of this modern species (see Clark, 1971).

Stratigraphically, *Dunbarella* seems to be confined to the dark layers of the major laminae; in a very few cases a section will expose the thin edge of a shell within a light layer, but as many *Dunbarella* shells have curvatures of a millimeter or more, these may well be the ends of shells whose centers are in the dark layers. We have seen no exposures where the main part of the shell is in a light layer.

Although some *Dunbarella* occur in each major lamina, this fossil becomes abundant at intervals of 4-10 major laminae. In these horizons the shells may cover 20-40% of exposed surfaces, and, as the rock naturally tends to split along such surfaces, it is easy to overestimate the abundance of *Dunbarella*. The areal distribution of the shells seems to be quite random; there is no indication of concentrations along preferred directions, for example.

The *Dunbarella* shells range from less than 3 mm to about 30 mm in height (the largest dimension in this bivalve), although most are in the upper third of that range. There is no obvious sorting by size. There is likewise no consistent orientation of the shells, either by compass direction or by "convex up" or "convex down."

The shells are frequently articulated, either with valves closed or with the valves "butterflied," attached at the hinge line but lying open. There is no evidence, such as the formation of concretions or pervasive pyritization, to suggest that soft tissues were still attached to the shells during deposition. In fact, the presence of so many butterflied valves suggests that decay was far advanced (muscle attachment lost) but not complete (organic ligament intact) at deposition.

Terrestrial-plant fossils, although not abundant, are common in the *Dunbarella* beds. Most occur within the dark layers of the major laminae, but a few are in the light layers. The dark layers are so colored by an abundance of black flakes, probably carbonized plant remains. Surprisingly, the plant fossils tend to be either substantially intact or completely reduced to these tiny flakes; no small, partially decayed but recognizable remnants have so far been observed.

Another important consideration is the lack of trace fossils or bioturbation disturbing the fine laminae, and the absence of trackways or other types of surficial markings on the bedding surfaces. This is a strong evidence that the depositional surface was unsuited for bottom dwellers. The good preservation noted in the soft plant fossils suggests an environment unfavorable even to bacteria.

Cyclic sedimentation

Flat laminations can be found within fine-grained rocks that form in at least four very different environments. These are varves, stromatolites, turbidites, and tidal deposits.

Varves, the product of seasonal variations in sedimentation rate and sediment composition, are usually expressed as alternating layers of light and dark sediment. We are unaware of any varves with a strong and systematic second periodicity expressed. If the *Dunbarella* beds contain varves, the other cycle of laminations must have a very different origin, such as tides. Given the similarity in expression of the two orders of laminae, this seems unlikely.

Stromatolites are the product of sediment trapping by algae or bacteria, and may include both daily and tidal cycles in their lamination. They usually express the lamination as alternating layers of relatively coarse sediment and organic material, the latter of which may be replaced by cements. The *Dunbarella* beds do not exhibit the characteristics of stromatolites.

Turbidites are generally much thicker than the laminae observed here, but we cannot reject them as models for the *Dunbarella* beds for that reason alone. Typically, a turbidite is recognized by graded bedding; the *Dunbarella* beds exhibit some sorting by grain size, but nothing that can be definitely related to graded bedding. Turbidites are also very unlikely to form with two different scales of regular cyclicities, and it is difficult to see how any other type of cyclic sedimentation could be involved in a traditional turbidite system.

Tidal deposits generally involve fine-grained sediments and are likely to express more than one cyclicity. A diffusion of organic particulates, rather than exclusively organic layers, would be expected in tidal deposits. Some sorting would be expected, but graded bedding would be rare. The lamination patterns found in the *Dunbarella* beds would be quite compatible with a tidal environment. We conclude that the *Dunbarella* beds are most likely tidal deposits, as any other explanation seems to involve a combination of factors that somehow produce different cyclicities while expressing them in an essentially identical fashion.

Tidal deposits

Tidal periodicities

Tides exhibit an impressive range of periodicities. In addition to the common semidaily, daily, and fortnightly, there are monthly, seasonal, semiannual, annual, and even longer cycles. Although the exact periods of these cycles have changed during the Phanerozoic (due to the retarding effects of tidal friction on the speed of the Earth's rotation), the hierarchical relationships of the cycles remain the same. Thus, predictive tidal-height data, as generated by NOAA (1988) for modern navigation and coastal activities, can be used to model ancient tidal sedimentation.

All tidal systems exhibit a rise and fall of tides on at least a daily basis; this is related to the Earth rotating within the combined gravitational fields of the Moon and the Sun. Theoretically there should be two separate high and low tides daily, as the Moon's gravity causes tidal bulges on both the front and back sides of the Earth. The actual time to complete these two tidal cycles is 24 hours and 52 minutes, as the Moon is moving while the Earth is rotating under it. In practice, the tides are so influenced by the resonant qualities of different ocean basins that in some cases there is only one tidal cycle per day. Such tidal cycles are termed "diurnal" (Fig. 5A), while the more normal circumstance of two tidal cycles per day is termed "semi-diurnal" (Fig. 5C). Situations in which the tides are diurnal part of the time and semidiurnal for the rest are called "mixed tides" (Fig. 5B).

In addition, there are systematic increases and decreases in tidal height, termed "neap—spring" periods. During the new and full moons, the gravitational effects of the Sun and Moon are in alignment and the highest, or "spring," tides occur. Conversely, during the first and last quarter phases of the Moon, the gravitational effects of the Moon and Sun are at right angles and the lowest, or "neap," tides occur. Thus, during any lunar orbital period (28.5 days, or approximately one month) two neap—spring tidal cycles will occur (Fig. 5).

Tidal sediments

Tidal periodicities can be readily encoded within sediments, which ultimately become preserved within the rock record. Many examples of such periodicities have been presented, including systematic thickness variations observed both in foresets (Visser, 1980; Allen, 1981) and within laminations (Kvale & Archer, 1990). For example, elevated current velocities produced during rising or falling tides will transport and deposit sediment and the amount of sediment

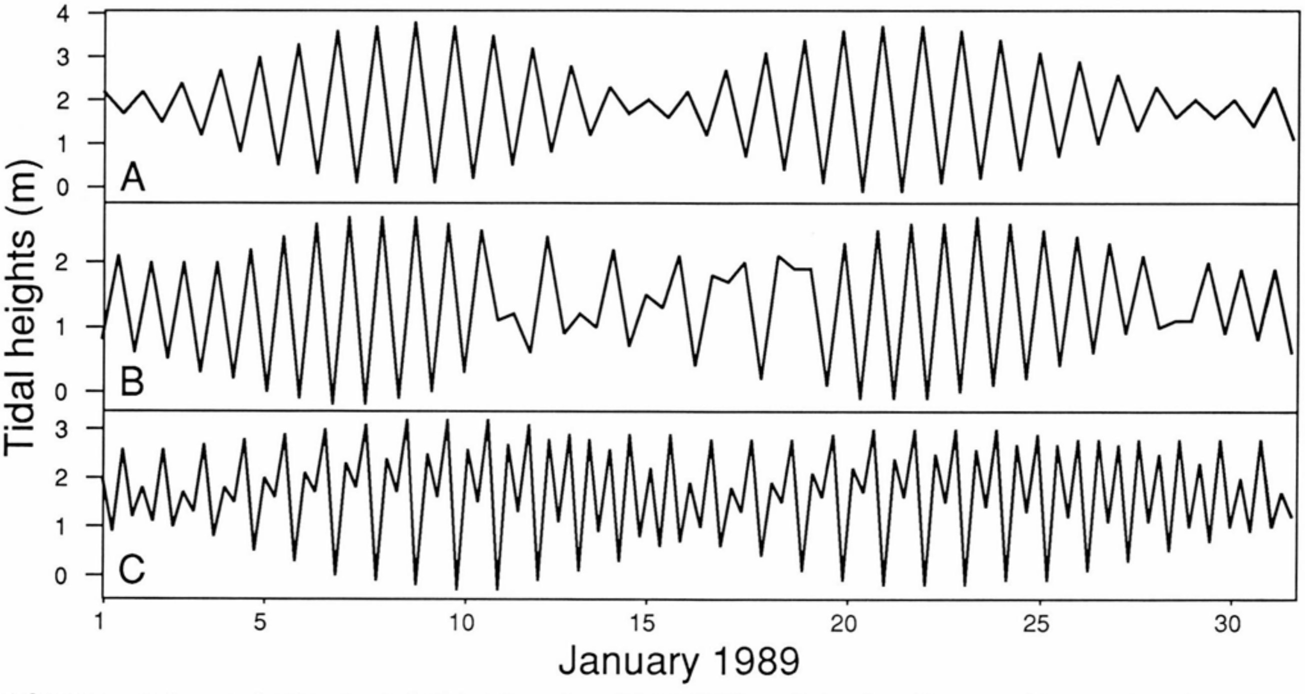

FIGURE 5—Tidal curves for three tropical tidal stations, from NOAA (1988) prediction data. Time period is approximately one lunar month and tidal heights exhibit two neap–spring tidal periods. The stations are: **A,** Do Son, Vietnam; **B,** Barito River, Borneo; **C,** Kolaka, Sulawesi.

deposited will be proportional to the height of the tide. Within bays or estuaries tidal currents wane as the tides reach their peak. During tidal maxima there is little to no water movement in areas not subject to rotary tides. During this "stillstand," fine-grained materials such as clays, or hydrodynamically light materials, such as plant debris, will accumulate from suspension. If sufficiently cohesive, this layer of fine-grained materials can protect the underlying coarser sediment from erosion during subsequent episodes of elevated tidal-current velocities.

Assumptions regarding depositional models

Constraints

Any models considered must conform to a number of observed facts. Some of the most important facts here are: (1) the two orders of lamination in the sediments; (2) the presence of clay, silt, and carbonate in the sediments; (3) the presence of both *Dunbarella* and terrestrial-plant fossils; (4) the absence of bioturbation; and (5) the presence of shrinkage cracks. Taken together, these facts restrict the possible depositional models to nearshore environments dominated by tides or tidal currents and influenced by both marine and nonmarine water masses. To narrow the model further requires making various assumptions.

Assumptions on laminations

The pattern of major and minor laminations can only be explained in a few ways. Because the major laminations contain minor laminations, it is clear that the major laminations cannot have daily or semidaily periodicities. On the other hand, the major laminations are so strongly expressed that the relatively weak seasonal or longer tidal periodicities are unlikely stimuli. We can further narrow the field by pointing out that strong monthly periodicities should enclose prominent fortnightly bands, which is not the case here. Thus the major laminations are almost certainly fortnightly.

This leaves the minor laminations as either semidaily or daily. There are of course too few of them to represent entire tidal cycles in either case, so the major dark bands must conceal the positions of some missing minor laminae. These dark bands are relatively thin compared to the major light bands, so they presumably represent some reduction in sedimentation rate. Still, if the minor laminae represent semidaily tides, the dark bands would have to accumulate over as much as 80% of the time, while physically occupying less than 20% of the sediment thickness. Although this is possible, it seems preferable to assume a diurnal tidal regime.

There is also the question of how the tidal cycle might have influenced the sedimentation. The pattern is 4 to 10 minor laminae within the major light band, separated by major dark bands in which minor laminae are not visible. The major light bands could represent events that happen only during extreme high tides, with the minor laminae marking the individual tides, and the major dark bands could represent those times between extreme high tides. Fig. 6 illustrates this concept.

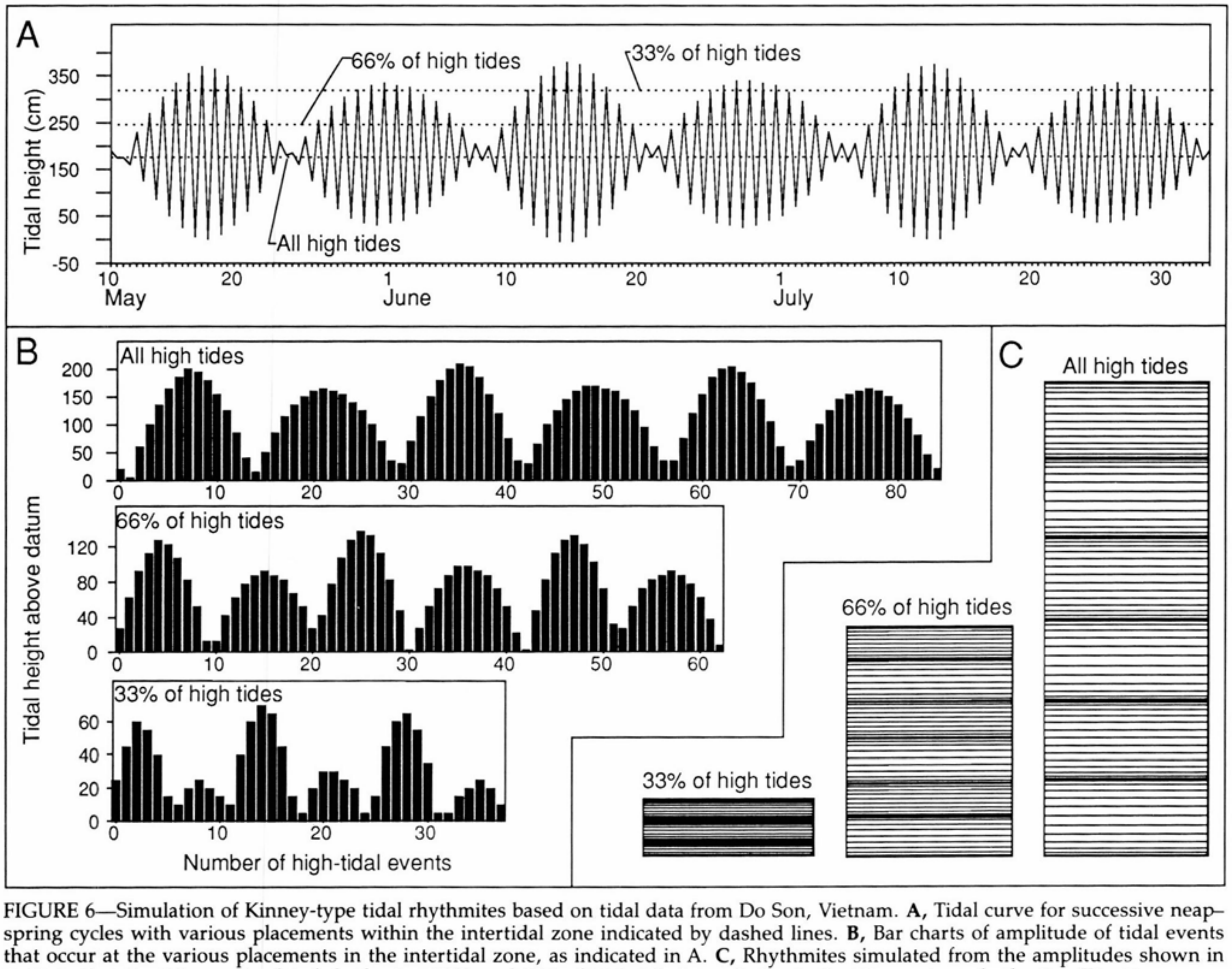

FIGURE 6—Simulation of Kinney-type tidal rhythmites based on tidal data from Do Son, Vietnam. **A,** Tidal curve for successive neap–spring cycles with various placements within the intertidal zone indicated by dashed lines. **B,** Bar charts of amplitude of tidal events that occur at the various placements in the intertidal zone, as indicated in A. **C,** Rhythmites simulated from the amplitudes shown in B. Note that the thinner simulated rhythmites (33% and 66% of high tides) are similar to the Kinney-type rhythmites (Fig. 2).

Tidal currents, rather than tide heights, could also cause the laminations. In this case, we have the problem that there are twice as many stillstands as high tides, and thus the relatively small number of minor laminae recorded is once again a difficulty. However, if the tidal current is being offset by a river current (Fig. 7: location D, Fig. 11), this problem disappears and we once again have a reasonable number of events.

Assumptions on sediments

The presence of clay and silt in the sediments is evidence for a terrestrial source of sediment. The carbonate fraction might of course be secondary, but the occurrence of calcite shells certainly demonstrates both that a marine source of sediment is possible and that the water was not that of an acidic marsh. On the other hand, the flakes of organic material might best be explained by the reworking of older marsh sediments, as their contrast to the well-preserved plant fossils is otherwise puzzling.

The fact that the mineralogical components of the sediment are essentially the same in both the light and dark layers of the major laminae suggests that their mechanism of deposition is independent of tidal action, although their rate of deposition apparently is not. On the other hand, the concentration of flakes of organic matter in the dark layers defines the tidal cycles, so it must be deposited in a different manner. The near-restriction of fossils to the major dark layers can also be considered a sedimentary effect dependent on the tides.

Assumptions on fossils

The fossils with the most significance to the depositional environment are the plant fossils and *Dunbarella.* The plant fossils, relatively rare and not confined to the dark layers, tell us that currents over the site of deposition must have sometimes come from land. Their fine state of preservation suggests both rapid burial and interstitial waters not favorable to bacterial decay.

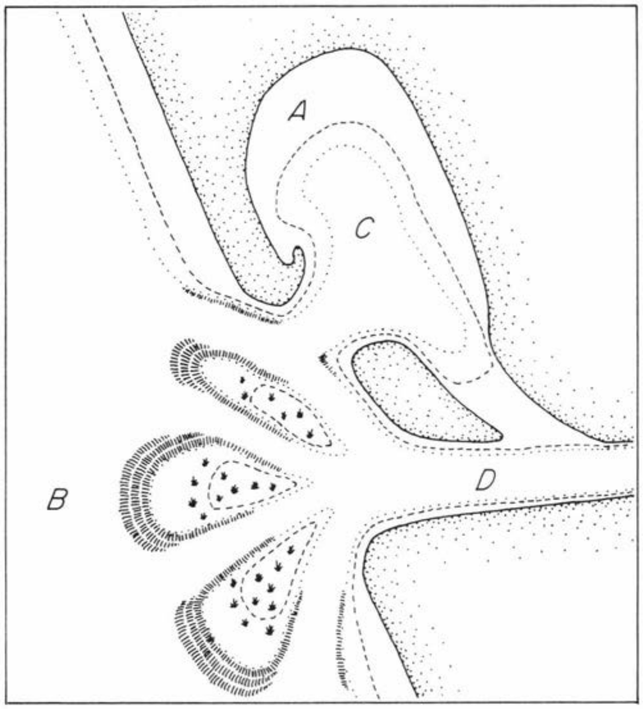

FIGURE 7—Map of theoretical coastline showing a variety of tidally influenced depositional sites. Solid lines = coastline (extreme high tide line), dashed lines = mean low water line, dotted lines = extreme low tide line, hachures = underwater embankments; vegetation shown on upper levels of tidal bars. A = Tidal flat (see intertidal model and Fig. 8), B = delta front (see prodeltaic model and Fig. 9), C = estuary basin (see estuary-basin model and Fig. 10), D = river estuary (see estuary-pycnocline model and Fig. 11).

Dunbarella has far more to offer as evidence for the depositional environment. Its impressive abundance, relatively uniform distribution, and concentration in certain bedding planes are clearly important constraints on modeling, but their significance requires careful interpretation. We can best approach the problem by making some assumptions about the paleoecology of *Dunbarella.* Not, of course, that *Dunbarella* lived on the surface of deposition; as pointed out earlier, it seems unlikely that anything lived there.

Much of the discussion to follow includes observations made by one of us (GRC) during 10 years of research in the ecology and growth of modern pectinids.

All bivalves distribute their progeny by means of free-swimming larvae, which settle over wide areas in periodic "spatfalls." In temperate waters such spawning occurs once or twice a year, regulated by seasonal factors. In equatorial waters, such as those in the Kinney Quarry site in the Pennsylvanian, spawning can be much more frequent. Most bivalves, including pectinids and all close relatives, are suspension feeders and do not require sediments as a food source. As juveniles, all pectinids attach to substrates such as shells, coral, or seaweed, and many continue the practice as adults. The strong byssal notch of *Dunbarella* places it in the latter group. No pectinids today can tolerate intertidal exposure; this is why inland restaurants do not ship live scallops as they do clams and mussels. Many modern pectinids can tolerate moderate variations in temperature and salinity; many others cannot. Finally, among byssate bivalves thin shells usually mean fast growth.

From these data we can safely assume that *Dunbarella is* a bysally attached suspension feeder that can settle a suitable substrate in enormous numbers if conditions are right at spatfall. The shells probably grow rapidly, accommodating minor temperature and salinity variations. Catastrophic death could be caused by excessive changes in temperature or salinity, or by exposure to air.

For a little more insight we could turn to a possible analog. *Leptopecten latiauratus is* a modern pectinid with a striking resemblance to *Dunbarella* (Clark, 1971). It is about the same size and shape, even to the shell curvature. It has a similar shell sculpture and a similarly thin shell. Like *Dunbarella,* it has a well-developed byssal notch. If form follows function, the two should have a similar ecology.

Leptopecten is an opportunistic colonizer. If a spatfall finds available substrates (and marine plants are frequently used), the population can explode overnight. Individuals can reach adult size in a matter of weeks, dominating some environments. In many environments, however, extreme low tides or other periodic factors can produce mortality as impressive as the initial settlements.

Interestingly, *Leptopecten* tends to remain attached by its byssus for some time after death; decay of the soft tissues is generally well advanced before the shell falls away from the substrate. Often the shell leaves the remains of the soft tissues still attached by the byssus; the shells, being very thin and relatively flat, are then readily transported by even slow currents.

Although we cannot assume that *Leptopecten* is a perfect analog for *Dunbarella,* there is enough independent evidence to justify consideration of *Leptopecten* ecology in paleoenvironmental models.

Assumptions on water chemistry and exposure to air

Both the lack of bioturbation and the presence of shrinkage cracks have implications for the sedimentary environment. The former tells us that the sediment surface was hostile to life either continuously or at frequent intervals, and the latter tells us that there were times when large amounts of water were drawn out of the sediments. General situations hostile to life include water deficient in oxygen, water of excessive salinity or alternating between fresh and marine, water too hot or alternating too rapidly between warm and cold, or intertidal equatorial environments. Situations in which water could be drawn from the sediments include subaerial exposure on a tidal flat and subaqueous sediments saturated with fresh water but covered with sea water (see Plummer & Gostin, 1981, and Wightman et al., 1987).

Depositional models

Intertidal model

A simple model of tidal sedimentation can be generated, in which thicknesses of laminae are directly proportional to tidal heights and the dark layers are produced during high-water stillstands. Based upon the tidal curves described above (Fig. 5), a simulated series of tidally produced laminae can be generated (Fig. 6). This type of simulation will produce a series of vertically stacked laminations that exhibit rhythmic variations in thickness, or "tidal rhythmites." Visual inspection of these simulated tidal rhythmites indicates that diurnal tidal systems will potentially produce rhythmites with dearly expressed neap-spring cycles.

Comparing the simulated rhythmites (Fig. 6) with the *Dunbarella-bed* laminations (Fig. 2) suggests that the hierarchy of laminations observed within the shale is best explained by invoking sedimentation within a diurnal tidal system. Based upon such a model, the dark layers of the major laminae are produced during neap tides, and the minor laminae represent individual tidal events; the latter are best developed during spring tides.

It is evident, however, that there are fewer than the approximately 15 minor laminae per major lamina that would be predicted by this tidal model. The model can be further refined to explain such occurrences. As described above, our tidal model predicts that lamina thickness will be proportional to tidal height. Maximum tidal heights vary during a neap-spring cycle; if we consider the model sedimentation site at various heights within the intertidal zone, then successively greater heights will expose the site to fewer and fewer tides. Based upon a tidal-height curve from a diurnal tidal system, such as that from Do Son, Vietnam (NOAA, 1988), lines representing various heights within the intertidal can be drawn (Fig. 6A). High tides which exceed these various lines can be extracted (Fig. 6B) and these sets, which can be termed "truncated neap-spring" data, can be used to generate simulated tidal rhythmites (Fig. 6C). The simulated rhythmites can be compared to the *Dunbarella* beds; there are many similarities of the thinner laminae (Fig. 2A) to the simulations that used only 33% of the highest tides (Fig. 6C). Similarly, the thicker major laminae of the *Dunbarella* beds contain more minor laminae (Fig. 2B) and are similar to the simulated rhythmites that used 66% of the highest tides (Fig. 6C).

Although placing the model sedimentation site high in the intertidal range (Fig. 7: location A, Fig. 8: A2-C2) succeeds in producing patterns similar to those found in the *Dunbarella* beds (Fig. 2), it would not serve to explain either the sedimentology or the distribution of fossils. In the model, the intervals between deposition at extreme high tides would have no deposition at all; in fact, the major dark layers in the *Dunbarella* beds contain sediments much the same as the light layers, as well as nearly all the fossils. A more sophisticated version of the intertidal model is needed.

A better solution would be a model deposition site at the middle of the intertidal range (Fig. 7: location A, Fig. 8: A1-C1); here the same relationship between extreme high tides and light-layer deposition could exist if the deposition depended upon tidal currents rather than tide range. At the center of the intertidal range, tidal currents are at a maximum when tide range is greatest; if deposition of silt and clay were more-or-less continuous, and deposition of the dark organic debris required currents below a certain threshold, then such a model might match the sedimentology of the *Dunbarella* beds.

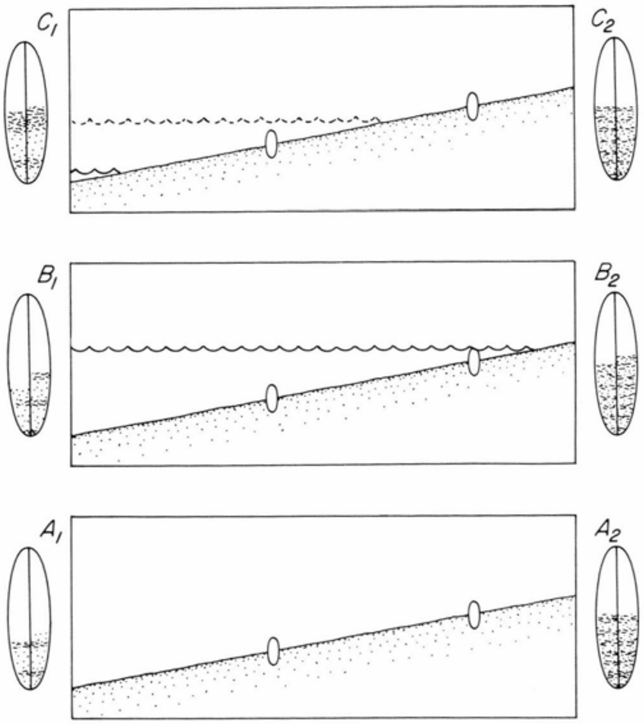

FIGURE 8—Intertidal depositional model showing different tide levels. Ellipses at left show sediment accumulation at mid-tide level (small ellipses in left center of diagrams); ellipses at right show sediment accumulation near extreme high tide level (small ellipses in right side of diagram); for each ellipse, compare its right half to its left half to see any deposition during the preceding rise or fall of the tide. **A_1–A_2,** Extreme low tide, no sediment accumulation at A_2, some clay and silt at A_1. **B_1–B_2,** Extreme high tide, sediment accumulation at both sites (more at B_1), consisting of clay and silt followed by settling of organic debris at slack water. **C_1–C_2,** Neap tides (solid line = mean low tide, dashed line = mean high tide), sediment accumulation at C_1 only, consisting of mixed clay, silt, and organic debris.

Although the intertidal environment would not necessarily collect *Dunbarella* shells, it is at least possible. For example, high tidal currents during spring tides could be too energetic for the deposition of such lightweight shells and plant remains, whereas the gentle currents of neap tides might spread them out over the tidal flats. The *Dunbarella* could have populated some hypothetical vegetation at extreme low tides, perhaps reached only every second or third spring tide, and have grown to adult size before the next exposure. Some four to six days after being killed by such an exposure, the shells would come loose from their attachments and be distributed by the neap tides. This would fit their observed distribution.

The intertidal model could accommodate the lack of bioturbation and the shrinkage cracks, but the absence of other features poses problems. Modern tidal flats commonly exhibit significant erosion, including rilling, small-scale channeling, and cut-banks associated with such channeling. Shells on such tidal flats would serve as focal points for these erosional effects. Erosional truncations of any type are not apparent within the *Dunbarella* beds. Indeed, the sections illustrated in Fig. 2 show no evidence of any erosion, even where the pectinid shells must have protruded above the surface during deposition. The lack of even fine-scale erosion is a serious impediment to an intertidal model.

Prodeltaic model

Based on observations of modern environments and a model generated by Smith et al. (1990), tidal rhythmites can be formed in a prodeltaic setting (Fig. 7: location B). In such a system, fluvial sediments that would normally be deposited on the delta top are, during the largest daily tidal oscillations produced during spring tides, transported basin-ward as density currents (turbidites). The amount of sediment transported is directly related to the height difference between lowest and highest tides (Fig. 9). Graded laminae, produced by sediment-gravity flows generated by tidal action, have been reported in sediment traps placed in 25 m of water (Smith et al., 1990). Sedimentologically, this model is of considerable importance because it serves to explain a tidal control of sedimentation in waters that are significantly deeper than those generally affected by tidal activity. The deeper-water tidal laminae would exhibit considerable lateral continuity as well as lack of erosional features. Thus, this model explains such features that are not readily explained by an intertidal model.

The presence of *Dunbarella* is difficult to explain unless the water is shallow enough for tidal currents to transport the shells from nearshore areas. It is possible for the *Dunbarella* to be living attached to floating seaweed above the prodelta basin, but then there is no easy way to involve a cyclic mortality. Thus, if the prodelta model is possible at all, it must be very near shore and quite shallow.

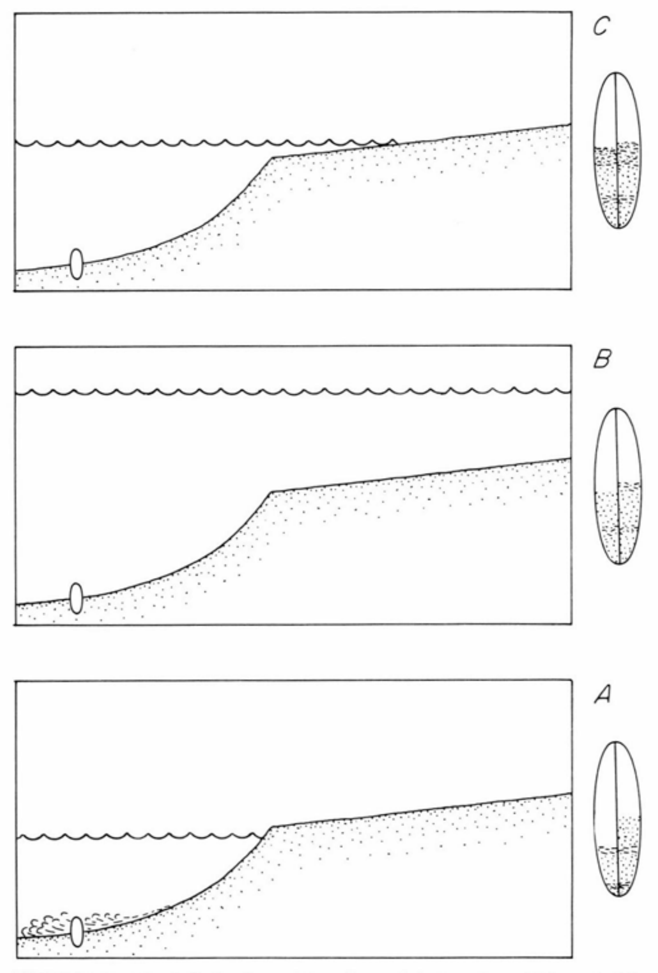

FIGURE 9—Prodeltaic depositional model showing different tide levels. Ellipses at right show sediment accumulation at position of small ellipse in diagrams (ellipses split as described in Fig. 8). **A,** Extreme low tide, sediment accumulation dominated by mini-turbidity flows triggered by exposure of lip of delta front. **B,** Extreme high tide, sediment accumulation mostly organic debris. **C,** Neap tide, mean low water shown, sediment accumulation of mixed clay, silt, and organic debris.

The real problem with this model comes with trying to explain the shrinkage cracks. As discussed in the next section, such cracks can be generated subaqueously if significant salinity fluctuations occur; however, sedimentation within this prodeltaic model would be in deeper-water, moreor-less marine settings and would probably not involve significant salinity fluctuations.

Estuary-basin model

This model invokes sedimentation within a tidally influenced estuary (Fig. 7: location C). Such a model shares similarities with both models described above; however, the rhythmites could be developed in a similar manner to that described in the prodeltaic model. Thus, fine-grained fluvial sediments are being secondarily reworked and deposited by tidal energies. The fluctuations of these tidal energies, related to oscillating tidal heights, produce a hierarchy of major and minor laminae, which are related to spring—neap and daily tidal-height variations, respectively (Fig. 10). An estuarine setting provides for significant fluctuations in salinity, and such variation is in turn related to spring—neap tidal cycles. During neap tides the tidal effects are minimized and the relative effect of the fluvial input is maximized. Thus the salinities of the depositional system during neap tides are likely to become brackish to fresh water. Conversely, during spring tides the tidal effect may become dominant, and the salinities will become more marine. Salinity variations within estuaries are complicated and involve effects beyond the scope of our discussion (see Feldman et al., this volume). Nonetheless, it is sufficient for our model to state that a more fluvial, fresh-water aspect is generally developed during neap tides and that a more marine, brackish aspect is generally developed during spring tides.

It is these salinity fluctuations, which correlate with the tidal cyclicity, that can serve to explain features such as the *Dunbarella* and shrinkage cracks that are not readily explained by the prodeltaic model. If the pectinids were epiplanktonic (attached to floating seaweeds) inhabitants of marine to brackish waters, spring tides could serve to concentrate large numbers of them in the brackish surface waters of the estuary. During the following periods of neap tides, tidal flux would be reduced and fluvial influence and resultant hyposaline waters could cause mass mortality. The shells would accumulate on the estuary floor in muds deposited from more-or-less hyposaline waters. As tidal flux increased during the ensuing spring tides, estuarine waters would become more saline. These overlying more saline waters would tend to draw out the hyposaline interstitial waters from the muds that had been formed during neap tides, and subaqueous shrinkage cracks would be formed (fluctuating salinities for such crack generation have been described by Wightman et al., 1987, and Plummer & Gostin, 1981).

Estuary-pycnocline model

Similar to the estuary-basin model, this model places the site of deposition well inside a river-dominated estuary (Fig. 7: location D). The river is bringing silt and clay to the deposition site, and the river flow is about the same speed as the maximum tidal currents. Marshes along the shores of the estuary provide a source for both reworked plant fragments and fronds of vegetation. Assuming the site was equatorial (see Scotese et al., 1979), the fresh water of the

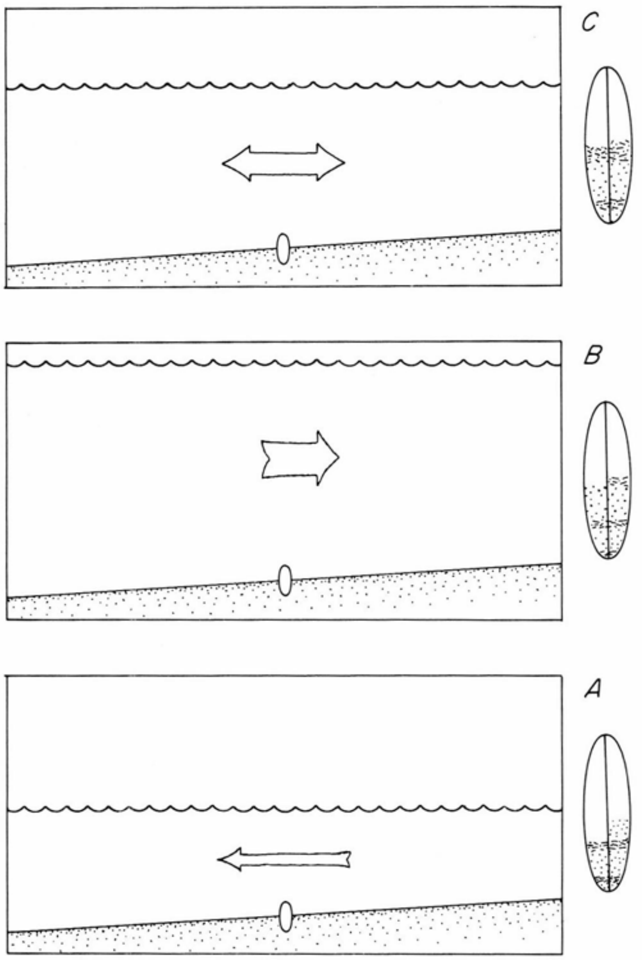

FIGURE 10—Estuary-basin depositional model showing different tide levels. Ellipses at right show sediment accumulation at position of small ellipses in diagrams (ellipses split as described in Fig. 8). **A,** Extreme low tide, sediment accumulation largely silt and clay from estuarine tidal flats, little organic debris accumulates under strong tidal current. **B,** Extreme high tide, sediment accumulation largely organic debris settling in slack water. **C,** Neap tides, sediment accumulation largely organic debris settling in relatively weak tidal currents, little silt or clay as tides do not reach source area in upper tidal flats.

river and the brackish water of the upper marsh would have been quite warm.

Strong tides introduce potentially cooler, saline (marine) waters into the estuary, and, because of the considerable density differences, this forms a wedge-shaped water mass at the bottom (Fig. 11). Rising tides carry the wedge farther up the estuary, opposing the river, and falling tides permit it to be carried out. Even though the wedge remains under the river, an incoming tide will slow the river's flow, and an exceptionally high tide will bring the river nearly to a halt.

Considering only the deposition of clay and silt, it can be seen that this model will result in continual deposition. Exceptionally heavy deposits will form at times of highest spring tides, when the river is slowed to the point that it drops nearly its entire load. During neap tides and the lesser spring tides deposition will be markedly less, but will continue.

To explain the dramatic variations in deposition of particulate plant debris, we invoke a pycnocline. This is nothing more than the strong density gradient between the warm, fresh river water and the cold, saline sea-water wedge. Even a slight density gradient can keep organic debris from settling through it; one of us (GRC) has observed thick clouds of organic debris above a thermocline in Bermuda. A density gradient involving not only temperature but also salinity would be even more effective.

We envision, then, a site along the bottom of an estuary where plant debris can settle to the bottom only when the pycnocline is absent, or at least considerably reduced in degree. During spring high tides the wedge would extend far upriver and the strong pycnocline would permit the passage of silt and clay from the river, but would hold back the organic material. During spring low tides the wedge would be far downriver, and the plant debris would be deposited along with the silt and clay. This would produce the minor laminae observed within the major light layer. During neap tides the diffuse tip of the wedge would sweep back and forth across the deposition site, permitting variable amounts of plant material to be deposited, but never completely cutting off the supply. The relatively low deposition rate of silt and clay during this stage would permit the accumulation of a strong major dark layer. This cycle is illustrated in Fig. 11.

A corollary to this depositional model is the observation that the number of minor laminae within major light layers would depend in part on river flow rates.

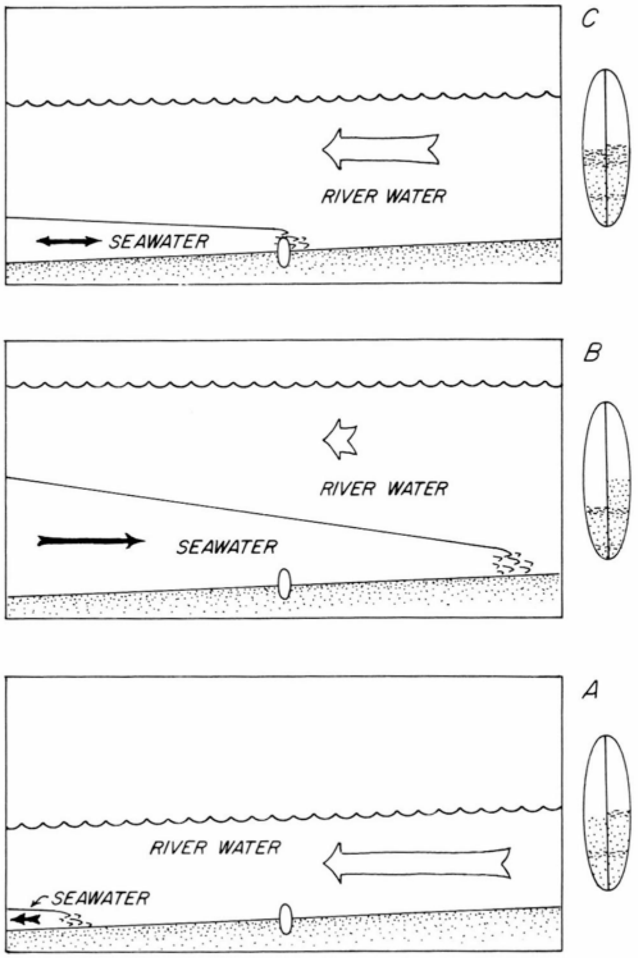

FIGURE 11—Estuary-pycnocline depositional model showing different tide/river levels and positions of sea-water wedge. Ellipses at right show sediment accumulation at position of small ellipses in diagrams (ellipses split as described in Fig. 8). **A,** Extreme low tide, sediment accumulation minimal, largely plant debris. **B,** Extreme high tide, sediment accumulation maximal, no plant debris. **C,** Neap tides, sediment accumulation minimal, with plant debris, lack of extreme tides results in a grouping of many tidal accumulations.

The distribution of *Dunbarella* follows a scheme much like that proposed for the intertidal model. Coastal marshes, either outside the estuary or enough seaward to be essentially marine, are periodically populated by *Dunbarella* spat-fall. No spat survive in the intertidal zones, except for the lowest intertidal where extreme spring tides might not expose the shells for several weeks. When exposure does occur, the dead pectinids would not release their shells for several days, just right for their distribution by the weak neap tides.

This model accounts for the lack of bioturbation, as the bottom environment is alternately swept by fresh and saline waters of different temperatures. This would be entirely too hostile for even common bacteria to flourish. Shrinkage cracks could form in this environment when layers of sediment deposited with interstitial fresh water are exposed to sea water.

Conclusions

Several lines of taphonomic and sedimentological evidence can be used to constrain the range of environments involved in the *Dunbarella* beds. The shales exhibit two orders of laminae, with major laminae delineated by darker zones. Some darker zones exhibit shrinkage cracks. *Dunbarella* occurrences are restricted to these darker zones. Minor laminae lack *Dunbarella.* Although a few layers display pyritization, lack of pervasive pyritization and the presence of butterflied valves suggest deposition after death. The two orders of laminae strongly suggest an origin by tidal processes, with the minor laminae formed during daily tidal events and the major laminae related to fortnightly (neap-spring) tidal cycles. Such patterned laminae have been referred to as "tidal rhythmites" and have been documented from modern and ancient settings.

Potential depositional models include tidal flat, tidally influenced prodeltaic, and tidal estuaries (basin and river). Lack of erosive features argues against a tidal-flat model. Lack of tidal currents (at least in a typical, deep-water prodelta) to explain the *Dunbarella* concentrations and lack of variations in water chemistry to explain shrinkage-crack occurrences serve to preclude a prodeltaic model. Within an estuary, oscillations of salinity related to tidal cycles could serve to explain both the *Dunbarella* concentrations and the production of subaqueous shrinkage cracks. Therefore, in this preliminary assessment we favor a subaqueous setting in a tidally influenced estuary (such as C or D in Fig. 7) as a reasonable depositional site.

Acknowledgments

We thank Keith Miller and Page Twiss for their suggestions on earlier versions of this paper. Fieldwork for this project was partially supported by NSF grant EAR-9018079.

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Faunal distribution, seasonal deposition, and fish taphonomy at the Upper Pennsylvanian (Missourian) Kinney Brick Company Quarry, central New Mexico

Phillip Huber

75 Meadow St., Seymour, Connecticut 06483

Abstract—The Kinney Brick Company Quarry exposes a 28 m thick coarsening-upward sequence which includes prodelta laminar micrite, microlaminated shale, silty shale interbedded with lenticular, very fine- and fine-grained sandstone, fluvial medium-grained sandstone, and limestone-pebble conglomerate. Invertebrate distribution and gross sedimentology indicate deposition in a basin characterized by poor circulation, reduced oxygen levels, fluctuating salinities, and gradually increasing sedimentation rates. These parameters suggest progressive shoaling and infilling of an interdistributary embayment which became increasingly isolated from interaction with open-shelf marine environments.

Seven autochthonous invertebrate assemblages are identified, which exhibit a general trend of decreasing taxonomic diversity upsection; successive assemblages are largely composed of survivor taxa from the preceding ones. Allochthonous organisms from terrestrial and fresh-water environments (e.g. plants, conchostracans) were transported into the embayment during "wet" phases of a seasonal monsoonal climatic regime, when increased discharge from landward source areas resulted in deposition of dark-colored, organic-rich microlaminae. During "dry" seasons, clastic particles settled out of suspension and formed light-colored laminae; in some units (e.g. fish bed) clastic influx was restricted enough to allow carbonate precipitation. Seasonal density stratification of the water column caused synchronous mortality events among both invertebrates and fish; fish preservation at the quarry is due to anaerobic substrate conditions rather than rapid burial.

Introduction

The Kinney Brick Company Quarry is developed in strata assigned to the Upper Pennsylvanian Wild Cow Formation (Madera Group), which is widely exposed along the dip-slope of the Manzano and Manzanita Mountains of central New Mexico. Exposures at the quarry have been referred to the early Virgilian Pine Shadow and La Casa Members (Myers, 1969; Myers & McKay, 1976; Lorenz et al., this volume), but conodont (Mapes & Boardman, this volume) and brachiopod data suggest a middle or late Missourian age, in which case the quarry section might correlate with the lower portion of the Pine Shadow or upper part of the Sol se Mete Members (cf. Myers, 1973, 1988). At present, 28 m of strata outcrop in the walls and floor of the quarry and include (ascending) laminar and finely laminated micrite, microlaminated shale, laminated shale and claystone, silty shale and interbedded sandstone, and limestone-pebble conglomerate. This sequence was deposited in a variety of nearshore-marine prodeltaic environments, and the section as a whole comprises a regressive facies sequence (Huber et al., 1989a, b; Lucas & Huber, 1991).

The most controversial aspect of Kinney Quarry geology and paleoecology is the mechanism(s) by which the fine-grained clastic fades exposed at and near the base of the quarry section was deposited. Some workers view these lithofacies as the product of tidal-rhythmite sedimentation (Archer & Clark, 1991, this volume; Feldman et al., 1991b, this volume), while another theory, advocated by Lehman (1991) and further developed below, regards the Kinney Quarry sequence as a product of seasonal deposition, recording the gradual shoaling and infilling of an interdistributary embayment. This latter model impacts on paleoecological and taphonomic interpretations of the quarry sediments and biota. Sedimentological features and biotic distribution suggest that the composition of faunal assemblages was largely dictated by restricted water circulation, reduced oxygen levels, and fluctuating salinity values and sedimentation rates. I argue that the entire stratigraphic section preserved at the quarry, except for the upper few meters (unit 17 of Lucas & Huber, 1991), is of marine origin and that terrestrial and fresh-water organisms (e.g. plants, conchostracans) were transported into the Kinney embayment during periods of increased clastic sedimentation initiated by the onset of the "wet" phase of a monsoonal climatic regime.

The following abbreviations are used in the text: CM, Carnegie Museum of Natural History, Pittsburgh; KU, University of Kansas, Lawrence; NMMNH, New Mexico Museum of Natural History, Albuquerque; USNM, U.S. National Museum, Washington, D.C.; UNM, University of New Mexico, Albuquerque.

Structure, stratigraphy, and sedimentology

At present, the Kinney Brick Company Quarry exposes a 28 m thick section in the lower, active pit. These strata define a regressive facies sequence which reflects the pro-gradation of a clastic delta (Huber et al., 1989a, b). The depositional history of this delta was interrupted on at least two occasions by marine transgressions which probably resulted from rising base level exceeding basin subsidence rate. The stratigraphy utilized in this paper is that of Lucas & Huber (1991), reproduced by Kues & Lucas (this volume).

The Kinney Quarry includes an upper, inactive pit, a lower, active pit, and a rear area which was worked before 1987. These three outcrop areas encompass most of the S^{1}/2 sec. 18, T9N, R6E, Bernalillo County. Structure within the confines of the quarry is simple. Strata in the upper, inactive pit dip gently to the southwest, but are horizontal in the active pit and rear area. The lower and upper areas of the quarry are separated by vegetation cover which conceals a north—south-trending normal fault with a displacement of approximately 20 m. Small-scale faults which trend roughly east—west and show displacements of 1 m or less are present in the upper and lower pits. Folding was observed only in the upper pit where a laterally restricted interval of unit 3 is folded and contorted along strike for less than 1 m. Interestingly, the underlying micrite and overlying fissile shale are relatively undisturbed, implying the occurrence of a syndepositional tectonic event. It is possible, however, that the folded zone is related to the major normal fault located within 15 m of the outcrop.

The section begins with 1 m or more of black, laminar to platy, pelletal, ostracode-rich micrite with a high content of black clay (unit 1). Feldman et al. (this volume) report that this unit includes thin (3-5 mm) laminated beds which alternate with burrowed zones up to 1 cm thick. The upper 7 cm of the micrite (unit 2) has uniform, fine laminations, and the transition from laminar to finely laminated bedding is sharp but gradational. Both units are petroliferous. The presence of pyrite on bedding surfaces and on valves of lingulid and articulate brachiopods indicates deposition under reducing conditions.

The overlying olive-black, calcareous shale (unit 3) is 14 cm thick and well indurated. This unit is characterized by rhythmic couplets of alternating organic- and clay-rich laminae interspaced with thin layers of pelletal, ostracode-rich micrite (Lehman, 1991). The organic- and clay-rich laminae are continuous along strike for 10 m or more; carbonate laminae pinch and swell in thickness and grade upward into detrital layers (see Feldman et al., this volume, fig. 2A, B). Carbonate deposition may have occurred in response to seasonal fluctuation of clastic input into the Kinney embayment. Analogous microstratigraphic sequences are common in many lacustrine deposits (e.g. Olsen, 1984) and Holocene facies of the Black Sea (Muller & Stoffers, 1974: fig. 4a). Other features of unit 3 include extensive yellowish-orange (10 YR 6/6) mottling and a complete absence of bioturbation. This unit is gradational with the overlying 22 cm of microlaminated fissile shale (unit 4) which displays the same colors. Unit 4 contains rare, centimeter-scale levees which truncate bundles of laminae, implying agitation by low-velocity bottom currents. Carbonate layers are less conspicuous in the lower 5 cm of the unit and are absent higher up. The thickness of individual laminae is slightly greater when compared to unit 3. I interpret this, absence of carbonate layers, and presence of small-scale levees as reflecting a subtle increase in sedimentation rate.

The fissile shale grades upward into olive-gray, microlaminated shale over an 8 cm interval. The olive-gray shale is 1 m thick, non-bioturbated, and lacks the tripartite bundles of laminae characteristic of unit 3. Archer & Clark (this volume) describe this subfacies as consisting of laminae packages comprising two orders of alternating light and dark bands and "zones," and note that fossils (mainly plants and the pectinid *Dunbarella)* are largely restricted to the major dark-colored laminae. Feldman et al. (1991b, this volume) report numerous horizons of what they interpret to be desiccation cracks throughout units 4 and 5, but Kues & Lucas (this volume) believe these structures to be weathered joint patterns. There is some support for the latter interpretation, as the infilled margins of these rectangular and polygonal structures do not penetrate the underlying microlaminated beds to a depth greater than 1-2 mm. Also, the underlying fish bed (unit 3) fractures very easily upon weathering and large areas of bedding surfaces (10 m^2) show similar joint-like patterns. The olive-gray shale is transitional with the overlying finely laminated and interbedded shale and claystone (unit 6). It is important to note that the thickness of individual laminae gradually increases upsection and parallels a progressive increase of the silt fraction from unit 2 through unit 6. The contact of units 6 and 7 is sharp, and the latter is a greenish-gray, highly fossiliferous shale which is platy to finely laminated and finer-grained than unit 6. This 20 cm thick bed contains an invertebrate assemblage which suggests that deposition occurred during an accelerated rise of base level (i.e. transgression).

The transition to silty shale occurs over an interval of 0.75 m (unit 8). Silty shale is the dominant lithology of the quarry exposure and includes a 9.9 m thick, laminar, bioturbated, micaceous facies (unit 9) and one or more beds (0.1-1.1 m thick) intercalated with very fine- and fine-grained sandstone. The sandstone beds (e.g. units 10, 12, 14) are lenticular, laminar to ripple laminar, and at least one tabular unit displays trough crossbedding (unit 16). The sandstones have been interpreted as interdistributary mouth bars (Lucas & Huber, 1991; Lorenz et al., this volume). The section is completed by 0.1-2.1 m of sandstone and limestone-pebble conglomerate which rest unconformably on unit 16. This facies (unit 17) most likely is a fluvial channel-lag deposit.

Faunal distribution

Most of the fossils obtained for this study were collected over a two-year period from the lower 8 m of the quarry exposure (units 1-9). No systematic effort was made to collect bulk census samples of invertebrates for paleoecological analysis, but the numerous excavations made in this interval provide an accurate, though only qualitative, assessment of invertebrate abundance, diversity, and distribution in these beds. The provenance of the vertebrates was carefully noted; preliminary census counts of taxa present in collections at CM, KU, NMMNH, UNM, and USNM, and those maintained by several private collectors, are indicated in Fig. 1. Note that certain groups, particularly palaeoniscoid fishes, are currently under study and the results have not been incorporated into this paper. Hence, most fusiform chondrosteans are referred to the form genus *"Elonichthys'* or "other palaeoniscoids" in Fig. 1, unless a confident generic identification could be made.

Invertebrates

Seven invertebrate assemblages are readily discernible in the 28 m of outcrop. The first (stratigraphically lowest) is the *Lingula—Solemya—Myalina* community found in the basal micrite (units 1-2) and described in detail by Kues (1991, this volume). This assemblage also includes the pectinids *Dunbarella* and *Aviculopecten*, cephalopods (see Mapes & Boardman, this volume), high-spired gastropods, articulate brachiopods *(Composita, Antiquatonia, Chonetinella, Linoproduct us, Neospirifer)*, and conodonts, which comprise the in-situ fauna. Kues (this volume) describes additional invertebrates (mostly molluscs) from this assemblage, but their indigenous and/or allochthonous origin cannot be clearly demonstrated because of small sample size and fragmentary preservation. Clearly allochthonous organisms derived from both open-shelf and fresh-water/terrestrial environments are plants (mainly calamitalean trunks and pinnules of *Neuropteris* spp.), spirorbid worms, crinoid columnals, echinoderm plates, bryozoans, conchostracans, smooth ostracodes, and insect wings. A marine environment with restricted circulation, though maintaining near-normal salinity, with a reduced oxygen content is indicated by the assemblage composition and taphonomy (note unbroken spines on articulate brachiopods and soft-part preservation of insects; Kues, 1991).

Assemblage 2 occurs in the basal microlaminated shale (unit 3). This interval contains a diverse palynoflora (Willard, 1991, this volume) and abundant, though poorly preserved, megafossil plants dominated by pteridosperms. Other allochthonous elements are crinoid columnals, fragments of fenestrate bryozoans (both uncommon), *Lingula*, conchostracans (Fig. 2), smooth ostracodes, and insects. The autochthonous fauna is strongly dominated by molluscan taxa which include small *Dunbarella*, *Myalina*, high-spired gastropods, ammonoids and nautiloids (including a phrag-

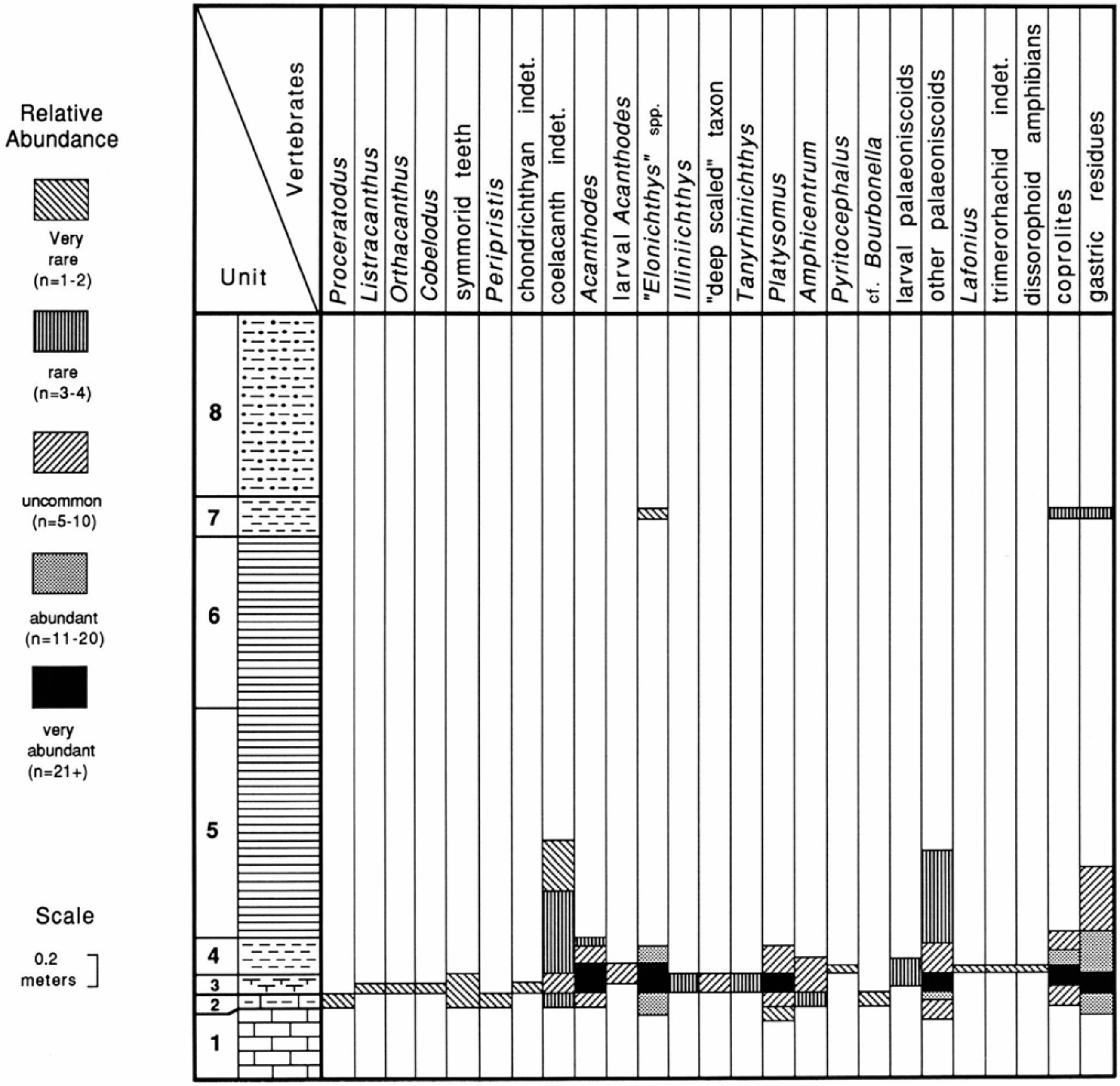

FIGURE 1—Distribution and relative abundance of vertebrates at the Kinney Quarry. Preliminary census counts of genera are based on collections at CM, KU, NMMNH, UNM, and USNM.

mocone 0.3 m long), along with common articulate brachiopods (e.g. *Antiquatonia, Neospirifer).* The assemblage is composed entirely of taxa found also in the underlying micrite, but taxonomic diversity and relative abundance of certain groups (especially articulate brachiopods) are greatly diminished. The presence of the conodont genera *Streptognathus, Anchignathodus,* and *Idiognathodus* (Mapes & Boardman, this volume), cephalopods, and articulate brachiopods requires a water column maintaining near-normal salinity for long periods of time (months or longer). The mass of heavier organisms (e.g. cephalopods, articulate brachiopods), when viewed in light of the microlaminated bedding, lack of current structures and bioturbation, uniform grain size, and reducing color of sediment, precludes the possibility that they were transported into the environment (cf. Mapes & Boardman, this volume).

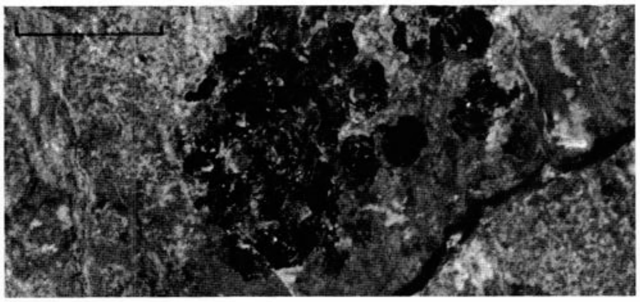

FIGURE 2—"Pseudestheria" sp., current-deposited grouping of disarticulated carapaces. Unit 3, NMMNH collection, uncatalogued. Scale bar equals 1 cm.

Assemblage 3 occurs in microlaminated, fissile shale (unit 4). Again, most taxa present are faunal constituents derived from the immediately underlying assemblage. Molluscs are still dominant and include small *Dunbarella, Myalina,* and the same high-spired gastropod found in units 1-3. Articulate brachiopods are not common and fewer than 10 badly crushed and generically indeterminate specimens have been collected. Other faunal trends are a decreased abundance of fish (discussed later) and the first appearance of malacostracans *(Aenigmacaris* and *Uronectes;* Schram & Schram, 1979), which are largely restricted to a 7 cm thick zone. Allochthonous elements in this assemblage are crinoid columnals, fenestrate bryzoans, *Chonetinella* cf. *flemingi,* all rare, and common *Lingula,* smooth ostracodes, and conchostracans. The presence in this unit of rare, small-scale levees, which truncate bundles of laminae 0.5-1.5 cm thick, suggests that low-velocity currents occasionally scoured the substrate surface. These structures also provide evidence of a mechanism which accounts for transport of allochthonous marine organisms into the embayment.

Assemblage 4 is of extremely low diversity and is dominated by the pectinid *Dunbarella. Dunbarella* in this assemblage (found in units 5-6) occurs in all growth stages from spat to valves up to 40 mm long (Mamay, 1990; Kues, this volume) and the density of specimens can exceed 700/m^2 on a bedding plane (Feldman et al., this volume). Other taxa are not common in these beds, but include ostracodes, *Myalina,* occasional gastropods, numerous fragmented conchs of ammonoids (cf. *Prothalassoceras),* and specimens of the eurypterid *Adelopthalamus luceroensis* Kues 1985. The occurrence of *Myalina* and ammonoids demonstrates a marine origin for these beds and counters Kues' (this volume) assertion that certain Kinney Quarry *Dunbarella* are indicative of fresh-water depositional environments.

Assemblage 5 is confined to the 20 cm thick bed of unit 7. The assemblage is much more diverse than that found in units 5 and 6 and includes most of the same taxa, a nautiloid (UNM 10945), high-spired gastropods, *Lingula,* ostracodes, and a large specimen of the malacostracan *Aenigmacaris.* Allochthonous organisms include abundant pteridosperm pinnules and walchian conifers, rare conchostracans, blattoid wings, and a single myriapod. This unit maintains its thickness and bedding character across the south half of sec. 18, T9N, R6E, Bernalillo County, while stratigraphically adjacent units tend to thin or thicken (e.g. units 6, 8, 9) across the same area. The faunal content suggests that this shale was deposited during a brief marine transgression (note presence of *Myalina,* gastropods, nautiloids, and *Lingula).*

The prodelta silty shale (units 8 and 9) is sparsely fossiliferous when compared with underlying beds. These units contain a megaflora dominated by walchian conifers, and the only invertebrates found thus far are small valves of *Dunbarella* (assemblage 6). The overlying interbedded shale, siltstone, and sandstone (units 10-16) are unfossiliferous with two notable exceptions. A lenticular sandstone bed exposed in the upper pit (which has no apparent lateral correlative in other areas of the quarry) contains abundant crinoid columnals and productid brachiopods. The broken and abraded condition of the specimens indicates that they were probably transported from source-area sediments. Higher in the exposure, Lucas & Huber (1991) reported a low-diversity invertebrate assemblage from unit 15 (assemblage 7). The assemblage is dominated by the nearly ubiquitous *Dunbarella;* less common taxa are *Myalina, Lingula,* and conchostracans.

Preliminary analysis of the Kinney Quarry invertebrate fauna indicates seven autochthonous fossil assemblages, most of which also contain a variety of organisms transported from both open-marine and terrestriaUfresh-water environments. A trend is apparent where each successive assemblage is composed of survivor taxa from the preceding one (Fig. 3). Most of the assemblages are transitional with one another over short stratigraphic intervals (usually under 10 cm), the only exceptions being assemblages 5 and 7 which are found in units interpreted as transgressive facies.

The faunal content in general indicates that almost the entire succession of lithofacies was deposited under marine conditions with fluctuating salinity values (cf. Huber et al., 1989b). Taxa which are 'considered indicators of fresh-water environments are limited to conchostracans (Petzold & Lane, 1988), smooth ostracodes (Kaesler, 1988), and possibly eurypterids (Kues, 1985, 1988). Conchostracans, however, are intimately associated with marine facies throughout much of the Permo-Carboniferous, and may have tolerated salinity values approaching 3% (Calver, 1968: 162). The rarity of eurypterids (three partial specimens) limits their usefulness in any paleoecological analysis which determines possible depositional environments, as the exact provenance of all the specimens is only assumed to be from somewhere in unit 5. Also, the same species found at the Kinney Quarry is otherwise known only from a dense concentration (over 150 specimens/m^3) in sediments of presumed fresh-water origin (Kues & Kietzke, 1981), making the latter occurrence a poor comparative analog.

Smooth ostracodes are generally considered indicators of fresh-water conditions (Kaesler, 1988). Their abundance in some beds which also contain stenohaline marine invertebrates (especially units 1-7) suggests an allochthonous origin. The restriction of these ostracodes in some units to bedding planes which also contain conchostracans (S. Lucas, pers. comm. 1991) is consistent with this interpretation and suggests that both groups were transported seaward during periods of increased clastic sedimentation (during "wet" seasons).

Much has been said in this volume about the taxonomy, distribution, and paleoecology of the pectinid *Dunbarella.* Kues (this volume) provides the taxonomic treatment, and he, Archer & Clark (this volume), Clark (1978), and Feldman et al. (this volume) discuss the distributional and paleoecological aspects of this taxon. Kues (this volume) believes that the large concentrations of *Dunbarella* in units 5 and 6 indicate deposition, at least in part, under fresh-water conditions. To the contrary, most previous workers concluded that *Dunbarella* thrived in environments with near-normal salinities (e.g. Zangerl & Richardson, 1963; Calver, 1968). Some authors have interpreted the occurrence of this taxon in lithofacies closely associated with coal-bearing portions of cyclothems to infer a brackish-lagoon environment (e.g. Murphy, 1967; Hickey & Younker, 1981). However, Donahue & Rollins (1974) demonstrated that similar dark-gray, laminated shales between the Harlem coal and Ames Limestone (early Virgilian) actually reflect offshore deposition at or near the maximum stillstand of a rapid transgression. This interpretation was modified by Boardman et al. (1984) and applied to analogous facies of another Conemaugh Group marine "event," the Brush Creek Cyclothem (early Missourian), which, incidentally, contains the type locality of *Dunbarella striata* (Murphy, 1967). Boardman et al. (1984) also identified this pectinid as an abundant constituent of offshore, deep-water communities *("Caneyella, Dunbarella*-Ammonoid—Radiolarian Community"). If the rapid transgression model (Donahue & Rollins, 1974; Boardman et al., 1984) is accepted, then an abundance of *Dunbarella* and its association with taxa such as *Lingula* and *Myalina* may not necessarily be indicative of an environment characterized by "brackish" salinities. Many of these assemblages are more suggestive of dysaerobic environments which probably maintained normal or nearly normal marine salinities. This interpretation explains the distribution of autochthonous invertebrate assemblages at the Kinney Quarry, as these assemblages mostly lack in-situ, burrowing infaunal organisms (except *Lingula* in assemblages 1, 5, and 7), contain low diversity and low abundance of sessile epifaunal and nektonic taxa, and are dominated by pseudoplanktonic suspension feeders (i.e. *Dunbarella).* I interpret primary factors which constrained invertebrate-assemblage composition and

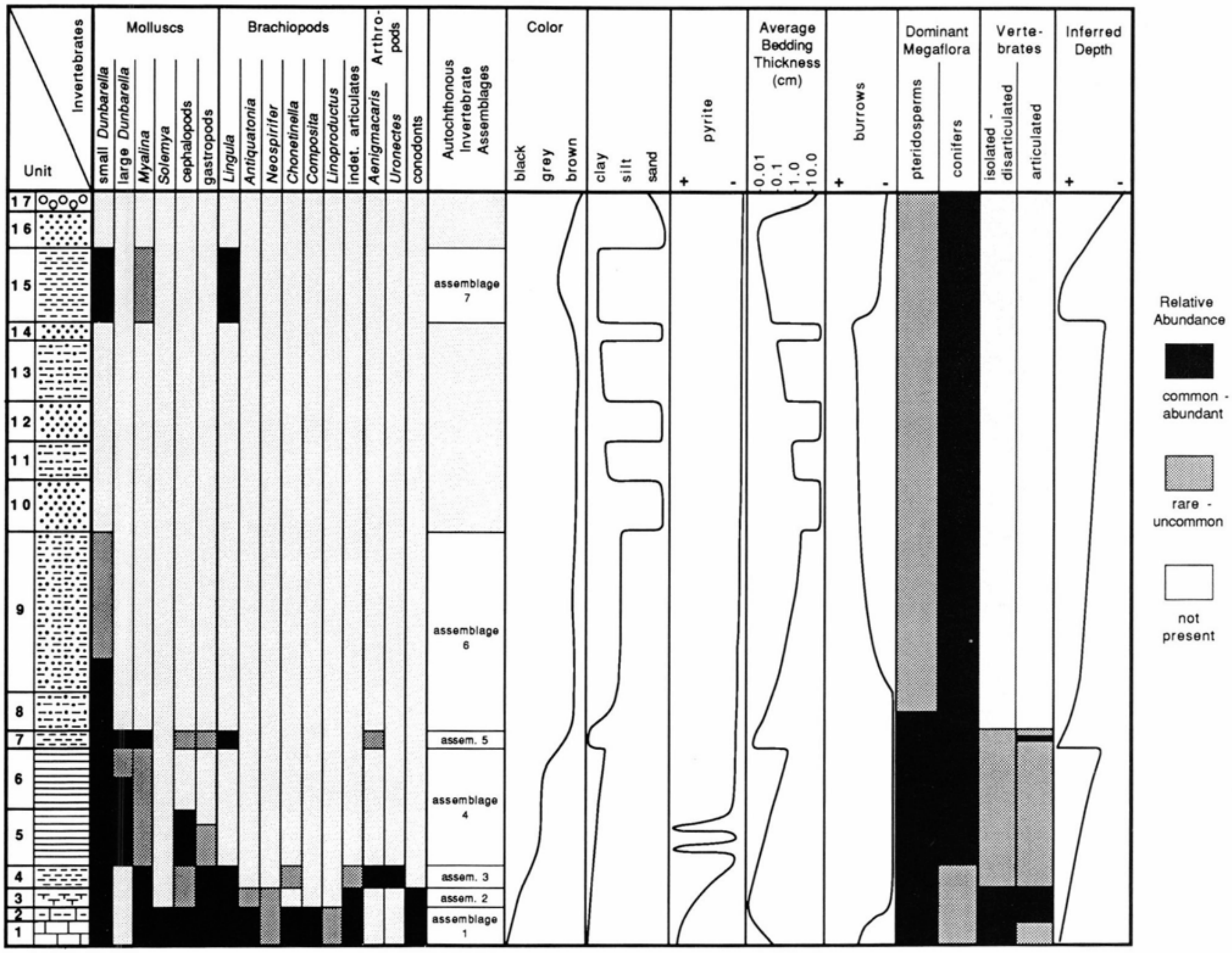

FIGURE 3—Distribution of primary in-situ invertebrate genera, autochthonous invertebrate assemblages, and inferred paleoecological trends at the Kinney Quarry. Graphic log for lithologic units is not to scale.

relative abundance as relating to dysaerobic/anaerobic substrate conditions, restricted circulation, seasonal hyposalinity, and, higher in the section (units 8-15), increased sedimentation rates. This interpretation is supported by the taphonomy of the vertebrate assemblage discussed below.

Vertebrates

Vertebrate remains occur throughout the lower 3 m of the quarry exposure (Fig. 2), but are mostly concentrated in a zone extending from the upper, finely laminated micrite (unit 2) into the fissile shale (unit 4). With the exception of Mazon Creek (early Westphalian D), the Kinney Quarry fishes comprise the most diverse Late Pennsylvanian fish fauna so far documented. At least 17 genera representing 12 families of chondrichthyan, dipnoan, coelacanthid, acanthodian, and actinopterygian fishes have been collected, along with rare specimens of trimerorhachid and dissorophoid amphibians. Most of the fishes are articulated and the quality of preservation is directly correlative with stratigraphic provenance and lithology. All vertebrates are preserved as phosphatic compressions up to 0.4 cm thick.

Chondrostean-grade actinopterygians are the most diverse group found at the locality. At least eight genera are known from articulated specimens and include several species of the form genus *"Elonichthys," Illiniichthys,* the long-snouted *Tanyrhinichthys mcallesteri* (Gottfried, 1987b), an aeduelliform (cf. *Bourbonella;* Gottfried, 1987a), a new deep-scaled taxon (Gottfried, 1991a, b), platysomoids provisionally referred to *Platysomus* and *Amphicentrum* (Zidek, 1991, this volume), and a new species of the haplolepid *Pyritocephalus* (Huber, this volume). Actinopterygians dominate the Kinney Quarry fish fauna. Articulated specimens are most common in unit 3, while fewer specimens have been collected from units 2 and 4. In contrast, disarticulated and/or disassociated individuals are common in the upper portion of unit 1 and in unit 2. Fish remains are rare higher in the section, and with a few notable exceptions are represented by isolated scales or badly decomposed carcasses.

Fusiform *"Rhadinichthys"-grade* palaeoniscoids include as many as five different species (D. Bardack, pers. comm. 1991), including two referable to *"Elonichthys,"* an additional form resembling *Illiniichthys* in possessing smooth, unornamented and/or non-denticulated scales, and a third morphotype which is characterized by a slender, narrow body and a slightly protruding rostrum. These specimens (NMMNH collection), the deep-scaled taxon (Gottfried, 1991a, b), and all material referred to *Tanyrhinichthys mcallesteri* (Gottfried, 1987b) were collected from unit 3. A single undescribed large palaeoniscoid was recovered from the upper pit by the author and Allan Lerner in 1989. While not yet prepared, this deeply fusiform specimen shows a standard length approaching 40 cm and presently displays most of the badly crushed skull and pectoral girdle. A smaller individual was obtained by the Black Hills Research Institute and, while not complete, it has a standard length on the order of 20 cm (M. Gottfried, pers. comm. 1989). The specimen was probably collected from a horizon correlative with unit 3 in the rear area of the quarry and is preserved in a dark-gray, unmottled, shaley limestone. Several platysomids in the LaFon (CM) collection are also in similar matrix and have the same provenance. Reconnaissance of this bed revealed moderately abundant isolated palaeoniscoid scales, but no generically identifiable material was collected. It should be noted for the record that Case (1982) illustrated two Kinney Quarry actinopterygians which he misidentified. These specimens are not *"Phanerorhynchus"* (p. 288, fig. 25-43) and *"Platysomus"* (p. 288, fig. 25-44) but *Tanyrhinichthys* and *Amphicentrum,* respectively.

A single aeduelliform showing affinity with the Permian taxon *Bourbonella* was obtained from the basal micrite (units 1 or 2) and described by Gottfried (1987a). The specimen is nearly complete but has a poorly preserved skull. Its significance lies in that it is the earliest known representative of the Aeduellidae and the only specimen of this family ever found in North America. This actinopterygian group is otherwise restricted to the Autunian lacustrine deposits in France. The youngest known haplolepid has also been collected at the Kinney Quarry. It is a well-preserved specimen from unit 4, which Huber (this volume) describes as a new species of *Pyritocephalus* Fritsch. The species is closely related to the type species, *P. sculptus,* from the Plzen Basin, Czechoslovakia, rather than to other American, Canadian, or European species. The New Mexico occurrence of this taxon further supports Gottfried's (1987a) hypothesis that interchange between piscine faunas of Europe and central-western North America must have occurred during the Permo-Carboniferous.

Platysomoids from the Kinney Quarry include both *Platysomus* and *Amphicentrum.* The former genus is perhaps the most common vertebrate taxon found at the locality; complete specimens occur in units 2-4. Based on the total known sample of Kinney fishes, *Platysomus* outnumbers *Amphicentrum* by a ratio of 10:1, a trend which is also apparent at Mazon Creek (Zidek, this volume). An outstanding feature of the Kinney Quarry *Platysomus* is the consistent in-situ preservation of phyllodont tooth plates, also preserved in the platysomoid *"Schaefferichthys"* (Dalquest, 1966), and found more commonly as isolated elements in ichthyolith assemblages in the Permo-Carboniferous of the midcontinent (e.g. Johnson & Zidek, 1981; Schultze, 1985). It is probable that all North American examples of the platysomids (sensu Moy-Thomas & Miles, 1971) pertain to a single genus and possibly species, with a broad temporal distribution spanning early Westphalian D through late Leonardian.

Most of the chondrichthyans were collected from unit 3. These include isolated *Peripristis* and symmoriid teeth, and a *Listracanthus* spine described by Zidek (1975, 1991, this volume); and two articulated specimens of the symmoriid *Cobelodus* and a cephalic spine and braincase of a new species of the xenacanthid *Orthacanthus* (Zidek, this volume). A third specimen may be an immature symmoriid, but poor preservation prevents generic identification. The xenacanthids mentioned by Lucas & Huber (1991) were misidentified and the material actually pertains to one or more of the symmoriid specimens and a poorly preserved coelacanth. With one exception, all articulated chondrichthyans were collected from the lower 5 cm of unit 3. The possible exception is the best preserved symmoriid, obtained by D. Gillette for NMMNH in 1984 from an unrecorded horizon. The matrix of the specimen is similar to that of unit 3 exposed in the rear area of the quarry, and B. Jurgena (pers. comm. 1989) has indicated this to be the exposure from which a large fish was obtained by the museum field crew around 1984-85. Other chondrichthyan and dipnoan fossils occur in unit 2, but are not common. These specimens include two symmoriid teeth and the holotype of *Proceratodus hlavini* Zidek 1975.

Acanthodes is abundant in unit 3 as articulated individuals up to 35 cm in length, but specimens are usually poorly preserved. Over 100 specimens have been collected since their presence in the quarry was first noted by Zidek (1975), and the material has been referred to a new species (Zidek, this volume). *Acanthodes* is also found in units 2 and 4, but specimens from these horizons are not common and largely consist of scale patches and isolated fin spines. Coelacanths are known from six or less specimens which range from isolated scales and pelvic plates (e.g. Zidek, 1975) to fully articulated individuals. I have collected two nearly complete specimens from unit 3 and have noted isolated scales in units 4 and 5. Other material has been obtained from the basal micrite (units 1 and 2). Most of the existing material is described by Schultze (this volume).

When compared to other Late Pennsylvanian faunas, tetrapods are unusually rare at the Kinney Quarry and, so far, comprise under 2% of the total vertebrate sample. Four articulated specimens are documented by Hunt et al. (this volume), which includes the trimerorhachid *Lafonius* (Berman, 1973), another trimerorhachid taxon of uncertain affinity, and two examples of a dissorophoid closely resembling the widespread and broadly contemporaneous *Amphibamus* (D. Baird, pers. comm. 1991). Isolated limb bones and centra occur more rarely. All the tetrapods, the malacostracans described by Schram & Schram (1979), and the new species of *Pyritocephalus* (Huber, this volume) were collected from a 7 cm thick interval in the lower portion of unit 4.

Coprolites, cololites, and gastric residues are found throughout the fish-bearing interval. These trace fossils were identified using criteria of Zangerl & Richardson (1963) and McAllister (1988); differentiation between ejecta and fecal residues is not in agreement with Hunt's (this volume) diagnosis of the same specimen sample. Coprolites are represented by black, ovoid and cylindrical carbonaceous masses rarely exceeding 5 cm in diameter. These residues lack internal structure and surficial morphologic detail, and as such cannot be related to any constituents of the diverse vertebrate fauna. Cololites are not common and their presence is inferred by the occurrence of knobby and grainy masses in the posterolateral trunk region of several palaeoniscoid specimens. Gastric residues appear to be more abundant than coprolites, but this impression may be the result of collecting bias. Gastric residues can be classified as two types, based on their content. Most are composed of broken and disarticulated skull elements, ribs, and scales of actinopterygian fishes (Fig. 4), while others, particularly from unit 4, include abundant macerated arthropods which are not identifiable (F. Schram, written comm. 1990). Coprolites and ejecta from the Kinney Quarry fish bed are covered more extensively by Hunt (this volume), based primarily on material collected by the author (NMMNH collection). Many coprolites and gastric residues were encountered, but only exceptional specimens were collected—less than 10% of the specimens observed. Any faunistic or paleoecological inferences based on quantitative data thus should be regarded with caution.

Fish taphonomy

Vertebrate preservation at the Kinney Quarry is the result of anaerobic substrate conditions and not of rapid burial, as suggested by Feldman et al. (this volume). The abundance of fully articulated fish (80% of sample; Fig. 5A) argues against flotation of carcasses for an extended period of time (cf. Elder & Smith, 1988). Likewise, individuals with partially disarticulated skulls always show disassociated dermal elements within a short distance from their point

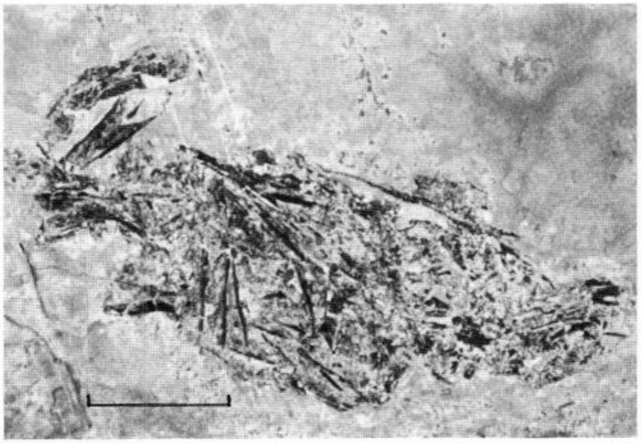

FIGURE 4—Gastric residue composed of crushed platysomoid rib and scale elements. Unit 3, NMMNH collection, uncatalogued. Scale bar equals 1 cm.

of origin, and always on the surface of the same lamina. This indicates that disarticulation resulted from eruption of gaseous-decay bubbles while the carcass lay on the substrate surface. In warm, subtropical waters fish carcasses float to the surface in a matter of hours and experience decomposition and internal expansion of a buoyant gas bubble (Elder & Smith, 1988). When the gas-filled body cavity ruptures, weakly connected elements of the dermal skull sink first, followed shortly by the deflated body. Such process results in a random (or current-directed) scattering of disassociated bones over a wide area, which to some degree is constrained by depth to substrate. The paucity of disarticulated specimens in the Kinney Quarry fish sample strongly suggests that most carcasses did not undergo postmortem flotation and instead remained on the substrate surface (Fig. 5B). Incomplete specimens usually have intact bodies and display a random dispersion pattern of lighter and/or smaller dermal-skull bones which are confined to distances of 6 cm or less from point of origin. In contrast, heavier dermal elements (e.g. shoulder-girdle bones) show only displacement or, at most, minimal disarticulation (Fig. 5C). Thus, the only mechanism which would keep fish carcasses "anchored" to the bottom of a warm, subtropical embayment of moderate depth is a substrate composed of flocculated fine clay and silt (cf. Feldman et al., this volume). Disassociation by carcass eruption and/or scavenging is, however, the exception rather than the rule. Most fishes from units 3 and 4 are articulated, whole, and show minimal evidence of predation (e.g. "bite marks"; Zangerl & Richardson, 1963). Also, many fishes (particularly *Acanthodes* and palaeonsicoids) are bent in angles between 40 and 120°, and numerous palaeoniscoids are preserved with their mouths open. These phenomena indicate poisoning.

Demaison & Moore (1980) discussed geochemical and paleoecological factors which operate in a variety of generalized anoxic environments. These authors conclude that substrates with an oxygen content between 0.7 and 0.3

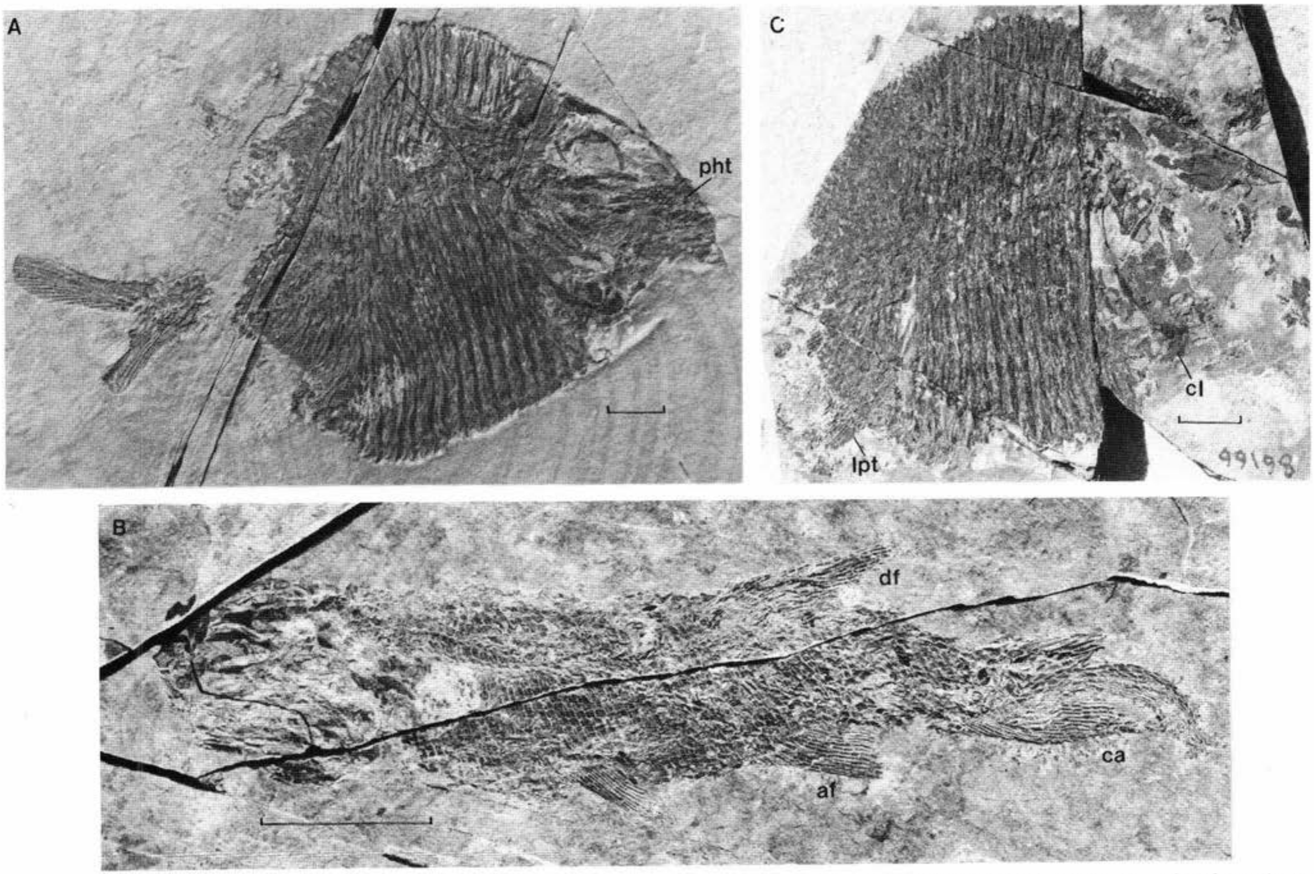

FIGURE 5—Taphonomic features of some Kinney Quarry fishes. **A,** *Platysomus* sp., fully articulated lateral compression, distal portions of fins covered by matrix. Note in-situ preservation of phyllodont tooth plates (pht). Unit 3, Allan Lerner Collection. **B,** Unidentified palaeoniscoid; disarticulation of distal portions of paired and median fins probably occurred while specimen lay exposed on substrate surface. Unit 3, Kaye Toolson Collection. Scale bars equal 1 cm. **C,** *Platysomus* sp., disarticulation and scavenging(?) probably occurred while carcass lay exposed on substrate. Note articulated skull roof and shoulder girdle vs. dispersion of smaller, anterior skull bones and disjointed lepidotrichia. Unit 3, KUVP 86166. Abbreviations: **af,** anal fin; **ca,** caudal fin; **cl,** cleithrum; **df,** dorsal fin; **lpt,** lepidotrichia; **pht,** phyllodont tooth plates.

m1/1 serve to dramatically depress metazoan diversity, and that at levels between 0.3 and 0.1 ml/l deposit feeders are rare and soft-bodied only. Below this threshold, only anaerobic bacteria remain as active processors of organic matter. However, the absence of a burrowing infauna can serve to further depress oxygen levels of interstitial water in sediments, which may contribute to reducing conditions and subsequent release of toxic metals for chelation with sediment-contained organic compounds (Demaison & Moore, 1980). Such reactions further contribute to substrate toxicity and constrain the activity of anaerobic bacteria, especially phosphate-recycling microbes which aid in the degradation of fish skeletons.

The presence of an abundant, though low-diversity, epifauna in units 3 and 4 requires long periods (months) of bottom oxygenation at a minimal level between 0.7 and 0.3 m1/1. If the substrate below the water—sediment interface was composed of flocculated clay and fine-silt grains, then substrate toxicity could be maintained during periods of benthos propagation. This would explain both the presence of oxygen-dependent epifaunal marine taxa and the complete absence of an infauna. It is significant that the in-situ fauna of units 3 and 4 is dominated by the pectinid *Dunbarella,* which was byssally attached to floating vegetation (Clark, 1978; Mamay, 1990; Mamay & Mapes and Archer & Clark, this volume). Other shelly taxa are restricted to specific bedding planes and the density of some of them, particularly gastropods, often exceeds 30 specimens/0.3m^2, suggesting mass-mortality events. These data support a seasonal sedimentation model where sustained influx of fresh water would provide the mechanism (i.e. hyposalinity) which caused mortality of epifaunal and pseudonektonic shelly taxa and also fish. This model also explains why most fish carcasses show minimal to no evidence of scavenging, as mortality in both groups would have been broadly synchronous (days or weeks, at most).

Zidek (pers. comm. 1991) has identified a consistent, slight disarticulation along the opercular line in specimens of *Platysomus.* Initial colonization of endoskeletal tissue by bacteria is through the gill slits, where initial degradation of the musculature would be expected to occur. If anoxia, aided by chelation reactions, was a controlling factor over fish preservation, it may be assumed that only bacteria capable of attacking soft tissue were sustained, while the resulting end-product reactions were not sufficient to promote scavenging by bone-dephosphatizing microbes. Thus, slight disarticulation of resistant dermal elements would result from the decomposition of supporting soft tissue. These observations also explain the consistent slight disarticulation of platysomoid lepidotrichia, which by modern analogy requires weeks (Elder & Smith, 1988), and the paucity of well-preserved acanthodian skulls and articulated elasmobranchs, which are composed primarily of poorly ossified/ calcified cartilage and mostly lack resistant, phosphate-rich dermal bone.

In contrast, fish from units 1 and 2 are predominantly disarticulated into isolated dermal-skull bones and patches of scales, which indicates that a considerable amount of scavenging occurred before burial. Articulated fish, and even isolated scales, are rare in stratigraphically higher units. Two articulated palaeoniscoids have been collected from units 5 and 7, respectively. The unit 5 specimen is a fusiform taxon that preserves several scales and dermal-skull elements which have a rotted appearance within a reduction zone approximating the original outline of the carcass. The specimen is very instructive because it suggests that a considerable amount of microbial scavenging occurred shortly after the carcass settled on the substrate and, unlike fish from units 3 and 4, also attacked the more durable, protein-rich squamation and fins. The single fish from unit 7 is also a fusiform palaeoniscoid identifiable as *"Elonichthys."* The specimen is articulated but has a poorly preserved skull and is bordered by a yellowish-brown (10 YR 5/4) reduction zone, as are many other fossils in assemblage 5. I interpret the poor skull preservation and reduction halo as the product of selective scavenging, where skull bones were favored by phosphate-recycling microbes over proteinaceous scales and fin rays (cf. McDonald & LeTourneau, 1989). The absence of fish remains in higher units may be correlated with increased sediment oxygenation evidenced by numerous burrowed horizons in units 8-16.

Discussion

Lithologic, taphonomic, and invertebrate diversity and distribution data indicate that the fossiliferous strata exposed at the Kinney Quarry were deposited in a variety of prodeltaic marine environments. Strata which reflect freshwater deposition are found only in the uppermost few meters of the section and are represented by a fluvial channel-lag deposit. Initial clastic sedimentation was restricted to clay-size particles which settled through suspension onto a carbonate shelf which was probably of moderate depth (30 m). The uniform grain size, laminar bedding, reducing color, low-diversity benthic and nektonic fauna, and preservation of delicate morphologic features and soft-bodied arthropods suggest a paleoenvironment of normal or nearly normal salinity, but with semirestricted circulation and reduced oxygen levels. I interpret this facies (units 1 and 2) as deposited in the distal portion of a developing bay or lagoon.

Deposition of the finely laminated upper micrite (unit 2) and overlying microlaminated shales (units 3 and 4) were affected by further restriction of the Kinney embayment by an as of yet unknown mechanism; possibly lobe encroachment and/or sill development at the bay mouth. The microlaminated bedding of these units, and especially the tripartite organic/clay/carbonate lamina bundle of unit 3, suggest that sedimentation was strongly influenced by anoxic bottom conditions and a climatic regime which produced varve-like bedding under a seasonally stratified water column. This model is compatible with a subtropical monsoonal climate, which has dominated the southwest and midcontinent during the Late Pennsylvanian (e.g. Kutzbach & Gallimore, 1989).

Stratification of the water column would have occurred during "wet" seasonal phases, when increased discharge from source areas flowed over more dense saline water, creating a density gradient. Depressed salinity values and increased influx of elastics resulted. Carbonate precipitation and deposition of pelletal, ostracode-rich layers occurred during "dry" seasons when clastic input slacked off. Evidence for this depositional model (applied primarily to units 2-4) is provided by microlaminated bedding, presence of cyclic carbonate laminae, reducing colors, high organic-matter content, pervasive mottling caused by incomplete decomposition of matted vegetation, absence of burrowing infauna, decreasing diversity and abundance of epifaunal taxa upsection, restriction of fresh-water organisms (conchostracans and smooth ostracodes) to specific bedding planes, soft-part preservation of arthropods, and presence of abundant, well-preserved fish.

The so-called *"Dunbarella* beds" (units 5-7) actually represent three distinct subfacies containing two invertebrate assemblages (assemblages 5 and 6). Archer & Clark (1991, this volume) identify two orders of laminations in these units, major (2nd order) light-colored laminae which are further subdivided into as many as 10 dark zones (1st order "laminations"), each composed of organic flakes (probably macerated plant debris). To account for such bedding these authors invoke a tidal-rhythmite sedimentation model which is tightly constrained by numerous hypothetical variables. It is also plausible that these laminations formed as a result of seasonal sedimentation in a wet/dry climatic regime (Fig. 6). The slight increase of the silt fraction upsection from unit 2 to unit 6 parallels a successive increase in lamina thickness through the same units, which probably reflects progressive shoaling of the embayment and closer proximity of silt-dominated fades of the prograding source area. First-order laminations are restricted to the light-colored major laminae, which were probably deposited during dry seasons. Hence, episodic increases in sediment discharge could provide pulses of macerated organic debris which would settle quickly on the substrate, forming thin, discrete dark layers interbedded with thicker, light-colored silt beds deposited by suspension throughout dry months. There is no support for the conclusions that the large concentrations of *Dunbarella* in units 5 and 6 indicate fresh-water deposition (Kues, this volume) or tidal-rhythmite sedimentation. The restriction of this pectinid to organic-rich, dark-colored laminae which alternate with unfossiliferous, light-colored laminae which alternate with unfossiliferous, light-colored laminae is suggestive of repetitive, seasonal mass-mortality events. Cyclic mortality among successive *Dunbarella* populations could have been induced by hyposalinity resulting from increased flow of fresh water into the environment during "wet" seasons.

The remainder of the Kinney Quarry section has been described by Lucas & Huber (1991) and Lorenz et al. (this volume). The silty-shale fades (units 8 and 9) is laminated (bed thickness varies between 0.5 and 10 cm), moderately burrowed, and contains a monotypic faunal assemblage composed entirely of small *Dunbarella*. The combined thickness of this facies exceeds 10 m, and it is overlain by a 10 m thick sequence of intercalated sandstone and silty shale (units 10-14) interpreted as delta-front, distal bayhead mouthbars interbedded with prodelta muds (Lorenz et al., this volume). This interval reflects a substantial increase in sedimentation rate and further shoaling of the embayment or lagoon. Water depth was probably 5-10 m. The relatively thick shale-sandstone fades near the top of the quarry section (units 15 and 16) represents a sustained rise of base level. The duration of this transgression cannot be reliably estimated, as the lower and upper unit contacts are not conformable. The stratigraphic section is completed by a limestone-pebble conglomerate which is lenticular and has a scoured base (unit 17). This unit is probably a channel-lag deposit (Huber et al., 1989a, b).

While this sedimentation model may be regarded as tentative, evidence for tidal-rhythmite deposition provided by Archer & Clark (1991, this volume) and Feldman et al. (1991b, this volume) is not definitive by any means. Modem tidal environments usually include such features as a pervasive lebenspuren, well-oxygenated substrates (e.g. Yeo & Risk, 1981), and diverse biotas. Sedimentary structures include bi-directional current indicators, flaser bedding, large-scale tidal bundles, graded coarse—fine couplets with laminae separated by clay drapes, preferred orientation of fossils, and evidence suggesting occasional periods of subaerial exposure (see Kvale et al., 1989; Kvale & Archer, 1990; and Feldman et al., this volume, for summary and discussion). The only convincing examples of Carboniferous tidal-rhythmite sedimentation which include finely laminated mud-rocks are found in laterally and stratigraphically restricted intervals of the Mansfield (Morrowan), Brazil (Atokan), and Carbondale (Desmoinesian) Formations in the Illinois Basin (Kvale et al., 1989; Kvale & Archer, 1990; Baird et al., 1985, respectively). These authors identify a variety of microstratigraphic (i.e. 10 cm or less) cycles comprised of alternating graded mud/mud, mud/silt, or mud/sand couplets which are interpreted as the product of deposition during daily and neap—spring tidal events. Evidence supporting rapid sedimentation includes climbing ripples, upright-standing trees, edgewise-buried pteridosperm pinnules, and infaunal organisms entombed in escape burrows (Baird et al., 1984, 1985; Kvale et al., 1989). These high-frequency cycles reportedly modulate to form 3rd and 4th order cycles which may represent monthly and seasonal tidal records; in some instances, these cycles have been identified in continuous stratigraphic sequences up to 8 m thick (Kvale et al., 1989; Kvale & Archer, 1990). These authors suggest that syndepositional compaction of underlying coal beds created the space necessary to accommodate such high sedimentation rates (35-100 cm/yr).

With the exception of alternating graded laminae which either form couplets (units 4-6) or tripartite bundles (units 2-4), structures indicative of tidal sedimentation are not present at the Kinney Quarry. Even if the basal 2.5 m of shale (units 3-7) are the only interval considered, the ap-

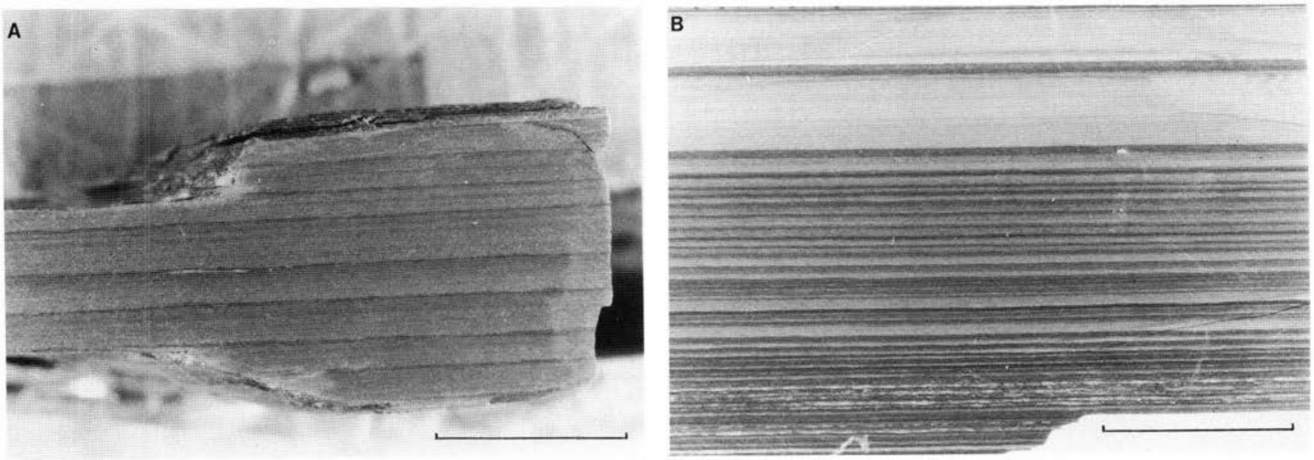

FIGURE 6—Microlaminated mudrocks from deltaic marine (A) and lacustrine rift-basin (B) depositional environments. **A,** Unit 5 ("*Dunbarella* beds"), Kinney Quarry. Major light-colored laminae range from 1.6 to 2.5 mm and average 1.8 mm in thickness. Note development of minor-lamina bundles within major light-colored zones. **B,** Ukranian Village Member of the Passaic Formation (Upper Triassic: Norian), Newark Supergroup, Pennsylvania. Thickness of polished slab is 2.54 cm; combined thickness of two major light-colored and intervening dark-colored zones is 7.8 mm. Note discontinuous carbonate laminae in lower 5 mm of slab (analogous to unit 3 at Kinney Quarry). Minor-lamina bundles are especially well developed within the two major light-colored zones near top of slab. Photo courtesy of P. E. Olsen. Scale bars equal 1 cm.

parent restriction of fossils to specific bedding surfaces and the presence of *cyclic* carbonate laminae are difficult to reconcile with a depositional environment supposedly characterized by rapid, daily sedimentation events. There is no preferred orientation of fossils among both invertebrates and vertebrates, and, except for centimeter-scale levees in unit 4, structures indicative of currents are not present. In addition, the vertebrates show no evidence of preservation due to rapid burial. To the contrary, the preservation of some specimens indicates prolonged exposure on the substrate surface. This is evidenced by disarticulation of lepidotrichia in platysomoids (Fig. 7) and by the fact that disarticulated dermal elements are always close to the point of their origin and always on the same lamina surface. Many fish carcasses show evidence of asphyxiation (tetany of fins and mandibles). Overall, the mode of preservation of the fauna suggests a mechanism (e.g. hyposalinity) capable of inducing repetitive mortality events. Thus, contrary to Feldman et al. (1991a), it seems unlikely that preservation of the Kinney Quarry Lagerstatte could be due to tidal-rhythmite sedimentation.

Age

The age of the Kinney Quarry strata is far from certain. Most workers accept Myers' (1973, 1988) fusulinid-based biostratigraphy of the Madera Group, which divides the Wild Cow Formation into three members spanning early Missourian through basal Wolfcampian. Myers (1969) and Myers & McKay (1976) show SE1/4 sec. 18, T9N, R6E to include both the upper Pine Shadow and basal La Casa Members, but at best demonstrate very poor outcrop control and do not identify the quarry on their respective bedrock maps. Stukey's (1967) map shows this area to be structurally complex, but his stratigraphy is difficult to compare with that of Myers (1973, 1988) and other papers in this volume. For instance, Stukey (1967) shows 20 m of interbedded limestone and shale above unit 17 at the Kinney Quarry, while field reconnaissance by Lucas & Huber (1991) failed to locate any stratigraphically higher strata contiguous with the quarry section. The remarkably diverse invertebrate fauna of the Kinney Quarry is notable for an almost total lack of biostratigraphically significant taxa. Fusulinids have been purportedly found at the Kinney Quarry (R. Anderson, pers. comm. 1990), but the specimens were not identified or retained for study, and extensive sampling of the basal micrite by this author, S. Krukowski, and B. Kues failed to procure additional material. Because of this and reasons stated above, the Kinney Quarry sequence cannot at present be correlated with any of the Wild Cow Formation fusulinid zones defined by Myers (1973, 1988).

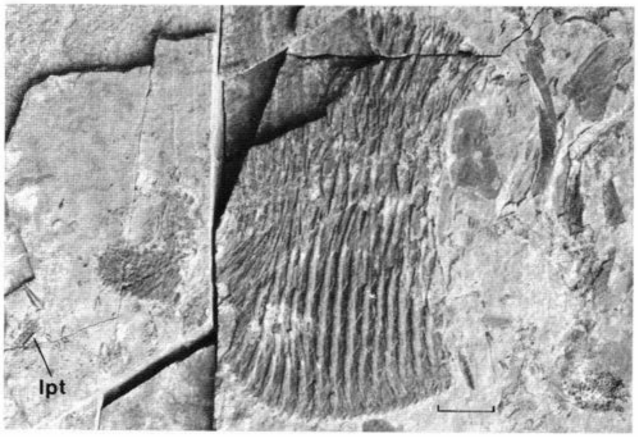

FIGURE 7—*Platysomus* sp., disarticulated, scavenged(?) specimen; carcass probably experienced eruption of gaseous-decay bubble while floating. Note disarticulated lepidotrichia **(lpt)** of caudal fin, implying a long time (weeks) of exposure on substrate surface. Unit 3, Allan Lerner Collection. Scale bar equals 1 cm.

Recent refinement of chonetid-brachiopod zonation in the Appalachian basin suggests reassignment of the Kinney Quarry strata to the Missourian. Hoare & Sturgeon (1984) demonstrated a close correspondence between chonetid and fusulinid distributions, with the zone of *Chonetinella* and the *Triticites ohioensis* assemblage subzone found in the lower and middle Conemaugh Group (Missourian) and the zone of *Neochonetes semiacanthus* and thick-walled *Triticites* species (including T. *cullomensis)* found only higher in the basin (e.g. Ames "cyclothem"). This distribution suggests correlation of the middle—upper Conemaugh Group with early Virgilian cyclothems (e.g. Oread) in the midcontinent and the middle Pine Shadow Member (sensu Myers, 1988). Kues (1991, this volume) identifies the chonetid *Chonetinella flemingi as* a moderately abundant (3-5% of sample) constituent of assemblage 1 (units 1 and 2). This taxon has a wide distribution in the Appalachian and midcontinent basins, where it is mostly restricted to Missourian formations and is range-concurrent with the *Triticites ohioensis* subzone (cf. Hoare & Sturgeon, 1984). Myers (1988) indicated that this fusulinid subzone encompasses the early and middle Missourian Sol se Mete Member, and suggested that upper Missourian strata are not present in the Madera Group. However, the Kinney Quarry occurrence of *C. flemingi* suggests that either the upper Sol se Mete Member or the lower Pine Shadow Member records deposition during late Missourian. On this basis, the quarry strata are reassigned to the middle or late Missourian; this conclusion is supported by conodont data reported by Mapes & Boardman (this volume).

Because Late Carboniferous fishes and tetrapods either have long stratigraphic ranges or are unique to specific localities, most of Kinney Quarry vertebrate taxa have little or no biochronologic value. However, of the fishes, haplolepid actinopterygians are otherwise known from Chesterian through Desmoinesian (Namurian—Westphalian) deposits (Huber, this volume), and their occurrence at the Kinney Quarry favors a Missourian rather than early Virgilian age. The meager tetrapod fauna is not particularly age-diagnostic, except in containing amphibamid dissorophoids which are restricted to the Late Pennsylvanian (Westphalian D through Stephanian C; Carroll, 1984).

Acknowledgments

I wish to express gratitude to Bob Jurgena for allowing access to the Kinney Brick Company Quarry. Thanks are due to Barry Kues, Spencer Lucas, Roy Mapes, and Jiri Zidek for numerous discussions and/or unpublished data pertaining to diverse aspects of Kinney Quarry geology and paleontology. Additional data and comments were provided by Donald Baird, David Bardack, David Berman, Fred Collier, Howard Feldman, Michael Gottfried, Adrian Hunt, Nicholas McDonald, Paul Olsen, Fred Schram, and Hans-Peter Schultze. Allan Lerner, Andrew Newhall, Michael Ripperger, Kaye Toolson, and the New Mexico Museum of Natural History Friends of Paleontology extended invaluable help in the field and generous donation of specimens. The New Mexico Museum of Natural History provided partial logistical support for this project. I am grateful to Ron Rukstela for aid in drafting figures, and I especially thank Tom Lehman, Gene Mapes, Roy Mapes, and Jiri Zidek for their helpful reviews of this paper.

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Early Virgilian palynofloras from the Kinney Quarry, Manzanita Mountains, New Mexico

Debra A. Willard

U.S. Geological Survey, MS 970, Reston, Virginia 22092

Abstract—Virgilian palynofloral assemblages examined from the Pine Shadow Member of the Wild Cow Formation (Kinney Brick Quarry, New Mexico) include abundant cordaitean, conifer, and pteridosperm pollen and a diverse suite of spores. Vertical transects from two sites in the quarry were analyzed. The Mamay–Watt collection is dominated by cordaite and conifer pollen, whereas the Huber collection is dominated by fern spores and spores of unknown affinity. In the MamayWatt samples, the cordaite pollen genus *Florinites* is dominant, and pollen of callistophytean pteridosperms *(Vesicaspora)* and walchian conifers *(Potonieisporites)* are common. The lycopsid spore *Endosporites* also is present, as are fern spores and, rarely, sphenopsid spores. In the Huber samples, fern spores and a spore of unknown affinity, *Lalmatiasporites indicus,* are dominant. Cordaite and conifer pollen are still abundant, however, and pteridosperm pollen and sphenopsid, lycopsid, and tree-fern spores are common components of the assemblages.

The Mamay–Watt assemblage suggests a local arboreous macroflora dominated by cordaites and conifers, with *Psaronius* tree ferns and medullosan pteridosperms present. The understory of this assemblage included at least one lycopsid *(Chaloneria),* one pteridosperm *(Callistophyton),* several small ferns, and two as yet unknown plants, which produced *Lalmatiasporites indicus* and *Cadiospora sphaera.* At the Huber site, the great abundance of lower-vascular-plant spores, the high percentage of fern spores and *Lalmatiasporites indicus,* and the greater abundance of sphenopsid spores are consistent with a higher level of soil moisture than at the Mamay–Watt site. This could reflect differences in topography or differing proximities to a fluvial system.

The Kinney Quarry palynofloras are unusual in their composition and diversity, but they share taxa with assemblages from the Upper Pennsylvanian and Lower Permian of the Western Interior, Illinois Basin, and Appalachian Basin in Euramerica, Upper Carboniferous and Lower Permian of Europe, and with Gondwanan floras from Australia, South America, Africa, and India.

Introduction

Strata in the Kinney Brick Quarry of central New Mexico preserve a Late Pennsylvanian (Virgilian) biota that is unusual in its paleogeographic position and in its composition. The locality has yielded megafossils of fishes, amphibians, bivalves, insects, eurypterids, and plants (Ash & Tidwell, 1982; Berman, 1973; Carpenter, 1970; Clark, 1978; Kelley & Northrop, 1975; Kues, 1985; Mamay, 1981, 1990; Schram & Schram, 1979; Zidek, 1975), permitting reconstruction of the ecosystem in considerable detail. The diversity of organisms from Kinney Quarry shales offered an opportunity to broaden the paleobotanical analysis by including a quantitative study of the palynoflora to generate additional data on the vegetation of the region and for comparison with other Late Pennsylvanian palynofloras. Palynological analysis of these strata provides an opportunity to expand the limited knowledge on the palynological composition of seasonally dry floras from the Late Pennsylvanian of Euramerica.

Most analyses of Late Pennsylvanian palynofloras have focused on coals that accumulated in peat-forming swamps (Cross, 1954; Grady & Eble, 1990; Habib, 1968; Willard, 1985, 1990a) and organic-rich shales deposited in low-lying clastic swamps (Clendening, 1974; Peppers, 1964). Both environments supported plant communities on poorly drained, waterlogged soils. Megafossil evidence indicates that these floras consisted primarily of tree ferns, medullosan pteridosperms, sigillarian lycopsids, and calamites, with occasional occurrences of cordaites (Phillips et al., 1985; Pryor, 1988; Willard, 1985, 1990a). Both palynological and paleobotanical studies of Late Pennsylvanian floras from relatively drier, extrabasinal environments (sensu Pfefferkorn, 1980) are less common, but such floras typically are dominated by cordaites and conifers (Ash & Tidwell, 1982; Leisman et al., 1988; Read & Mamay, 1964; Rothwell and Mapes, 1988; Winston, 1983). In addition, megafloras from the Kinney Quarry include abundant walchian conifers and medullosan seed ferns, and a suite of taxonomically enigmatic plants (*Charliea manzanitana, Plagiozamites planchardii, Dicranophyllum readii,* and *?Podozamites* sp.) (Mamay & Mapes, this volume). The diversity and composition of the megafloral assemblage suggests that palynological assemblages also should contain palynomorphs characteristic of extrabasinal environments, in moderate contrast with those from Late Pennsylvanian coal- and clastic swamps of Euramerica and Lower Gondwanan assemblages. This study was designed to (1) characterize the palynofloral composition of the Pine Shadow Member in the Kinney Quarry, (2) study vertical patterns of vegetational change through Kinney strata, (3) compare two laterally separate collections to establish preliminary estimates of vegetational heterogeneity, and (4) assess the paleoecology of the Kinney assemblage. The data also are compared with palynological evidence from other depositional settings and floral provinces to provide insights into the relation of the Kinney Quarry flora to others in Late Pennsylvanian time.

Materials and methods

The two collections from the Kinney Quarry that were available for palynological analysis were obtained by S. H. Mamay and A. Watt in 1969 and by P. Huber in 1990. Both collections consist of samples from different stratigraphic levels within the sampling area, but neither represents the full thickness of the section. The Mamay—Watt collection consists of 10 samples ranging from the basal micrite through calcareous shales of the uppermost plant-bearing beds (Fig. 1) and three samples consisting of pieces of rock matrix from each plant-bearing unit. These samples were collected in the inactive pit north of the presently active pit, but more specific information on sample thickness or collection location within the quarry is not available. The Huber collec-

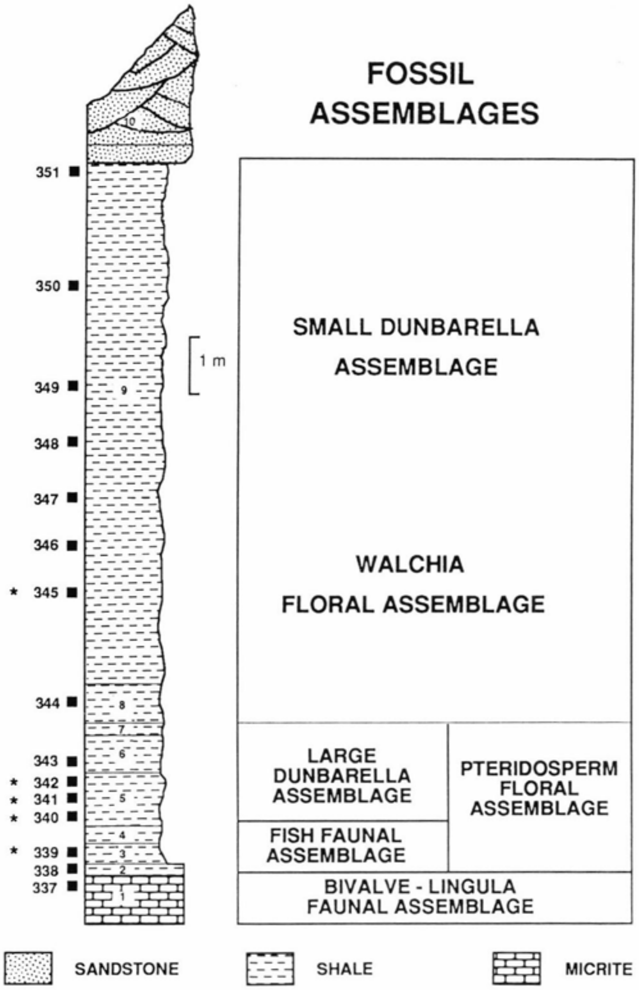

FIGURE 1—Stratigraphic section of Kinney Quarry strata from which the Huber collection was sampled. Each palynological sample site is marked with a black box and the maceration number. Asterisks indicate productive samples. The uppermost sample of the Mamay–Watt collection corresponds approximately to the upper part of unit 9 in this figure (modified from Lucas & Huber, 1991).

tion consists of 15 samples ranging from 0.05 m below the micrite-shale contact to 13.9 m above that contact, directly below the first sandstone unit of the section (Fig. 1). This collection was made in the currently active portion of the pit at least 150 m from the Mamay-Watt collection. Every sample from both collections consists of micrite or calcareous shale.

Each sample was crushed into pieces 2-5 mm in diameter and covered with 20% HCl to decalcify the material. Once the reaction was completed, the residue was neutralized with repeated water washes. Samples then were covered with 52% HF and left overnight to dissolve silicates. After neutralization with water washes, the residue was mixed with dilute detergent to suspend clay-size particles and centrifuged slowly for one minute. The slow centrifugations in detergent were repeated until most of the clays were removed as supernatant and the supernatant was transparent. After a water wash to remove the detergent, the residue was mixed with $ZnCl_2$ (specific gravity = 2.0) and centrifuged to separate organics from mineral material. Organic material was pipetted off, rinsed once with 10% HCI, and neutralized with distilled water before treatment with 5% KOH for 1-5 minutes. After the KOH solution was neutralized with water washes, the residue was mixed with glycerin jelly and mounted on microscope slides. For each sample, six slides were prepared. These were examined at x 250 magnification to identify the species that were present in each sample. For each productive sample, 100-200 palynomorphs were counted using a magnification of x 400; the number counted depended on the quality of preservation and relative abundance of palynomorphs in the sample. Rock samples, slides, and residues are deposited in collections of the National Museum of Natural History under USNM catalog numbers 455160-455191.

Results

Only four of thirteen samples from the Mamay-Watt collection and five of fifteen samples from the Huber collection were productive. The two collections differed in which lithologies yielded palynomorphs. In the Mamay-Watt collection only dark-gray shales (Munsell color code N3, N4) were productive (Table 1). Three of these samples were collected in the lower parts of the section; the fourth was collected near the top of the section in strata that approximately correlate with unit 9 of the Huber collection. A greater variety of lithologies is represented by productive samples in the Huber collection, including light-gray shales (Munsell color code N6) and olive-gray shales (Munsell color code 5Y 5/2, 5Y 6/1) (Table 1). The relatively low yield of palynomorphs from these strata is related to the high calcareous fraction of the rocks. Calcareous rocks typically are barren of palynomorphs because of oxidizing conditions associated with their deposition and subsequent diagenesis (Traverse, 1988).

Mamay-Watt collection

Gymnosperm pollen are dominant in the upper three samples from the Mamay-Watt collection, comprising 6883% of the assemblage in macerations 298, 299, and 306 (Fig. 2). **In** these three samples, *Florinites* (Fig. 7A, B) is the most abundant genus of gymnosperm pollen (29-41%), followed by *Vesicaspora* (Fig. 7E) (8-12%), *Potonieisporites* (Fig. 7D) (3-10%), and *Protohaploxypinus* (Fig. 7F) (0-10%) (Fig. 3). Spores of unknown affinity also are common in these samples; *Cadiospora sphaera* comprises 5-11.5% and *Lalma-*

TABLE 1—Lithologies of productive samples in the Mamay–Watt and Huber collections, Kinney Brick Quarry.

MAMAY-WATT COLLECTION			HUBER COLLECTION		
Maceration Number	Lithology	Munsell Color Code	Maceration Number	Lithology	Munsell Color Code
306	Dark gray, calcareous shale	N3	345	Olive-gray, calcaeous shale	5Y 5/2
299	Dark gray, calcareous shale	N4	342	Olive-gray, calcaeous shale	5Y 5/2
298	Dark gray, calcareous shale	N4	341	Light-gray, calcareous shale	N6
352	Dark gray, calcareous shale	N3	340	Medium-gray, calcareous shale	N6
			339	Olive-gray, calcaeous shale	5Y 6/1

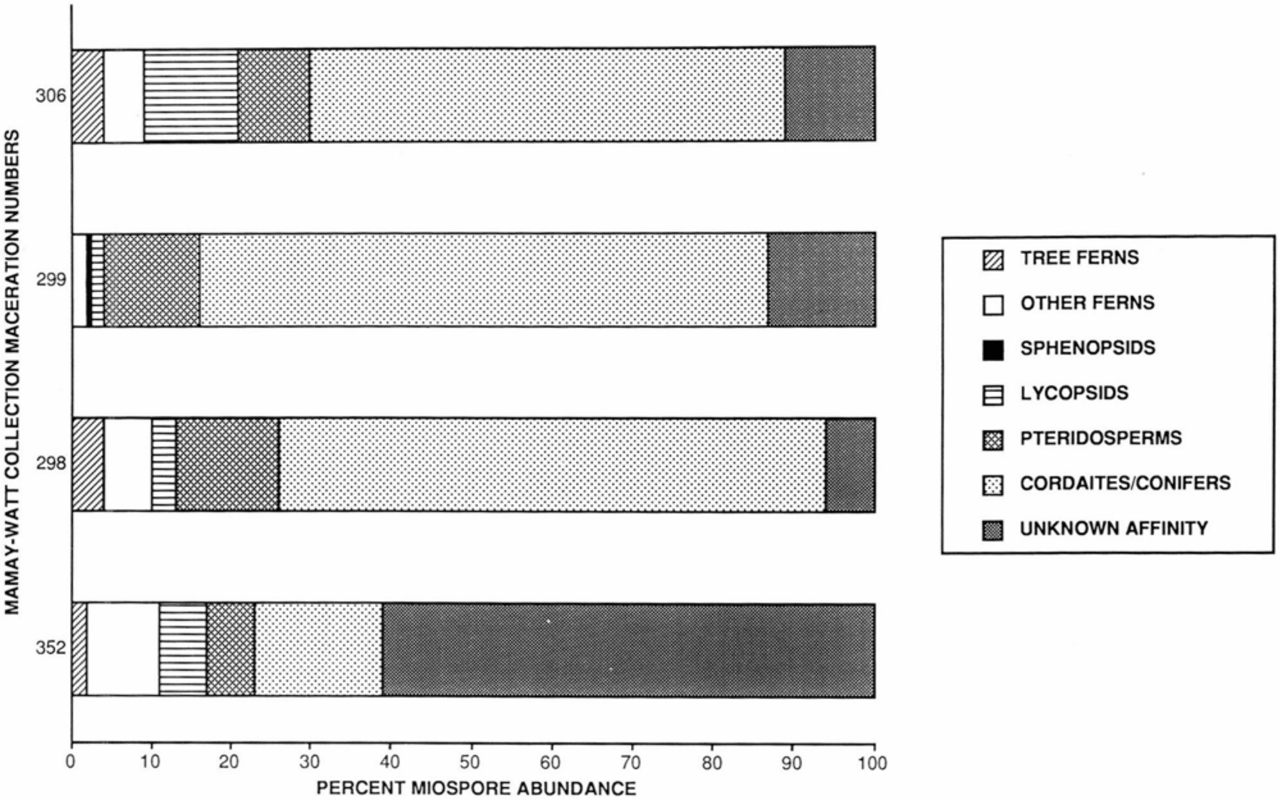

FIGURE 2—Percent abundance of pollen and spores of major plant groups in productive samples of the Mamay–Watt collection. The figure has no vertical scale.

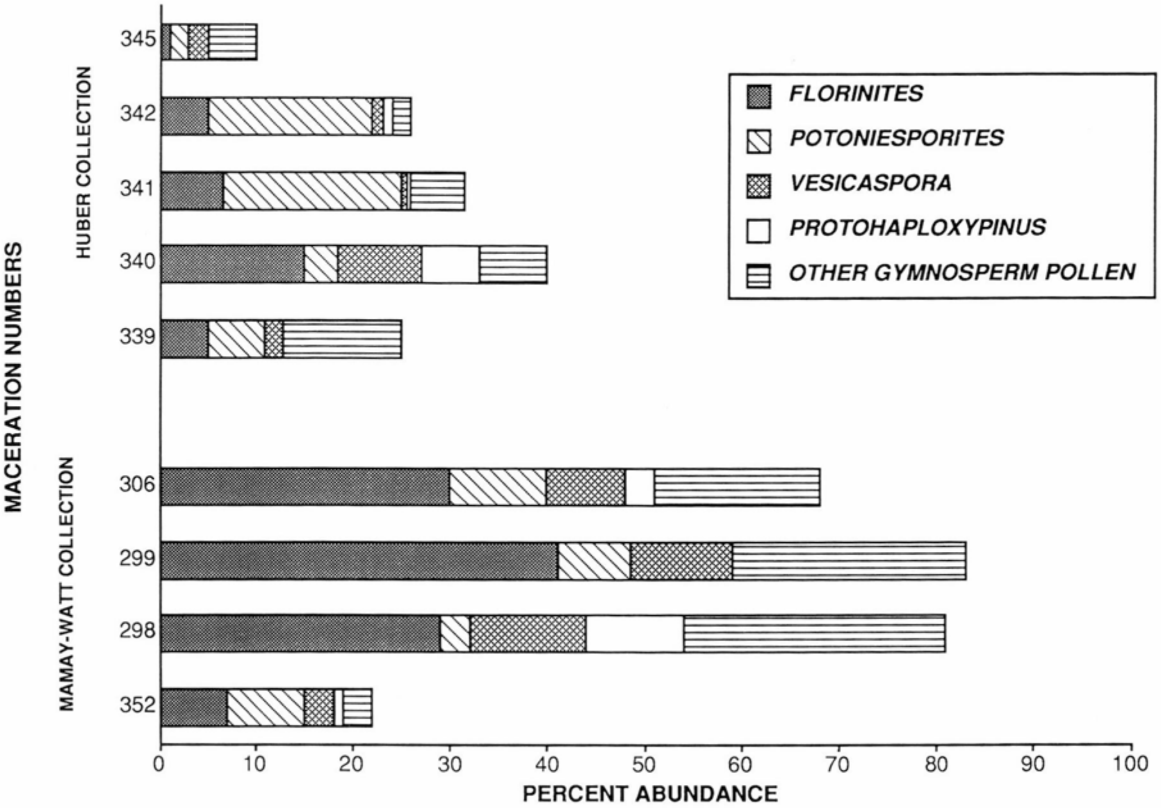

FIGURE 3—Percent abundance of gymnosperm pollen genera in productive samples of the Huber collection (top) and the Mamay–Watt collection (bottom). The figure has no vertical scale.

tiasporites indicus (Fig. 7G) up to 5% of the palynoflora. In the basal sample (maceration 352), gymnosperm pollen (22%) are outnumbered by spores of unknown affinity, which represent 61% of the palynoflora (Fig. 2). Of these, *Lalmatiasporites indicus* is the most abundant species (34%) followed by *Cadiospora sphaera* (27%) (Fig. 4). In the gymnosperm-pollen component, both *Potonieisporites* and *Florinites* are common (8% and 7%, respectively), and *Vesicaspora* and *Schopfipollenites* each comprise 3% of the palynoflora.

Lycopsid spores are present in all four samples but are most abundant in the uppermost sample (12%), maceration 306 (Fig. 2). The lycopsids are represented almost entirely by *Endosporites globiformis*, with *Crassispora kosankei* only present in macerations 298 and 306 (Table 2). Fern spores are fairly common (2-9%) and are represented by species of *Convolutispora*, *Deltoidospora*, *Granulatisporites*, *Laevigatosporites*, *Raistrickia*, *Triquitrites*, and *Verrucosisporites.* Tree-fern spores also are present in every sample, comprising up to 4% of the palynoflora; these consist primarily of species of *Cyclogranisporites* and *Punctatisporites.* Sphenopsid spores are rare and were recorded from only two macerations (Table 2).

Huber collection

Palynofloras from the Huber samples generally are dominated by fern spores and spores of unknown affinity, although gymnosperm pollen also are abundant (Fig. 5). The lower two samples (macerations 339 and 340) differ from the others in the dominance (33-38%) by fern spores, richness of conifer, cordaite, and pteridosperm pollen, and poorness (18-28%) of spores of unknown affinity (Fig. 5). Palynological assemblages of the three overlying samples (macerations 341,342, and 345) are dominated by spores of unknown affinity (42-55%), and cordaite and conifer pollen and fern spores comprise up to 26% and 33% of the palynofloras, respectively. Tree-fern spores are present in all five samples (2-9%), as are spores of lycopsids and sphenopsids (each <5%).

The most abundant species in the Huber collection *is Lalmatiasporites indicus, a* large trilete spore of unknown affinity that commonly is preserved in tetrads; it comprises up to 50% of the palynological assemblages from the Huber collection (Fig. 4) and is most abundant in the upper three samples. *Cadiospora sphaera* is less common than *L. indicus* in every sample, representing from 3% to 12% of the assemblage (Fig. 4). Fern spores are dominant in the lower two samples and abundant in the upper three. The most abundant genus is *Verrucosisporites* (up to 25%); both *V. donarii* and *V. morulatus* are common elements in the Huber samples (Table 2). Other common fern spores include *Laevigatosporites minor*, *Microreticulatisporites sulcatus*, and species of *Convolutispora*, *Deltoidospora*, *Granulatisporites*, and *Triquitrites*. Most tree-fern spores are species of *Punctatisporites*, most commonly larger ones such as *P. aerarius* and *P. nitidus.* Other tree-fern species present are *Laevigatosporites minimus*, *Cyclogranisporites aureus*, and *C. multigranus* (Table 2).

Cordaite and conifer pollen are abundant (18-30%) in the lower four samples and less common (6%) in the top zone (Fig. 5). *Potonieisporites simplex* and species of *Florinites* are the most abundant (up to 19% and 15%, respectively). *Wilsonites vesicatus* comprises up to 4% of the palynoflora, and *Protohaploxypinus* also is present (up to 6%). Several other bisaccate species are present, including *Lueckisporites virkkiae*, *Striatoabeites richteri*, *Rhizomaspora radiata*, and *Alisporites zapfei* (Table 2).

Pteridosperm pollen are present in every sample of the Huber collection (2-11%), and *Vesicaspora wilsonii* is the most common pteridosperm species (1-9%). *Schopfipollenites* also is present in every sample, comprising up to 6% of the palynological assemblage. Sphenopsids are represented by *Calamospora*, which is present in every sample but never

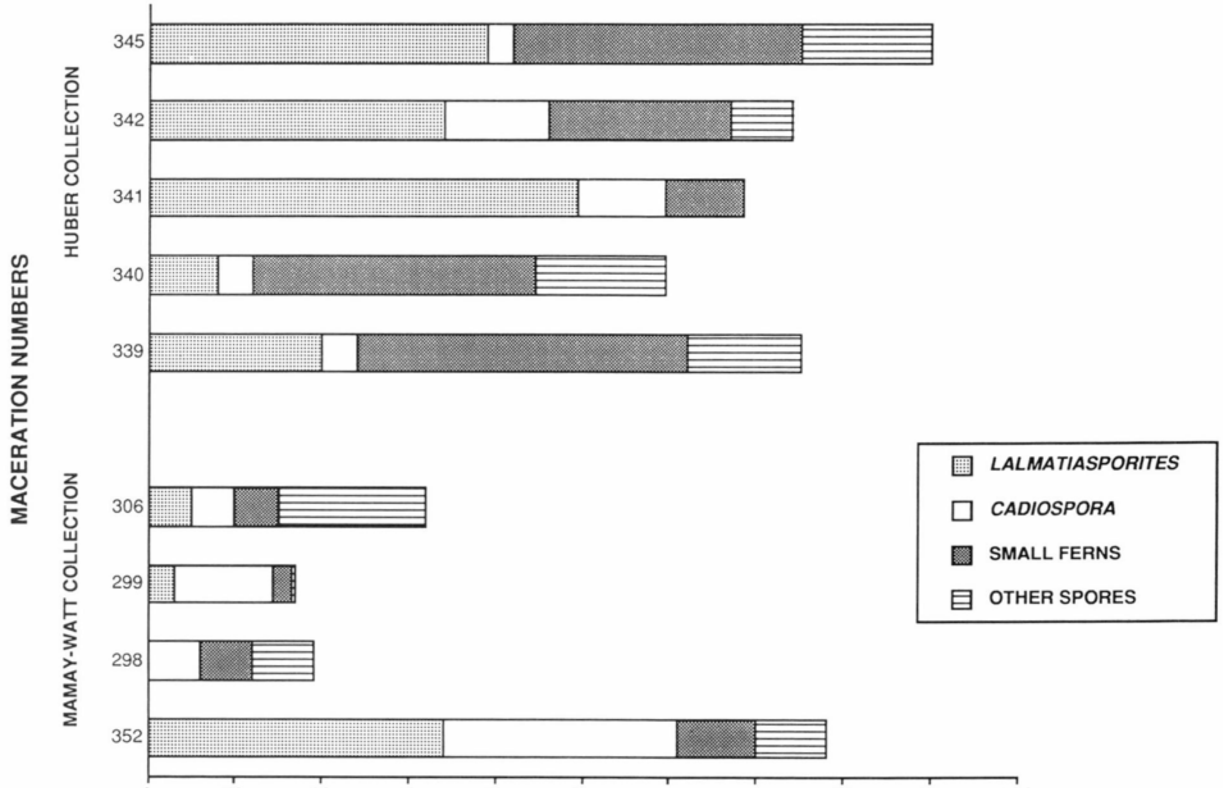

FIGURE 4—Percent abundance of *Lalmatiasporites indicus*, *Cadiospora sphaera*, fern spores, and all other lower-vascular-plant spores in productive samples of the Huber collection (top) and the Mamay–Watt collection (bottom). The figure has no vertical scale.

TABLE 2—Palynomorphs present in Mamay–Watt and Huber collections, Kinney Brick Quarry. P = Present but not encountered in count; R = Rare (<2%); U = Uncommon (2–5%); C = Common (5–10%); A = Abundant (>10%).

	MAMAY-WATT COLLECTION				HUBER COLLECTION				
	352	298	299	306	340	341	342	345	339
FERNS/TREE FERNS									
Punctatisporites curviradiatus								R	
P. decorus						U			
P. minutus	R	U			R			U	
P. aerarius								R	
P. nitidus					U		R	R	
Punctatisporites sp.	R						R		A
Cyclogranisporites aureus					P				
C. multigranus				U	P				U
Laevigatosporites minimus							P		R
Spinosporites sp.								R	
Punctatosporites minutus		R							
P. punctatus					U			P	
Acanthotriletes sp.					P				
Laevigatosporites ovalis					U				
L. minor	R		R	R	C		R	R	C
Apiculatisporites latigranifer			R	R					
A. spinulistratus	R				R	R	R	P	
Verrucosisporites donarii	R	R			A	U	U	C	R
V. verrucosus		R							
V. microtuberosus					R				
V. morulatus					R	C	C	C	
V. sifatii								R	P
Verrucosisporites sp.		R			R				
Microreticulatisporites sulcatus					U	R	U	C	
Convolutispora florida					P			R	
C. tessellata	U				U	R	P	U	
Convolutispora sp.								P	P
Savitrisporites nux					P				
Laevigatosporites desmoinesis					R			P	
Deltoidospora guennelii					R			P	P
D. levis	P	R			C	R	R	R	C
D. parvus									U
D. priddyi					R				
Granulatisporites adnatus							R	P	
G. granularis	R				R				R
G. parvus					R				
G. minutus	P	P							
Lophotriletes microsaetosus				P	U				
Lophotriletes sp.	P				R				R
Gillespiesporites venustus									U
Raistrickia aculeata				P					
R. saetosa									R
Raistrickia sp.		P	R	R		R			
Triquitrites bransonii		R		R	R			P	U
T. sculptilis	R					R			

(continued on next page)

TABLE 2, continued

	MAMAY-WATT COLLECTION				**HUBER COLLECTION**				
	352	**298**	**299**	**306**	**340**	**341**	**342**	**345**	**339**
SPHENOPSIDS									
Calamospora mutabilis									R
C. parva	P				C	R	R	R	R
Calamospora sp.			R						
LYCOPSIDS									
Crassispora kosankei		P		R					
Endosporites globiformis	C	U	U	A	R	U	R		
Cirratriradites surangei						R			
Cirratriradites sp.			P					U	
CORDAITES/CONIFERS									
Illinites unicus		R							
Wilsonites vesicatus	P	P	P		R		R	U	U
Florinites florini		U	A	R					
F. mediapudens	U	A	A	A	A	U	U	P	U
F. millotti					R	R		R	
F. similis	P	A	A	A	U	U	R		R
F. volans	U	U	U	U	U	U	P		
Phillipsites tenuis		U	C	R					
Striatosaccites tractiferinus		R	U						
Protohaploxypinus chaloneri					C	R	P		
Protohaploxypinus sp.	R	C		U	U		R		
Pityosporites sp.		R							
Potonieisporites simplex	C	U	A	C	C	A	A	R	C
Rhizomaspora radiata			U						P
Striomonosaccites sp.			U						
Species A					R				
Alisporites zapfei									U
Lueckisporites virkkii					U				
Lueckisporites sp.	P				P				
Striatoabeites richteri					U				
PTERIDOSPERMS									
Vesicaspora wilsonii	U	A	A	C	A	R	R	R	R
Schopfipollenites sp.	U	R	U	R	U	A	R	R	U
UNKNOWN AFFINITY									
Species B				R	C	P			
Lalmatiasporites indicus	A		U	U	A	A	A	A	A
Cadiospora sphaera	A	C	A	U	U	A	A	U	U

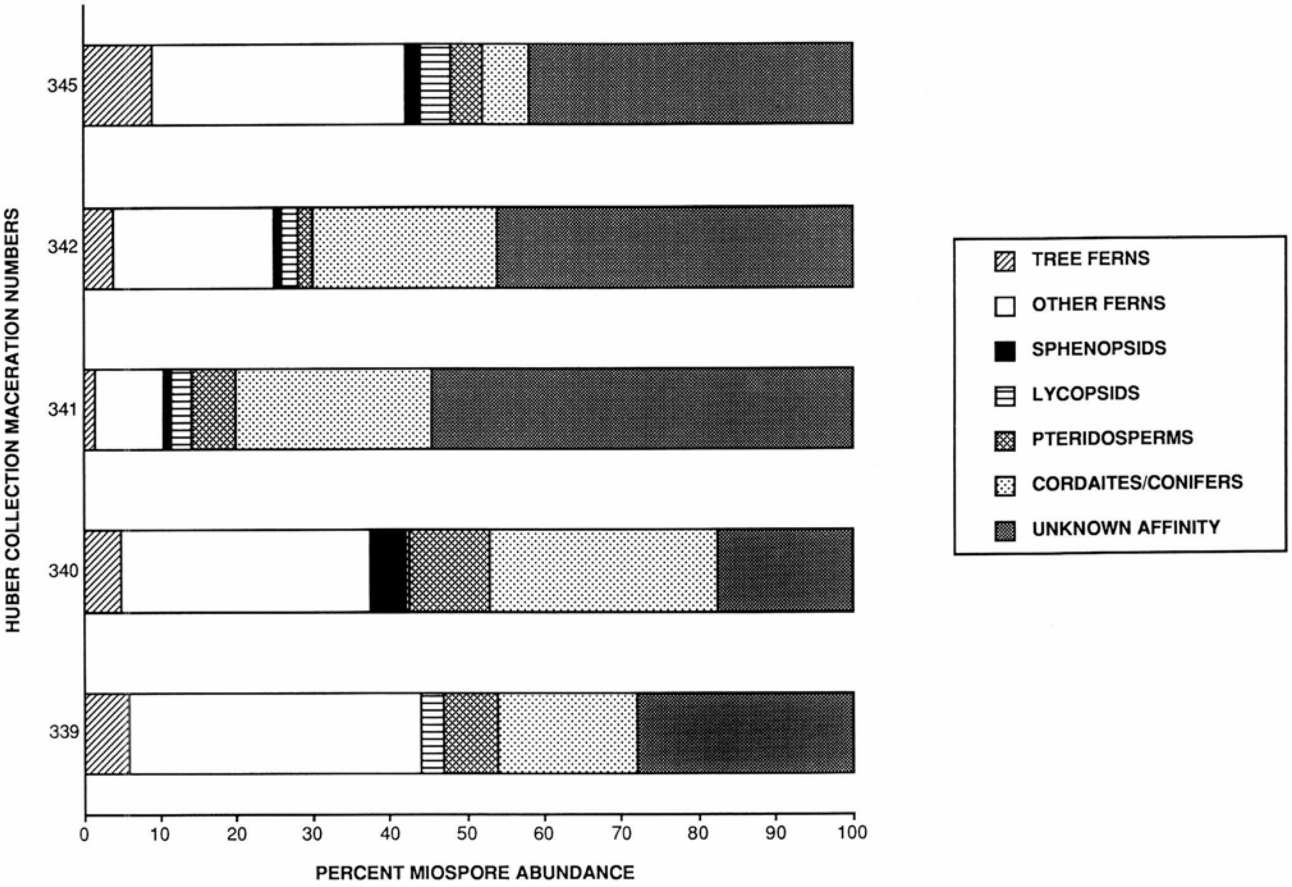

FIGURE 5—Percent abundance of pollen and spores of major plant groups in productive samples of the Huber collection. The figure has no vertical scale.

exceeds 5% of the assemblage; the most common species is C. *parva* (Fig. 7C). Lycopsids also are present in every sample (1-4%). Only two lycopsid species were identified in the Huber collection, *Endosporites globiformis* and *Cirratriradites surangei;* neither exceeds 2% of the assemblage.

Discussion

Vertical distribution of palynomorphs

Vertical patterns of change in species abundance differ between the two collections. In the Mamay-Watt collection, the basal sample is dominated by spores of unknown affinity, but the other three samples consist primarily of cordaite and conifer pollen (Fig. 2). In contrast, the Huber collection produced two lower samples with higher abundances of fern spores and pteridosperm pollen and three upper samples dominated by spores of unknown affinity (Fig. 5). Inferences regarding vertical distribution of taxa derived from these two collections must be considered cautiously because (1) only one-third of the samples was productive, (2) neither collection represents the full thickness of the section, and (3) the relative stratigraphic positions of productive intervals between the two collections are uncertain. Therefore, both due to differential preservation of palynomorphs and sampling strategies, neither collection provides a continuous record of Late Pennsylvanian pollen/spore accumulation during deposition of the sediments which became the Pine Shadow Member at the Kinney Brick Quarry. More complete lateral and vertical sampling is necessary to fully understand "successional" patterns in vegetation at the Kinney site. Observations on vegetational trends are listed below.

Mamay-Watt collection—The bottom sample (maceration 352) is the most unusual in the Mamay-Watt collection; 61% of its palynoflora are spores of unknown affinity. Of these spores, *Lalmatiasporites indicus* is slightly more abundant than *Cadiospora sphaera.* The upper three samples are dominated strongly by gymnosperm pollen (68-81%); *Florinites* is the most common genus (29-41%) in all three samples, and both *Potoniesporites simplex* and *Vesicaspora wilsonii* are common (Fig. 3). The most noteworthy difference among the three upper samples is the relatively great abundance (12%) of *Endosporites globiformis* in the top sample (maceration 306).

Huber collection—The lower two samples in the Huber collection have fewer (17.5-28%) spores of unknown affinity and more fern spores (32.5-38%) and pteridosperm pollen (7-10.5%) than the upper three samples, which are dominated more strongly by spores of unknown affinity. In all five samples, *Lalmatiasporites indicus* is the most abundant problematic taxon, with much lower abundances of *Cadiospora sphaera* (Fig. 4). No consistent pattern of vertical change in abundance of cordaite and conifer pollen is evident (Fig. 5), but *Potoniesporites simplex* is more abundant than species of *Florinites* in every sample except maceration 340, where *Vesicaspora wilsonii* also is unusually common (Fig. 3). Gymnosperms are at their lowest abundance (10%) in the uppermost sample (maceration 345).

Lateral variation in palynomorph abundance

The two collections differ radically in species composition, abundance, and diversity, reflecting the spatial heterogeneity within the plant community surrounding the depositional basin. Palynofloral assemblages from the Huber samples are collectively more diverse (64 species) than those from the Mamay-Watt collection (45 species). This diversity reflects the greater number of lower-vascular-plant species in palynological assemblages of the Huber collection. Both collections include 16 species of gymnosperm pollen, but the Huber collection contains 48 spore species, compared with 29 in the Mamay-Watt collection. Most of the extra spore species in the Huber collection are correlated with ferns (Table 2) and other small understory plants.

The species diversity exhibited by palynological assemblages (up to 64 species) is about two times greater than that of the megafossil assemblage (30 species: S. H. Mamay, pers. comm. 1991). Such a pattern has been noted in other studies of Pennsylvanian strata that have included both paleobotanical and palynological assemblages. In the Upper Pennsylvanian Bristol Hill and Friendsville Coals, 61 palynomorph species were present compared to 23 megafossil species (Willard, 1985), and in the Middle Pennsylvanian Springfield Coal, 115 palynomorph species were present versus 30 megafossil species (Willard, 1990b). Several factors control the differences in diversity from the two records: (1) Palynomorphs usually are preserved better and more abundantly than plant megafossils. The diversity of megafloral assemblages is affected strongly by preservational biases; plants with high proportions of lignified tissue such as periderm or wood (i.e. lycopsids or conifers) are preserved preferentially over plants of a more parenchymatous construction (i.e. ferns). Palynomorphs are extremely resistant to degradation, and a fundamental bias in the palynological record results from differential rates of palynomorph production; this variation affects interpretation of the relative abundance of different taxa more strongly than interpretation of the diversity of palynological assemblages. (2) Palynomorphs may be transported over great distances by wind currents (Traverse, 1988), therefore presenting a regional view of the source vegetation and incorporating species from several different environments. Transport of larger plant fragments typically involves shorter transport distances; megafossil assemblages thus illustrate vegetational composition on a more localized scale, including plants from fewer different settings than palynological assemblages. (3) Palynomorph species are "form" taxa differentiated purely on morphological characteristics (Traverse, 1988), and, in many cases, the genera may have been split into an artificially high number of species. In contrast, paleobotanical researchers still are striving to combine organ taxa into "whole-plant" assemblages, and the resulting species may more realistically represent genera or even families. Therefore, there is not yet a one-to-one correspondence between palynomorph and plant-megafossil species. Although taphonomic biases can never be discounted, a closer correspondence between the two records should be approached as in-situ spores from fructifications are examined to establish the degree of intraspecific palynomorph variation within a megafossil species and as palynomorph species are correlated with source plants.

Generally, palynomorphs from the Mamay-Watt collection indicate a high proportion of tree species, whereas those in the Huber collection were produced by smaller, understory plants. The upper three Mamay-Watt samples are composed primarily of tree pollen (72-85%) which consist of abundant cordaitean and walchian pollen and common pteridosperm pollen and tree-fern spores. In the Huber collection, palynomorphs produced by tree species are less common (19-45%), and spores produced by ferns and those of unknown affinity are dominant. Lycopsid and sphenopsid spores also are more abundant than in the Mamay-Watt collection.

Floristic differences between the two collecting sites also have been observed in megafossil records (Mamay & Mapes, this volume). Plant megafossils from the Mamay-Watt site include abundant *Neuropteris* and *Walchia; Dicranophyllum, Sphenopteris,* sphenopsids, sigillarian lycopsids, and tree ferns also were present. The Huber collection consists primarily of *Neuropteris* and includes *Walchia*, *Pecopteris*, and sphenopsids. The differences in composition between the two sites reflect the spatial heterogeneity typical of many terrestrial landscapes. The sites are from quarry pits at least 150 m apart, and the compositional differences may be real or may reflect taphonomic bias; further field study is necessary to document the relative influences of pre- and post-depositional factors.

Paleoecological implications

Palynological assemblages from the two sites differ markedly in the abundance of lower-vascular-plant spores and pollen. The Huber samples are dominated strongly by spores (59.5-90%), whereas the upper three Mamay-Watt samples consist predominantly (68-83%) of pollen (Fig. 6). When compositional differences, species abundance, and species diversity are considered jointly, it suggests that the variation between the two sites reflects differences in relative soil moisture. Although the topographic differences between the two sites may have been relatively minor, seasonal dryness is known to exacerbate the effects of topography and other edaphic factors on vegetational composition (Stebbins, 1952). Edaphically dry patches with distinctive floras also have been documented within a few meters of more extensive, wetter soils; such coexistence of locally wet and dry soils is typical of plant communities (Axelrod, 1972). Thus, the existence of seasonality during deposition of the Pine Shadow Member would have exaggerated the effects of topography and soil wetness, resulting in locally very different plant communities such as those from the two collection sites. Lower vascular plants typically require at least periodic free water for reproduction, whereas the evolution of the seed habit and wind-dispersed pollen released seed plants from that requirement (Rothwell & Mapes, 1988). The high proportion of lower-vascular-plant spores and the relatively great diversity of fern and sphenopsid spores at the Huber site suggest that the plant assemblage there may have grown in relatively wetter, more poorly drained soils than that at the Mamay-Watt site. Such a site could represent a topographic low, a site with a less permeable substrate, or a site near a river channel.

Comparison of the Kinney Quarry assemblage with other Late Pennsylvanian assemblages

The extensive differences between palynological assemblages from the two sites in the Kinney Quarry make direct comparison with other assemblages more challenging. In the Kinney Quarry, some samples are dominated by monosaccate pollen, but others are dominated by large trilete spores. These differences correspond to those seen in separate Permo-Carboniferous paleofloristic provinces. Below, palynological assemblages from Upper Pennsylvanian and Lower Permian strata in Euramerican and Gondwanan sites are summarized and compared with the Kinney Quarry palynological assemblages.

Euramerica—Late Missourian strata at Garnett, Kansas, have yielded abundant plant megafossils and palynomorphs. *Potonieisporites* contributes up to 75% of the palynoflora (Winston, 1983), and other common genera are *Vesicaspora, Protohaploxypinus,* and *Pityosporites.* Tree-fern and fern spores also are present in low abundance throughout the Garnett section. Virgilian palynofloral assemblages from shales and coals of Kansas and Oklahoma were studied by Clendening (1974) for comparison with the Dunkard Group of the Appalachian Basin. Although gymnosperm pollen are present in these strata, the palynofloras are dominated by species of *Laevigatosporites* with common occurrences of *Ca-*

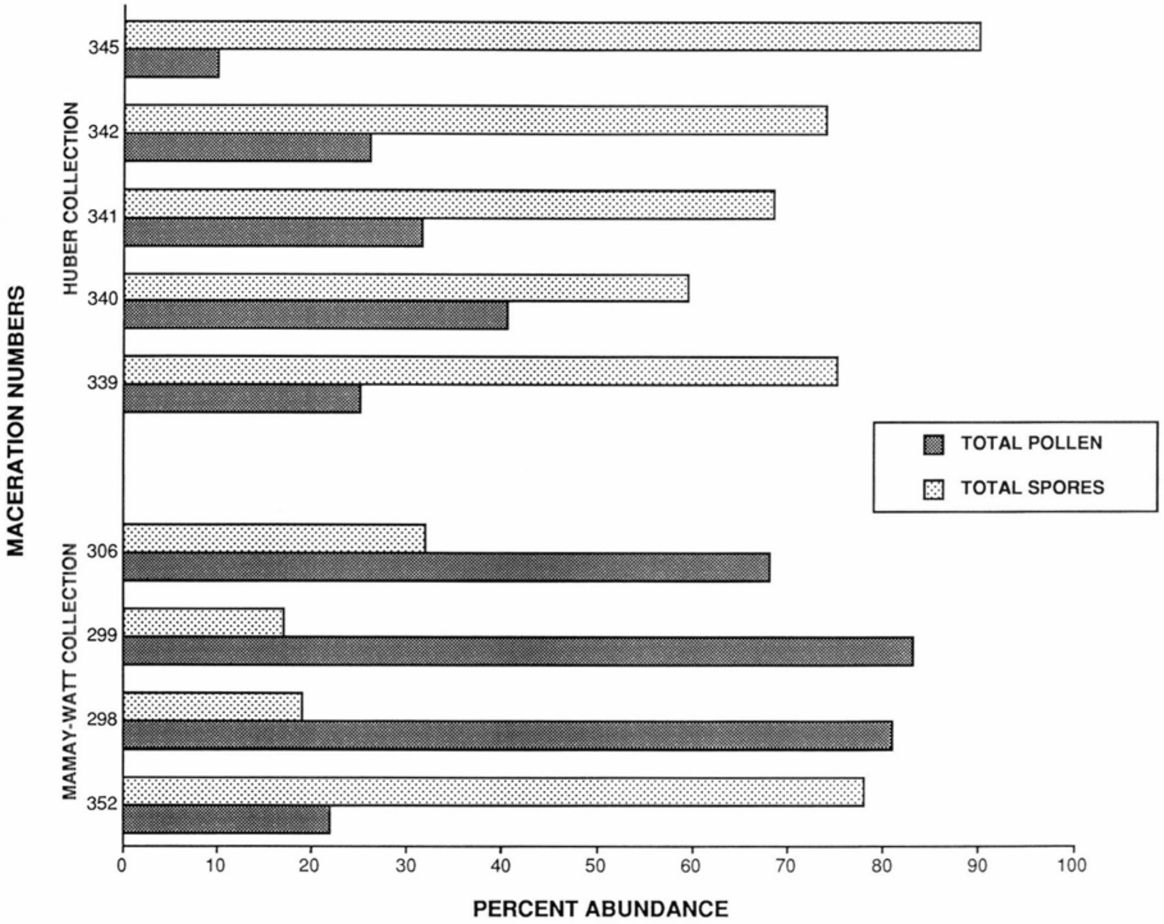

FIGURE 6—Percent abundance of pollen and spores in productive samples of the Huber (top) and Mamay–Watt (bottom) collections. The figure has no vertical scale.

lamospora and *Vesicaspora.* Saccate pollen are more abundant in overlying Lower Permian strata. Palynofloras of Late Pennsylvanian to Early Permian age from the Western Interior have been described by Taggart & Ghavidel-Wyooki (1988) and Wilson (1962). Channel-fill deposits in the Hamilton Quarry, Kansas, are thought to be of Late Pennsylvanian age and are dominated by *Potonieisporites,* with *Alisporites* abundant. Striate bisaccate forms are common, and spores are relatively rare (Taggart & Ghavidel-Wyooki, 1988). The Lower Permian Flowerpot Formation of Oklahoma is dominated even more strongly (90%) by pollen with striate bisaccate forms abundant (Wilson, 1962). Both the Hamilton Quarry and Flowerpot Formation samples have many elements in common with the Kinney palynological assemblages, but the relatively greater abundance of striate bisaccate pollen and lesser abundance of spores are most consistent with a Permian age.

Most palynological analyses of Late Pennsylvanian strata in the Illinois Basin have focused on Missourian-age units (Kosanke, 1950; Peppers, 1964; Willard, 1985). The coals, which have been of primary interest, typically are dominated strongly by tree-fern spores with spores of calamites, small ferns, and sigillarian lycopsids common. Underclays tend to have more diverse palynological assemblages with tree-fern, calamite, and fern spores (Peppers, 1964; D. A. Willard, unpubl. data 1991). The only assemblages with abundant cordaite pollen are those from marine units above the coals. Even in these samples, however, spores of tree ferns and lycopsids outnumber cordaite pollen in the assemblage (Peppers, 1964).

Shales of the lower part of the Dunkard Group in the Appalachian Basin were analyzed palynologically by Clendening (1974), who established them as Late Pennsylvanian in age. Although a great variety of saccate forms were identified from Dunkard coals and shales, the most abundant taxa of the Washington Formation are species of *Laevigatosporites* and *Thymospora.* Gymnosperm pollen, particularly *Vesicaspora* and *Cordaitina,* are more abundant in the younger Greene Formation but do not reach the abundance recorded in Kansas (Clendening, 1974).

In Europe, palynological data have been used extensively in developing palynostratigraphic zonation schemes (see Clayton et al., 1977). Generally, the Stephanian is dominated by spores, particularly those of ferns and lycopsids (Alpern, 1954). Lower Stephanian palynomorphs include abundant *Lycospora, Densosporites, Laevigatosporites, Torispora, Thymospora,* and *Florinites,* with some bisaccate pollen present. In upper Stephanian strata, most of the same genera are abundant, and *Potonieisporites* is present consistently. By the Autunian, the change from spore- to pollen domination occurred; in rocks of this age, *Potonieisporites* and *Florinites* are very abundant, bisaccate pollen and *Vittatina* are more common than earlier, and fern and lycopsid spores are rare (Clayton et al., 1977).

Gondwana—By far, the most widely studied palynofloras of Late Carboniferous to Early Permian age are from Gondwanan strata in Australia, South America, and India. Each is characterized by a distinct vertical change in palynofloral composition from dominance by large, monosaccate pollen such as *Parasaccites* and *Potonieisporites* and abundance of large trilete spores *(Punctatisporites gretensis, Callumispora* spp., *Lalmatiasporites indicus)* in glacial deposits of Late Pennsyl-

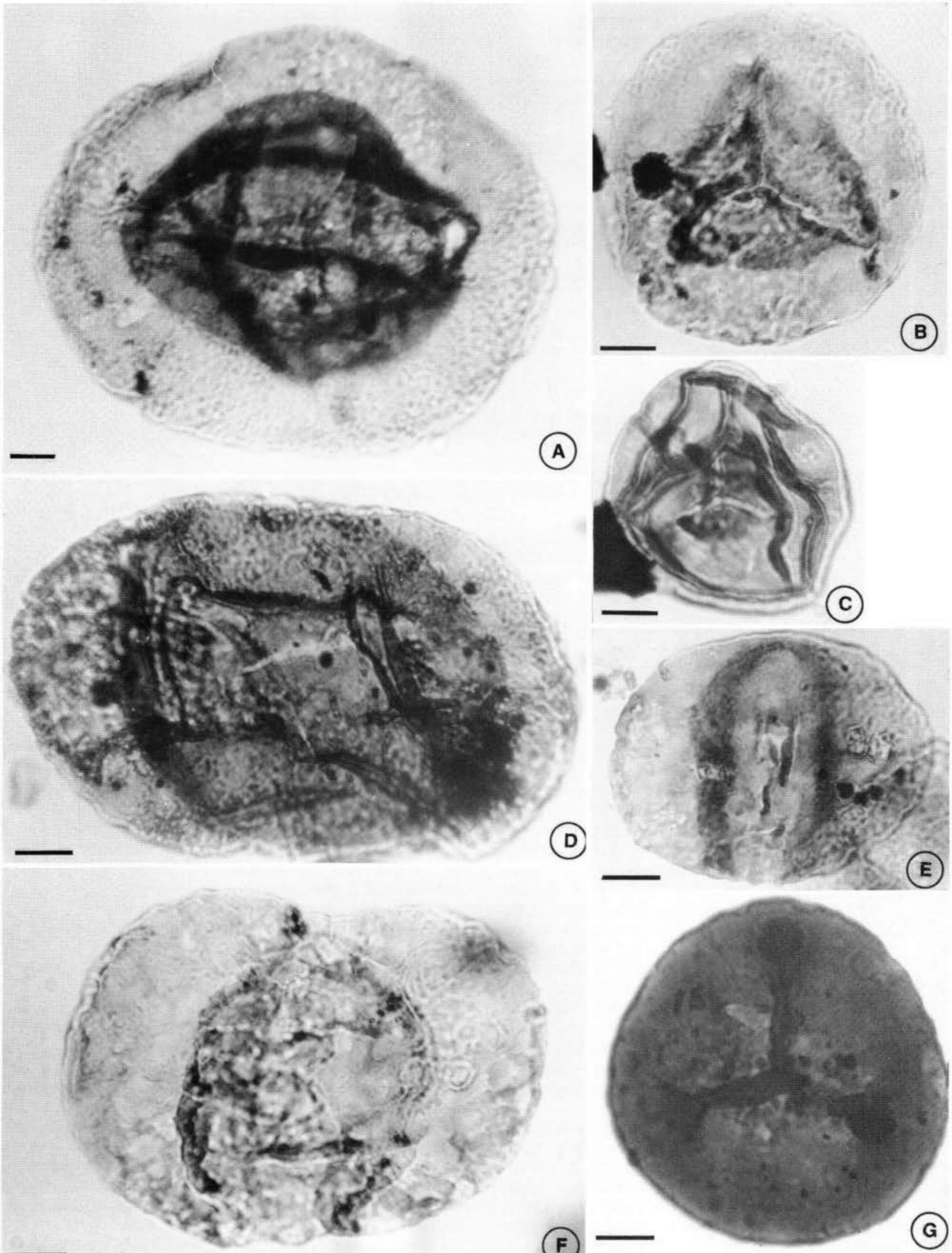

FIGURE 7—Common pollen and spores from Kinney Quarry palynofloras. All figures × 1000 unless indicated otherwise. Scale bar equals 10 μm. **A,** *Florinites similis* Kosanke 1950, USNM 455189 (×750); **B,** *Florinites volans* (Loose) Potonie & Kremp 1956, USNM 455190; **C,** *Calamospora parva* Guennel 1958, USNM 455185; **D,** *Potonieisporites simplex* Wilson 1962, USNM 455186; **E,** *Vesicaspora wilsonii* (Schemel) Wilson & Venkatachala 1963, USNM 455187; **F,** *Protohaploxypinus* sp. (Samoilovich) Hart 1964, USNM 455191; **G,** *Lalmatiasporites indicus* D'Rozario & Banerjee 1987, USNM 455188.

vanian age to eventual dominance of striate bisaccate pollen such as *Protohaploxypinus* and *Faunipollenites in* post-glacial deposits of the Permian (Schopf & Askin, 1980). Similar patterns have been documented with minor variations in Australia (Kemp et al., 1977), Argentina, Uruguay, Brazil (Archangelsky & Toigo, 1980; Bharadwaj et al., 1976), India (Bharadwaj, 1966; Navale & Tiwari, 1965), and Zaire (Pierart, 1979).

Kinney Quarry—Despite the great palynological variation between the two sites at the Kinney Quarry, the dominance of monosaccate pollen and trilete spores definitely places it as Late Pennsylvanian in age. Importantly, however, elements from both the Euramerican and Gondwanan provinces are present. The abundance of *Florinites* and *Potonieisporites* is more characteristic of Euramerican palynofloras of the Late Pennsylvanian, whereas *Lalmatiasporites indicus* and similar large, trilete spores are much more abundant in Gondwanan assemblages. Such a mixture of elements from different floral provinces also is evident in the plant megafossils. Although the abundance of walchian conifers and neuropterid pteridosperms is similar to other Late Pennsylvanian-Early Permian floras of the Euramerican province, a suite of plants resembling Mesozoic and Gondwanan forms *(Charliea, Dicranophyllum, Plagiozamites, ?Podozamites)* also is present (Mamay & Mapes, this volume). Eventual correlation of these megafossil taxa with their palynomorph species would facilitate identification of these plants at other sites using the palynological record and would greatly increase our knowledge of the biogeographic distribution of these enigmatic species.

Summary

The Kinney Quarry palynological assemblages suggest that two ecologically distinct but laterally close plant communities were present at the quarry. The Mamay-Watt collection represents a typical Late Pennsylvanian extrabasinal forest adapted to occasional, perhaps seasonal, dry periods, as documented by abundant cordaite, conifer, and pteridosperm pollen, the presence of tree-fern spores, and the rarity of sphenopsid spores. The abundance of wind-dispersed pollen in the samples suggests that these palynofloras may include elements of the regional vegetation. The Huber collection is dominated by spores of small ferns and one problematic taxon, *Lalmatiasporites indicus,* includes spores of sphenopsids and other lower vascular plants, and consistently is more diverse than samples of the Mamay-Watt collection. These palynological characteristics and the dominance of lower-vascular-plant spores in the Huber samples are consistent with deposition in a locally wetter environment, perhaps with poorly drained, everwet soil. This site could have been topographically lower than the MamayWatt site or nearer a fluvial channel. Further fieldwork and analyses are necessary to clarify the validity of this hypothesis.

The combined characteristics of both Euramerican and Gondwanan provinces in the Kinney palynological assemblage reflect strong compositional differences between the two sample sites. The Mamay-Watt collection most closely resembles Late Pennsylvanian palynofloras from the Garnett site and the Hamilton Quarry in Kansas on the basis of cordaite and conifer pollen abundance. The Huber collection, dominated by fern spores and *Lalmatiasporites indicus,* is more similar to assemblages from Late Pennsylvanian glacial deposits of Gondwana. Therein lies the most remarkable aspect of the Kinney Quarry flora; both the plant megafossil and microfossil assemblages contain an admixture of typical Virgilian species with others known from no other Late Pennsylvanian sites.

Acknowledgments

I thank W. A. DiMichele, S. H. Mamay, R. J. Litwin, and R. M. Bateman for their careful, critical reviews of the manuscript and informal discussions while the work was in progress. Samples for palynological analysis were provided by 5. H. Mamay and P. Huber. F. M. Hueber provided access to laboratory facilities. I thank R. J. Litwin for assistance with processing techniques and for access to photomicrographic equipment. The research was conducted during my tenure as a postdoctoral fellow at the National Museum of Natural History.

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Early Virgilian plant megafossils from the Kinney Brick Company Quarry, Manzanita Mountains, New Mexico

Sergius H. Mamay[1] and Gene Mapes[2]

[1]*Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560;*
[2]*Botany Department, Ohio University, Athens, Ohio 45701*

Abstract—The Pine Shadow Member of the Wild Cow Formation, exposed at the Kinney Quarry, contains about 30 species of plant megafossils preserved as compressions/impressions among animal fossils characteristic of nearshore assemblages. The undamaged condition of the plants suggests nearby growth sites and quiet depositional conditions, consistent with recognition of a sheltered lagoonal environment.

Conifers and neuropterid pteridosperms share dominance in the flora. The conifers appear as branching systems of *Walchia piniformis* with minor occurrences of W. *schneideri.* Other gymnosperms are abundant *Neuropteris* (chiefly *N. ovata)* and *Sphenopteridium,* rare *Odontopteris,* and sparse cordaitean leaves and ovulate parts. The ferns consist of abundant material of a fertile alloiopteroid, rare *Pecopteris feminaeformis, P.* sp., and *Danaeites emersonii.* The lycopsids consist of rare impressions of *Sigillaria brardii,* whereas the sphenopsids are only moderately represented by *Calamites, Annularia, Asterophyllites,* and *Calamostachys.*

Unusual taxa are *Dicranophyllum readii, Charliea manzanitana, Plagiozamites planchardii,* and *?Podozamites* sp., all seemingly discordant with Pennsylvanian biostratigraphy. *Dicranophyllum readii* is very similar to certain Triassic sphenobaierans, whereas *Charliea* and *Plagiozamites* have parallel-veined, cycad-like foliage, and the *?Podozamites* material resembles certain Mesozoic conifers. Aside from these stratigraphically "precocious" anomalies and the characteristically Mississippian *Sphenopteridium,* the Kinney flora is basically similar to Upper Pennsylvanian/Lower Permian conifer-rich floras from Carrizo Arroyo, New Mexico, Garnett and Hamilton, Kansas, and Saar–Nahe, Germany.

Introduction

The sediments exposed at the Kinney Brick Company Quarry in Bernalillo County, central New Mexico, contain a wide variety of both plant and animal fossils. These rocks comprise part of the Pine Shadow Member of the lower Virgilian (Upper Pennsylvanian) Wild Cow Formation. The geographic and geologic particulars of the locality were most recently described by Lucas & Huber (1991), who also presented a brief summary of the biota.

Plant megafossils are a very conspicuous element in the Kinney biota. These were first noted by professional paleontologists in October 1961, when S. R. Ash led C. J. Felix and G. D. Glover to the quarry while prospecting for Pennsylvanian palynological material (C. B. Read, pers. comm. 1961; Ash and Tidwell, 1982). That expedition in fact marked the very beginning of paleontological investigations of this remarkable site.

As a result of that and subsequent collecting trips by Ash and Read—both then of the U.S. Geological Survey Fuels Branch Office in Albuquerque—a modest amount of plant material was accumulated, though only one specimen was ever described or illustrated (Mamay, 1990). On the basis of preliminary identifications by Read, however, floral lists and brief discussions were published, first by Kelley & Northrop (1975) and later by Ash & Tidwell (1982).

In 1967, Mamay and A. D. Watt, then with the Paleontology and Stratigraphy Branch of the U.S. Geological Survey, visited Read and were introduced to Tom J. Kinney, who granted permission to collect at the quarry. Mamay and Watt spent four weeks collecting during a subsequent visit in 1969. Quarrying was essentially in full-time operation at the time, and freshly dug material was in ample supply—attractive not only to Mamay and Watt, but also to school classes and Scout groups, as well as the occasional unidentified amateur collector. A substantial collection was made; along with the Read and Ash specimens, this material was brought to Washington, DC, and accessioned permanently to the custody of the U.S. National Museum (USNM).

The Mamay–Watt collection is the principal source of information incorporated in this survey of the Kinney flora; two obvious taxonomic novelties were described in earlier publications by Mamay (1981, 1990). Other material made available for this study included a suite of New Mexico Museum of Natural History (NMMNH) specimens collected by Phillip Huber, as well as specimens collected by Neal LaFon that are now the property of the Carnegie Museum (CM). Nearly all of the material illustrated here, however, is from the USNM collection. Specimens from the Huber or LaFon collections that are mentioned here are referred to with their respective museum catalogue numbers (NMMNH, CM).

Preservation of the plant fossils

Plants are predominantly represented by detached leaf fragments derived from several groups of vascular plants, with some specimens sufficiently large to demonstrate the two or three ultimate orders of division of compound pteridophyllous fronds. Many coniferous shoots are present, some representing penultimate branches with many of the ultimate branchlets, fully clothed with leaves and attached in relatively undistorted attitudes. A few sphenopsid cones are present, along with a fair abundance of gymnosperm ovules. Bark impressions are rare, as are small detrital fragments or layers of comminuted "plant hash." The plant material is preserved mostly as clear-to-vague impressions and compressions; three-dimensional casts, molds, and permineralized specimens are extremely rare, and cuticular material has not been observed.

Many specimens appear as faint impressions with neither organic residue nor mineral stains to enhance their outlines with contrasting coloration. Others are variously stained with limonitic or manganese compounds that delineate faithfully the outline of the fossils. In some instances, the staining creates a striking light-colored halo between the dark plant material and generally darker matrix (Fig. 7B), thus enhancing the fossils' outlines. However, the mineral stains often obscure important details such as venation patterns. Similarly, some specimens are preserved with a thick coalified residue that sharply outlines the plant while obscuring the venation (Fig. 4E). On the other hand, a remarkable amount of fine surface detail is visible in some specimens with neither organic nor mineral enhancement (Fig. 2A). Venation is indistinct or obscure in many specimens (Fig. 3A, E), but is exceptionally clear in others (Figs. 5F, 9C).

Composition, general description of the flora

Despite its preservational deficiencies, the Kinney plant material lends itself to generic assignments of all but a few elements. Several specific identifications are warranted, but because of insufficient diagnostic details, some species are distinguished with only the "cf." designation. The assemblage is remarkably diverse, containing representatives of several groups of Paleozoic vascular plants: lycopsids, sphenopsids, ferns, pteridosperms, dicranophylls, cordaites, conifers, and parallel-veined, compound-leaved plants of uncertain taxonomic affinity.

Lycopsids

Only three positively identifiable lycopsid specimens have been found; these are small areas of sigillarian bark impressions, most similar to *Sigillaria brardii* Brongniart. The best of these (Fig. 2A) exhibits several of the transversely elongate leaf scars characteristic of the species. Each shows the median vascular scar, flanked by well-defined parichnos scars, with a faint ligule scar above each leaf scar. These features, along with the well-defined rugosities between leaf scars, represent one of the best examples of preservation of surface features in the absence of organic or mineral residues.

The only other putative lycopsid specimen appears in Fig. 2B; it shows an aggregate of acuminate foliose structures with closely arranged, expanded bases; this may be the terminal portion of a sigillarian vegetative shoot.

Sphenopsids

Representatives of the Calamitaceae appear as impressions and poorly defined compressions of stems, foliage, and cones. Foliage and stem material are moderately frequent, whereas fructifications are very rare.

The axial fragments range from very narrow segments 2 cm or less in width to 12 cm in the widest; the internodal lengths are generally about twice as great as the width, and nodal anatomy and transnodal relationships of the ribs are mostly too obscure for taxonomic application. In the larger specimens (cf. Fig. 2C), the ribs attain widths of only about 2 mm. With their straight, very narrow ribs, these axes conform in most characters to the common species *Calamites cistii* Brongniart. However, the presence of a few ribs continuing directly across a node (e.g. Fig. 2C) suggests assignment of these axes to the subgenus *Mesocalamites;* Remy & Remy (1977) applied the binomial *Mesocalamites cistii* to similar material.

Both *Annularia* and *Asterophyllites* occur in the Kinney sediments, with *Annularia* being the more abundant genus. The long-leaved form shown in Fig. 2F appears referable to *Annularia pseudostellata* H. Potonié; the smaller-leaved specimens (Fig. 2D, E) are tentatively assigned to *A. radiata* (Brongniart) Sternberg and A. *asteris* **Bell,** respectively. The only species positively identified is *Annularia sphenophylloides* (Zenker) Gutbier, shown in Fig. 2G; the very symmetrical whorls of wide-tipped leaves readily distinguish this common species. *Asterophyllites* is represented in the USNM collection only by the very small-leaved, specifically indeterminate specimen shown in Fig. 2H. However, the CM collection contains two specimens (CM 15101, 15102) with very narrow leaves reaching 5 cm in length; these are typical examples of *A. equisetiformis* (Schlotheim) Brongniart.

The few calamitean cones available appear to represent two species, based on the size differences between apparently mature specimens. The larger of these (Fig. 2J) is provisionally referred to *Calamostachys pedunculata* Weiss, and the smaller (Fig. 21) to *C. ludwigii* Weiss. The difficulty of arriving at dependable taxonomic assignments (even on the generic level) in dealing with calamitean cones in this type of preservation was discussed by Gastaldo (1981). Because of the obscure nature of such critical features as number of sporangia and insertion of sporangiophores, it remains possible that the Kinney specimens are correctly assignable to *Palaeostachya* rather than to *Calamostachys.*

Ferns

Only five taxa of ferns are recognizable in the Kinney flora: *Danaeites emersonii* Lesquereux, *Pecopteris feminaeformis* (Schlotheim) Sterzel, *Aphlebia* sp., and two undeterminable pecopteroid forms, one of which is fertile.

The genus *Danaeites* Goeppert is represented by four fertile specimens, which are referred here to *D. emersonii* Lesquereux. These fragments are portions of a large, probably tripinnately compound frond with distantly spaced, alternating pinnae bearing large, broadly oblong pecopteroid pinnules with slightly constricted bases (Fig. 3C). The chief identifying characteristic of this taxon lies in the fructifications, which consist of closely spaced, linear marattialean synangia that cover almost the entire abaxial surface of the pinnule and obscure the ultimate venation. Sterile specimens have not been recognized.

Pecopteris feminaeformis is represented by a single small pinna fragment comprising only six pinnules (Fig. 3F). However, this meager material is clearly referable to *P. feminaeformis* by reason of its simple venation with the sparse, undivided lateral veins passing through the lamina at a very narrow angle, each terminating in a sharp, distally directed marginal tooth; the pinnules are characteristically broadly attached, basally confluent, and taper to a pointed tip.

A third taxon *(?Pecopteris* sp.), exemplified by Fig. 3A, B, and G, constitutes the most prominent—albeit the most problematical—element in the fern assemblage. It consists of many penultimate pinna fragments, some as much as 20 cm long. Although these display only bipinnate architecture, one specimen (USNM 455005) contains two penultimate pinna fragments with unusually thick rachises (approximately 6 mm wide), which lie parallel to each other in an orientation suggesting derivation from a common superior rachis. It thus appears likely that the fronds of this plant were quite large and at least tripinnate. The ultimate pinnae are alternate, widely spaced so as not to overlap, narrow, and rigid-appearing. The pinnules are small (up to 7 mm long), alternate, and rather widely spaced. They tend to be slightly constricted at the base (Fig. 3A) and taper distally, presenting a subdeltoid general outline with a **blunt,** rounded tip. The lateral margins are shallowly crenulate in many areas (Fig. 3A), but are mostly indistinct or ambiguous under magnification. The ultimate venation is also unclear or totally obscure. The difficulty of delineation of these features is partly due to the inferior preservation, but is also attributable to the presence of abundant fructifications that mask or interfere with observation of the veins or margins. The fructifications appear as submarginal rows of poorly defined radial synangia (Fig. 3G), each apparently composed of several sporangia. In some specimens the individual sporangia can be distinguished, and are preserved in such a way as to extend beyond the lamina and impart a crenulate appearance to the pinnule margin. This condition is shown in Fig. 3A, where the coalified walls of **the elongate** sporangia simulate a confusing pattern of ultimate venation and a crenulate or erose pinnule outline.

Fructifications aside, the Kinney foliage might be placed among the pecopterids, sphenopterids, alloiopterids, or possibly other taxa. Because of its lax, open habit of pinnulation, some might prefer the genus *Alloiopteris* H. Potonié as the proper taxonomic receptacle for this plant. However, the fructifications, as far as can be determined, are of the *Asterotheca* or *Acitheca* type; in deference to this indication of marattialean affinity, it seems appropriate to provisionally assign this material to the common late Paleozoic genus *Pecopteris* Brongniart, simply as *?Pecopteris* sp. The ambiguities and otherwise unsatisfactory definition of critical characters discourage a more committal taxonomic assignment.

Palynomorphs could not be recovered from this plant or from the fertile *Danaeites* material (D. A. Willard, pers. comm. 1991).

The presence of another fern, more suggestive of the arborescent Marattiales, is established by a few specimens representing very large, at least tripinnate fronds with rachises reaching 2 cm in width (e.g. USNM 455006, not figured). Penultimate pinna fragments reach at least 20 cm in length and are alternately attached at intervals of about 8 cm; the closely spaced ultimate pinnae essentially span the distance between the penultimate pinnae. The overall architecture is typical of the common cyatheoid pecopterids (e.g. *Pecopteris cyathea* Schlotheim; *P. arborescens* Schlotheim), but a specific determination of this sparse material is precluded by the absence of venation features and the indistinct pinnule outlines. This foliage is designated here only as *Pecopteris* sp.

The generic name *Aphlebia* Presl embraces several types of modified, stipule-like foliar appendages that are fairly common in Paleozoic floras, principally in association or direct connection with marattialean fern fronds. However, only two incomplete specimens of *Aphlebia* sp. have been found in this flora. The illustrated specimen (Fig. 3D) shows the deeply pinnatifid outline typical of most aphlebias.

Pteridosperms

This group is represented by four genera based on foliage: *Neuropteris* (Brongniart) Sternberg, *Odontopteris* Brongniart, *Sphenopteridium* Schimper, *Cyclopteris* Brongniart, and one on ovules *(Trigonocarpus* Brongniart). The presence of other taxa is suggested by a few nondescript ovules. *Odontopteris* is rare, occurring as only two specifically undeterminable terminal pinna segments (Fig. 3E).

Neuropteris is a co-dominant component of the flora; specimens occur with approximately the same frequency as the walchian conifers. The Kinney neuropterids consist mainly of more-or-less articulated specimens of the highly variable species *Neuropteris ovata* Hoffman (e.g. Fig. 4C, one of the best examples). This is possibly the most extensively studied species in late Paleozoic floras; the works of Crookall (1959), Laveine (1967, 1989), Wagner (1963), Zodrow & Cleal (1988), and others amply demonstrate the great morphological variability and attendant difficulties inherent to taxonomic treatment of the European *N. ovata.* The most recent meaningful appraisal of the North American neuropterids is that of Cridland et al. (1963). In reference to *N. ovata,* they stated (1963: 78) that "Several species are quite closely related to it and are only differentiated with difficulty. . . . Until these, and other species of the *N. ovata* group of plants, are the subject of extensive restudy and are more clearly defined, we feel that anything but a broad and conservative view of *N. ovata* is unmanageable." For the above reasons, compounded by the preservational deficiencies of the present material, we endorse those cautious views in approaching the abundant Kinney neuropterids.

A "typical" specimen of *N. ovata,* with its characteristically oblong, blunt-tipped and basally auriculate pinnules, is seen in Fig. 4E. Fig. 4A, C—D illustrates slight variants of this form; Fig. 4A is of further interest in the presence of many *Dunbarella* shells, evidently preserved in their living positions of attachment to the foliage. The narrowly attached, suborbicular pinnules of the specimen shown in Fig. 4B are suggestive of *N. heterophylla* Brongniart. Specimens with those pinnule configurations are rare, however, and an identification of *N. heterophylla* at this point can only be extremely tentative.

N. scheuchzeri Hoffman is a minor component of the neuropterids. It occurs only as a few detached but specifically recognizable pinnules (Fig. 5B, C). Their large size, linear-linguiform outline with cordate base, and bluntly acute tips are dependable characteristics of this species, the absence of hairs notwithstanding. The basal cyclopterid lobe shown in Fig. 5C is a further point of distinction.

Fig. 5D—E shows features that are characteristic of neither *N. ovata* nor *N. scheuchzeri.* The relatively short, wide pinnules with sinuate margins, distal auriculation, paired insertion, and variable attitudes suggest an affinity with *N. macrophylla* (cf. Crookall, 1959: pl. 40/2). Several examples of this form are present in the collection. Yet another form appears in Fig. 5H. The pinnules show a decurrent basal attachment and deltoid, acute tips that recall some examples of *N. obliqua* (Brongniart) Zeiller (cf. Crookall, 1959: text-fig. 54). Given the paucity of material, however, this specimen cannot even be attributed with confidence to *Neuropteris.*

Other items attributable to *Neuropteris* are seen in Fig. 5. Defoliate axes of the type shown in Fig. 5A are commonly associated with *Neuropteris* foliage and are thought to represent denuded main rachises, with the "spurs" representing remains of pinna rachises. The non-fimbriate specimen of *Cyclopteris* sp. (Fig. 5F) is a rare form here; its entire margin probably indicates derivation from a frond of *N. scheuchzeri,* inasmuch as the cyclopterid appendages of *N. ovata* have fimbriate margins. Finally, the ovule shown in Fig. 5G (a limonitic cast) is apparently three-ridged and therefore referable to an unidentified species of *Trigonocarpus.*

Sphenopteridium Schimper is one of the more prominent constituents of this flora. Its abundance marks one of several unusual features of the Kinney flora, for *Sphenopteridium* is characteristically a Lower Carboniferous genus. Tidwell (1967) reported *Sphenopteridium* from the lowermost Pennsylvanian Manning Canyon Shale of Utah, but the genus is otherwise absent from the American Pennsylvanian.

The illustrated specimens (Fig. 6A, C—E) show the salient features of this unnamed species of *Sphenopteridium.* The foliage consists of fairly large (at least 40 cm long) bipinnate fronds with a long (at least 13 cm), stout (to 14 mm wide) petiole that dichotomizes acutely to form two equal rachial segments that bear laxly arranged, opposite to alternate, narrow pinnae below the point of petiolar division (Fig. 6D) as well as above. In some specimens the rachial surface is ornamented by narrow, closely spaced transverse ridges indicative of cortical sclerotic plates such as those that characterize the pteridosperm *Heterangium.* Each pinna bears several-to-many narrowly attached, mostly alternate, very deeply lobed pinnules, whose narrow, linear-to-cuneiform ultimate divisions terminate in rounded, sometimes emarginate tips; this is the only example of this type of deeply dissected lamination in the Kinney flora. The venation is simple and open (Fig. 6C), with an indistinct, apparently single vein entering the base of a pinnule and dichotomizing sparsely, each division ending at the distal margin of a pinnule lobe.

Foliar outlines of this plant are generally sphenopteroid, and its resemblances to *Sphenopteris elegans* Brongniart are notable; especially close comparisons may be drawn between Fig. 6A of this paper with Brongniart, 1828: pl. 53/1, and Amerom, 1975: pl. 1. However, the aggregate of its other known features (dichotomously divided petiole, transversely ridged rachial surface, and simple dichotomous venation lacking a dominant vein) supports the assignment of this plant to *Sphenopteridium* sp. rather than to *Sphenopteris.* A detailed account of this taxon is in preparation by Mamay for publication elsewhere.

Dicranophyllum

This genus is a major element in this flora, being represented by abundant specimens of the leaves described as *Dicranophyllum readii* by Mamay in 1981 (see Fig. 7E, F). Although it conforms to the generic concept in qualitative features—long, slender, twice-dichotomous leaves—this species is a startling element in this flora because of the great size of the leaves, which reach lengths of 75 cm while less than 2 cm wide at the base. It is unique to the Kinney flora; equally spectacular foliage of this morphotype is not known from anywhere else in the Paleozoic. A close comparison may be made between these leaves and those of certain species of *Sphenobaiera* (i.e. *S. pontifolia* Anderson & Anderson 1989) from the Triassic of South Africa. Although they are considerably smaller than *Dicranophyllum readii* leaves, reaching only 9 cm in length, the long, slender *Sphenobaiera* leaves display much the same morphology, even though they may fork as many as three times. Given no other morphologic characters for comparison, only the geographic and stratigraphic disparities between their occurrences presently discourage an interpretation of generic identity between the American and African plants, rather than the *Dicranophyllum* alliance.

Cordaites

The cordaiteans are inconspicuous, with a sparse representation of less than a dozen incomplete leaf fragments, a few detached ovules, and one partial fertile axis; none of these specimens is specifically identifiable. The linear, parallel-veined leaves are 1.5 to 2.0 cm wide, none with the tip preserved; one specimen (Fig. 7D) shows a concave basal configuration representing the line of attachment. Associated platyspermic ovules *(Samaropsis* sp.; Fig. 7A, B) are small (approx. 1.5 cm wide) and have a wide, circular wing notched at either or both ends. The fertile organ *(Cordaianthus* sp.; Fig. 7C) consists of a broken axis with a bilateral arrangement of dwarf shoots, mostly broken. It is not known if this strobilus was ovuliferous or polleniferous.

Conifers

Walchian conifers are a co-dominant element, occurring with approximately the same frequency as *Neuropteris.* Although abundant, these specimens are not subject to refined taxonomic analysis because of the lack of information regarding their cones, cuticles, or other anatomical details; they are therefore treated here as representatives of the form-genus *Walchia* Sternberg (Mapes & Rothwell, in press, discuss the most recent developments in the taxonomy and nomenclature of the walchian complex).

The specimens consist of leafy shoots with their full complements of leaves intact in most examples. Nearly all the specimens entail the two highest orders of branching: the penultimate axes, showing the characteristic plagiotropic arrangement of the closely spaced, parallel ultimate branchlets. The largest specimens are 20-22 cm long, with as many as 27 branchlets on either side; the latter reach 12 cm in length. The branchlets create a broadly acute angle (approx. 50°) with the supporting axis; they are mostly straight, rigid-appearing, and fully formed. One unusual specimen (Fig. 8F), however, shows three penultimate shoots bearing a number of apparently young lateral branchlets in early stages of development and pendent positions. The generally large size and undamaged condition of most specimens attests to gentle deposition within relatively close distances from the growth sites.

The leaves vary in length from about 2 to 5 mm, usually with an inwardly curved tip (Fig. 8A, B); in some specimens the tip is straight (Fig. 8C). The variations are apparently within the ranges commonly accepted for the widely distributed species *Walchia piniformis* (Schlotheim) Sternberg, to which we assign most of the Kinney material. A few specimens, however, have longer, more laxly distributed leaves, inserted nearly perpendicularly (Fig. 8D); none of these ultimate shoots are attached to a superior axis. Because of the size and attitude of the leaves, these specimens are provisionally referred to *Walchia schneideri* Zeiller.

Reproductive specimens are absent except for one poorly preserved cone and a few ambiguous ovules. A single specimen of the bifid leaf *Gomphostrobus* sp. (Fig. 8E) completes the walchian assemblage.

Parallel-veined foliage of uncertain affinity

Three taxa characterized by parallel-veined ultimate foliai segments comprise an unusual and distinctive aspect of the Kinney flora. These were recently reported by Mamay (1990) as *Charliea manzanitana* n.gen., n.sp., *Plagiozamites planchardii* (Renault) Zeiller, and an unnamed element compared with *Podozamites* (Brongniart) Braun.

Charliea is known only from its foliage, which consists of compound leaves (only once-compound as now known) with sessile, oblique, and partly clasping, linear-oblong pinnae that have truncated tips, deeply incised into 2-4 nearly equal lobes (Fig. 9B). The lateral margins are smooth and the venation is open, with parallel veins that dichotomize sparingly and end at the tip of a distal lobe (Fig. 9C, D). The overall aspect of *Charliea* foliage is reminiscent of that of *Russellites* Mamay or a zamioid cycad. Only a few articulated frond specimens have been found, but the easily recognized detached pinnae are fairly common. This plant has not been found elsewhere.

Plagiozamites, represented by *P. planchardii* (Renault) Zeiller, is identified here on the basis of two pinnate frond fragments, the better of which is shown in Fig. 9A. The genus is characterized by compound leaves in which the sessile, oblanceolate pinnae are obliquely attached, slightly clasping, and, unlike *Charliea,* have denticulate margins and rounded, undissected tips. The venation is open; the veins are parallel to somewhat spreading, with each vein terminating in a sharp marginal tooth. This material, like *Charliea,* exhibits characteristics that are strikingly reminiscent of the zamioid cycads.

The single specimen shown in Fig. 9F resembles the genus *Podozamites,* although the limited material prevents confident generic determination. Nonetheless, the specimen, with its narrow, linear, basally constricted and slightly clasping laminae and blunt, rounded to truncated tips, suggests the morphology of *Russellites* or *Podozamites.* The venation is open and sparsely dichotomous, with all veins ending in the laminar tips. Precise taxonomic evaluation of this specimen depends on morphological identification of its ultimate segments as either the distichous pinnae of a compound, cycad-like frond or the disguised helical leaves of *a Podozamites-like* coniferous shoot.

Other problematica

The three specimens shown in Fig. 9E, G, and H are insufficient for identification of even the category of organs represented. They do show characters, however, that are incongruous with any of the known associated entities. The epaulette-like structure seen in Fig. 9G apparently consists of an expanded lamina traversed by a strong midvein, with its margin dissected into several acute-acuminate segments, possibly of sporangial nature. This configuration suggests a *Crossotheca-like* fructification with pendent sporangia arranged along the margin of a terminal receptacle. The other two specimens are obviously parts of parallel-veined foliose structures that stand apart from *Charliea* or the other parallel-veined associates. The specimen shown in Fig. 9E, with its deep, narrow marginal laciniations, is reminiscent of *Rhacopteris* (cf. *R. asplenites* [Gutbier] Schimper; see Laveine, 1989: pl. 49/1). The remaining problematicum (Fig. 9H) again shows a dissected marginal outline that superficially recalls *Charliea* but is otherwise not comparable. It might more aptly be regarded as a form of *Aphlebia,* albeit not as convincingly aphlebioid as the specimen shown in Fig. 3D.

Although the foregoing specimens contribute no points of taxonomic distinction to the Kinney assemblage, they alert one to the probability of eventual discovery of more complete material that will broaden our understanding of the flora.

Discussion

Vertical distribution of the plants

Only two detailed descriptions of the Kinney Quarry rock section have incorporated observations on plant-fossil distribution. The earlier account (Stukey, 1967: 28) reported "Abundant plant remains: *Callipteris conferta, Walchia gracillima, Neuropteris* sp. cf. *N. clarksoni, Mixoneura* sp. cf. M. *ovata, Plagiozamites* sp. nov. . . ." (the identifications were attributed to C. B. Read, but we cannot confirm the presence of the genus *Callipteris;* see Kelley & Northrop, 1975: 48). These plants occurred in the 2 ft thick, thin-bedded, black limestone immediately above the basal micrite. Stuckey also reported *Neuropteris ovata* in the next higher, black to light-gray shale unit that extended vertically to about 10 m above the base of the section. The later, less detailed stratigraphic section diagrammed by Gottfried (1987: fig. 7) indicated plant occurrences as high as about 14 m above the quarry floor, but identifications were not provided.

The latest rock description (Lucas & Huber, 1991) indicates plant occurrences beginning in the basal micrite (their unit 1) and extending upward through unit 9—a vertical distance of about 15 m. They distinguish a lower "pteridosperm floral assemblage" (units 2-7) and an upper *"Walchia* floral assemblage" (units 8-9).

When Mamay and Watt collected in 1969, the lower pit was inactive and attention was focused on the fresh material being exposed daily in the upper pit. Nonetheless, the lower beds—presumably equivalent to the present units 2-7 of Lucas & Huber—were sufficiently exposed that extensive sampling was possible (see Fig. 1). Abundant plants occurred there, with conspicuous representatives of *Neuropteris, Sphenopteridium,* and particularly *Dicranophyllum.* These beds also contained the epiplanktonic *Dunbarella* material mentioned earlier. Calamiteans and *Walchia* were present but not abundant. The underlying basal micrite produced only a few plant fragments; however, one of these was a small specimen of *Walchia* sp., establishing a lower range limit for the conifers at the Kinney site.

The upper pit was then being excavated for the predominantly tan and olive shales and siltstones that are thought to have been the approximate equivalents of Lucas & Huber's units 8, 9, and possibly 10. Plants were less abundant

FIGURE 1—View of the Kinney Quarry ("lower pit") photographed in May 1969. Arrow at right indicates location of D. H. Dunkle's "fish quarry"; arrow at left indicates the approximate highest level from which Mamay and Watt obtained plant fossils. The vehicles are parked on the highly fossiliferous fissile dark-gray shale immediately overlying the fish beds.

than in the lower shales, but nonetheless were frequent and often better preserved. All the taxa discussed here were present in those beds. *Sphenopteridium*, *Dicranophyllum, Neuropteris,* and *Walchia* were prominent, with *Neuropteris* and *Walchia* sharing dominance. There was no apparent segregation or concentration of taxa. Plants tended to occur in small, discontinuous pockets of mixed taxa. *Dunbarella* shells were closely associated with most plants and included both large and small individuals; small ones seemed more predominant toward the top of this interval. The highest occurrence of plants was observed in a thin (to 10 cm) series of very thinly bedded, highly fissile, tan silty shales with prominent Liesegang banding. These beds contained abundant *Neuropteris,* conspicuous *Calamites* stems and foliage, and only rare *Walchia* and *Pecopteris; Dunbarella* was absent.

On the basis of the Mamay-Watt collection, it was apparent that most of the plant taxa were long-ranging in the Kinney section, with essentially uninterrupted distributions. Their variable densities are not clearly correlative with lithologies or position within the rock section. Any inconsistencies between the Lucas & Huber (1991) observations and those presented here probably reflect spatial heterogeneity revealed by retreating rock faces exposed by more than 20 years of intermittent mining operations. The discrepancies between the early and recent floristic observations suggest that definition of a floral zonation within the Kinney section would be premature.

An unusual biotic association

There are probably many types of ecological interactions preserved in an assemblage as taxonomically diverse and physically compact as the Kinney biota. One presently obvious and spectacular example is that involving *Dunbarella* shells preserved in direct juxtaposition with plant material. Several specimens in the USNM collection strikingly demonstrate this association.

These are mostly leaf fragments of *Neuropteris ovata* (e.g. Fig. 4A); also noted are an unidentified plant axis with many shells arranged along one side as though in a preferential distribution (Fig. 6B), and a single pinna of *Charliea* with a lone shell positioned with its byssal area in contact with the *Charliea* lamina (Fig. 9D). One of the better examples, shown in Fig. 4A, consists of several articulated pinnae of *Neuropteris ovata* with many *Dunbarella* valves lying in contact with the foliar lamina. The shells are mostly small (4 to 8 mm in greatest dimension), with only one large shell appearing on this specimen. Isolated shells are not evident in the surrounding matrix of this bedding surface. None of the other plant taxa have been seen with juxtaposed *Dunbarella* shells, although examples of close association are abundant and plant parts may be surrounded by numerous shells on very thinly separated bedding layers (Fig. 6A).

Archer & Clark (1991: 3) regard the Kinney *Dunbarella as* ". . . an opportunistic colonizer of floating or bottom-dwelling vegetation, much like the modern kelp scallop, *Leptopecten latiauratus* . . . ," and the modern scallop was described by Clark (1978: 380) as ". . . settling favorable sites in enormous numbers and growing to maturity in only a few months." There can be little doubt that the dunbarellas were bysally attached to, and preserved in growth positions on, the plant structures. The two ecologies—modern and fossil—involve parallel situations, except that a presumably dead, terrestrially derived supporting substrate (notably *Neuropteris)* and a living aquatic colonizer *(Dunbarella)* were involved in the Kinney association, whereas both substrate and colonizer are living aquatic organisms in the case of *Leptopecten.*

The *Dunbarella-laden* leaves probably had been shed not long before being introduced into the Kinney lagoon and were still afloat when the *Dunbarella* spat settled thereon; the plant axis with shells apparently preferentially arranged along one side (Fig. 6B) was likewise probably afloat, with spat attaching themselves on the submerged side, to result in the illustrated distribution. The plant material deteriorated very slowly while the dunbarellas grew quickly, resulting in fairly well-preserved plant fossils with mostly small shells attached. This process of colonization was obviously accomplished in a very quiet depositional setting.

An intriguing aspect of this plant-animal association derives from the almost total absence of *Dunbarella* shells on plant remains other than *Neuropteris ovata;* presumably all plant specimens were equally exposed to colonization by *Dunbarella,* yet only the *Neuropteris* seemed to attract the mollusks. A similar example of substrate selectivity, involving *Spirorbis* tubes adherent exclusively to foliage of *Tinsleya texana* in a flora containing several other plant species, was described by Mamay (1966) from the Permian of Texas. This preferential distribution was attributed to some unknown characteristic of gaseous decay products that was both unique to *Tinsleya* in that flora and attractive to the spirorbids. It is probable that a similarly attractive quality of the neuropterid decay products can explain the colonization of *Neuropteris* by *Dunbarella,* to the evident exclusion of most other floral elements.

Comparisons with similar occurrences

With the exceptions of the abundant *Sphenopteridium,* the unique *Charliea,* the rare *Plagiozamites,* the unusual *Dicranophyllum,* and the very problematical *Podozamites-like* specimen, the Kinney flora shares several taxa with other North American and European assemblages of Late Pennsylvanian or earliest Permian age; some of these are summarized in Table 1. The walchian conifers are conspicuous in each of these assemblages and usually represent dominant elements. While very abundant at the Kinney site, however, the conifers seem to have shared dominance with the neuropterid pteridosperms. The prominence of conifers, along with the sparse representation of pteridophytes, is consistent with the absence of coal (Mapes & Gastaldo, 1986) and suggests that water stress was a strong factor in the Kinney paleoenvironment. Salinity fluctuations may also have influenced the characteristics of faunal assemblages in these deposits (Table 1).

Other gymnosperms in the Kinney flora include a very minor representation of *Cordaites,* along with the pteridosperms *Odontopteris* (rare), *Sphenopteridium* (abundant), and *Neuropteris* (very abundant). These are predominantly coal-swamp and clastic-sediment inhabitants (Scott, 1979, 1980). Although individual species occur in varied associations, their ecologic tolerances are not fully known. That *Neuropteris* and *Sphenopteridium* both occur throughout the Kinney section indicates a certain degree of ecologic versatility. *Odontopteris* is evidently equally rare at the other sites considered here. It probably was an inconspicuous element in those floras, and is mentioned here chiefly because it was sufficiently common in parts of the Appalachian Pennsylvanian that it was considered a useful stratigraphic guide fossil by Read & Mamay (1964). The same can be said of the fertile pecopterid fern *Danaeites,* which makes its westernmost known appearance in the Kinney flora.

The genus *Callipteris* Brongniart, a gymnosperm recorded from the other North American and the Saar-Nahe floras, is absent from the Kinney assemblage. Conifer-rich late Paleozoic deposits commonly contain one or more species of *Callipteris,* and it has been identified at the other sites considered here (Table 1). The genus is known from early Abo deposits (Wolfcampian, Permian) south of Jemez Springs, New Mexico (Read & Mamay, 1964), but if it was established in the Manzanita area by Virgilian time, its presence there has not been detected.

TABLE 1—Common biotic features occurring in three or more of five selected late Paleozoic conifer-rich biotas, derived from personal observations and literature, including: Ash & Tidwell, 1982; Haubold, 1983; Kerp & Fichter, 1985; Lucas & Huber, 1991; Mapes & Gastaldo, 1986; Mapes & Mapes, 1988.

	KINNEY, TIJERAS, NM Pine Shadow Mbr. Wild Cow Fm. Late Pennsylvanian	CARRIZO ARROYO, NM Red Tanks Mbr. Madera Fm. Late Penn./Early Permian	HAMILTON, KS in Topeka Limestone Shawnee Group Late Pennsylvanian	GARNETT, KS Rock Lake Shale Mbr. Stanton Limestone Fm. Missourian Late Pennsylvanian	GERMANY, EUROPE Unterrotliegendes Saar-Nahe Lauterecken-Odernheim Schichten, L-03 Early Permian
GYMNOSPERMS					
conifers	Walchia spp.	Walchia spp.	Walchia spp.	Walchia spp.	Walchia spp.
cordaites	Cordaites sp.	Cordaites	Cordaites	Cordaites	Cordaites
seed ferns	Sphenopteridium	Sphenopteris	Sphenopteris		
	Neuropteris	Neuropteris	Neuropteris	Neuropteris	Neuropteris
	Odontopteris	Odontopteris	Odontopteris		Odontopteris
	*Unique taxa (see text)	Callipteris	Callipteris	Callipteris	Callipteris
PTERIDOPHYTES					
ferns	Pecopteris			Pecopteris	Pecopteris
lycopsids	Sigillaria		Sigillaria	Sigillaria?	
sphenopsids	Calamites				Calamites
	Annularia	Annularia	Annularia	Annularia	Annularia
	Asterophyllites	Asterophyllites	Asterophyllites		Asterophyllites
INVERTEBRATES					
	molluscs	molluscs	molluscs	molluscs	
	eurypterids	eurypterids	eurypterids	eurypterids	
	spirorbids	spirorbids	spirorbids		
	ostracods		ostracods		ostracods
	brachiopods	brachiopods	brachiopods	brachiopods	
	insects	insects	insects	insects	insects
VERTEBRATES	tetrapods	no data	tetrapods	tetrapods	tetrapods
	acanthodians		acanthodians		acanthodians
	palaeoniscids		palaeoniscids		palaeoniscids

Significance of the Kinney flora

This flora is important from the standpoint of its extraordinary variety of taxa, particularly when considered in the context of the very restricted geographic area and the thin stratigraphic interval involved; few Paleozoic plant localities entail as compact a population with comparable taxonomic variety. Here the potential exists for future detailed systematic studies of several plant groups and their responses to environmental conditions.

Biostratigraphic anomalies enhance the interest of the Kinney flora. A prime example is the "late" appearance of *Sphenopteridium.* This marks a notable upward extension of the known stratigraphic range of this predominantly Mississippian genus, which has been useful as a guide fossil for Upper Mississippian rocks in parts of the Appalachian and Midcontinent regions (Read & Mamay, 1964).

More important, however, is the abrupt appearance in the Kinney flora of plants that are both morphologically incongruous and biochronologically anachronistic with more "normal" Pennsylvanian foliar assemblages. These plants-*Charliea manzanitana, Plagiozamites planchardii,* and the *Podozamites-like* specimen—possess compound or pseudocompound foliar architecture with parallel ultimate venation reminiscent of the Permian *Russellites,* Mesozoic cycadophytes, or the Mesozoic conifers. While *Plagiozamites* had a circumboreal distribution, it is known largely from Permian or early Mesozoic occurrences in the Eastern Hemisphere; the Kinney occurrence is noteworthy as only the second credible Paleozoic occurrence in North America. *Charliea,* however, is known from no occurrence other than the Kinney site, nor are there any clues as to its ancestry.

Dicranophyllum readii, with its simple dichotomous laminar morphology, resembles not only *Dicranophyllum* but also the South African Triassic species *Sphenobaiera pontifolia,* providing some grounds for speculation regarding a Gondwana lineage in the Kinney flora. Perhaps the present taxonomic assignment of the plant should be reassessed. Whether it be a true *Dicranophyllum* or a *Sphenobaiera,* however, the Kinney plant is strangely unique by virtue of the enormous size of its leaves, which recalls the foliar gigantism displayed by *Evolsonia* from the Early Permian of Texas (Mamay, 1989). Both ancestry and progeny of this taxon, like those of *Charliea,* are unknown.

Any of the foregoing plants, if found singly in a "normal" Pennsylvanian flora, would evoke surprise; that they all occur together is truly astonishing. Collectively they seem to reflect a precocious and geologically sudden evolutionary insurgence that produced foliar differentiations ". . . presageful of the Early Mesozoic floras .....(Mamay, 1990: 865). Therein lies the greatest significance of the Kinney flora.

Acknowledgments

We are indebted to R. M. Bateman, W. A. DiMichele, G. W. Rothwell, and M. L. Trivett for their thorough, thoughtful, and expeditious reviews of the manuscript. Informal discussions with **J.** T. Dutro, Jr. and D. A. Willard were also helpful. Jiri Zidek kindly lent us CM specimens, with the approval of David Berman, and Phillip Huber placed at our disposal some NMMNH material that he had collected. S. R. Ash corroborated certain historical details, and Sherri Myer and R. H. Mapes assisted with preparation of

Table 1. We are particularly grateful to J. P. Ferrigno, who prepared all the fossil photographs. This study was partially supported by Ohio University Baker Fund and Research Committee (#9783) awards to Mapes, and by National Science Foundation grants BSR 86-00660 and EAR 8903792.

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Figures 2-9

FIGURE 2

All figures natural size unless otherwise indicated

A, *Sigillaria brardii* Brongniart. Bark fragment showing several vertically elongate leaf scars. USNM 450764, x 2.

B, Undetermined aggregate of acuminate foliose structures, probably lycopsid. USNM 450765, x 2.

C, *Calamites cistii* Brongniart. Segment of a large stem showing one node. USNM 450766.

D, *Annularia* cf. *radiata* (Brongniart) Sternberg. Two foliate branchlets, each with several leaf whorls. USNM 450767, x 2.

E, *Annularia* cf. *asteris* Bell. Branch segment with three whorls of branchlets, each bearing several leaf whorls. USNM 450768, x 2.

F, *Annularia* cf. *pseudostellata* H. Potonié. Axis with several leaf whorls. USNM 450769.

G, *Annularia sphenophylloides* (Zenker) Gutbier. Axial fragment with a single leaf whorl. USNM 450770, x 2.

H, *?Asterophyllites* sp. Calamitean stem segment bearing several very thin branches with extremely small whorls of *?Asterophyllites* leaves (below); above are portions of two poorly preserved cones. USNM 450771.

I, *Calamostachys? ludwigii* Weiss. Series of small cones. USNM 450772.

J, *Calamostachys? pedunculata* Weiss. Large, compact cone. USNM 450773.

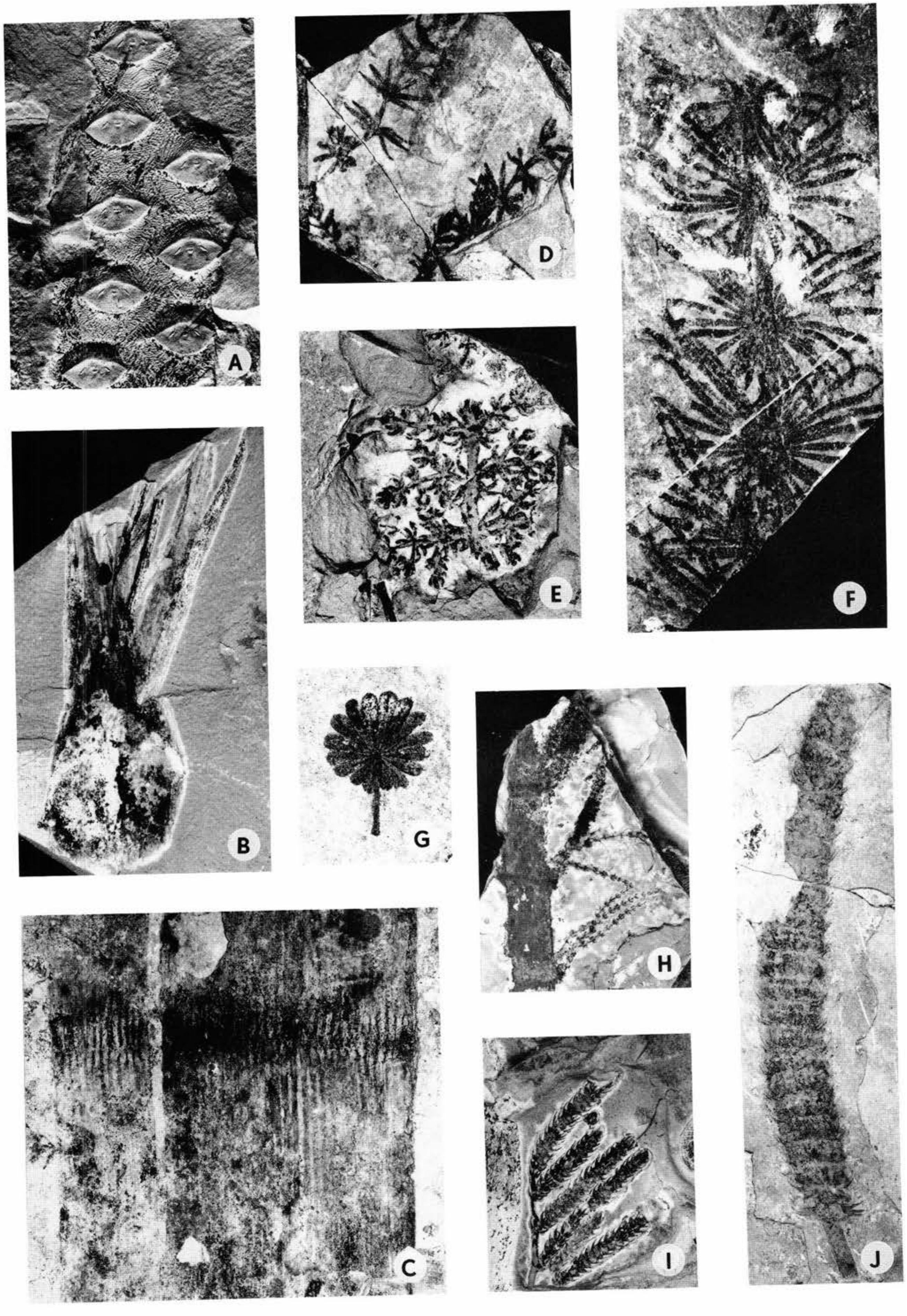
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FIGURE 3

All figures natural size unless otherwise indicated

A, B, G, *?Pecopteris* sp. A, Part of ultimate pinna with several pinnules. Note constricted pinnule bases, variably crenulate margins, and many groups of narrow, pointed sporangial remains, some extending across pinnule margins into the matrix. USNM 450774, x 4. B, Penultimate pinnule showing lax arrangement of pinnae and pinnules, and alloiopteroid appearance of pinnules. USNM 450775. G, Several pinnae; some pinnules, particularly at bottom left, showing submarginal rows of circular objects suggestive of *Asterotheca* synangia. USNM 450780.

C, Danaeites emersonii Lesquereux. Several pinnae with fertile pinnules showing densely arranged linear synangia. USNM 450776.

D, Aphlebia sp. Fragmentary specimen showing deeply pinnatifid lamina. USNM 450777.

E, Odontopteris sp. Terminal portion of a pinna. USNM 450778.

F, Pecopteris feminaeformis (Schlotheim) Sterzel. Several pinnules showing simple, acute ultimate veins terminating in marginal denticulations of tapering, pointed pinnule laminae. USNM 450779, x 4.


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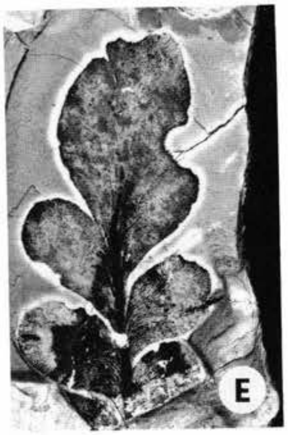
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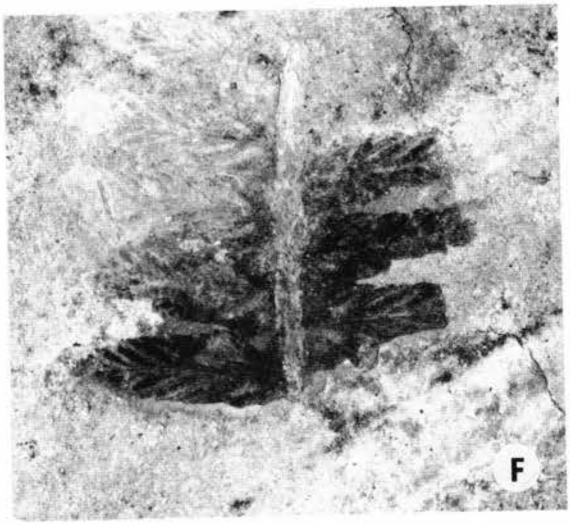
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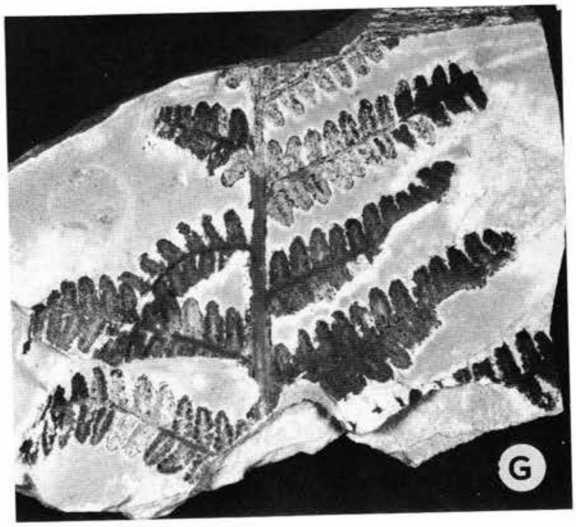
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FIGURE 4
All figures natural size

A, C—E, Variable foliage of *Neuropteris ovata* Hoffman. In A, note the many *Dunbarella* shells positioned directly on the leaf. A, USNM 422631; C, USNM 450781; D, USNM 450782; E, USNM 450784.

B, *Neuropteris* pinna fragment; the rounded, widely spaced and narrowly attached pinnulation is suggestive of *N. heterophylla* Brongniart. USNM 450783.

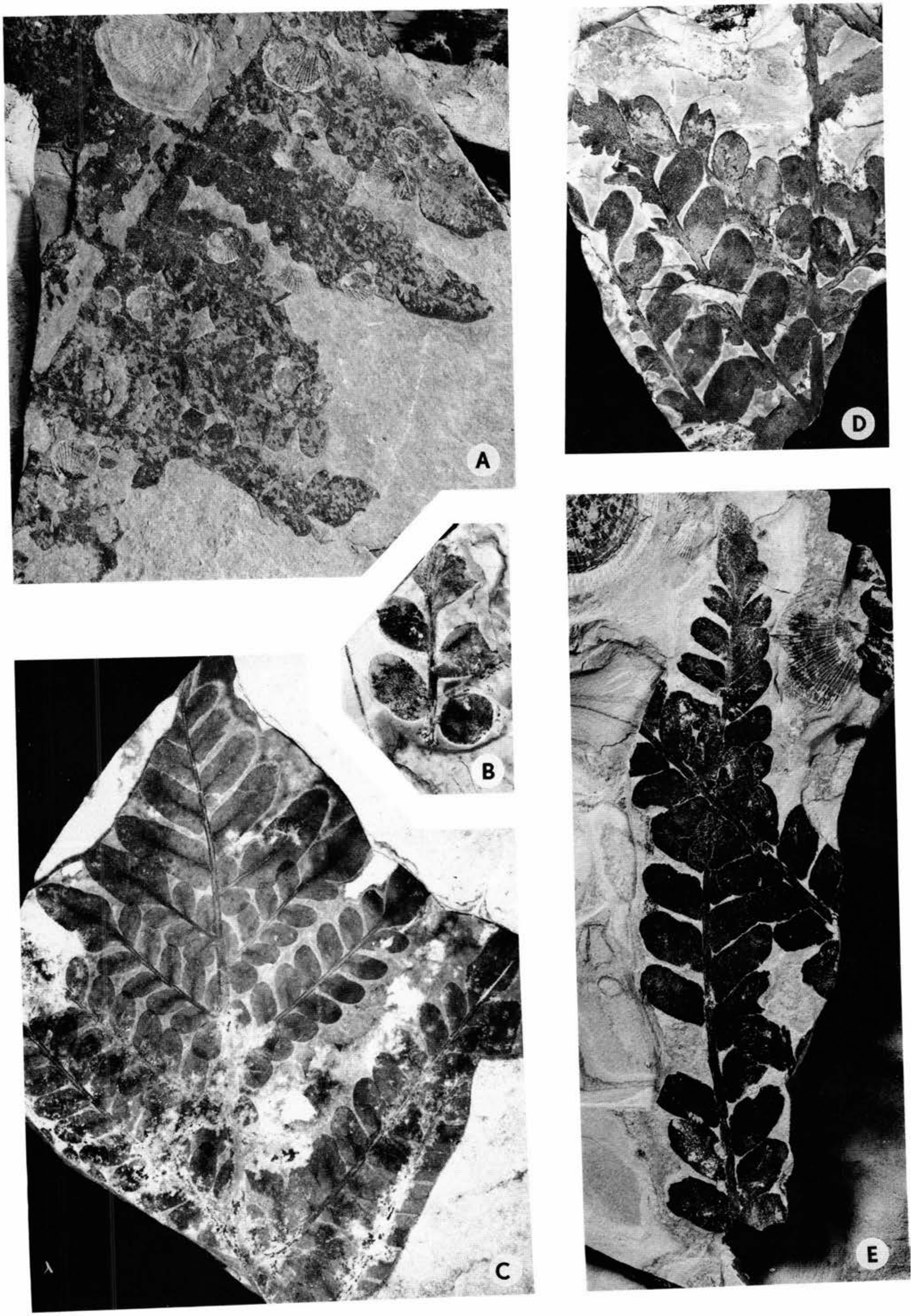
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FIGURE 5

All figures natural size unless otherwise indicated

A, Axis presumed to be a neuropterid rachis, the "stubs" representing pinna rachises. USNM 450785.

B, Incomplete pinnule of *Neuropteris scheuchzeri* Hoffman. USNM 450786.

C, Pinnule of *Neuropteris scheuchzeri,* showing a cyclopteroid basal pinnule. USNM 450787.

D, E, *Neuropteris* sp. (cf. *N. macrophylla* Brongniart). D, USNM 450788; E, USNM 450789.

F, Leaflet of *Cyclopteris* sp. USNM 450790.

G, Cast of ovule of *Trigonocarpus* sp. USNM 450791, x 2.

H, ?Neuropteris sp. (cf. *N. obliqua* [Brongniart] Zeiller). USNM 450792.

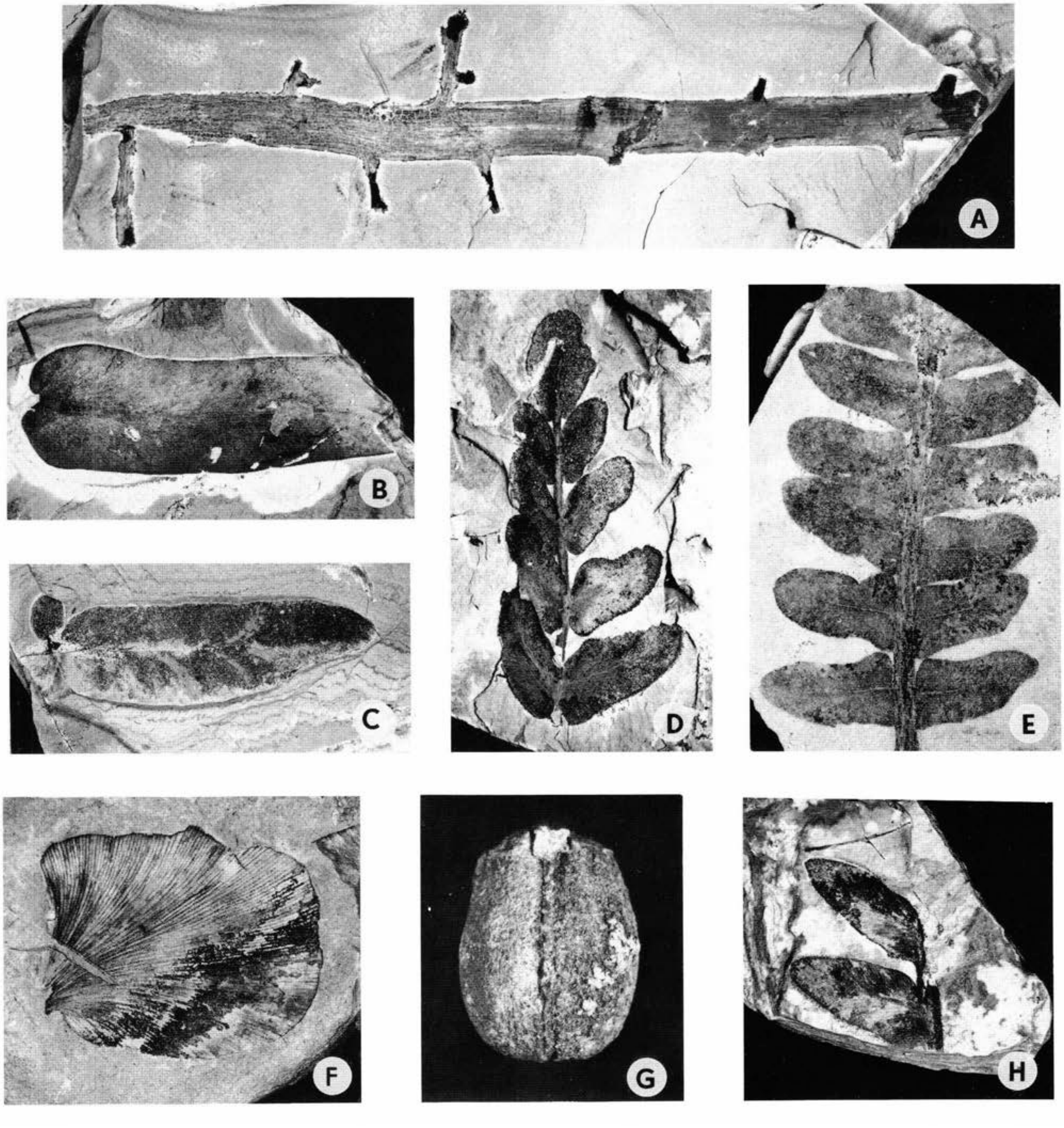
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FIGURE 6

All figures natural size unless otherwise indicated

A, C—E, *Sphenopteridium* sp. A, Single pinna showing the deep pinnule lobation characteristic of the species. Note the several large associated *Dunbarella* shells. USNM 450793. C, Parts of three pinnae; pinnules show the open dichotomous venation. USNM 450794, x 2. D, Part of frond showing division of petiole into equal rachises and large pinnae produced below the point of dichotomy. USNM 450795. E, Frond showing equally bipartite architecture, long petiole, and petiolar pinnae. USNM 450796, x 0.8.

B, Unidentifiable plant axis with many small *Dunbarella* shells associated, probably in growth positions along the lower surface of the axis. USNM 422632.

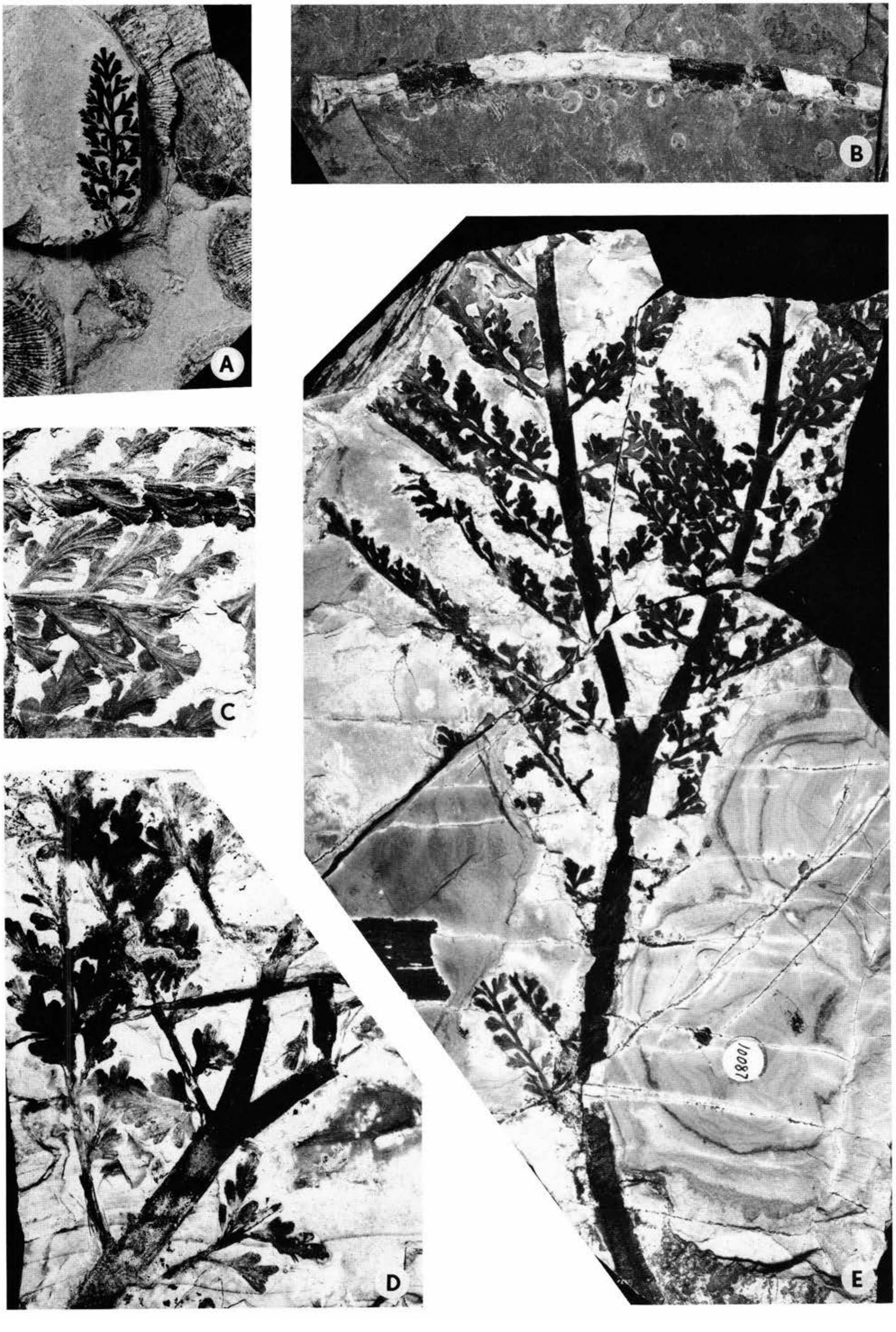
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FIGURE 7

All figures natural size unless otherwise indicated

A, B, Platyspermic cordaitean ovules *(Samaropsis* sp.) showing broad, circular wing. A, USNM 450797, x 2; B, USNM 450798, x 2.

C, Cordaianthus sp. Cordaitean fertile axis with several bilaterally arranged dwarf shoots. USNM 450799, x 2.

D, Cordaites sp. Basal portion of a leaf with split lamina; note concave configuration of leaf base. USNM 450800.

E, F, *Dicranophyllum readii* Mamay. E, Distally incomplete leaf showing the enlarged base, the initial dichotomy, and dichotomy of the resultant laminar segments. USNM 267281, x 0.35. F, Leaf fragment showing two orders of dichotomy. USNM 267283, x 0.95.


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FIGURE 8

All figures natural size

A—C, F, *Walchia piniformis* (Schlotheim) Sternberg; examples of variability within this species. F illustrates an unusual specimen with apparently young, pendent leafy shoots, preserved in different stages of development. A, USNM 450803; B, USNM 455002; C, USNM 450804; F, USNM 455004.

D, Walchia cf. *schneideri* Zeiller. Leafy axial fragment with long, lax leaves. USNM 455001.

E, Gomphostrobus sp. Single bifid leaf. USNM 455003.

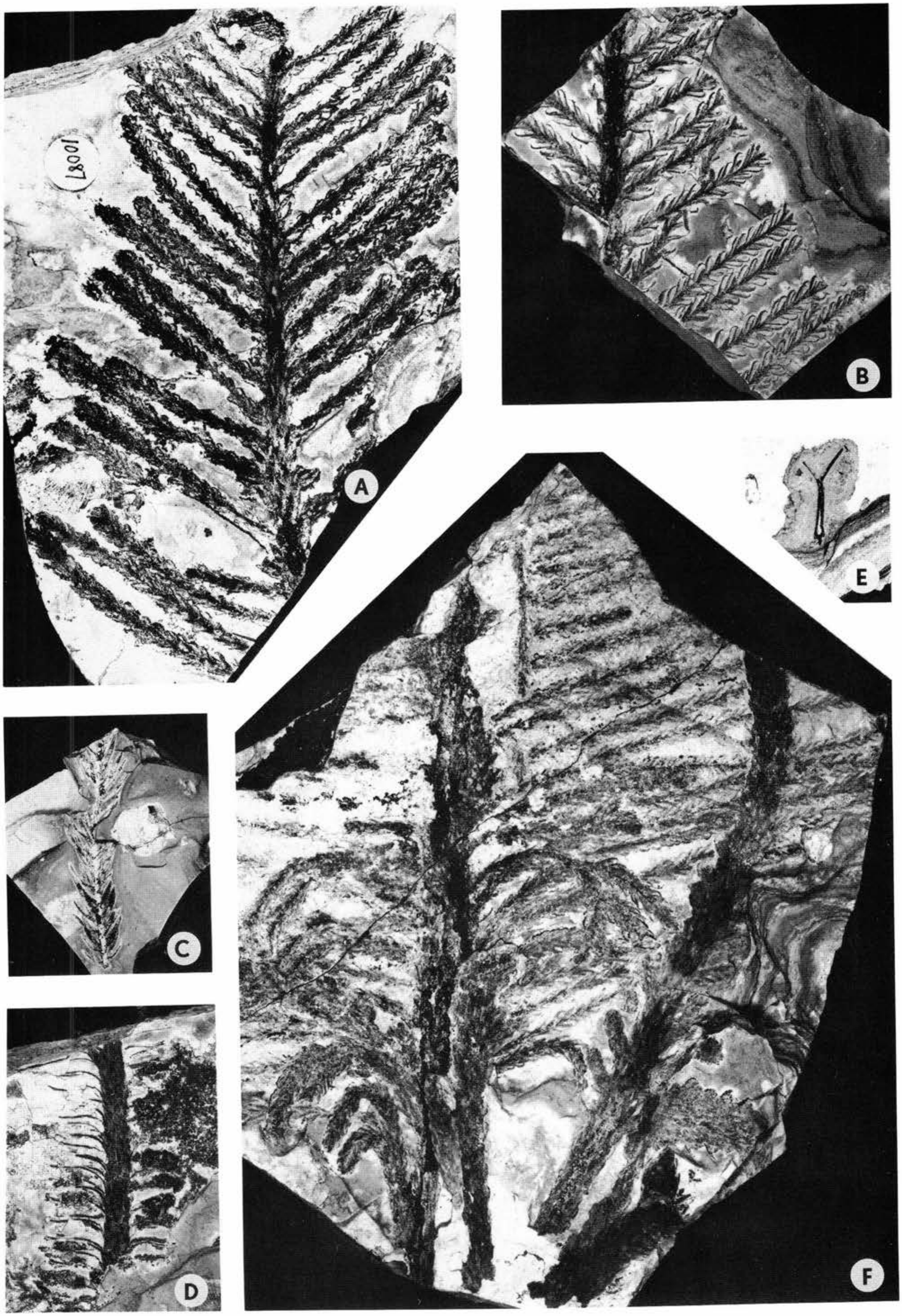
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FIGURE 9

All figures natural size unless otherwise indicated

A, *Plagiozamites planchardii* (Renault) Zeiller. Frond fragment, showing parallel-veined pinnae. USNM 422621.

B, *Charliea manzanitana* Mamay. Frond fragment, showing parallel-veined pinnae with truncated, deeply incised tips. USNM 422628.

C, *Charliea manzanitana.* Single pinna, showing parallel, open venation and trilobate tip. USNM 422623, x 3.

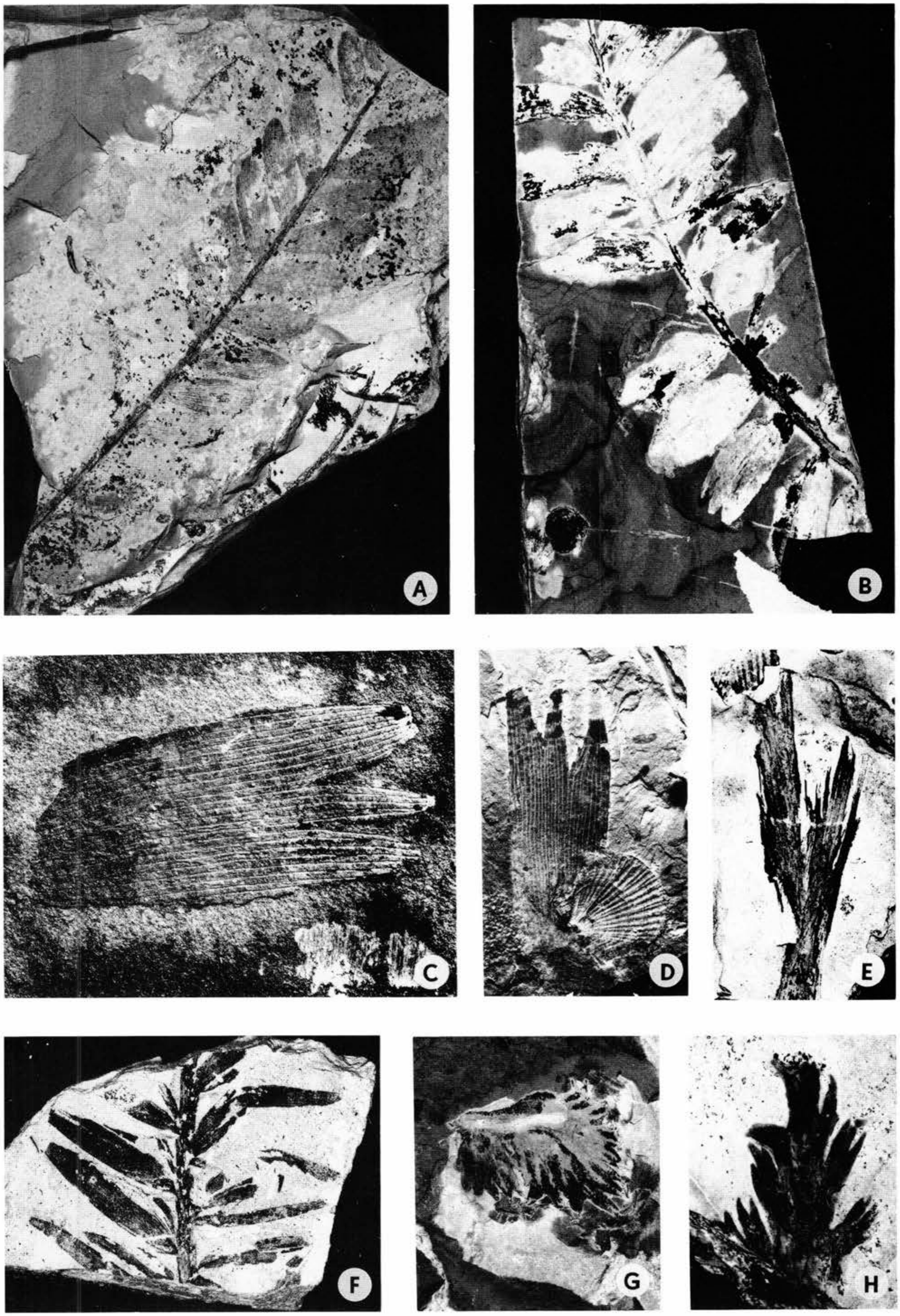
D, *Charliea manzanitana.* Single pinna with unequally trilobate tip and superimposed *Dunbarella* shell. USNM 422625, x 2.

E, Problematical foliose structure with deep, narrow, marginal laciniations. USNM 450901, x2.

F, Problematical foliate axis, reminiscent of a cycad-like frond or a *Podozamites-like* leafy conifer shoot. USNM 422630.

G, Problematical epaulette-like structure, reminiscent of *Crossotheca.* NMMNH P-14413 (Huber collection), x 2.

H, Problematical foliose structure with deeply incised margins. USNM 450802, x 2.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A Late Pennsylvanian restricted-marine fauna from the Kinney Quarry, Manzanita Mountains, New Mexico

Barry S. Kues

Department of Geology, University of New Mexico, Albuquerque, New Mexico 87131-1116

Abstract—The basal, dark-gray, argillaceous limestone forming the floor of the Kinney Quarry contains a Late Pennsylvanian marine fauna that is dominated by the inarticulate brachiopod *Lingula carbonaria* and the pelecypods *Solemya* and *Myalina.* These genera comprise about 57% of the total abundance of specimens sampled. Important subsidiary members of this fauna (each representing 4 to 9% of total abundance) include conchostracans, unornamented ostracodes, the pectinacean pelecypod *Dunbarella,* the ammonoid *Prothalassoceras,* and the articulate brachiopod *Chonetinella flemingi.* Typical stenohaline inhabitants of Pennsylvanian offshore marine environments (e.g. fusulinids, corals, echinoderms, bryozoans, and most articulate brachiopods) are sparse or absent. The dominant genera in this fauna were salinity-tolerant *(Lingula, Myalina)* or preferred low oxygen concentrations and probably high levels of dissolved organic matter *(Solemya),* based on the ecology of modern representatives or analogues and on Pennsylvanian occurrences of these taxa elsewhere. The relatively high percentages of articulated *Lingula* and pelecypod valves, lack of significant shell fragmentation, and preservation of delicate spines on some specimens of *Chonetinella* indicate quiet conditions and little, if any, post-mortem transport. Fragments of plants and fishes (common in the overlying nonmarine units), much disseminated organic material, siliciclastic sediments, and maybe conchostracans and ostracodes were derived by possibly seasonal influx from a nearby vegetated, prograding delta complex, which composes the overlying strata at the quarry. The basal-limestone fauna contains only a small proportion of stenohaline benthic organisms, and very few benthic browsers/detritus-feeders and infaunal deposit-feeders. Taken together, the composition of the fauna and other observations noted above suggest a nearly normal-marine environment that was subject to fluctuating salinity and reduced circulation, with depleted oxygen and elevated levels of organic material near the substrate. Deposition of the basal limestone in a bay or lagoon that experienced progressive restriction as a prograding delta advanced toward and around it is consistent with this paleoenvironmental interpretation. A perplexing, unidentified, soft-bodied, worm-like fossil from the top of the basal limestone is illustrated.

Introduction

A fossiliferous sequence of Upper Pennsylvanian strata about 28 m thick is exposed at the Kinney Quarry, Bernalillo County, New Mexico. Most of this sequence consists of tan to gray shale, claystone, and siltstone from which a variety of terrestrial plants, nonmarine invertebrates, fishes, and amphibians have been collected (Lucas & Huber, 1991; Kues & Lucas, this volume; see also other papers in this volume). However, the basal unit is a dark-gray to black argillaceous limestone containing a restricted-marine fauna discussed briefly by Kues (1990). The purpose of this paper is to provide more detailed information concerning the composition and paleoecology of this fauna. Comprehensive taxonomic description of the fauna is not pursued here; instead, the main intention is to illustrate the most important brachiopod and bivalve species and to provide sufficient descriptive information to justify the identifications. All specimens discused here are in the paleontology collections of the Department of Geology, University of New Mexico (UNM).

Location and stratigraphic setting

The Kinney Quarry is located along the west side of New Mexico Highway 337 (formerly NM-14 south), 13 km south of the town of Tijeras (Fig. 1). The section in the quarry is part of the Pine Shadow Member of the Wild Cow Formation, Madera Group. The entire member has an average thickness of about 70 m in the Manzanita/Manzano Mountains, and has been reliably dated as early to middle Virgilian on the basis of fusulinids described from localities elsewhere in these mountains (Myers, 1973, 1988). However, no fusulinids have been found in the Kinney Quarry strata.

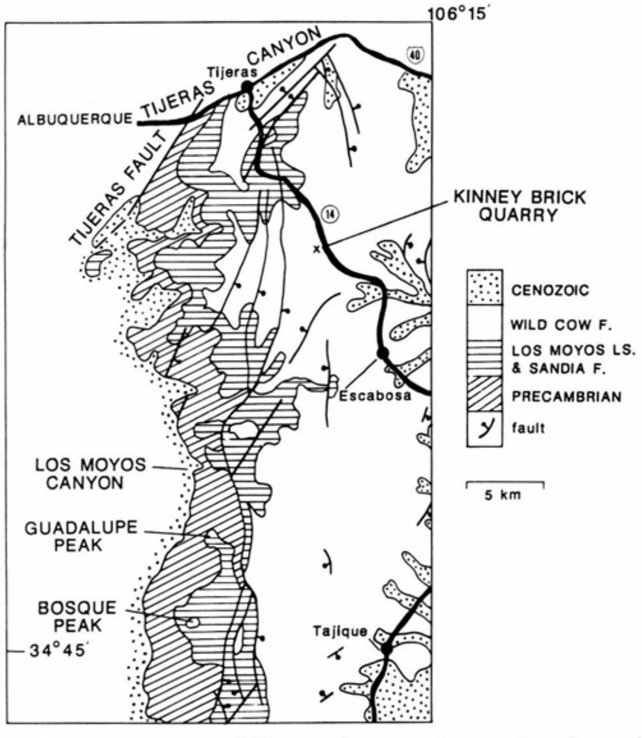

FIGURE 1—Location of Kinney Quarry and general geology of Manzanita Mountains (from Lucas & Huber, 1991).

The dark limestone containing the marine fauna discussed here forms the floor of the quarry and is the basal unit (unit 1) of the stratigraphic section exposed in the quarry (Kues & Lucas, this volume). Total thickness of this limestone unit is not known; it does not crop out significantly in areas immediately around the quarry. About 0.5 m is exposed in the quarry, and the upper 20 to 30 cm are widely present there. The limestone is a hard, dense, splintery, dark-gray to black, argillaceous micrite rich in organic material and producing a faintly fetid odor when broken. It becomes platy to laminated and less calcareous through a 10 cm thick transitional zone (unit 2), above which the lithology becomes a soft, fissile, brown to gray shale with little calcium carbonate. Most of the characteristic marine invertebrates of the basal limestone disappear rather abruptly through the transition zone.

Sampling and preservation

The upper part of the limestone was sampled for fossils across an area of approximately 400 m^2 along the floor of the eastern ("upper") part of the quarry. All fossils observed in the field were collected and samples were examined further in the laboratory. Specimens were identified, counted, and their relative abundance determined. The conclusions and interpretations presented in this paper are based upon examination of nearly 1000 specimens. A much larger sample could have been easily obtained; however, although additional rare taxa might have been discovered, it is doubtful that the relative-abundance figures for various taxa reported here would change significantly with increased collecting.

Most of the bivalves are preserved as molds, with the exception of *Myalina* and *Dunbarella*, which typically retain shells in a reasonably good state of preservation. Ammonoids and nautiloids are almost invariably steinkerns, whereas all brachiopods, conchostracans, ostracodes, and other invertebrates are represented by their shells. Fragments of terrestrial plants and fish debris are moderately common in the limestone. The plants are typically broken stems and branches; little leaf material was preserved. Fishes are represented by isolated scales and by some disarticulated but dense accumulations of scales and bones consisting in some cases of several dozen elements. Nearly all of the major invertebrate taxa were preserved in an unbroken state, although small fragments constitute the entire record of some of the rarer brachiopods, crinoid stems, and bryozoans.

Composition of the fauna

The fauna of the basal limestone is moderately diverse; a list of identified taxa and their abundance in the sample is given in Table 1. No attempt was made to identify genera or species of ostracodes, conchostracans, cephalopods, fishes, or plants. The cephalopods from this unit were studied by Mapes (1991) and Mapes & Boardman (this volume).

Three different abundance measures for bivalved taxa are

TABLE 1—Abundance of taxa observed in the basal limestone (unit 1) at the Kinney Quarry. For bivalved taxa, counted articulated specimens also include slightly disarticulated but overlapping right and left valves. TS, total specimens; AS, articulated specimens; MI, minimum individuals; MEA, mean estimated abundance; FM, feeding method. For feeding methods, ISF, infaunal suspension-feeder; IA, infaunal absorber; ESF, epifaunal suspension-feeder; EDF, epifaunal browser or detritus-feeder; NS, nektonic carnivore. Abundance of fish and plant fragments and of spirorbid worms not tabulated.

Taxon	TS	AS	MI	MEA	%TS	%MI	%MEA	%AS	FM
Brachiopoda									
Lingula carbonaria	191	26	109	150	20.9	18.9	20.1	17	ISF
Chonetinella flemingi	33	33	33	33	3.6	5.7	4.4	100	ESF
Antiquatonia sp.	4	?	4	4	0.4	0.7	0.5	?	ESF
Linoproductus sp.	2	?	2	2	0.2	0.3	0.3	?	ESF
Composita subtilita	2	2	2	2	0.2	0.3	0.3	100	ESF
Derbyia sp.	1	?	1	1	0.1	0.2	0.1	—	ESF
Total brachiopods	233	—	151	192	25.5	26.1	25.7	—	—
Pelecypoda									
Solemya radiata	169	23	96	133	18.5	16.6	17.8	17	IA
Solemya trapezoides	45	27	36	41	4.9	6.2	5.5	66	IA
Myalina aff. *wyomingensis*	134	14	74	104	14.7	12.8	13.9	13	ESF
Dunbarella striata	58	4	33	46	6.4	5.7	6.1	9	ESF
Streblochondria? sp.	6	0	6	6	0.7	1.0	0.8	—	ESF
Clinopistha levis	3	?	3	3	0.3	0.5	0.4	—	ISF
Aviculopecten basilicus	2	0	2	2	0.2	0.3	0.3	—	ESF
Leptodesma (*Leptodesma*) sp.	1	0	1	1	0.1	0.2	0.1	—	ESF
Parallelodon? sp.	1	0	1	1	0.1	0.2	0.1	—	ESF
unidentified bivalves	21	—	21	21	2.3	3.6	2.8	—	—
Total pelecypods	440	—	273	358	48.1	47.1	47.8	—	—
Gastropoda									
Glabrocingulum (*Glabrocingulum*) sp.	8	—	8	8	0.9	1.4	0.9	—	EDF
high-spired, unidentified	3	—	3	3	0.3	0.5	0.4	—	EDF
Euphemites sp.	1	—	1	1	0.1	0.2	0.1	—	EDF
other unidentified	1	—	1	1	0.1	0.2	0.1	—	EDF
Total gastropods	13	—	13	13	1.4	2.3	1.5	—	—
Ammonoidea	42	—	42	42	4.6	7.3	5.6	—	NC
Nautiloidea	11	—	11	11	1.2	1.9	1.5	—	NC
Conchostraca	87	?	44	66	9.5	7.6	8.8	?	ESF
Ostracoda	86	?	43	65	9.4	7.4	8.7	?	EDF
Crinoidea (stems)	1	—	1	1	0.1	0.2	0.1	—	ESF
Bryozoa	1	—	1	1	0.1	0.2	0.1	—	ESF
Total	914	—	579	749	99.9	100.1	100.0	—	

included in Table 1: (1) total number of specimens includes each articulated specimen and each isolated valve, and represents the maximum possible number of individuals in the sample; (2) minimum number of individuals is the number of articulated specimens plus one-half the number of isolated valves, the assumption being that each pair of valves in the sample belonged to a single individual; (3) estimated mean abundance is the average of maximum and minimum abundances, based on the assumption that some pairs of isolated valves belonged to single individuals but that other individuals are represented by only one valve. This figure probably most closely approximates the true number of individual organisms that existed in the volume of sediments sampled. Organisms having a single shell, of course, have the same abundance figures in all three columns. For some bivalved taxa (e.g. pectinaceans) represented by few specimens, isolated valves were determined to be from different individuals based on size differences or preservation of only left valves, and the estimated mean abundance is the same as the number of specimens. Fragments of plants and fishes are not included in abundance estimates owing to difficulty in determining accurately how many individuals were represented. The few spirorbid worms observed attached to plant fragments were likewise excluded from abundance calculations. Ostracodes were probably undercounted because their tiny valves were not searched for as rigorously as remains of large organisms. Because of small size compared to other elements of the fauna, the biomass represented by ostracodes and conchostracans was relatively much smaller than their abundance figures would indicate. No conodonts were observed in this study, but their presence in the basal limestone was reported by Kelley & Northrop (1975), Krukowski (pers. comm. 1991), and Lehman (pers. comm. 1991). According to Lehman, the conodonts appear to be more similar to late Missourian than to early Virgilian forms.

The fauna of the Kinney Quarry basal limestone is dominated by the inarticulate brachiopod *Lingula* and the bivalves *Solemya* and *Myalina*. These genera comprise about 57% of the mean estimated abundance. Important subsidiary members of the fauna are conchostracans, unornamented ostracodes, *Chonetinella* (the only moderately common articulate brachiopod), *Dunbarella,* and small ammonoids. Stenohaline groups, such as corals, bryozoans, crinoids, fusulinids, and many articulate brachiopods, which are common to abundant in Late Pennsylvanian open carbonate-shelf environments of the Wild Cow Formation, are absent or poorly represented in the basal limestone at the Kinney Quarry. Bivalves compose about 48% of the estimated mean abundance in this fauna, with all molluscs totaling about 56%. Further discussion of modes of life and relationships between the taxa in this fauna are presented in the section on paleoecology. Brief descriptions of the major brachiopod, bivalve, and gastropod taxa are presented below.

Brachiopods

Lingula carbonaria Shumard 1858

Abundant *Lingula* valves (Fig. 2.1) attain a length of about 13 mm and have a mean length/width ratio of 1.56, based on 10 measured specimens. The beak is low and rather acute, and ornamentation consists of numerous fine (15/ mm near center of valve), concentric growth lines and obscure, fine radial striae. Shape of the posterior valve margin varies from rather pointed to blunt. The Kinney specimens are distinctly broader than typical examples of *L. carbonaria* from the Midcontinent (Dunbar & Condra, 1932) and Appalachian basin (Sturgeon & Hoare, 1968), which have length/ width ratios of about 1.65 to 1.85. Specimens with a relatively blunt posterior margin approach *L. kanawhensis* Price in shape. *Lingula carbonaria is* a broadly defined species, and the name has been applied to most lingulas reported from the Pennsylvanian of North America.

Antiquatonia sp.

A few incomplete pedicle valves (Fig. 2.2) with an extrapolated length of 35 to 45+ mm are assigned to *Antiquatonia* on the basis of strong radial and concentric ornamentation of about equal magnitude on the posterior part of the valve. Intersection of radial costae and concentric wrinkles forms prominent, evenly spaced, isolated nodes. The fragments available for study do not clearly show the complete valve marginal profile, spine distribution, or hinge-line features; thus, assignment to species was not attempted.

Chonetinella flemingi (Norwood & Pratten 1855)

Small chonetoids, by far the most common articulate brachiopods in the Kinney basal limestone, agree well with examples of *Chonetinella flemingi* from the Midcontinent. The pedicle valves (Fig. 2.3, 2.4) are relatively wide and short, the largest having a width of 12 mm and a length of 6.5 mm. This valve is marked by a relatively deep median sulcus beginning above the hinge line, and moderately steep lateral slopes. The hinge line bears about five spines on each side of the beak. These are typically oriented at an acute angle from the hinge line and are represented by spine bases, but on some specimens one or two spines several millimeters long are preserved. The valves are ornamented with fine, conspicuous radial lirae that are relatively widely spaced and are crossed by irregular concentric growth lines of about the same magnitude. About five or six lirae per millimeter were measured in the center of a valve near its anterior margin. The brachial valve is strongly concave.

The range of *Chonetinella flemingi* extends to about the Missourian—Virgilian boundary in the Midcontinent (Dunbar & Condra, 1932), and to the middle Conemaugh (mid-Missourian) in the Appalachian basin (Hoare & Sturgeon, 1984). The Kinney specimens thus represent an unusually late occurrence for the species. They are not significantly different from specimens (reported by Kues, 1985) collected from the Missourian Sol se Mete Member of the Wild Cow Formation, about 13 km south of Kinney Quarry. In that unit *C. flemingi* occurs with a wide variety of other articulate brachiopods and other stenohaline **invertebrates.**

Pelecypods

Clinopistha levis Meek & Worthen 1870

The few available specimens (Fig. 2.5, 2.6) are composite and internal molds that are partially embedded in the limestone matrix. The entire margin of these specimens is not exposed, but they display moderately high, acutely rounded, posteriorly situated beaks and a broadly convex, high anterior margin. Judging from the molds, the valves were strongly inflated. The visible portions of the Kinney specimens are similar in all respects to equivalent areas of the numerous type and other specimens of *Clinopistha levis* illustrated by McAlester (1968) and Pojeta (1988). In addition, internal molds, such as the lectotype illustrated by Mc Alester (1968: pl. 4/1), possess faint radial lirae across their surface, representing mantle muscle scars and tracks (Pojeta, 1988). The Kinney specimens display identical radial lirae.

The type specimens of *Clinopistha levis* are from the Carbondale Formation (Desmoinesian) of Fulton County, Illinois (fide Pojeta, 1988). The species ranges from the Desmoinesian to the top of the Missourian in Ohio (Hoare et al., 1979), and is present in the Wolfcampian of Nevada (Yancey, 1978).

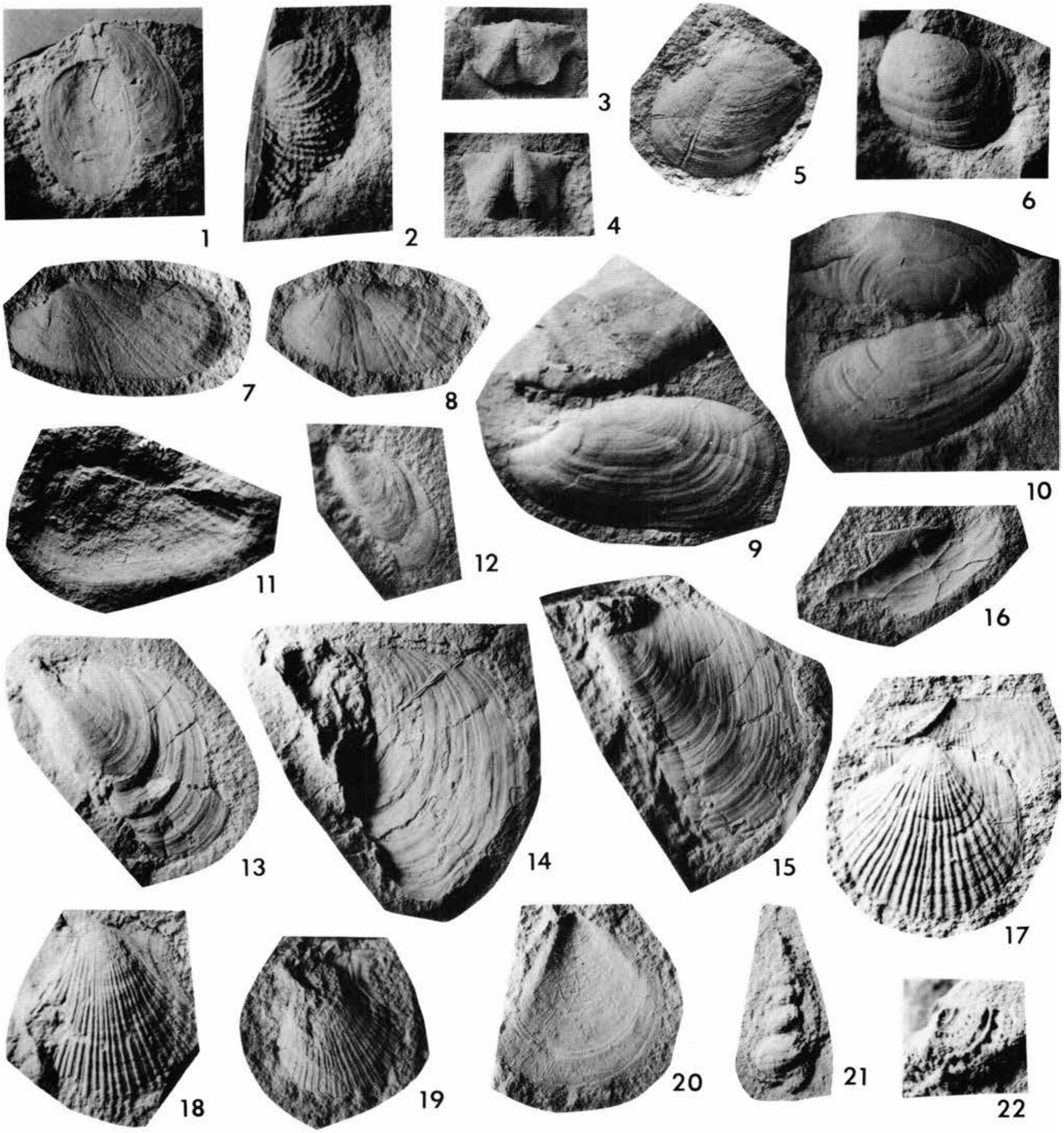

FIGURE 2—Virgilian invertebrates from the basal limestone (unit 1), Kinney Quarry. **1,** *Lingula carbonaria* Shumard, two overlapping valves, UNM 11126, ×2.5. **2,** *Antiquatonia* sp., posterior part of pedicle valve, UNM 11127, ×1.75. **3, 4,** *Chonetinella flemingi* (Norwood & Pratten), pedicle valves, UNM 11128 and 11129, respectively, both ×2. **5, 6,** *Clinopistha levis* Meek & Worthen, left valve view of composite mold, UNM 11130, and right valve view of composite mold, UNM 11131, both ×2. **7, 8,** *Solemya radiata* Meek & Worthen, right valve views of composite molds, UNM 11132 and 11133, respectively, both ×2. **9, 10,** *Solemya trapezoides* Meek, right valve view of composite mold articulated with part of left valve mold, UNM 11134, and composite molds of articulated left (lower) and right valves, UNM 11135, both ×1. **11,** *Paralellodon*? sp., concave, partially shelled external mold of right valve, UNM 11136, ×2. **12–15,** *Myalina* aff. *wyomingensis* (Lea); 12, external view of left valve of small specimen, UNM 11137, ×2; 13, external view of left valve, UNM 11138, ×1.5; 14, internal view of large right valve, UNM 11139, ×1.5; 15, external view of left valve, UNM 11,140, ×1.75. **16,** *Leptodesma* (*Leptodesma*) sp., internal (concave) view of incomplete left valve, UNM 11141, ×2.5. **17,** *Dunbarella striata* (Stevens), left valve partially overlapping internal surface of right valve, UNM 10964, ×2.5. **18, 19,** *Aviculopecten basilicus* Newell, partial left valves, UNM 11142, ×1.5, and UNM 11143, ×2, respectively. **20,** *Streblochondria*? sp., internal (concave) surface of outer layer of left(?) valve, UNM 11144, ×3. **21,** Unidentified high-spired gastropod (Kinney unit 3), UNM 11146, ×4. **22,** *Glabrocingulum* (*Glabrocingulum*) sp., mold of part of spire showing nodose subsutural ornamentation, UNM 11145, ×4.

Solemya radiata Meek & Worthen 1860

Solemya radiata (Fig. 2.7, 2.8) is abundant in the Kinney limestone unit, but is preserved only as composite molds. The valves are elongate and most are 15 to 25 mm long. Measurements of 30 specimens yielded a mean length/height ratio of 2.34 (range, 2.14 to 2.71), with maximum valve height a little in front of the beaks. The beaks are relatively low and are situated about three-quarters of the distance from the anterior to posterior end. A short posterodorsal margin is straight to slightly concave and slopes gently to the relatively blunt posterior margin. The anterior margin is typically higher and more broadly convex than the posterior margin. Dorsal and ventral valve margins are straight to very gently convex, and are subparallel for much of the length of the valve in front of the beaks. Ornamentation consists of numerous conspicuous fine grooves that radiate from the umbo across all parts of the valve. These grooves are typically rather widely but fairly evenly spaced, and are best developed across the center of the valve, beneath and a little anterior to the beaks. In this area, two or three pairs of unusually closely spaced grooves define narrow, low, flat, costa-like areas of the valve surface on many specimens. Growth annulations are inconspicuous compared with the radial ornamentation.

This species has been widely reported in the central and eastern United States, mainly from Desmoinesian and Missourian units (see Hoare et al., 1979, for synonymy; and Pojeta, 1988, for excellent illustrations). Variability in valve shape appears to be moderately high in the Kinney assemblage, but the species is nonetheless distinctive in shape and ornamentation, and is easily distinguished from the larger *S. trapezoides.*

Solemya trapezoides (Meek 1874)

This large bivalve is represented mainly by composite molds of open but articulated valves (Fig. 2.9, 2.10). It attains a maximum length of about 50 mm in the basal limestone, and length/height ratio varies from 1.92 to 2.20. The valves are compressed laterally, with the beaks situated about two-thirds of the distance from the anterior to posterior margins. Valve height increases anteriorly, and the anterior margin is high and bluntly convex. The posterior margin is lower and more acutely rounded than the anterior margin. A conspicuous arcuate groove extends along the base of the posterior umbonal slope, near the posterodorsal margin. Above this groove, the restricted posterodorsal region is a gently inflated, flange-like area marked by sharp, closely spaced growth lines. In addition, a shallower groove extends posteroventrally from the beak through the center of the umbo on the valve molds, reflecting the position of a low, internal valve ridge. Relatively strong, low, concentric wrinkles are conspicuous across most of the external surface of the valves. A few faint radial lirae were observed near the posterior end of some valves, but conspicuous radial ornamentation, such as characterizes *S. radiata*, is absent. *Solemya radiata is* also much smaller, more elongate, and possesses more posteriorly situated beaks than *S. trapezoides.*

Parallelodon? sp.

The single, incomplete specimen (Fig. 2.11) includes part of the shell preserved with its external surface down against the matrix and a partial external mold where the shell has flaked off the rock. The valve is elongate, relatively wide, about 19 mm in length, and bears more than 30 broad costae that radiate from the umbo to the anterior, posterior, and ventral margins. These costae are strongest across the anterior and posterior ends of the valve, becoming faint in the center. The radial costae are crossed by finer, more closely spaced growth lines. The hinge area and beaks are not preserved, but the presence of an elongate, flattened posterodorsal area seems indicated by a change in valve profile at the posterior end of the preserved shell material. The incomplete nature of this specimen prevents positive identification.

Myalina aff. wyomingensis (Lea 1853)

Myalinids are common in this assemblage (Fig. 2.12-2.15), but nearly all valves are embedded in the hard matrix to the extent that it is difficult to determine the nature of the beak, anterior end, and anterior margin of the valves. The largest valves are estimated 35 to 40 mm along their maximum dimension near the anterior margin, with the hinge length approximately two-thirds of the maximum dimension. The valves are prosocline and subtriangular, with the umbonal ridge meeting the hinge margin at an angle of about 65° in larger specimens (angle a of Newell, 1942). The umbonal ridge is relatively high and sharp-crested, and tends to curve gently anteriorly. The size and position of the beaks, presence or absence of an anterior lobe, and profile of the anterior margin could not be accurately determined in any of the available specimens, hindering confident identification. The hinge line is straight and curves relatively sharply into the broadly convex posterior margin, forming an obtuse angle of about 120° (angle ß of Newell, 1942). There is no trace of a sinus along the posterior margin. The valves are thin and their external surface displays numerous irregular growth lamellae, but these are not especially rugose and no spines are present. Right valves are rather flattened compared to left valves. The interior features of the valve were not observed. Smaller specimens (Fig. 2.12) have a narrower, more elongate shape and a smaller angle a, about 55°.

General valve shape and profile of the hinge and posterior margins of the Kinney Quarry specimens are most similar to valves of *Septimyalina scitula* Newell 1942, *Myalina (Myalina) wyomingensis* (Lea 1853), and *Myalinella meeki* (Dunbar 1924). All of these species occur in the Virgilian of the Mid-continent, and they are superficially similar in form (Newell, 1942). Compared to the Kinney Quarry specimens, *S. scitula* appears to have flatter, thicker valves with less curved umbonal ridges, and a more acutely pointed anterior end. *Septimyalina* also possesses a septum within the internal umbonal cavity. The presence or absence of such a septum could not be determined in the Kinney Quarry specimens. Further preparation, involving grinding away the matrix to expose the umbonal cavity, is required in order to determine whether a septum is present.

Myalina (Myalina) wyomingensis possesses an inflated, curved umbonal ridge and has moderately lamellate growth increments, similar to the Kinney form. However, the umbonal ridge of M. *(M.) wyomingensis* is broadly convex, rather than sharp-crested as in the Kinney Quarry specimens. M. *(M.) wyomingensis* also displays a prominent beak elevated well above the hinge line, and an anterior lobe—features that are not exposed for examination in the Kinney Quarry specimens. Small valves (e.g. Fig. 2.12) resemble *Myalinella meeki,* but appear to have a more rounded intersection of hinge and posterior margins and a more convex posterior margin.

Additional preparation of present specimens or collection of more complete specimens is required to observe certain critical morphological features of the Kinney Quarry myalinid valves that would allow confident identification. At present, the common myalinids in this unit are referred tentatively to M. aff. *wyomingensis.* Clearly, the Kinney Quarry specimens are quite distinct from most other Late Pennsylvanian myalinid species, which generally are either larger and possess a posterior sinus near the hinge margin [e.g. M. (M.) *miopetina* Newell 1942], or have more upright, subrectangular valves with a larger angle a and a smaller angle 13 [e.g. M. (M.) *glossodoidea* Newell 1942; M. *(Orthomyalina) slocomi* Sayre 1931].

Leptodesma (Leptodesma) sp.

A single incomplete left valve (Fig. 2.16), with its external surface down against the substrate, is referred to *Leptodesma (Leptodesma).* The valve body is elongate and rather narrow, and the preserved portion of it is about 13 mm along its maximum dimension. The valve is unornamented except for numerous comarginal wrinkles. The posterior auricle is elongate and nearly flat, with a strongly concave posterior margin. Valve shape and the morphology of the posterior auricle both indicate that this specimen may represent either *L. (L.) ohioense* (Herrick 1887) or *L. (L.) longa* (Geinitz 1866).

Dunbarella striata (Stevens 1858)

Dunbarella striata is the most common pectinacean in the Kinney Quarry limestone fauna. The valves are typically unbroken and well preserved, and some specimens are articulated or nearly so (Fig. 2.17). The species is relatively small (maximum height is about 15 mm) and has nearly acline, orbicular valves. The left valve is moderately convex and bears 20 to 30 prominent ribs which increase by intercalation. The right valve is less convex, approaching flatness, with relatively broad costae that increase by bifurcation. The anterior auricles are small and triangular, with that of the right valve associated with a deeply indented byssal notch. The posterior auricles of both valves are larger, have gently convex posterior margins, and are indistinctly separated from the valve body. Incomplete *Dunbarella* valves may superficially resemble *Aviculopecten,* but the latter genus has well defined, triangular, posterior auricles that are well set off from the valve body. More detailed information on *D. striata* and its relationships with the dunbarellas occurring in the nonmarine part of the Kinney sequence is presented by Kues elsewhere in this volume.

Aviculopecten basilicus Newell 1937

Two incomplete left valves (Fig. 2.18, 2.19) agree well with *Aviculopecten basilicus,* known from Virgilian strata in Kansas and Texas (Newell, 1937). The largest valve is about 20 mm high, moderately convex, with height and length being approximately equal. The posterior auricle is large, triangular, and bears several small, obscure radiating rib-lets. The posterior auricular sinus is broad and strongly concave; anterior auricles were not preserved. Ornamentation consists of about 40 strong, broadly rounded to flattened ribs separated by narrower interspaces. Typically, one fine rib is intercalated between each pair of major ribs. The valves show no evidence of spines or imbrications. Newell (1937) noted that some ribs of *A. basilicus* split distally into two or three smaller ones, but this was not observed in the Kinney specimens. However, a few large ribs on one valve appear to have been formed by coalescence of two smaller ones near the center of the valve.

Streblochondria? sp.

Several small, gently convex pectinacean valves may represent *Streblochondria* (Fig. 2.20), but the auricles and shape of the shell are poorly preserved, making positive identification difficult. All specimens in which the shell is preserved are oriented with the external surface down against the substrate, leaving only the interior surface of the outer layer exposed to view. The valves attain a maximum height of about 12 mm and are higher than long. They display slight to moderate obliquity, with a straight, relatively strong posterior umbonal fold and a more convex, rounded anterior fold. Ornamentation consists primarily of relatively strong, fine, closely spaced, concentric growth lines. Less conspicuous fine radial ribbing is also present, but there is no indication of the cancellate external ornamentation that characterizes many species of *Streblochondria.* All internal valve surfaces also have relatively prominent, elongate, radial, undulatory to zig-zag and branching pustules of unknown origin.

Gastropods

Gastropods are few and poorly preserved in the Kinney basal-limestone fauna. Their shell material commonly has been altered to an almost featureless soft, chalky substance; impressions provide the best record of whorl shape and external ornamentation. *Glabrocingulum (Glabrocingulum)* is the most common genus (Fig. 2.22). Molds indicate a low-spired shell with whorls embracing nearly to the periphery. Ornamentation consists mainly of several spiral lirae on the upper whorl surface, with the subsutural lira being largest and distinctly nodose. Whorl morphology and ornamentation suggest affinities to *G. (G.) grayvillense* (Norwood & Pratten 1855). Except for one mold of a small portion of a bellerophontid with spiral lirae *(Euphemites),* no other gastropod specimens are well enough preserved for even generic identification.

In the upper part of the basal limestone, and continuing higher in the section through the fish bed (unit 3), are moderate numbers of a small, high-spired gastropod up to about 7 mm in height (Fig. 2.21). These are invariably flattened and too poorly preserved for positive identification. The whorl profile is evenly convex and several spiral lirae are present. Possibly these shells are *Donaldina. Glabrocingulum (Glabrocingulum), Euphemites,* and *Donaldina* have all been described from the underlying Missourian Sol se Mete Member in the Manzano Mountains (Kues, 1985).

Paleoecology

The taxonomic composition and preservation of the Kinney Quarry limestone fauna provide information relating to its paleoecology and to the depositional environment in which it lived. This fauna is dominated numerically by the genera *Lingula, Solemya,* and *Myalina,* which together comprise about 57% of the total mean estimated abundance (Table 1). The main subsidiary elements of the fauna (conchostracans, ostracodes, small ammonoids, *Chonetinella, Dunbarella)* total additional 34% of mean estimated abundance. Because these subsidiary taxa are small to minute animals, the percentage of total biomass (of preserved taxa) represented by the dominant species very likely exceeds their numerical abundance. In addition, two of the three dominant genera *(Lingula* and *Solemya)* are extraordinarily conservative in their evolution and are represented by modern species, whose ecology has been studied. The third dominant genus, *Myalina,* is extinct, but is believed to be ecologically closely analogous to the modern genus *Mytilus* (Newell, 1942; Hickey, 1987). The following discussion focuses first on the paleoautecology of the dominant taxa, then considers the paleoecology of other taxa, and finally integrates this information together with other observations into a consideration of the depositional environment of the limestone unit.

Modern species of *Lingula* live an infaunal, suspension-feeding existence in intertidal to shallow subtidal marine environments. Often they are found in periodically exposed mudflats and in other conditions where reduced salinities may occur (Craig, 1952; Rudwick, 1970). Lingulas excavate relatively deep burrows in sediments ranging from clean sand to fetid muds. In the late Paleozoic, *Lingula is* most conspicuous in nearshore faunas of relatively low diversity, which often occur in dark shales (e.g. Ferguson, 1963; Calver, 1968; Hickey & Younker, 1981). Although tolerance of brackish conditions is generally attributed to Paleozoic lingulas, the genus also occurs in more diverse, shallow, normal-marine faunas.

The valves of *L. carbonaria* in the basal limestone of Kinney Quarry are generally well preserved and almost invariably unbroken, with 17% of the specimens consisting of paired valves in life position or slightly displaced. In life, the two valves were connected by muscles, without direct articulation. The lack of fragmentation and significant number of paired valves in the Kinney Quarry assemblage strongly suggest quiet conditions with little or no post-mortem transport. Occurrence of some small to medium-sized valves (36 mm long) reflects age differences in the original population and indicates that current-winnowing processes were minor to absent.

Most living species of *Solemya* inhabit shallow marine environments (intertidal to about 40 m), where they burrow to depths of about 50 cm or more and have the ability to swim for short distances (Pojeta, 1988). Ecological studies of some species indicate preference for organic-rich, oxygen-poor, reducing mud or muddy-sand substrates (Reid, 1980; Cavanaugh, 1983). These species have poorly developed guts, or lack them entirely, and gain nourishment by assimilating dissolved organic matter or by utilizing symbiotic, sulfur-oxidizing, chemoautotrophic bacteria for internal CO, fixation (Cavanaugh, 1983). Pennsylvanian species have been reported almost exclusively from shallow-marine black-shale and black-limestone lithologies (e.g. Johnson, 1962; Hoare et al., 1979), and in some cases have been subject to pyritization (Pojeta, 1988). *Solemya* shell morphology has changed very little since the late Paleozoic, and this appears to be true of their ecology as well.

Kinney Quarry *Solemya* specimens are preserved entirely as composite molds of unbroken shells, with 17% of S. *radiata* and 66% of the larger S. *trapezoides* specimens being open, articulated valves. As *Solemya* shells are thin and lack teeth, this mode of preservation suggests quiet water. Living species produce distinctive Y-shaped burrows (Pojeta, 1988), but no burrows of any kind have been observed in the Kinney Quarry limestone. The open, articulated valves suggest that death occurred on the sediment surface rather than within burrows, but little or no transport of valves before burial is indicated. The two species of *Solemya* living in the limestone environment may have differed subtly in behavior, but evidently little or no competition between them for food or living space existed. In terms of biomass, the two species appear to have been approximately equal; specimens of *S. trapezoides* are less than one-third as abundant as *S. radiata,* but are much larger. The abundance of *Solemya* in the dark, organic-rich limestone of the Kinney Quarry is consistent with ecological preferences similar to those of modem species. Co-occurrence of *S. radiata* and S. *trapezoides* has been reported elsewhere in the Pennsylvanian of North America (Wanless, 1958; Johnson, 1%2; Hoare et al., 1979).

Myalinids are perhaps the most conspicuous inhabitants of Pennsylvanian shallow-marine clastic and impure-carbonate environments along open shorelines. In Midcontinent cydothems, myalinid-dominated assemblages typically overlie *Lingula* assemblages in transgressive phases and immediately underlie them in regressive phases (e.g. Elias, 1937; Boardman et al., 1984). Newell (1942) noted that myalinids preferred quiet nearshore environments, and their presence in a variety of intertidal and lagoonal environments and lithologies (in addition to open-shelf conditions) has been documented (e.g. Hickey, 1987). Most workers consider myalinids to have been ecologic analogues of modern eurytopic mytiloids, particularly in their unusually wide tolerance of salinity variations (Newell, 1942; Calver, 1968; Hickey, 1987). As is true of *Lingula,* they appear to have been able to live successfully in environments subject to brackish salinities. *Myalina* was adapted to a benthic, soft-substrate, byssally attached existence, resting on its right valve. Stanley (1972) described a correlation between change from an endo- to epibyssate mode of life and change in valve morphology from small and strongly prosocline to larger, with upright, acme valves. *Myalina wyomingensis* was considered a transitional form that was virtually epifaunal; the same seems true of the Kinney Quarry myalinids, which are similar to M. *wyomingensis* in valve size and shape.

The Kinney myalinas are mostly represented by disarticulated valves; about 13% of the specimens are articulated. Although medium-sized to relatively large valves predominate, numerous smaller valves (5-10 mm along anterior margin) are also present. *Myalina* specimens were preserved in a moderately wide range of orientations, from horizontal to inclined. Possibly this reflects variation in the death positions of byssally attached individuals, perhaps accentuated by slight current activity and an inherently greater tendency of the valves to sink into the sediments than was the case with the thinner *Lingula* and *Solemya* valves.

Of the main subsidiary elements of the Kinney Quarry limestone fauna, the pectinacean *Dunbarella* was a eurytopic suspension-feeder that may have lived byssally attached to floating vegetation and seaweed (e.g. Johnson, 1962; Clark, 1978). The genus occurs widely through overlying non-marine facies in the Kinney Quarry sequence; its paleobiology is discussed in more detail by Kues elsewhere in this volume. *Chonetinella flemingi,* the only moderately common articulate brachiopod, is a common constituent of diverse, normal-marine, Late Pennsylvanian shelf communities. Chonetoids dominate some assemblages in the central and eastern U.S. (e.g. Johnson, 1962; Moore, 1964; Sturgeon & Hoare, 1968), as well as in the Manzanita Mountains of New Mexico (e.g. Kues, 1983). They appear to have been most successful in quiet, nearshore environments, in which salinity might have been slightly subnormal, enough to be unfavorable for less euryhaline organisms (Moore, 1964; West, 1972). Hickey & Younker (1981), for example, reported *Chonetinella* in Virgilian black- and gray-shale lithologies containing low-diversity assemblages, as well as in argillaceous limestones associated with a large, diverse, marine fauna. The specimens of *Chonetinella* in the Kinney limestone unit are complete, articulated, and some have retained one or more of the delicate spines that extend from the hinge line of the pedicle valve.

All of the ostracodes observed in the Kinney limestone are smooth, unornamented forms represented mainly by unbroken, isolated valves. Smooth-shelled taxa generally increase relative to ornamented taxa in brackish to freshwater late Paleozoic environments (Benson, 1961) and often are good indicators of nonmarine conditions (Kaesler, 1988). Conchostracans—small, bivalved, thin-shelled crustaceans — are mostly confined to brackish- to fresh-water environments in the late Paleozoic, to the extent that occasional occurrences in normal-marine faunas are considered evidence of transport from nonmarine into marine waters (Petzold & Lane, 1988). Calver (1968) summarized conchostracan distribution in the Carboniferous of England, concluding that they lived in a variety of brackish- to fresh-water deltaic environments. In some cases, they are abundant in beds immediately preceding or following a marine incursion, and may even be mixed with nearshore marine fossils. In other cases, they apparently inhabited inland bodies of nearly fresh water completely cut off from the sea.

The cephalopods (small ammonoids, exclusively *Prothalassoceras,* and larger orthoconic and coiled nautiloids) are typically considered to be stenohaline nektonic organisms.

Their occurrence in the Kinney basal limestone has been studied by Mapes (1991), and Mapes & Boardman (this volume), who conclude that the low-diversity cephalopod fauna probably inhabited an environment with slightly reduced salinity and low bottom-oxygen levels, with mortality mainly due to predation. Little to no post-mortem transport is indicated.

Although not tabulated in the abundance calculations, fish remains (isolated teeth and scales, and larger concentrations of numerous scales) are moderately common in the Kinney Quarry limestone. The fish remains are both less abundant and more highly fragmented than in beds (units 2-4) immediately overlying the basal limestone. These higher units, which have yielded many partial to complete fishes, contain a biota that is almost certainly brackish (see below and Kues & Lucas, this volume). Similarly, fragments of terrestrial plants preserved in the limestone (mainly small stems and branches, with occasional small leaf fragments) are much less abundant and worse preserved than in overlying units. Spirorbid worms, observed attached to plant fragments both in the limestone and overlying units, are common in both nearshore-marine and nonmarine environments in the late Paleozoic (e.g. Calver, 1968).

Taken together, the composition and preservation of this biota lead to several conclusions regarding the environment in which it lived. The fauna is composed predominantly of benthic marine invertebrates that occupied shallow-shelf environments. However, many groups that are common constituents of such environments in the Pennsylvanian of North America (such as bryozoans, corals, crinoids, echinoids, most articulate brachiopods, and fusulinids) are rare to absent in the Kinney Quarry limestone unit. Most of the shallow-marine brachiopod and bivalve taxa that are present in this limestone are uncommon to rare, whereas they are more conspicuous in gray limestone and calcareous shale units in Late Pennsylvanian exposures elsewhere in central New Mexico. In contrast, the numerically dominant elements of the Kinney limestone fauna include marine genera *(Lingula, Myalina)* known to have been tolerant of subnormal salinities, and a marine bivalve *(Solemya)* probably adapted to unusual ecological conditions involving high concentrations of dissolved organic material and relatively low oxygen concentrations. Further, the chonetoid *Chonetinella,* the only moderately common articulate brachiopod, represents one of the most eurytopic groups of articulates. *Dunbarella,* the most common pectinacean, lived in both marine and brackish waters during the late Paleozoic, as did the spirorbid worms.

All of the dominant genera *(Lingula, Solemya, Myalina)* have been widely reported in nearshore, low-diversity Pennsylvanian marine faunas in North America. No assemblages that closely approximate the composition of the Kinney limestone fauna appear to have been reported from western Midcontinent cyclothemic sequences. In Illinois, however, an association of species from calcareous concretions in Desmoinesian black shales *(Orbiculoidea* association of Johnson, 1962) is taxonomically similar to the Kinney assemblage, although the relative abundance of the species in this association is unknown. Seven of the 10 taxa that characterize this association (including both species of *Solemya, Lingula, Myalina, Dunbarella, Clinopistha,* and spirorbids) are also present in the Kinney assemblage. The common inarticulate brachiopod *Orbiculoidea* that characterizes the Illinois association is conspicuously absent from the Kinney assemblage, however. The *Orbiculoidea* association was interpreted by Johnson (1962) as living on/in soft, organic-rich muds in nearshore, shallow marine environments, an environment similar to that postulated for the Kinney limestone fauna.

The faunal evidence thus strongly suggests that the Kinney limestone organisms lived in shallow water, near a shoreline, in a restricted-marine environment that was significantly affected by salinity fluctuations. The presence of terrestrial-plant fragments, unusually high levels of organic detritus in the sediments, and dilution of shelf carbonates with fine siliciclastic sediments also suggest a vegetated land area nearby. Modeling of late Paleozoic climates across Pangaea (e.g. Kutzbach & Gallimore, 1989) has shown that New Mexico was situated about 10° north of the equator, in a generally hot, relatively arid climatic regime that experienced summer monsoonal air flow and increased rainfall during the summer months. This seasonal increase in rainfall and consequent increase in fresh-water runoff and stream input to the nearshore marine environment might well have produced salinity fluctuations, especially if the Kinney marine environment were somewhat restricted.

Immediately above the basal limestone unit, the lithology changes to a fissile, grayish-brown shale (units 2-4). Most elements of the marine fauna disappear abruptly and are replaced by a biota consisting of abundant pteridosperms, some *Walchia* fronds and other plants (Mamay & Mapes, 1991, and this volume), a variety of fishes, rare amphibians, insects, millipedes, conchostracans, unornamented ostracodes, small dunbarellas, and malacostracan crustaceans. This biota reflects replacement of the argillaceous carbonate marine environment by prograding clastic deltaic sediments and brackish aqueous environments that were responsible for most of the overlying Kinney Quarry sequence (e.g. Lorenz et al., 1991, and this volume). The elements of the Kinney limestone assemblage that appear to have preferred brackish conditions (conchostracans, ostracodes, and perhaps fishes) were probably derived from laterally adjacent, nearby brackish deltaic environments. Like the plant fragments, they were washed or migrated into the marine environment during times of elevated rainfall. Possibly, they survived temporarily in areas of lowered salinity produced by mixing of marine and fresh water near the shoreline, or in a less dense surface layer of fresh or brackish water above the more normal marine waters near the substrate. Such periodic influxes of fresh water would also have made the Kinney limestone environment unsuited for long-term habitation by most stenohaline marine taxa.

The lack of fragmentation of most invertebrate shells (including the thin, fragile valves of *Lingula, Solemya,* and *Chonetinella),* the significant percentages of bivalved taxa preserved in articulated condition (including taxa with organic rather than skeletal structures holding the valves together, e.g. *Lingula, Solemya),* and the retention of delicate spines on some *Chonetinella* valves all strongly indicate quiet conditions with little or no post-mortem transport. No evidence of current agitation or significant disruption of the sediments by bioturbation was noted in the limestone unit.

If the interpretations presented above are accurate, it is clear that most of the Kinney basal-limestone taxa, including the three dominant genera, were buried and preserved in essentially the same area of bottom they had inhabited. Thus, they probably represent the main preserved elements of a distinctive benthic community that lived in the Kinney environment. As noted above, some elements of the limestone fauna, such as the ostracodes, conchostracans, and fishes, may have been transitory inhabitants, or were washed in from onshore brackish environments. Most cephalopods, requiring stabile, normal-marine salinity, were excluded from the Kinney environment. As Mapes (1991) and Mapes & Boardman (this volume) note, cephalopod diversity is low (one ammonoid and two nautiloid species), suggesting that variable salinity might have been a barrier to the entry of most cephalopod and other stenohaline species.

Consideration of the modes of life and feeding processes of the Kinney Quarry limestone fauna indicates that the mean estimated abundance of infaunal suspension-feeders and probable dissolved-organic-matter absorbers (chiefly *Lingula* and *Solemya)* exceeded the abundance of epifaunal suspension-feeders (mainly *Myalina,* other bivalves, and *Chonetinella),* if probably allochthonous groups such as ostracodes and conchostracans are excluded. Several of the epifaunal suspension-feeders *(Dunbarella* and other pterioid bivalves) may have lived attached to floating vegetation rather than directly upon the substrate. Motile epifaunal browsers/detritus-feeders, such as gastropods, constitute only a small proportion of the fauna. Infaunal deposit-feeders are virtually absent, although they are an important element of many Pennsylvanian nearshore, muddy-substrate, marine communities. *Clinopistha* is the only such species observed in the Kinney limestone, and its abundance is less than 1%.

Trace fossils that might indicate the presence of soft-bodied deposit-feeders are likewise absent, but this is true also of traces of known burrowing taxa, such as *Lingula* and *Solemya.* Possibly the sediment was too soft and fluid for burrows to remain intact.

The carnivorous taxa represent a significant component of the Kinney limestone assemblage, amounting to more than 7% of the specimens. Presumed nektonic carnivores are limited to cephalopods and fishes, which occupied the top levels of the food web. As the ammonoids are moderately common but generally small (10-15 mm in diameter), ostracodes and conchostracans would seem to be their most likely food source, although the distribution and abundance of these small arthropods may have varied seasonally.

The composition, modes of life, and feeding methods of the Kinney limestone fauna differ considerably from that of most Pennsylvanian shallow-marine faunas. Generally these are dominated by epifaunal suspension-feeders (e.g. articulate brachiopods, bryozoans, crinoids, corals) in offshore shelf environments, and by epifaunal browsers, detritus-feeders, and suspension-feeders (gastropods, many bivalves) or infaunal deposit-feeders (e.g. nuculoid bivalves) in many nearshore environments, including prodelta and delta-front areas (e.g. West, 1972). In contrast, both deposit-feeders and epifaunal browsers/detritus-feeders were quite uncommon in the Kinney limestone environment, and epifaunal suspension-feeders were subsidiary elements of the permanent fauna. This reflects the unusual nature of this environment, indicated by previously mentioned lines of evidence. Fluctuating, occasionally subnormal salinity undoubtedly eliminated many epifaunal suspension-feeding organisms, and augmented the adverse effects of low oxygen concentrations and perhaps unusually acidic water associated with high levels of organic material within the sediment. Low water pH was suggested as a limiting factor for conchostracans in somewhat similar conditions by Petzold & Lane (1988). Infaunal deposit-feeders and epifaunal browsers/detritus-feeders may have been restricted by these factors, even if some were relatively euryhaline.

The evidence presented above leads to the conclusion that the Kinney Quarry limestone fauna lived in a sheltered, quiet bay or lagoon connected sufficiently with more open marine waters to maintain salinity and carbonate content at normal or near-normal levels. Little study of other Pine Shadow Member sections in the Manzanita—Manzano Mountains has yet been done, so it is not possible to estimate the areal extent of this bay or lagoon. By analogy with Midcontinent Missourian shoreline environments (Schutter & Heckel, 1985), the Kinney limestone probably reflects an originally shallow, open-marine carbonate-shelf environment that was beginning to experience the effects of delta-edge progradation into the area. As portions of the delta built out across this shelf, the Kinney environment become progressively restricted, and influx of fine siliciclastic sediments, organic detritus, pulses of fresh water, and some brackish organisms increased. Salinity fluctuations, perhaps related to seasonal variations in rainfall and runoff, become significant, especially in the more landward areas of the lagoon. High levels of organic material accumulated in the sediments, possibly making them unusually acidic. The dissolved organic components in the water column favored, and were utilized by, unusual taxa like *Solemya* that were adapted to that nutrient source.

Restriction of the Kinney environment would also have tended to dampen turbulence from waves and currents. This may have been augmented by the density contrast between inflowing fresh water and underlying denser marine or near-marine water. Such density contrasts are known to suppress vertical circulation in modern deltaic environments (Bates, 1953). Decrease in circulation would have in turn lowered oxygen levels near the substrate, favoring organisms like *Lingula* and *Solemya.* Deterioration of the formerly stabile, well-oxygenated shallow-marine environment resulted gradually in the retreat of most benthic stenohaline invertebrates out of the lagoon, while eurytopic species increased. Overall diversity declined. Eventually, this portion of the shelf was covered by deltaic nonmarine sediments and environments, which produced the overlying, much thicker portion of the Kinney sequence.

Postscript

One other fossil is worthy of note. It was collected from the top of the basal limestone or possibly from the base of the transitional interval (unit 2). It is a well-defined, flattened compression of a large, elongate, soft-bodied organism preserved in a U-shaped curve (Fig. 3). The specimen is covered by an orange, ferruginous film that contrasts sharply with the surrounding dark-gray limestone, and is locally affected with what appear to be dendritic manganiferous deposits. Total length of this fossil exceeds 25 cm. It tapers very gradually from a maximum width of about 28 mm near one end (anterior?) to as little as 15 mm near the other end, but then expands slightly beyond and is truncated by the edge of the slab on which it is preserved. The anterior(?) margin appears to divide into two blunt lobes with diffuse distal outlines. Possibly the lobes ramify into tendrils or tentacles, but details cannot be seen clearly. Most areas of this compression bear numerous small spirorbid-worm tubes attached to the external surface of the organism. This suggests that it must have been exposed to colonization by the spirorbids for a relatively long period of time before being buried.

This specimen appears to represent an animal. It does not display the veinous, fibrous, or cellular structures typical of carbonized plants, and morphologically is unlike any plant part known to me. Close examination of the specimen revealed no evidence of segmentation, appendages, or internal body parts. Likewise, scales and other mineralized skeletal elements are apparently lacking. The cuticle or skin comprising the external surface of the organism appears to be smooth or very minutely pebbled. Small areas of carbonized integument may be present, but this is uncertain owing to dendritic precipitations of similar color and texture on and near the specimen.

At present, the affinities of this organism remain to be determined. Lack of segmentation removes it from consideration as an annelid or arthropod. It does not resemble any of the fishes reported from slightly higher in the Kinney section, and absence of scales, bones, and other mineralized elements rules out most kinds of fishes. Pennsylvanian lampreys (Bardack & Zangerl, 1968) are comparable in shape and size, and lack appendages and bony scales. However, compressed specimens from Mazon Creek retain well-defined portions of their internal cartilaginous skeletons;

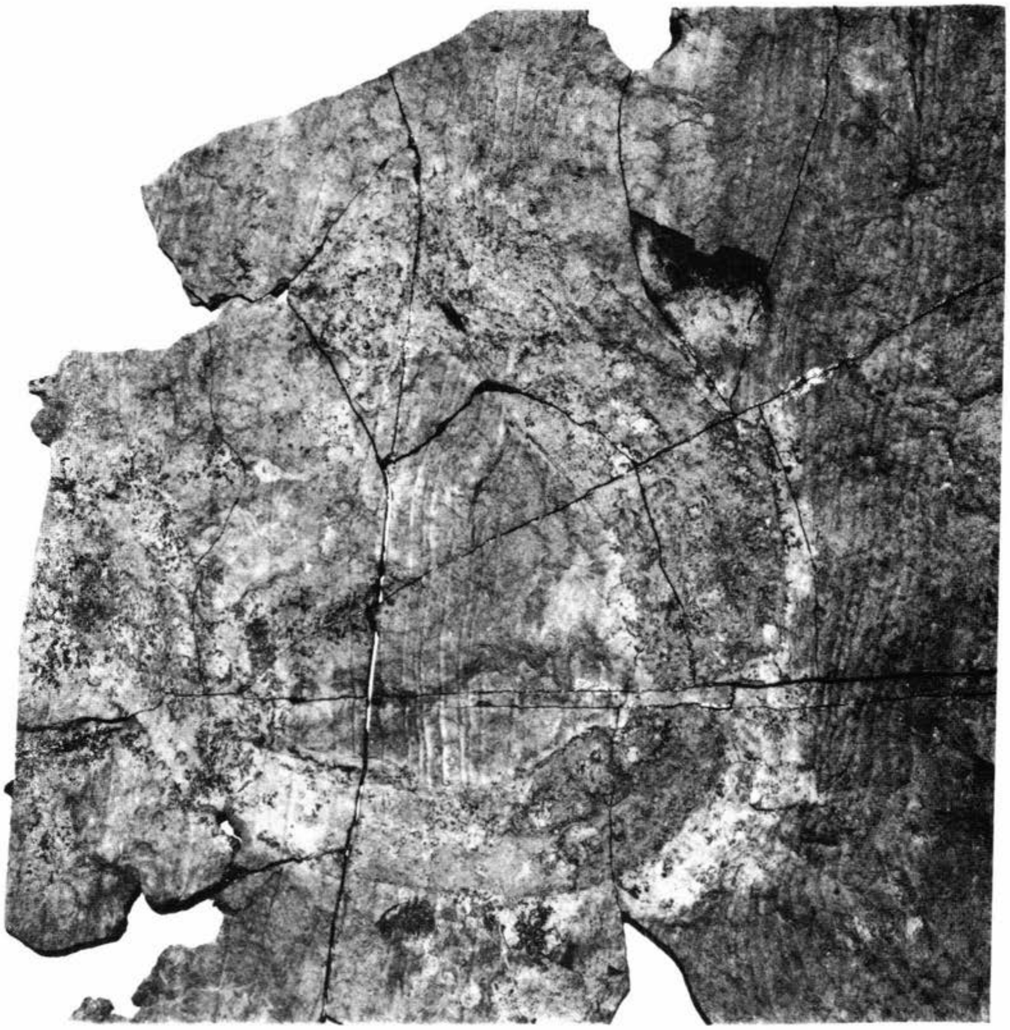

FIGURE 3—Unidentified soft-bodied organism from the top of Kinney unit 1 or base of unit 2, ×0.80. Presumed anterior end is toward upper part of slab.

nothing comparable can be seen in the Kinney specimen. Several groups of soft-bodied, worm-like, unsegmented invertebrates (e.g. holothurians, sipunculids, phoronids) are known from modern marine environments, but have a poor to nonexistent fossil record. The occurrence of conodonts in the Kinney limestone unit and elongate shape of the Kinney specimen might suggest another candidate for a conodont-bearing animal. However, no conodonts were observed associated with the compression, and the Early Carboniferous conodontan described by Briggs et al. (1983) is narrower and less than one-fifth the size of the Kinney specimen.

Obviously, these brief comments provide neither a comprehensive description nor a complete survey of the possible affinities of this organism. More study will probably reveal additional morphological details and provide a better basis for determining the affinity of this organism. The specimen is available to anyone interested in examining it.

Acknowledgments

I thank John Pojeta, U.S. Geological Survey, and Royal Mapes, Ohio University, for reviewing an earlier version of the manuscript, and Pojeta for a subsequent enlightening discussion of matters relating to Pennsylvanian pelecypods. I am also grateful to Kaye Toolson for the loan of some specimens in her personal collection.

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The bivalve *Dunbarella* in marine and nonmarine facies of the Upper Pennsylvanian sequence at the Kinney Quarry, Manzanita Mountains, New Mexico

Barry S. Kues

Department of Geology, University of New Mexico, Albuquerque, New Mexico 87131-1116

Abstract—Late Pennsylvanian assemblages of *Dunbarella* are present in restricted-marine and brackish environments at the Kinney Quarry. Small specimens (*D. striata*) are a subsidiary element of the bivalve-dominated, restricted-marine fauna in argillaceous limestone at the base of the quarry section, whereas unusually large (40+ mm long) valves of *D. rectalaterarea* occur in great numbers together with abundant carbonized remains of terrestrial plants in a 1.8 m thick brackish facies (units 5 and 6) beginning about 0.4 m above the basal limestone. All growth stages, including tiny spat attached to plants, are present in the unit 5 and 6 assemblages, which display significant ontogenetic and probable ecological variability in such features as valve shape and proportions, position of the beak along the hinge line, and number of ribs on the valve body and auricles. This intraspecific variability in features that have been utilized as specific characters by past workers suggests that North American Pennsylvanian *Dunbarella* assemblages may represent a slowly evolving complex of ecomorphs within, at most, two species, *D. striata* and *D. rectalaterarea.* The unit 5 and 6 dunbarellas attained large size in especially favorable conditions, probably within a deltaic bay or estuary where marine influence was slight. Valves are virtually limited to bedding planes between successive 1-4 mm thick laminae, and display numerous growth lines that probably represent daily growth increments, by analogy with some modern pectinaceans. These assemblages appear to represent r-selected, opportunistic populations that proliferated rapidly, attained large population sizes, and experienced elevated, possibly seasonal, mortality rates in conditions of unstable salinity and sediment influx. Small dunbarellas occur in other nonmarine intervals of the Kinney sequence, in which the exact combination of favorable ecological conditions necessary to sustain rapid growth to large sizes apparently was not present.

Introduction

The pectinacean bivalve *Dunbarella* is a moderately common constituent of some North American Pennsylvanian offshore- to nearshore-marine assemblages, and it also occurs in brackish-water faunas. Three Pennsylvanian species are presently recognized in North America, based mainly on taxonomic studies of specimens from the central and eastern U.S. (e.g. Newell, 1937; Murphy, 1967; Hoare et al., 1979). Other species are common in the Late Carboniferous of Great Britain. The North American species have been cited in a moderate number of faunal lists, but the genus appears to be less common than other pectinaceans, such as *Aviculopecten.* No dunbarellas have been previously described from the southwestern United States.

Dunbarella is common throughout the Upper Pennsylvanian sequence exposed in the Kinney Quarry, Manzanita Mountains, southeast of Albuquerque. Specimens are abundant and well preserved in some beds, and may represent the dominant element of the biota in these intervals. The genus occurs in several lithologies and is associated with different biotic assemblages, indicating that it was successful in a variety of paleoenvironments. In this report, the morphology and variability of *Dunbarella* in three different assemblages are compared and related to the taxa known from the central and eastern United States. In addition, some observations on the taxonomy of *Dunbarella* and the paleoecology of the Kinney assemblages are presented.

All specimens discussed and illustrated here are in the University of New Mexico (UNM) Department of Geology collections.

Location and occurrence

The Kinney Quarry is located about 13 km south of the town of Tijeras, along the west side of New Mexico Highway 337 (formerly NM-14 south), Bernalillo County, New Mexico (Fig. 1). About 28 m of predominantly gray to brown shale, mudstone, and siltstone beds, with several sandstone units, are exposed in the quarry walls, with dark-gray argillaceous limestone forming the quarry floor (Fig. 2). The

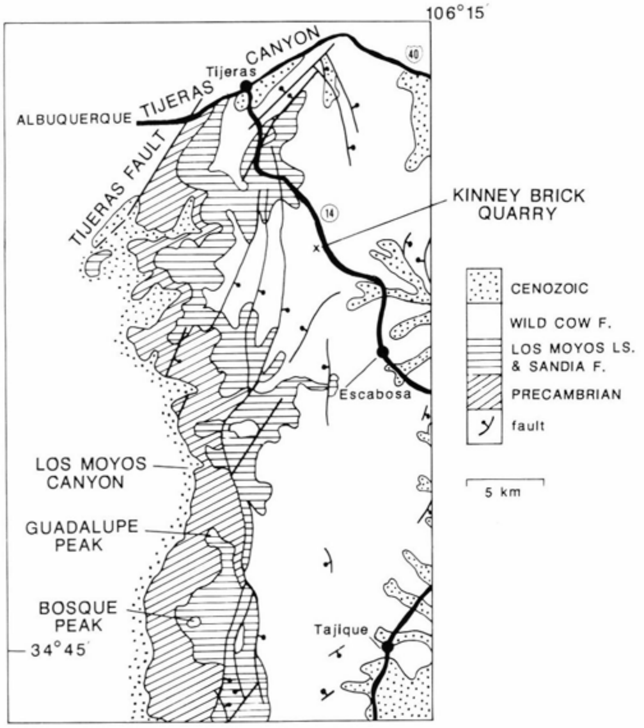

FIGURE 1—Map showing location of Kinney Quarry and general geology of Manzanita and northern Manzano Mountains (from Lucas & Huber, 1991).

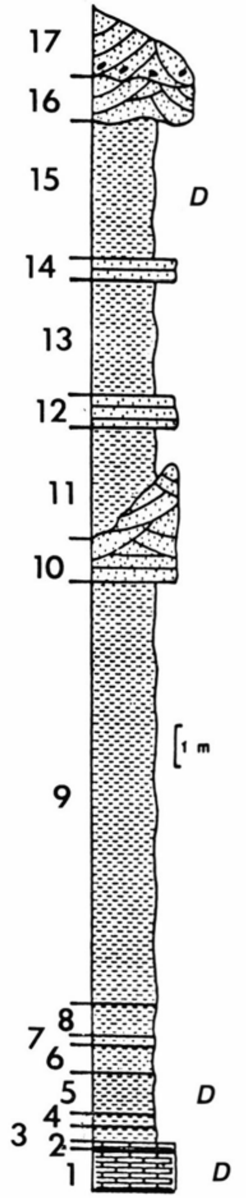

FIGURE 2—Generalized stratigraphic section of part of Pine Shadow Member, Wild Cow Formation, exposed in Kinney Quarry (from Lucas & Huber, 1991). Intervals yielding *Dunbarella* samples discussed in this paper are indicated by *D*.

quarry sequence forms part of the Pine Shadow Member, Wild Cow Formation (Madera Group), a unit that was dated as early Virgilian based on fusulinid studies (Myers, 1973, 1988) at nearby localities. Except for the basal limestone, the Kinney sequence appears to represent deposition primarily in brackish- to fresh-water environments associated with a nearby prograding delta system (Lucas & Huber, 1991; Kues & Lucas, this volume). Numerous groups of non-marine fossils have been reported in these beds, especially in the 0.5 m thick horizon (units 2-4) immediately overlying the basal limestone. These fossils include terrestrial plants, insects, myriapods, eurypterids, unornamented ostracodes, conchostracans, malacostracans, fishes, and amphibians (see other papers in this volume).

Three units (1, 5, and 15; Fig. 2) were sampled for *Dunbarella* and associated fossils. The basal, restricted-marine limestone facies yielded only small valves, typically no longer than 15 mm. *Dunbarella* comprises about 6% of the total number of specimens from this limestone. Unit 5 is composed of laminated, argillaceous to calcareous, dark-gray shale containing large numbers of valves representing all growth stages. Nearly all of the larger (20+ mm long) valves observed in the Kinney sequence occur in unit 5, including some that attained a maximum length of 42 mm, unusually large for the genus in North America. The valves occur locally in high densities and are concentrated at the contacts between successive laminae. *Dunbarella* is by far the most abundant fossil in unit 5, but carbonized terrestrial plants are also common. Unit 15 is a slope-forming, soft, fissile, gray-to-tan-mottled shale. Small *Dunbarella* valves are the most abundant element of the low-diversity biota, which also includes moderately common specimens of *Lingula* and conchostracans, rare *Myalina* valves, and fragments of plants. More detailed information on the paleoenvironments of these three units is presented later in this report.

Sampling and preservation

Specimens from each of the three sampled Kinney Quarry units consist mainly of complete or nearly complete valves displaying excellent preservation of surficial features. About 50 specimens of *Dunbarella* were obtained from the basal limestone (unit 1), of which nine were measured (Table 1). Approximately 100 specimens (15 measured) from the upper shale unit (unit 15) were examined. The greatest effort was directed toward the prolific unit 5 fauna; more than 500 *Dunbarella* specimens were examined and 123 were measured. In all units the thin, fragile shells are composed mainly of recrystallized calcite, which tended to flake off from bedding planes as the rock was split. The inner, aragonitic layers of the valves were not preserved; therefore, nothing can be said about muscle scars, hinge features, and other characteristics of the inner valve surfaces.

Contrary to the observations of Clark (1978), only a few pairs of articulated, closed valves were observed. Most specimens were isolated single valves, and a small number were articulated but open. Nearly all of the valves in the three assemblages were preserved originally in an unbroken state. Depending on the original orientation of a valve on the substrate, either the external surface or the inner surface of the outer shell layer was exposed on a bedding plane. In some specimens most of the shell was absent, but excellent molds were preserved. Minor distortion, caused by flattening of originally convex valves during lithification, affected some valves, but many are essentially undistorted. No measurements of valve orientation on bedding planes were made, but subjective inspection revealed no obvious preferred orientation. Approximately two-thirds of the valves have been preserved with their convex outer surfaces facing upward, the most stable position for valves of this shape.

The left and right valves of pectinaceans are slightly to greatly dissimilar in convexity. The right valve is typically less convex than the left, with more subdued ornamentation, and rested on the substrate below the left valve during the life of epifaunal forms. In *Dunbarella*, the right valve is only slightly less convex than the left, and the number and general appearance of the radiating costae is similar on both valves. Right valves differ in adding new costae by bifurcation rather than intercalation, and in having a narrower, more elongate anterior auricle associated with a deeper byssal notch. Thus, distinguishing between right and left valves in well-preserved specimens presents few difficulties.

In each of the three assemblages, the number of isolated left valves greatly exceeds the number of right valves. Right valves represented 11%, 5%, and 25% of the total measured valves from units 1, 5, and 15, respectively. The actual proportion of preserved right valves is believed to be somewhat greater, based on the presence of broken, unmeasured right valves in these assemblages, but falls far short of 50%. This disparity in preserved left and right valves of late Paleozoic

TABLE 1—Summary of measurements of *Dunbarella* left valves from Kinney units 1, 5, and 15. N, number of measured specimens; H, valve height; L, maximum valve length; HL, length of hinge line; Beak position is distance of beak from anterior end of hinge line/total hinge length. Large = >15 mm in height.

		H/L			HL/L			Beak Position	
Assemblages	mean	range	N	mean	range	N	mean	range	N
Unit 1	1.02	0.96–1.07	7	0.78	0.72–0.81	6	0.44	0.35–0.48	6
Unit 5									
Large	1.00	0.83–1.18	63	0.79	0.69–0.93	54	0.46	0.37–0.56	55
Small	0.98	0.80–1.14	44	0.79	0.68–0.92	39	0.46	0.37–0.59	38
Unit 15	0.99	0.92–1.04	9	0.83	0.76–0.94	10	0.43	0.37–0.48	10

pectinaceans, even in quiet environments where winnowing was not a factor, has been noted by previous workers (e.g. Newell, 1937; Watkins, 1975). The flatter, more fragile right valves were more likely to be broken and less likely to be quickly buried than the left valves (Watkins, 1975).

Taxonomic history

Dunbarella was established by Newell (1937) for Carboniferous pterinopectinids having an orbicular to subquadrate prosocline shape, intercalate costae on the left valve and bifurcate costae on the slightly less convex right valve, and a high but not well differentiated posterior auricle that is quite different in shape from the anterior auricle. Three North American Pennsylvanian species—D. *whitei* (Meek), *D. rectalaterarea* (Cox), and *D. knighti* Newell—were assigned to the genus. Maximum length of each species was reported to be approximately 25 mm (Newell, 1937). *Dunbarella whitei* (the designated type species) was characterized as having relatively few (up to about 30) rather broad, flattened costae on the body of the valve, non-costate auricles, and anteriorly situated beaks, with valve height and length being subequal. *Dunbarella knighti* was distinguished by the presence of costae on both auricles, a large number of valve costae (70 to 90), and a subcentral beak, but was similar to *D. whitei* in valve size and shape. The type specimens of *D. rectalaterarea* have been lost, but Newell considered the species distinctive in its high, subquadrate shell (height greater than length), numerous (77 to 83) crowded costae on the valve, costate auricles, and the nearly right angle formed at the intersection of the hinge line and outer margin of the posterior auricle. *Dunbarella whitei* was described from Virgilian strata, whereas the other two species were Desmoinesian in age.

Few workers have studied North American species of *Dunbarella* since Newell first recognized the genus. Lintz (1958) erected *D. appalachiensis* for specimens from the Missourian of Maryland having a shell higher than long, a median beak, costate auricles, and up to 48 rounded costae. Murphy (1967) reviewed these species and provided some information on variability and paleoecology based on collections from the Desmoinesian and Missourian of Ohio. He synonymized *D. whitei* with *D. striata* (Stevens), a poorly known species that Newell had referred questionably to *Aviculopecten.* Murphy noted that some specimens of *D. striata* possess definite costae on both auricles and may display as many as 50 costae on the valve body, trends that approach the typical condition of *D. knighti. Dunbarella striata* was distinguished from *D. knighti* by its smaller number of valve costae, absence or obsolescence of auricular costae, anterior position of the beak, and generally smaller size. One unusually large specimen of *D. knighti,* measuring more than 40 mm in height, was recorded from a Desmoinesian brackish-water shale facies. *Dunbarella appalachiensis* was considered a synonym of *D. striata,* but *D. rectalaterarea* was retained as a distinct species on the basis of its extremely high form.

Hoare et al. (1979) described *D. striata, D. knighti,* and *D. rectalaterarea?* from Middle and Upper Pennsylvanian strata in Ohio. Their specimens of *D. knighti* ranged from about 19 to 24 mm in height and most displayed 42 to 56+ valve costae, whereas *D. striata* was limited to specimens 16 mm high or less, with 16 to 28 body costae and 0 to 3-4 obsolescent costae on the anterior auricle. Several subquadrate specimens up to 34 mm in height were questionably assigned to *D. rectalaterarea,* but the authors noted that shell shape was the only feature distinguishing these specimens from the more abundant *D. knighti* in the same unit. They suggested that *D. rectalaterarea?* might be a growth variation of *D. knighti.* None of the authors who studied *Dunbarella* provided information on ontogenetic variations or juvenile specimens of the three species.

This taxonomic review illustrates that the features believed to characterize each species have been modified somewhat by the authors who have studied them, and that some valve features that are variable within single assemblages (e.g. valve size, shape, number of body and auricle costae) have been utilized in distinguishing between *Dunbarella* species. The large number of *Dunbarella* specimens of all growth stages present at different intervals of the Kinney Quarry sequence provides an excellent record of the morphological variability within assemblages. Study of this variability, described below, has implications for the species-level taxonomy of North American dunbarellas.

Systematic paleontology

Class BIVALVIA Linnaeus 1758
Order PTERIOIDA Newell 1965
Superfamily PECDNACEA Rafinesque 1815
Family PTERINOPECTINIDAE Newell 1937
Genus *DUNBARELLA* Newell 1937

DUNBARELLA RECTALATERAREA (Cox 1857)

Figs. 3K-V, 4A-F

1857. *Avicula rectalaterarea* Cox, p. 571, pl. 9/2.
1937. *Dunbarella rectalaterarea* (Cox): Newell, p. 40, pl. 2/5-7.
1944. *Pterinopecten (Dunbarella) rectilaterarius* (Cox): Shimer & Shrock, p. 403, pl. 160/4-5.
1979. *Dunbarella rectalaterarea?* (Cox): Hoare, Sturgeon & Kindt, p. 37, pl. 6/24.

Description—Valves large, up to 42 mm long, slightly to moderately prosocline; shape ranges from nearly orbicular to subquadrate, typically with minor to conspicuous posterior obliquity; height and length about equal; maximum length at about mid-height; hinge length approximately 80% of maximum length; beak situated slightly anteriorly in most specimens, averaging about 0.45 of distance from anterior to posterior end of hinge-line margin; left valve moderately convex, with short triangular anterior auricle and shallow, gently concave byssal sinus; ornamentation of left valve consists of bold, relatively narrow, rounded, straight to slightly undulatory radial ribs that increase gradually by intercalation to number about 50 to 60 at periphery of large valves; radial ribbing crossed by numerous, fine, closely spaced growth filae and occasional stronger concentric wrinkles that may deflect or offset radial ribs; right valve slightly less convex than left valve, with small, elongately

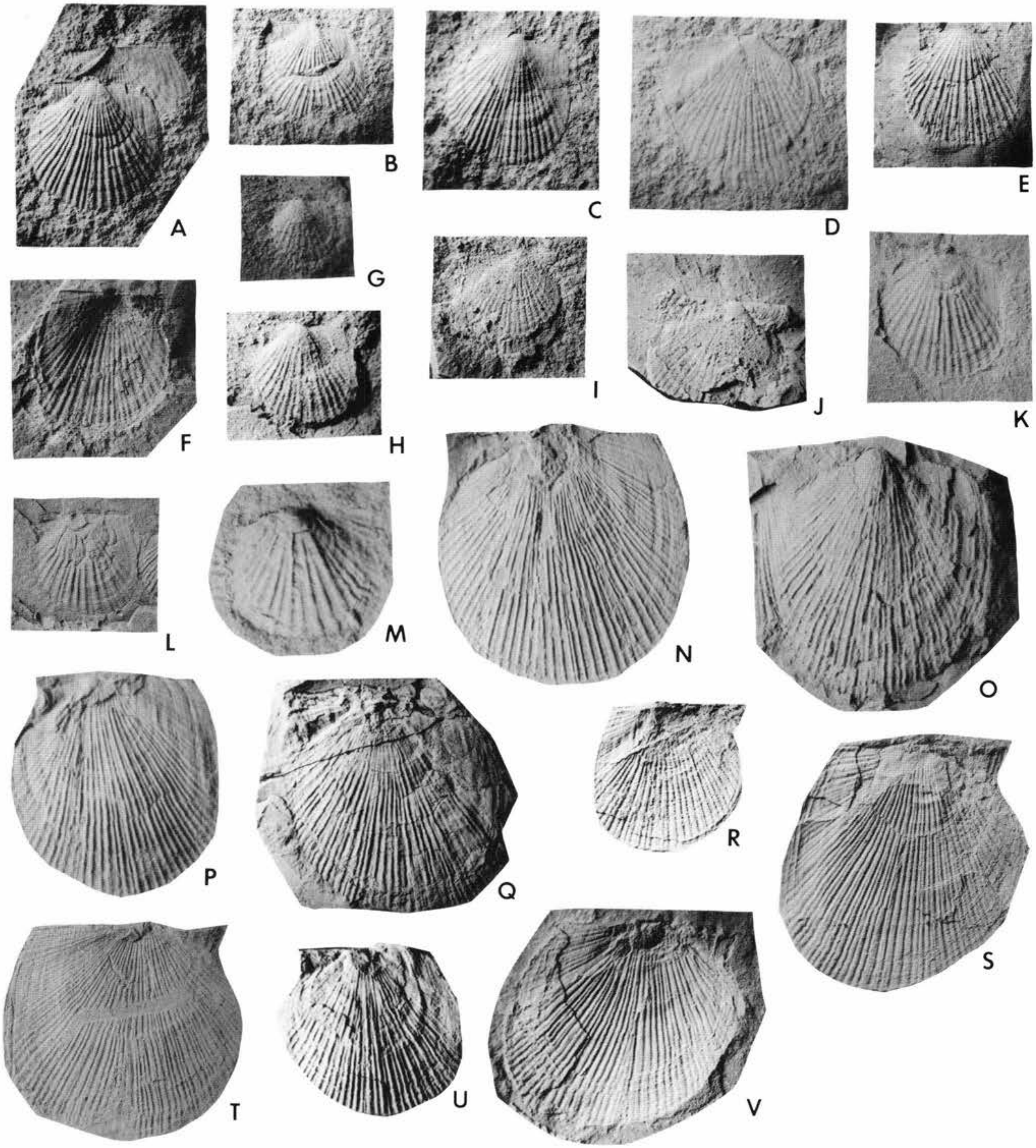

FIGURE 3—*Dunbarella* from the Kinney Quarry; A–D from unit 1; E–J from unit 15; K–V from unit 5. **A–D,** *Dunbarella striata:* **A,** external view of left valve partially overlapping internal surface of right valve, UNM 10964, ×2; **B,** external view of left valve, UNM 10965, ×1.75; **C,** external view of left valve, UNM 10966, ×2; **D,** external view of right valve, UNM 10967, ×2. **E–J,** *Dunbarella* sp.: **E,** external view of left valve, UNM 10968, ×2; **F,** internal view, concave impression of left valve, UNM 10969, ×2.5; **G,** external view of left valve, UNM 10970, ×3; **H,** external view of left valve, UNM 10973, ×2; **I,** external view of right valve, UNM 10971, ×2.5; **J,** external view of right valve, UNM 10972, ×2.75. **K–V,** *Dunbarella rectalaterarea:* **K,** external view of small left valve, UNM 10974, ×3.75; **L,** external view of small left valve (note pit on beak), UNM 10975, ×2.75; **M,** external view of small left valve, UNM 10976, ×5.5; **N,** external view of left valve, UNM 10977, ×1.5; **O,** external view of left valve, UNM 10978, ×1.5; **P,** external view of left valve, UNM 10979, ×1.5; **Q,** external view of left valve, UNM 10980, ×1.4; **R,** internal view, concave impression of left valve, UNM 10981, ×1.5; **S,** internal view, concave impression of left valve with some shell material adhering, UNM 10982, ×1.5; **T,** internal view, concave impression of left valve, UNM 10983, ×1.0; **U,** external view of left valve, UNM 10984, ×1.35; **V,** internal view, concave impression of left valve with some shell material adhering, UNM 10985, ×2.

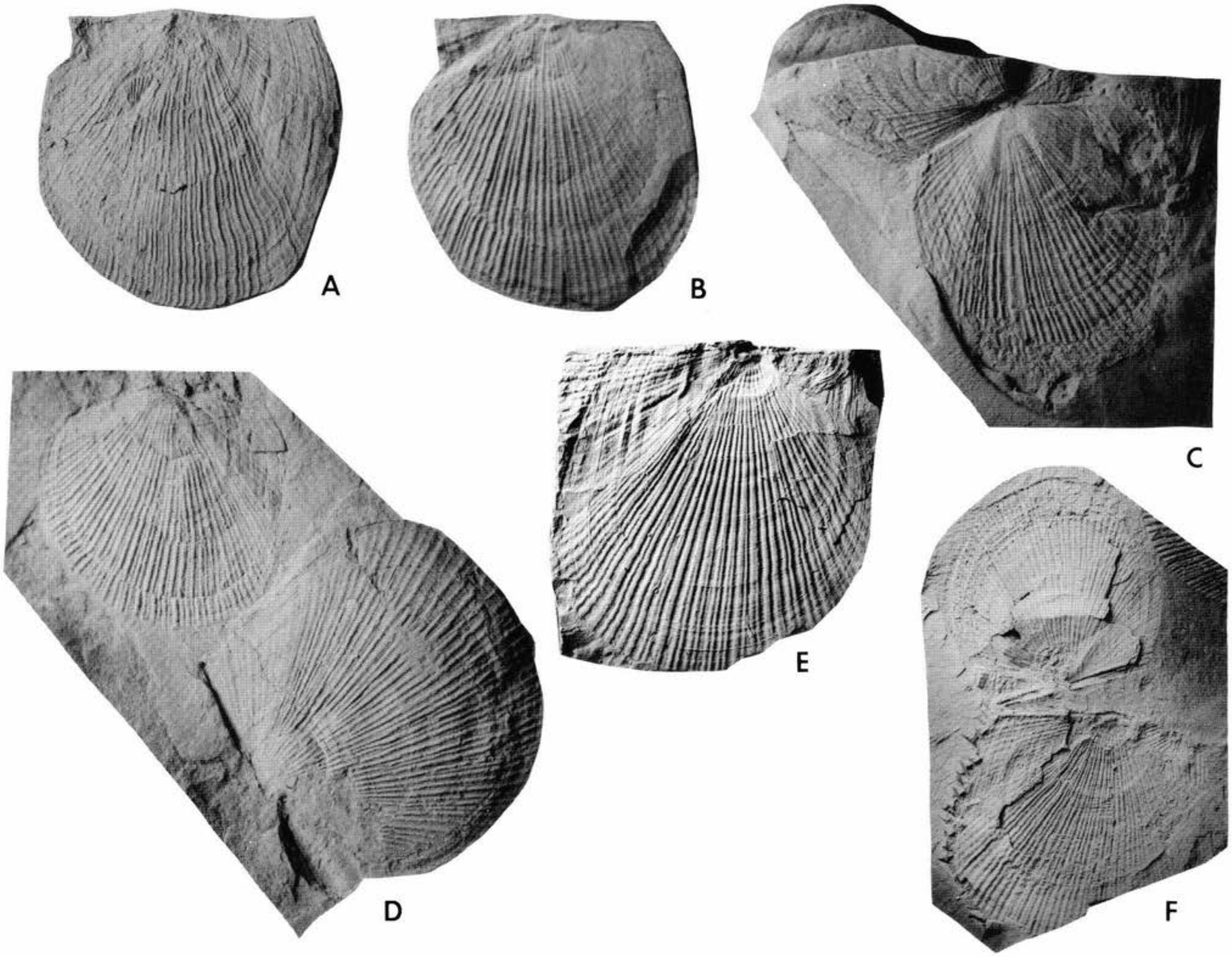

FIGURE 4—*Dunbarella rectalaterarea*, unit 5 of Kinney Quarry; all figures ×1.5 unless otherwise indicated. **A,** External view of left valve, UNM 10986; **B,** external view of left valve, UNM 10987; **C,** external surface of right valve (lower) with part of articulated left valve, UNM 10988; **D,** external views of two left valves, UNM 10989 (upper) and UNM 10990 (lower); **E,** internal view, concave impression of left valve with some shell material adhering; note anterior auricle of right valve resting on anterior auricle of left valve of this once-articulated, closed specimen, UNM 10991; **F,** external views of two right valves, UNM 10992 (upper) and UNM 10993 (lower), ×1.

triangular anterior auricle and deep byssal notch, with ornamentation similar to that of left valve but increasing by bifurcation; anterior auricle of both valves typically with strong growth lines but either lacking radial costae or displaying two to four low, obscure costae; posterior auricle of both valves large, high, merging indistinctly with valve body, ornamented typically with 8 to 20 obscure to conspicuous, sharp, fine riblets often best expressed near hinge line and close to valve body; posterior margin of posterior auricle nearly straight to gently convex, slightly concave in some small specimens, meeting hinge line at an obtuse angle ranging from about 100° to 135°; internal valve and hinge features poorly preserved.

Measurements are given in Table 1.

Discussion—The description is based on specimens from Kinney unit 5 and emphasizes the features of large valves. However, specimens of all sizes, down to very small valves 2 mm high, are present in this assemblage and provide information on ontogenetic changes. Valve shape is the most obviously variable feature of these bivalves; the range in variability among left valves is shown in Fig. 5. Typically, the valve is suborbicular to subquadrate, with only slight posterior obliquity. Four major gradational trends were observed, leading to valves that are: (1) more strongly orbicular, with convex anterior and posterior margins and a broadly obtuse angle at the intersection of the hinge line and posterior margin; (2) relatively low, with increasing posterior obliquity and nearly straight posterior margins; (3) relatively high, with conspicuous posterior obliquity; and (4) relatively high, with an almost acline, subquadrate shape. This variation in valve shape encompasses forms with relatively low, orbicular valves similar to those of *Dunbarella knighti* and *D. striata* on one end of the spectrum, and the relatively high, subquadrate shape characteristic of *D. rectalaterarea* as well.

Variation in other measured valve features is displayed in several scatter diagrams (Figs. 6-10). Variation in height/length ratios among all sizes is minor and does not change significantly with growth (Fig. 6). Smaller valves show a slight tendency toward being a little longer than high, and larger valves a little higher than long, but the difference is almost imperceptible. Mean height/length ratio for large valves (more than 15 mm high) is 1.00, compared with 0.98 for smaller valves (Table 1). Position of the beak is typically slightly anterior to the midpoint of the hinge line, but in 22% of the measured valves the beak was at, or slightly posterior to, the midpoint (Fig. 7). Variability in beak position is great, ranging from 0.37 to 0.59 of the distance from anterior to posterior end of the hinge line.

In all specimens, maximum valve length significantly ex-

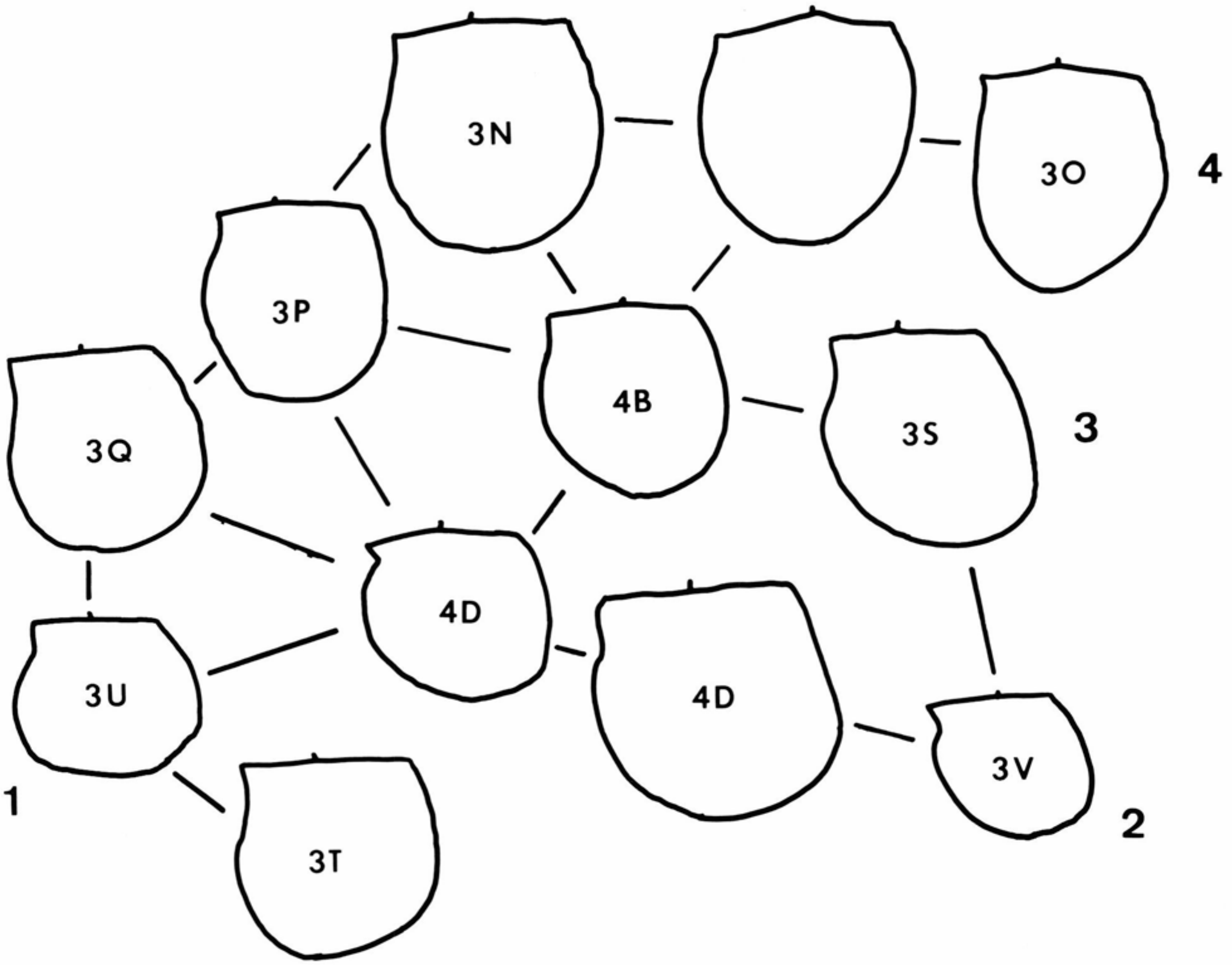

FIGURE 5—Variation in outline of left valve among *Dunbarella rectalaterarea* specimens in unit 5, shown in slightly less than natural size. Photographed valves are indicated by their figure numbers; dots along hinge line indicate position of beak. In a few cases the outlines are reversed for specimens preserved as concave impressions, so that profile is consistently of left valve exterior, with anterior end to left. 1, low, suborbicular shape; 2, low, prosocline shape; 3, high prosocline shape; 4, high, nearly acline shape.

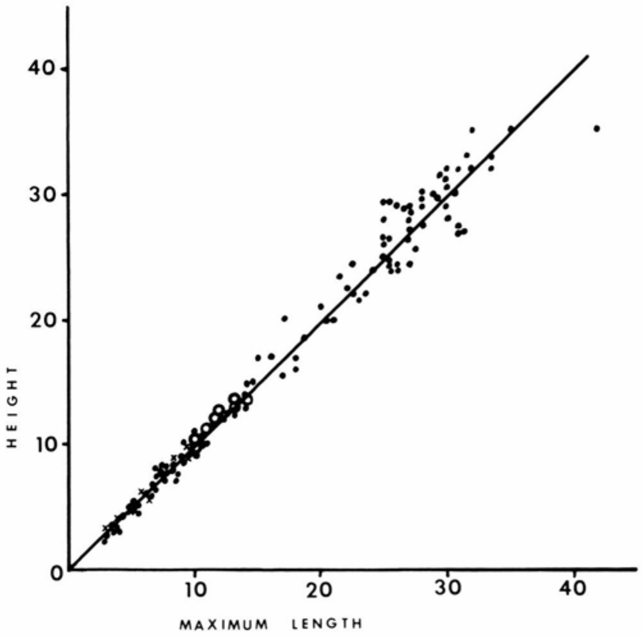

FIGURE 6—Scatter diagram showing relationship between height and maximum length (in mm) of *Dunbarella* left valves from unit 1 (open circles), unit 5 (solid circles), and unit 15 (X).

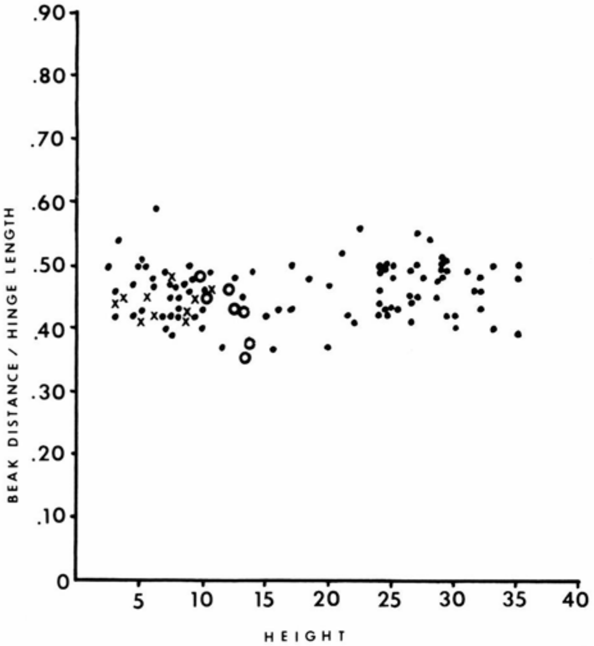

FIGURE 7—Scatter diagram showing relationship of beak position (distance of beak from anterior end of hinge line/hinge length) to size (height, in mm) of *Dunbarella* left valves from unit 1 (open circles), unit 5 (solid circles), and unit 15 (X).

ceeded the hinge-line length. The rather great variability in this ratio (Fig. 8, Table 1), from hinge length/maximum length ratios of 0.64 to 0.93, reflects the variability in valve shape. The more orbicular valves generally expand considerably ventrally from the hinge line and thus display relatively low ratios, whereas the high, subquadrate valves tended to expand anteriorly and posteriorly to a lesser degree, resulting in higher ratios. Similarly, the obtuse angle formed by the intersection of the posterior and hinge margins varies depending on the general shape of the valve. The more strongly convex posterior margin of relatively low, orbicular valves produces a high angle, up to 135°. Higher, subquadrate valves have a nearly straight posterior margin that intersects the hinge line at a nearly right angle.

A plot of the number of ribs on the body of left valves relative to valve size (Fig. 9) displays a fairly consistent rate of rib increase with growth. Increase in number of ribs is greatest in smaller valves. By a height of 10 mm, all valves in the unit 5 assemblage had developed at least 20 ribs; large valves 25 to 35 mm in height possess about 40 to 60 ribs. Intercalation of new ribs occurred consistently with valve growth, beginning about 3 mm from the beak. Thus, in any restricted area of the valve there is a gradational spectrum from narrow, small, newly intercalated ribs to larger primary ribs, with discrete ranks of rib sizes being absent. A greater degree of initial rib intercalation occurs around the anterior one-half to two-thirds of the valve body of smaller specimens, but rate of intercalation is about evenly developed in all areas of larger valves. Occasional intercalated ribs fade out with growth, but most ribs, once they appear, terminate at the valve margin.

About one-third of the specimens display low, inconspicuous costae on the anterior auricle. Typically, two to four costae are present in these specimens. No correlation between valve size and presence or number of costae on the anterior auricle was observed. The posterior auricles generally bear numerous fine, radiating costae, but wide variability exists in the number present on valves of a given size (Fig. 10). A general trend toward increase in costae with valve growth is apparent. Most small valves (less than 10 mm high) lack costae on the posterior auricle, and all valves 15 mm or more in height have them, although they may be faint in some specimens. In many valves these costae are best developed near the hinge line and near the border with the valve body, with the intervening central area being smooth or possessing only obscure costae. Transition from the posterior auricle to the valve body is not obvious and is best indicated by a fairly abrupt increase in the size of the costae onto the valve body.

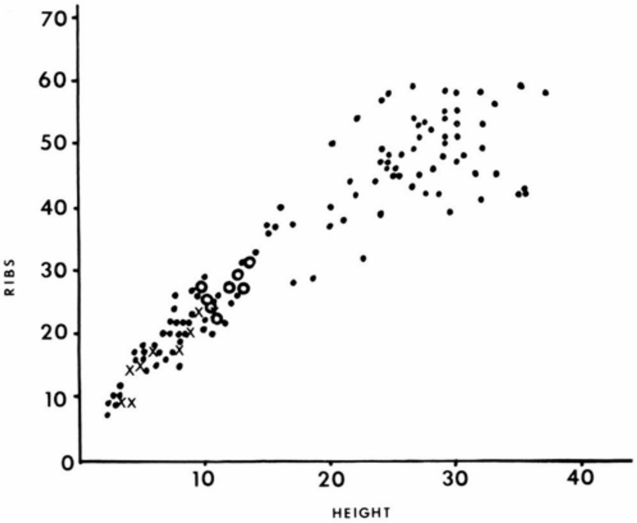

FIGURE 9—Scatter diagram showing number of ribs on valve body relative to height (in mm) of *Dunbarella* left valves from unit 1 (open circles), unit 5 (solid circles), and unit 15 (X).

Small specimens in the unit 5 assemblage are typically vaguely subrectangular, with length exceeding height in most specimens. Radiating ribs on the valve body are relatively broad and coarse relative to the size of the valve in

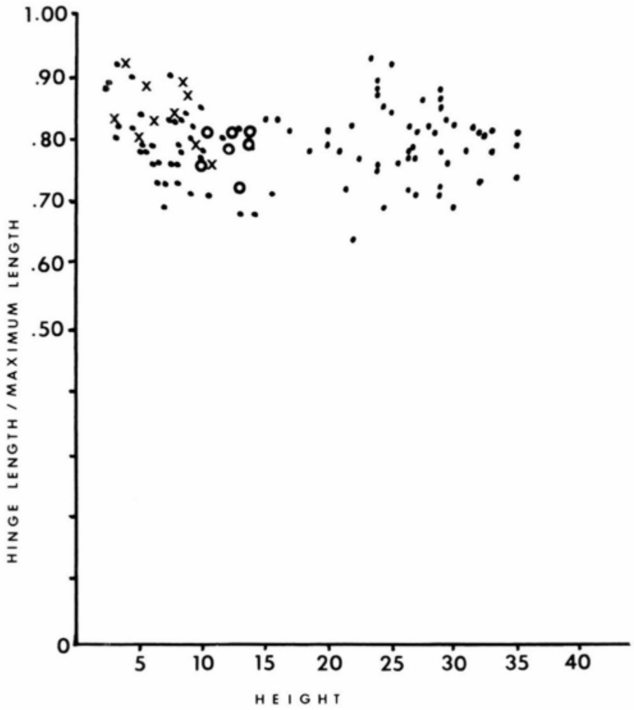

FIGURE 8—Scatter diagram showing relationship of hinge length/maximum length to size (height, in mm) of *Dunbarella* left valves from unit 1 (open circles), unit 5 (solid circles), and unit 15 (X).

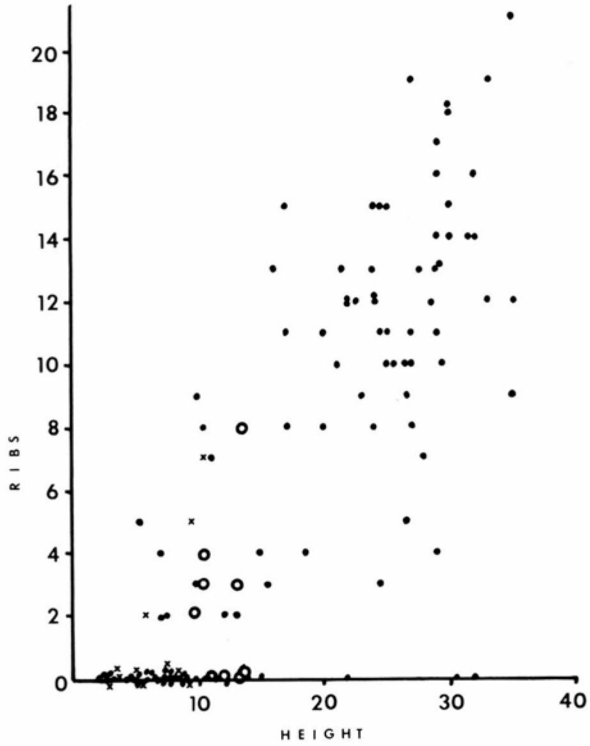

FIGURE 10—Scatter diagram showing number of ribs on posterior auricle relative to valve height (in mm) of *Dunbarella* left valves from unit 1 (open circles), unit 5 (solid circles), and unit 15 (X).

many specimens. The smallest measured specimen (height = 2.3 mm) possess about seven low, wide ribs and three prominent concentric wrinkles. The number of ribs on the left valve body increases rapidly by intercalation; at a height of 7.5 mm valves have 15 to 25 ribs, and at 10 mm 20 to 30 ribs are present. Specimens less than 5 mm high invariably lack costae on both auricles, as do many specimens up to about 15 mm in height. Most specimens less than 10 mm in height display only a slightly obtuse angle at the intersection of the posterior and hinge margins. In addition, the posterior margin immediately below the hinge line tends to be slightly concave, rather than straight to broadly convex as in large specimens. Several small specimens (e.g. Fig. 3L) have a deep circular pit on the beak of the left valve. These pits resemble valve attachment scars on some nonpectinacean pterioids. However, *Dunbarella* lived byssally attached to the substrate rather than cemented to it; thus, the origin and functional significance, if any, of these pits is at present unknown. Identification of the smaller valves in this assemblage as juveniles of the taxon represented by the large valves is consistent with morphological trends common to the assemblage as a whole.

DUNBARELLA STRIATA (Stevens 1858)

Fig. 3A-D

1858. *Posidonomya striata* Stevens, p. 265.
1872. *Aviculopecten whitei* Meek, p. 195, p1. 4/11a-c.
1937. *Dunbarella whitei* (Meek): Newell, p. 39, pl. 1/9-11, pl. 2/12-18.
1958. *Dunbarella appalachiensis* Lintz, p. 111, pl. 16/21-23.
1967. *Dunbarella striata* (Stevens): Murphy, p. 1500, pl. 195/8-12.
1969. *Dunbarella whitei* (Meek): Newell *in* Cox et al., p. 334, fig. 5.
1979. *Dunbarella striata* (Stevens): Hoare et al., p. 36, pl. 6/11-14.

Description-Valves small, up to 15 mm high, nearly acline to slightly prosocline; shape ranges from orbicular to slightly subquadrate, with minor posterior obliquity; height and maximum length about equal; hinge length approximately 80% of maximum length; beak situated from 0.35 to 0.48 of distance from anterior to posterior end of hinge line; left valve moderately convex, with short, triangular anterior auricle and shallow, gently concave byssal sinus; ornamentation of left valve consists of 20 to 30+ strong, somewhat broadly to narrowly rounded radiating ribs crossed by fine, obscure, concentric growth lines, number of ribs increases by intercalation; right valve less convex than left valve, nearly flat in some specimens, with a low posterior umbonal fold, a small, elongate anterior auricle, and fairly deep byssal notch; ornamentation of right valve consists of 20 to 30+ radiating ribs, typically lower and broader than ribs of left valve, number of ribs increases by bifurcation; anterior auricle of both valves either lacks costae or has up to four obscure costae; posterior auricle of both valves large, high, typically lacking radiating riblets but displaying up to about seven obscure riblets on a few specimens; posterior margin of posterior auricle nearly straight to moderately convex, meeting hinge margin at a moderately obtuse angle of about 120°; internal valve features poorly preserved.

Measurements are given in Table 1.

Discussion-The description is based on specimens from unit 1. Unit 15 dunbarellas are quite similar in most features, but display an even lesser tendency to develop auricle rib-lets, possibly owing to their generally smaller size. For reasons mentioned below, the unit 15 specimens are referred to *Dunbarella* sp. In all important valve features, the Kinney specimens agree closely with topotypes of *D. striata* described by Murphy (1%7). They differ from specimens of *D. whitei* and *D. striata* described by Newell (1937) and Hoare et al. (1979), respectively, in having bolder, more sharply rounded radial ribs on the left valve, and in being typically less posteriorly oblique. Some Kinney specimens (e.g. Fig. 3A) closely resemble some specimens from Ohio assigned by Hoare et al. (1979) to *D. knighti* (e.g. pl. 6/15) in valve shape and rib development, although they are much smaller. The specimens from Kinney unit 1 and unit 15 are also closely similar to specimens of *D. rectalaterarea* of equivalent size from unit 5. The latter are typically more quadrate and somewhat longer relative to height. However, the plots of various valve proportions (Figs. 6-10) show no significant differences between the specimens from units 1 and 15 and smaller specimens of *D. rectalaterarea* from unit 5. If the large valves of unit 5 had not been present, the smaller valves from this interval probably would not have been separated taxonomically from the unit 1 and unit 15 specimens.

Taxonomic discussion

The specimens from Kinney unit 5 are assigned to *Dunbarella rectalaterarea* on the basis of their typically subquadrate shape, large size, numerous, relatively sharply rounded radiating ribs, and generally costate posterior auricle. The Kinney specimens differ slightly from Desmoinesian specimens described by Newell (1937) in developing fewer ribs on the valve body (50 to 60 compared to *77+* to 83 in Newell's specimens), and in either lacking or possessing a few low costae on the anterior auricle, in contrast to the five to eight strong costae reported by Newell. As noted above, valve shape of the Kinney specimens is variable; suborbicular valves that trend toward the typical shape of *D. knighti* are gradationally connected to subquadrate forms in unit 5.

The high valve form of *D. rectalaterarea,* invariably cited as a distinctive feature of the species by previous workers, is most pronounced in Newell's (1937) measured specimens. Height/length (H/L) ratios averaged about 1.06, compared to 0.93 for both *D. striata* and *D. knighti* specimens measured by Newell. However, measurements presented by Hoare et al. (1979) for the three species indicate H/L ratios averaging 1.04 for *D. striata* (if one aberrently high specimen is omitted), 0.97 for *D. knighti,* and 1.04 for *D. rectalaterarea?.* These figures suggest a greater range of variability in H/L ratios within each species than is indicated by Newell's measured specimens. Certainly, relatively great variation characterizes the assemblages of *D. rectalaterarea* in Kinney unit 5 (Table 1). The mean H/L ratio is 1.00, but about 21% of the measured specimens are relatively high (H/L = 1.05 or higher) and thus similar to the specimens of *D. rectalaterarea* reported by Newell (1937). One of the three specimens of this species illustrated by Newell (1937: pl. 2/10) has a somewhat suborbicular shape that closely resembles some Kinney unit 5 specimens.

Dunbarella knighti may also attain a large size comparable to that of the Kinney unit 5 specimens (Murphy, 1967). The orbicular valve shape and the larger obtuse angle formed by intersection of the posterior and hinge margins (actually a consequence of orbicular shape) were the only significant features noted by Newell (1937) that separate this species from *D. rectalaterarea.* Hoare et al. (1979) separated *D. rectalaterarea?* from co-occurring specimens of *D. knighti* solely on the basis of subquadrate shape and suggested that the two forms might only be growth variants. Specimens assigned to both *D. rectalaterarea?* and *D. knighti* by Hoare et al. (1979) generally possess fewer radial ribs than the specimens described by Newell (1937), but about the same number as in the large Kinney specimens. Taken together, the observations of these workers suggest that the two species are variable and closely related.

As presently recognized, *D. striata* (encompassing *D. whitei* of Newell, 1937) includes smaller specimens no more than 24 mm high (Murphy, 1967). This species has the orbicular shell shape of *D. knighti* (Newell, 1937) and converges with that species in possessing costae of variable number and prominence on the anterior and posterior aurides (Murphy, 1967). *D. striata* has generally been characterized as having fewer radial ribs than *D. knighti* (although Murphy noted as many as 50 on one *D. striata* valve), with the costae tending toward flatness, and possessing a beak more anterior to the hinge midpoint. However, Murphy (1967) noted that the position of the beak may be of doubtful significance, given the wide variation he observed in this character in *D. knighti.* Even greater variation in beak position was observed in the Kinney specimens assigned to *D. rectalaterarea* and *D. striata.* The studies of previous workers indicate significant morphological overlap between *D. knighti* and *D. striata.*

High variability in several major valve features, including shape, angle formed by intersection of posterior and hinge margins, number of ribs, degree of development of costae on the anterior and posterior auricles, and beak position, characterizes the dense assemblages of *Dunbarella* in Kinney unit 5. One could choose specimens from a single bedding plane that appear to belong to each of the three presently recognized North American species. Rather than believing that representatives of three genetically isolated biospecies lived together at the same time in an environment where few other taxa existed, it appears more reasonable to interpret the gradational variation within these assemblages as being related to ontogenetic and ecological factors. In this regard, it is worth noting that the measured specimens of *D. striata, D. knighti,* and *D. rectalaterarea?* reported by Hoare et al. (1979) are segregated by size, from smallest to largest in the order listed above. This is suggestive of a growth series, with the morphological differences noted for the three species being related to size and to differences in the environments in which they lived.

Significant environmental control of the expression of many pectinacean valve characters has been documented in studies of modern species. Clark (1971), for example, studied two nominal subspecies of *Leptopecten latiauratus,* a common inhabitant of the California coast. The two subspecies live at different depths and are distinguished by numerous morphological differences, including number and prominence of ribs, presence of conspicuous growth lines, shell obliquity, ratio of hinge length to maximum valve length, and thickness of shell. However, when individuals of both subspecies were placed in constant conditions approximating the natural environment of one subspecies, the morphology of the other subspecies changed to that of the former. These morphologically distinct forms were found to be ecomorphs rather than true subspecies, with various valve characters determined by ecology, in this case differences in temperature and substrate stability.

While one cannot uncritically apply the results of such studies of modern pectinaceans to rather remotely related late Paleozoic taxa, many of the valve features that are ecologically variable in modern forms are among the most variable features of the morphologically similar *Dunbarella* valves in unit 5. This suggests that ecological factors, in concert with ontogenetic changes, likely had a significant effect on this variability. The fact that the presently recognized North American species of *Dunbarella* have been distinguished mainly on the basis of features that are ecologically labile in modern pectinaceans raises the question of whether these species are truly distinct taxonomic entities or ecological variants of one or two variable species.

Answering this question definitively would require considerably more study of *Dunbarella* assemblages in North America. Present knowledge of the genus is restricted to a few descriptive studies, some with information on variability, from only a few points in its temporal, geographic, and paleoenvironmental ranges. The three North American species have each been reported from Desmoinesian to Virgilian strata, and the genus ranges geographically from Maryland, through Illinois and Kansas, to New Mexico. Moreover, *Dunbarella* occurs from offshore-marine to a variety of nearshore-marine and lagoonal brackish-water environments (see below). In the latter environments, short-term fluctuations in important ecological factors such as salinity, input of sediment and organic matter, water chemistry, and perhaps temperature were probably pronounced. Variation in valve morphology, influenced by one or more of these factors, may well have developed as individual populations grew in somewhat different environments. Murphy (1967: 1501) noted that *Dunbarella,* while sensitive to ecological conditions, was also tolerant of a variety of conditions, "so that complete intergradation between described species may be expected." When possible geographic and temporal variation is also considered, *Dunbarella* may be visualized as encompassing a complex of evolving, variable, gradational ecomorphs, in which discrimination of probable biospecies based on preserved shell morphology on any consistent basis is difficult.

In this study, *Dunbarella* assemblages consisting of large, subquadrate to suborbicular valves and the earlier growth stages occurring with them are assigned to *D. rectalaterarea.* These assemblages are limited to an approximately 1.8 m thick horizon, mostly in unit 5, in which there is little evidence of marine influence. Specimens of small (maximum length about 15 mm), more consistently orbicular valves having fewer valve body and auricular costae, and occurring in the restricted-marine fauna of the basal limestone (unit 1) are referred to *D. striata.* Murphy (1967: 1501) observed that "as marine conditions set in, *Dunbarella* populations tended to produce smaller individuals bearing fewer body costae, the auricular costae growing obsolescent." This observation is generally supported by some of the Kinney Quarry assemblages, but the actual relationship between size/morphology and salinity is certainly more complex. Some British marine species, such as *D. papyraceus, attain* a larger size than any reported North American nonmarine specimens of *Dunbarella.*

Assemblages of small dunbarellas are also present in other intervals of the Kinney Quarry sequence, such as unit 15. These are not formally identified to species. They may be a morph of *D. rectalaterarea* that was limited to small size because of less favorable ecological conditions. Alternatively, they may represent a morph of *D. striata* adapted to brackish water, or immigrants of *D. striata* from normal-marine environments washed into the restricted Kinney lagoon as larvae and surviving in somewhat brackish conditions for a while. A third possibility is that the entire range of *Dunbarella* morphologies present in the Kinney sequence represents a single, highly eurytopic biospecies, with size and morphology strongly influenced by salinity and other factors.

Dunbarella knighti appears to be a morph that is transitional between *D. rectalaterarea* and *D. striata, similar* to the former in attaining relatively large size, numerous radial ribs, and costae on the auricles, and similar to the latter in valve shape and proportions. Beak position, considered an important feature distinguishing *D. knighti from D. striata* (Murphy, 1%7), is so variable a character that it seems to be of little taxonomic significance. Thus, *D. knighti* is not regarded here as a separate species.

Paleoecology

Previous studies have demonstrated that *Dunbarella* occurs in a wide variety of marine facies and is a constituent of several different marine communities in North America (see Wanless, 1958, for a useful catalog of lithologies and taxa associated with *Dunbarella* in Pennsylvanian cyclothems of Illinois). In some black, fissile shales it is part of an epipelagic fauna of low diversity, traditionally considered a nearshore-lagoonal environment (e.g. Zangerl & Richardson, 1963) but now recognized by many workers as representing the farthest offshore, deepest-water facies of Midcontinent cyclothems (Boardman et al., 1984). *Dunbarella* occurs in offshore dark shales and argillaceous limestones stratigraphically adjacent to black, fissile shales, but in association with a diverse, mollusc-dominated fauna (the *Sinuitina—juvenile ammonoid—Anthraconeilo* subcommunity of Boardman et al., 1984). The genus is present in gray, grayish-green, and black shales representing nearshore-marine conditions, deposited during the initial transgressive or penultimate regressive phases of cyclothems, where it is typically associated with *Lingula, Orbiculoidea,* and *Myalina* (Wanless, 1958; Johnson, 1%2; Boardman et al., 1984). Locally, especially in thin intervals of dark shales and limestones, *Dunbarella* may occur in large numbers as the dominant element of an assemblage (Willman & Payne, 1942; Wanless, 1958; Zangerl & Richardson, 1963; Hickey & Younker, 1981). *Dunbarella* also occurs commonly in a similar range of marine fades in the Upper Carboniferous of Great Britain, but is not present in nonmarine environments (Calver, 1968a, b).

The genus is present, although less often reported, in nonmarine fades in North America. Murphy (1967) noted that it occurs in three distinct lithologies in the Pennsylvanian of Ohio: black, fissile shales typically overlying coal beds *(D. knighti),* marine calcareous shales *(D. striata),* and argillaceous shales containing a brackish-water fauna. As mentioned above, the largest specimens appear to occur in brackish conditions. *Dunbarella is* a subsidiary element of, and restricted to, a fauna occurring in black shales overlying nonmarine, coal-bearing strata in the initial transgressive phase of the Virgilian LaSalle cyclothem in Illinois (Hickey & Younker, 1981). In these shales, interpreted as brackish deposits, the unidentified species of *Dunbarella* occurs in a low-diversity assemblage dominated by the brachiopods *Crurithyris, Orbiculoidea, Leiorhynchus,* and *Lingula,* and the bivalve *Streblopteria.* Clearly, based on the observations of previous workers, *Dunbarella* was tolerant of an unusually broad range of ecological conditions.

The morphology of *Dunbarella,* particularly the unequal auricles and deep byssal notch of the right valve, suggests strongly that it was epibyssate, remained byssally attached throughout life, and thus was unable to swim (Stanley, 1972; Hoare et al., 1979). Some authors have suggested that it commonly lived attached to seaweed or floating vegetation (e.g. Johnson, 1962; Clark, 1978, for Kinney dunbarellas; Boardman et al., 1984). This appears to have been the case for Kinney specimens in unit 5. Mamay (1981, 1990) and Mamay *&* Mapes (this volume) describe numerous small *Dunbarella* valves whose position relative to large plant fronds strongly indicates byssal attachment. One similar occurrence of a large pteridosperm frond with numerous very small dunbarellas in apparent life position was observed during this study. This specimen is in a private collection and currently unavailable for detailed study and illustration. These observations suggest strongly that *Dunbarella* spat attached to floating vegetation. It is likely that attachment was maintained throughout the life of an individual, although no large valves were observed in my collections that would definitely indicate byssal attachment.

The Kinney Quarry sequence has been interpreted by most workers as having been deposited in a restricted bay or lagoon bordered by a vegetated, prograding delta (Kues & Lucas, this volume). The basal dark-gray limestone (unit 1) contains a moderately diverse, restricted-marine fauna dominated by *Lingula, Solemya,* and *Myalina,* with a subsidiary component of articulate brachiopods (especially *Chonetinella),* conchostracans, unomamented ostracodes, small ammonoids, and *Dunbarella striata* (Kues, 1990, this volume). The Kinney environment at this stage was sufficiently connected with more open marine waters to maintain salinity at normal or near-normal levels, but was also subject to influx of fresh-water runoff, plant detritus, and siliciclastic sediments from the adjacent land areas. All of the bivalved taxa in this unit, including *Dunbarella striata,* are preserved in an unbroken state, with most species represented by numerous articulated specimens, suggesting that conditions were quiet and little transport prior to burial had occurred.

Following deposition of the basal limestone, the environment became less saline. Most elements of the marine fauna disappear within a few centimeters above the limestone, in a transition zone (unit 2) that abruptly becomes a fissile, grayish-brown shale. Characteristic fossils in units 3 and 4 are a variety of fishes, numerous terrestrial plants, amphibians, malacostracans, insects, spirorbid worms, snails, small *Dunbarella* valves, and sparse nautiloids, brachiopods, and fenestrate bryozoans. Limited connection with the sea persisted, but salinity had dropped substantially below 35 ppt.

In unit 5, *Dunbarella attained* its maximum abundance and size, presumably due to optimal ecological conditions. The first occurrence of a thin layer of dense, large *Dunbarella* valves is about 0.4 m above the top of the basal limestone (about at the base of unit 5), in fissile to platy, locally calcareous, dark-gray to brown shales. Concentrations of large valves are common through unit 5 and into the lower part of unit 6. In the upper part of unit 6, beginning about 1.9 m above the basal limestone, intervals with *Dunbarella* appear to be more widely separated and large valves become uncommon, although numerous small valves are present. At the top of unit 6, about 2.2 m above the limestone, *a Dunbarella* horizon is composed entirely of valves less than 15 mm long, with most being considerably smaller.

In units 5 and 6, the valves typically are concentrated on bedding planes separating successive laminae, and a wide range of valve sizes is represented. Valves on a single unit 5 bedding plane were pyritized, and disseminated pyrite particles are present in the surrounding sediment. In these horizons, *Dunbarella* is by far the most abundant faunal element; fronds and small fragments of terrestrial plants, mainly pteridosperms and *Walchia,* are also abundant. In a platy calcareous-shale fades near the base of unit 5, well-preserved platysomid fishes and a single *Myalina* shell were observed among large *Dunbarella* valves, and this is probably the horizon that produced the two eurypterid specimens known from the quarry (Kues, 1985). Rare, unornamented ostracodes and small masses of macerated ostracode valves (probably fecal material) are also present in unit 5 *Dunbarella* horizons. The virtual absence of marine organisms and abundance of well-preserved terrestrial-plant remains through most of units 5 and 6 suggest brackish conditions of relatively low salinity, with slight marine influence. A single orthocerid nautiloid specimen, the only stenohaline marine fossil observed in unit 5, probably swam in and died of osmoregulatory shock (Mapes, 1991; Mapes & Boardman, this volume).

Thickness of the laminae varies from about 1 to 4 mm in unit 5; in one 25 mm thick slab, 10 laminae were counted, ranging from 1.4 to 3.5 mm in thickness. These laminae represent cyclically deposited packages of sediment, and consist generally of a thicker, poorly fossiliferous portion and a much thinner, organic-rich layer containing the concentrations of *Dunbarella* and terrestrial plants. Numerous finer laminations are also present within each major lamina. The major laminae have been interpreted as varves (Clark, 1978; Anderson, oral comm. 1990), but Feldman et al. (1991 and this volume) and Archer & Clark (1991 and this volume) have suggested that tidal cycles were responsible.

If the general view of the Kinney sequence as representing the progressive restriction and sedimentary infilling of a bay or lagoon (Lucas & Huber, 1991) is correct, varves might be the more reasonable interpretation, as tidal influence on sedimentation would have been slight in a nearly or completely enclosed pool. Conversely, sedimentation in an open estuarine system might have been strongly influenced by tidal cycles. Feldman and Archer argued convincingly at the Kinney symposium (April 1991) that deposition of the lower laminated part of the Kinney sequence occurred in a tidal environment. They noted that the effects of two-weekly tidal cycles are manifested far upstream, in low or fresh-water salinities far from the marine environment, and that tidal effects may be amplified in the narrower portions of bays and estuaries. According to this interpretation, each major lamina represents rapid sediment deposition within a two-week period. Study of the depositional environments of the Kinney sequence by several workers is continuing; clearly, accurate interpretation of some aspects of unit 5 *Dunbarella* paleobiology depends on which model for the genesis of the laminae proves to be correct.

During the Late Pennsylvanian, New Mexico was situated along the west coast of Pangaea, at a latitude of approximately 10° or less north of the equator (Scotese et al., 1979; Bambach et al., 1980). Climates in this area became increasingly arid beginning as early as the Desmoinesian, with an expansion of arid climates from west to east through the remainder of the Pennsylvanian and Early Permian. This is indicated by eastward development of evaporites and a marked change from wetter- to drier-adapted floras at the beginning of the Missourian (Phillips et al., 1985; Schutter & Heckel, 1985). Climatic modeling of Pangaea during the Permian (Kutzbach & Gallimore, 1989; Crowley et al., 1989) suggests arid, high-temperature (30°C +) conditions across the southwestern United States, with precipitation barely exceeding evaporation only during the summer months (Kutzbach & Gallimore, 1989: fig. 5). Summer monsoonal flow passed northeastward from the equator across this area (Kutzbach & Gallimore, 1989: fig. 3).

If this model of late Paleozoic climate is accurate, the Kinney area would have experienced relatively higher levels of rainfall during the summer than in the winter, with increased runoff and sediment input resulting during the summer. Such seasonal changes may have affected the viability of *Dunbarella* populations. If tides were not a factor and the laminae are varves, the thin concentrations of *Dunbarella* valves between successive laminae could represent several months worth of accumulated valves in a winter regime of very slow sedimentation, or seasonal mass-mortality events, as suggested by Clark (1978). Such mortality-enhancing seasonal changes would probably not be related to temperature (temperature variation in west equatorial Pangaea was slight and the tropics were hot year-round; Kutzbach & Gallimore, 1989), but rather to changes in rainfall, runoff, and nutrients entering the *Dunbarella* habitat.

If the laminae were the result of tidal cycles, concentrations of *Dunbarella* valves at the top of each lamina must represent die-offs of part of the population every two weeks. If the unit 5 dunbarellas were living in shallow water, near the head of an estuary or in sluggish streams feeding an estuary, they might have been subjected to stranding and death on exposed mudflats during times when the range between high and low tide was greatest (i.e. at maximum spring tides). Only a small proportion of a population would be so affected during each two-week cycle, but thin concentrations of dead dunbarellas would result. Estuaries are complex, dynamic systems in which salinity fluctuations are influenced by the shape and depth of the estuary, the interplay between tidal range and amount of fresh-water runoff, variations in river discharge, and other factors (Emery et al., 1957). The optimum ecological conditions in which the Kinney dunbarellas were able to attain large sizes almost certainly existed in only a small portion of the larger bay—estuary environment represented by much of the Kinney sequence.

Other aspects of the biology of *Dunbarella* are indicated by the unit 5 assemblages. In each concentration of valves, all sizes, from 2-3 mm to more than 35 mm in length, are present. This strongly suggests that spawning occurred more or less continuously, rather than once or twice a year, which is typical of modern marine pectinaceans (e.g. Mason, 1957; Hayami, 1984). Numerous fine concentric growth filae are present on some well-preserved valves (e.g. Figs. 3V, 4A). Approximately 80 to 100 growth lines were counted on several valves having heights of about 30 mm, producing an average interval between the lines of about 0.3 mm. The number and spacing of these lines correspond closely to measurements made on modern pectinaceans (Clark, 1968) for daily-growth increments. Although it is not certain that fine growth increments are deposited daily by all modern pectens, interpretation of fine growth lines in *Dunbarella* as daily increments is a reasonable hypothesis. If true, this would indicate rapid growth of *Dunbarella* valves to maximum size in less than a year, and would be consistent with a yearly mass-mortality scenario. Detailed study of growth lines on many valves in a single assemblage would allow comparison of individual growth patterns. Similar patterns on numerous valves that end at the same point would reflect environmental fluctuations during growth for a community that perished during a mass-mortality event (Clark, 1968).

The *Dunbarella* populations in unit 5 exhibit many of the characteristics of r-selected opportunistic species discussed by Pianka (1970) and Levinton (1970). Such species tend to live in variable environments, undergo rapid development and high growth rates, attain large population sizes dominating the assemblages in which they occur, and may suffer catastrophic, density-independent mortality. Apparent production of spat continuously rather than periodically by the unit 5 dunbarellas is consistent with an r-selection adaptive strategy; Hickey & Younker (1981) previously noted the opportunistic nature of some *Dunbarella* assemblages in Illinois cyclothems. Pianka (1970) also cited small body size as a feature of an r-strategist species, but the reverse seems to be the case with the unit 5 dunbarellas. Apparently, optimal ecological conditions•during deposition of unit 5 enhanced growth rates and maximum valve size far beyond what was possible for dunbarellas in the marine or other brackish environments preserved in the Kinney Quarry sequence.

Further, these optimal conditions apparently persisted for only a short time in the area of the quarry. The total number of laminae within the approximately 1.9 m thick interval containing large *Dunbarella* valves was not counted, but may be estimated at less than 1000, assuming an average lamina thickness of 2 mm. If each lamina was deposited within a single two-week tidal cycle (26 laminae/year), the thickness of the entire interval containing large dunbarellas could have been deposited in as little as 37 years. Large dunbarellas developed only in what must have been a restricted range of brackish salinities, in relatively soft, muddy environments. Siltier lithologies with fewer plants and less disseminated organic debris above units 5 and 6 lack large *Dunbarella* valves.

Unit 15, a brownish-gray, soft, fissile shale near the top of the Kinney sequence, contains a low-diversity assemblage dominated by small *Dunbarella* specimens. Isolated and articulated valves of *Lingula* are moderately common; a few conchostracans and one *Myalina* valve were the only other elements of the fauna observed. Small fragments of plants are moderately common. The invertebrate shells are unbroken and some are articulated, indicating quiet conditions. The occurrence of *Lingula* and *Myalina* suggests some marine influence, but diversity is much less than in the restricted-marine fauna of the basal limestone (unit 1). The Kinney environment was brackish at this stage, but subject to the influx of normal marine waters that raised salinity to probably the lowest levels tolerated by *Lingula* and *Myalina*. Conchostracans are typically limited to brackish water in the Pennsylvanian (Calver, 1968a, b; Petzold & Lane, 1988). Their occurrence in unit 15 may reflect a few individuals living at the upper range of their salinity tolerance, or they may have been transported from more landward, less saline portions of the bay or estuary.

Small *Dunbarella* valves similar to those in unit 15 occur widely in the Kinney sequence, both below (units 2-4) and above (upper unit 6 and unit 7) the interval containing large valves. Lucas & Huber (1991) reported small *Dunbarella* specimens through much of the thick interval of relatively unfossiliferous silty claystones and shales (units 8-9) that composes the middle third of the Kinney sequence, but their distribution and abundance remain to be documented.

Many of these paleoecological observations should be regarded as preliminary. More detailed study of size-frequency variations and growth-line patterns of *Dunbarella* valves, and of relative abundances of the associated biota within each of the Shelly intervals is needed. Studies of this nature would allow better understanding of population structure and fluctuations within the *Dunbarella* communities and identification of subtle changes in ecological conditions accompanying them. For example, the abundance of large and medium-size (15 + mm long) valves dwindles considerably relative to small valves through the upper part of unit 6. Study of this transition might more definitely suggest the nature of the environmental changes that progressively restricted *Dunbarella* assemblages to small individuals. Fine-scale stratigraphic and sedimentological studies of the entire Kinney sequence will improve our understanding of changes in depositional environments and better constrain possible mechanisms regulating the conspicuous cyclic sedimentation in the lower part of the sequence.

Acknowledgments

I thank Royal Mapes, Ohio University, and Spencer Lucas, New Mexico Museum of Natural History, for reviewing an earlier version of this paper and offering suggestions that improved it. Discussions with Howard Feldman, Kansas Geological Survey, and Allen Archer, Kansas State University, concerning the origin of the laminae in the lower Kinney sequence were also helpful. W. R. Jurgena kindly allowed access to the quarry for collection of specimens.

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Late Pennsylvanian cephalopods from the Kinney Quarry, Manzanita Mountains, New Mexico

Royal H. Mapes[1] and Darwin R. Boardman II[2]

[1]Department of Geological Sciences, Ohio University, Athens, Ohio 45701; [2]Department of Geosciences, Texas Tech University, Lubbock, Texas 79409

Abstract—With one exception, Kinney Quarry cephalopods were recovered from the basal black to brownish-black micritic limestone in association with inarticulate brachiopods, bivalves, arthropods, and numerous fish remains. A single additional specimen was recovered from a shale unit several meters above the basal limestone.

All but one of the cephalopods (N = 41) are crushed molds or casts. Ammonoids dominate the assemblage (N = 26); straight nautiloids (N = 14) and coiled nautiloids (N = 1) occur less frequently. The single identifiable straight nautiloid is referred to *Pseudorthoceras knoxense* (McChesney). All of the more complete fragments and entire specimens are tightly umbilicate, and one individual retains a suture pattern. All of the ammonoids are provisionally assigned to *Prothalassoceras kingorum,* which ranges from middle Missourian to middle Virgilian. The low ammonoid diversity suggests an autochthonous population in a restricted environment rather than an allochthonous assemblage which would be more diverse. Additionally, the large percentage of fragmented ammonoid specimens (63%) suggests extensive and possibly size-selective predation of an autochthonous cephalopod population rather than damage by post-mortem transport. A single complete ammonoid specimen contains a thick carbon film by position suggestive of mandibles and stomach contents similar to those documented from the Bear Gulch Lagerstatte (Mississippian: Chesterian) of Montana.

Introduction

Overall, the stratigraphic units at the Kinney Clay Quarry in New Mexico have yielded a diverse assemblage of significant fauna and flora. Among the faunal elements are relatively rare straight and coiled cephalopods. These cephalopods are, with one exception, recovered from only the lowermost units. Ammonoids are the most common cephalopod group recovered, with orthoconic nautiloids and coiled nautiloids making up a smaller portion of the collections. None of the cephalopod taxa recovered thus far are particularly diagnostic in a biostratigraphic sense; hence their usefulness for effecting precise correlations with the extensive cephalopod occurrences in the Midcontinent (see Boardman, 1991, and Boardman et al., in press, for a summary) is limited. Nevertheless, their occurrence does provide significant insight into paleoecologic conditions and certain paleobiological phenomena including documentation of conch fragmentation by scavenging or predation, along with evidence of soft-part preservation.

In this report, UNM refers to University of New Mexico and NMMNH to New Mexico Museum of Natural History.

Location, occurrence, and preservation

The Kinney Quarry is located approximately 13 km south of Tijeras, Bernalillo County, New Mexico, on the west side of New Mexico Highway 337 (see fig. 1 of Kues, this volume). At the locality, approximately 28 m of gray and brown shale, mudstone, siltstone, and sandstone units form the quarry walls; the base of the quarry is a dark-gray argillaceous limestone (see fig. 2 of Kues, this volume). The entire sequence has been assigned to the Pine Shadow Member of the Wild Cow Formation (Madera Group) that Myers (1973, 1988) dated as early to middle Virgilian on the basis of fusulinids recovered from strata near, but not at, the quarry. However, conodonts from the Kinney Quarry may indicate a slightly older age (late Missourian to earliest Virgilian). Recently, James E. Barrick and Thomas M. Lehman of Texas Tech University (written comm. 1991) recovered conodonts from a small number of samples including the fish bed and surrounding strata at the Kinney Quarry. The conodonts identified by Barrick include representatives of *Streptognathodus firmus* and *Idiognathodus simulator*. The co-occurrence of *S. firmus* and *I. simulator* indicates latest Missourian to early Virgilian for the Kinney Quarry based on range data from the Midcontinent presented by Barrick & Boardman (1989) and Boardman & Heckel (1990). According to Barrick, preliminary analysis of the specimens of *I. simulator* recovered from the Kinney Quarry demonstrates more similarity to late Missourian representatives of the species when contrasted to those of the early Virgilian.

The cephalopods that form the basis of this report were, with one exception, recovered from the basal limestone units. The single exception is an orthoconic nautiloid (UNM 10945; Fig. 1.2) recovered from a brown shale several meters above the basal limestone. The faunal groups recovered from the limestone units in association with the cephalopods include conodonts *(Idiognathodus, Streptognathodus,* and *Anchignathodus* from unit 2 or 3 of Lucas & Huber, 1991), spirorbid worms, brachiopods, ostracodes, conchostracans, several groups of fishes, bivalves, gastropods, and extremely rare bryozoans and crinoid-stem fragments (Kues, this volume). Fossil plants preserved as carbon impressions also co-occur with the cephalopods. Coprolites, presumably from both invertebrates and vertebrates, are also common.

The clastic units above the basal limestone appear to have been deposited in a distal to proximal prodeltaic environment (Lucas & Huber, 1991; Lehman, 1991). Nonmarine fossils recovered above the basal limestone include plants, arthropods (insects, millipedes, eurypterids, smooth-shelled ostracodes, conchostracans, malacostracans), fish, and amphibians (see other reports in this volume).

The preservation of the single cephalopod from a shaly unit higher in the section is different from the basal-limestone cephalopods in that it is preserved three-dimensionally (Fig. 1.2). All of the specimens from the basal limestone are crushed impressions and most lack the test (for the best preserved specimens see Fig. 1.1, 1.3-1.8). One orthoconic-nautiloid fragment (unnumbered) retains the impressions of spirorbid worms. The single three-dimensionally preserved orthoconic nautiloid (Fig. 1.2) exhibits a series of transverse breaks which show that the internal deposits are obscured by corrosion and/or recrystallization to sparry calcite.

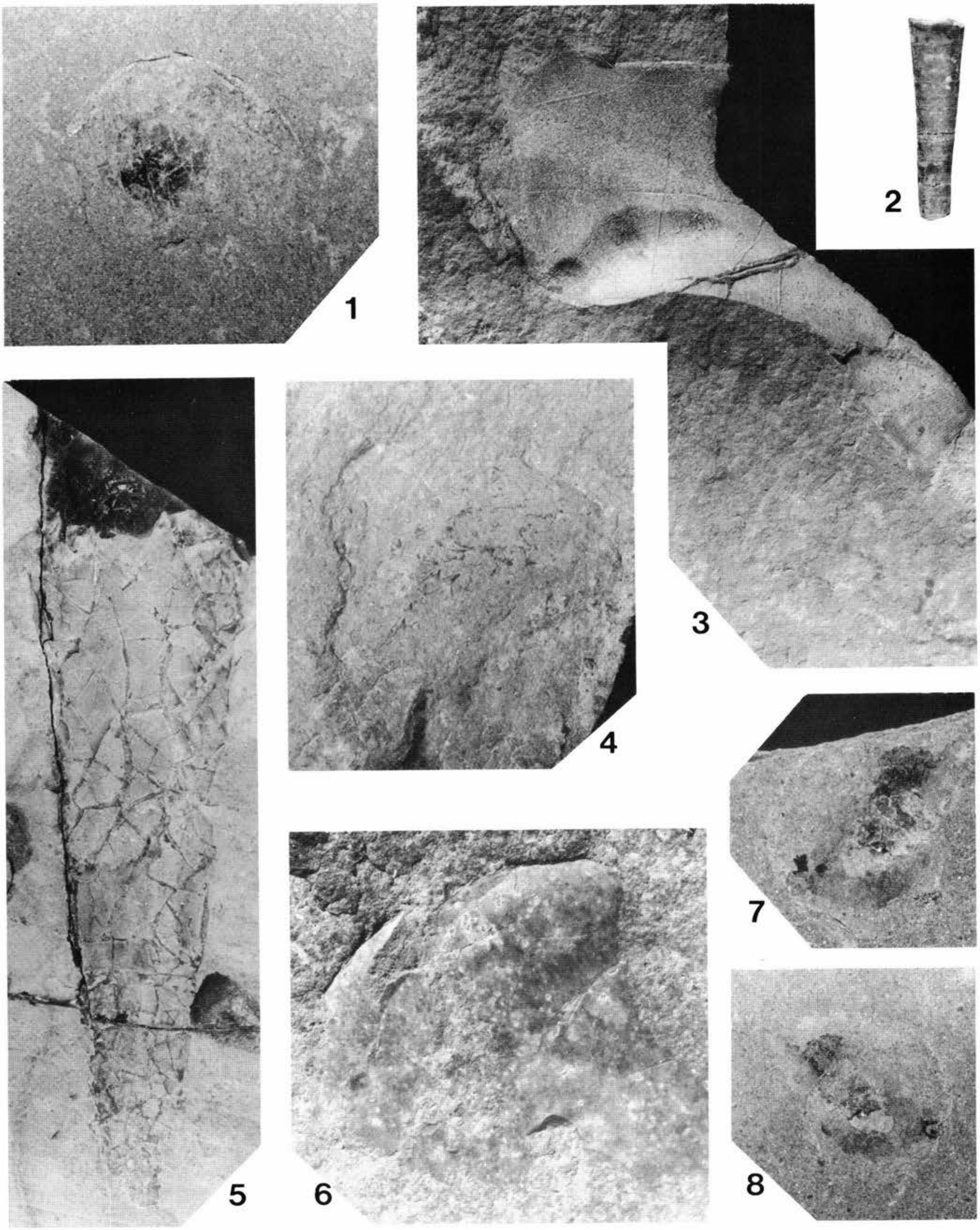

FIGURE 1—Cephalopods from the basal limestone (except number 2) at the Kinney Quarry, New Mexico. **1,** Crushed ammonoid with intact body chamber and a thick carbon area at the center of the specimen, NMMNH P-16062, ×4.5. **2,** *Pseudorthoceras knoxense* (Mc Chesney 1860) from unit 4 or 5 (see Kues, this volume, fig. 2), UNM 10945, ×1.3. **3,** Unidentified coiled-nautiloid fragment showing umbilical and ventrolateral nodes, UNM 10759, ×2.8. **4,** Internal mold of a crushed and distorted *Prothalassoceras kingorum* phragmocone showing traces of the suture pattern, UNM 10754, ×5.1. **5,** Unidentified crushed orthoconic nautiloid, unnumbered, ×1.4. **6,** Crushed ammonoid body-chamber fragment showing the venter and umbilical area, UNM 10763, ×3.5. **7, 8,** Counterpart and part, respectively, of a crushed but complete ammonoid. The body chamber contains two dark (carbon-rich?) areas that can be interpreted as possible mandibles and stomach/alimentary-canal contents. NMMNH P-16061, ×3.8.

Taxonomy and biostratigraphy

The collection of cephalopods contains 41 specimens. Ammonoids (both complete and fragmentary conchs) dominate the assemblage (N = 26). Orthoconic nautiloids are less numerous (N = 14), and coiled nautiloids are represented by a single impression of a conch fragment.

Late Paleozoic ammonoids are best identified by ornament patterns, conch proportions, and especially suture patterns. Only one of the ammonoids (UNM 10754) preserves a suture pattern (Figs. 1.4, 2). This suture pattern, together with the impressions of ornament and estimated conch shape and dimensions of the remaining specimens, strongly suggests that all of the ammonoids belong to *Prothalassoceras* (Late Pennsylvanian to Early Permian). Several species of this taxon have been described from Upper Pennsylvanian strata (see Beinert, 1971, for a summary). The suture configuration in the Kinney Quarry specimen (Fig. 2) is closest to *P. kingorum*, which ranges from middle Missourian to perhaps middle Virgilian.

Orthoconic nautiloids from the Kinney Quarry are, with one exception (Fig. 1.2), poorly preserved impressions that are crushed and fragmentary; Fig. 1.5 is the best preserved specimen. All but the single exceptional specimen (UNM 10945; Fig. 1.2) from the shaly unit are unidentifiable. The UNM 10945 specimen is smooth-shelled, with no discernible ornament. The preserved phragmocone is approximately 78 mm long with an oral lateral diameter estimated, due to partial crushing, at 11.5 mm, and an uncrushed apical lateral diameter of 3.2 mm. The total length of the specimen based on the body-chamber impression in the sediment must have exceeded 117 mm; the apical end, including several chambers and the protoconch, is not preserved. Overall, the conch is slightly depressed, with the dorsoventral diameter being slightly less than the lateral diameter.

Internal structures of this three-dimensional specimen are not particularly well preserved in the dorsal portion of the phragmocone due to significant crushing and corrosion of the cameral deposits. The small-diameter siphuncle (0.5 mm at a dorsoventral diameter of 4.5 mm) is placed slightly ventrad of the center. The configuration of the septal necks and cameral deposits cannot be determined on the basis of the available material. Nevertheless, external morphology, siphuncle position, as well as size and general configuration of the internal deposits as viewed on broken surfaces, suggest strong similarities to *Pseudorthoceras knoxense* (Mc Chesney 1860). This is a rather common taxon in the middle and Upper Pennsylvanian marine sediments, which tended to prefer moderate-depth to shallow water and well oxygenated environments (Boardman et al., 1984).

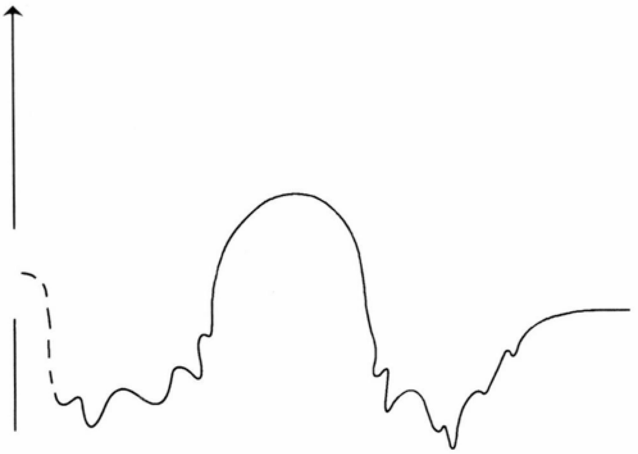

FIGURE 2—Composite sutural diagram of *Prothalassoceras kingorum* from specimen UNM 10754, showing digitations on the prongs of the ventral and lateral lobes. Conch height and diameter are estimated to be 5.8 mm and 13.0 mm, respectively.

The single coiled-nautiloid specimen (UNM 10759; Fig. 1.3) is an impression of a fragment of a widely umbilicate taxon which exhibits blunt umbilical and ventrolateral nodes. The maximum diameter of the intact specimen is estimated to have exceeded 60 mm, with a corresponding umbilical diameter at the umbilical shoulder of 33 mm. The specimen apparently represents a fragment of body chamber, since no traces of septa are preserved. Growth lirae outline a shallow lateral (ocular) sinus and part of a ventrolateral salient. Although the fragmentary nature of this specimen precludes positive generic reference, its widely umbilicate, nodose conch form is reminiscent of both *Metacoceras* and *Tainoceras.* As both of these genera are known to range throughout the Pennsylvanian and Permian, the specimen cannot be considered a diagnostic biostratigraphic index.

Preservation of soft parts

Preservation of soft parts in late Paleozoic cephalopods is an extraordinarily rare phenomenon. To date, there are three major preservational modes that preserve cephalopod soft parts including arm impressions, mandibles, radula, and stomach/gut contents. Two of these three preservational modes are best typified by the classic regional occurrence, namely the Pennsylvanian-age Mazon Creek ironstone concretions in Illinois (and elsewhere) (Baird, 1979; Saunders & Richardson, 1979; Baird et al., 1984) and the Mississippian Bear Gulch Limestone in Montana (Williams, 1981; Cox, 1986; Mapes, 1987). The third and less well known occurrence ranges in age from Mississippian to Permian, with preservation of soft parts being confined to the interiors of phosphate nodules that formed in basinward marine shales deposited in low-oxygen environments (Mapes, 1987).

A single specimen (NMMNH P-16061; Fig. 1.7 counterpart and 1.8 part) from the Kinney Quarry exhibits features within its body chamber that probably reflect preservation of soft parts. A comparison of specimen NMMNH P-16061 with similarly preserved ammonoids from the Bear Gulch fauna of Montana (Mapes, 1987: fig. 2) suggests that the dark (carbon-rich?) area at its aperture is the remnants of mandibles. Similarly, a second carbon-rich area farther within the body chamber could conceivably represent stomach or alimentary-canal contents. A second specimen (NMMNH P-16062; Fig. 1.1) contains dark areas within the phragmocone that may correspond to the ventrally positioned siphuncle.

Paleoecology and taphonomic/biostratonomic considerations

Of all the cephalopods, the ammonoids provide the best data set that can be utilized for determination of paleoecological interpretations and taphonomic/biostratonomic considerations. The coiled and orthoconic nautiloids are less helpful in determining these phenomena because their paleoenvironmental tolerances are less restricted. Because of the overall poor preservation, small data-base size, and questionable identification for many of the ammonoid specimens, the conclusions suggested herein must be considered speculative.

As interpreted herein, the entire ammonoid population is monospecific. Considering that more than 60% of the ammonoids are represented by fragmentary body chambers that would have no ability to maintain independent buoyancy when separated from the phragmocone, the assemblage must represent the product of either scavenged shells derived from an autochthonous (or allochthonous) population on the bottom, or the predation of a living, low-diversity population at the Kinney Quarry site. If the population was transported from the nearby marine environment as a nekroplantic accumulation into the Kinney area, a higher diversity of ammonoids would be expected. Virtually all Midcontinent Pennsylvanian occurrences interpreted as allochthonous contain at least three to five genera when 25 or more specimens are recovered. Occurrences interpreted as autochthonous almost always have five or more genera unless severe salinity and/or oxygen stress are a factor. As for the possibility that the shell fragments are a product of scavenging of empty conchs on the bottom, there is no fossil evidence at Kinney Quarry that scavenging occurred. The only known potential scavengers at Kinney Quarry that co-occur with the cephalopods are fish. Modern fish are known to break the conchs of living *Nautilus* (Saunders et al., 1989), but there is no documentation of fossil or modern fish scavenging by shell breakage of ectochleate cephalopod conchs. Additionally, there is no evidence for bioturbation or current activity sufficiently strong to break the conchs (Kues, this volume). Conversely, there is abundant direct evidence that modern cephalopods are opportunistic predators and cannibals (see Saunders et al., 1987, for a summary); fossil cephalopods presumably were similar in this respect. Additionally, fish of several types recovered at Kinney Quarry could also fill the role of cephalopod predator.

An additional piece of evidence supporting predation is the size ratio of complete conchs and conch fragments. In the ammonoid populations recovered from the Midcontinent, conclusions on predation are based in part on presence or absence of body chambers (Sims et al., 1987) and tooth marks (Kauffman & Kesling, 1960; Mapes & Hansen, 1987; Hansen & Mapes, 1990). In the Midcontinent samples, there is a clear pattern of size selection of cephalopod prey. Small-diameter conchs appear to be less frequently predated (i.e. exhibit no puncture holes and retain body chambers), whereas larger conchs tend to be represented by incomplete phragmocones lacking body chambers, and sometimes the conchs exhibit punctures. Preliminary non-statistical analysis of more than 50,000 Midcontinent middle to Late Pennsylvanian (Desmoinesian—Virgilian) ammonoids suggests that a size threshold separating non-predated from predated ammonoids occurs at a conch diameter of about 30 mm. At the Kinney Quarry, approximately 50% of the conchs below 15 mm diameter are complete, whereas 100% of the conchs above 15 mm are preserved as fragments (compare A, B, and C in Fig. 3). All but one of the ammonoid fragments are pieces of body chamber. These fragments do not exhibit any punctures, suggesting the predators had a crushing or cutting attack mode rather than a stabbing offensive armament that would produce shell punctures. There is also a clear selection toward body chambers of the larger ammonoids which contain the soft parts rather than the phragmocones which contain virtually no tissue.

The mode of some ammonoid preservation in the basal limestone unit at Kinney Quarry resembles that of the Bear Gulch Limestone (see Mapes, 1987, and Landman & Davis, 1988, for additional examples). In some of the Bear Gulch cephalopod fauna (which is moderately diverse, with collections containing hundreds of ammonoids and coiled and orthoconic nautiloid specimens) preservation of soft parts is moderately common. At Bear Gulch, in-situ mandibles are frequently preserved as carbon films and stomach/alimentary-canal contents have been documented (Mapes, 1987; Landman & Davis, 1988). The single occurrence from the Kinney Quarry of an intact complete ammonoid (Fig. 1.7, 1.8) with similar carbon thickenings in the body chamber in the appropriate places for mandibles and perhaps stomach/alimentary-canal contents is striking in its similarity with the Bear Gulch Limestone occurrences which have been interpreted as deposited in a deep-water, normal marine salinity environment with low oxygen (see Cox, 1986, Mapes, 1987, and Williams, 1981, for summaries).

The paleoecologic conditions that prevailed during the time the basal limestone unit was being deposited will continue to be a subject of debate by paleontologists. The cephalopod fauna only indirectly provides information on depositional conditions prevailing during deposition of the basal limestone. Autochthonous ammonoids in Pennsylvanian deposits of the Midcontinent tend to be recovered from offshore, shelf-edge and middle-shelf deposits with normal marine salinities (see Boardman et al., 1984, for a summary). Typically the cephalopod diversities in these conditions are moderate to high, with 5 to 20 ammonoid taxa being recovered. Some instances of low-diversity ammonoid assemblages associated with low-oxygen conditions have been documented (Boardman et al., 1984). Ammonoids recovered from the most offshore parts of Pennsylvanian cyclothems (black, fissile shales deposited under very low-oxygen conditions) commonly contain fewer than five species. Offshore, very low-oxygen conditions are manifested by lack of benthic organisms (with no evidence of bioturbation) along with a diverse pelagic fauna including radiolarians and conodonts. Additionally, abundant non-skeletal phosphate and a wide variety of geochemical signatures add corroborative support to the contention that the black shales were deposited under very low-oxygen conditions.

Salinity was probably not responsible for the low ammonoid diversity at Kinney Quarry. In a number of Pennsylvanian cyclothems in the Midcontinent and Appalachian Basin, essentially monotypic ammonoid autochthonous occurrences of large numbers of *Neoaganides* have been observed at sites where independently confirmed nearshore, brackish-water conditions existed. In these settings, *Neoaganides* occurs with the conodont genus *Adetognathus*. The *Adetognathus (= Cavusgnathus* of some workers) biofacies is widely accepted as representing a nearshore, euryhaline environment (Heckel & Baesemann, 1975; Merrill & von Bitter, 1976). *Adetognathus* has not yet been recovered at Kinney Quarry, only *Streptognathus*, *Anchignathodus*, and *Idiognathodus* have been recovered from the cephalopod-bearing limestone. These latter taxa are considered to be exclusively marine.

In conclusion, the low-diversity ammonoid fauna (one genus and species) at Kinney Quarry is interpreted on the basis of indirect evidence as an autochthonous population subjected to significant size selection by predators. Larger ammonoids were probably preyed upon more frequently than smaller individuals. The coiled and orthoconic nautiloids from the basal limestone presumably also formed part of this community, and were similarly preyed upon since they are preserved as highly fragmented body chambers and partial phragmocones. Paleoecologic conditions as based on Midcontinent occurrences and the Bear Gulch lithic and preservational similarities suggest that the cephalopods at Kinney lived in somewhat deeper water as compared to nearby water depths, and that low-oxygen conditions prevailed at or below the sediment/water interface. Salinities can probably be ruled out as a cause for environmental stress because normal-marine conodonts which are intolerant of reduced salinities coexisted with the cephalopods. The cephalopod diversity was probably limited because of the low oxygen levels and perhaps little connection with other offshore areas (Lehman, 1991).

The single orthoconic-nautiloid specimen recovered somewhat higher in the stratigraphic succession is probably a stray from the nearby marine environment that managed to swim into the restricted prodeltaic environment. The animal could not have floated into the environment after death because the internal cameral deposits in the phragmocone

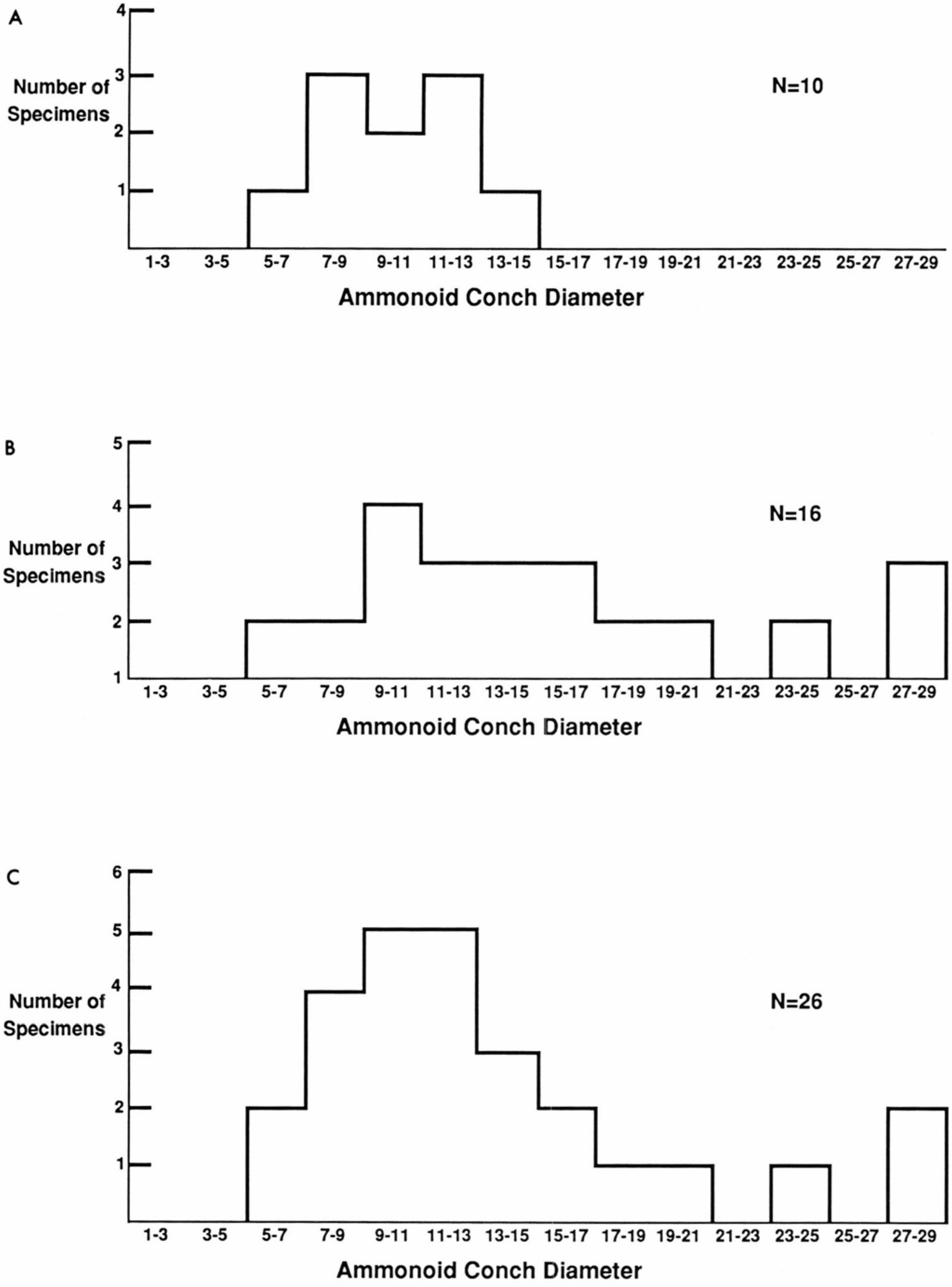

FIGURE 3—Frequency diagrams of **(A)** diameter distribution (in mm) of complete (body chamber and phragmocone) ammonoid conchs, **(B)** estimated-diameter distribution (in mm) of body-chamber and phragmocone (only one) fragments of ammonoid conchs, and **(C)** estimated-diameter distribution (in mm) of conch fragments and complete ammonoid conchs from the basal limestone unit at the Kinney Quarry, New Mexico. No corrections for diameter increase due to crushing have been calculated.

would have caused the conch to immediately sink. Also, the overall completeness of the phragmocone and body chamber would appear to rule out that the conch has been brought into this environment by, or inside, a predator. Thus, the animal was probably killed by osmoregulatory imbalances produced when a stenohaline marine organism enters a brackish- to fresh-water environment.

Acknowledgments

We wish to thank Barry Kues, Sergius H. Mamay, and Jiri Zidek for their assistance in obtaining the Kinney Quarry specimens used in this analysis. Also, the helpful discussions and the manuscript review by Barry Kues regarding the locality provided meaningful insight and background into the cephalopod occurrences at Kinney Quarry. We also wish to thank David Work for his very helpful review of this manuscript. Acknowledgment is made to the donors of the Petroleum Research Fund, administered by the American Chemical Society, for partial support of this research (PRF No. 15821AC2 and PRF No. 20742-B8-C) to R.H.M. and to the Ohio University Research Committee.

Postscript

After this manuscript was completed, Mr. Phil Huber indicated that specimens NMMNH P-16061 and 16062 are from unit 2 which immediately overlies the basal limestone, and that the unique three-dimensionally preserved orthoconic nautiloid UNM 10945 is from unit 7 of Lucas & Huber (1991). The unique nature of the specimens from unit 2 with their preservation of soft parts has already been described, and the information that they were obtained from a different unit is appreciated. Also appreciated is the information about the precise interval that yielded the orthoconic nautiloid; the osmoregulatory scenario given herein is not negated by this new information.

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Enigmatic vermiform fossils from Upper Pennsylvanian rocks at the Kinney Brick Quarry, New Mexico

Joseph T. Hannibal

Cleveland Museum of Natural History, 1 Wade Oval Drive, University Circle, Cleveland, Ohio 44106-1767

Abstract—Two elongate specimens from the Kinney Brick Quarry, New Mexico, show indications of segmentation. These vermiform specimens differ from other forms described from the Kinney Brick Quarry but the lack of clearly delineated features precludes identification.

Introduction

In the course of a study of terrestrial arthropods from the Kinney Brick Quarry, Dr. Sergius Mamay of the U.S. National Museum (USNM) brought to my attention a small collection of elongate fossils in the USNM. He collected these specimens from the Kinney Brick Quarry during the late 1960's. One of these specimens (USNM 450760) has been identified as a diplopod and is described and illustrated by Shear et al. (this volume: fig. 3B, C). The identity of the other specimens in this collection proved to be enigmatic. However, two of these specimens are of special interest because of their relatively large size and the presence of features dissimilar to those of other described specimens from the Kinney Brick Quarry. These specimens may document the presence of additional taxa in the Kinney biota.

Descriptions

USNM 450761

This elongate, flattened specimen (Fig. 1A) has a preserved length, measured along its axis, of 46 mm. It has an irregular outer boundary and varies in width (exclusive of a light halo) from 4.2 to 7.2 mm. The specimen is preserved primarily as a layer of light-brown material against darker matrix. There is finely comminuted carbonized material in this light-brown area and there are several polygonal, carbonized, platelike elements on the sides of the specimen at about its midpoint, where the width is most restricted. A light yellowish-brown rim, or halo, extends from the specimen into the matrix. At places, irregularly elongate "fingerlike" portions of the halo extend outward.

Light-colored halos similar to the one surrounding this specimen are also found surrounding plant material from the Kinney Brick Quarry (see, for instance, fig. 7b in Mamay & Mapes, this volume). Small ovoid molds that may represent ostracodes are associated with both the fossil and the halo.

USNM 450762

This elongate specimen (Fig. 1B-D) has a preserved length, measured along its axis, of approximately 13.5 cm. Its width averages about 5 mm. The specimen has slightly raised areas, resembling segments, preserved on one half of the matrix (USNM 450762B, "the part") and grooves and wedge-shaped indentations on the other half of the matrix (USNM 450762A, the "counterpart"). More than 50 "segments," ranging from about 1 to 2 mm in length, are present. In places a thin layer of carbon is associated with the specimen. Originally, a carbonized layer may have covered the entire specimen.

This specimen is larger and has more indication of segmentation than USNM 450761. In its segmentation it more closely resembles a fragmentary specimen (USNM 235643) noted by Schram & Schram (1979) as being a possible myriapod and noted as being unidentifiable by Shear et al. (this volume). The fragmentary specimen is 11 mm long and has indications of about 14 "segments."

Some arthropod remains, including a fairly complete specimen of the crustacean *Uronectes kinniensis* Schram & Schram 1979, are located about 1 cm away from, and on the same bedding plane as, USNM 450762. Because the crustacean fossil includes relatively well preserved cuticular material, the absence of such material associated with USNM 450762 might be taken as an indication that USNM 450762 lacked similarly robust cuticular material. There are also ostracodes associated with this specimen.

Discussion

Both USNM 450761 and USNM 450762 are in the same general size range and both have an elongate shape, but differences such as the presence or absence of carbonized plates indicate that these two specimens are probably unrelated, representing two separate taxa.

Although these specimens are associated with carbonized material, they do not seem to have any morphological features to suggest that they are plants. Furthermore, Mamay, who has long worked with plant material from the Kinney Brick Quarry and who has collected these specimens, asserts (pers. comm.) that they are not plants. Because they are associated with some organic, carbonized material, as are some other Kinney Brick Quarry fossils, they are probably not trace fossils—at least not ones representing movement of an animal through sediment.

In their overall shape and in the various indications of segmentation, these forms resemble, at least superficially, some soft-bodied vermiform organisms such as onychophorans and various worms. Vermiform organisms, particularly polychaete worms, are known in great numbers from the Mazon Creek deposits of Westphalian D age in Illinois (Thompson & Johnson, 1977; Thompson, 1979). Such fossils could be expected in other Carboniferous rocks that were deposited in similar settings. Indeed, Lucas & Huber (1991: 84) noted the presence of fossil worms at the Kinney Brick Quarry. However, those worms were not documented with descriptions or illustrations.

The mode of preservation of soft parts in the Mazon Creek polychaetes, "as light color markings against the darker rocks, as carbon films; as molds; and as the altered cuticle"(Thompson, 1979: 172), also resembles the mode of preservation of the Kinney Brick Quarry specimens described here. These Kinney Brick Quarry enigmatic fossils are also in the same size range as the Mazon Creek polychaetes. One or both of the Kinney Brick Quarry specimens may represent the remains of worms, but the lack of clearly delineated features precludes identification.

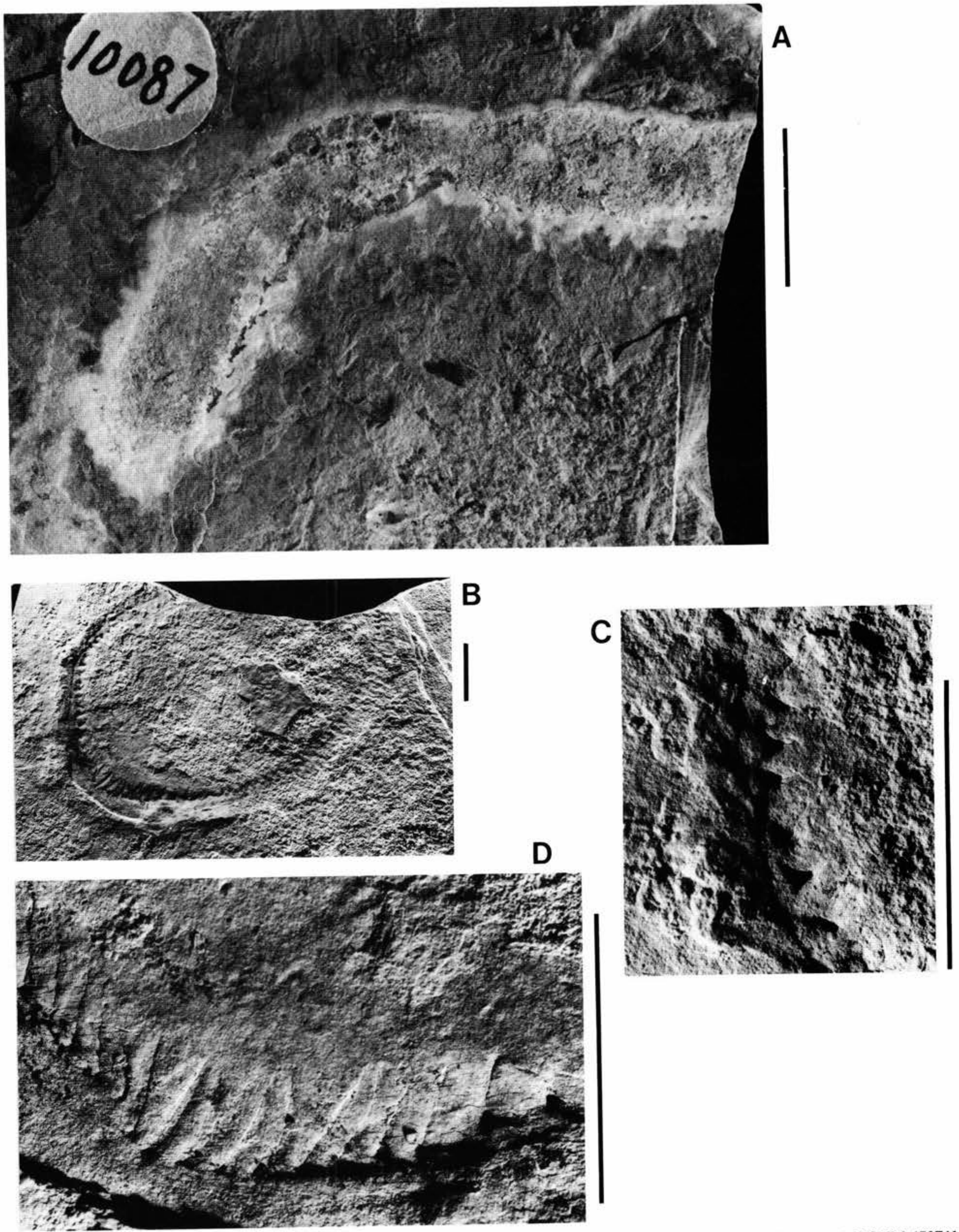

FIGURE 1—Vermiform fossils from the Kinney Brick Quarry (specimens unwhitened). All scale bars equal 1 cm. **A,** USNM 450761. **B,** USNM 450762A ("counterpart"). **C,** Close-up of portion of USNM 450762A seen in upper left of B; note wedge-shaped indications of segmentation. **D,** Close-up of groovelike indications of segmentation along midsection of USNM 450762A.

Acknowledgments

Sergius Mamay, U.S. National Museum, initiated the loan of, and provided information on, the specimens described herein. Bruce Frumker, Cleveland Museum of Natural History, took the photographs reproduced in Fig. 1. This paper was improved by the comments of Drs. Rodney Feldmann of Kent State University and Loren Babcock of Ohio State University.

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Preliminary report on Late Pennsylvanian Conchostraca from the Kinney Brick Quarry, Manzanita Mountains, New Mexico

Heinz Kozur[1], Spencer G. Lucas[2], and Adrian P. Hunt[2]

Reis a *u. 83, H-1029 Budapest, Hungary;* [2]*New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, New Mexico 87104*

Abstract—The conchostracan *Pseudestheria* sp. is present in the upper part of unit 1 and the lower part of unit 3 of the lower Virgilian(?) strata exposed at the Kinney Brick Quarry, Manzanita Mountains, New Mexico. Conchostraca are rare in the upper part of unit 1 and are represented almost exclusively by juveniles and subadults who have not attained sexual maturity. The unit 1 immature conchostracans occur on bedding planes with pliohaline brackish-water to low-salinity brachyhaline marine invertebrates, whereas the one bedding plane in unit 1 with adult conchostracans produces a mesohaline brackish-water fauna. In contrast, the lower part of unit 3 produces conchostracans of all ontogenetic stages, and the adult stages, some with preserved eggs, dominate. In unit 3, fossils on the same bedding planes as the conchostracans indicate a mio- to mesohaline brackish-water environment. On one bedding plane, only subadult specimens of *Pseudestheria* are present with small specimens of the pectinid bivalve *Dunbarella,* indicating that the salinity-tolerance boundary for conchostracans was exceeded.

Introduction

Nearshore marine and lagoonal strata exposed at the base of the Virgilian (?) section in the Kinney Brick Quarry contain a diverse biota characterized by many excellently preserved specimens (Lucas & Huber, 1991). Lucas & Huber (1991: table 1) listed the flora and fauna from the Kinney Brick Quarry reported through 1990, including unidentified conchostracans which are reported on here.

These conchostracans were collected from the upper part of unit 1 and the basal portion of unit 3 of the measured section of Lucas & Huber (1991: fig. 4; also see Kues & Lucas, this volume). Some conchostracans are present in units 2 and 4, but these were not studied. Unit 1 is dark-gray to black manly limestone, whereas unit 3 is a gray, calcareous shale. Conchostracans are rare and occur mostly as isolated individuals in unit 1, but in unit 3 they are very common and occur both in unidentifiable clusters and as isolated individuals. Their shells are usually phosphatized and deformed to some extent. However, some slightly deformed or undeformed specimens can be identified as *Pseudestheria* sp. Further studies of the Kinney conchostracans and their comparison with latest Carboniferous and Early Permian Conchostraca from the European Rotliegendes (Holub & Kozur, 1981; Kozur, 1989) are underway by Kozur. All specimens described here are in the collection of the New Mexico Museum of Natural History (NMMNH).

Systematic paleontology

Genus *PSEUDESTHERIA* Raymond 1946

PSEUDESTHERIA sp.

Figs. 1, 2

Description—Carapace medium large and high, with greatest height somewhat behind the midline; dorsal margin long and straight, 0.62-0.69 of carapace length; anterior margin broadly rounded, its lower part somewhat obliquely rounded, and its largest rounding at mid-length; posterior margin somewhat higher than anterior margin, sharply set off from the dorsal margin, in the oblique upper part straight or only slightly rounded and in the lower part broadly rounded, greatest rounding somewhat below mid-height; ventral margin strongly convex, nearly symmetrically rounded, and with the greatest rounding somewhat behind mid-length; smooth umbonal area small, 0.9 mm in maximum length and about 0.5 mm high; the following 24 growth lines very indistinct and not visible in poorly preserved specimens, suggesting a larger umbonal area than is actually present; inner 11-16 growth lines (until subadult stage) narrow to moderately wide, outer growth lines narrow, and outermost growth lines very narrow; 28-41 growth lines present in adults; growth lines smooth to finely pitted; eggs sometimes present; representative measurements listed in Table 1.

Occurrence—Pine Shadow Member of Wild Cow Formation, early Virgilian?, Kinney Brick Quarry, Manzanita Mountains, New Mexico. Based on fusulinids, Myers (1982, 1988) assigned a Virgilian age to the entire Pine Shadow Member. However, some fossils suggest an age as old as Missourian for the strata exposed at the Kinney Quarry. Thus, conodonts identified by R. Burton and listed, but not illustrated or described, by Kelley & Northrop (1975) include only one taxon restricted to the Virgilian, *Streptognathodus elegantulus.* The other taxa listed either are long ranging conodonts or indicate a Missourian or even older age (Kozur, 1984).

TABLE 1—Measurements (in mm) of selected specimens of *Pseudestheria* sp. from unit 3 at the Kinney Brick Quarry. Measurements follow the protocol of Tasch (1987: fig. 18) but, because of distortion of many specimens, not all of the measurements he lists are presented.

length	height	growth lines	ontogenetic stage
3.2	2.5	13	subadult
3.3	2.4	12	subadult
3.3	2.3	12	subadult
3.5	2.6	—	subadult
3.2	2.6	20	subadult
4.0	3.5	35	adult
4.0	3.4	38	adult
4.1	3.5	41	adult
4.3	3.5	35	adult
4.8	3.6	28	adult
5.0	4.3	29	adult

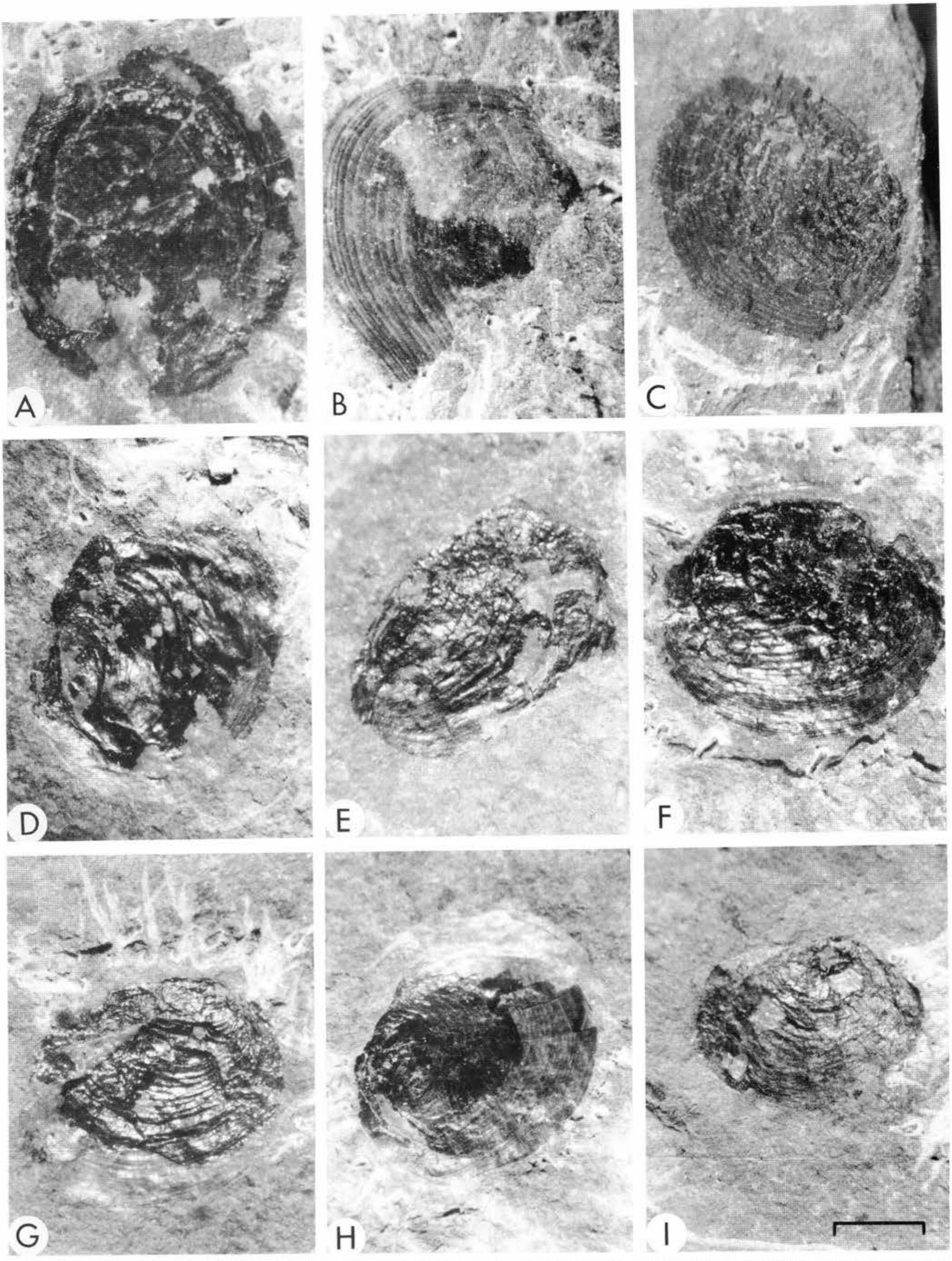

FIGURE 1—*Pseudestheria* sp. from unit 3 at the Kinney Brick Quarry. **A,** NMMNH P-19123; **B,** NMMNH P-19124; **C,** NMMNH P-19125; **D,** NMMNH P-19126 (note eggs); **E,** NMMNH P-19127; **F,** NMMNH P-19128; **G,** NMMNH P-19129; **H,** NMMNH P-19131; **I,** NMMNH P-19129. Scale bar = 1 mm.

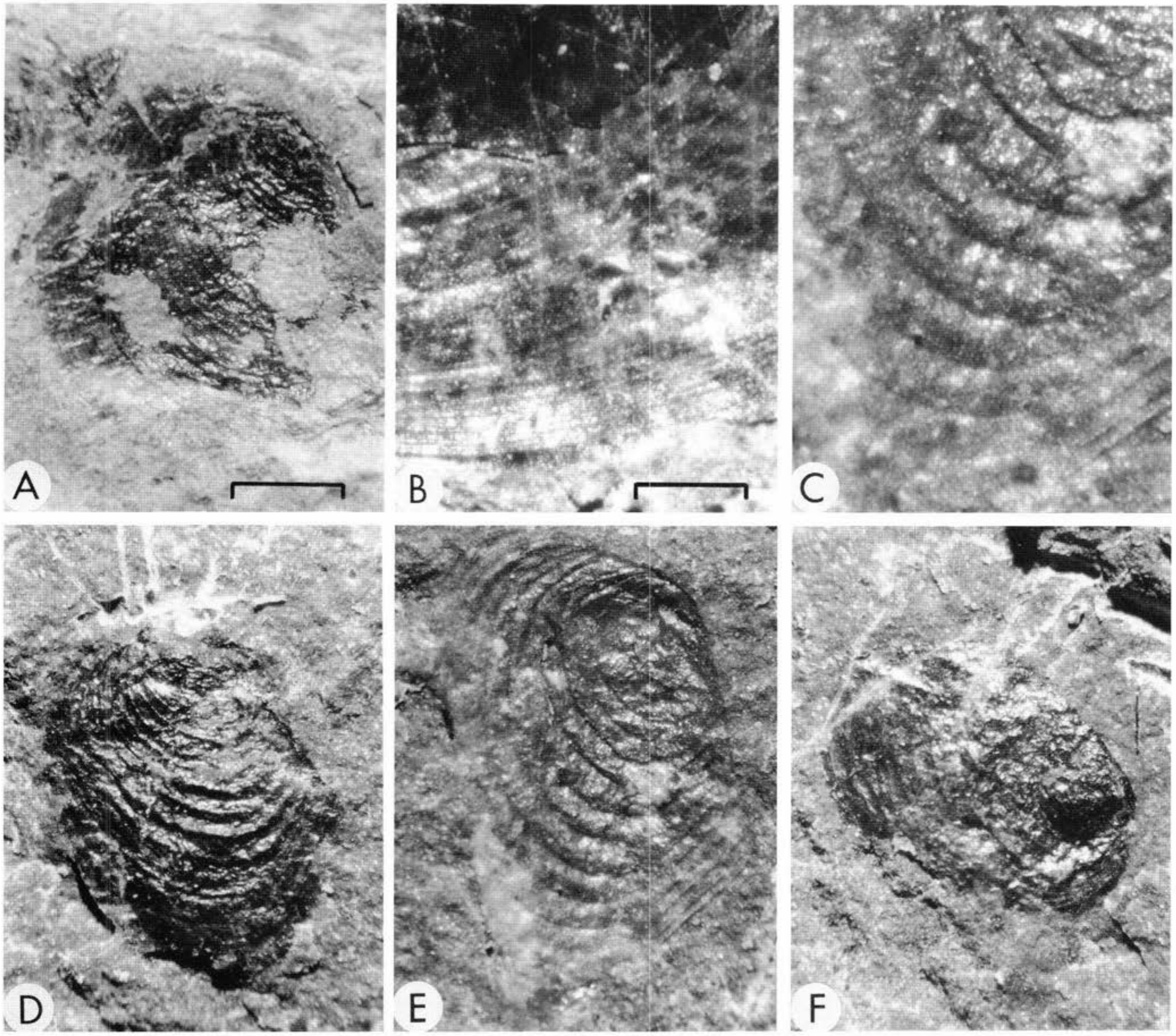

FIGURE 2—*Pseudestheria* sp. from unit 3 (A–C) and unit 1 (D–F) at the Kinney Brick Quarry. **A,** NMMNH P-19130; **B,** outer growth lines of NMMNH P-19131; **C,** inner growth lines of NMMNH P-19132; **D–F,** NMMNH P-19132. Scale bar = 1 mm for A and D–F, and 0.5 mm for B and C.

Fossil-plant assemblages from most of the Kinney Quarry section are dominated by *Walchia,* but lack callipterids (Lucas & Huber, 1991). The oldest callipterids are of late Missourian age, and callipterids generally are present in meso- to xerophilic Virgilian plant assemblages. The lack of callipterids at the Kinney Quarry may be related to provincialism, or it may indicate an age older than latest Missourian.

Remarks—The Kinney conchostracans clearly pertain to *Pseudestheria* as originally defined by Raymond (1956). Tasch (1969) considered *Pseudestheria* to be a junior subjective synonym of *Cyzicus (Lioestheria),* but we use the name *Pseudestheria* pending a revision of the European *Pseudestheria* fauna underway by Kozur. The identity at the species level of the Kinney conchostracans will have to await completion of this revision.

Paleoecology

Carboniferous to Recent associations that include adult Conchostraca occur only in fresh-water to mesohaline brackish-water environments (Tasch, 1969; Kozur, 1971; Webb, 1979; Kozur & Seidel, 1983). In environments where salinity may have changed rapidly, such as those represented by the strata exposed at the Kinney Brick Quarry, conchostracans can only be used to interpret the paleoecology of the actual bedding planes on which they are present.

The upper part of unit 1, except for one bedding plane, produces only juvenile and subadult conchostracans. No mass occurrences, as are common in unit 3, are present in unit 1 where conchostracans are always found as isolated, scattered specimens. This suggests that the unit 1 conchostracans were not able to attain maturity and reproduce in the habitat in which they lived. Thus, it seems likely the unit 1 conchostracans reproduced in a different habitat than that in which they are fossilized, probably one of lower salinity. Indeed, the megainvertebrate assemblage of unit 1 (Kues, this volume) contains bivalves and brachiopods indicative of a brachyhaline marine environment. This is reinforced by the unit 1 ostracode fauna, which consists almost exclusively of *Paraparchites,* a euryhaline marine ostracode genus with a salinity tolerance that ranges from pliohaline brackish to slightly hypersaline. A few *Geisina* also are present. These ostracodes suggest a unit 1 environment within the range of pliohaline brackish (salt content 1.0-1.8%) to low-salinity brachyhaline marine (brachyhaline I of Kozur, 1971, 1972; salt content about 2%).

Juvenile conchostracans apparently invaded this environment from adjacent, more favorable habitats of lower salinity, but only lived for a short time, dying before they could reach sexual maturity. The salinity of water in which unit 1 was deposited exceeded the upper tolerance for the reproductive phase of the conchostracan life cycle. One bedding plane in unit 1, however, is an exception. This bedding plane yielded two adult specimens of *Pseudestheria* and no indicators of pliohaline brackish to brachyhaline marine water, such as *Dunbarella, Myalina,* and *Paraparchites.* It does, however, contain a specimen of *Carbonita.* This suggests a brief influx of fresh water during the deposition of this bedding plane, and lowering of salinity to mesohaline brackish.

The bedding planes with conchostracans from the lower part of unit 3 also contain the following fossils: ostracodes (abundant *Carbonita* and *Darwinula,* and less common *Geisina),* rare specimens of the inarticulate brachiopod *Lingula,* fish scales, and, on one bedding plane that contains only subadult specimens of *Pseudestheria,* small specimens of the pectinacean bivalve *Dunbarella.*

Bedding planes with abundant specimens of the freshwater ostracodes *Carbonita* and *Darwinula, a few Geisina* (marine to brackish-water ostracodes), and abundant conchostracans suggest miohaline (0.3-0.5% salt) brackish-water environments. Those with abundant perprimitiids, rare *Carbonita,* and abundant conchostracans indicate mesohaline (0.5-1.0% salt) brackish-water environments. The co-occurring *Lingula* (only tiny juveniles) has a lower salinity tolerance of meso-/pliohaline, and the co-occurring *Dunbarella* must have been euryhaline. Clearly, more detailed, bedding plane by bedding plane collecting in the basal part of unit 3 is needed to develop a precise salinity history of this unit, which includes beds deposited under mesohaline to miohaline conditions. However, in general the abundance of a low-diversity conchostracan fauna in this unit indicates a mesohaline brackish-water environment for the basal part of unit 3.

Only the bedding plane in unit 3 with abundant small *Dunbarella* could have been deposited under pliohaline conditions. This plane only produces juvenile and subadult specimens of *Pseudestheria,* all of which belong to the same ontogenetic stage. These conchostracans seem to have died prior to maturity, probably because salinity briefly exceeded the upper limit of tolerance for conchostracans. If so, a high-tide event may be postulated (cf. Archer & Clark, 1991).

These paleoecological inferences have some bearing on the lower salinity tolerance of *Dunbarella.* Bedding planes at the Kinney Quarry where *Dunbarella* abound lack conchostracans. These beds normally might be interpreted to reflect brachyhaline marine (small *Dunbarella)* or marine (large *Dunbarella)* waters. However, at the Kinney Quarry it is likely that bottom waters were euxinic and that *Dunbarella* was pseudoplanktic (Lucas & Huber, 1991; Archer & Clark, 1991). On those bedding planes in units 1 and 3 with a few small *Dunbarella* associated with conchostracans, the conchostracans are almost exclusively juveniles and subadults. These bedding planes, as discussed above, suggest pliohaline to brachyhaline I marine brackish water. This suggests the lower boundary of salinity tolerance for *Dunbarella* is pliohaline brackish (1.0-1.8% salt).

Acknowledgments

We thank Bob Jurgena and the Kinney Brick Company for permission to collect at the Kinney Brick Quarry, Phillip Huber for collecting some of the specimens reported here, and Ken Kietzke and an anonymous reviewer for their comments on the manuscript.

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Late Pennsylvanian Ostracoda from the Kinney Brick Quarry, Bernalillo County, New Mexico, with notes on other microfossils

Kenneth K. Kietzke[1] and Roger L. Kaesler[2]

[1]*New Mexico Museum of Natural History, 1801 Mountain Rd. NW, Albuquerque, New Mexico 87104;*
[2]*Department of Geology, Paleontological Institute, and Museum of Invertebrate Paleontology, University of Kansas, Lawrence, Kansas 66045*

Abstract—The ostracodes from the Kinney Brick Quarry are a low-diversity, brackish-water assemblage containing a transitional fauna from a more marine *Paraparchites* zone at the base through a zone characterized by *Geisina* to a relatively fresh-water brackish fauna at the top that is dominated by *?Carbonita* and *Darwinula*. All three assemblages contain essentially the same ostracodes but differ in their relative proportions. The ostracodes are apparently absent or very rare in the units with *Dunbarella* and fossil plants higher in the section. Whether this is a result of sedimentation rate or some other environmental factor is not known.

Other microfossils found in this unit include rare foraminifera, charophytes, *Spirorbis* worms, and ichthyoliths. More detailed taxonomic and paleoecologic work remains to be done on this interesting unit.

Introduction

Ostracodes are an inconspicuous, low-diversity element in the unique fauna from the upper Pine Shadow Member of the Wild Cow Formation at the Kinney Brick Quarry (Fig. 1). Most are relatively long-ranging Middle to Late Pennsylvanian species that do little to resolve the question of the age of the Kinney Quarry strata. They do, however, have paleoecological significance. Ostracodes appear to be restricted to the lowest 2 m of section (units 1-4)—the basal limestone and the beds below the bed containing the large *Dunbarella* valves (unit 5 of Lucas & Huber, 1991).

Late Paleozoic Ostracoda of New Mexico have been little studied. Perhaps the most relevant study devoted primarily to ostracodes in nearby areas is Werrell (1961). Unfortunately, he did not study ostracodes from the Kinney Brick Quarry nor any of the taxa reported herein. Most other reports of ostracodes from the late Paleozoic of New Mexico consist of descriptions of single species as part of studies of other faunas (e.g. Girty, 1908) or taxonomic reviews (e.g. Sohn, 1972). Numerous species have been cited in abstracts and lists, but these are difficult to verify taxonomically. Some recent papers have documented ostracodes from some well-known New Mexico fossil localities (e.g. Kietzke, 1990).

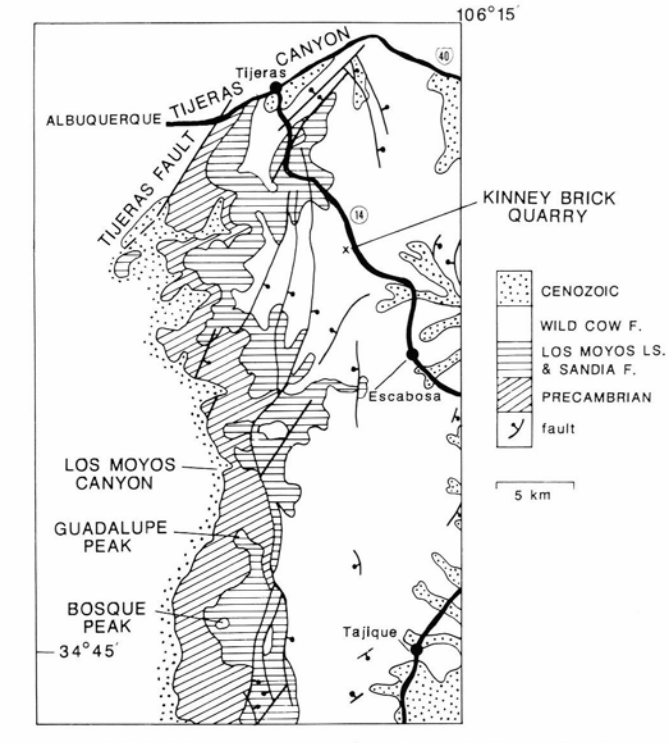

FIGURE 1—Locality map (from Lucas & Huber, 1991).

This study is preliminary, more detailed studies will be needed to refine the taxonomy and the paleoecologic observations made here. The following text is intended to provide a starting point for future studies and a general introduction to the Kinney ostracodes and other microfossils.

Methods

The calcareous and indurated nature of the units (Fig. 2) that contain the ostracodes has made the usual collection methods difficult. Thus, we have examined the bedding surfaces, physically removing the ostracodes observed. Only unit 4 of Lucas & Huber (1991) could be disaggregated, and a somewhat richer fauna was recovered from this unit. The specimens recovered were picked, sorted by morphotype, identified, and photographed with a scanning electron microscope (SEM). Associated microfossils were also collected and identified to genus. All specimens are catalogued into the collections of the New Mexico Museum of Natural History (NMMNH).

Stratigraphic and geologic setting

The stratigraphic sequence (Fig. 2) used here is that of Lucas & Huber (1991). Collections have been made to refine this stratigraphy to the centimeter scale for future studies. Units 1-3 are gradational in nature. The strongest breaks occur between units 4 and 5 and 1 and 2. Other authors in this volume cover the details of the stratigraphic sequence.

The paleogeographic setting of the Kinney Quarry is Manzanita Platform between the Lucero Basin to the west and the Estancia Basin to the east (Kottlowski, 1961). The major highland source of sedimentation in the area is the Pedernal landmass, a north-south-trending uplift about 50 km east of the Kinney Quarry. This is almost certainly the source of the arcosic sandstones typical of the lower Pine

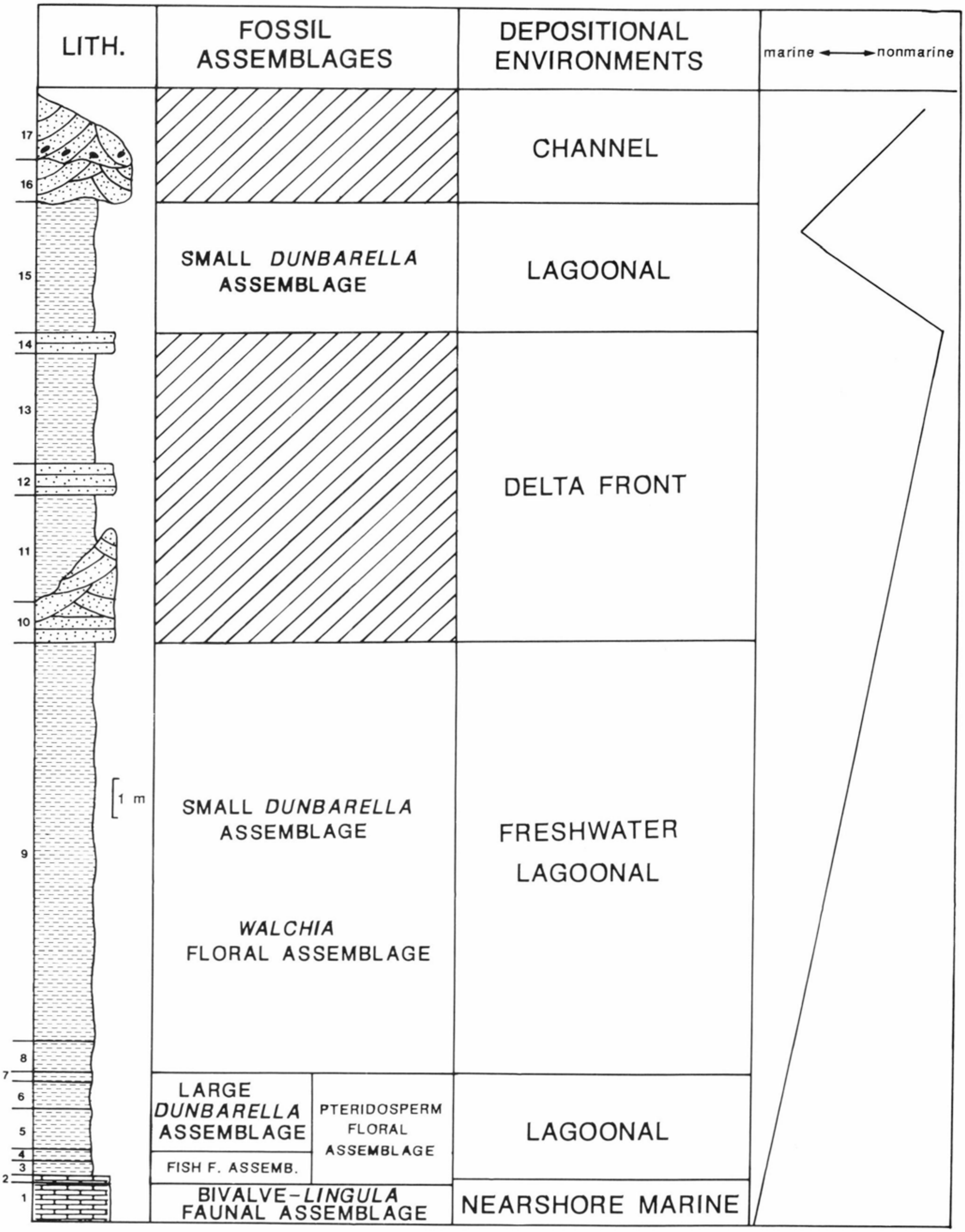

FIGURE 2—Stratigraphic section at Kinney Brick Quarry (from Lucas & Huber, 1991).

Shadow Member of the Wild Cow Formation below the level of the Kinney Quarry.

Taxonomy

Class OSTRACODA Latreille 1806
Order PALAEOCOPIDA Henningsmoen 1953
Family HOLLINIDAE Swartz 1936
Genus HOLLINELLA Coryell 1928

HOLLINELLA cf. GRAHAMENSIS (Harlton 1927)
Fig. 3G

This species has a low anterior node and minutely papillose surface characteristic of the holotype of this species. Only a single, broken valve was found (in unit 4), making assignment provisional. This species has been reported from the Virgilian of Texas (Melnyk & Maddocks, 1988).

Family GEISINIDAE Sohn 1961 Genus GEISINA Johnson 1936

GEISINA GREGARIA (Ulrich & Bassler 1906)
Fig. 3D, E

Sexual dimorphism in this genus is expressed by the inflation of the posterior region of the valves. Most specimens from the Kinney Quarry are adult females, although crushed specimens in some units makes this observation tentative. *G. gregaria* is found rarely in unit 1 and more commonly in units 2 through 4. The proportional abundance decreases upward from its peak in unit 2. This species has been reported from the Desmoinesian, Missourian, and Virgilian of Texas and the Midcontinent (Ulrich & Bassler, 1906; Melnyk & Maddocks, 1988; Hecht & Kaesler, 1991).

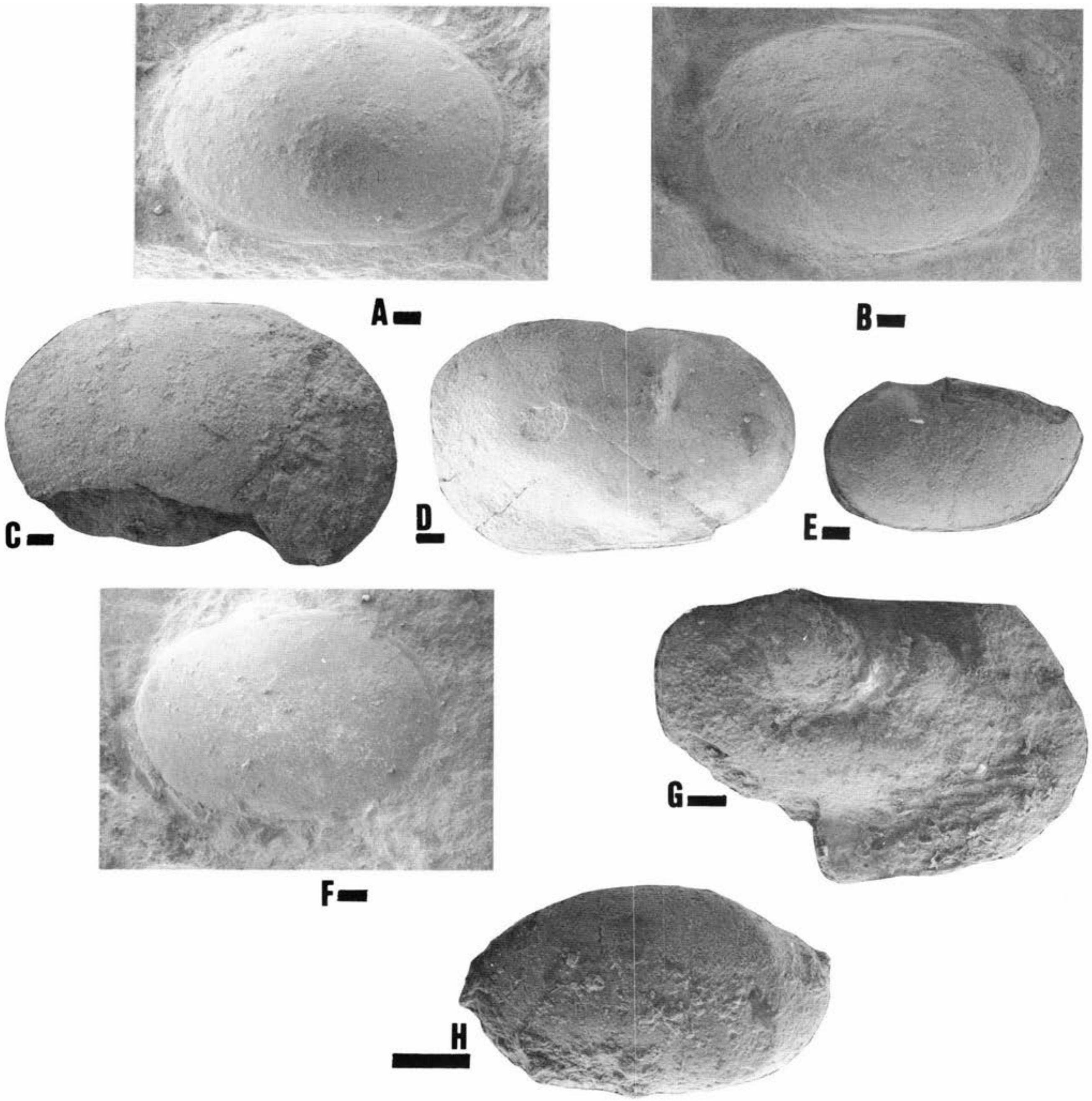

FIGURE 3—Ostracoda from Kinney Quarry, all in lateral view. **A–C, F,** *Paraparchites* cf. *kellettae;* A, left valve, unit 1 (NMMNH P-14707); B, right valve, unit 1 (NMMNH P-14708); C, right valve, unit 4 (NMMNH P-14706); F, left valve, unit 1 (NMMNH P-14726). **D, E,** *Geisina gregaria;* D, left valve, unit 4, mature specimen (NMMNH P-14704); E, left valve, unit 4, late instar (NMMNH P-14705). **G,** *Hollinella* cf. *grahamensis,* right valve, female, unit 4 (NMMNH P-14703). **H,** *Healdia* sp., left valve, unit 4 (NMMNH P-14713). All scale bars = 100 μm.

Family PARAPARCHITIDAE Scott 1944
Genus *PARAPARCHITES* Ulrich & Bassler 1906

PARAPARCHITES Cf. KELLETTAE Sohn 1971
Fig. 3A—C, F

The excellent preservation, lack of crushing, and large size made this a conspicuous member of the unit 1 (basal micrite) fauna. This species has previously been reported from the Upper Pennsylvanian and Lower Permian of the Midcontinent region (Sohn, 1971).

Order PODOCOPIDA Müller 1894
Family CARBONITIDAE Swain 1976
Genus *CARBONITA* Strand 1928

?*CARBONITA* sp.
Fig. 4A—C, F

A rather highly arched dorsum makes assignment to *Carbonita* tentative. Similar species were described as *Carbonita fabulina* by Joes & Kirkby (1889) from the Carboniferous of Nova Scotia and as *Darwinuloides puris* by Shao-zeng (1985) from the Late Permian of China. As currently understood (Sohn, 1985), *Carbonita* apparently has an indentation of the lateral surface of the valves in the area of the muscle scar, which would appear to exclude the form described by Jones & Kirkby from this genus. Bless (1973) illustrated specimens assigned to this genus, that do not have this feature, from the Carboniferous of Europe, where a broader definition of the genus is in use. The muscle scars of the Chinese specimens suggest a relationship to *Whipplella* or *Suchonella.* Eventual discovery of muscle scars in the Kinney Quarry ostracodes would aid in determining their true relationships. This species is common in units 2-4 of the Kinney Quarry. It increases in abundance proportionally upward in the section.

Family DARWINULIDAE Brady & Norman 1889
Genus *DARWINULA* Brady & Robertson 1885

?*DARWINULA* sp.
Fig. 4D, E, G

Darwinula is a fresh- to brackish-water ostracode still living in such environments today. The Kinney specimens lack the tapered anterior end that is characteristic of most species of Carboniferous *Darwinula.* In this regard they resemble in outline *Darwinula* sp. 3 of Sohn (1985) from the Mississippian of Virginia. Unfortunately, Sohn's material consists only of two steinkerns, making more detailed comparisons impossible. The Kinney specimens are also similar in some aspects to a form from the Late Permian of Brazil (Sohn & Rocha-Campos, 1990: fig. 17/7-9). Other reported late Paleozoic *Darwinula* from North America include *Darwinula hollandi* Scott 1944, a similar or identical species from the Pennsylvanian of Illinois referred to by Cooper (1946) as *Darwinula pungens* (Jones & Kirkby 1879), and several forms from the late Paleozoic of West Virginia listed in open nomenclature by Sohn (1977). An extensive foreign literature exists, particularly in Russian and Chinese. *?Darwinula* sp. is rare in unit 1 and more common in units 2-4 at the Kinney Quarry, and appears to increase in abundance upward in the section.

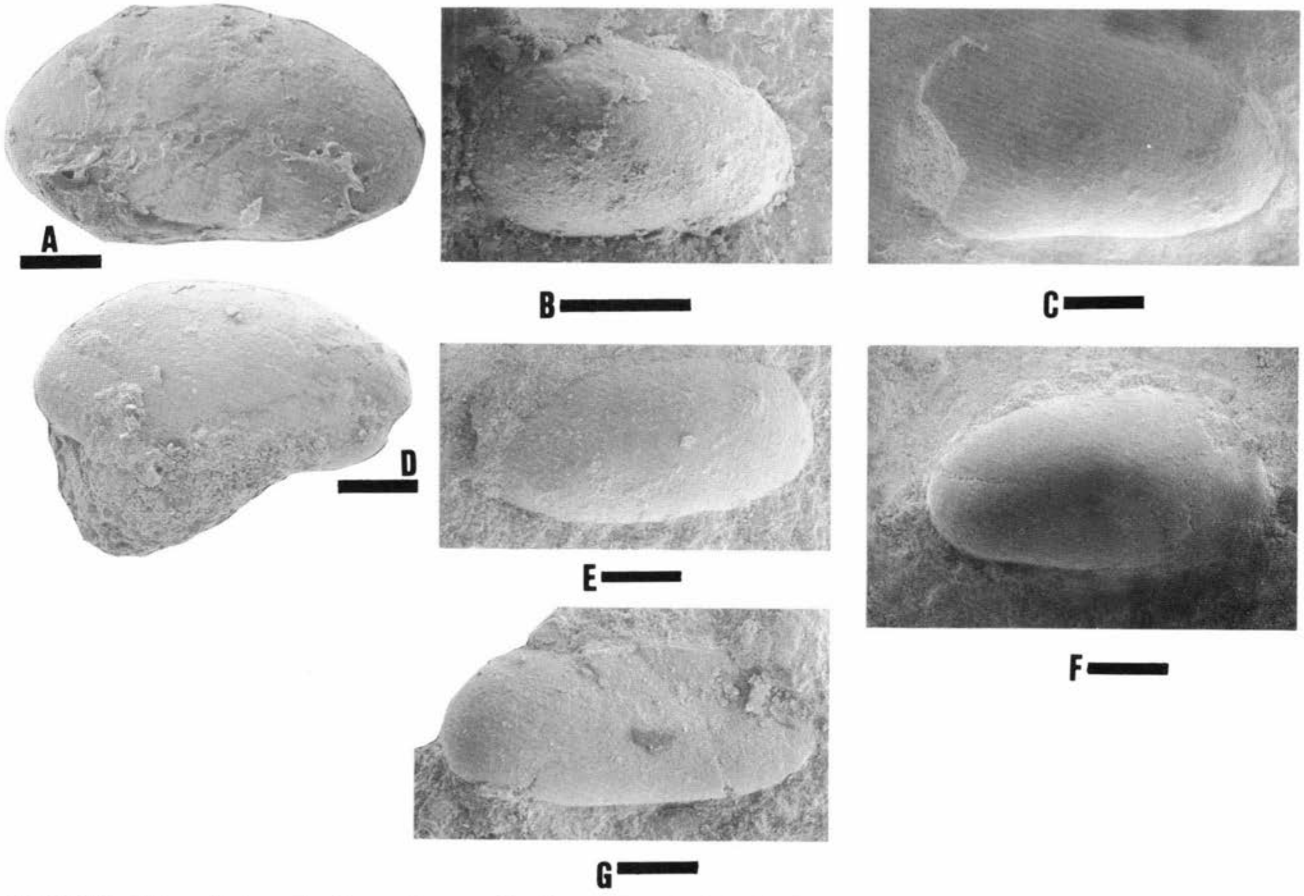

FIGURE 4—Ostracoda from the Kinney Quarry, all in lateral view. **A–C, F,** ?*Carbonita* sp.; A, left valve, unit 4 (NMMNH P-14709); B, right valve, unit 4 (NMMNH P-14710); C, right valve, unit 4 (NMMNH P-14711); F, left valve, unit 1 (NMMNH P-14712). **D, E, G,** ?*Darwinula* sp.; D, right valve, unit 4 (NMMNH P-14714); E, left valve, unit 4 (NMMNH P-14715); G, right valve, unit 4 (NMMNH P-14716). All scale bars = 100 µm.

Family **HEALDIIDAE** Harlton 1933
Genus *HEALDIA* Roundy 1926

HEALDIA sp.
Fig. 3H

A single specimen from unit 4, with a pronounced posterior rim, may be *Healdia* aff. *simplex* Roundy 1926. However, an unequivocal assignment cannot be made on the basis of a single valve. A similar ostracode was recovered from the Flechado Formation (Desmoinesian) near Talpa, New Mexico, by Kietzke (1990: fig. 9A) and identified as *Healdia* sp. The Kinney specimen is lower in proportion to length and more posteriorly extended past the ridge.

Paleoecology

Overall, the ostracodes are characteristic of a mixed nearshore-marine and brackish-water fauna that appears to have become less marine above the basal limestone. The absence of ostracodes in the *Dunbarella* beds is perhaps the result of higher sedimentation rates in these units. If the very thin layers in the *Dunbarella* beds are formed by tidal cyclicity as suggested by Archer & Clark (1991), then higher sedimentation rates for these beds are likely. Non-preservation and other factors, while possible, are less likely in view of the excellent preservation of both plants and the calcareous *Dunbarella* valves. Two ostracode faunas can be recognized, the *Paraparchites* fauna from the basal micrite and the *Geisina—Darwinula—Carbonita* fauna from the overlying units. The latter fauna may have a higher proportion of *Geisina* in the lower part and a higher proportion of *Darwinula* and *Carbonita* in the upper part, but differential preservation and possible collecting biases make this uncertain. Relative abundances of these taxa, found in examination of bedding surfaces, are shown in Fig. 5. These proportions are based on relatively small sample sizes (n = <100) and are thus fraught with the statistical ambiguities inherent in such samples (Sokal & Rohlf, 1981). Fig. 3 shows the transition from the basal limestone (unit 1) dominated by *Paraparchites* to the upper ostracode-bearing unit (unit 4) dominated by *Carbonita*. This suggests a rapid transition from marine and brackish-water to a more nearly fresh, brackish-water environment in the thin interval from the limestone to the base of the bed containing the large *Dunbarella* (unit 5). Since this is also the interval which contains the more striking vertebrate fossils, a more detailed discussion seems warranted.

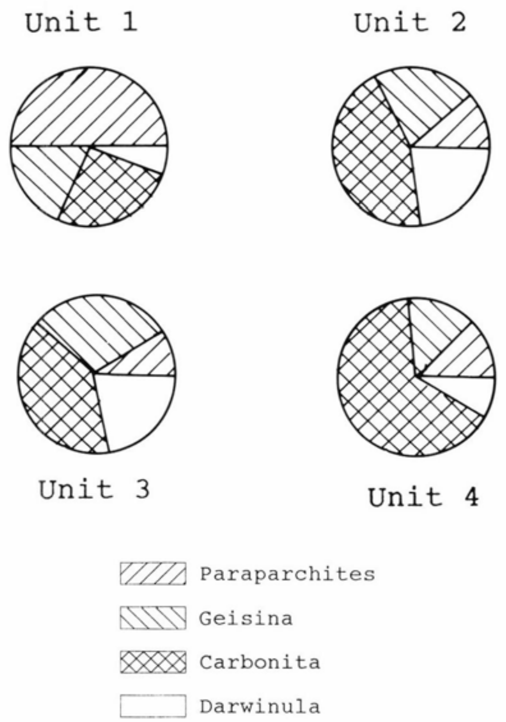

FIGURE 5—Distribution of Ostracoda in various units from counts of individuals on bedding planes. Numbers counted for each unit: unit 1, n = 22; unit 2, n = 65; unit 3, n = 77; unit 4, n = 56.

Previous work on rocks from similar environments has been limited. The only ostracode reported from the Middle Pennsylvanian Mazon Creek fauna in Illinois is *Paraparchites mazonensis* Sohn 1977, although some unidentifiable ostracodes were previously illustrated by Langford (1963). The ostracodes of the Hamilton Quarry in Kansas have been reported in a preliminary fashion by Kaesler (1988), who found *Darwinula* sp., rare *Carbonita*, and a single *Bairdia*. The Hamilton fauna appears to be slightly less brackish in lacking the *Geisina* and *Paraparchites* components found in the Kinney fauna. The fauna from the Early Permian Carrizo Arroyo locality in New Mexico has not been studied paleoecologically, but one of us (KKK) has found abundant *Darwinula* in that assemblage, suggesting a more fresh-water environment for that locality.

Kaesler & Denver (1988) found *Paraparchites* to be characteristic of nearshore lagoonal or hypersaline environments in the Americus Limestone (Wolfcampian) of Kansas. Dewey (1987) considered *Paraparchites* characteristic of hypersaline environments. This ostracode may be more indicative of abnormal salinity than of reduced or increased salinity specifically. Another species common in Early Permian lagoons was *Sansabella bolliaformis*, a kloedenellacean species morphologically similar to *Geisina gregaria* . Bless et al. (1969), in studies of the Westphalian of The Netherlands, established a nearshore phase characterized by and named after *Geisina*. Only their *Carbonita* phase was more shoreward. Melnyk & Maddocks (1988) considered *Darwinula* to be most characteristic of nearshore environments, with *Geisina* extending more seaward and overlapping with *Paraparchites* at about the prodelta—lagoon interface. The Kinney Quarry ostracodes of the basal limestone appear to have lived in a lagoon. Terrigenous influences and reduced salinity increased with time. The rapid transition indicated by the ostracodes suggests a period of rapidly changing salinity in an already restricted environment.

The ostracodes from the basal micrite (unit 1, Fig. 2) typically occur as articulated valves, suggesting little transport or wave action. The ostracodes in units 2-4 are frequently single valves, indicating some post-mortem disturbance. These ostracodes from the upper units are usually also crushed or cracked, but lack of disassociation of the fragments suggests this to be a diagenetic rather than a taphonomic feature. Preservation is generally excellent. Considerable variation in abundance of ostracodes occurs among bedding planes, although whether this is due to vertical or lateral variations in abundance is not clear.

Associated microfossils included two crushed charophyte oogonia (Fig. 6A—C) from unit 4 and one from unit 3. Charophytes lived in fresh to brackish water, but their oogonia could have been washed into distant environments. Their rarity and lack of associated vegetation suggest this to be the case in the Kinney Quarry. A single specimen of the foraminifer *Globivalvulina* was recovered from unit 2 and another from unit 3. *Globivalvulina* is a widely ranging benthic species typical of nearshore-marine units of the Pennsylvanian and Permian. Also present are uncommon *Spirorbis* (Fig. 6H—J) in unit 4. These were not attached to any substrate, indicating possible attachment to plants in life. Several fossil plants with attached *Spirorbis* specimens are in the NMMNH paleontology collections, further supporting this hypothesis. Scattered brachiopod spines and bryozoan fragments were also recovered from units 1-4. Numerous

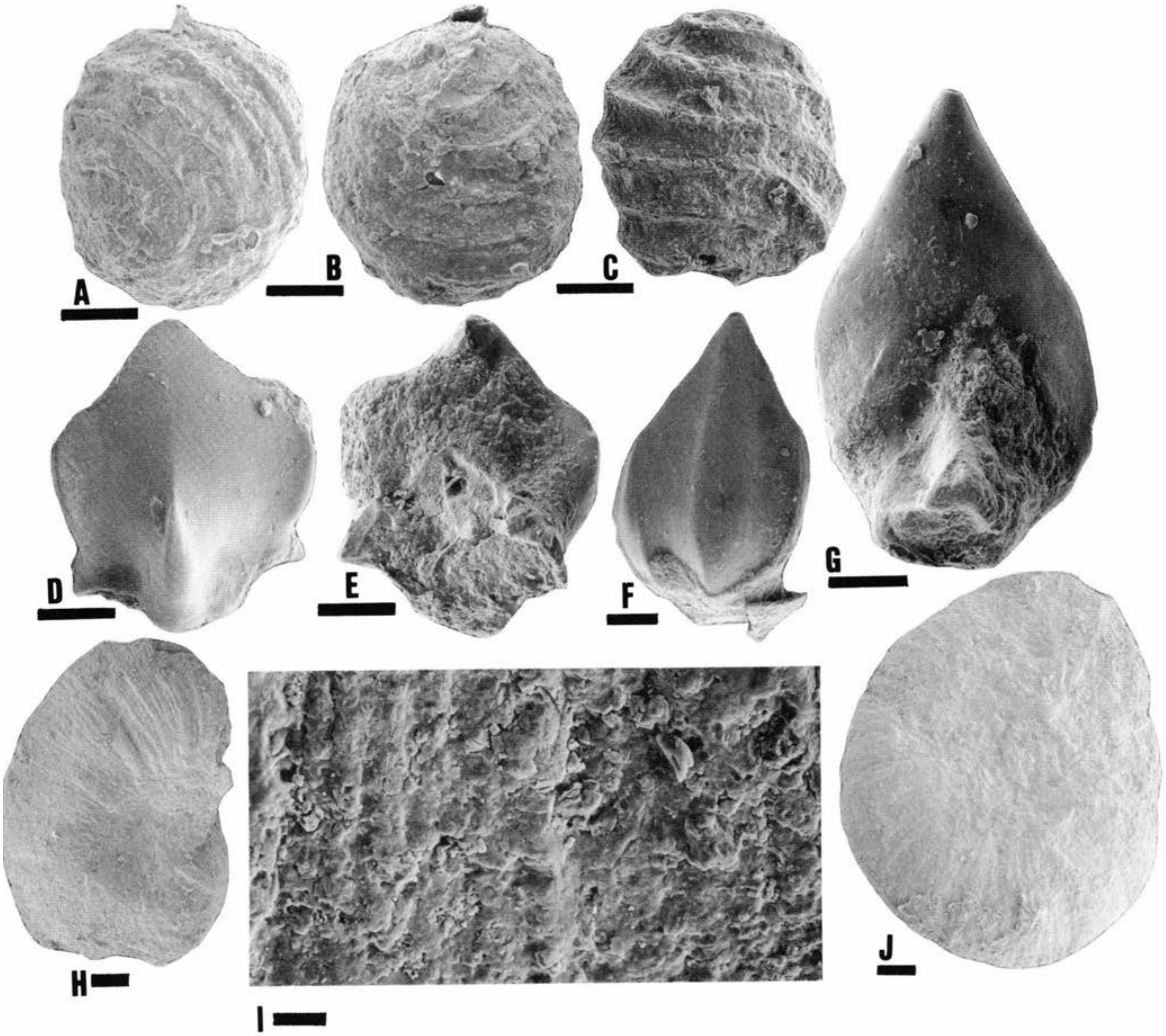

FIGURE 6—Non-ostracode microfossils from unit 4 of the Kinney Brick Quarry. **A–C,** Charophyte oogonia, crushed, near-lateral views; A, B (NMMNH P-14717), C (NMMNH P-14718). **D–G,** Vertebrate ichthyoliths, top and basal views; D, E (NMMNH P-14721), F, G (NMMNH P-14722). **H–J,** *Spirorbis* sp., top view (H), closeup (I), top view (J) of another individual; H–I (NMMNH P-14719), J (NMMNH P-14720). Scale bars = 100 µm for A–H and J, and 10 µm in I.

invertebrate megafossils, particularly molluscs and conchostracans, also occur in these units and are dealt with by other authors in this volume. Vertebrate debris, including numerous ichthyoliths (Fig. 6D—G), as well as well-preserved vertebrate skeletons described in this volume, are abundant in units 1-4.

Conclusions

(1) The Ostracoda from the Kinney Quarry form a low-diversity, brackish-water assemblage. Dominant genera are *Paraparchites, Geisina, Carbonita,* and *Darwinula.*

(2) The salinity was reduced from a more nearly normal-marine level near the base (unit 1) to a much more brackish level near the top of the ostracode-bearing zone (unit 4). The reduction of salinity occurred in the same interval where most of the more spectacular vertebrate and arthropod fossils are found.

(3) The Ostracoda were reduced dramatically, and for all practical purposes disappeared, at the base of the *Dunbarella* zone (unit 5). This could be the result of higher sedimentation rates or some other, still unrecognized, environmental factor.

(4) Associated microfossils include charophytes, *Globivalvulina,* and *Spirorbis,* and further support the environmental conditions indicated by the ostracodes.

Acknowledgments

We would like to thank Dr. **J.** Zidek for suggesting the need for this paper in the symposium volume and giving us the time to prepare a manuscript. We also thank Drs. Barry Kues, Collette Burke, Cranston Christopher, and Spencer Lucas for kindly reviewing this paper on such short notice and suggesting improvements. The New Mexico Museum of Natural History is the repository for our specimens and brought us together in the context of the Kinney Quarry Symposium in the first place.

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Terrestrial arthropods from Upper Pennsylvanian rocks at the Kinney Brick Quarry, New Mexico

William A. Shear[1], Joseph T. Hannibal[2], and Jarmila Kukalová-Peck[3]

[1]Department of Biology, Hampden-Sydney College, Hampden-Sydney, Virginia 23943-0096;
[2]Cleveland Museum of Natural History, 1 Wade Oval Drive, University Circle, Cleveland, Ohio 44106-1767;
[3]Geology Department, Carleton University, Ottawa, Ontario, Canada K1S 5B6

Abstract—Terrestrial arthropods from the Kinney Brick Quarry, New Mexico, are rare and most are poorly preserved. The specimens we studied are all incomplete, fragile, and many are simple carbon films lacking appreciable relief. Two major groups, Diplopoda (millipeds) and Insecta, are represented. A unique specimen is a myriapodous arthropod with single segments; it may be a centiped (Chilopoda).

Too little is known of the terrestrial arthropod fauna of the Kinney Brick Quarry to characterize the fauna ecologically or to compare it in detail to other, better known faunas. However, as fossil insect faunas of the Rocky Mountain region become better known, they show promise that they may be distinct from the faunas of the eastern United States and Europe.

Introduction

The geological setting, paleoecology, and taphonomic aspects of the Kinney Brick Quarry deposits are discussed in Lucas & Huber (1991) and in other papers in this collection. Our study of the terrestrial arthropods adds little to what is already known of these topics. An overview of the paleoecology of terrestrial arthropods in the Paleozoic is provided by Shear & Kukalová-Peck (1990), while Shear (1991) discusses Paleozoic terrestrial ecosystems in a community context.

The purpose of this paper is to document the occurrence at the Kinney Brick Quarry of fossil myriapods and insects, and to briefly review similar records from the Rocky Mountain region.

Although more than 130 species and perhaps more than 50 genera of fossil millipeds have been described (Hannibal & Farago, 1984), the absence of any synthetic taxonomic work (but see Burke, 1973, 1979) makes it difficult to place new material in systematic and phylogenetic perspective. Specimens from the western parts of North America are rare. Most previous reports of fossil myriapods in the Rocky Mountain region consist of descriptions of Cenozoic forms. Schram & Schram (1979), however, reported a possible myriapod from the Kinney Brick Quarry. This specimen (USNM 235643) is very poorly preserved and its identity cannot be determined. Hannibal & Feldmann (1988) reported on a small collection from Hamilton, Kansas, limestones of latest Carboniferous or earliest Permian age. An indeterminable juliform diplopod and a probable new genus of euphoberiid were mentioned. Paleozoic juliforms are very similar to some groups of modern diplopods (Hoffman, 1969), but euphoberiids belong to the "group" Archipolypoda, an assemblage of usually very large, heavily spined myriapods limited to the late Paleozoic. Hoffman (1969) treated them as a class, but as of this date no synapomorphic characters have emerged which would allow them to be unequivocally separated from the class Diplopoda. Burke (1979), whose studies of these animals are the most detailed yet published, regarded the Archipolypoda as an order of Diplopoda.

Paleozoic insects are only a little better known from the Rocky Mountain region, though the fauna is potentially rich. Durden (1988) provided a list from which may be extracted more than 60 generic names, scattered through 14 nominal orders, of Late Carboniferous and Permian insects found at three main Rocky Mountain sites: Carrizo Arroyo, Valencia Co., New Mexico; Fairplay, Colorado; and "Manzano," New Mexico. This latter name undoubtedly refers to the Wild Cow Formation at the Kinney Brick Quarry. Durden's list lacks documentation, especially for many genera he reports from Carrizo Arroyo and Fairplay; until more detailed descriptions are published, it must be regarded as suggestive only.

An additional locality from which only a single species has been named is near Lehi, Utah, in the Manning Canyon Shale (Nelson & Tidwell, 1987). This insect, *Brodioptera stricklani* Nelson & Tidwell (Megasecoptera, Brodiopteridae), is of interest here because it is distantly related to one of the specimens described below from the Kinney Brick Quarry. More generally, the Manning Canyon Shale has been characterized by Durden (1984) as the oldest insect-bearing stratum in North America, and indeed is comparable in age to the important new site at Hagen—Vorhalle in Germany (upper Namurian B) now producing a wealth of insect fossils (Brauckmann, 1988). According to Nelson & Tidwell (1987), there is disagreement about the age of the Manning Canyon Shale; estimates range from upper Namurian A to Namurian C. Based on the flora, they considered the formation to be lowermost Namurian B.

Insects from the Carrizo Arroyo were described by Kukalová-Peck & Peck (1976). The deposit is of Virgilian age. The collection included the calvertiellid palaeodictyopteran *Carrizopteryx arroyo* Kukalová-Peck, the oldest known member of its family. Other Calvertiellidae are known from the Permian. Without describing the material, they also mentioned the presence of a single wing of a syntonopterid, two protorthopterans, and several blattoids. Evidently Durden (1988) has seen more extensive collections, and lists more genera and families, especially of blattoids. He also records the genus *Carrizopteryx* from Fairplay, Colorado.

Carpenter (1970) was the first to describe insects from the Kinney Brick Quarry, though in his paper he referred only to "an exposure of the Madera Formation, southeast of Albuquerque, New Mexico." Carpenter's material was collected by Sergius Mamay, who has told one of us (JH) that the owners of the quarry at that time shunned publicity and thus asked that a more specific locality not be published. In contrast to the material we have examined, Carpenter's shows good preservation. Carpenter described a new genus and species of palaeodictyopteran of the family Lycocercidae, *Madera mamayi*. It is the oldest known lycocercid and the only one from North America. *Pseudobiella fasciata* Carpenter, of the order Caloneurodea, family Permobiellidae, belongs to an order that is poorly represented in American deposits, and the family has only two other monotypic genera (Carpenter, 1980). Carpenter also mentioned a "thysanuran" and several blattoids from this collection. The "thysanuran" may well have been in fact a monuran, specimens of which have also been found at Carrizo Arroyo (Kukalová-Peck, 1985, caption of figs. 23-27). The blattoids have not been described formally, but Durden (1988) listed a number of families and genera from the Kinney Brick Quarry.

In his 1970 paper, Carpenter also named *Sandiella readi*, which he assigned to the family Eugereonidae of the order Palaeodictyoptera. This specimen came not from the Kinney Brick Quarry but from "the Sandia Formation on an exposure on the north side of Santa Fe Creek in the eastern suburbs of the city of Santa Fe, New Mexico (locality no. 8941, Geological Survey)." This insect was characterized as being very close to members of the genus *Dictyoptilus* from Commentry, France (Kukalová, 1%9). No additional insects have been recovered from this locality, but we do not think there has been any searching done.

In conclusion, though little has been published on Paleozoic fossil insects from the Rocky Mountains, what has appeared is very suggestive of a distinctive faunal composition and the potential for locating deposits near in time to the earliest known occurrences of winged insects. Of the few named species, two are the oldest known of their families.

We have examined insect and myriapod material present in the collections of the New Mexico Museum of Natural History, Albuquerque, New Mexico (NMMNH), as well as additional material from the U.S. National Museum of Natural History, Washington, D.C. (USNM), the University of New Mexico, Albuquerque (UNM), and the Carnegie Museum of Natural History, Pittsburgh (CMNH). The numbers given are those of the respective institutions. The general quality of preservation of these fossils is poor; most are vague impressions or carbonaceous "shadows" lacking much detail. For this reason we have not provided descriptions or discussions of all the specimens listed in Table 1, selecting only those of reasonable quality and some paleontological interest. Kukalová-Peck & Peck (1976) speculated that the material had been redeposited, but it is perhaps more likely that the material had decayed somewhat and suffered damage during transport to the site by streams. For these reasons we name no new taxa based on these specimens. Table 1 lists by number the specimens we have studied and gives our identifications.

TABLE 1—Terrestrial arthropods from the Kinney Brick Quarry examined for this study.

Museum number	Comments
NMMNH P-14349	Diplopoda
NMMNH P-14350	Diplopoda?
NMMNH P-12990	Megasecopteran (near Brodiidae), body and wing fragments
NMMNH P-14340	Megasecopteran?, anterior part of body
NMMNH P-14335	Large blattoid
NMMNH P-14336	Blattoid wing fragment
NMMNH P-14337	Blattoid wing fragment (Phyloblattidae)
NMMNH P-14338	Blattoid wing fragment
NMMNH P-14341	Blattoid wing fragment
NMMNH P-14342	Nearly complete blattoid wing
NMMNH P-14343	Blattoid wing fragment
NMMNH P-14345	Blattoid wings
NMMNH P-14346	Insect wing? Probably blattoid
NMMNH P-14347	Blattoid (Phyloblattidae?)
NMMNH P-14348	Large blattoid
UNM 10692	Myriapoda incertae sedis
CMNH 34962	Diplopoda?
USNM 450760	Diplopoda

Diplopoda

Specimen NMMNH P-14349

At least 14 segments, most seen in lateral view, are preserved (Fig. 1A-C). The pleurotergites are roughly quadrangular, about 3 mm long and 4 mm wide, but it is likely that at least half the width has been lost or is folded under the visible part. The pleurotergites have convex, gently rounded anterior borders, rounded anterolateral corners, finely crenulated margins, and are ornamented with shallow pits (possibly impressions of warts or nodules, but this is not likely). The posterior borders are concave and the posterolateral corners are sinuous. About midway in the length, but closer to the anterior margin, of some pleurotergites is a larger and deeper pit, which could represent the broken base of a hollow spine, or possibly the opening of a repugnatorial gland. There are two sternites for each pleurotergite; the sternites are about 1.4 mm long. Preserved portions of sternites, representing less than one-hall the total width, are up to 2.6 mm wide (as measured on the counterpart); it is likely that the entire sternite was approximately 6 mm wide. The anterolateral corners of the sternites are emarginated and the preserved portions bear a single slitlike spiracle, about 0.6 mm long, located between the site for articulation of the leg and the lateral margin of the sternite. The spiracle is oriented subparallel to the long axis of the sternite.

This specimen has been twisted 180° at its midpoint; the dorsal—ventral portions of the posterior are reversed from that of the anterior. A small bit of carbonized plant material is preserved on a bedding plane about 1 mm above that of the specimen; also on the slab on a bedding plane about 1 mm below that of the milliped is a bivalve mollusc.

This fragmentary specimen lacks features which allow even a tentative assignment, except that the presence of *a* pair of sternites for each pleurotergite places it in the Diplopoda. While wide, paired sternites occur in archipolypods, they are found in some living milliped taxa as well, and probably (as a plesiomorphic feature) occurred in many groups of Paleozoic diplopods (see Almond, 1985: fig. 2). Unless the large pit referred to above is a broken spine base, the absence of the characteristic euphoberiid spines would probably exclude this specimen from that group.

Specimen NMMNH P-14350

This specimen presents a dorsal aspect and consists of more than 40 tergites, each about 1 mm long and 2.3 mm wide (Fig. 2A, **B).** The fact that there is little or no change in tergite length throughout the specimen suggests that even more segments were present in life. Each tergite is divided into anterior and posterior sections by a transverse sulcus; the anterior division is slightly longer. The lateral edges are gently convex. Associated with one tergite is an ovoid impression (0.7 mm in diameter; Fig. 2B) of unknown significance. The posterior sections of the tergites are ornamented with undulatory transverse grooves.

The transverse division of the segments suggests a diplopod, but there are no diagnostic features.

Specimen CMNH 34962

This specimen consists of portions of about 28 tergites exposed in dorsal view, and is curved into a "C" shape. Each tergite is about 0.9 mm long and 2.6 mm wide. A few tergites have traces of a transverse sulcus, but others do not. The lateral edges of the tergites are gently convex.

This specimen resembles NMMNH P-14350 in the size

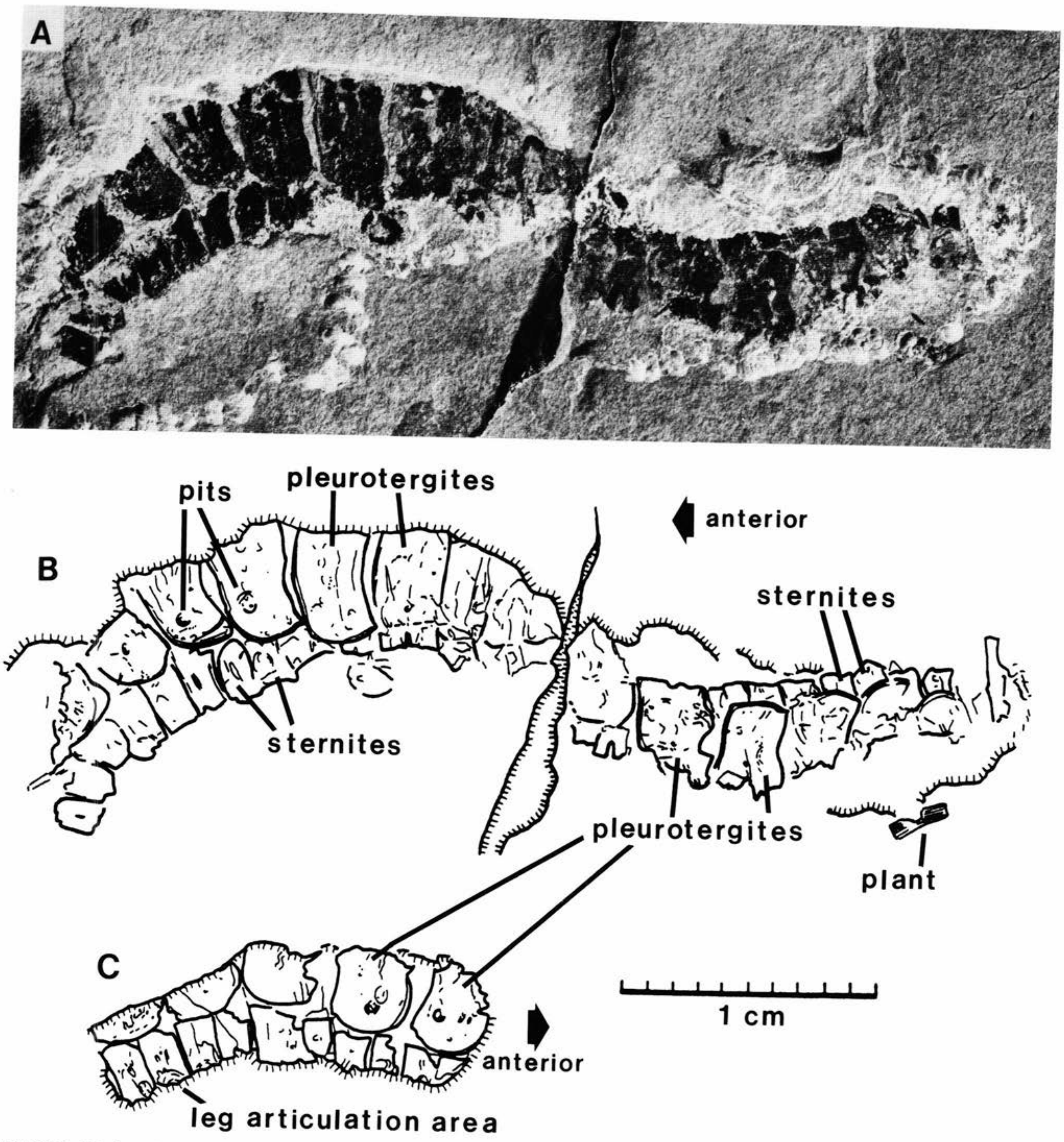

FIGURE 1—Diplopod NMMNH P-14349 from the Kinney Brick Quarry. **A,** Specimen preserved primarily in lateral view; the area of the fossil to the left of the crack in the matrix is shown with dorsum up; the portion to the right is reversed due to twisting of the specimen. **B,** Interpretive drawing of the morphology shown in A; this drawing done with the specimen whitened, thus some details differ from those seen in A; hachure lines extend from higher to lower planes. **C,** Interpretive drawing of counterpart.

and shape of the tergites, but can be differentiated from it by the lack of a prominent sulcus on most tergites and by the lack of tergal ornamentation. Some of these differences may be due to poor preservation of CMNH 34962.

Specimen USNM 450760

Approximately 54 tergites in lateral view, each about 0.8 mm long and 1.7 mm high, can be discerned in this specimen (Fig. 3B, C). A possible gut infilling about 0.6-0.8 mm wide is present in about 23 segments. The gray color of the infilling easily distinguishes it from the brown color of the remainder of the fossil. Each tergite is divided into a larger, presumably anterior portion and a smaller, presumably posterior portion by a shallow transverse sulcus. Very fain and extremely fine striations are present on some segments, and most of them appear to be transverse. The head region of the specimen appears to be present but is indistinct.

The general form, attitude of preservation in a semicoiled position, and the transverse division of the segments of this specimen indicate that it is a diplopod.

Myriapoda incertae sedis

Specimen UNM 10692

About 13 tergites in oblique dorsal view are preserved in this specimen. Each is about 1 mm long and 2.5 mm wide;

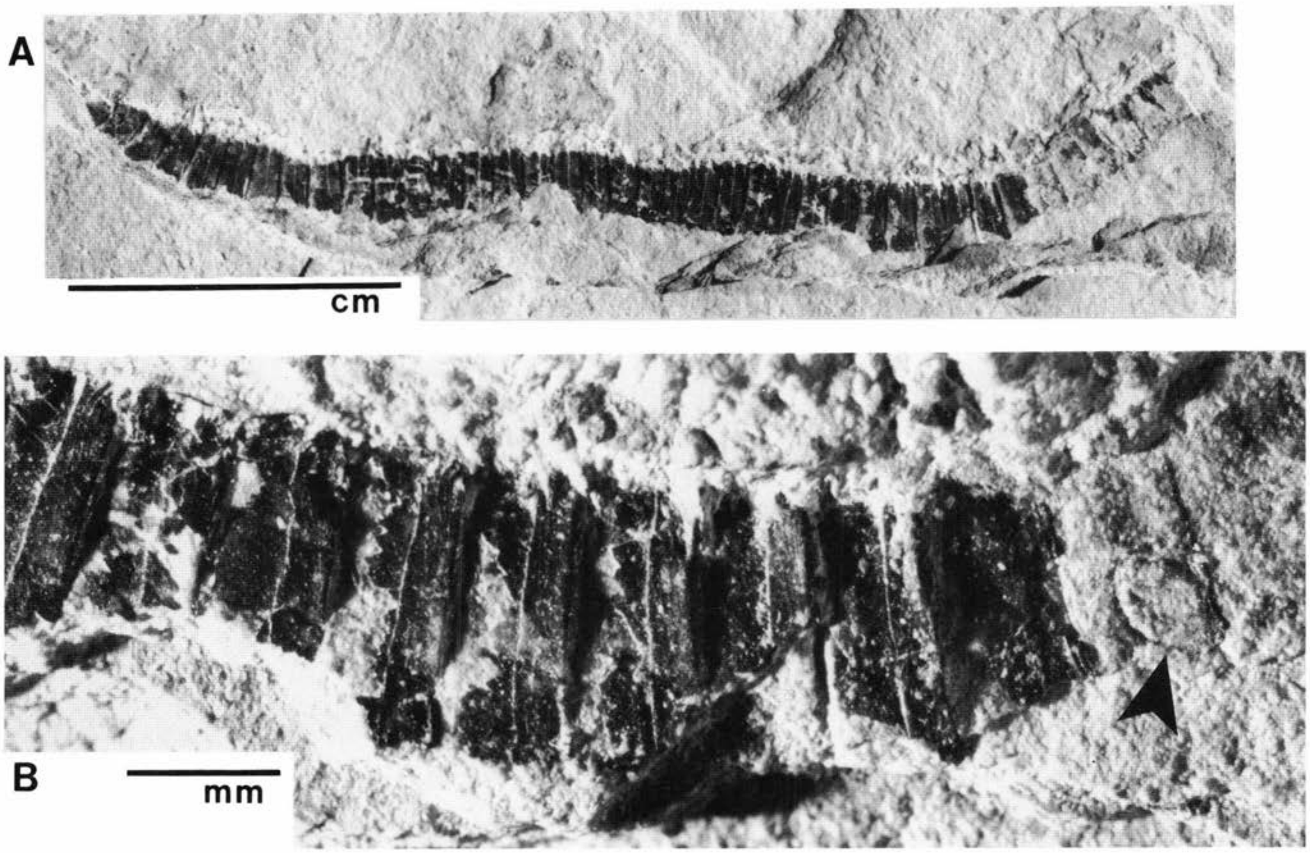

FIGURE 2—Diplopod(?) NMMNH P-14350 from the Kinney Brick Quarry. **A**, Dorsal view, anterior is to the left. **B**, Close-up of specimen; ovoid object referred to in text is indicated by arrow.

they are not divided by transverse sulci (Fig. 3A). From nine of these segments project elongate elements at most about as long as half the tergite width, but abruptly diminishing in apparent length ?posteriorly. Some have acute tips. These may be tergal spines or perhaps legs. At the ?anterior end the elongate elements are longest and ?posteriorly, where the view is more directly dorsal, they are shorter. This is consistent with their being legs attached either laterally or to the ventral surface, but not with tergal spines, which would appear shorter in a more lateral view and longer in a direct dorsal view. The shortening ?posteriorly may be due to the partial concealment of ventrally attached legs by the tergites. Also, the tergite edges of the ?anterior segments seem to overlap the bases of the elongate elements without any sign of attachment. On the other hand, there are no clear signs of segmentation, such as would be expected in legs.

If the single elements associated with each segment are legs, the specimen cannot be a milliped and may be a centiped. While no Paleozoic members of the order Geophilomorpha have been described in detail (but see Matthew, 1894, for some possibilities), the similar dimensions of the tergites in this specimen suggest a geophilomorph, if indeed it is a centiped. For information on Paleozoic centipeds see Mundel (1979) and Shear & Bonamo (1988).

Insecta

Specimen NMMNH P-12990

This specimen is in two fragments and comprises the anterior part of the body (Fig. 4A, B; Lucas & Huber, 1991: fig. 5D), including the head, antennae, and parts of three or four legs, and partial impressions of three wings (Fig. 5A), two of them superimposed. The body is simply a broken carbonaceous film over the surface of the coarse matrix. Little detail or relief can be seen, so some of the sutures between the leg segments, for example (Fig. 4B), should be regarded as partly conjectural. Of interest is the apparent presence of four large antennal elements at the base of the antenna—a primitive feature. The maxillary palpi can be seen on either side of the ventral head surface and the long, typical beak extends straight ventrally. The tarsus of one of the legs appears to be five-segmented.

The ventation of a probable hindwing is shown in Fig. 5A. In addition to the numerous crossveins, only the faintest traces of a possible archedictyon can be made out; it may not really be present. Vein ScP must have ended at or proximal to midwing. RP has three successive and nearly equally spaced branches, the branching of MA and MP has not been preserved, and only a small distal fragment of CuA is present. The proximal part of the wing and the entire anal area are missing. The general pattern resembles that in the megasecopteran family Brodiidae (= Brodiopteridae; Carpenter, 1963; Nelson & Tidwell, 1987), but the differences in the body and in some details of the wings suggest that a new, somewhat more primitive family may be represented. More material is required to determine the taxonomic placement of this insect.

Specimen NMMNH P-14337

This specimen (Fig. 5B) is part of a well-preserved blattoid wing (tegmen), probably belonging to a phyloblattid (Schneider, 1983). While close to *Phyloblatta,* this specimen differs in having ScA with five straight serial veinlets, a unique plesiomorphy within the Phyloblattidae. In *Phyloblatta*, ScA is transformed into a blunt ridge and the veinlets are lost. Unfortunately, the matrix is so coarse that we cannot make out any sculpture between the veinal branches; in *Phyloblatta* this would be a pebbled surface of small nodules.

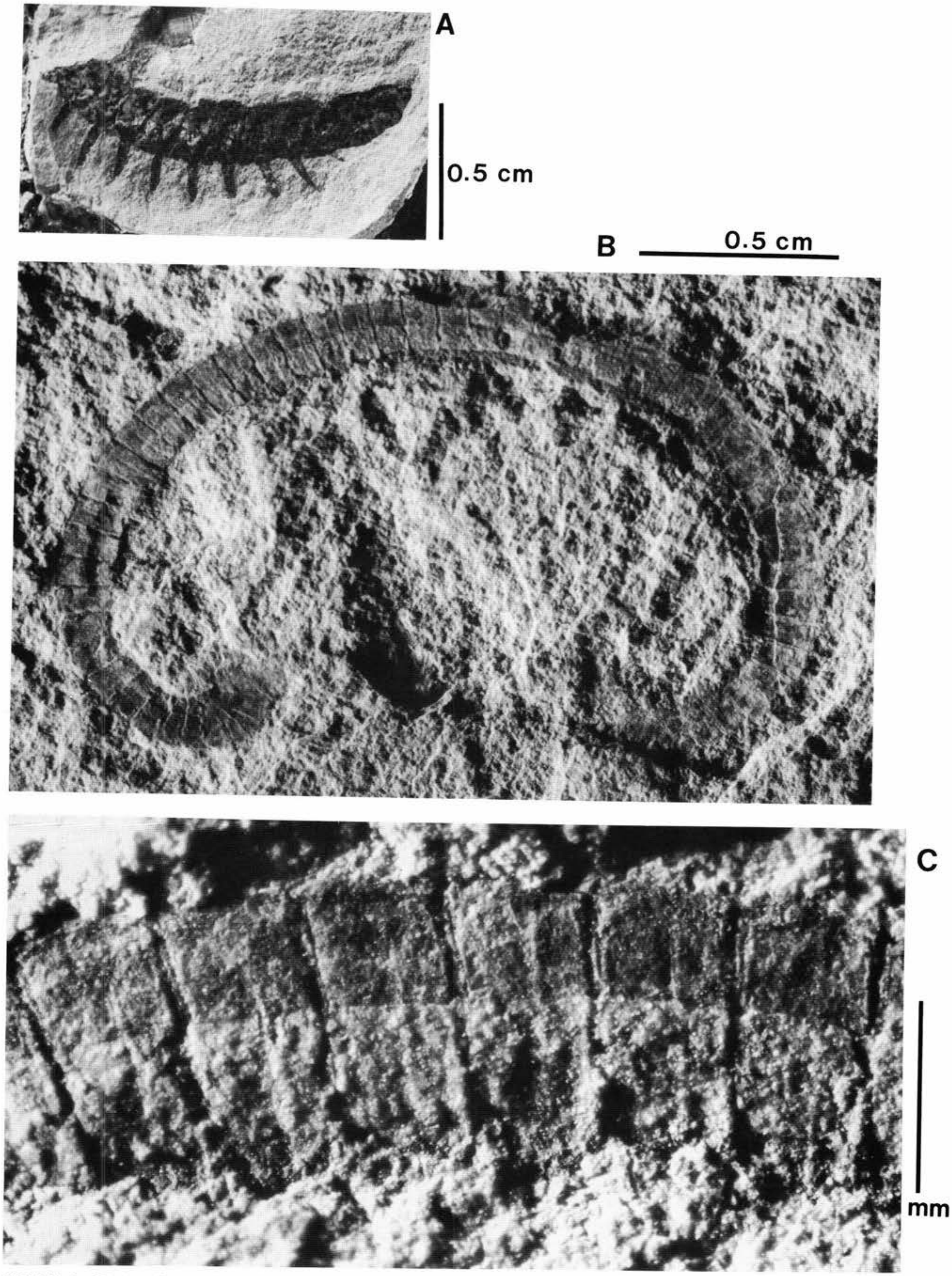

FIGURE 3—Myriapodous arthropods from the Kinney Brick Quarry. **A,** Possible centiped, UNM 10692, preserved in dorsal aspect; found 18 inches above main fish bed (floor of lower pit). **B,** Diplopod USNM 450760 in lateral view, curled ventrally; presumed anterior is to the left; possible gut infilling is represented by the lighter area to the ventral side of the body. **C,** Close-up of midbody segments of USNM 450760; gut infilling as described above.

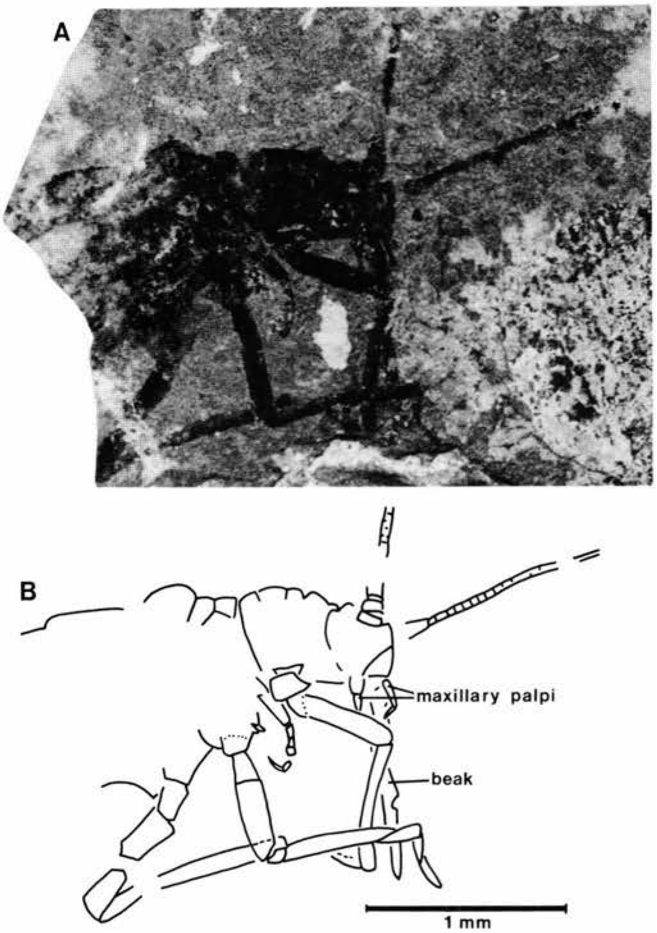

FIGURE 4—Possible brodiid, NMMNH P-12990. **A,** Photo of head and part of body. **B,** Interpretive drawing of same.

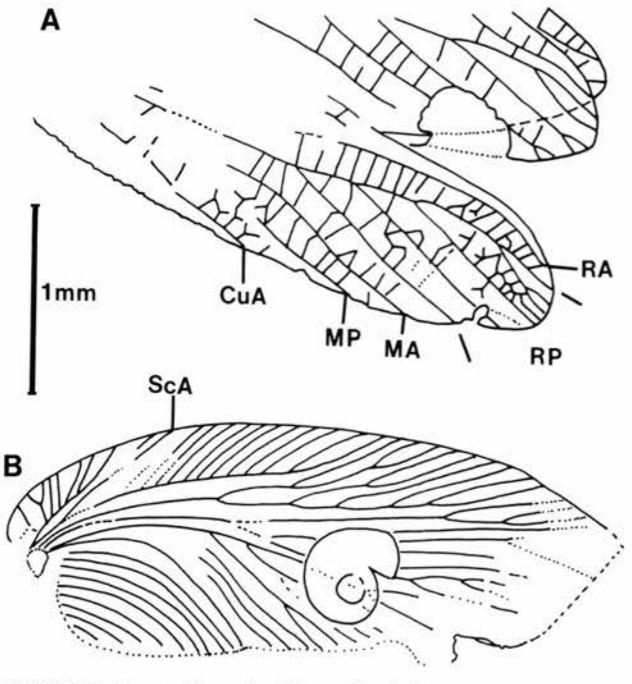

FIGURE 5—Insects from the Kinney Brick Quarry. **A,** Interpretive drawing of wings of a possible brodiid, NMMNH P-12990; compression precluded direct observation of (+) and (−) orientation of veins. **B,** Blattoid stem-group wing, NMMNH P-14337; coiled object is a small gastropod shell.

In this context we use the term "blattoid" loosely, since these fragments are not from members of the modern order Blattodea but represent the stem group from which the later roaches were derived. At least some of these ancestral types had prominent ovipositors and did not produce oothecae.

Clearly, other families of the blattoid stem group are also represented, including some poorly preserved specimens that show bodies as well as wings. Durden (1986) lists *Spiloblattina* (Spiloblattinnidae) from "Manzano, New Mexico," and Carrizo Arroyo. From Carrizo Arroyo, he also mentions *Amoeboblatta, Penetoblatta,* and *Puknoblattina* (Petrablattinidae), *Bradyblatta* (Bradyblattidae), *Distatoblatta* (Anthracoblattinidae), *Acmaeoblatta, Amblyblatta, Epheboblatta,* and *Nearoblatta (Acmaeoblattidae), Neorthroblattina* (Neorthroblattinidae), and several undescribed taxa.

Acknowledgments

Staff of the New Mexico Museum of Natural History provided loans of most of the specimens examined in this study. Sergius Mamay and others at the U.S. National Museum of Natural History, Washington, D.C., provided information on and loans of additional material from the Kinney Quarry. Bruce Frumker, Cleveland Museum of Natural History, took many of the photographs reproduced in Figs. 2 and 3. The photograph reproduced in Fig. 4 is from Lucas & Huber (1991, fig. 5D) and is reproduced here courtesy of Spencer Lucas. The comments of Conrad Labandeira and Rodney Feldmann materially improved this paper.

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Conodont platform elements from the Madera Formation (Pennsylvanian) at the Kinney Brick Company Quarry, Manzanita Mountains, New Mexico

Stanley T. Krukowski

Chemstar Lime Company, P.O. Box 127, BMI Complex, Henderson, Nevada 89015

Abstract—The floor of the lower, active pit of the Kinney Quarry is composed of a dark-gray to black, carbonaceous lime mudstone which grades upward into a brown, carbonaceous shaley lime mudstone. Samples from these two units were processed for conodonts, but only two platform elements of *Adetognathus lautus* and 10 platform elements of *Idiognathodus delicatus* were recovered. All the elements are unusually small and appear to be from juvenile specimens. The depositional environment was transitional between marine and brackish to fresh water, and was hostile to conodonts. The sample is not adequate for determining the age of the units.

Introduction

The first Pennsylvanian conodont fauna from New Mexico was reported by Robert C. Burton in 1964 in an unpublished paleoecological study of the Madera Formation at the Kinney Quarry. According to Kelley & Northrop (1975), Burton claimed to have approximately 500 specimens from 2 kg of rock. A partial list of these conodont elements includes the following:

Idiognathodus acutus
Idiognathodus delicatus
Idiognathodus humerus
Idiognathodus meekerensis
Spathognathodus minutus
Streptognathodus cancellosus
Streptognathodus elegantulus
Streptognathodus simulator
Streptognathodus tenuis
Synprioniodina microdenta

Due to Burton's prolonged absence, it was not possible to borrow his collection; therefore, it became necessary to sample units in the Kinney Quarry which reportedly contain conodonts.

The floor of the lower, active pit is composed of a very dark-gray to black, fossil-bearing, carbonaceous lime mudstone of the upper Madera Formation (Pennsylvanian). This unit grades upward into a brown, carbonaceous, fossiliferous shaley lime mudstone which is about 2.5 feet thick. Eight bulk grab samples were collected from various places in the lower-pit floor in March 1990, mostly from these units.

One kilogram from each sample was processed for conodonts using a 10% solution of hydrochloric acid. No conodonts were recovered from the three samples of the lower unit, the fossil-bearing, carbonaceous lime mudstone. Four samples from the brown, carbonaceous, fossiliferous shaley lime mudstone yielded a dozen conodont platform (Pa) elements and several small, broken pieces of other discrete elements (probably M, Sa, Sc, and Sb elements). One sample collected from the overlying sequence of shales and claystones was barren.

Systematic paleontology

ADETOGNATHUS LAUTUS (Gunnell)

(Not illustrated)

1967. *Adetognathus lauta* (Gunnell): Lane, pp. 933-934, pl. 121, figs. 1-5, 7, 10, 11, 15, 17, 18. (For synonymy see Baesemann, 1973).
1991. *Adetognathus lautus:* Kaiser & Manger, figs. 5:6(?), 6:14, 15.

Description—A thin, narrow left-sided platform element. The anterior free blade extends from the left platform margin. The blade is shorter than the platform. Blade denticles are fused but free at the tips. A deep medial trough is present along the length of the platform and is open at the anterior end. The margins are ornamented with short transverse ridges. In lateral view the platform element is slightly arched. The basal cavity is deep and asymmetrical, extending as a narrow groove along the lower margin of the blade.

Remarks—Two specimens were recovered from the brown, carbonaceous, fossiliferous shaley lime mudstone of the quarry floor. The diminutive size of these specimens, their poorly developed transverse ridges, and the few short dentides along the blade suggest that these are juvenile forms.

IDIOGNATHODUS DELICATUS Gunnell

Fig. 1a–c

1971. *Idiognathodus delicatus* Gunnell: Merrill & King, p. 658, pl. 76, figs. 13-16, 18, 22.
1973. *Idiognathodus delicatus* Gunnell: Baesemann, pp. 699-700, pl. 47, figs. 18, 19, 23, 24.
1991. *Idiognathodus delicatus:* Kaiser & Manger, figs. 5:3, 6:5.

Description—In upper view the platform is narrow, lanceolate, and tapers posteriorly. Anteriorly, accessory lobes may be present and ornamented with nodes arranged randomly or in rows. The upper surface of the platform is ornamented with parallel transverse ridges. The free blade is long, about half the length of the element, and composed of 10 or more fused denticles which are free at the tips. The blade is widest at the base of the denticles. The free blade extends onto the platform as a medial, fused carina which occupies from one-third to two-thirds of the platform length. The carina may terminate in a shallow trough posteriorly, transecting transverse ridges. A large, flaring, asymmetrical basal cavity extends anteriorly along the bottom of the free blade. In lateral view the element is slightly to moderately arched.

Remarks—Ten specimens were recovered from the brown, carbonaceous, fossiliferous shaley lime mudstone of the quarry floor. They appear diminutive, smaller than "normal" specimens. Fig. la, c illustrates longer carinae for this species. This is reminiscent of *Streptognathodus parvus* Dunn 1966, but the rudimentary or weak development of lateral lobes on both inner and outer platform margins is indicative of *I. delicatus.* The small size, longer carinae, poorly developed lateral lobes, and incomplete or absent transverse ridges (particularly posteriorly) suggest juvenile forms of *I. delicatus.* In addition, the shaley lime mudstone represents a

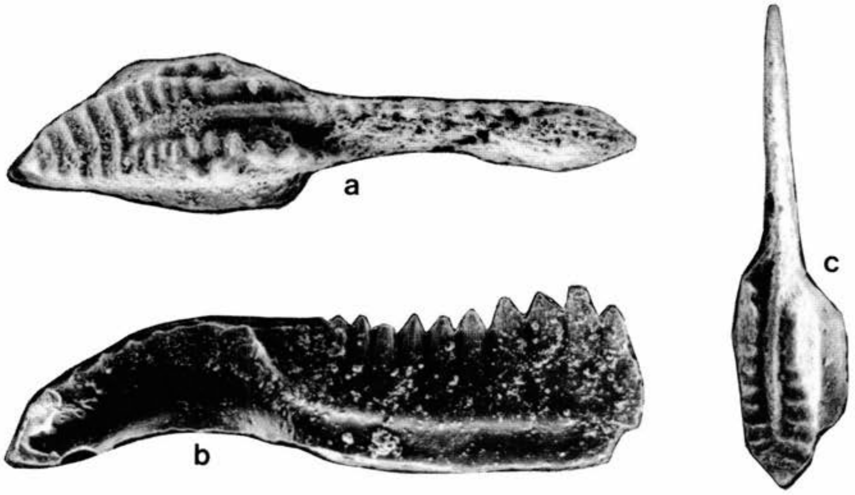

FIGURE 1—*Idiognathodus delicatus* from Kinney Quarry, New Mexico. **a,** Upper view, ×75; **b,** right lateral view, ×100; **c,** upper view, ×75.

transitional, i.e. harsh, environment of deposition between the marine lime mudstone below and the overlying shales and claystones.

Conclusion

No attempt is made here to assign an age to the upper Madera Formation in the Kinney Quarry based on so few conodont platform elements representing only two species, *Adetognathus lautus* (Gunnell) and *Idiognathodus delicatus* Gunnell. The rock units composing the quarry floor, the lower gray, fossil-bearing lime mudstone and the brown, carbonaceous, fossiliferous shaley lime mudstone, and the gradational contact between them represent an environment which is transitional between marine and brackish to fresh water, respectively. This environment was hostile to conodonts. Only a few juvenile specimens apparently lived there.

In April 1991 it was discovered that the lower lime mudstone grades laterally into a crinoidal grainstone which is exposed in the floor of the upper pit, near the quarry entrance. Additional samples of this facies have been collected, and it is anticipated that they will yield a larger conodont fauna.

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Late Pennsylvanian Chondrichthyes, Acanthodii, and deep-bodied Actinopterygii from the Kinney Quarry, Manzanita Mountains, New Mexico

Jiri Zidek

New Mexico Bureau of Mines & Mineral Resources, Socorro, New Mexico 87801

Abstract—The Kinney Brick Company Quarry fish beds contain a diverse assemblage of chondrichthyans, *Acanthodes* (Acanthodii), actinopterygians, a dipnoan, and a coelacanth (Actinistia: Sarcopterygii). The first two groups and the deep-bodied actinopterygians are described in this paper. The chondrichthyans include *Orthacanthus huberi* n. sp. (Xenacanthiformes), *Cobelodus aculeatus* (Symmoriiformes), *Symmorium reniforme* (Symmoriiformes), *Peripristis cf. semicircularis* (Petalodontiformes), and *?Listracanthus* (Chondrichthyes inc. sedis). The class Acanthodii is represented by *Acanthodes kinneyi* n. sp., and the deep-bodied actinopterygians include *Amphicentrum jurgenai* n. sp. (Palaeonisciformes), *Platysomus schultzei* n. sp. (Bobasatraniiformes), and Platysomidae indet. (?Bobasatraniiformes). Only *Amphicentrum* may possibly bear on the age of the site, because this genus has not been hitherto known from Stephanian B (= Virgilian) deposits.

Platysomus is a collective genus that contains lower actinopterygians of two orders, the Palaeonisciformes and the Bobasatraniiformes, and what should or should not be retained in the genus cannot be decided without a species-by-species revision. The Kinney species, *P. schultzei,* exhibits a number of advanced features and is the most primitive and oldest bobasatraniiform fish known. A single headless specimen identified only as Platysomidae indet. is the only North American platysomid that possessed pelvic fins. It is tentatively assigned to the Bobasatraniiformes because of a parasagittal arrangement of the caudal fulcra, which is interpreted as an advanced feature. A definitive ordinal placement must await the discovery of more complete specimens in which the structure of the head can be examined.

Acanthodes and most of the actinopterygian taxa are common at the Kinney Quarry, whereas the other groups (Chondrichthyes, Dipnoi, Sarcopterygii) are exceedingly rare. The abundance vs. paucity is profound and cannot be explained by different fossilization potentials of cartilage and bone. The explanation clearly lies in environmental requirements of the various taxa and in their respective positions in the trophic web. *Symmorium* was a large and agile predator that quite certainly was at the top of the tropic web, followed by the smaller but equally agile *Cobelodus,* whose dentition of minute teeth may not have necessarily prevented taking large prey. The chondrichthyan predators should be expected to be far less numerous than their osteichthyan and invertebrate prey; in addition, the paucity of their shed teeth suggests that they were only occasional visitors to the Kinney lagoon. The dentition of *Amphicentrum jurgenai* is not known and can only be extrapolated from *A. granulosum,* in which it consists of massive coronoid and ectopterygoid plates bearing conical teeth and capable of crushing mollusc shells. The phyllodont tooth plates of *Platysomus schultzei are* a more fragile apparatus better suited for crushing crustacean carapaces than mollusc shells. In the toothless *Acanthodes,* gill-rakers functioned as a straining apparatus for filter-feeding as well as a holding device preventing larger prey from escaping. It is very likely that the diet of *A. kinneyi* included both invertebrates and smaller fishes.

The prevailing mode of disarticulation of the deep-bodied and other actinopterygians at the Kinney Quarry is a rupture along the opercular line which represents a major zone of weakness. Several ruptured specimens of *Platysomus* provide strong evidence against the floating of fish carcasses claimed by some authors and used as an indication of shallow water. The rupture invariably resulted in disarticulation over a very small area (25-36 are), indicating that it occurred on the substrate and not on the water surface.

Introduction

The Kinney Brick Company Quarry (hereafter referred to 27 the Kinney Quarry) is located in the Manzanita Mountains southeast of Albuquerque (Bernalillo County, NW^1/4 SW^1/4 SE1/4 sec. 18, T9N, R6E) and exposes a Late Pennsylvanian paralic sequence of shales, claystones, and sandstones, with a micritic limestone at the base. The exposure is in the Pine Shadow Member of the Wild Cow Formation (Madera Group) and is 28 m thick (Lucas & Huber, 1991). Based on fusulinids recovered from other exposures in the area, Myers (1973, 1982, 1988) dated the Kinney Quarry deposits as early Virgilian; however, it is possible that they are wholly or in part late Missourian (see Huber and Mapes & Boardman, this volume). Fusulinids are said to occur in the micritic limestone that forms the quarry floor (P. Huber, pers. comm. 1991), but few have been collected and none studied. A future study of them should prove helpful to resolving the question of age of the Kinney Quarry strata.

The Kinney Quarry fish beds (units 2-4 of Lucas & Huber, 1991; see also Kues & Lucas, this volume) have produced a diverse ichthyofauna composed of chondrichthyans, *Acanthodes* (Acanthodii), actinopterygians, *Proceratodus* (Dipnoi), and a coelacanth (Crossopterygii). The actinopterygians and *Acanthodes* are common, whereas the other groups are exceedingly rare. *Proceratodus hlavini* Zidek 1975 is known only from the holotype (CMNH 8311, a left mandibular tooth plate with incomplete prearticular); the coelacanthid is known from scales, neural arches, fin rays, a pelvic basal plate (USNM 187143 and 187149; Zidek, 1975), and three partial specimens plus one nearly complete specimen in the KUVP collection (Schultze, this volume); and the chondrichthyan taxa are known from only one or two specimens each. The abundance vs. paucity is profound and cannot be explained by different fossilization potentials of cartilage and bone. The explanation clearly lies in environmental requirements and preferences of the various taxa, and in their respective positions in the trophic web.

There is nothing new to say about *Proceratodus hlavini,* the coelacanth is treated by Schultze (this volume), and the fusiform actinopterygians are described by Bardack, Gottfried, and Huber (all in this volume). The account below thus is restricted to the chondrichthyans, *Acanthodes,* and the deep-bodied actinopterygians.

Institutions that house Kinney Quarry specimens, and specimens from other localities used for comparisons, are abbreviated as follows: AMNH, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio; FMNH/PF/UC, Field Museum of Natural History, Chicago, Illinois; KUVP, University of Kansas Museum of Natural History, Lawrence; NMMNH, New Mexico Museum of Natural History, Albuquerque; OMNH, Oklahoma Museum of Natural History, Norman (formerly OUSM, University of Oklahoma Stovall Museum of Science and History); TMM, Texas Memorial Museum, Austin; UI, University of Illinois at Urbana–Champaign; USNM, U.S. National Museum of Natural History, Washington, D.C.; YPM, Yale Peabody Museum, New Haven, Connecticut; YPM/PU, Princeton University collection at the Yale Peabody Museum.

Acknowledgments

Spencer Lucas and Ruby Williamson made available NMMNH specimens, and Adrian Hunt often brought and returned them for me. Hans-Peter Schultze and John Chorn made available KUVP specimens and helped with stratigraphic information on the Kansas *Peripristis* included for comparison. Loans of Kinney and other deep-bodied actinopterygians were extended also by Donald Baird (formerly of PU), David Berman of CM, Daniel Blake of UI, John Bolt of FMNH, Wann Langston (formerly of TMM), William Purdy of USNM, Bobb Schaeffer (formerly of AMNH), and Mary Ann Turner of YPM. Ted Cavender of the Ohio State University, William Melton of the University of Montana, and Gerard Case of Jersey City kindly provided information on platysomid and amphicentrid occurrences in South Dakota, Montana, and Iowa plus Nebraska, respectively. The holotype of *Acanthodes kinneyi,* NMMNH P-19208, was expeditiously prepared by Pete Reser of NMMNH. *Cobelodus aculeatus* NMMNH P-19182 was prepared by Shannon Krause and Wayne Wentworth, formerly of New Mexico Tech, and x-rayed by Ted Steinbock of X-Ray Associates, PA, Albuquerque. Allan Lerner and Kaye Toolson, Albuquerque, kindly let me examine and photograph specimens in their personal collections. Lynne McNeil typed the manuscript. Discussions with David Bardack, University of Illinois at Chicago, Michael Hansen, Ohio Geological Survey, Hans-Peter Schultze, University of Kansas, and Rainer Zangerl, Rockville, Indiana, were exceedingly helpful and their reviews much improved the manuscript. This is contribution 72 to the International Geological Correlation Programme No. 328.

Systematic paleontology

Class **CHONDRICHTHYES** Huxley 1880
Subclass **ELASMOBRANCHII** Bonaparte 1838
Order **XENACANTHIFORMES** Berg 1940
Family **XENACANTHIDAE** Fritsch 1889
Genus *ORTHACANTHUS* Agassiz 1843

ORTHACANTHUS HUBERI n. sp.
Figs. 1, 2

Material—Holotype NMMNH P-19146a + b, the distal half (a) and the proximal end (b) of an occipital spine; and paratype NMMNH P-19146c, a partial braincase.

Type locality and horizon—Kinney Brick Company Quarry, NW^1/4 SW^1/4 SE^1/4 sec. 18, T9N, R6E, Bernalillo County, central New Mexico. Unit 3 of Lucas & Huber (1991; see also Kues & Lucas, this volume), Pine Shadow Member of Wild Cow Formation, Madera Group, Upper Pennsylvanian.

Etymology—Named after the collector, Phillip Huber.

Diagnosis—Occipital spine with maximum diameter to length ratio of 1:26; straight or very slightly curved posteriorly; tubercle rows situated posterolaterally, number of tubercles in each row approaches or may exceed 100; cross section circular except flat to slightly concave posterior face between denticle rows. Braincase with dorsal otic ridge that issues at level of anterior margin of otic process and extends back into occipital area.

Description—A slender, straight spine 129 mm (NMMNH P-19146a) plus 40 mm (NMMNH P-19146b) in preserved length and 8 mm in maximum diameter. The 19146b segment (Fig. 1A$_2$) is the proximal end with a fragment of calcified cartilage attached. Its anterior surface is collapsed and crushed but nevertheless exhibits a sculpture of short, interrupted striae. Since the distance of this segment from the proximal end of 19146a has not been recorded during collection, it is of no use in estimating the spine's total length.

NMMNH P-19146a (Fig. 1A$_1$, B) is nearly complete distally, with only 2 mm of the tip missing. Sculpture of fine, uninterrupted longitudinal costae is preserved in the proximal one-fourth and a posterolateral denticle row 105 mm long and consisting of ca. 100 denticles is exposed on the left side. The denticles gradually diminish in size distally, from 7/cm at the proximal end of the row to 15/cm near the tip. In the proximal half of the row the denticles are stubby and are separated from each other by gaps roughly equal to the diameters of their bases, whereas in the distal half they are more pointed, more obviously curved proximally, and progressively more closely spaced, with the bases of the distalmost denticles touching. The specimen (19146a) is split longitudinally throughout the proximal two-thirds and its right side is elevated above and somewhat over the left side. When restored, the cross section becomes circular with only the posterior surface between the denticle rows either flat or slightly concave (Fig. 1E).

NMMNH P-19146c (Fig. 2) is the posterior part of a flattened braincase that was found closely associated with the spine. It is exposed in dorsal view and shows the right otic process, the paired dorsal otic ridge, the lateral otic ridges, and the occipital crest. The preserved part is 5 cm long and amounts to somewhat less than one-half of the entire braincase, which thus would be ca. 11 cm long. The dorsal otic ridge issues on the level of the anterior margin of the otic process and extends back into the occipital area; in effect, it surrounds much of the occipital crest.

Discussion—Orthacanthus spines differ from those of other xenacanthids in the cross section and position of denticle rows. The cross section either remains essentially circular throughout the spine length or changes from deeply oval (i.e. somewhat antero-posteriorly compressed) in the proximal part to circular in the central part and to laterally compressed oval in the distal part. The dentide rows are situated either posteriorly or posterolaterally and are restricted to the distal third to half. The denticles of the left and right rows may form pairs or may alternate, but this is not unique to the genus. Although *Orthacanthus* spines may be characterized as gently curved posteriorly either through most of their length or in the distal third to half, the curvature tends to be quite variable within species and straight spines, although uncommon, occur as well. The *0. huberi* spine has numerous hairline transverse fractures, and it is thus possible that a minor curvature was originally present but succumbed to pressure during burial and diagenesis.

Should the spine occur alone rather than in association

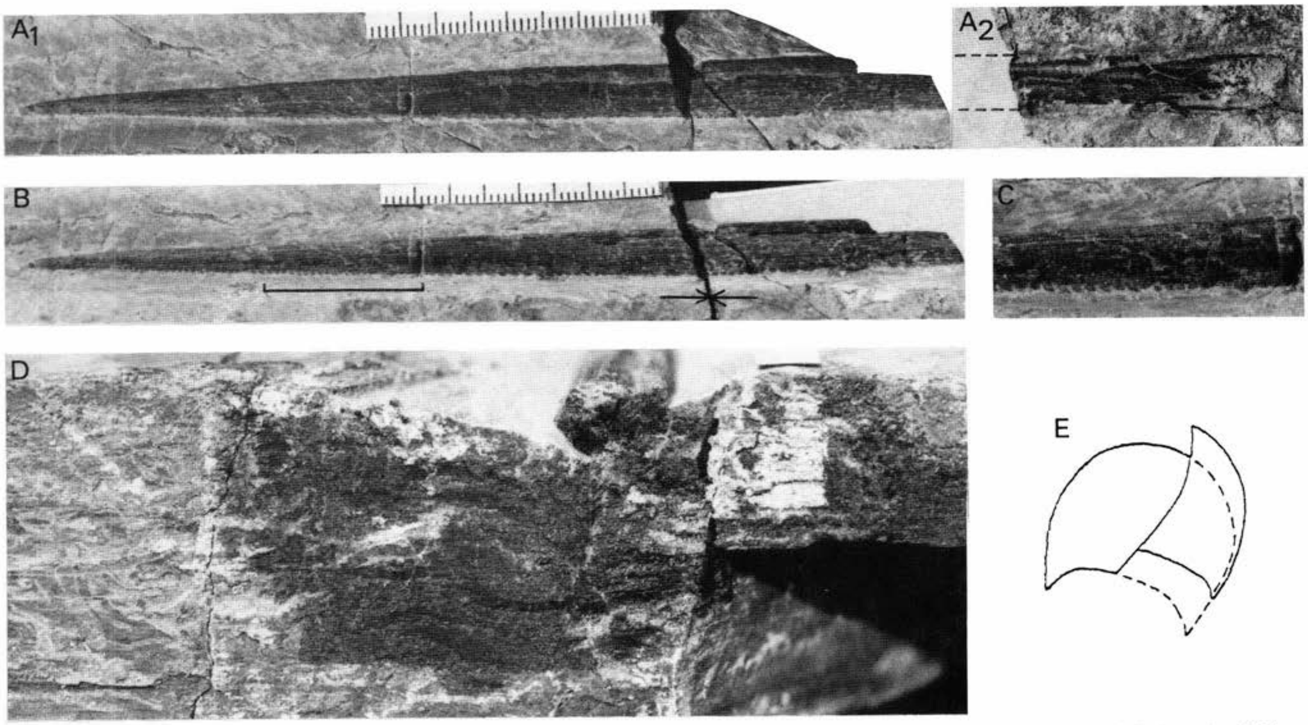

FIGURE 1—*Orthacanthus huberi* n. sp., holotype NMMNH P-19146a (A_1) and 19146b (A_2), Kinney Quarry, New Mexico. **A,** Oblique anterior view; **B,** lateral view; **C,** enlarged section marked by the bar in B to show denticulation; **D,** enlarged (×2) cross section at the break marked by arrows in B, showing associated mass of calcified cartilage with discrete fragments of radials; **E,** enlarged (×3) cross section as preserved (solid line) and restored (interrupted line). Scale in A and B in millimeters.

with the braincase, its length could be estimated only very roughly, at between 210 mm (if the entire distal half was denticulated) and 315 mm (if only the distal third was denticulated), and its maximum diameter to length ratio would thus range anywhere between 1:26 and 1:39. Fortunately, the length of the braincase can be estimated quite confidently at ca. 11 cm, which helps to refine the unsatisfactorily rough estimate of the spine's length. A braincase 11 cm long indicates a fish ca. 100 cm long. In most xenacanthids the spine length to total specimen length ratio varies between 1:5 and 1:6, which for a spine 210 mm long translates to a fish 105-126 cm long. This estimate is quite compatible with that derived from the braincase, and it can thus be concluded that the spine was only ca. 210 mm long, its entire distal half was denticulated, its maximum diameter to length ratio was 1:26, and that it belonged to a fish ca. 1 m long.

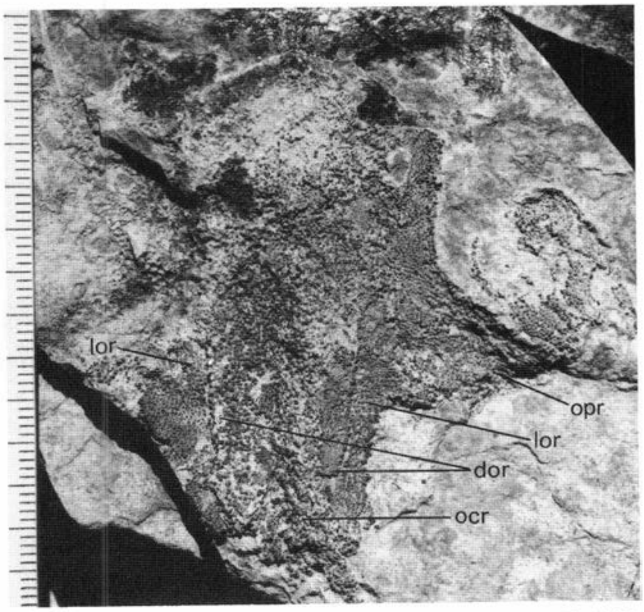

FIGURE 2—*Orthacanthus huberi* n. sp., paratype NMMNH P-19181, Kinney Quarry, New Mexico. Scale in millimeters. The posterio part of a braincase showing the right otic process **(opr)**, the paire dorsal otic ridge **(dor)**, the lateral otic ridges **(lor)**, and the occipita crest **(ocr)**.

At least 20 xenacanthid species are based on isolated spines (Woodward, 1889; Davis, 1892), and approximately half of them can be assigned to *Orthacanthus.* The largest such spine is *0. cylindricus* Agassiz 1843, the type species of the genus, with some spines 50 cm long. The *0. huberi* spine most closely resembles *0. cylindricus* from the British Coal Measures (Westphalian) and *0. kounoviensis* Fritsch 1889 and *0. pinguis* Fritsch 1889, both from Stephanian B of Bohemia, Czechoslovakia. In *0. cylindricus* the curvature is minor and some spines are straight (Davis, 1892: pl. 73/1), and in *0. kounoviensis* and *0. pinguis* the curvature is minor as well (Fritsch, 1889: pl. 87). The cross sections of *0. pinguis* (Fritsch, 1889: pl. 87/3-4) and of some specimens of *0. cylindricus* (Davis, 1892: pl. 73/4) match that of *0. huberi* better than does *0. kounoviensis,* but Davis' illustrations of *0. cylindricus* indicate a substantial amount of variation in this regard. The *0. huberi* spine differs from all these species in the maximum diameter to length ratio and in the denticulation. In *0. huberi* the maximum diameter to length ratio is 1:26, whereas in *0. cylindricus* and *0. kounoviensis* it is 1:20, and in *0. pinguis* only 1:15. The left denticle row of *0. huberi* contains ca. 100 denticles, which is 25-50% more than in *0. cylindricus* (entire distal half denticulated), 50% more than in *0. kounoviensis* (entire distal half denticulated), and ca. 70% more than in *0. pinguis* (only the distal third denticulated). The *0. huberi* spine thus is significantly more slender and more finely/densely denticulated than in the other three species.

The braincase does not quite match any other xenacanthid braincase so far described. The difference is in the position of the dorsal otic ridge, which normally extends from behind the postorbital process to the level of the otic process (see Schaeffer, 1981: fig. 6). In the *0. huberi* braincase the dorsal otic ridge is situated much more posteriorly, starting at the level of the anterior margin of the otic process and extending well back into the occipital area. In effect, it surrounds much of the occipital crest instead of ending, as usual, approximately at the level where the occipital crest starts. Although the posterior extent of the ridge may be somewhat exaggerated due to dorso-ventral compression, the condition certainly is real (i.e. not an artifact of preservation) and thus of diagnostic value.

Orthacanthus is the most inadequately known xenacanthid genus (Zidek, in press, a, *b).* Since the majority of its species are based solely on spines and teeth, and a few are known from associations of teeth, jaws, and braincases (invariably devoid of spines), it is impossible to determine with any degree of confidence which of the organ-based species are valid and which are synonymous with others. The *0. huberi* spine would be no exception, the question of whether it really is a new species or whether it rather belongs to a species already known from other hard parts obviously could not be answered. However, its association with a braincase of distinctive morphology makes it possible to conclude that *0. huberi* indeed is a new species.

Both the spine and the braincase are equally diagnostic. The reasons why the spine is designated as holotype and the braincase as paratype and not vice versa is that (1) future finds will more likely be spines than braincases and (2) xenacanthid spines usually are species-diagnostic, whereas braincases present problems even on the generic level (Zidek, in press, a, *b).* Although *0. huberi* is an exception in the latter regard, basing it on the spine makes the species more compatible with the criteria normally applicable to the Xenacanthidae. The reason why both the spine and braincase cannot be designated as the holotype is that they are discrete specimens. Although they were found closely associated, the spine was not actually attached to the braincase, and the possibility, however small, thus exists that the two do not belong to the same fish.

Since the spine is *Orthacanthus-like* whereas the braincase is not, the question arises whether the assignment to *Orthacanthus* is correct. One possibility is that the new species in fact belongs to the genus *Triodus* Jordan 1849, whose spine has been described as "an *Orthacanthus-like* spine of perfectly circular (drehrund = circular, as if turned on a lathe) cross section" (Zangerl, 1981: 65, translation of Jordan, 1849). *Triodus* had remained an enigmatic genus until recently, when virtually complete articulated specimens were discovered in the Saar—Nahe Basin of southwestern Germany. These specimens are being studied at the Johannes Gutenberg University, Mainz (see Schneider & Zajíc, 1990: 27), and data on morphology of the spine and braincase are not yet available. The second possibility of course is that the Kinney material represents a new genus, but, because of the work in progress on *Triodus*, it would not be prudent to erect one.

Order SYMMORIIFORMES Zangerl 1981
Family SYMMORIIDAE Dean 1909
Genus *COBELODUS* Zangerl 1973

COBELODUS ACULEATUS (Cope 1894)
Figs. 3-6

Two symmoriid skeletons, NMMNH P-19180 and 19182, have been found at the Kinney Quarry so far, but only the 19182 specimen can be unequivocally assigned to *Cobelodus.* The 19180 specimen consists of an occipital fragment of the braincase, the left epihyal, fragments of branchial arches, left and right scapulocoracoids, anteriorly displaced left metapterygium, about a dozen pectoral radials, vertebral column back to the level of the dorsal fin, and poorly preserved dorsal radials. The elements are on the order of size of those in the 19182 skeleton and there is nothing incompatible with *Cobelodus* in their morphology. However, there is nothing incompatible in them with the other symmoriid genera *(Symmorium* and *Denaea)* either, and the 19180 specimen thus cannot be identified any better than Symmoriidae indet. The entire description and discussion below are based on the 19182 specimen.

The NMMNH P-19182 skeleton (Fig. 3A) is 45 cm in standard length and lacks only the anterior half of the braincase and the dorsal lobe of the tail. It is exposed by the right side, with the backbone gently arched. A 28 mm long, ovoid coprolite (cololite) is preserved between the neural and anterior haemal arches (further see Hunt, this volume), i.e. somewhat posteriorly of where the vent would be.

The braincase is distorted and difficult to interpret. Its maximum length is 34 mm and little more than the otico-occipital region is preserved (Fig. 4A). From Zangerl (1981: figs. 77, 78, 80) it appears that symmoriid braincases averaged 13-14% of standard specimen length (13% in *Cobelodus),* and for a 45 cm long fish the entire braincase thus should be 58.5 mm long. Since the otico-occipital region takes about 40% of the braincase length (Zangerl, 1981: 70), it should occupy 23.4 mm of the preserved part and the anterior 10.6 mm should be the hind part of the orbital region. This is precisely the case, from the occipital condyle to the arrow in Fig. 4A the distance is 23.5 mm. Symmoriid braincases are quite deep dorso-ventrally and the foramen magnum is situated near the base. The ventral surface bears paired otic depressions (Fig. 4B) separated by a median ridge which floors the medulla. Both the occipital condyle and the otic depression(s) are visible in the Kinney braincase, documenting that it is exposed in ventral to ventrolateral aspect. The postorbital arcade was crushed, pressed against the braincase wall, and became a mere ridge.

The visceral skeleton and pectoral girdle—fin complex can be discerned in more detail from a radiograph (Fig. 5). It shows the palatoquadrate to be shorter than the Meckel's cartilage, the ceratohyal about as long as the palatoquadrate, and the epihyal matching the length of the palatoquadrate crest. The branchial arches are not well preserved and there is no evidence of basibranchial elements. The three epibranchials all appear to be the right ones, whereas two of the ceratobranchials could be the left-side elements. The Meckel's cartilage is longer than the palatoquadrate also in *Symmorium*, and the skeletons of the two genera are in all respects so similar that they can be reliably differentiated only by their teeth. Fortunately, etching with 10% acetic acid succeeded in uncovering several teeth between the jaws (Fig. 6, area circled in Fig. 3A, B). They are minute (barely over 2 mm long), slender, monocusped, finely striated, with expanded, convex bases and in no way differ from the monocusped *Cobelodus* teeth illustrated by Zangerl & Case (1976: fig. 16) and Hansen (1986: fig. 22D—E, p1. 4/ 14, 15). Although poorly preserved, they nevertheless provide unequivocal evidence that the specimen ís *Cobelodus.* Since the lower teeth of *Cobelodus* were cladodont, those in the Kinney specimen must be from the palatoquadrate.

The scapulocoracoids and metapterygia are well preserved and those of the right side are fully visible. The right scapulocoracoid appears to have lost the lower, coracoid part (Fig. 3A, B), but the radiograph (Fig. 5) shows this part to be merely covered up. It also reveals a small, claw-like sternal element (Zangerl & Case, 1976: fig. 17d—f), whose distal end is not discernible, however. The metapterygium is a compound structure of fused axial segments and basal rods (Zangerl & Case, 1976: 134, figs. 17, 20); 16-17 basals are evident in the right metapterygium of the Kinney spec-

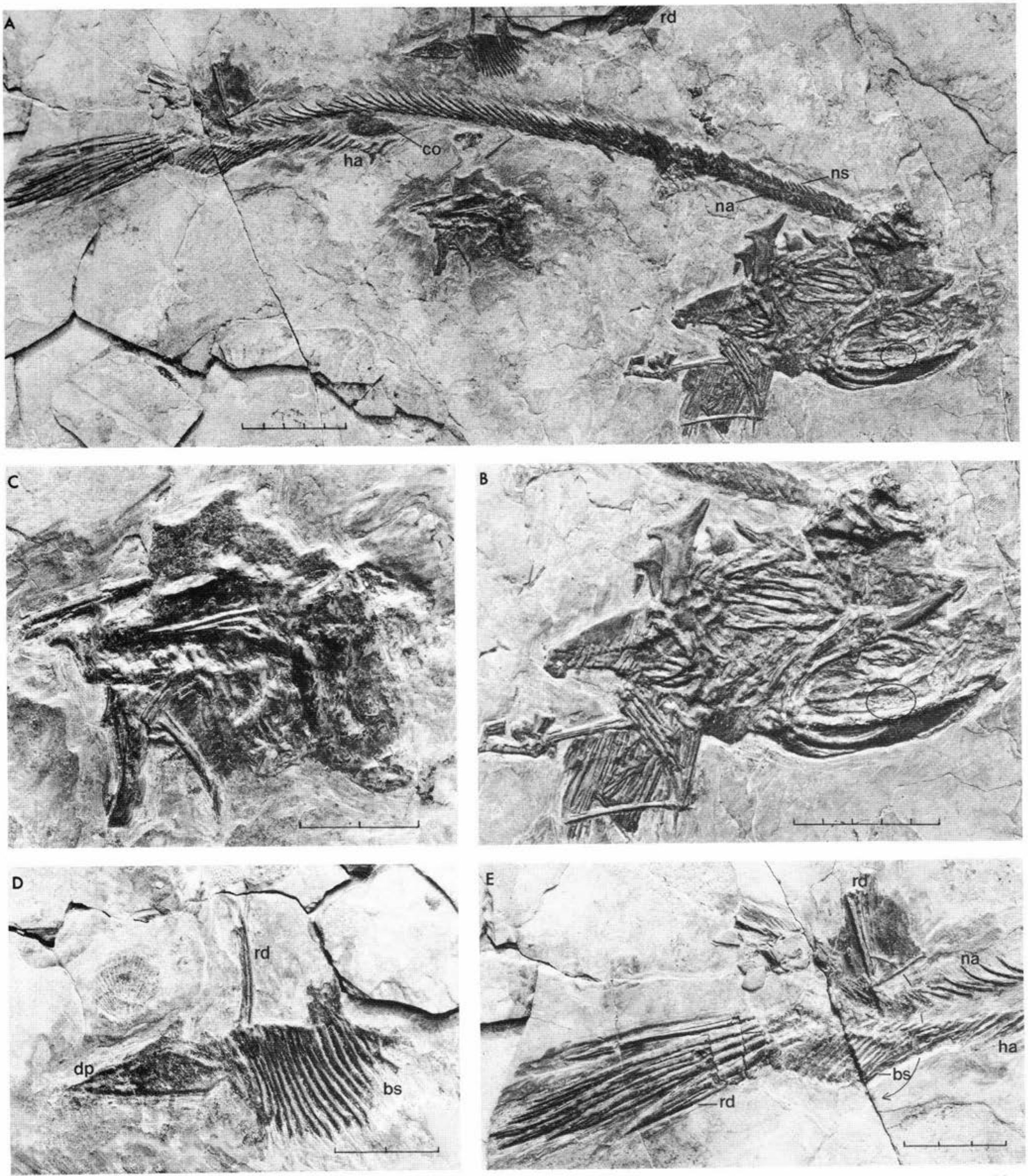

FIGURE 3—*Cobelodus aculeatus* NMMNH P-19182, Kinney Quarry, New Mexico. Overall view **(A)** and close-ups of head and shoulder **(B)**, pelvic plate **(C)**, dorsal fin **(D)**, and caudal fin **(E)**. The elements shown in B are labeled in Figs. 4 and 5. The area circled in A and B contains teeth and is detailed in Fig. 6. Arrows in A and E show original positions of displaced radials. Scales in centimeters. Abbreviations: **bs,** basal; **co,** coprolite (cololite); **dp,** dorsal plate; **ha,** haemal arch; **na,** neural arch; **ns,** neural spine; **rd,** radial.

imen, and the first discrete axial segment, i.e. the proximal end of the whip, is at the distal end of the metapterygium. The more distal segments of the whip and all radials are detached and disarrayed.

Little can be said about the pelvic plate and fin (Fig. 3C). The plate shows an anteroventral beak-like projection and a ventral concavity (lower right of figure), but otherwise its margins are broken up, incomplete, and/or covered with disarrayed basal rods and a few radials. What appears to be a more robust proximal clasper element (lower left of figure) actually consists of two basal rods. Due to poor preservation, however, the lack of clasper elements cannot be used as evidence for female sex. The sex simply cannot be determined in the Kinney specimen. The only other observation worth mentioning is size, the pelvic plate is relatively larger than those of Zangerl & Case (1976). As restored in their fig. 33, the anteroventral—posterodorsal length of the pelvic plate should not exceed the length of the dorsal

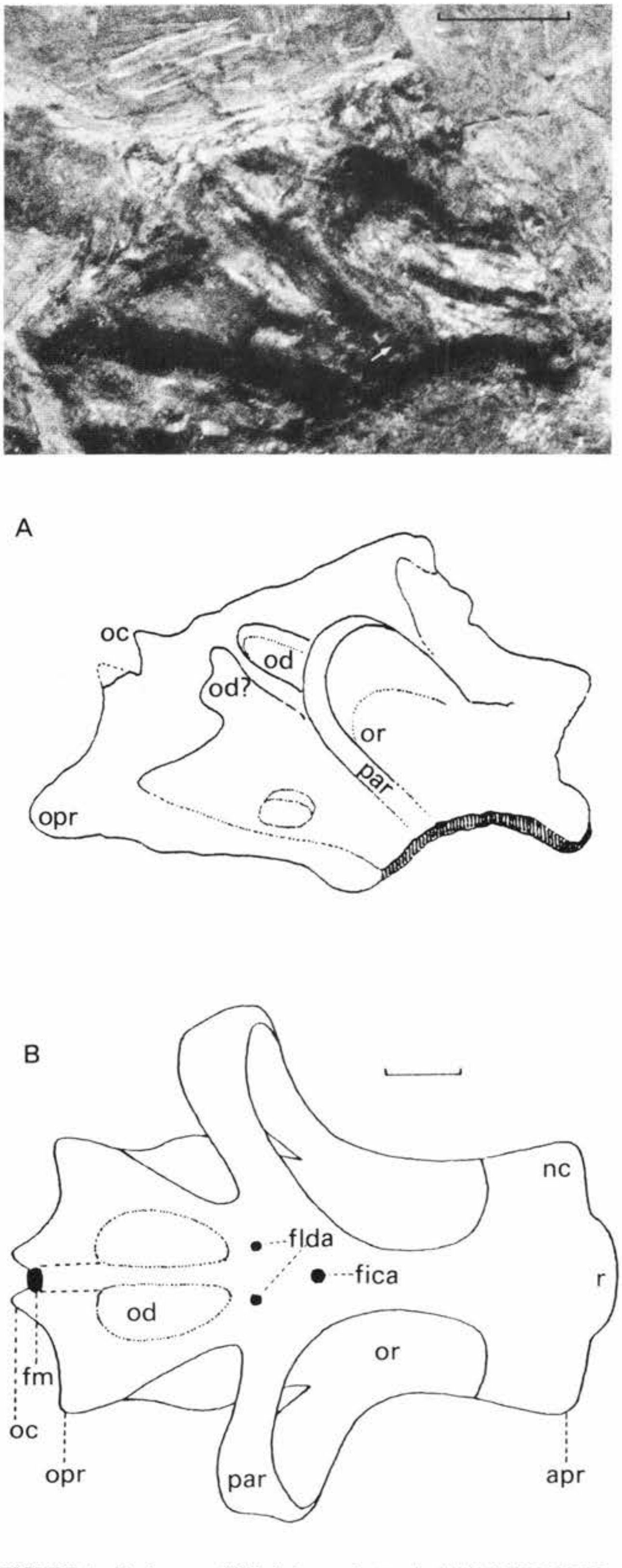

FIGURE 4—Braincase of *Cobelodus aculeatus*. **A,** NMMNH P-19182, Kinney Quarry, New Mexico. **B,** Morphology of ventral surface, chiefly after Zangerl & Case (1976: figs. 3, 5); braincase faces right to facilitate comparison with A. Scale bars equal 1 cm, arrow denotes anterior limit of otico-occipital region calculated in text. Abbreviations: **apr,** antorbital (nasal) process; **fica,** foramen for internal carotid artery; **flda,** foramina for lateral dorsal aorta; **fm,** foramen magnum; **nc,** nasal capsule; **oc,** occipital condyle; **od,** otic depression; **opr,** otic process; **or,** orbit; **par,** postorbital arcade; **r,** rostrum.

plate, but in the Kinney specimen it is nearly twice as long. This is of interest because it does not appear that the pelvic area could actually be a composite of right and left pelvic plates.

The dorsal fin (Fig. 3A, D) consists of 22 basal rods which support a series of (presumably 22) radials, and an arrow-shaped dorsal plate (V-shaped element of Zangerl & Case, 1976: 145-146) at the posterior end of the basal series. All the basal rods are in place and the last four overlap the open anterior end of the basal plate. Of the radials only two more posterior ones are in place, nine have been displaced anteriorly and overturned (top of Fig. 3A), and the remaining rods (presumably 11) are not preserved. In both the basal and radial series the longest rods are in the center and the length diminishes anteriorly and posteriorly. The longest basal measures 26 mm and the longest radial measures 37 mm. The radials are as sturdy as the basals, but their distal ends are more pointed than the proximal ends of the basals. The dorsal plate is 32 mm long and its dorsal and ventral edges are thickened into narrow rims. Zangerl & Case (1976: 146) reported that the thin sheet of cartilage which forms the body of the plate sometimes contains circular perforations, but it appears to be solid in the Kinney specimen.

The vertebral column (Fig. 3A) consists of 90 neural arches and 23 haemal arches. There are no ventral arches corresponding to the first through 74th neural arches. The last neural arch is just before the upturn into the dorsal lobe of the tail, which is not preserved. Assuming ca. 30 neural arches involved in the dorsal lobe, the total number is estimated at around 120. The first 10 haemal arches are free and correspond to the 75th through 84th neural arches. The 11th through 23rd haemal arches articulate with basal rods of the ventral lobe of the tail. All the arches are paired, the right and left members of each pair being in contact with each other but not fused except possibly for the posterior haemal arches involved in the ventral lobe of the tail. That area (Fig. 3E) is not preserved well enough to permit a decision, however. The first four neural arches are the shortest and the most robust, and in the first 25-30 arches there is a clear division between the arch proper and its spine. The division shows in Fig. 3A—B as a line that runs somewhat diagonally through the segments, higher up anteriorly (= arch taller than its spine) and lower down in the more posterior segments (= arch as tall or shorter than its spine). Also, the first 25-30 segments are sigmoidal, a shape that results from posterior inclination of the lower part of an arch and upper part of its spine and vertical position of the upper part of that arch and lower part of its spine. Beyond the 25-30th segment the arch/spine division disappears and the neural arches become straight to gently upturned rods with slightly expanded (in the more anterior segments) to unexpanded bases.

Zangerl & Case (1976: 144, figs. 30, 31, 33) found a consistent change in appearance of the vertebral column directly beneath the dorsal fin, where the column rises toward the fin and the neural arches suddenly become much more steeply inclined posteriorly. It looks as if muscle contraction pulled the vertebral column toward the dorsal fin, bending and possibly even rupturing the column at that point. In the Kinney specimen the dorsal fin is located above the 63rd through 75th neural arches and, as can be seen in Fig. 3A, no change is evident in that area. It implies that the feature observed by Zangerl & Case (1976) is a post-mortem development and, therefore, that the beginning of their region of tail peduncle would be better placed somewhat more posteriorly, at the 75th segment, which is the first neural-haemal segment. Also the extent of Zangerl & Case's (1976) cervical region (first through 15th neural arches) is not the

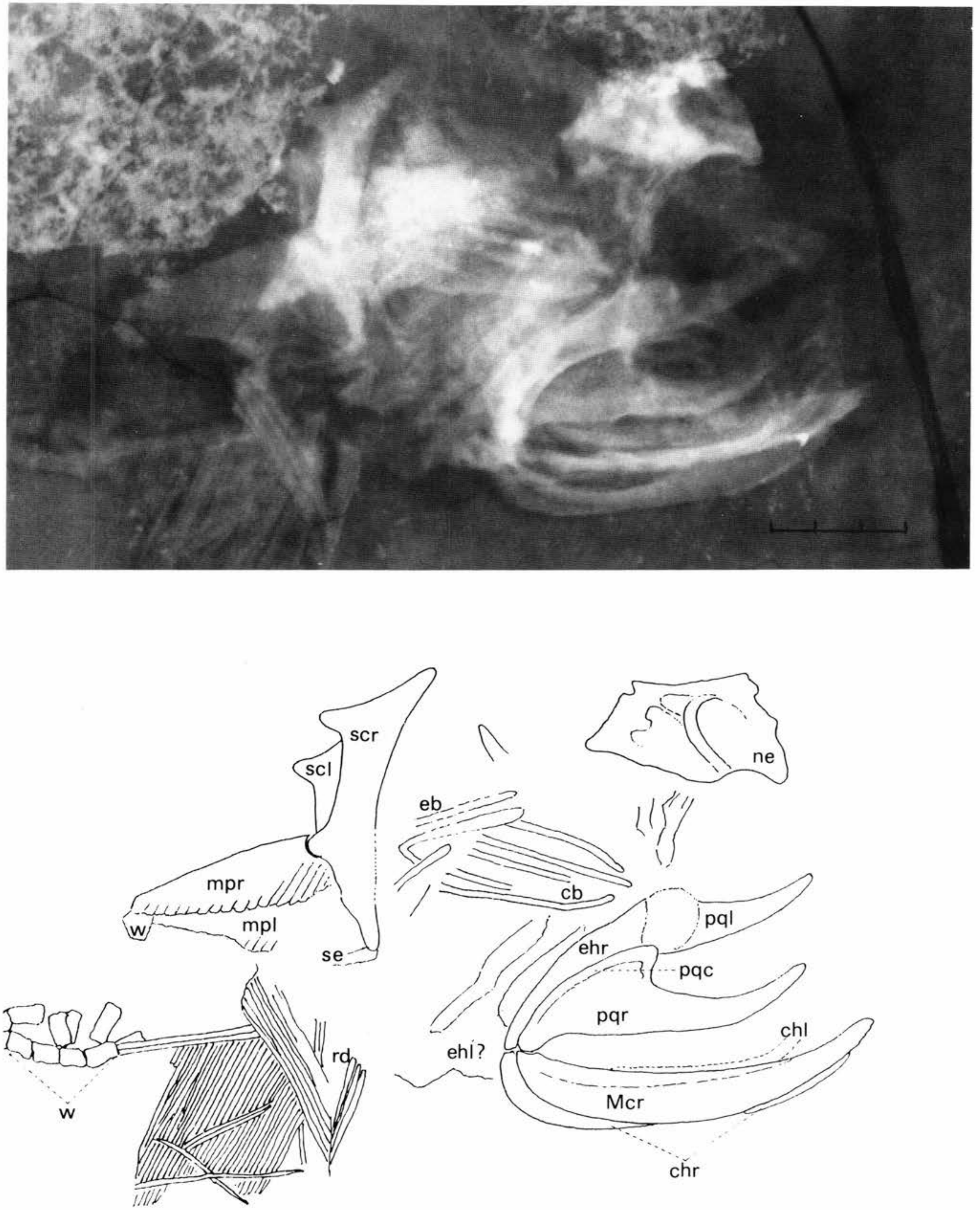

FIGURE 5—*Cobelodus aculeatus* NMMNH P-19182, Kinney Quarry, New Mexico. Radiograph and tracing of braincase, visceral skeleton, and pectoral girdle and fins. Scale in centimeters. Abbreviations: **cb,** ceratobranchials; **chl,** left ceratohyal; **chr,** right ceratohyal; **eb,** epibranchials; **ehl,**left epihyal; **ehr,** right epihyal; **Mcr,** right Meckel's cartilage; **mpl,** left metapterygium; **mpr,** right metapterygium; **ne,** neurocranium; **pqc,** palatoquadrate crest; **pql,** left palatoquadrate; **pqr,** right palatoquadrate; **rd,** radialia; **scl,** left scapulocoracoid; **scr,** right scapulocoracoid; **se,** sternal element; **w,** whip segments.

FIGURE 6—Teeth of *Cobelodus aculeatus* NMMNH P-19182, Kinney Quarry, New Mexico. Better preserved teeth are denoted by arrows and their location in the specimen is circled in Fig. 3A, B. Scale in millimeters.

same as in the Kinney specimen, in which it is at least 10 segments longer.

The tail (Fig. 3E) lacks the dorsal lobe and the ventral lobe is incomplete and preserved in a fashion that gives it an aberrant appearance. Eight or nine anterior radials are missing and two have been displaced to the dorsal side of the fin. The aberrant appearance is caused by articulation of posterior radials with seemingly much thinner basal rods. However, the posterior basals are in fact not preserved, all that is left of them are a few faint impressions that create the illusion of thinness. Preserved are only the anterior basals. Their number (10-11) combined with the number of posterior radials (6) gives an estimate of 16-17 segments for the ventral lobe. Some of the radials are distally branched, however. Once the above preservational peculiarities are discerned, the ventral lobe can be easily restored into one characteristic of a symmoriid.

Adult *Cobelodus* reached 150 to 200 cm (Zangerl, 1981: 69), and the Kinney specimen thus is a juvenile. *C. aculeatus* is the only presently recognized species. The size of the pelvic plate and the length of the cervical region of the vertebral column are the only features in which the Kinney specimen differs from C. *aculeatus* as described by Zangerl & Case (1976). However, the former could be due to the young ontogenetic age, sex, or even post-mortem compressional enlargement (the pelvic plate is the worst preserved part of the specimen), and the latter due to either intraspecific variability or differences in preservation. Neither feature precludes assignment of the Kinney specimen to *C. aculeatus.*

Genus *SYMMORIUM* Cope 1893

SYMMORIUM RENIFORME Cope 1893

Fig. 7

USNM 187135 (Fig. 7A) and CM 47847 (Fig. 7B) are cladodont teeth with striated cusps. Another similar but fragmentary tooth is NMMNH P-19206. The teeth are quite large, with the base 12 mm long in the USNM specimen and 18.5 mm long in the CM specimen. They both have a carinated main cusp and two pairs of accessory cusps of which the lateral pair is the larger. All the accessory cusps are incomplete and, therefore, the question whether they too were carinated cannot be answered. In oral view the bases of all the cusps are roughly circular, but the labial face of the main cusp is flattened. In aboral view, which is available only in the CM specimen (Fig. 7B$_2$), the base is longitudinally concave and so is its labial margin (upper in the figure) which bears a pair of bosses (basolabial articulating bosses) situated underneath the intermediate cusps. The bosses are low, with slightly concave centers, and thus have the character of facets rather than tubercles. In lingual view, also available only in the CM specimen (Fig. 7B1), a pair of low apical bosses occupies the sloping lingual margin opposite the intermediate cusps. The CM tooth is rather abraded, which accounts for the relative indistinctiveness of these features. In lateral view (Fig. 7B$_3$), the main cusp of the CM specimen is vertically oriented and exhibits a sigmoidal flexure. The small amount of striation that is preserved on the main cusp of the CM tooth is finer than that in the USNM specimen.

According to Lund (1985: 8-13, fig. 8), teeth of the just

FIGURE 7—*Symmorium reniforme*, Kinney Quarry, New Mexico. **A,** USNM 187135, labial face. **B,** CM 47847 in lingual (B_1), aboral (B_2), and lateral (B_3) views. Arrows denote apical boss in B_1, basolabial boss in B_2, and carina in B_3. Scales in millimeters.

described morphology belong to *Stethacanthus* and *Cladodus*, but there is a good reason for rejecting his assignment and regarding the teeth as symmoriid. A feature considered characteristic of *Stethacanthus* teeth is a trapezoidal basolabial projection or boss beneath the main cusp (see Williams, 1985: 119, pl. 8/3-4), which articulates with an apical boss in the center of the lingual margin of the successive tooth. The articulation thus is medial. Cladodont teeth of symmoriids, on the other hand, exhibit a paired articulation, i.e. a pair of basolabial bosses articulates with a pair of apical bosses on the lingual margin of the successive tooth. This arrangement is shown very clearly in the teeth of *Symmorium reniforme* described and illustrated by Williams (1985: 107-109, pl. 7/1-13), which differ from the Kinney Quarry teeth only in the presence of a labial sulcus on the main cusp and finer striation. However, a labial sulcus is apparent between the basolabial bosses of both Kinney specimens (Fig. 7A, B_2) in precisely the same way as it is illustrated by Mapes & Hansen (1984: fig. 2A) and Hansen (1986: fig. 20A, pl. 4/19). Clearly, the differences in extent of labialsulcus development and fineness of striation on the cusps are within the limits of infraspecific variation, and the Kinney Quarry *Symmorium* teeth thus are assignable to the species S. *reniforme.*

The CM tooth is 24 mm tall and 21 mm long, which according to Mapes & Hansen (1984) translates to a fish over 2.5 m long. This is nowhere near the size limit of the species, however; Hansen (1986: 193) reports *S. reniforme* teeth from the Pennsylvanian black shales of the Eastern Interior Basin that are up to 40 mm in maximum dimension and must have been shed by fishes at least 4 m long.

Order PETALODONTIFORMES Zangerl 1981

Family PRISTODONTIDAE Woodward 1889

Genus *PERIPRISTIS* St. John 1870

PERIPRISTIS aff. *SEMICIRCULARIS*
(Newberry & Worthen 1866)
Fig. 8A

USNM 187133 is the right half of a labially exposed crown which bears four obliquely triangular cusps that increase in size toward the midline (left edge as preserved). The cusps are broad, apically rounded, and their edges are not serrated. The crown is smooth, labio-lingually curved, and lacks a basal ridge. Assuming that the largest preserved cusp is medial, the entire crown would have seven or nine cusps.

This specimen has been previously identified as *Ctenoptychius* (Zidek, 1975: 7, fig. 1A), another petalodontiform genus (inc. sedis) with cuspidate tooth crowns. It is being reassigned to *Peripristis* because the cusps are broad and apically rounded, the notches between them are very short and weakly developed, and the crown has a pronounced labio-lingual curvature and no basal ridge. In *Ctenoptychius* the cusps are more pointed and narrower, are demarcated by notches that run down one-fourth to one-third of the crown height on both labial and lingual faces, the crown is either flat or only very slightly labio-lingually curved, and a basal ridge is present on the labial face (Hansen, 1985: pl. 1/12-14, and written comm. 1991; see also *Belantsea montana* of Lund, 1989: figs. 5-6, whose dentition is indistinguishable from *Ctenoptychius* and which most likely *is* a *Ctenoptychius).*

Hansen (1978: 55) included also the genera *Pristodus* Davis 1883 and *Megactenopetalus* David 1944 in the family Pristodontidae, which is characterized by dentitions consisting of a single multicusped dental element in the upper jaw and a single monocusped acuminate element in the lower jaw (whereas *Ctenoptychius* has several tooth families in each jaw). Compared to *Peripristis,* the cusps of *Pristodus are* much taller, more pointed, more numerous (10-14), and there is no medial cusp (Hansen, 1985: 536, fig. 10). In *Megactenopetalus* the shape of the cusps is similar to *Peripristis,* but the individual cusps are demarcated by lingual and labial notches at least to the extent seen in *Ctenoptychius,* both faces of the cusps bear short, radiating grooves (see Ossian, 1976: pl. 1), there is no medial cusp, the tooth base is reduced to a concave surface of attachment on the basolabial portion of the dental element (in *Peripristis* the tooth base is long, tumid, and flattened lingually), and the teeth are among the largest petalodont teeth known.

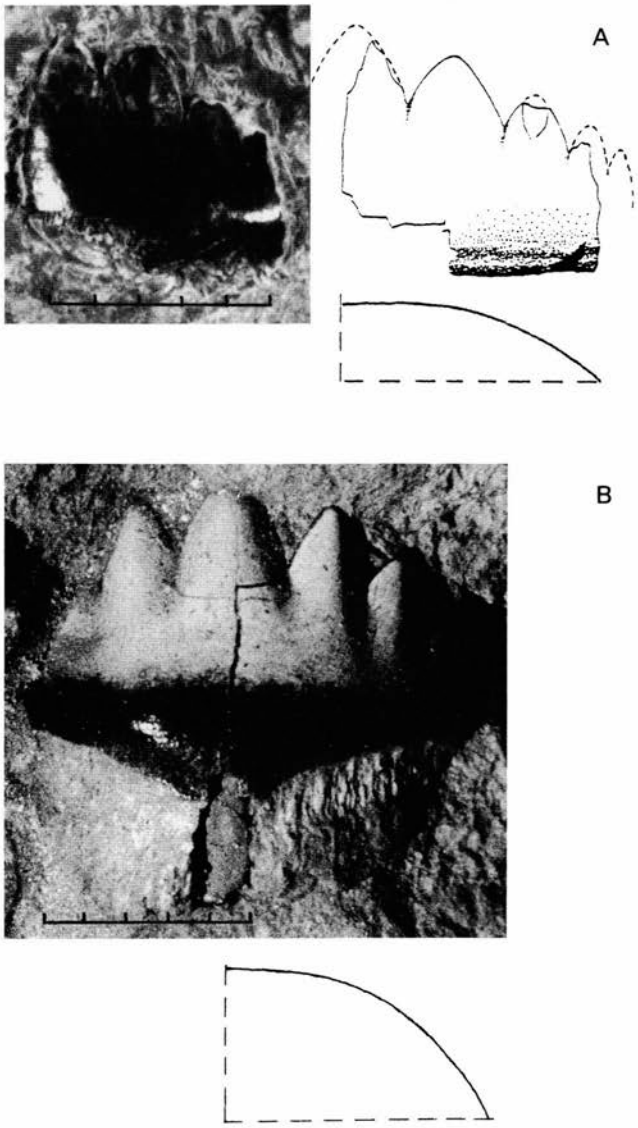

FIGURE 8—Upper dental elements of *Peripristis*. **A,** USNM 187133, partial crown of *P.* aff. *semicircularis*, Kinney Quarry, New Mexico. **B,** KUVP 82937, partial crown and tooth base of *P. semicircularis*, Stanton Limestone Member of Kiewitz Shale, Missourian, at the Ash Grove Cement Company's Louisville E Quarry, southeastern Nebraska. Curves show labio-lingual curvature of the crown. Scales in millimeters.

Hansen (1985: 534) recognized only one *Peripristis* species, *P. semicircularis* (originally described as *Ctenoptychius).* Although there is nothing incompatible with *P. semicircularis* in the Kinney specimen, its fragmentary condition nevertheless mandates only a tentative species assignment.

P. semicircularis KUVP 82937 (Fig. 8B) from the Stanton Limestone, Missourian, of southeastern Nebraska has four lateral cusps (the crown thus was nine-cusped) and its labio-lingual curvature is more pronounced than that of the Kinney crown. Yet, it is the least curved of a lot of seven teeth, four of which approach an arc of 180°. In KUVP 14386 and 55293 (Fig. 9) from the Virgilian of Kansas the arc is full 180° and the lingual views (A_2, B_2) show the cup-like pit at the crown's base and the short, radial grooves rimming the cutting edges of the cusps, both features characteristic of *Peripristis.* When restored, also these teeth appear to have had four cusps on each side of the medial cusp, and, moreover, this appears to be the case in all other specimens of *Peripristis* in the KUVP collection (777, 899, 55073, 55293, 68114, 68115, 68117, and 85563). Nine thus seems to be the prevailing number of cusps in *P. semicircularis,* and the Kinney specimen is restored accordingly.

CHONDRICHTHYES INCERTAE SEDIS

Genus *?LISTRACANTHUS* Newberry & Worthen 1870

Fig. 10A

USNM 187132 (counterparts) has been previously identified as *Listracanthus* (Zidek, 1975: 7), but that generic assignment is equivocal because of the very poor preservation of the specimen. The preserved part is 15 mm long and is longitudinally split in the sagittal plane. Its ornamentation thus is not visible, and an attempt to remove the specimen from the hard calcareous shale would most likely result in its destruction. Therefore, it can only be said that the specimen resembles *Listracanthus* more than any other dermal denticle or ichthyodorulite presumed to belong to the Chondrichthyes (see Zangerl, 1981: 103-106, for an account of such elements).

Listracanthus is a spine-like dermal denticle with a brush of slender projections along either the entire anterior and posterior margins (Fig. 10C) or along much of the concave, presumably posterior margin and the distal part of the (presumably) anterior margin (Fig. 10B). The length varies between ca. 15 and 70 mm. Such denticles have been recorded from many Carboniferous localities and stratigraphic levels (starting with upper Tournaisian; Patterson, 1965: 162, fig. 33, *Deltoptychius armigerus)* in North America and Europe (Zangerl & Richardson, 1963; Chorn & Reavis, 1978; Zangerl, 1981; Lang & Štamberg, 1979), and Lower Triassic deposits of British Columbia, Canada (Schaeffer & Mangus, 1976: 525, fig. 5). In some instances they occur together with *Petrodus-type* denticles (e.g. in *Deltoptychius armigerus).* So far, *Petrodus* has not been found at the Kinney Quarry. Zangerl (1981: 104) concluded that *"Listracanthus is* a fish with a dermal skeleton consisting of large numbers of both listracanthi and petrodi. *Petrodus,* on the other hand, probably is a very large animal whose skin is armored exclusively with petrodi, and whose dentition may consist of *Carcharopsis* teeth." Since these elements clearly occur in a number of chondrichthyan taxa, Chorn & Reavis (1978: 4) suggested that *"Listracanthus* and *Petrodus* should be formally regarded as *nomina dubia* and retained to represent organ-genera only." Form genera would be a more appropriate term, however, because it concerns forms with generically unrelated species (see Wells, 1944: 11, footnote).

According to R. Zangerl (written comm. 1991), *Listracanthus* is now known to have had a dentition consisting of

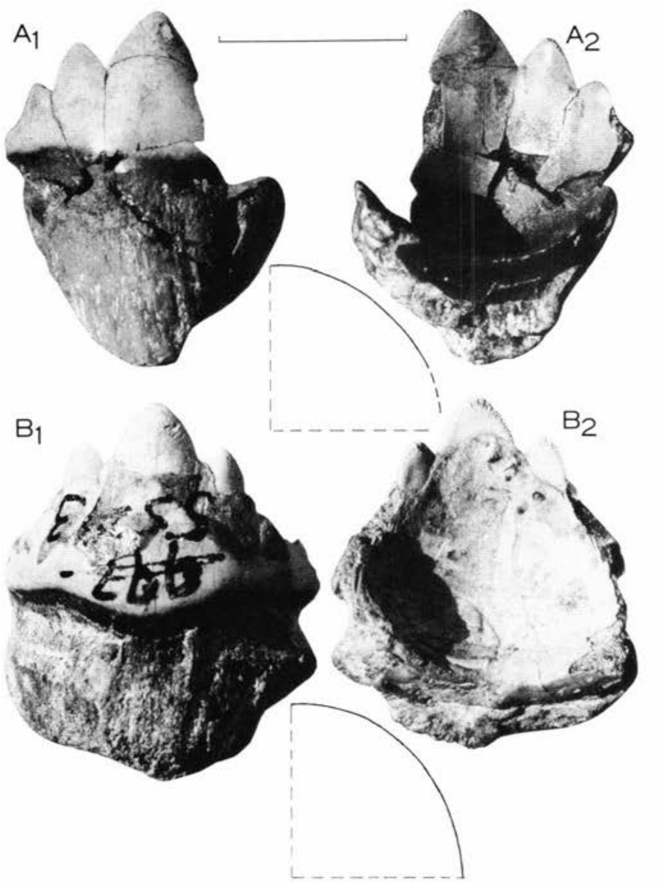

FIGURE 9—Upper dental elements of *Peripristis semicircularis* in labial (A_1, B_1) and lingual (A_2, B_2) views. **A,** KUVP 14386, Virgilian, Chautauqua County, Kansas (30 mi E of Arkansas City, Coll. J. W. Glydden 1912). **B,** KUVP 55293, Virgilian near Lyndon, Osage County, Kansas (5 1/2 mi S of Lyndon, Coll. A. K. Stanely 1938). Curves show labio-lingual curvature of the crown. Scale bar equals 1 cm and applies to both specimens.

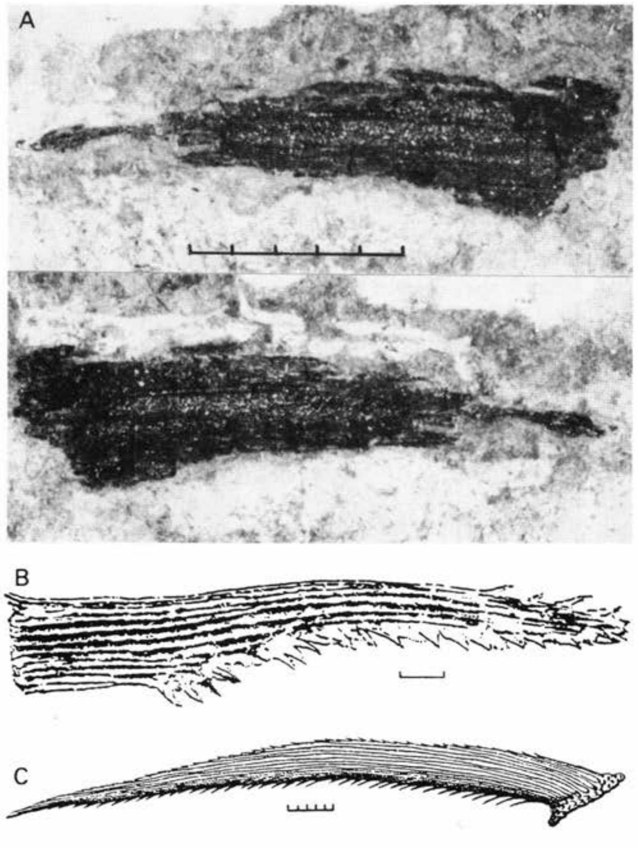

FIGURE 10—**A,** *?Listracanthus,* USNM 187132 (counterparts), Kinney Quarry, New Mexico. **B,** *Listracanthus eliasi* Hibbard 1938, Cedarvale Shale (Wabaunsee Group, Virgilian) of Missouri (drawn from a photograph of the holotype published by Hibbard, 1938; pl. 19); according to R. Zangerl, written comm. 1991, this is probably an abnormal denticle of *Listracanthus hystrix* Newberry & Worthen 1870. **C,** *Listracanthus* sp., Little Osage Shale Member of Fort Scott Limestone, Desmoinesian, Kansas (from Chorn & Reavis, 1978: fig. 3C). Scales in millimeters.

Calopodus apicalis teeth (*Calopodus* St. John & Worthen 1875 is regarded by Hansen, 1985: 538, as a chondrichthyan inc. sedis); although both *Listracanthus* and *Petrodus* were very large fishes, in neither of them was the skeleton calcified.

Class ACANTHODII Owen 1846
Order ACANTHODIFORMES Berg 1940
Family ACANTHODIDAE Huxley 1861
Genus *ACANTHODES* Agassiz 1833

ACANTHODES KINNEYI n. Sp.
Figs. 11, 12A

1975. *Acanthodes* sp., Zidek, pp. 12-17, *fig.* 2, pls. 1, 2.

Material—Holotype NMMNH P-19208, nearly complete fish. Paratypes CM 47842a + b, USNM 187147, OMNH 00447, 00448, 00449. The USNM and OMNH paratypes were described 17 years ago as *Acanthodes* sp. and many specimens have been found at the Kinney Quarry since then. However, although *Acanthodes* is common at the site, of all the specimens collected between 1975 and 1991 only the holotype and the CM paratype are preserved well enough to add to the old description (Zidek, 1975).

Type locality and horizon—Kinney Brick Company Quarry, NW^1/4SW^1/4 SE^1/4 sec. 18, T9N, R6E, Bernalillo County, central New Mexico. Units 2-4 of Lucas & Huber (1991; see also Kues & Lucas, this volume), Pine Shadow Member of Wild Cow Formation, Madera Group, Upper Pennsylvanian.

Etymology—Named after the locality, which carries the company founder's name.

Diagnosis—Squamation development unusually rapid (specimens 145 mm long are fully scaled), ossification of endoskeleton commencing unusually late in ontogeny (in specimens ca. 145 mm long). Dorsal and anal spines directly opposite each other. Long, probably vestigial pelvic fins. Ventral/pectoral spine length ratio 0.25; ventral spine situated at least one-third of pectoral-anal distance behind pectoral. Hyoid and branchial gill-rakers of same morphology, slender, thinly lenticular in cross section; blade with faint longitudinal ridges, separated from base by constriction; base short and narrower than proximal portion of blade.

Description—The holotype NMMNH P-19208 (Fig. 11B) is 280 mm in total length, which places it among the largest specimens known from the site. It is fully scaled and the count of the largest scales, located near the main lateral line in the postdorsal-precaudal region, is three per millimeter in a row (3 sc/mm). Measurable lengths are: mandibular splint 25 mm, branchial region 20 mm, scapulocoracoid 11 mm (height), pectoral spine 51 mm, ventral spine 13 mm, dorsal spine 28 mm, pectoral-ventral spine distance 55 mm, pectoral-dorsal spine distance 155 mm, and dorsal spine-tip of tail distance 80 mm. The anal spine cannot be measured because only its base is preserved, but it is of interest that the base is inserted directly below, rather than anteriorly of, the base of the dorsal spine. The ventral spine is bilaterally symmetrical. As in a majority of *Acanthodes* species, the suprascapula was not fused with the top of the scapular blade and is not preserved. The jaws (Fig. $11B_2$) are articulated and show the posterior (articular) meckelian ossification with the dermal mandibular splint attached, and the quadrate and metapterygoid ossifications of the palatoquadrate. The posterior meckelian ossification is unusually long and appears to include co-ossification with the anterior (mentomandibular) meckelian ossification. The branchial region (Fig. $11B_2$) is poorly preserved and shows only two series of gill-rakers, probably of the first and fifth branchial arches.

The CM 47842a +b (Fig. 11A) is only 145 mm in total length, yet its scale cover is developed as fully as in the holotype. It has four scales per millimeter in a row (4 sc/ mm) near the main lateral line in the postdorsal-precaudal region, where the scales are the largest. Measurable lengths are: outer diameter of circumorbital ring 8 mm (corrected for distortion), mandibular splint 15 mm, branchial region 12 mm, pectoral spine 31 mm, dorsal spine 13 mm, anal spine 13 mm, pectoral-dorsal/anal spine distance 80 mm, and dorsal spine-tip of tail distance 38 mm. The ventral spine is missing. The anal spine is inserted directly below the dorsal, as in the holotype. The anterior region back to the pectoral girdle is preserved much better in the counterpart CM 47842b (Fig. $11A_2$), which shows circumorbital rings, mandibular splints, branchiostegal rays, gill-rakers of all five branchial arches, part of the left scapulocoracoid and pectoral spine, the medial ventral, supraorbital, infra-orbital, and supramaxillary sensory lines, and the anteriormost squamation. Only a few tesserae are present, but a large number of them is preserved between the circumorbital rings of the part CM 47842a. They are polygonal, no larger than 0.2 mm in diameter, and have raised centers. Minute rhombic scales, much smaller than the tesserae, are present throughout the branchial region in both the part and counterpart. With the exception of the scapulocoracoid, all these parts are components of the exoskeleton. The only other trace of the endoskeleton is a fragment of the posterior (articular) meckelian ossification which is exceedingly thin, indicating that ossification of the endoskeleton has barely begun. The circumorbital ring consists of five bones, of which the posterior and posteroventral are shorter than the anterior, dorsal, and ventral. Both rings are overturned, exposing the smooth inner surfaces of the bones. However, one bone in the left ring is preserved with the outer surface exposed (arrow in Fig. $11A_2$) and reveals ornamentation of faint ridges radiating from the concave inner margin. The gill-rakers (Fig. 12A) are 1-4 mm long, slender, and thinly lenticular in cross section. The blade bears faint longitudinal ridges and is separated from the base by a constriction. The base is short and narrower than the proximal portion of the blade. There is no difference in morphology between the hyoid and branchial gill-rakers.

Discussion—Squamation development was unusually rapid and ossification of the endoskeleton commenced unusually late in ontogeny of *A. kinneyi.* The only other species in which the scale cover developed equally fast or faster are *A. ovensi* (Toumaisian) and *A. lundi* (Namurian), in which, however, ossification of the endoskeleton commenced much earlier than in *A. kinneyi* (Zidek, 1980, 1985: addendum; Forey & Young, 1985). In *A. bronni* (Early Permian), specimens 150 mm long have only the caudal-precaudal region covered with scales, and even in specimens 300 mm long the squamation does not reach the pectoral region (Heidtke, 1990: fig. 52B, D). In *A. bridgei* (Virgilian), specimens ca. 150 mm long have squamation developed only to a level slightly anterior of the ventral spine, and in specimens around 280 mm long scales reach the pectoral region only ventrally, around the ventrolateral and median ventral sensory lines (Zidek, 1976: fig. 13, 1985: fig. 5). In both *A. bronni* and *A. bridgei* ossification of the endoskeleton commenced earlier in ontogeny than in *A. kinneyi,* and ossified parts of the labyrinth are present in specimens well under 100 mm long (Zidek, 1985: 152; Heidtke, 1990: fig. 50).

The position of the dorsal and anal spines directly opposite each other is known to occur in only one other species, *A. ovensi,* in which, however, some variation in this regard appears to be present (Forey & Young, 1985: 55). In *A. kinneyi* the two spines are inserted opposite each other in both the above described specimens as well as in OMNH 00447 and 00449 (Zidek, 1975: pls. 1B, 2B). Finding the same position in all four specimens suggests that it could be a character more stable than in *A. ovensi.*

Gill-rakers of *A. bridgei* (Fig. 12B) have bulbous bases which are not separated from the blades by a constriction,

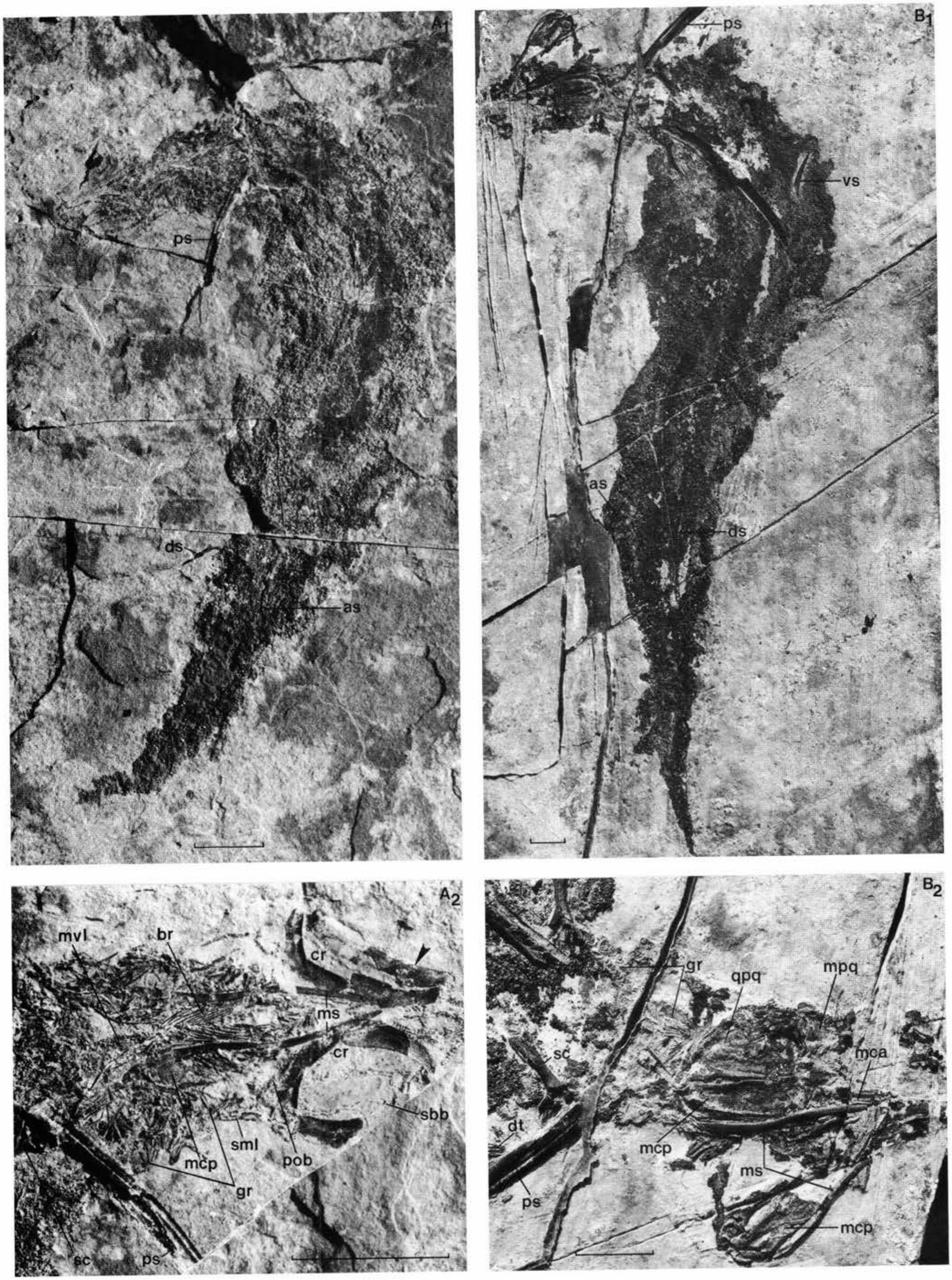
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FIGURE 11—*Acanthodes kinneyi* n. sp., Kinney Quarry, New Mexico. **A,** Paratype CM 47842a + b, part (entire specimen, A_1) and counterpart 47842b (prepectoral region only, A_2). **B,** Holotype NMMNH P-19208, entire specimen (B_1) and detail of pectoral–prepectoral region (B_2). Arrow in A_2 denotes ornamented circumorbital plate. Supraorbital canals and commissure between circumorbital rings in A_2 are not labeled for lack of space. Scale bars equal 1 cm. Abbreviations: **as,** anal spine; **br,** branchiostegal rays; **cr,** circumorbital ring; **ds,** dorsal spine; **dt,** dermotrichia; **gr,** gill-rakers; **mca,** anterior (mentomandibular) meckelian ossification; **mcp,** posterior (articular) meckelian ossification; **mpq,** metapterygoid ossification of palatoquadrate; **ms,** mandibular splint; **mvl,** median ventral sensory line; **pob,** postorbital branch of infraorbital sensory line; **ps,** pectoral spine; **qpq,** quadrate ossification of palatoquadrate; **sbb,** suborbital branch of infraorbital sensory line; **sc,** scapulocoracoid; **sml,** supramaxillary (quadratojugal) sensory line; **vs,** ventral spine.

←

and the ornamentation consists of very fine, faint, interrupted striae. Gill-rakers of *A. lundi* (Fig. 12C) have strongly developed longitudinal ridges on the blade which is separated from the base by a constriction, but the base is bulbous, as wide or wider than the proximal part of the blade, and twice as tall as in *A. kinneyi*. Gill-rakers of *A. bronni* (Fig. 12F) have been described by Watson (1937: 105) as follows:

> Each one consists of a blade, relatively wide from side to side, widening greatly at the middle of its length but extremely narrow from back to front. It has a lenticular transverse section and its free extremity is pointed. The surface bears a series of irregular low longitudinal ridges and furrows which lie in the main parallel to its length. The blade of the gill-raker is a little narrowed just above its base. The base itself is a hollow bone expanded in a plane at right angles to the breadth of the whole element. It is thick so that its cavity is nearly circular in section. The attached surface, which lies in very close contact with the underlying bone of the hyoid arch, is a hollow half-cylinder placed transversely to the length of the hyoid arch.

This description agrees with Reis' (1896) drawing shown here in Fig. 12F. Reis (1896: pl. 6/3) shows the hyoid and branchial gill-rakers as morphologically identical, and Watson (1937) does not mention that the branchial gill-rakers would in any way differ from those on the hyoid arch. Yet, the branchial gill-rakers of *A. bronni* illustrated by Heidtke (1990: fig. 25) appear to be quite different from those shown by Reis and described by Watson, and the possibility thus exists that either those figured by Heidtke belong to another species or *A. bronni* has gill-rakers of two distinct morphologies. The latter possibility has been hinted at by Zajíc (1985), although it is not entirely clear whether he regards the two different morphologies (Fig. 12D, E) as belonging to the same species. Zajic's (1985) hyoid gill-raker (Fig. 12D) is very similar to the gill-rakers of *A. kinneyi* (Fig. 12A) except that they are very thinly lenticular in cross section, whereas that of Zajíc has an oval cross section.

The median ventral sensory line can be discerned in USNM 187147 and CM 47842. In the CM specimen it is much better preserved in the counterpart (Fig. $11A_2$), which, however, ends at the pectoral girdle. The ventrolateral sensory line is apparent in USNM 187147 and OMNH 00447, but its anterior end is not preserved. These specimens suggest that the median ventral line reached all the way to the pectoral girdle and branched into the paired ventrolateral line at a point somewhat posterior of the girdle. This is different from *A. bridgei* (Zidek, 1980: fig. 4C) and *A. lundi* (Zidek, 1980: fig. 1A), in which the median ventral line branches into the ventrolateral lines anterior of the pectoral girdle. The situation in *A. bronni* was described by Watson (1937: 111) in terms so general (". . . pair of ventral lateral-like canals which arise quite anteriorly between the pectoral fins . . .") that the location of the branching point cannot be stated.

When measurements of *A. kinneyi* (presented here and in Zidek, 1975: 15) are conbined into the ratios used for *A. bridgei* and *A. lundi* and *A. lundi* (Zidek, 1976: table 2, 1980: 54-55) and the three species are compared biometrically, the results indicate remarkable similarity in proportions. Close proportional similarity can most likely be extended to the whole genus, although the other *Acanthodes* species remain to be treated quantitatively. The only ratios that appear to indicate proportional differences of any substance are the ventral/pectoral spine length and the pectoral—ventral/pectoral—anal distance which gives the relative forward or backward position of the ventral spine. The ventral/pectoral spine length ratio is 0.25 in *A. kinneyi* (NMMNH P19208, OMNH 00447), 0.35-0.45 in *A. brídgei* (Zidek, 1976, table 2), 0.27-0.35 in *A. lundi* (Zidek, 1980: 55), and 0.27—

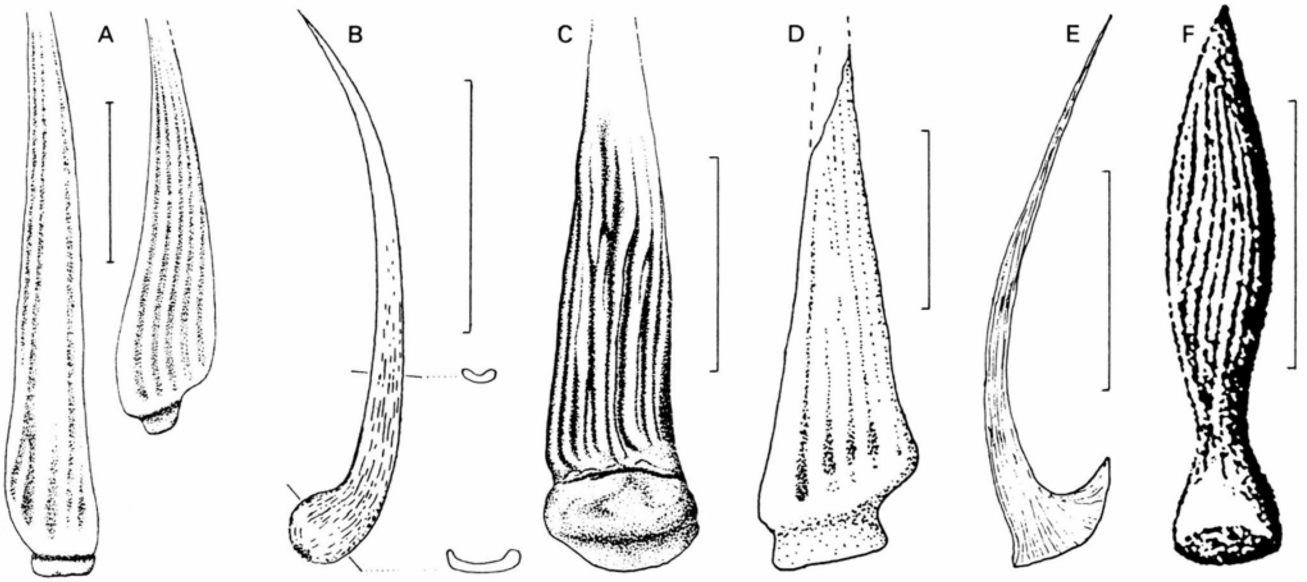

FIGURE 12—Gill-rakers of *Acanthodes*. **A,** Branchial gill-rakers of *A. kinneyi* n. sp.; **B,** ceratohyal gill-raker of *A. bridgei* (from Zidek, 1976: fig. 4B); **C,** hyoid gill-raker of *A. lundi* (from Zidek, 1980: fig. 4C); **D, E,** hyoid (D) and branchial (E) gill-rakers of *Acanthodes* sp. indet. from Stephanian B of Bohemia, Czechoslovakia (from Zajíc, 1985: figs. 1, 2); **F,** gill-raker of *A. bronni* (from Reis, 1896: pl. 6/18). Scale bars equal 1 mm.

0.28 in *A. bronni* (Watson, 1937: fig. 21; Heidtke, 1990: fig. 36). *A. kinneyi* thus differs quite markedly in this regard from *A. bridgei,* but not from *A. bronni* and *A. lundi.* The position and morphology of the ventral spine (pelvic in pre-1990 publications) are interesting. In *A. kinneyi* and *A. bronni* the ventral spine is situated at least one-third the pectoral-anal distance behind the pectoral spine, whereas in *A. bridge* it is less than one-third the distance behind the pectoral, and in *A. lundi* only one-fourth the distance behind the pectoral. Forward position of the ventral (pelvic) spine/plate) girdle is an advanced feature, and one of the earliest species of the genus, *A. lundi* (Namurian), thus is more advanced in this respect than the Late Pennsylvanian and Early Permian species.

The morphology of the ventral spine presents a dilemma because in *A. kinneyi* (Fig. 11B,), *A. bridgei* (Zidek, 1976: fig. 8b), and *A. bronni* (Boy, 1976: 34; Heidtke, 1990: 50-51, fig. 36) it is bilaterally symmetrical (in *A. lundi* and *A. ovensi* ii is too poorly preserved to tell) and, to my knowledge, no specimen shows two ventral spines. For these reasons, Heidtke (1990: 50) called the spine unpaired and ventral rather than pelvic, to emphasize that in *A. bronni* it was not supported by a pelvic basal plate. An unequivocal basal plate is preserved only in the holotype of *A. bridgei,* but its morphology cannot be discerned because it is exposed in an on-edge view and cannot be freed from the matrix (Zidek, 1976: 18, fig. 8B). There can only be one reason for the uniqueness of the plate, it must have been cartilaginous (or, if ossified to any extent, the ossification commenced late in life) and, therefore, is virtually never preserved. From the standpoint of comparative anatomy it is exceedingly unlikely that a basal plate would be present in one species and absent in all other species of the genus, more likely it has not been found because of the rarity of its preservation. It appears though that if a plate of discernible morphology is ever found, it will turn out to be a median, bilaterally symmetrical element. As such it should be called ventral rather than pelvic plate. The suggestion that the "infraclaviculae" of *A. gracilis* figured by Fritsch (1893: fig. 270, pl. 107/10) could be pelvic basal plates (Zidek, 1976: 18, fig. 8) must be withdrawn because the "infraclaviculae" are paired, transversely asymmetrical plates that would have supported paired, transversely asymmetrical (at least proximally) spines. However logical and expectable this may sound, in reality it is not so and *Acanthodes* turns out to be a genus specialized even more than previously thought. In *A. kinneyí* (OMNH 00447) there are two lines of dermotrichia between the ventral and anal spines, indicating the presence of long, probably vestigial pelvic fins (Zidek, 1975: 13, fig. 2A, D), wherein lies the above mentioned dilemma. One would expect paired fins to be supported by paired spines, or fusion of paired basal plates into a median element and loss of one of the spines (however unlikely this may be) to *follow* disappearance of the fins and not vice versa.

A. kinneyi exhibits several primitive features unexpected in a Late Pennsylvanian species. These include the position of dorsal and anal spines directly opposite each other, the position of the ventral spine relatively far behind the pectoral, long pelvic fins, and rapid squamation development. In sharp contrast to this is the ontogenetically late beginning of ossification of the endoskeleton, which is in accord with the general regressive trend apparent in the evolution of the genus (Zidek, 1985: 164) but is unexpectedly extreme in comparison with other roughly contemporaneous species.

Class ACTINOPTERYGII Klein 1885

At least two deep-bodied actinopterygian genera, *Amphicentrum* and *Platysomus,* have been recovered from the Kinney Quarry fish beds and are described below. The anatomical terminology follows Gardiner & Schaeffer (1989; except in Fig. 20C, D, where Campbell & Le Duy Phuoc's (1983) determinations are left unchanged to facilitate comparison with those in Figs. 13, 14, 20A, B, and 24C. Although Gardiner & Schaeffer (1989) could perhaps lx criticized for using certain terms more appropriate for tetrapods than actinopterygians, their paper nevertheless is widely known and well suited for application in a descriptive work such as this, dealing with only a limited number of taxa from a single locality. Lengthy discussion of questionable homologies, some of which may never be resolved to everyone's satisfaction, obviously are beyond the scope of this study.

Order PALAEONISCIFORMES Goodrich 1909

Family AMPHICENTRIDAE Moy-Thomas 1939

Genus *AMPHICENTRUM* Young 1866

Gardiner & Schaeffer (1989) use the generic name *Cheirodusa* M'Coy 1855 (= *Chirodus* M'Coy 1848) which, however, Dyne (1939) found to be based on a broken bone with only one tooth *(C. pesranae)* and therefore invalid as a definable generic name (this was stated already by Woodward, 1891: 536, who, however, let the name *Cheirodus* stand). Dyne thus revived the name *Amphicentrum* which had been applied by Young (1866) to the best known species of the genus *(A. granulosum)* and thus is definable beyond reproach.

Summary of occurrences and taxonomic comments

Amphicentrum is a relatively rare genus known from only a small number of localities. A review of the occurrences is needed before describing the Kinney Quarry species.

Illinois—Amphicentrum occurs in the Francis Creek Shale Member of the Carbondale Formation (Desmoinesian; lower Westphalian D) in the Mazon Creek area, Grundy and Will Counties. The first specimen found at Mazon Creek was named *Platysomus orbicularis* by Newberry & Worthen (1870: pl. 3/1), who unfortunately neglected to describe it. The description was provided by Eastman (1903: 193, 1917: 276), who transferred the species to the genus *Cheirodus.* The whereabouts of the holotype were not known to Eastman, his description was instead based on several YPM specimens and USNM 4404. My inquiries about the holotype have also been in vain. As regards the YPM specimens noted but not enumerated by Eastman, it appears that none of them have ever been catalogued and cannot be located in the YPM collections. The material of *Amphicentrum orbiculare* from Mazon Creek thus consists of only four specimens: USNM 4404 (R. D. Lacoe Coll.; Eastman, 1917: 277, pl. 9/2), PF 7339 (pit 11; catalogued as *Platysomus circularis),* YPM 3240 (S. S. Strong Coll.), and YPM 3241 (S. S. Strong Coll.). The two YPM specimens were identified by Eastman, but most likely they were not part of the suite of specimens used in his papers.

There is no hope that the holotype of *"Platysomus" orbicularis* Newberry & Worthen will ever be located, and it cannot be established that Eastman's descriptions and illustrations pertain to that species. Eastman (1903: 193) stated that one of the YPM specimens is labeled *"Platysomus orbicularis"* in Newberry's handwriting, but that specimen cannot be located either. The holotype of *P. orbiularis, as* illustrated by Newberry & Worthen (1870: pl. 3/1), was a headless fish with platysomid rather than amphicentrid body outline. Eastman (1903: 193) argued that "the type was very imperfectly preserved, in which case it is not to be wondered that the authors failed to observe the dorsal and ventral peaks." However, since the holotype was not available to Eastman, his argument has to be regarded as conjectural. Judged from Newberry & Worthen's illustration, their specimen does not deserve more than to be labeled an indeterminate deep-bodied actinopterygian, and the specimens described later by Eastman thus should be considered separately as *Amphicentrum orbiculare* (Eastman 1903, non Newberry & Worthen 1870). USNM 4404 (Fig. 13) is the best preserved of the four available specimens and is hereby declared the neoholotype. PF 7339 and YPM 3241 are neoparatypes because they add to the information provided by the neoholotype. YPM 3240 is headless and poorly preserved, and is thus noted only as a referred specimen.

Eastman (1917: 276-277) noted that *A. orbiculare* is a small species which attained a maximum length of about 4.5 cm, but PF 7339 (not available to Eastman) measures that much from the posterior margin of the cleithrum (the head is not preserved) to the caudal cleft and must have been at least 6 cm in standard length. The head is preserved to any extent only in the neoholotype and YPM 3241, and only the positions of some of the dermal bones can be discerned, not their morphology. The skull-roof bones bear an ornament of coarse tubercles, whereas those on the cheek and the pectoral girdle are ornamented with vertical cristae. The operculum is twice as deep as the suboperculum, and the preoperculum is a ventrally narrowing bone nearly as deep as the operculum and suboperculum combined. The snout and mandible are not preserved. The pectoral girdle consists of a clavicle, a cleithrum with a strong ventral embayment and a thin dorsal blade, and a supracleithrum that widens toward the dorsal margin where it attaches to the post-temporal. There is no postcleithrum.

The body is nearly twice as deep as it is long and has a pronounced, pointed dorsal peak composed of two scales and a less pronounced and more posteriorly situated ventral peak also composed of two scales. The dorsal and ventral marginal scales are short and tuberculated, whereas those on the mid-flank are up to three times deeper than wide and bear an ornament of vertical cristae that are much finer than those on the pectoral-girdle and cheek bones. The neoholotype has 18 vertical scale rows between the supracleithrum and the anterior end of the caudal peduncle (counting along the lateral line), and the much larger PF 7339 has 23 vertical scale rows. On the caudal peduncle the scales become much smaller and lozenge-shaped, and five rows of them extend onto the dorsal lobe of the tail.

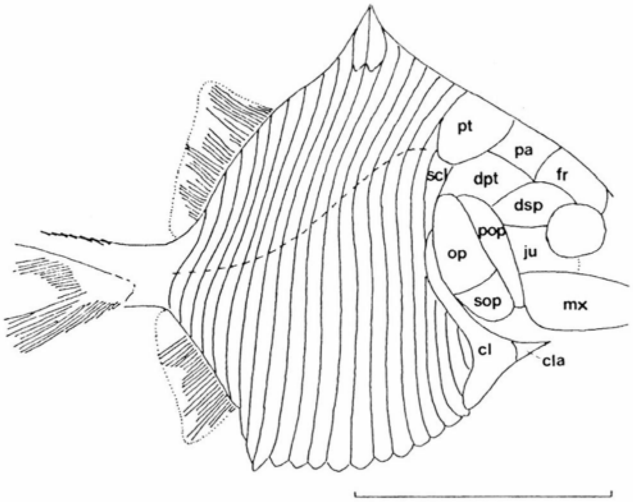

FIGURE 13—*Amphicentrum orbiculare*, Mazon Creek, Illinois. Camera-lucida drawing of USNM 4404 (neoholotype), with sop, pa, fr, and cla added from YPM 3241 and detail of the dorsal peak and fin contours from PF 7339. Scale bar equals 1 cm. Abbreviations: **cl**, cleithrum; **cla**, clavicle; **dpt**, dermopterotic; **dsp**, dermosphenotic; **fr**, frontal; **ju**, jugal; **mx**, maxillary; **op**, operculum; **pa**, parietal; **pop**, preoperculum; **pt**, post-temporal; **scl**, supracleithrum; **sop**, suboperculum.

The fins are best preserved in the PF 7339 which shows a few pectoral fin rays in the glenoid fossa of the coracoid and has the dorsal, anal, and caudal fins complete. The dorsal and anal both are the highest anteriorly and gradually become lower toward the caudal peduncle. The longer dorsal has 56 fin rays, whereas the anal has 42. The caudal fin is heterocercal but equilobate and has 15 fin rays in the ventral lobe and 25 or 26 in the dorsal lobe. Bifurcation of the first and second order occurs in both lobes. In all fins the rays are segmented and the segments are four to six times longer than wide. Fulcra are present only in the tail, where 15 or 16 long, narrow, deeply imbricating fulcra are arranged in a sagittal row. There is no pelvic fin.

A. orbiculare is quite distinct from *A. granulosum* and *A. jurgenai* n. sp. described below (see Discussion under *A. jurgenai).* I suspect it to be more closely related to *A. striatum* which, however, is based on a specimen too fragmentary to be useful for a comparison.

Iowa and Nebraska—Case (1982) illustrated *Amphicentrum* sp. from the Stark Shale (Dennis Formation, Bronson Group, Missourian) at Winterset, Madison County, Iowa (fig. 25-37), and Sarpy County, Nebraska (fig. 25-38). The Iowa specimen is indeterminate to species, whereas the Nebraska specimen is somewhat better preserved and appears to be assignable to the new species described below. In addition, G. R. Case obtained a specimen from the Wea Shale (Westerville Formation, Missourian) at the Hansen Quarry #6 between Papillion and Bellevue, Sarpy County, Nebraska, which he donated to the Field Museum of Natural History (PF 8371). This specimen is very similar to that from the Stark Shale in Sarpy County (Case, 1982: fig. 2538) and probably also belongs to the new species described below.

The only other North American occurrence consists of a single tooth from Linton, Jefferson County, Ohio (late Westphalian D), described by Newberry (1856: 99) as *Chirodus acutus.* However, the name is conspicuously missing from Newberry's later accounts of the Linton fauna and according to Miller (1889: 589) it is "too poorly defined to warrant recognition." The whereabouts of Newberry's holotype are unknown, but from his brief description and from Dyne's (1939) comments on the holotype of *Chirodus pesranae* M'Coy, whose preservation is similar to that of *C. acutus*, it can be concluded that the fossil is indeterminate to genus and probably to family as well.

Great Britain—Apart from the United States, Great Britain is the only other country where *Amphicentrum* is known to occur. Three species, *A. granulosum* Young 1866 (the type species of the genus), *A. striatum* Hancock & Atthey 1872, and *A. crassum* (Traquair 1890) have been described, of which the former is best known. The holotype of *A. striatum* is a very small and imperfectly preserved fish from the Northumberland coal field (Westphalian), with the body much deeper than long, the dorsal and ventral scales tuberculated, and the mid-flank scales having the tubercles fused into vertical cristae (Woodward, 1891: 540). The only other known examples are two isolated ectopterygoids at the British Museum (Natural History), both from Newsham near Newcastle-upon-Tyne.

A. crassum is based on isolated scales from the Carboniferous Limestone at Abden, Fifeshire, and Beith, Ayrshire, but several articulated specimens allegedly belonging to this species have recently been found in the basal Millstone Grit (Pendleian, basal Namurian) at Bearsden near Glasgow, which has yielded a diverse assemblage of marine invertebrates and fishes (Wood, 1982). The specimens are up to 31 cm long—a full third longer than *A. granulosum*and are said to possess pelvic fins, which would be a very unusual feature for the genus. Unfortunately, Wood's (1982) account is exceedingly sketchy and an in-depth study is urgently needed to confirm the affinity of the specimens.

A. granulosum (Fig. 14) is a large species from the Coal Measures (Westphalian) of Staffordshire and Lancashire, England, and Lanarkshire, Scotland. It was described by Young (1866) and discussed at length by Traquair (1875, 1879), and the structure of its skull has been redescribed by Dyne (1939). This species is known from a number of well preserved specimens and, therefore, can serve as a model for describing the Kinney Quarry *Amphicentrum*.

Apart from articulated fishes, isolated ectopterygoids belonging to indeterminate *Amphicentrum* have been recorded from the Upper Carboniferous Limestone (Visean) at Richmond and Wensleydale, Yorkshire (see Woodward, 1891: 540).

AMPHICENTRUM JURGENAI n. sp.

Material—Holotype CM 47845a + b (Fig. 15D). Paratypes CM 47843a + b (not figured), CM 47844a + b (Fig. 15B), CM 47846 (Fig. 15A); NMMNH P-19112a + b (Fig. 15C), NMMNH P-19116 (Fig. 15E); KUVP 86170a + b (Fig. 15F). Referred specimens USNM 187148; CM 30727, 30733, 30734a + b, 30735a + b; KUVP 86174a + b. One unnumbered specimen is in the A. Lerner Collection, Albuquerque; its preservation is very similar to that of the holotype (Fig. 15D).

Type locality and horizon—Kinney Brick Company Quarry, NW^1/4 SW^1/4 SE1/4 sec. 18, T9N, R6E, Bernalillo County, central New Mexico. Units 2-4 of Lucas & Huber (1991; see also Kues & Lucas, this volume), Pine Shadow Member of Wild Cow Formation, Madera Group, Upper Pennsylvanian.

Etymology—Named in honor of Bob Jurgena, President of the Kinney Brick Company of Albuquerque, without whose permission most of the specimens could not have been collected.

Diagnosis—Small species 5.5 to 7.5 cm in standard length. Head amounts to one-quarter of standard length; body more than one-and-half times deeper than long, dorsally and ventrally angulated without spine-like peaks; ventral angle situated directly under dorsal angle. Ventral end of cleithrum does not reach body margin. Thirty to thirty-three vertical scale rows between cleithrum and anterior end of caudal peduncle; marginal scales short and lozenge-shaped, mid-flank scales up to four times deeper than wide; all scales ornamented with vertical, parallel cristae. Dorsal and anal fins start at body angles and reach to caudal peduncle; anterior dorsal and anal fin rays modified into rigid keels; anal fin longer than dorsal fin.

Description—The preservation of *Amphicentrum* is similar to that of *Platysomus*, which is discussed in the following section. *A. jurgenai* ranges between 5.5 and 7.5 cm in standard length; CM 47846 is the largest specimen. The head amounts to one-quarter of the standard length and the body is more than one-and-half times deeper than long. The body shape is somewhat atypical of *Amphicentrum* because it lacks the spine-like dorsal and ventral peaks. Instead it is only angulated, with the ventral angle situated directly under the dorsal angle (Figs. 15D, 16). The CM 47846 (Fig. 15A) is misleading in this regard because it is posterodorsally incomplete and appears to have the ventral angle situated more forward. However, this is a preservational artifact resulting from compression that pushed the ventral part of the body forward (see diagonally displaced scales above the ventral angle).

The skull roof and cheek invariably are poorly preserved and the entire type series is needed to restore the pattern (Fig. 16). The post-temporal is preserved to some extent in all specimens, but its ornament of radiating cristae broken up into drop-shaped tubercles can be seen only in NMMNH P-19116 (Fig. 15E). This specimen also shows the parietal and its suture with the frontal, but the ornament is not preserved. All other bones are ornamented with uninterrupted cristae which undulate and form concentric patterns on the dermosphenotic, dermopterotic, fugal, lachrymal, nasal, and the mandible, and are essentially straight and anteroposteriorly or vertically oriented on the rostral, premaxillary-antorbital, maxillary, and the opercular series. The frontal is separated from the orbit by the dermosphenotic and the nasal. The rostral and premaxillary-antorbital are best seen in CM 47846 (Fig. 15A), where they appear to be of an extent comparable to *A. granulosum*. The operculum

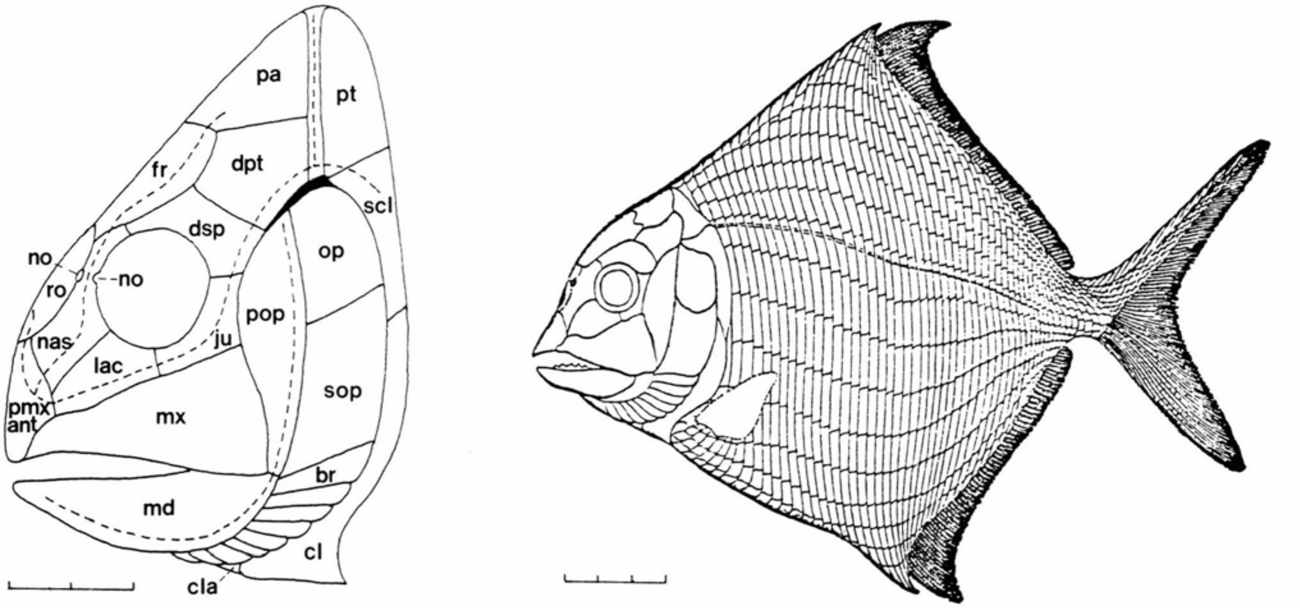

FIGURE 14—*Amphicentrum granulosum* Young 1866 from Westphalian of England and Scotland. Habitus drawing from Traquair, 1879: pl. 5/1, and restoration of the head from Dyne, 1939: text-fig. 1. Scales in centimeters. Abbreviations: **br,** branchiostegals; **cl,** cleithrum; **cla,** clavicle; **de,** dentary; **dpt,** dermopterotic; **dsp,** dermosphenotic; **fr,** frontal; **ju,** jugal;**lac,** lachrymal; **md,** mandible; **mx,** maxillary; **nas,** nasal; **no,** nostril; **op,** operculum; **pa,** parietal; **pmx-ant,** premaxillary-antorbital; **pop,** preoperculum; **pt,** post-temporal; **ro,** rostral; **scl,** supracleithrum; **sop,** suboperculum.

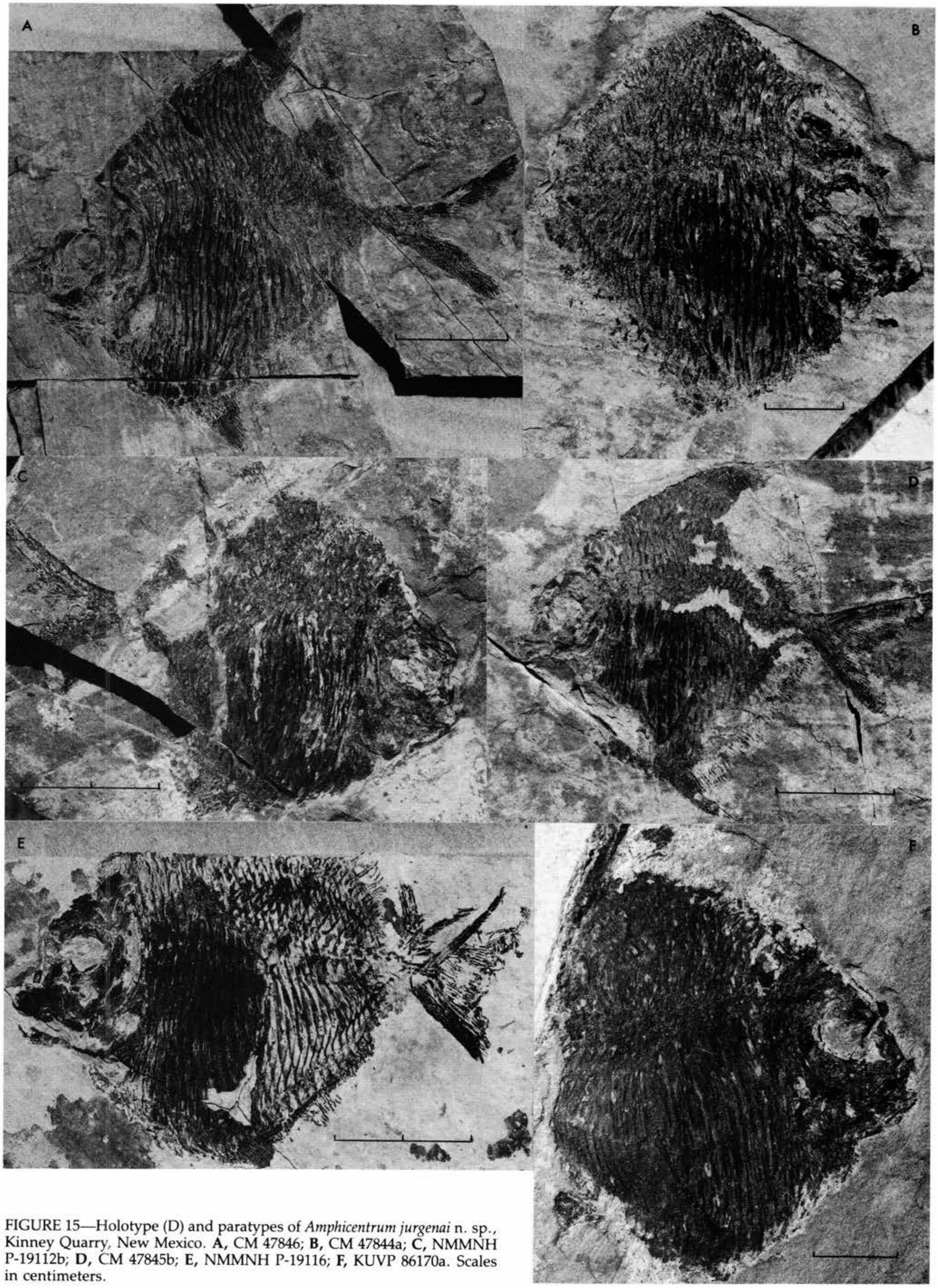

FIGURE 15—Holotype (D) and paratypes of *Amphicentrum jurgenai* n. sp., Kinney Quarry, New Mexico. **A,** CM 47846; **B,** CM 47844a; **C,** NMMNH P-19112b; **D,** CM 47845b; **E,** NMMNH P-19116; **F,** KUVP 86170a. Scales in centimeters.

is twice as deep as the suboperculum, but this is apparent only in CM 47843b and 47846; in all other specimens the opercular series is so damaged that the division cannot be recognized. The preoperculum is a ventrally narrowing bone as deep as the suboperculum anmd operculum combined; it is best seen in the holotype (Fig. 15D). Three displaced branchiostegals are preserved in NMMNH P-19116, but the space between the suboperculum and the ventral end of the cleithrum could have accommodated at least twice as many. The jaws are edentulous and the mandible is as long as the maxilla and its premaxillary-antorbital overlap. The preservation of the mandible is not good enough to recognize its components. In CM 47846 the posterodorsal edge of the maxilla is crushed and several narrowly conical teeth about 0.5 mm tall are scattered in this area. They are too high above, and posterior of, the inner edge of the maxilla (which in *A. granulosum* is tooth-bearing) and are thus interpreted as derived from the posterior end of the ectopterygoid. Most of the specimens show a scleral ring composed of four segments.

The dermal pectoral girdle consists of the cleithrum and the supracleithrum. The cleithrum extends to the body axis where it articulates with the supracleithrum, which widens dorsally and attaches to the posterolateral edge of the posttemporal. Both bones bear an ornament of uninterrupted longitudinal cristae. The presence of a clavicle is assumed because it is present in other *Amphicentrum* species (see Figs. 13, 14), but it is not visible in any specimen of *A. jurgenai*. One likely reason is that the cleithrum does not reach the anteroventral body margin and its ventral embayment invariably is obscured by a mass of scales. Another possibility is that the clavicle is attached anteromesially rather than anteriorly and is thus covered by the anterior margin of the embayment.

CM 47846 (Fig. 15A) is the only specimen that shows a part of the pectoral fin in the glenoid fossa of the coracoid. Only the proximal, unsegmented parts of 12 fin rays are preserved, but it nevertheless appears that the fin was very small, probably 10-15 mm long and not much over 5 mm wide. There is no evidence of fulcra, but the poor preservation precludes deciding whether the fin originally bore them. There is no pelvic fin.

The dorsal and anal fins definitely do not bear fulcra, instead their anterior ends are strengthened by a special arrangement of the fin rays. The first ca. 20 dorsal fin rays and the first 15 anal fin rays form solid veils of interlocking segments that must have functioned as rigid (non-undulating) keels (Fig. 15A, D). In contrast, the more posterior fin rays are shorter and spaced apart, with each gap being about as wide as the width of the adjoining rays. The distal ends of the free rays bifurcate, whereas those of the anterior keels do not. The holotype (Fig. 15D) shows several baseosts underneath the dorsal keel, with each baseost supporting three fin rays. Conversely, NMMNH P-19116 (Fig. 15E) shows baseosts underneath both the anal and dorsal free rays, with each anal baseost supporting only one fin ray and each dorsal baseost supporting three fin rays. Both fins reach all the way to the caudal peduncle where the fin rays are the shortest and are inclined and curved toward the peduncle. The fin-ray segments in the keels are twice as long as they are wide, but in the free fin rays they become shorter, about one-and-half times longer than wide. The anal fin is complete in the holotype (Fig. 15D), where it has 67 rays. The dorsal fin is only partially preserved in the holotype, NMMNH P-19116, and CM 47846. Since the dorsal fin is 20% shorter than the anal, it is estimated that the total number of dorsal fin rays was 53-55.

The caudal fin is heterocercal but equilobate and the depth of its cleft amounts to one-half of the fin length. It is best preserved in the holotype (Fig. 15D) which has 12 fin rays in the dorsal lobe. The fin rays of the ventral lobe are more easily and accurately counted in CM 47846 (Fig. 15A) where they number 20. The dorsal fin rays are shorter. In both lobes the fin rays gradually diminish in length toward the center of the fin and so do their unsegmented proximal parts which are thinner and much shorter than the segmented parts. The individual segments are twice as long as they are wide and in the ventral lobe gradually thicken toward the margin of the fin while maintaining the 2:1 length to width ratio. Few of the ventral fin rays bifurcate and second-order bifurcation is rare. In the dorsal lobe the distal thickening of the fin rays appears to be negligible or absent and filling of the fin web is achieved by first- and second-order bifurcation. The tip of the dorsal lobe consists of a flange of short, delicate rays. Despite the first- and second-order bifurcation, the dorsal rays remain spaced apart, whereas those of the ventral lobe form a solid veil. The lowermost ray of the ventral lobe is much shorter than the successive rays which are the longest in the entire fin.

The squamation of the dorsal lobe is preserved only in NMMNH P-19116 (Fig. 15E), where it consists of four rows of lozenge-shaped, non-imbricating scales that cover the uppermost part of the lobe, and deeply imbricating fulcra that form the ridge of the tail. The fulcra are incompletely preserved and cannot be counted, but it is apparent that they are quite small, narrow, and arranged in a sagittal row. The non-imbricating scales are proximally short and ornamented with parallel cristae, but toward the tip of the lobe become exceedingly flat, prolonged and narrow, and lose the ornament. The lowermost row ends about halfway up the lobe, whereas the three remaining rows reach nearly to the tip.

On the caudal peduncle and body margins the scales are short, lozenge-shaped, and ornamented with 10-15 cristae that run parallel to the scale margin. On the mid-flank the ornament remains the same, but the scales become up to four times deeper than wide and display prominent anterior ridges that dorsally and ventrally extend into spines for peg-and-socket articulation with the adjoining scales. Counting vertical scale rows is difficult because of scale disruption and an error of plus/minus two or three rows is to be expected. However, in all specimens the count is at least 30 and may be as high as 33 vertical scale rows between the top of the cleithrum and the anterior end of the caudal peduncle. The scale rows are essentially vertical over much of the body, only anterodorsally and in a small area around the pectoral fin they become inclined forward. In front of the caudal peduncle the orientation is not clear in any of the specimens, which is largely responsible for the expected counting error. Marginal scales of three rows are involved in formation of dorsal and ventral body angles.

Discussion—The skull-bone pattern of *A. jurgenai* (Fig. 16) is virtually identical to that of *A.orbiculare* (Fig. 13). These two species differ from *A. granulosum* (Fig. 14) in having the operculum deeper than the suboperculum, the post-temporal extending more anteriorly, and the dermopterotic relatively larger. The cleithrum/supracleithrum proportions are about the same in *A. jurgenai* and *A. granulosum,* whereas in *A. orbiculare* the supracleithrum is relatively shorter. *A. jurgenai* differs from the other two species in that the cleithrum does not reach the anteroventral body margin.

The three species are quite different in body shape and in morphology of the dorsal and anal fins. In *A. granulosum* the body is rectangular with nearly straight margins, in *A. orbiculare* the anterodorsal and posteroventral margins are straight and short whereas the anteroventral and posterodorsal margins are convex and long, and in *A. jurgenai* all the body margins are convex and the anterodorsal and posteroventral margins are longer. In *A. granulosum* and *A. orbiculare* the body culminates in dorsal and ventral spine-

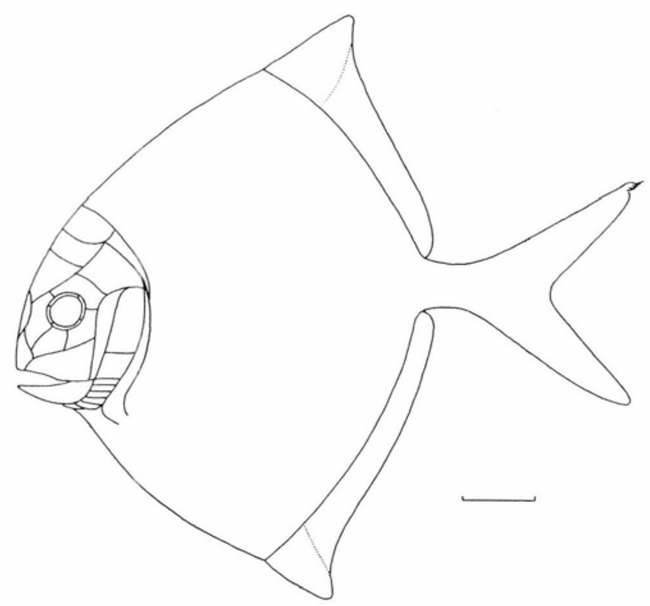

FIGURE 16—Composite restoration of *Amphicentrum jurgenai* n. sp. with fins and body outline based on the holotype and CM 47846, and structure of the head and pectoral girdle on the entire type series. Extent of the rigid dorsal and anal anterior keels is shown by dotted line. Individual bones are labeled in Fig. 14. Scale bar equals 1 cm.

like peaks which in the former curve backward and in the latter point straight up/down, and in both species the ventral peak is situated posteriorly of the dorsal. In *A. jurgenai,* on the other hand, the dorsum and ventrum are only angulated, without pronounced peaks, and the ventral angle is situated directly under the dorsal angle.

The dorsal and anal fins of *A.jurgenai* are more similar to those of *A. granulosum* which also span the entire posterodorsal and posteroventral body margins. However, the differentiation into rigid anterior keels and posterior undulatory fin webs present in *A. jurgenai* is, as far as known, absent in *A. granulosum,* where instead of fin keels the dorsal and ventral body peaks functioned as such. In *A. orbiculare* the dorsal and anal fins are much shorter and do not exhibit any specialized features. Whereas in *A. granulosum* and *A. orbiculare* the dorsal fin is longer, in *A. jurgenai* the reverse is the case and the anal fin is ca. 20% longer than the dorsal fin. Another species which might have had the dorsal and anal fins differentiated into rigid anterior keels and posterior undulating membranes is *A. crassum* from Bearsden, Scotland, but until the specimens are described this is to be regarded only as a suggestion stemming from differential preservation of the fins in one photographed specimen (see Wood, 1982: fig. 3).

Differences can be seen also in the number of vertical scale rows between the pectoral girdle and the anterior end of the caudal peduncle (18-23 in *A. orbiculare,* 30-33 in *A. jurgenai,* and 40-45 in *A. granulosum),* and in the number of marginal scales involved in formation of the body peaks or angles (2 in *A. orbiculare,* 3 in *A. jurgenai,* and 5-6 in *A. granulosum).* The numbers are substantially higher for *A. granulosum* which is a large species (up to 20 cm in standard length) and, correspondingly, they are somewhat higher for *A.jurgenai* (7.5 cm in standard length) than for *A. orbiculare* (6 cm in standard length). It is thus clear that these differences correlate with species size.

Finally, the three species differ also in ornamentation of the scales and dermal bones of the skull and pectoral girdle. In *A. granulosum,* as the species name implies, the ornament of coarse tubercles prevails; in *A. orbiculare* tubercles are restricted to the marginal scales and skull roof, and all other scales, the cheek, and the pectoral girdle are ornamented with cristae; and in *A. jurgenai* the ornament of uninterrupted cristae prevails even more than in *A. orbiculare* and tubercles are restricted to the post-temporal and possibly the parietal (whose ornament is not known).

The dentition of *A. granulosum* consists of conical teeth on the inner surface of the maxilla and on ectopterygoids modified into plates, and on coronoids fused to form a massive lower plate (Dyne, 1939). In *A. orbiculare* and *A. jurgenai* the dentition is not known, but the conical teeth scattered behind the maxilla of *A. jurgenai* CM 47846 and interpreted as derived from the ectopterygoid would seem to suggest that the dentition was similar to that of *A. granulosum.*

Order BOBASATRANIIFORMES Berg 1940
Family PLATYSOMIDAE Young 1866

Genus *PLATYSOMUS* Agassiz 1835

Summary of occurrences and taxonomic comments

A review of the North American occurrences of *Platysomus* is needed before describing and placing the Kinney Quarry species. Occurrences in Europe, Asia, and Greenland are treated only briefly because a full-scope review would be lengthy and beyond the scope of this paper. Certain taxonomic comments are necessary, however, because a recent study (Campbell & Le Duy Phuoc, 1983) of the type species, *P. gibbosus* (Blainville 1818), resulted in its transfer to the Bobasatraniiformes.

Oklahoma—Cope (1891: 460, pl. 33/10) based *P. palmaris* on "about a hundred fragments of bodies of various sizes, some of which include the scapular arch, but none the fins." They were collected in 1884 by W. F. Cummins from one of the Deep Red Run sites (Garber Formation, Lower Permian) in today's Cotton County. The lectotype (Dalquest & Kucurko, 1988: 265), AMNH 7281, consists of an incomplete flank with vertically cristated scales and the cleithrum. A similarly preserved specimen from the type locality, presumably also collected by Cummins, is AMNH 9160. However, it is impossible to tell whether this specimen has been used in Cope's original description, and it thus is only a topotype or tophomeotype. Case (1915: 96) listed *P. palmaris* from the Pond Creek site (Garber Formation) in Grant County, and Wegemann (1915: 25) recorded *Platysomus* scales from Cotton County, within the range of the Southwest Taylor site of Olson (1967: 22). The deposits of this site lie below the Ryan Sandstone in the Oscar Formation of the Gearyan Series, which the Oklahoma Geological Survey considers to be latest Pennsylvanian in age (see Zidek, 1972: 174). The Oklahoma Gearyan remains to be satisfactorily defined, however, and the Kansas Geological Survey regards correlable units as the lowermost Permian. Olson (1967: 44, 68, 102; 1970: 377-378, 381, 392-393) found *Platysomus* scales and flank plus skull fragments in the Wellington Formation, Lower Permian, at the Perry 6 site in Noble County and the McCann Quarry in Kay County; he noted (Olson, 1970: 393) that the remains of *Platysomus* are accompanied by *Sphaerolepis* tooth plates and, therefore, that it is not inconceivable that these plates in fact are of platysomid derivation. Olson's specimens from Perry 6 (UF 1006, 1013) and McCann Quarry (UF 1025-1028) were examined by Johnson & Zidek (1981), who found them to be phyllodont tooth plates of platysomid derivation. More recently, an occurrence of articulated specimens of *Platysomus* was recorded from the base of the Hennessey Group, Lower Permian, at the East Manitou site in Tillman County (Fig. 17; Simpson, 1973, 1974). Schultze (1985) reported platysomid scales from the Schroyer Limestone (Gearyan) in Kay County.

The material available to Cope was exceedingly poorly

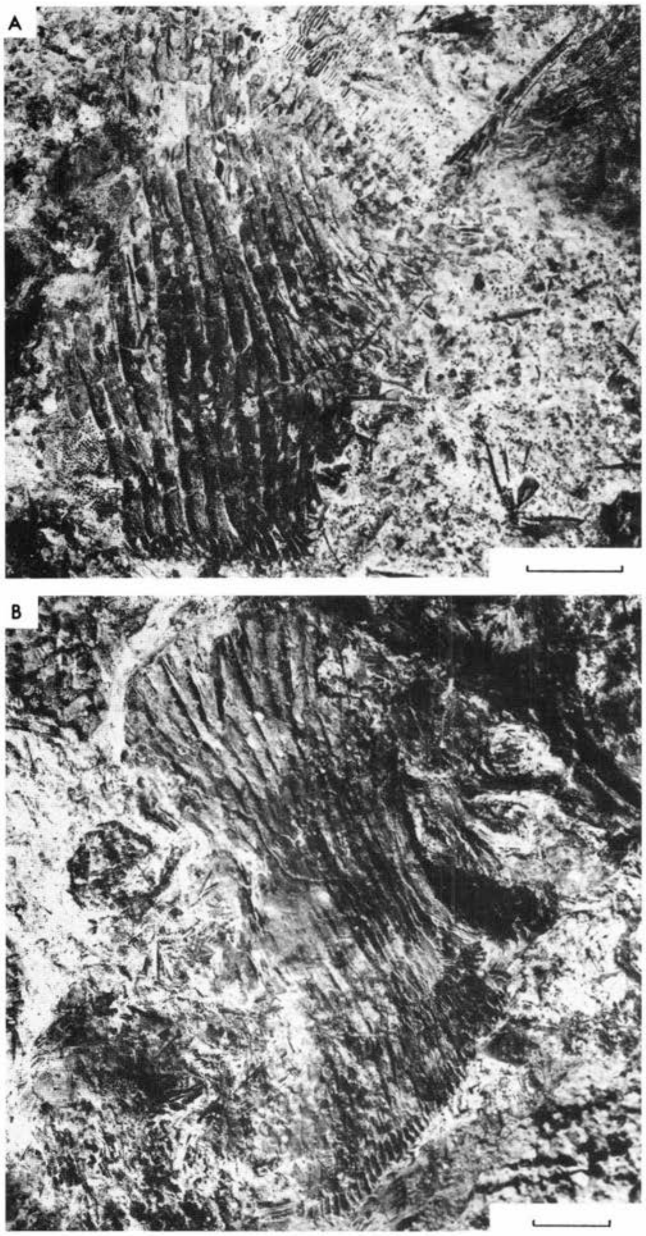

FIGURE 17—*Platysomus* sp. (OMNH, uncatalogued) from the base of the Hennessey Group, Lower Permian, at the East Manitou site, Tillman County, Oklahoma. **A,** Flank, dorsal fin, and dorsal lobe of the tail. **B,** Incomplete flank and poorly preserved head. *Acanthodes* scales scattered around the specimen in A. Scale bars equal 1 cm.

preserved and resulted in a description so generic that the species *P. palmarís* is undefinable. This is best apparent from comparing Cope's (1891) plate 33 with Fig. 17 of this paper. The East Manitou specimens are preserved better than those illustrated by Cope, yet they can be identified only generically. Cope's specimens thus can be recognized only as *Platysomus* sp. and the species name *P. palmaris* is declared nomen dubium.

Texas—Beede (1907: 120) and Udden (1912: 18) listed *Platysomus* scales from the Wichita Group, Wolfcampian, and Hussakof (1911: 173, fig. 56A) referred an incomplete flank and fins except the pectoral (AMNH 7935) from Dundee, Archer County (Belle Plains Formation, uppermost Wichita Group), to *P. palmaris* Cope. Wilson (1950) described four partial specimens of *Platysomus* sp. (TMM 953-1 through 4) from the Blaine Formation (Double Mountain Group, Guadalupian) in King County. This is one of only two Late Permian occurrences of platysomid fish in North America. Dalquest (1966) described a new platysomid, *Schaefferichthys leudersensis* [sic] n. g. et sp. (holotype only, USNM 23109; Fig. 18) from the Lueders Formation, Wichita Group, near Lake Kemp in Baylor County. Johnson (1975, 1979) reported abundant dentigerous plates with a phyllodont type of tooth replacement in microvertebrate samples collected from early Leonardian deposits in Baylor County, and expressed the opinion that these plates are of either platysomid or coelacanthiform derivation. This question was further dealt with by Johnson & Zidek (1981), who concluded that the tooth plates are of platysomid derivation, and that also the tooth plates of an alleged coelacanth (Wilson, 1949) from the Vale Formation (Clear Fork Group, Leonardian) in Taylor County are phyllodont and belong to a platysomid. Fracasso & Hovorka (1987) found a single phyllodont tooth plate in the San Andres Formation, Guadalupian, in the Texas Panhandle. It is the second platysomid occurrence in the Late Permian of North America. Dalquest et al. (1988) argued against the platysomid derivation of phyllodont tooth plates on the ground that such plates are common in their study area (Lueders Formation in Baylor County) whereas platysomid scales or any other skeletal elements are absent, and that the plates would be too large for platysomid fishes which usually do not exceed 10 cm in length. Therefore, they tentatively assigned the tooth plates to an unidentified coelacanth. Although the absence of platysomid scales and any other skeletal elements certainly is odd, the Kinney Quarry *Platysomus* described below eliminates any doubt that might remain about the derivation of the phyllodont tooth plates.

Schaefferichthys leudersensis is based on a single specimen which is preserved as poorly as the East Manitou specimens shown in Fig. 17 (see also Johnson & Zidek, 1981: text-fig. 1H). The generic diagnosis of *Schaefferichthys* fits *Platysomus* and the species diagnosis is as for genus. In effect the species is undefinable and the generic name is a synonym of *Platysomus.* The interesting aspects of the specimen are traces of a phyllodont tooth plate (tritoral denticles of Dalquest, 1966: 760; see also Johnson & Zidek, 1981: 533) and a quadratojugal behind the maxilla (Fig. 18; see discussion under *Platysomus schultzei* n. sp.).

Illinois—Platysomus occurs in the Francis Creek Shale Member of the Carbondale Formation (Desmoinesian) in the Mazon Creek area, Gruney and Will Counties. I am aware of only nine specimens, six of *P. circularis* Newberry & Worthen 1870 and three of *P. lacovianus* Cope 1891, which came from both the predominantly fresh-water Braidwood fauna and the predominantly marine Essex fauna. The best preserved specimen of *P. circularis* is illustrated in Fig. 19A. The holotype of *P. círcularis,* UI X-489 (part) and OF 593 (counterpart) has the head preserved in outline only and the UI part is identified in Newberry's handwriting (Newberry & Worthen, 1870: 347, pl. 4/2). Other specimens identified by Newberry are AMNH 520 (headless, labeled "Cotype?" by Hussakof, 1908: 87), UC 14390 (head in outline only), and USNM 16358 (a nearly complete fish). The remaining two specimens are PF 5533 (headless) and PF 7066 (fiberglass mold of a nearly complete fish), both from pit 11, Will County. PF 7339, also from pit 11, is labeled *P. circularis,* but in reality it is an imperfectly preserved *Amphicentrum.* Of the three specimens of *P. lacovianus* two (AMNH 7400, YPM 3242) are nearly headless and the remaining one (USNM 4399) has the head preserved in outline only. AMNH 7400a + b is the holotype (Cope, 1891: 462, pl. 31/11; R. D. Lacoe Coll.), USNM 4399 (R. D. Lacoe Coll.) was erroneously labeled "Type" by Merrill (1907: 16), and YPM 3242 was identified as *P. lacovianus* by Eastman.

Cope (1891: 462) stated that the two species can be dif-

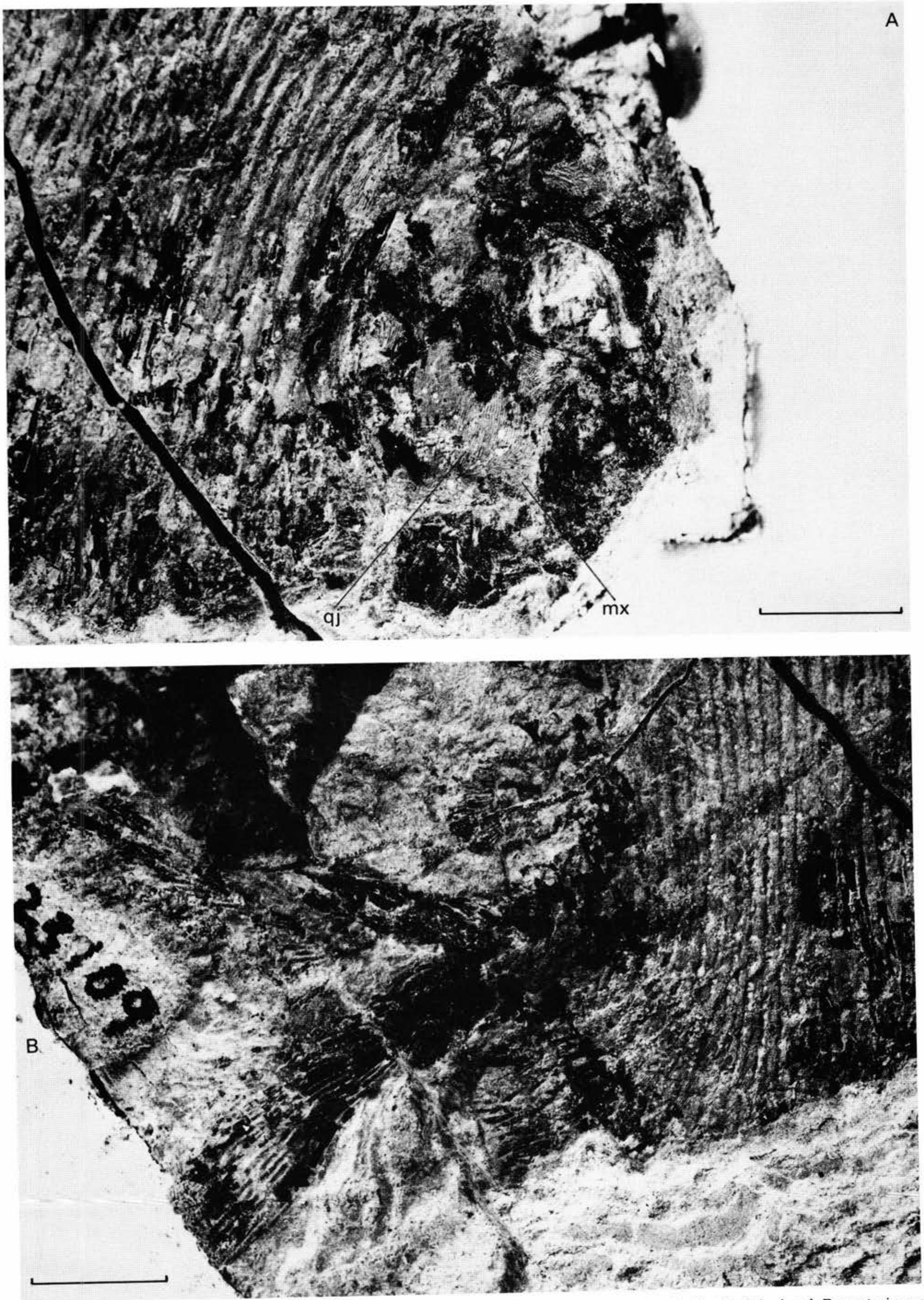

FIGURE 18—Holotype of *Schaefferichthys leudersensis*, counterpart not figured by Dalquest (1966). **A,** Detail of the head; **B,** posterior part of the body and fins. Scale bars equal 1 cm. Abbreviations: **mx,** maxillary; **qj,** quadratojugal.

ferentiated on fin-ray counts (D40, A30, C30 in *P. circularis* vs. D28, A25, C30 in *P. lacovianus)* and scale morphology (smooth in *P. circularis* vs. ornamented with parallel ridges in *P. lacovianus)*, but that is not the case. The scales of *P. circularis* are ornamented in exactly the same manner as those of *P. lacovianus* (see Fig. 19A) and the differences in fin-ray counts are an artifact of preservation. The fin-ray formula is approximately D40, A30-35, C28-30 in both species, and they both have 20-22 vertical scale rows between the supracleithrum and the anterior end of the caudal peduncle (counting along the main lateral line). Since there are no criteria on which the two could be separated, *P. lacovianus* is hereby placed in synonymy of *P. circularis.* It is a small species that probably has not reached over 60 mm in standard length. Baseosts are visible in PF 7066 (dorsal), AMNH 520 (dorsal), and USNM 16358 (anal), in which each baseost supports two fin rays. The cheek is preserved to any degree only in PF 7333 (Fig. 19A), PF 7066, and USNM 16358, which show evidence of a quadratojugal behind the maxilla.

USNM 16358 is only 28 mm in standard length and is markedly less deep-bodied than the other specimens. It has 22 vertical scale rows and 29 dorsal, 26 anal, and 27 caudal fin rays. Although the preservation does not allow to state categorically that the dorsal and anal fins are complete, the body shape nevertheless makes the specimen suspect. UC 14390 is only 20 mm in standard length and is as deep-bodied as all the larger specimens, which makes it unlikely that the lower body profile of USNM 16358 could be due to young ontogenetic age. It raises the possibility of another *Platysomus* species in the Mazon Creek fauna.

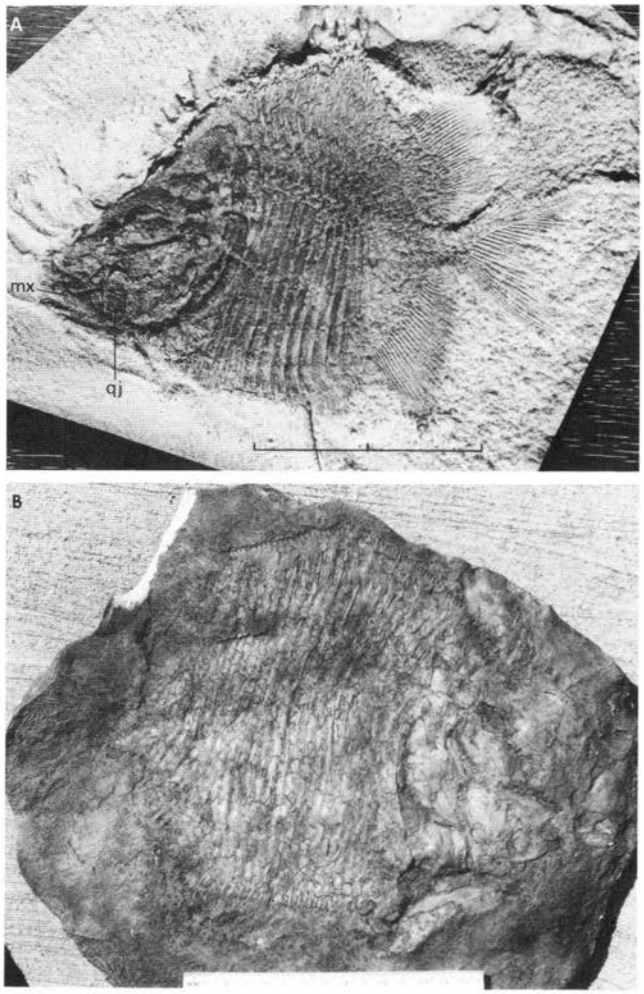

FIGURE 19—**A,** *Platysomus circularis* PF 7333 from the Francis Creek Shale Member of the Carbondale Formation, Desmoinesian, at Mazon Creek (pit 5), Will County, Illinois. Plaster cast of an expanded latex mold. Scale in centimeters. **B,** Plaster cast of a large platysomid YPM/PU 18126 from the Opeche–Minnekahta transition zone of the Phosphoria Group, Lower Permian, at the South Dakota State Cement Plant Quarry, northwest outskirts of Rapid City. The specimen is ca. 30 cm in standard length. Abbreviations: **mx,** maxillary; **qj,** quadratojugal.

South Dakota—A large platysomid occurs in a fish fauna recovered from the Opeche-Minnekahta transition zone of the Phosphoria Group, Lower Permian, at the South Dakota State Cement Plant Quarry, northwest outskirts of Rapid City. This fauna has been studied by T. M. Cavender of Ohio State University, according to whom (written comm.) the platysomid specimens are mostly isolated cranial and pectoral-girdle elements and scales, and a few articulated smaller individuals which may be juveniles or another species. Five specimens from this fauna are in the YPM/PU collection, but four of them (YPM/PU 19652-18655) cannot be located (M. A. Turner and P. Huber, pers. comm.) and the fifth (YPM/PU 18126) is preserved only as a plaster cast (Fig. 19B). This specimen, which appears to represent a new species, adorned a wall of "Swede" Nielsen's house which was swept away by a flood on Rapid Creek (west of Rapid City; D. Baird, written comm.). According to G. D. Johnson, University of South Dakota (pers. comm.), two articulated specimens of *Platysomus* were collected by him in 1985 at the State Cement Plant Quarry, and several specimens from that locality are at the South Dakota School of Mines in Rapid City.

Arizona—The Kaibab Limestone, Leonardian, has produced a number of phyllodont tooth plates. Hussakof's (1943) "detached teeth of a ganoid" are individual teeth from disintegrated phyllodont tooth plates (Johnson & Zidek, 1981: 425, table 1).

West Virginia—A fragmentary phyllodont tooth plate (CM 35137) has been found in the Windy Gap Limestone Member of the Greene Formation, Lower Permian, at Fairview Ridge near Wileyville (Johnson & Zidek, 1981).

Montana—Platysomid fishes occur in the Bear Gulch Limestone Member of the Heath Formation, Namurian E_2b (W. G. Melton and R. Lund, pers. comm.). According to L. Grande (pers. comm.), the Field Museum collection contains a number of well-preserved specimens of Bear Gulch *Platysomus* (s.l.) that can be separated into two distinct morphologies.

Kansas—Schultze (1985) reported phyllodont tooth plates from the Schroyer Limestone (Gearyan) in Cowley County and the Speiser Shale (Gearyan) in Butler County, and platysomid scales from the Funston Limestone (uppermost Virgilian) in Riley County and Threemile Limestone (Gearyan) in Cowley and Greenwood Counties.

Nebraska—According to L. D. Martin and H.-P. Schultze, University of Kansas (pers. comm.), Late Pennsylvanian (Virgilian) phyllodont tooth plates have been found at Peru, Nemaha County.

Greenland—Nielsen (1935:98) and Bendix-Almgreen (1976: 556) list *Platysomus* sp. from the Upper Permian marine deposits of the Foldvik Creek Formation in central East Greenland, where the actinopterygian fauna is closely related to that of the European marine Upper Permian (Kupferschiefer, Germany; Marl Slate, England). The occurrence concerns only isolated scales which were described by Aldinger (1937: 188-193).

China—Wei Feng (1977) described *Sinoplatysomus meishanensis* n. g. et sp. from the Changhsing Limestone, Upper Permian, at Meishan in Chekiang Province. He compared the new genus with *Platysomus, Amphicenturm (Cheirodus),* and *Cheirodopsis,* and cited Stensiö (1921) who, however, later transferred his specimens to *Bobasatrania* (see Stensiö, 1932). The description is brief and lacks an illustration; without the material at hand it is impossible to make any meaningful comments.

Soviet Union-Obruchev (1977: 7) listed *Platysomus?* sp. from the upper fish horizon of the Bystrianskaia Formation in the Minusinsk depressions and the Tuva Basin. This is the oldest occurrence so far recorded (lower Tournaisian = Kinderhookian). Minikh (1986) redescribed *Platysomus biarmicus* Eichwald 1857 and erected *Kargalichthys efremovi* n. g. et sp. which, however, is a questionable platysomid. *P. biarmicus* occurs in the late Kazanian (= late Guadalupian) and Tatarian (= late Guadalupian and Lopingian) of the East European Platform and the eastern foothills of the Urals, whereas *Kargalichthys* is known only from the Urzhumskyi Series, early Tatarian, in the southeast part of the East European Platform. Woodward (1891: 545) remarked that *P. biarmicus* is "evidently closely allied to *P. gibbosus,"* but Minikh's (1986) revision indicates otherwise.

Czechoslovakia-Fritsch (1912: 14-15, fig. 15) briefly described a small, poorly preserved specimen from the Lower Permian calcareous shales at Bitouchov (Krkonoše Piedmont Basin, northeast Bohemia) as *Platysomus pygmaeus* n. sp. The specimen has been lost, but from Fritsch's figure it is obvious that this is not a platysomid. Therefore, contrary to the published record, no platysomid fish, and no deep-bodied actinopterygian of any other kind, is known to occur in the Permo-Carboniferous of Czechoslovakia.

Germany-Platysomus occurs in the Kupferschiefer, whose deposition is considered by most stratigraphers to mark the beginning of the Late Permian (Zechstein), but Harland et al. (1990: fig. 3.7) regard it as the latest Early Permian (Rotliegendes). Two species, *P. gibbosus* (Blainville 1818) and *P. striatus* Agassiz 1835, have been described, the latter originally from the English Marl Slate. Woodward (1891) placed *P. striatus* in synonymy of *P. gibbosus,* but Schaumberg (1976, 1977) and Haubold & Schaumberg (1985) consider it a valid species. From their habitus restoration (1985: fig. 104) and restoration of the head (1985: fig. 81/4; Fig. 20B of this paper), both modified from Traquair (1879: pl. 6/1), it appears that *P. striatus* differs from *P. gibbosus* (redescribed by Campbell & Le Duy Phuoc, 1983: 65-68, text-fig. 17; Fig. 20C of this paper) in possessing a postcleithrum and toothed jaws, lacking pelvic fins, posteroventral angulation of the body, and a quadratojugal behind the maxilla, and in having the cheek less differentiated (only jugal and lachrymal instead of five infraorbitals as in *P. gibbosus,* and no suborbitals).

Great Britain-P. *gibbosus* occurs in the Marl Slate (Upper Permian) of England and, in turn, *P. striatus* which was originally described from the Marl Slate, occurs also in the German Kupferschiefer. Traquair (1879: 369) discussed the taxonomic history of the species included in *Platysomus,* and Woodward (1891: 542) placed several species, including *P. striatus,* in synonymy of *P. gibbosus.* Apart from *P. gibbosus* and *P. striatus* (which is here considered valid) five other species occur in Great Britain: *P. forsteri* Hancock & Atthey 1872 in the Coal Measures (Westphalian) of Yorkshire and Northumberland, England, and Lanarkshire, Scotland; *P. parvulus* Williamson 1849 in the Coal Measures of Staffordshire, Lancashire, Yorkshire, and Northumberland, England, and Midlothian and Lanarkshire, Scotland; *P. rotundus* Hancock & Atthey 1872 in the Coal Measures of Newsham and Northumberland, England; *P. tenuistriatus* Traquair 1879 in the Lower Coal Measures of Derbyshire, England; and *P. superbus* Traquair 1881 in the Viséan at Glencartholm (Eskdale, Dumfriesshire), Scotland.

The material of *P. forsteri* is exceedingly poorly preserved; the form and proportions of the head and body are not known, and only the scale morphology is discernible in any detail. *P. tenuistriatus* and *P. rotundus* are small species (9 and 7.5 cm long, respectively) known only from the holotypes. In both the body is rounded, without any dorsal and ventral angulations, the dorsal and anal fins are relatively low, and the head is poorly preserved. It is doubtful whether these two species are mutually separable. *P. parvulus* is a peculiar species with a steeply raised and pointed dorsum. It was redescribed by Young (1866) and discussed by Watson (1925), but the structure of its head remains essentially unknown; it may not belong in *Platysomus. P. superbus* is a geologically much older species known from several well perserved specimens. It has unusually high dorsal and anal fins. The head (Fig. 20A) and habitus were restored by Moy-Thomas & Dyne (1938: text-figs. 37, 39).

It is not known whether *P. forsteri, P. tenuistriatus,* and *P. rotundus* possessed pelvic fins. It is of interest that pelvic fins are present in *P. gibbosus, P. parvulus,* and *P. superbus,* whereas in *P. biarmicus* (Minikh, 1986: 14), *P. striatus* (Haubolt & Schaumberg, 1985: fig. 104), and the North American *Platysomus* they are absent (a single known exception is described below). Already Young (1866: 301-302) pointed out that "The genus *Platysomus,* as defined by Agassiz, . . . contains forms which cannot be included under the definition he has given," and included in his own generic diagnosis the character "No ventral fins"-only to go on redescribing *P. parvulus,* which does have pelvic (ventral) fins, and leaving it in *Platysomus.*

From the above account it is obvious that without a revision of all the noted species it cannot be decided what is and what is not a *Platysomus.* The only approach possible at the moment is to provisionally leave all the unrevised species in this collective genus and to describe a new species with the expectation that in the future it may have to be placed in a new genus and possibly a new family.

PLATYSOMUS SCHULTZEI n. sp.

Figs. 21-25

Material-Holotype NMMNH P-19195 (Figs. 22, 25). Paratypes CM 47832* (Fig. 21E), CM 47836* (Fig. 21D), CM 47840a + b (Fig. 21B); KUVP 86176 (Fig. 21C); NMMNH P-19114 (Fig. 21A), NMMNH P-19117a + b* (Figs. 21F, 23), NMMNH P-19194a + b (not figured). Referred specimens USNM 187134, 187145, 187148, 187150; CM 30727, 30728, 47831*, 47834*, 47835a + b*, 47837, 47838*, 47839*, 47841*; KUVP 86161, 86166, 86168*, 86171, 86172*, 86175*, 86182*; NMMNH P-19113, 19115, 19118*, 19145, 19194a +b (asterisk denotes presence of phyllodont tooth plates).

More than 100 specimens are in NMMNH, KUVP, CM, USNM, and several private collections. The 25 referred specimens listed above have been selected because they are better preserved. Specimens in private collections are not listed because they are unnumbered. It is worth mentioning, however, that the A. Lerner Collection, Albuquerque, contains five well preserved specimens, all of them with phyllodont tooth plates in-situ.

Type locality and horizon-Kinney Brick Company Quarry, NW1/4 SW1/4 SE1/4 sec. 18, T9N, R6E, Bernalillo County, central New Mexico. Units 2-4 of Lucas & Huber (1991; see also Kues & Lucas, this volume), Pine Shadow Member of Wild Cow Formation, Madera Group, Upper Pennsylvanian.

Etymology-Named in honor of Hans-Peter Schultze for his many contributions to the knowledge of Paleozoic fishes.

Diagnosis-Deep-bodied fish reaching 14-15 cm in standard length. Head and pectoral girdle amount to slightly less than one-third of standard length. Body about one-third deeper than long, with circular ventral margin and circular to more steeply arched dorsal margin; margins not angulated. Large lacuna between post-temporal, dermopterotic, operculum, and supracleithrum, left and right posttemporals entirely separated by ridge scales; premaxillary

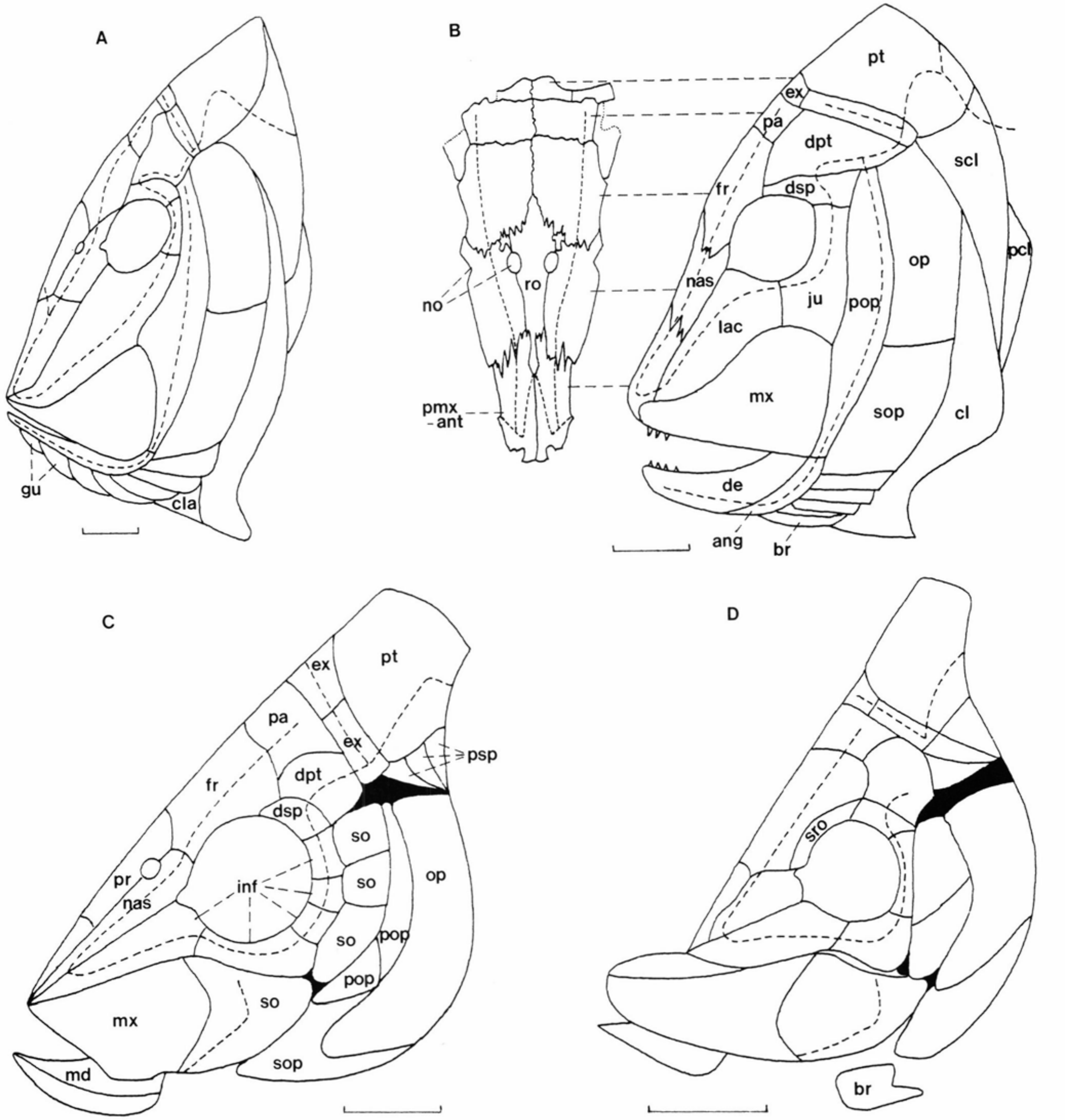

FIGURE 20—Restorations of the head of: **A,** *Platysomus superbus* (from Moy-Thomas & Dyne, 1938: fig. 37, pectoral girdle added from fig. 39). **B,** *Platysomus striatus* (lateral view from Haubold & Schaumberg, 1985: fig. 81/4; frontal view of skull roof from Schaumberg, 1976: fig. 2). **C,** *Platysomus gibbosus* (from Campbell & Le Duy Phuoc, 1983: text-fig. 17); anterior end of postrostral is tentative. **D,** *Ebenaqua ritchiei* (from Campbell & Le Duy Phuoc, 1983: text-fig. 4); inclusion of supraorbital and division into two preopercula are tentative. In A and B terminology follows Gardiner & Schaeffer (1989); in C and D Campbell & Le Duy Phuoc's (1983) determinations are left unchanged. Scale bars equal 1 cm. Abbreviations: **ang,** angular; **br,** branchiostegals; **cl,** cleithrum; **cla,** clavicle; **de,** dentary; **dpt,** dermopterotic; **dsp,** dermosphenotic; **ex,** extracapular; **fr,** frontal; **gu,** gular; **inf,** infraorbitals; **ju,** jugal; **lac,** lachrymal; **md,** mandible; **mx,** maxillary; **nas,** nasal; **no,** nostril; **op,** operculum; **pa,** parietal; **pop,** preoperculum; **pr,** postrostral; **pmx-ant,** premaxillary-antorbital; **psp,** postspiracular; **pt,** post-temporal; **ro,** rostral; **scl,** supracleithrum; **so,** suborbital (quadratojugal of this paper); **sop,** suboperculum; **sro,** supraorbital.

discrete from antorbital; quadratojugal between preoperculum and maxillary; extrascapulars and postspiraculars absent; jaws beak-like and edentulous, dentition consists of two phyllodont tooth plates supported by parasphenoid + vomer(s) and basibranchial + basihyal. Cleithrum and supracleithrum do not meet but are linked by postcleithrum; cleithrum carries large dermal clavicular plate. Flank with 25 vertical scale rows; scales up to six times deeper than wide, ornamented with 12-20 longitudinal cristae running parallel to scale margin; dorsal and ventral marginal scales modified into (1) unornamented parasagittal ridge scales that bear slender spines, and (2) sagittal ridge scales that are pebble-shaped and extend into short and blunt spines. Pectoral fins small. Pelvic fins absent. Dorsal and anal fins

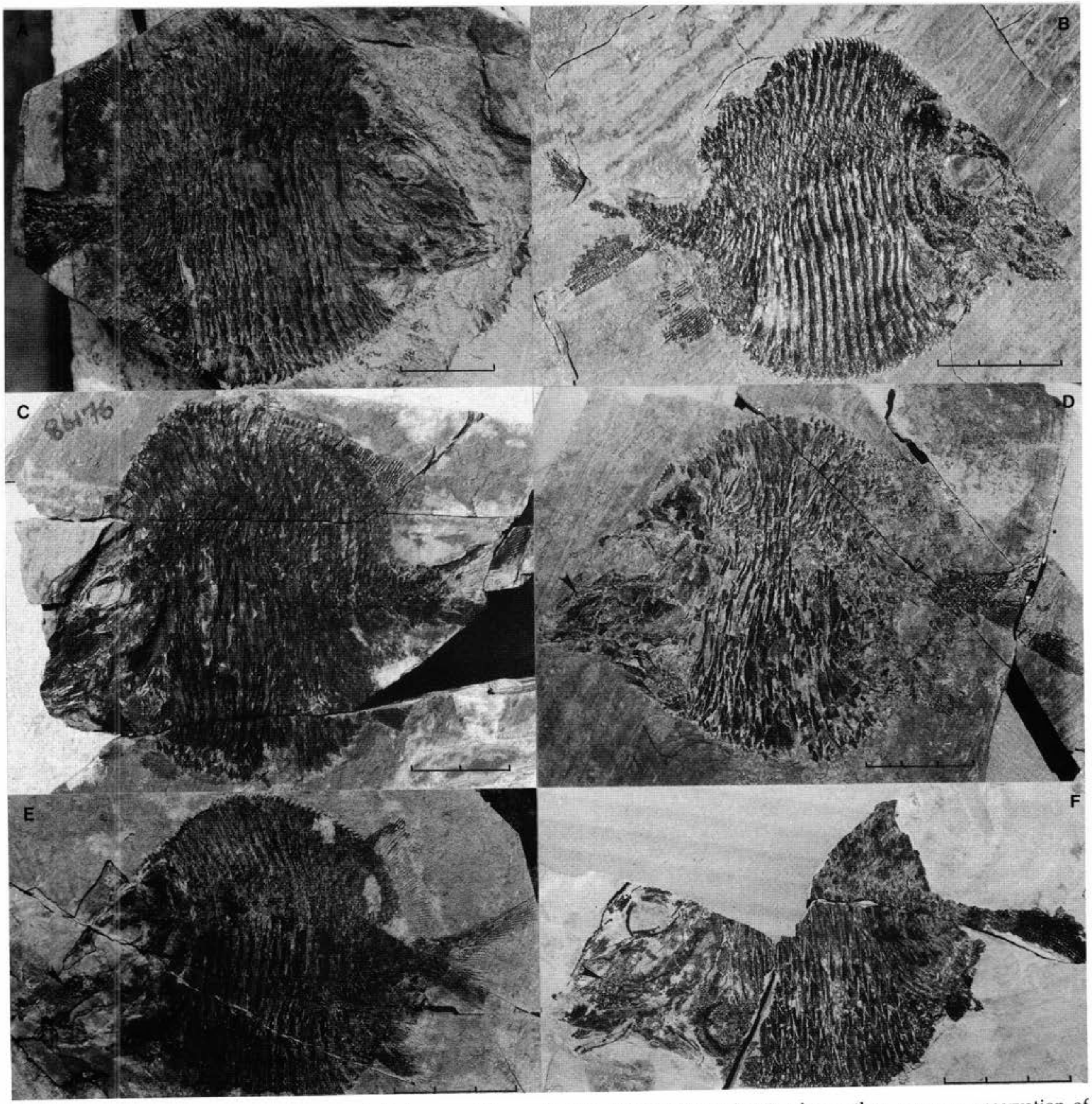

FIGURE 21—Six paratypes of *Platysomus schultzei* n. sp., Kinney Quarry, New Mexico, showing better than average preservation of *Platysomus* at the site. **A**, NMMNH P-19114; **B**, CM 47840a; **C**, KUVP 86176; **D**, CM 47836; **E**, CM 47832; **F**, NMMNH P-19117b. The specimen in C is antero-posteriorly compressed. The specimen in D is the largest known from Kinney, 14.2 cm in standard length. The specimen in F is stratigraphically the highest hitherto found at Kinney, from only two or three inches below contact with unit 4 of Lucas & Huber (1991), and has the best preserved phyllodont tooth plates (shown in more detail in Fig. 23). Arrows in D–F denote phyllodont tooth plates. Scales in centimeters.

reach to caudal peduncle; dorsal nearly one-third longer than anal. Caudal fin heterocercal but equilobate, with 17 rays in ventral lobe and 20 rays in dorsal lobe; rays bifurcate in both lobes; 31(+) long and narrow caudal fulcra. No fulcra in other fins. Rays of all fins segmented; segments shorter than wide to as long as wide.

Description—As all other bony fishes at the Kinney Quarry, the specimens of *Platysomus* are preserved as phosphatic compressions. Those recovered as counterparts are more difficult to interpret because they are split in the sagittal or parasagittal plane and therefore viewed from the inside. In the platysomid fishes the difficulty stemming from such preservation concerns primarily the skull, whose bones are not just exposed from the inside but often partially overlap and become dislocated. Compared to the skull, interpretation of a body preserved in counterparts presents little or no problem because platysomids had laterally much compressed bodies. Because of a blade-like body cross section, then post-mortem compression concerned a distance short enough to prevent any significant distortion, and in many specimens the left and right sides are superimposed exactly.

Most specimens are 10-12 cm in standard length. The largest specimen (CM 47836, Fig. 21D) is 14.2 cm in standard length, and the holotype (Fig. 22) is 12 cm in standard length. Specimens less than 10 cm long are very rare and the few known are poorly preserved.

The head and pectoral girdle amount to slightly less than one-third of the standard length, and the body (from the posterior edge of the cleithrum to the anterior end of the caudal peduncle) is approximately one-third deeper than long. The ventrum is perfectly circular, without any posteroventral angulation (Fig. 21B). The dorsum is either circular (Fig. 21D, E) or somewhat more steeply arched (Fig. 22), but again the curve is smooth, without any angulation. In a few instances the variation in arching of the dorsum is due to anteroposterior compression during burial (see Comments at the end of the paper), but in most specimens it appears to be the original, undistorted shape.

The dermal bones of the skull roof, cheek, and pectoral girdle are best preserved in the holotype, but several other specimens help to verify bone boundaries. Unfortunately, the sensory canals on the head are largely obscured and cannot be made out. The elements discussed below are shown in Figs. 20 and 22-24.

The post-temporal is the largest bone of the skull roof. It is obliquely quadrate with an extending ventral corner that meets the posterodorsal beak-like edge of the dermopterotic. The ornament consists of radiating cristae in the lower third, cristae broken into radiating rows of tubercles in the anterior to dorsal third, and undulating cristae roughly parallel to the margin in the posterior third. The anterior suture with the parietal is well developed, but anterolaterally there is a narrow lacuna and the posterolateral edge of the parietal and the dorsal edge of the dermopterotic are not in contact with the post-temporal. The posterolateral corner is attached to the supracleithrum, but the anterolateral edge is free since there is a large lacuna between the post-temporal, supracleithrum, operculum, and dermopterotic. The left and right post-temporals are entirely separated by parasagittal and sagittal ridge scales.

In all the other skull-roof bones (parietal, frontal, nasal, rostral, antorbital, premaxillary) the ornament consists of fine tuberdes. The dermosphenotic and dermopterotic, which are perhaps best regarded as transitional between the roof and cheek, are also tuberculated except for the posteroventral third of the dermosphenotic which bears oblique cristae running parallel to the bone margin. In contrast, the cheek bones are ornamented with fine cristae whose orientation helps to determine some difficult-to-recognize bone boundaries. The cristae break down into tubercles only in the mid-ventral portion of the maxilla, along the ventral margin of the suboperculum, and on the dentary. This would seem to indicate that the branchiostegals and the angular were also denticulated. However, no branchiostegals have been identified in the material, and none are tentatively included in Fig. 24C in order to show the clavicle. The presence of an angular is based on NMMNH P-19117a + b and CM 47840b which show the mandible to be as long as the maxilla, and on a well preserved suture at the hind end of the dentary in the holotype.

The anterior suture of the parietal is obliterated, but the anterior extent can be verified from the overlapping edge of the left parietal. The frontal forms the dorsal margin of the orbit and reaches down to the posterior edge of the anterior nostril. Campbell & Le Duy Phuoc (1983: 39) remarked that "it is not common for the frontal to be in contact with the orbit in the deep-bodied palaeoniscoids" (but see Fig. 20A-C) and tentatively included a supraorbital between the frontal and the orbit in their restoration of *Ebenaqua*. However, there can be no doubt that the frontal is in contact with the orbit in *P. schultzei*.

The rostral and nasal enclose the anterior nostril which is located on the posterior end of their common suture. The posterior margin of the nasal forms the anterodorsal and anterior margins of the orbit whose anterior embayment houses the posterior nostril. The antorbital is the second largest bone of the skull roof. Its posterior margin reaches all the way down to the maxilla, but the shape of the suture cannot be precisely determined because of a significant amount of uplifting and distortion of the adjacent lachrymal. Therefore the antorbital/lachrymal suture is drawn as a straight line (Fig. 24C), which probably is not too far from the truth. The anterior margin of the antorbital has a well preserved, strong suture. Below this suture is a small, wedge-shaped bone that rests on the anterodorsal margin of the maxilla. It bears an ornament of fine tubercles identical to those on the antorbital and clearly is accessoric to it; hence, it is interpreted as a discrete premaxillary. The only other alternative would be regarding the unpaired bone between the nasals as the postrostral and the paired bones anterior to it as the rostrals or rostro-antorbitals. However, the rostral is an unpaired bone that is subdivided into the rostral and postrostral in "some genera of redfieldiids and possibly some perleidids" (Gardiner & Schaeffer, 1989: 146), to which may be added the haplolepids (in *Pyritocephalus* there is a large postrostral, a small rostral, and premaxillaries; Štamberg, 1978: fig. 2; Huber, this volume: fig. 2). Gardiner & Schaeffer (1989: fig. 19E) considered the median bone between the nasals of *Platysomus superbus* to be the rostral and their interpretation is followed here (Fig. 20A, B). In *Platysomus* the paired bones anteriorly of the rostral and nasals thus are the premaxillary-antorbitals (Fig. 20B), which in *P. schultzei* are divided into discrete antorbitals and premaxillaries.

The ventral edges of the dermosphenotic and dermopterotic have been uplifted by a ceratobranchial that is exposed at the anterior margin of the operculum, and the posterior edge of the dermopterotic has been further uplifted by two additional branchial elements, cerato- or epibranchials, whose ends protrude through the large posterior lacuna (Figs. 22, 24A, B). Restored into its original position, the posterodorsal beak-like edge of the dermopterotic apparently was in contact with the extending posteroventral edge of the post-temporal. Due to the shapes of the margins involved, the contact must have been at least a minor overlap.

The jugal is a clearly defined thick and narrow bone that forms the posteroventral margin of the orbit. The lachrymal is a much broader bone that is uplifted and dislocated along the interrupted line in Fig. 24B (this is well apparent also in Fig. 22), causing the impression of two discrete elements. However, the line has the appearance of a fracture rather than a suture, and only the jugal and lachrymal are thus restored in Fig. 24C.

The operculum is approximately three times deeper than wide and covers two-thirds of the area between the pectoral girdle and the hind edge of the orbit. Its dorsal margin is obliquely quadrate and posteriorly is in contact with three bones of the dermal girdle (cleithrum, postcleithrum, supracleithrum). Ventrally it overlaps the suboperculum which is an even wider bone that fills the entire area between the cleithrum and the hind end of the jaws. Little can be said about the preoperculum because it is overlain by the displaced ceratobranchial and only its anterior portion is visible. However, enough is exposed to ascertain that only one preoperculum is present. The space available for the preoperculum is quite narrow; its ventral part must have been more than twice as wide as the dorsal part.

Between the preoperculum and the maxilla lies a bone that Campbell & Le Duy Phuoc (1983: 41) interpreted as a suborbital in *P. gibbosus* (Fig. 20C) and *Ebenaqua* (Fig. 20D). Its dorsal surface is continuous with that of the maxilla and the suture with the lachrymal and the preoperculum is well preserved except in the posteroventral corner which is covered by the displaced ceratobranchial. Since there is a minor notch in the anteroventral edge of the suboperculum, the posteroventral corner of this bone is restored somewhat extended to flexibly articulate with this notch as in *Ebenaqua* (Campbell & Le Duy Phuoc, 1983: text-fig. 5). The postero-

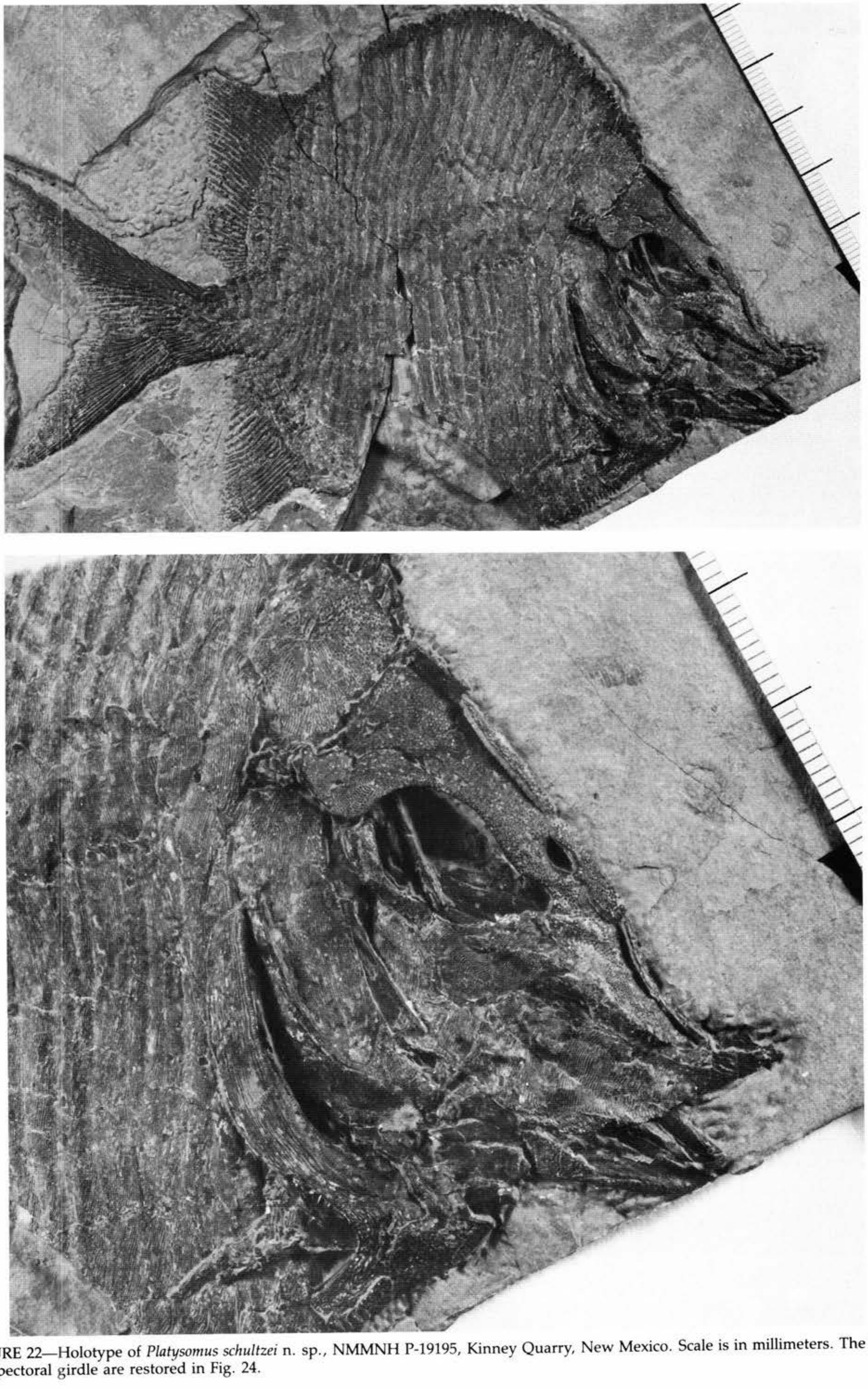

FIGURE 22—Holotype of *Platysomus schultzei* n. sp., NMMNH P-19195, Kinney Quarry, New Mexico. Scale is in millimeters. The head and pectoral girdle are restored in Fig. 24.

dorsal corner is also extended into a short process that appears to fit into a notch in the anteroventral edge of the preoperculum, but the preservation is not good enough to recognize whether this is a real articulation or an overlap. The anterior suture with the maxillary appears to be of an overlapping type as in *P. gibbosus* (Campbell & Le Duy Phuoc, 1983: 66) and the boundary between the two bones is best determined using ornament. On the maxilla the dorsal ends of the cristae curve anteriorly, whereas on the bone in question they curve posteriorly; the point of divergence coincides with the maxillary suture. Although the ornament is well preserved, no sensory canal can be detected. Since in all specimens the sensory canals are largely obscured, this may not be the original condition. If in *P. schultzei* this bone really is anamestic, then it differs from those in *a P. gibbosus, Ebenaqua,* and *Bobasatrania* which carry sensory canals. The lack of a sensory canal would weaken the interpretation of the bone as a suborbital because sensory canals normally do not cross suborbitals; this interpretation is further weakened by the bone's position and by its close suturing with the maxilla. Campbell & Le Duy Phuoc (1983: 41) considered two other homologies, supramaxillary and quadratojugal, and rejected the former for reasons with which I concur. That leaves the quadratojugal, which appears to be the least objectionable interpretation. The bone between the preoperculum and the maxillary of *P. schultzei* thus is interpreted as a quadratojugal that has become exposed and enlarged due to anterior migration of the jaw articulation, and that may not have (yet?) incorporated a sensory canal from the preoperculum. The latter part of the argument would seem to be supported by the relatively smaller size of this bone in *P. schultzei* (compare Fig. 24C with Fig. 20C, D).

The jaws are anteriorly incomplete in the holotype, but can be restored from NMMNH P-19117a + b (Fig. 23). The length and overall shape of the mandible are also apparent from CM 47840b (not illustrated, but its counterpart is Fig. 21B). The 19117a + b specimen shows the anterior ends of the maxilla and mandible to be rounded, slightly knoblike, and deflected medially to meet their antimeres. No divisions are apparent in the mandibles of these specimens, but in the holotype there is a suture at the end of the anterior piece, indicating a division into a dentary and a shorter angular.

The jaws are edentulous and the only dentition present consists of two median phyllodont tooth plates. They are preserved in about 50% of the specimens studied, but very few specimens show which element(s) supported the upper plate and none reveal which element(s) supported the lower plate. The holotype shows only seven marginal teeth of the upper plate under the uplifted edge of the rostral, but CM 47836 (Fig. 21D) and CM 47838 (Fig. 27A) show the upper tooth plate overhanging the anterior end of the parasphenoid, which implies that the supporting elements were both the parasphenoid and the vomers (or a median vomer as in *Bobasatrania).* Nielsen (1952: 199-202, fig. 2) described phyllodont tooth plates in *Bobasatrania groenlandica* and called the upper tooth plate vomerine, but considering how large the tooth plates are in *P. schultzei,* the vomers would be too short to form the sole support of the plate. The support of the lower tooth plate is more equivocal. Nielsen (1952) stated that in *B. groenlandica it* is supported by the massive unpaired basibranchial, and Nelson (1969: 495) wrote that the lower plate in *Bobasatrania* may be "a basihyal plate or basibranchial plate or one representing both." Unfortunately, the material of *P. schultzei* does not help to decide on the supporting element, but since the tooth plates are relatively larger than in *Bobasatrania*, the position is taken that the lower plate was supported by both the basibranchial and basihyal.

In *P. schultzei* the tooth plates amount to approximately one-third of the skull length (measured from the tip of the premaxillary to the anterior margin of the cleithrum). The upper plate has a concave occlusal surface, is narrower than the lower plate, and its narrower, more pointed end faces posteriorly. The lower plate has a convex occlusal surface, is about three times longer than wide, and its posterior end is transversely concave. The morphology and histology of late Paleozoic phyllodont tooth plates were described in detail by Johnson & Zidek (1981) and do not need to be repeated here. However, Johnson & Zidek could examine only isolated tooth plates and, therefore, had to make assumptions which can now be confirmed.

NMMNH P-19117a + b and CM 47840a + b preserve the

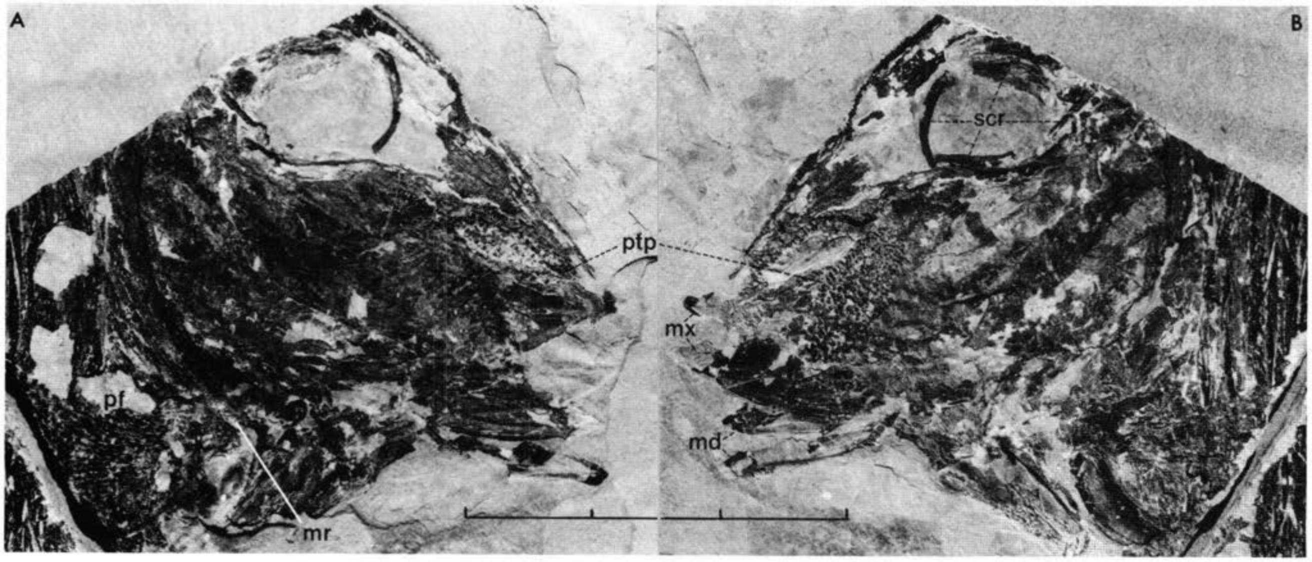

FIGURE 23—*Platysomus schultzei* n. sp., paratype NMMNH P-19117a + b (counterparts, a in A, b in B), Kinney Quarry, New Mexico, with well preserved upper **(A)** and lower **(B)** phyllodont tooth plates **(ptp)**, scleral ring **(scr)**, mandible **(md)** and pectoral fin **(pf)** whose articulation on margo radialis **(mr)** of the coracoid is visible in A. In B the photo gives the impression that another bone covers the central part of the maxilla, but this is only an artifact of preservation accentuated by lighting; microscopic examination shows this to be part of the maxilla which is as long as the mandible. Scale in centimeters.

scleral ring which consists of four thin and narrow bones with the ventral component longer than the others (Fig. 23). A cresent-shaped bone with an exceedingly thin margin is present below the dorsal component in both specimens, indicating that the eye capsule was not entirely cartilaginous.

The dermal pectoral girdle (Figs. 22, 24) consists of the cleithrum, clavicular plate, supracleithrum, and postcleithrum. The cleithrum is a thick bone with a denticulated anterolateral ridge that extends all the way up to the pointed dorsal end, a flattened body ornamented with fine longitudinal cristae, and a ventral pectoral embayment that is covered with tubercles and short, undulating cristae. Anteroventrolaterally the cleithrum carries a large, tuberculated clavicular plate. Anterior of the cleithrum the clavicle loses its ornamented dermal cover and turns medially to meet and overlap its antimere. The supracleithrum is a scale-shaped, flat bone whose concave dorsal margin is sutured to the oblique posterolateral margin of the posttemporal. The ventral margin of the supracleithrum is slanted and straight, and meets the equally slanted and straight dorsal margin of the postcleithrum. The cleithrum and supracleithrum thus do not meet; they are connected via the postcleithrum, which is a scythe-shaped, flat bone at the posterodorsal margin of the cleithrum. Both the postcleithrum and supracleithrum are ornamented with longitudinal cristae which become undulate only near the dorsal margin of the supracleithrum.

In Fig. 22 the posteroventrolateral edge of the cleithrum appears to be ornamented with four large denticles and a small tuberculated plate. These elements have been excluded from Fig. 24 because they clearly are out of place. The denticles actually are sagittal ridge scales (see below), and the small tuberculated plate is a dermal-bone fragment resting on the ornament of the cleithrum.

The coracoid part of the endoskeletal pectoral girdle is exposed in the holotype (Figs. 22, 24A) and in the paratype NMMNH P-19117a + b (Fig. 23), and shows the glenoid fossa with margo radialis and incomplete radials. In the holotype the pectoral fin rays are compacted into a rod-like mass. They are better preserved in the NMMNH P-19117a counterpart (Fig. 23A), where there are between 20 and 30 finely segmented rays up to 15 mm long. An incomplete pectoral fin is preserved also in CM 47836 (Fig. 21D), but does not add to the information provided by NMMNH P-19117. There is no evidence of fulcra in the pectoral fin of either specimen.

The dorsal fin reaches all the way down to the caudal peduncle, where its rays are the shortest and the most delicate. The fin rays gradually increase in length up the posterodorsal edge of the body. There are 43 dorsal fin rays in the holotype and the fin looks complete, but NMMNH P-19194a has 58 dorsal fin rays. Similarly, the anal fin reaches all the way up to the caudal peduncle and the fin rays gradually increase in length down the posteroventral edge of the body. There are 26 (estimated) anal fin rays in the holotype and, again, the fin looks complete, but other specimens (e.g. paratypes CM 47840a, NMMNH P-19117a, NMMNH P-19194a) have 34 anal fin rays. Since in the holotype there are ridge scales immediately above the uppermost dorsal fin rays (Fig. 22), the fin could not have been any longer. A likely explanation of the discrepancy in dorsal and anal fin-ray counts is sexual dimorphism, in which case the holotype probably is a female. In both instances (D43, A26 and D58, A34) the dorsal fin is nearly one-third longer than the anal fin. The dorsal and anal fin-ray segments are shorter than wide to as long as wide; longer than wide segments have not been observed in either the holotype or any other specimen. Baseosts are visible in CM 47832 (dorsal), 47834 (dorsal, anal), 47835a (dorsal), 47838 (dorsal, anal), and NMMNH P-19117b (anal), but only the first and last specimens have the fin rays preserved and show that each baseost supported two rays. Fulcra are absent in both dorsal and anal fins.

The caudal fin is heterocercal but equilobate and the depth of its cleft amounts to slightly less than half the fin length. It is best preserved in the holotype (Fig. 25) on which the following account is based. Examination of specimens in which the tail is sufficiently well preserved (CM 47832, CM 47840a, NMMNH P-19115, NMMNH P-19117a) indicates that variation in number of fin rays and in the extent of

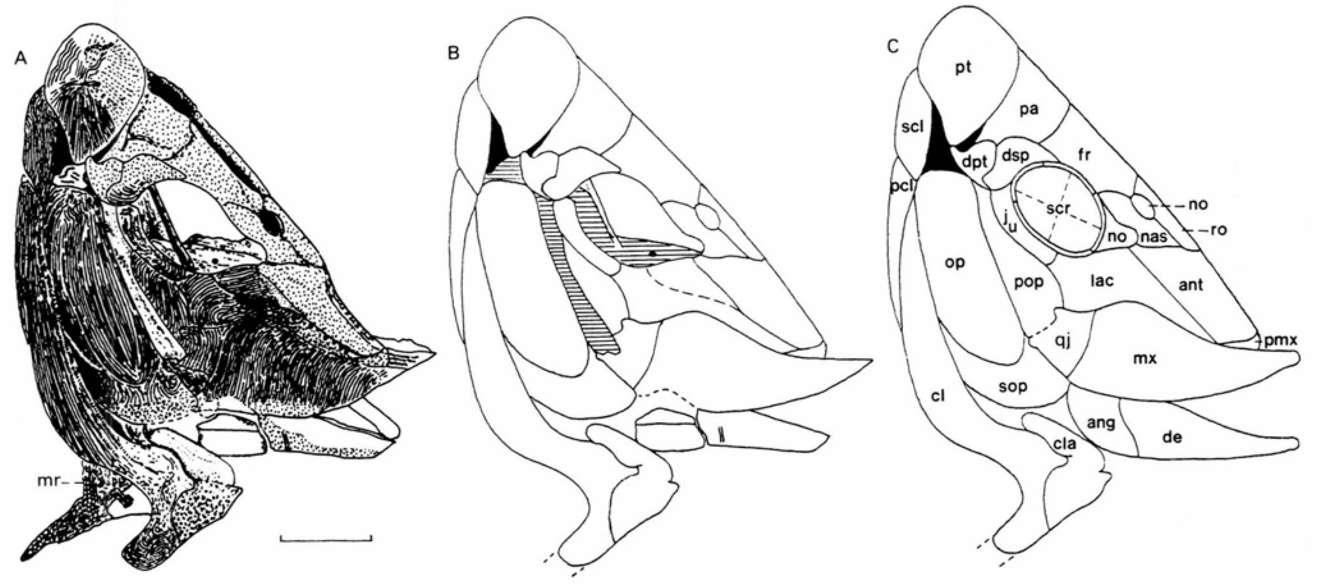

FIGURE 24—*Platysomus schultzei* n. sp. **A,** Ornament on the dermal bones of the skull as seen in the holotype. **B,** Contours of bones as preserved in the holotype; ceratobranchial and parasphenoid (in the orbit) hachured; **C,** Restoration of the skull and pectoral girdle; based on the holotype and paratypes CM 47840b (scleral ring, mandible) and NMMNH P-19117 (scleral ring, maxilla, mandible); lacunae in black. Scale bar equals 1 cm. Abbreviations: **ang,** angular; **ant,** antorbital; **cl,** cleithrum; **cla,** clavicle; **de,** dentary; **dpt,** dermopterotic; **dsp,** dermosphenotic; **fr,** frontal; **ju,** jugal; **lac,** lachrymal; **mr,** margo radialis; **mx,** maxillary; **nas,** nasal; **no,** nostril; **op,** operculum; **pa,** parietal; **pcl,** postcleithrum; **pmx,** premaxillary; **pop,** preoperculum; **pt,** post-temporal; **qj,** quadratojugal; **ro,** rostral; **scl,** supracleithrum; **scr,** scleral ring; **sop,** suboperculum.

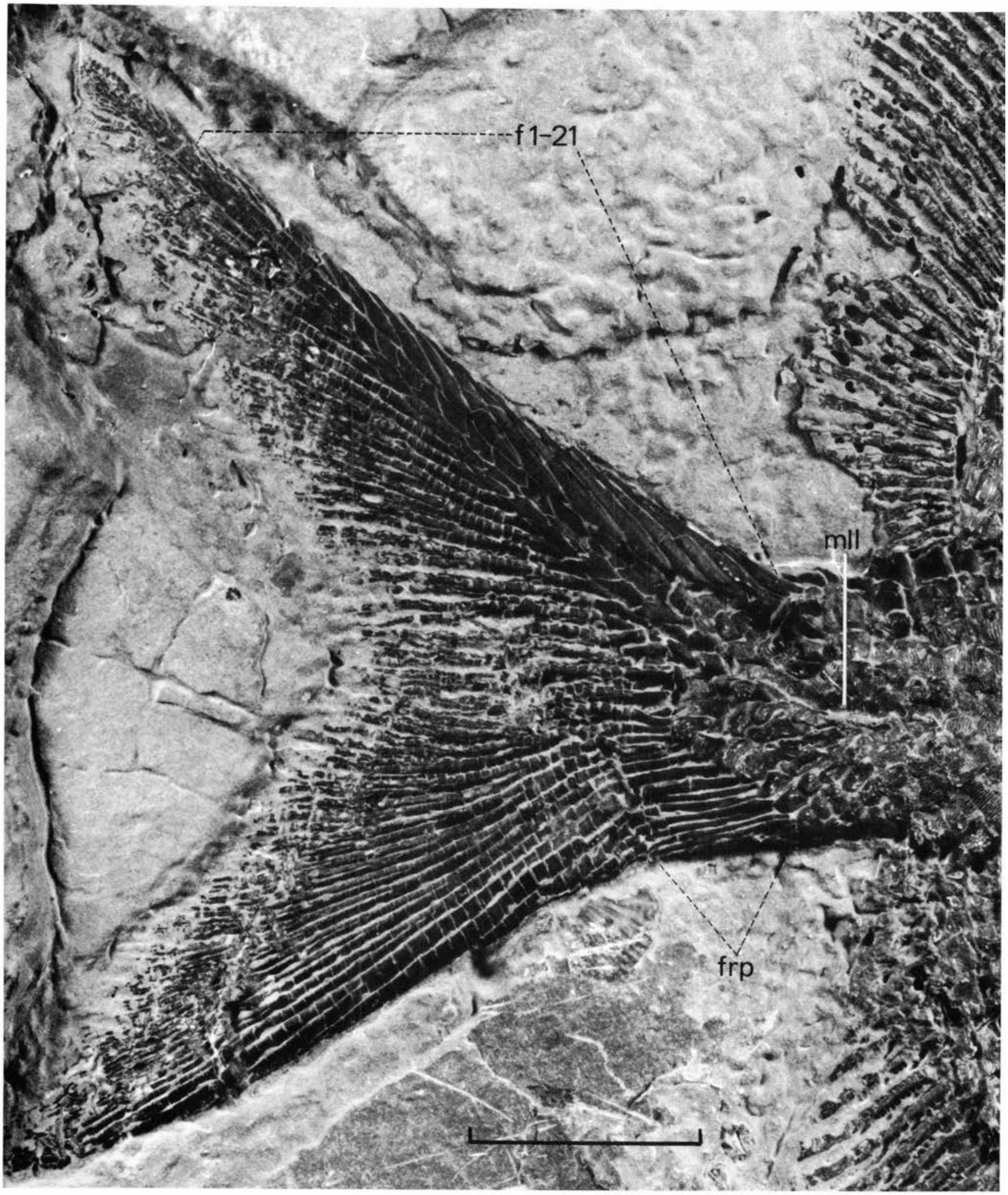

FIGURE 25—*Platysomus schultzei* n. sp., caudal fin and peduncle of the holotype. Scale bar equals 1 cm. Abbreviations: **f1–21,** fulcral scales 1–21; **frp,** unsegmented proximal parts of fin rays; **mll,** main lateral line.

scale cover is quite small (± 2 rays). There are 37 fin rays, 17 in the ventral lobe and 20 in the dorsal lobe. The fin rays gradually diminish in length toward the center of the fin. The reduction in length concerns the unsegmented proximal parts of the rays as well. These parts can be seen in their entirety in the ventral lobe and in the lower part of the dorsal lobe; higher up they are covered by scales. The unsegmented parts are not as closely packed as the much longer and somewhat thicker segmented parts, which form a solid veil through much of the fin. Only in the uppermost part of the ventral lobe, the lower one-fourth of the doral lobe, and along the fin periphery is there any free space between the rays. The fin-ray segments are shorter than wide to as long as wide; longer than wide segments have not been observed in either the holotype or any other specímen. The rays of the dorsal lobe are shorter than those of the ventral lobe. Bifurcation occurs in both lobes, but the shorter dorsal rays bifurcate only once, approximately at mid-length of the segmented part, whereas some of the longer ventral rays bifurcate twice—at about one-third of the segmented length and again at about two-thirds of the segmented length. The lowermost ray of the ventral lobe is exceptional in that it is much shorter than the successive rays, yet its unsegmented part is as long as those of the successive rays and nearly equals the length of the segmented part. Counting from the lower margin of the ventral lobe, the third and fourth rays are the longest in the entire fin.

The squamation of the dorsal lobe (Fig. 25) consists of three rows of flat, non-imbricating scales that cover only the uppermost part (only about 20%) of the lobe, and imbricating fulcra that form the ridge of the tail. The fulcra are very long and narrow (spine-like) scales arranged in a single left and right series. Twenty-one fulcra are present between the caudal peduncle and the distal part of the dorsal lobe, and a solitary one can be seen near the tip of the lobe. Since the distal fulcra are very small, at least 10 of them must have covered the distal end of the lobe. The total number thus can be estimated at 31(+). The flat, non-imbricating scales are essentially lozenge-shaped, but only two opposite edges are straight whereas the other two opposite edges are oblique. Only the upper row reaches near the tip of the lobe, the middle and lower rows end at about two-thirds the distance. No ornament is present on any of the caudal scales.

The scales of the caudal peduncle (Fig. 25) bear the same ornament of cristae as those on the flank, but are much shorter. Posteriorly and posteroventrally they diminish in size and become irregularly pebble-shaped and pitted. The main lateral sensory line runs in the center of the peduncle, turns up into the dorsal lobe of the tail, and ends abruptly beneath the fourth fulcral scale. This is the only discernible part of the lateral line; it is not preserved on the flank of any available specimen.

Since the lateral line is not preserved, vertical scale rows have to be counted along the arching vertebral column whose course is apparent as an impression in all specimens. The counts are not precise because of scale disruption, but in all specimens they vary between 23 and 26, and the most frequent count is 25 vertical scale rows between the posttemporal and the anterior end of the caudal peduncle. The scale rows are truly vertical only posterodorsally, whereas posteroventrally they bend backward and in the anterior two-thirds of the flank they are concave anteriorly, i.e. inclined forward both dorsally and ventrally of the vertebral column. This pattern is best seen in the holotype (Fig. 22) and the paratype CM 47840a + b (Fig. 21B). Counting the number of scales in a row is even more difficult, but an example from the mid-flank gives an idea about the scale proportions. There are three unmodified scales above the vertebral column and five unmodified scales below it. Starting from the vertebral column, the dorsal scales have depth to width ratios of 6:1, 4:1, and 3:1, whereas in the ventral scales the ratios are 5:1, 5:1, 4:1, 4:1, and 3:1. Each scale has a strong anterior ridge that dorsally and ventrally extends into spines for peg-and-socket articulation with the adjoining scales. The ornament consists of 12-20 longitudinal cristae that may slightly undulate on some of the shorter scales, but at the most part are straight and run parallel to the scale margin. The cristae in no way differ from those on the pectoral girdle and on the cheek bones.

The dorsal and ventral marginal scales are modified into (1) unornamented parasagittal ridge scales that dorsally/ventrally terminate in slender and often sinusoidally curved spines (modified ends of anterior ridges), and (2) sagittal ridge scales that are pebble-shaped and dorsally/ventrally extend into short and blunt spines. There are two parasagittal ridge scales above/below each scale row, whereas the sagittal ridge scales match the scale rows. This results in an interlocking arrangement that resembles a double-saw blade and strengthens the flank margins.

Discussion—P. *schultzei* differs from other platysomids in a number of features, but comparing it with all other species would be lengthy and, considering how poorly most of them are known, without much merit. Therefore, the following comparison is restricted to species that lack pelvic fins *(P. circularis, P. striatus, "Schaefferichthys leudersensis")* and two other species in which the structure of the head is fairly well known *(P. gibbosus, P. superbus).*

P. circularis (Fig. 19A) is a much smaller species that also has a quadratojugal behind the maxilla. However, it lacks a postcleithrum, there are only 20-22 vertical scale rows on the flank, and the body is dorsally and posteroventrally angulated. The jaws are less protruding than in *P. schultzei,* but their shape is similar and it is likely that they were edentulous.

Similarly, *"S. leudersensis"* has a quadratojugal behind the maxilla (Fig. 18A; Dalquest, 1966: text-fig. 1, unlabeled), lacks a postcleithrum, and the body is posterodorsally and posteroventrally angulated (Fig. 18B; Dalquest, 1966: text-fig. 1). There are 32 vertical scale rows on the flank. The jaws are edentulous and the dentition consists of phyllodont tooth plates. The Oklahoma specimens shown in Fig. 17, *"S. leudersensis"* (Fig. 18), and *P. schultzei* are about the same size. The former two may be conspecific and closely related to *P. schultzei,* but the head and fins of *"S. leudersensis"* are so poorly preserved that this cannot be demonstrated.

P. striatus has a postcleithrum and a round ventrum, but the body is posterodorsally angulated and relatively low, scales (31 vertical rows) are relatively short (max. depth to width ratio of 2.5:1) and modified marginal scales are absent, and the skull roof and cheek (Fig. 20B) are clearly different from *P. schultzei* (extrascapulars present, dermopterotic much larger than dermosphenotic, suboperculum nearly as deep as operculum, maxilla deep and tooth-bearing, and no quadratojugal).

P. superbus has a postcleithrum and the body depth to length ratio is similar to *P. schultzei* (3:2), but the body is dorsally and posteroventrally angulated, flank scales (38 vertical rows) are as short as in *P. striatus,* and modified marginal scales appear to be lacking. The dorsal and anal fins are exceptionally large and the pelvic fins are well developed. All fins bear fulcra. The dermal skull and pectoral girdle (Fig. 20A) are so similar to *P. striatus* that explaining how they differ from *P. schultzei* would be a repeat of the previous paragraph.

P. gibbosus (Fig. 20C) was redescribed by Campbell & Le Duy Phuoc (1983) who found it to be the most primitive bobasatraniid known. It shares with *P. schultzei* the presence of a quadratojugal behind the maxilla, but in most other respects it is a quite different fish. The body shape, the flank squamation, and the fins are virtually identical with *P. striatus* except that the pelvic fins are present and the pectoral girdle lacks a postcleithrum. Extrascapulars and postspiraculars (three) are present, the infraorbital and suborbital series contain five and three elements, respectively, and there are two preopercula and at least six branchiostegals. Although edentulous as in *P. schultzei,* the maxilla has a very different shape.

Campbell & Le Duy Phuoc (1983) listed the following features as distinctive of the order Bobasatraniiformes: (1) postspiraculars present; (2) two preopercula; (3) a large suborbital (quadratojugal of this paper) between the maxilla and preopercula; (4) maxilla large, edentulous, and placed well forward; (5) mandible slung well forward; (6) branchiostegals reduced or absent; (7) suspensorium vertical; (8) clavicle reduced or absent; (9) body deep; (10) flank scales elongated and vertically striated (cristated); (11) scale rows swing forward to meet the posterodorsal and anteroventral margins obliquely; (12) a row of spines (modified scales) on the anterodorsal and anteroventral body margins; (13) pelvic fin small or absent; (14) dorsal and anal fins extend to the caudal peduncle; and (15) caudal fin heterocercal but equilobate. Of these characters fully two-thirds (3, 4, 6, 915) are present in *P. schultzei;* however, characters 9-11 and 13-15 all are very weak and cannot be used to differentiate between the deep-bodied Palaeonisciformes (Amphicentridae and "lower platysomids"—P. *superbus, P. striatus)* and the Bobasatraniiformes ("higher platysomids," Bobasatranlidae, *Ebenaqua)* because they are present in both. They are related to deepening of the body in lower actinopterygians generally, regardless of lineage, and as such are of no value in assessing relationships. This leaves characters 1-8 and 12, to which may be added three new ones—(I) phyllodont tooth plates, (II) specialized postcleithrum, and (III) parasagittal caudal fulcra. Characters 2-5, 8, and 12 are absent in the deep-bodied Palaeonisciformes and can be safely considered advanced without further comment except noting that the shortening of the jaws (4, 5) is not nearly as profound as in *P. gibbosus* and *Ebenaqua.* Characters 1, 6, 7, and I-III require elaboration.

(1) Postspiraculars are present in *P. gibbosus* and *Ebenaqua* (Fig. 20C, D) and are lacking in *P. superbus* and *P. striatus* (Fig. 20A, B), indicating that their presence is an advanced character. However, a similarly situated bone is present in *Moythomasia* (Jessen, 1968) and *Pteronisculus* (Nielsen, 1952: 203), and there is some disagreement whether such bones in *Bobasatrania mahavavica* are postspiraculars (Lehman, 1956: 20-21) or postorbitals (White, 1932). Campbell & Le Duy Phuoc (1983: 40-41) stated that "These examples . . . suggest either that in primitive palaeoniscoids bones were developed in the angle between the shoulder girdle, the cranial roof, and the opercular, but that they were later lost in many genera; or alternatively that bones developed in this position to fill space as required," and added that "The causal mechanisms for the independent development of these bones may be different in each case." It thus seems that only the presence of *multiple* postspiraculars should be regarded as an advanced feature and that the presence of a lacuna between the post-temporal and the operculum may be viewed as the initial stage of development of this advanced condition.

(6) Campbell & Le Duy Phuoc (1983) found five jointed branchiostegals and at least one free branchiostegal in *P. gibbosus* and characterized its branchiostegal arrangement as complex. *P. gibbosus* thus is much like *P. superbus* and *P. striatus* in this regard. In *Ebenaqua,* on the other hand, the branchiostegals are reduced to a single pair of broad plates that probably functioned as second subopercula (Campbell & Le Duy Phuoc, 1983: 45, text-figs. 6, 7). Too little is known about the bobasatraniiform branchiostegals to decide whether such extreme reduction and modification is the norm for the more advanced members of the order or rather whether it is a specialization unique to *Ebenaqua.* I suspect it to be the latter and assume that a less profound reduction and modification is to be expected in other bobasatraniiforms.

(7) The suspensorium angle is a character hard and subjective to use, and it certainly should not be a criterion for deciding what is an advanced palaeonisciform or a primitive bobasatraniiform. As pointed out by Gardiner & Schaeffer (1989: 145-146), a truly vertical suspensorium is a neopterygian feature because only in neopterygians is the hyomandibular facet of the neurocranium horizontal. In the lower actinopterygians this facet is always slanted and, although the suspensorium may approach 90° (most nearly perhaps in the Haplolepiformes), it is never quite vertical and often exhibits a variable inclination within a family. In the Amphicentridae, for instance, it is nearly vertical (based on the orientation of the preoperculum) in *A. granulosum* (Fig. 14) and quite oblique in *A. orbiculare* (Fig. 13) and *A. jurgenai* (Fig. 16). And in the platysomid-bobasatraniiform lineage it is steeper in *P. superbus* and *P. striatus* (Fig. 20A, B) than in *P. schultzei* (Fig. 24C), although the latter is in all other respects more advanced. In this light the suspensorium angle becomes essentially meaningless and is assigned no weight in the final assessment of *P. schultzei.*

(I) The dentition of *Bobasatrania groenlandica* consists of phyllodont tooth plates supported by the vomer (unpaired in that genus) and/or parasphenoid and the basihyal and/ or basibranchial. Among the "lower platysomids," on the other hand, *P. striatus* has conical teeth lining the margins of the maxilla and dentary; the dentition of *P. superbus* is not known. Neither *P. gibbosus* nor *Ebenaqua* has the dentition preserved, but since in both the jaws are edentulous it is reasonable to assume that it consisted of tooth plates supported by similar palatal and visceral elements. Although the evidence is based on only three species, there nevertheless appears to be little doubt that in the platysomid-bobasatraniid lineage the presence of plates with phyllodont tooth replacement is an advanced feature.

(II) A single postcleithrum is a primitive actinopterygian condition (Gottfried, 1989), but it should be added that the primitive postcleithrum is small, amounts to little more than a modified scale, and does not contribute to the structural integrity of the pectoral girdle. This is the situation in *P. superbus* and *P. striatus,* whose postcleithra are unimportant accessoric bones. *P. gibbosus* and *Ebenaqua* lack a postcleithrum (Campbell & Le Duy Phuoc, 1983: 46, 68), but in *Bobasatrania groenlandica* it is a large bone whose contact with the supracleithrum is much more extensive than that of the cleithrum and which is very obviously important to the integrity of the girdle. If narrowing of the cleithrum-supracleithrum contact was a trend, then it was brought to an extreme in *P. schultzei* where the two are not in contact and the postcleithrum assumes the function of a link between them. Thus, although single, the postcleithra of *B. groenlandica* and *P. schultzei* are highly derived structures.

(III) In *P. schultzei* and the Platysomidae indet. specimen described below the caudal fulcra are arranged in parasagittal left and right rows that meet sagittally to form the ridge of the dorsal lobe. To my knowledge, this arrangement has not been explicitly recorded in the literature, but some illustrations of *Bobasatrania* seem to indicate that it might be present in that genus as well. This is clearly a derived feature not known to occur in the Palaeonisciformes, in which the caudal fulcra are arranged in a single, sagittal row.

The surfacing and enlargement of the quadratojugal (3) has to do with shortening of the jaws (4, 5), and these characters thus can as well be thought of as one (3-6 = 3). With character 7 (suspensorium angle) dismissed as essentially meaningless, nine characters that are deemed meritorious remain to assess the relationship of *P. schultzei.* Within this set *P. schultzei* is advanced on five counts (3, 12, I-III), in the initial stage of development of advanced features on two counts (1, 6), and primitive on two counts (2, 8). The assessment of (1) is based on the presence of a large lacuna between the post-temporal, operculum, supracleithrum, and dermopterotic, and that of (8) on the limited space available below the ventral margin of the suboperculum, which could have accommodated only three to four branchiostegals.

P. schultzei appears to be more derived than *Bobasatrania* in the structure of its dermal pectoral girdle and shares with *Bobasatrania* the presence of phyllodont tooth plates which are supported by the same skeletal elements and are morphologically as well as histologically strikingly similar. In comparison with *P. gibbosus,* which possesses three postspiraculars, two preopercula, and a larger, canal-bearing quadratojugal, *P. schultzei* clearly is more primitive. Yet, the presence of five advanced characters and the evidence of inception of two others (1, 6) indicate that it is not an advanced palaeonisciform or a transitional form, but the oldest and most primitive member of the Bobasatraniiformes discovered to date.

?BOBASATRANIIFORMES

PLATYSOMIDAE INDET.

Fig. 26

CM 47833 is a headless specimen, but its standard length can be confidently estimated at no less than 16 cm; it is thus the largest platysomid hitherto found at the Kinney Quarry. This specimen cannot be assigned to *P. schultzei* for the following reasons:

(a) It has pelvic fins. Twelve fin rays are preserved and above them lies a 30(+) mm long basal plate that reaches all the way back to the anal fin. The fin-ray segments are squarish, as wide as long, and the longest, anterior fin rays measure 21 mm. Small fulcra are present on the anterior margin of the fin, but are exposed in an on-edge view and their morphology cannot be described.

(b) The caudal fin rays, the extent of the caudal squamation, and the morphology of the fulcra all differ from *P. schultzei.* There are 20 fin rays in the ventral lobe and at least 30 in the dorsal lobe, i.e. a total of 50(+) as compared to only 37 in *P. schultzei.* The fin rays of the ventral lobe do not branch distally and the fin-ray segments are longer than wide (in *P. schultzei* distal branching does occur in the ventral lobe and the fin-ray segments are only as long as wide or shorter than wide). The scale cover of the dorsal lobe is more extensive than in *P. schultzei* and the scales are lozenge-shaped, with straight or nearly straight edges. They are quite short at the base of the tail, but become progressively more elongated toward the tip of the dorsal lobe. Half the width of the dorsal lobe is covered by scales, whereas in *P. schultzei* the scale cover is restricted to a narrow strip at the upper edge (less than one-quarter the width) of the dorsal lobe. The arrangement, relative size, and shape of the fulcral scales also are quite different. Instead of a single left and right parasagittal series of long, narrow, and unornamented fulcra *(P. schultzei),* there is a proximal series of lozenge-shaped scales and a distal series of longer, also lozenge-shaped scales. Each fulcrum thus is a unit consisting of two scales, proximal and distal, both with an ornament of shallow pits. Nine fulcra are preserved, and there may have been two to three more in the missing tip of the lobe. The fulcral scales thus are much more robust than those in *P. schultzei,* whose ridge of the dorsal lobe is formed by 30(+) fulcra.

(c) Only 22 anterior rays of the anal fin are preserved, but traces of proximal ray segments in the area toward the tail suggest that the anal fin had at least 45 rays (26-34 in *P. schultzei).* There are no fulcra on the anterior margin of the anal fin. The dorsal fin is not preserved, but traces of proximal ray segments suggest that the dorsal was about 25% longer than the anal. The number of dorsal fin rays thus can be estimated at 53-55 (43-58 in *P. schultzei).*

(d) The specimen has 40 vertical scale rows between the cleithrum and the caudal peduncle (25 in *P. schultzei).*

The above features leave no doubt that the CM 47833 specimen is distinct from all platysomids so far found in North America. Considering the abundance of platysomid fishes at Kinney, it is likely that additional, overlooked specimens are in museum and/or private collections which will have to be searched again. This is one reason why the specimen is not formally diagnosed and named. Another reason is that at this time the specimen cannot be compared with the European species, and it thus is not clear whether it represents a new species or is instead assignable to a species already known.

The parasagittal arrangement of the caudal fulcra indicates a derived, presumably bobasatraniiform, condition. However, in absence of other diagnostic features it cannot be unequivocally decided whether the specimen is a bobasatraniiform or an advanced palaeonisciform, and it is thus assigned to the former order only tentatively.

Comments

Taphonomy

The Kinney Quarry fish beds appear to have been deposited in a relatively low-energy environment below the

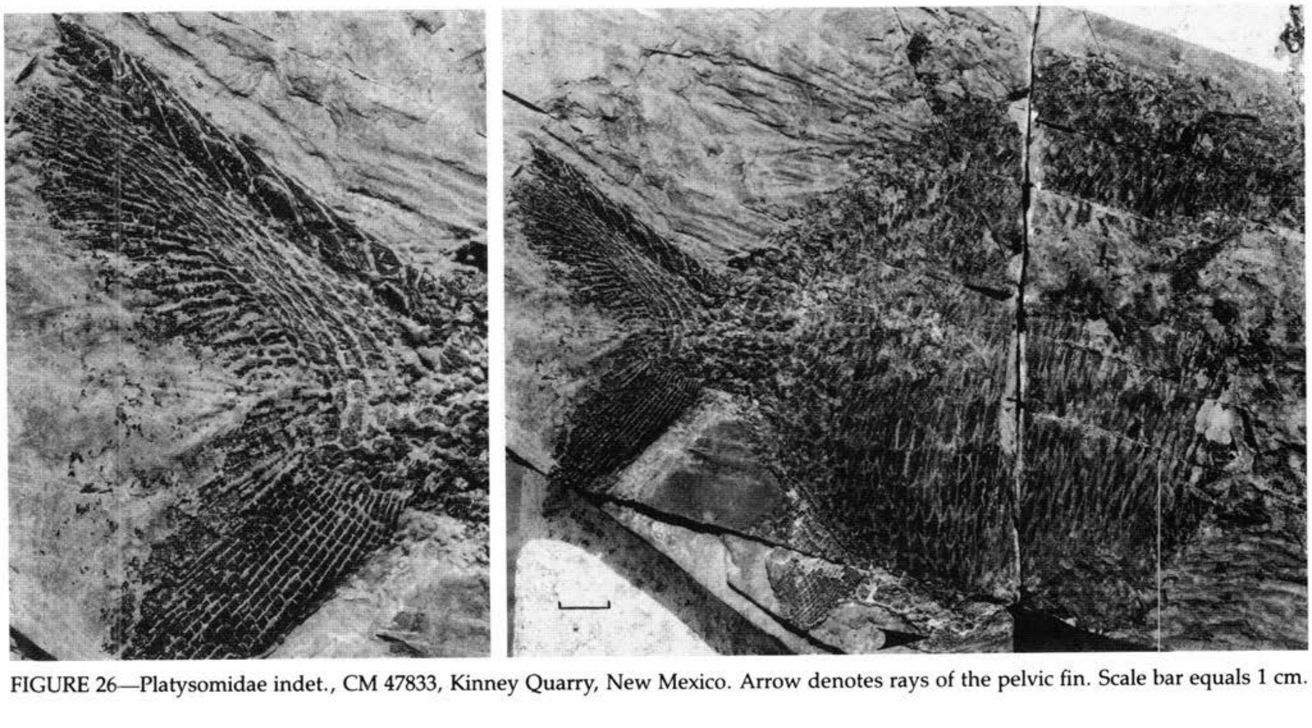

FIGURE 26—Platysomidae indet., CM 47833, Kinney Quarry, New Mexico. Arrow denotes rays of the pelvic fin. Scale bar equals 1 cm.

wave base, but some specimens nevertheless suggest fairly strong bottom or density currents. Most common is antero-posterior compression that must have taken place immediately before and/or during burial and is best apparent in *Platysomus* (Figs. 20C, 27A) and *Amphicentrum* (Fig. 15A). Although the peg-and-socket scale articulation is strong in these genera, the force was powerful enough to condense the vertical scale rows and increase the body depth to length ratio. An extreme example is shown in Fig. 27B, with the posterior part of the body folded over and the length of the specimen substantially reduced, interestingly without disrupting the fins. No preferred orientation of specimens can be discerned at the site, which may mean that the currents were localized and intermittent; in that case density currents would seem to be the most likely cause.

An interesting aspect of preservation of the Kinney Quarry fishes is that curved-up specimens with wide-open mouths, such as are encountered in mass-mortality events caused by desiccation or poisoning, do not occur at the site. Instead the backbones are straight or gently convex-up and the head point either straight ahead or down, indicating relaxed musculature. A case in point is *Cobelodus* which in the black shales of the midcontinent has the vertebral column beneath the dorsal fin almost always disrupted, apparently due to contraction of the epaxial musculature, whereas at the Kinney Quarry no disruption is evident (Fig. 3A). Desiccation, which can be excluded for other reasons as well (see water depth), and poisoning thus are the most unlikely causes of fish mortality at Kinney, and so is osmotic shock which would produce similarly spasmatic results. Although this observation does not reveal the prevailing cause of death, it does indicate that the fishes lived in an environment that was not toxic or in other ways hostile to them.

The prevailing mode of disarticulation of the deep-bodied and other actinopterygians at the Kinney Quarry is a rupture along the opercular line which represents a major zone of weakness and is caused by the increasing gaseous content of the carcass. Several so ruptured specimens of *Platysomus* provide strong evidence against floating of fish carcasses claimed by some authors and used as an indication of shallow water at the Kinney site. The rupture invariably resulted in disarticulation over a very small area (25-36 cm^2; Fig. 28), indicating that the event took place on the substrate and not on the water surface, which would have resulted in a much larger scatter. A variation on this theme would be to assume high depositional rates that would prevent floating by causing a fast burial, thus retarding decomposition. This is an unlikely scenario, however, because the sediment cover would either prevent rupture or, should

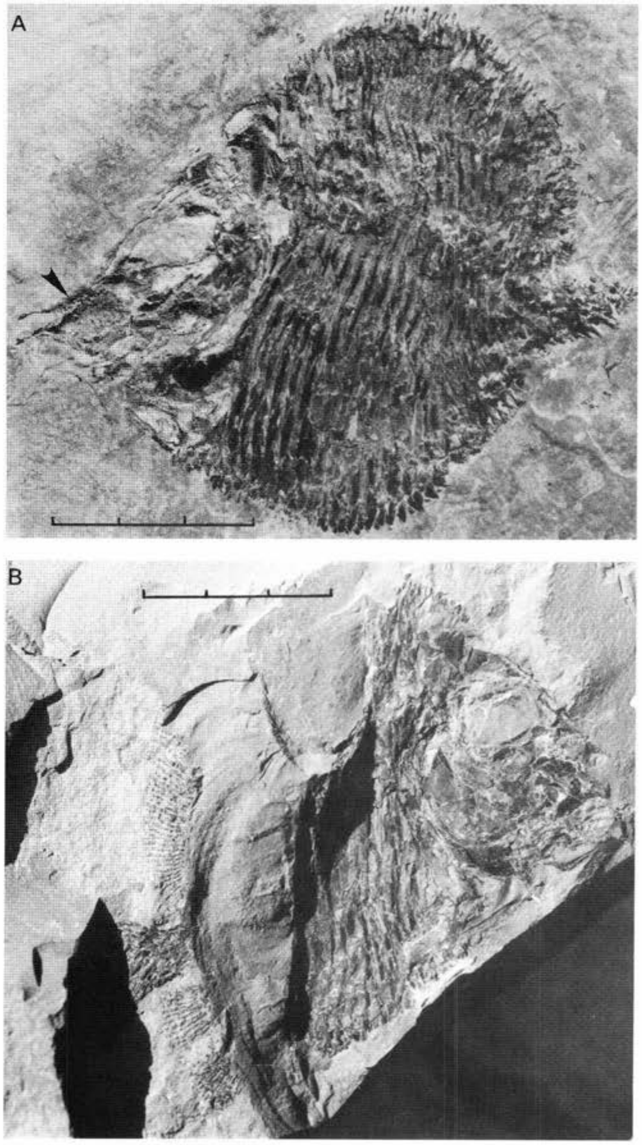

FIGURE 27—Antero-posterior compression of *Platysomus schultzei*, Kinney Quarry, New Mexico. **A,** CM 47838; **B,** KUVP 86161. In B the posterior end of the body folded and the superimposed part was lost during collection. Arrow denotes an upper phyllodont tooth plate; scales in centimeters.

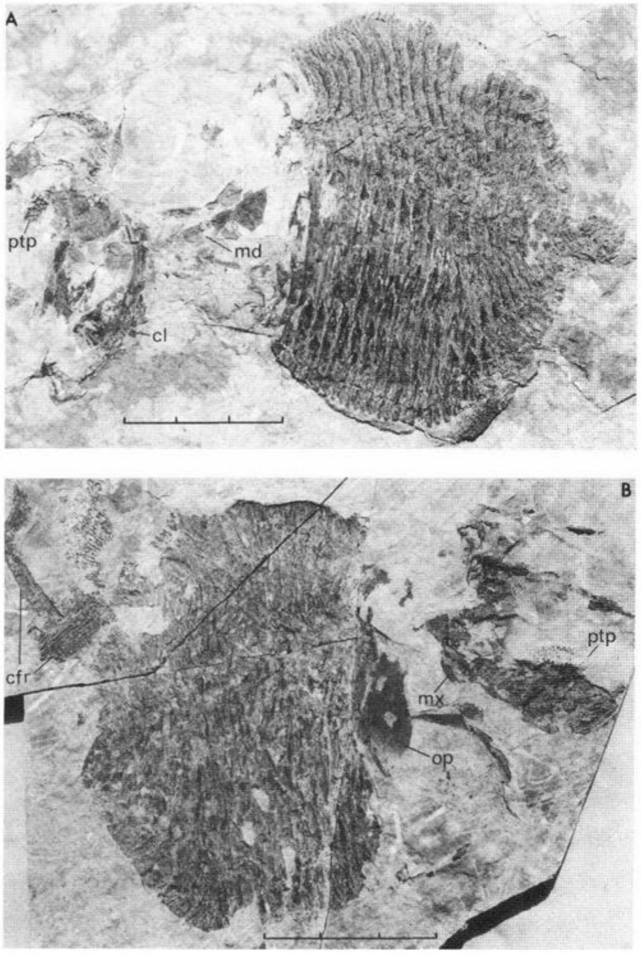

FIGURE 28—*Platysomus schultzei* CM 47834 **(A)** and CM 47835a **(B)** showing the prevailing mode of disarticulation, along the opercular line, in the Kinney Quarry fishes. Scales in centimeters. Abbreviations: **cfr,** caudal fin rays; **cl,** cleithrum; **md,** mandible; **mx,** maxillary; **op,** operculum; **ptp,** phyllodont tooth plate.

rupture occur, it would result in the disturbed sediment and a virtual lack of disarticulation of skull elements, neither of which has been observed at the site. Elder's (1985) data suggest that a water column more than 8-10 m deep (the range being a factor of temperature) prevents carcasses from floating; therefore, based on the above evidence, it is concluded that the depth of water at Kinney exceeded 10 m.

Distribution and ecology

Listracanthus ranges from late Tournaisian (Patterson, 1965: 162, fig. 33, *Deltoptychius armigerus)* into the Early Triassic (Schaeffer & Mangus, 1976: 525, fig. 5), however it is a form genus without merit other than indicating a marine environment. *Peripristis is* a marine genus known to range from Late Mississippian (Chesterian) into the Early Permian (Wolfcampian) of the North American midcontinent (Hansen, 1985: 534). The symmoriids are also known only from marine deposits. *Cobelodus* has been so far recorded from Desmoinesian (= Westphalian C + D) of the Eastern Interior Basin (Zangerl & Case, 1976), Desmoinesian through middle to late Virgilian (= Westphalian C through Stephanian B) of the Midcontinent Basin (Zangerl & Case, 1976; Tway, 1982; Virgilian of Iowa and Kansas; Hansen, 1986: Desmoinesian of Oklahoma), and Morrowan(?) through late Missourian (= Westphalian A? through Stephanian A) of the Appalachian Basin (Hansen, 1986). *Symmorium* ranges through the entire Pennsylvanian marine sequence of the United States (Hansen, 1986) and occurs as early as late Chesterian (= early Namurian; Lund, 1986: *Stethacanthus, Cladodus;* Miller, 1981: *Cladodus)* and as late as Early Permian (Branson, 1916: *Cladodus occidentalis). Cladodus neilsoni* Traquair from East Kilbride, Lanarkshire, Scotland, is also referrable to *Symmorium* (Zangerl, 1981: 71). It is from the Cement Limestone Shale, Lower Limestone Group, Viséan **P2**, and thus is the oldest *Symmorium* known to date. Hansen (1986: 195-196) reviewed the foreign literature, found occurrences of *Symmorium* (described as *Cladodus* and *Ctenacanthus)* also in the Carboniferous of the U.S.S.R., Greenland, and China, and concluded that *S. reniforme* will probably prove to be "nearly ubiquitous in marine rocks of Pennsylvanian age." *Orthacanthus is* a fresh-water genus ranging from Westphalian D of Europe and North America into early Late Permian (early Guadalupian = Kungurian) of North America (Texas, Oklahoma; Olson, 1962, 1965). It appears to be an allochthonous element which was washed into the Kinney lagoon from a stream. The Kinney Quarry occurrence establishes a new westernmost limit for most of these genera, but stratigraphically they are well within their known ranges.

Acanthodes ranges from early Viséan in Scotland *(A. sulcatus,* Lower Oil Shale Group; Denison, 1979: 45) into early Late Permian in Germany *(A.* sp., N4—N5 levels of the Nahe Group, Kungurian; Boy, 1987). In North America its occurrences range from Namurian E_2b in Montana (A. *lundi,* Heath Formation; Zidek, 1980) into the Early Permian in Texas *(A. luedersensis,* Lueders Formation, uppermost Wolfcampian; Dalquest et al., 1988). The Texas occurrence is considered shallow-water marine by Dalquest et al. (1988), whereas the Montana occurrence involves both shallow-water marine (Bear Gulch Limestone Member of the Heath Formation) and fresh-water (paper-shale zone somewhat lower in the Heath Formation) environments (Zidek, 1980, 1988: 158). Many other occurrences of *Acanthodes* are in freshwater, lacustrine, and fluvial deposits. For instance, the European species of intermontane basins far removed from seaways were either potamodromous (limnodromous) or nonmigratory. Even the species found in shallow-water marine deposits most likely were euryhaline anadromous fishes which migrated into streams and lakes to spawn. At the Kinney Quarry this appears to be documented by size distribution, all the specimens are adult to subadult fishes and there is no evidence of individuals small enough to be called fry. This is in marked contrast with other occurrences, most notably the Hamilton Quarry complex in Kansas (Zidek, 1976, 1988), where juvenile individuals greatly outnumber subadults and only one specimen can be regarded as "fully" grown. The prevalence of juveniles at Hamilton and the excellent preservation of their delicate structure indicate a very low-energy regime that could have served as a spawning site. Although most specimens of *A. kinneyi* are articulated or only slightly disarticulated, they usually do not show the detail seen in the Hamilton Quarry specimens of *A. bridgei* (the holotype of *A. kinneyi* is a rare exception). This suggests that adult and subadult *A. kinneyi* was autochthonous to the Kinney lagoon, but the depositional environment, which was a higher-energy regime than that at Hamilton, was less favorable to good preservation of its micromeric exoskeleton.

Amphicentrum ranges from the Viséan (England, Scotland) into the late Westphalian (England, Scotland., Illinois). It has not been previously recorded from Stephanian **B (** = Virgilian) deposits, but the significance of the Kinney Quarry occurrence is not clear. It could be interpreted as supplementary evidence for a Missourian age of the quarry strata (see Huber and Mapes & Boardman, this volume), or it could simply mean that the last occurrence of *Amphicentrum* is younger than previously thought. The question of which alternative is correct will have to be resolved on conodont and fusulinid evidence.

Platysomus ranges from either an early Tournaisian *(Platysomus?* sp. of Obruchev, 1977: 7) or Namurian E_2b (Montana) into the Late Permian (Germany, Great Britain, China). However, as pointed out above, this is a collective genus that contains lower actinopterygians of two orders, the Palaeonisciformes and the Bobasatraniiformes, and what belongs in each order cannot be determined without a speciesby-species revision. The Kinney species, *P. schultzei,* exhibits a number of advanced features that make it the most primitive bobasatraniiform fish known, which, contrary to *Amphicentrum,* would seem to give the site a younger-age flavor. However, similar contradictions are present in the Kinney Quarry flora (see Mamay & Mapes, this volume), and it is far more likely that *P. schultzei* indicates our inadequate knowledge of first and last occurrences than a younger geologic age of the Kinney section.

As is apparent from the summaries presented above, both *Amphicentrum* and *Platysomus* occur in marine, brackish, as well as fresh-water environments. In addition to different species inhabiting different environments, the available evidence indicates that certain species were either anadromous or amphidromous, i.e. freely moving between fresh and salt waters without the purpose of breeding. This appears to be the case at Mazon Creek, where *A. orbiculare* and *P. circularis* are present in both the predominantly freshwater Braidwood fauna and the predominantly shallow-water marine Essex fauna, and it may prove to be the case of *Platysomus* sp. from the fresh-water East Manitou site in Oklahoma (Simpson, 1974) and *"Schaefferichthys leudersensis"* from the shallow-water marine deposits at Lake Kemp, Texas (Dalquest, 1966; Dalquest et al., 1988), which I strongly suspect to be conspecific. Like *Acanthodes kinneyi,* the samples of *A. jurgenai* and *P. schultzei* consist almost entirely of large, presumably adult individuals and very small specimens are altogether absent. The virtual lack of size range encountered at Kinney is suggestive of catadromy, but other than circumstantial evidence to this effect is unlikely to become available.

As noted in the introduction, the abundance of *Acanthodes* and most actinopterygians versus the paucity of other piscine groups (Chondrichthyes, Dipnoi, Sarcopterygii) is profound and cannot be explained by different fossilization potentials of cartilage and bone. The explanation lies in environmental requirements of the various taxa and in their respective positions in the trophic web. *Symmorium* was a large and agile predator that quite certainly was at the top of the trophic web, followed by the smaller but equally agile *Cobelodus,* whose dentition of minute teeth may not have necessarily prevented taking large prey. *Peripristis* is hard to assess because it is known only by isolated teeth; it was a smaller and probably a more sluggish predator. The chondrichthyans should be expected to be far less numerous than their osteichthyan and invertebrate prey; in addition, the paucity of their shed teeth suggests that they were only occasional visitors to the Kinney lagoon. Although *Acanthodes* was toothless, it can be placed at the same trophic level as the smaller fusiform palaeoniscoids because its gill-rakers functioned as both a straining apparatus for filter-feeding and a holding device preventing a larger prey from escaping. Oral dentition is not necessary for swallowing a large prey, and small palaeoniscoids inside body cavities of *Acanthodes* are known from other localities; it is thus most likely that the diet of *A. kinneyi* included both invertebrates and smaller fishes. The Kinney coelacanthid (Zidek, 1975; Schultze, this volume) is a small species that seems best placed somewhat below the trophic level of *Acanthodes* and most palaeoniscoids. The only Kinney fishes that were restricted to invertebrate diet(s) are the deep-bodied actinopterygians and the lungfish *Proceratodus.* However, *Proceratodus* is best excluded from the scenario because it is known by only one tooth plate and it cannot be ascertained that it was an autochthonous element of the Kinney Quarry fauna. The dentition of *Amphicentrum jurgenai* is not known and can only be extrapolated from *A. granulosum,* in which it consists of massive coronoid and ectopterygoid plates bearing conical teeth and capable of crushing mollusc shells. The phyllodont tooth plates of *Platysomus schultzei* were a more fragile apparatus better suited for crushing crustacean carapaces than mollusc shells.

If at all present, articulated specimens of *Amphicentrum* and *Platysomus* are rare and usually poorly preserved at other localities. In contrast, *A. jurgenai* is not uncommon and *P. schultzei* is the most abundant fish at Kinney, outnumbering *Amphicentrum* and other actinopterygians by perhaps as much as 10:1. And, furthermore, it is now clear that a second platysomid species occurs at the site. The Kinney Quarry thus provides a unique opportunity for future studies of these inadequately known groups of deep-bodied actinopterygians.

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Pyritocephalus lowneyae n. sp., the youngest haplolepiform (Pisces: Actinopterygii) from the Pennsylvanian of central New Mexico

Phillip Huber

75 Meadow St., Seymour, Connecticut 06483

Abstract—The family Haplolepidae encompasses a monophyletic complex of small, Carboniferous-age actinopterygians with a previously reported stratigraphic range spanning Namurian A through late Westphalian D. The youngest (early Stephanian) haplolepid is described as a new species of *Pyritocephalus* Fritsch. The specimen was collected at the Kinney Brick Company Quarry in the Manzanita Mountains, central New Mexico. *Pyritocephalus lowneyae* n. sp. differs from other species of the genus by a ventrally wider preoperculum, larger cleithrum, and posteriorly situated dermosphenotics which accommodate enlarged nasals. As in *P. sculptus,* the rostrum includes a rostral and the fin rays do not bifurcate distally. The number of dorsal fin rays (10) is higher than in other species, while the number of caudal fin rays (12) is comparatively lower. The squamation contains 29 vertical scale rows along the main lateral line and virtually lacks ornamentation of parallel ridges on the anterolateral trunk region, which is otherwise characteristic for the genus.

The Kinney Quarry exposes 28 m of strata referable to the Pine Shadow (Missourian–Virgilian) Member of the Wild Cow Formation, Madera Group. The previously assigned early Virgilian age is now in doubt as conodont and brachiopod data suggest a middle or late Missourian age for the quarry strata. Nonetheless, the Kinney Quarry *Pyritocephalus* is the youngest known haplolepid and represents a western extension of the haplolepiform radiation, which peaked during Westphalian D.

Introduction

The family Haplolepidae Westoll 1944 comprises a monophyletic complex of Carboniferous-age actinopterygians marked by a unique combination of characters which collectively trend toward a "subholostean" level of organization. Members of this family show reduction of key elements including the rostrum, opercular series, branchiostegal rays, and fin rays. Other advanced tendencies are ossified centra in at least one species *(Microhaplolepis ovoidea)* and the possibility that the maxilla may have been freed from the cheek, a characteristic of neopterygians such as *Semionotus* and *Lepidotes* (Baum & Lund, 1974).

These small fishes (standard length seldom exceeds 7 cm) are a common constituent of many Carboniferous coal-swamp faunas in North America and Europe. Haplolepids have been previously recorded from Upper Mississippian (Namurian A) through Upper Pennsylvanian (Westphalian D) strata; based on the specimen described below, this range may now be extended to middle or late Missourian or early Virgilian (Stephanian A or B, respectively). The specimen is from the Wild Cow Formation (Madera Group) exposed in the Kinney Brick Company Quarry, 12 km south of the town of Tijeras, Bernalillo County, New Mexico. It was found in a layer of dark-gray, microlaminated, fissile shale which mottles yellowish brown; the shale belongs to unit 4 of Lucas & Huber (1991) and lies above the top of the laminar, clayey micrite which forms much of the quarry floor. Directly associated biota includes a variety of plants, spirorbid worms, molluscs *(Myalina, Dunbarella,* high-spired gastropods), arthropods (ostracodes, conchostracans, malacostracans, insects, myriapods), rare, allochthonous chonetid brachiopods and fenestrate bryozoans, other fishes, and trimerorhachid and dissorophoid amphibians.

Fossil fishes in the Kinney Quarry are largely confined to a 0.5 m thick interval of microlaminated calcareous and fissile shale. The new *Pyritocephalus* was found in the fissile shale and, like other Kinney fishes, is a phosphatized compression. Fishes from this locality usually have badly crushed skulls that obscure details of smaller dermal elements (e.g. suborbitals) and skull-roof morphology. However, the haplolepid has the skull well preserved in dorsolateral aspect and shows enough detail to warrant assignment to a new species. Preparation was accomplished manually with needles under a binocular microscope.

The following abbreviations are used throughout the text: NMMNH, New Mexico Museum of Natural History, Albuquerque; PU, Princeton University collection at YPM; USNM, National Museum, Washington, D.C.; YPM, Yale Peabody Museum, New Haven; ZP, Regional Museum of Western Bohemia, Plzen.

Systematic paleontology

Family HAPLOLEPIDAE Westoll 1944
Subfamily PARAHAPLOLEPINAE Lowney 1983
Genus *PYRITOCEPHALUS* Fritsch 1895

Revised generic diagnosis—Small actinopterygian fishes rarely exceeding 7 cm in standard length; head short and broad, with rostrum, postrostrum, and premaxillaries present; maxillary posteriorly expanded; skull roof deeply fenestrated; paired frontals and parietals variably fused to form a single ossification, or maintain faint to distinct frontoparietal and sagittal sutures; dermopterotics lost, replaced by lappet extension of parietals; parietals deeply embayed for reception of posttemporals; skull roof ornamented with linear to semiconcentric grooves and terrace rugae; opercular series reduced; antopercular present; quadratojugal present; branchiostegal rays reduced, with median and paired lateral and posterior gulars present; dorsal fin posterior to anal fin; caudal completely heterocercal; fin rays completely segmented and reduced in number; squamation mostly smooth, with variable parallel-ridge ornamentation in anterolateral trunk region; vertical scale rows number 25-32 along main lateral line.

PYRITOCEPHALUS LOWNEYAE n. sp.
Figs. 1, 2

Material—Holotype, NMMNH P-12988, is the only known specimen.

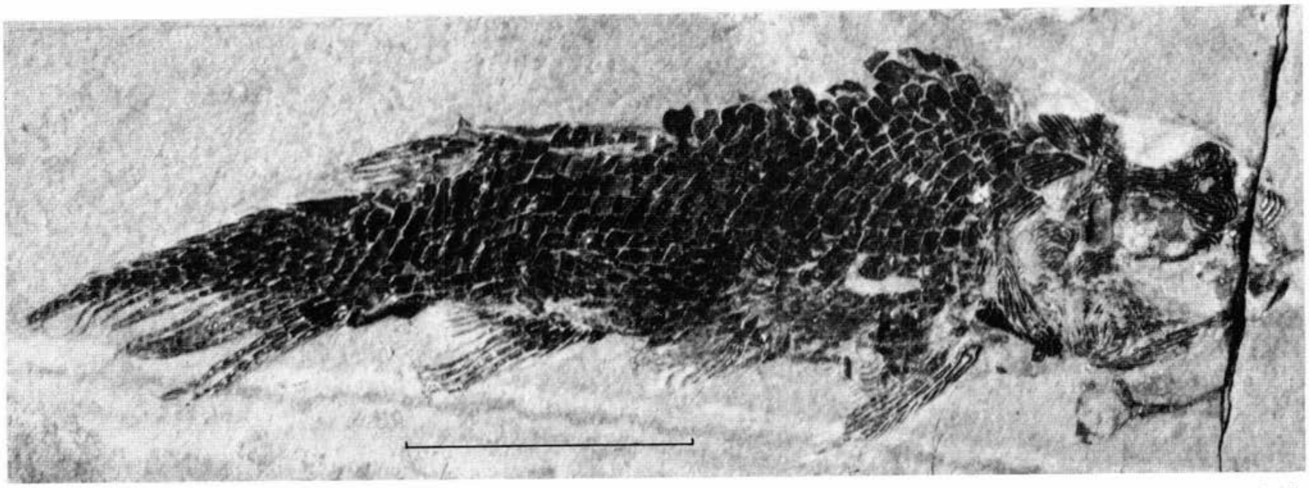


FIGURE 1—*Pyritocephalus lowneyae* n. sp., holotype NMMNH P-12988 from the Wild Cow Formation exposed at the Kinney Brick Company Quarry, New Mexico. Scale bar equals 1 cm.

Locality and horizon—Kinney Brick Company Quarry, SE1/4 sec. 18, T9N, R6E, Bernalillo County, New Mexico. Microlaminated fissile shale in the upper (northeastern) quarry pit, 24 cm above the clayey micrite which forms much of the quarry floor.

Etymology—Named after Karen A. Lowney in recognition of her contributions to haplolepiform systematics and evolution.

Diagnosis—Nasals and cleithrum enlarged, and preoperculum ventrally wider than in other *Pyritocephalus* species; postrostrum present as in *P. sculptus;* number of dorsal fin rays (10) higher than in other species; number of caudal rays (12) lower than in other species; ornamentation of parallel ridges on anterolateral trunk scales reduced to area adjacent to pectoral fin; fin rays not distally bifurcated.

Description—The frontals are lobate and coalesce with no sagittal suture visible. The posterolateral margin bordering the temporal fenestrae is not as well rounded as in *P. sculptus* (e.g. ZP 525, 875, and 860 of Štamberg, 1978), and the frontals progressively widen toward the snout and are anteromesially emarginated for reception of the postrostral. The frontoparietal is narrow and more similar to *P. gracilis* (e.g. YPM 3259) than to *P. sculptus* or other species. Stamberg (1978: 278, fig. 4b) noted a single specimen of *P. sculptus* (ZP 876) which displays "considerable irregular growth," having the left frontal nearly twice as large as the right. This condition is present in *P. lowneyae* and the dimensions of the frontals are nearly identical. Ornamentation of the dermal skull roof in both specimens is similar, but the origin of this anomaly remains speculative. Unlike ZP 876, the New Mexico specimen lacks a distinct median suture. Reduction of the skull roof by fusion of the paired frontals and parietals is a phenomenon variably present in all *Pyritocephalus* species for which an adequate sample is available *(P. lineatus* and *P. sculptus).* As in other *Pyritocephalus* species and *Parahaplolepis,* dermopterotics are absent and have been replaced by lappet extension of the parietals (cf. Baird, 1978). The parietals border the posterior margin

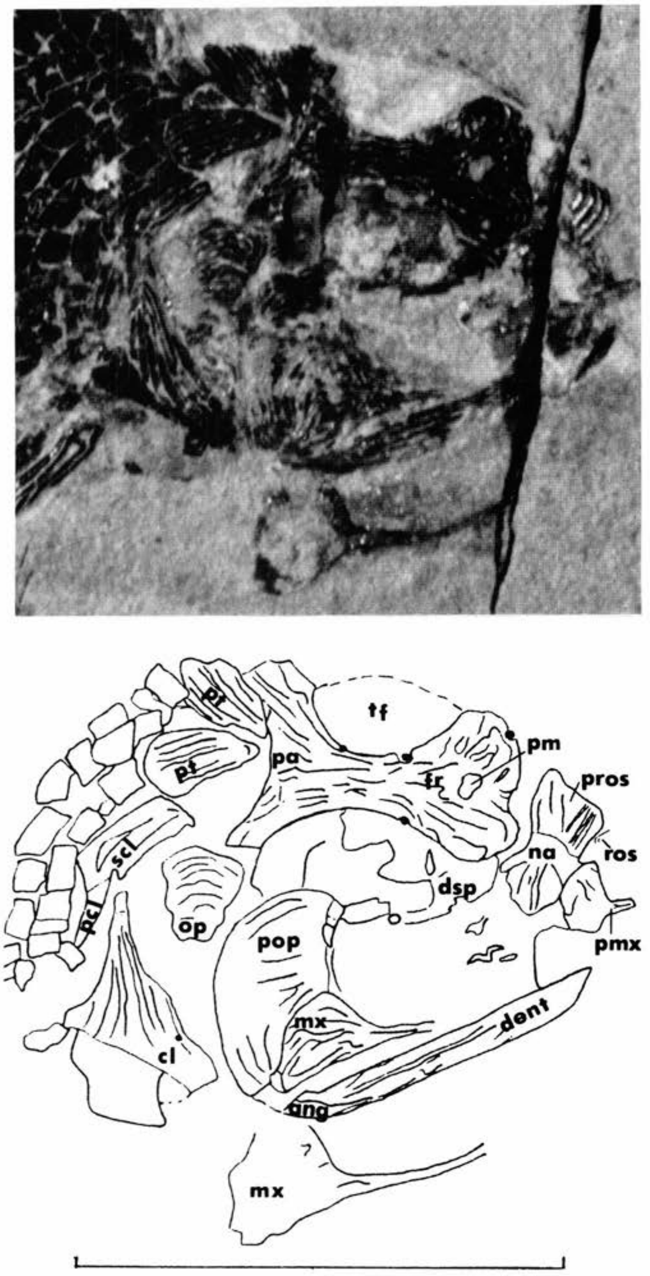


FIGURE 2—*Pyritocephalus lowneyae* n. sp., holotype NMMNH P-12988, skull in dorsolateral aspect. Tracing shows primary elements of the dermal skull. Scale bar equals 1 cm. Abbreviations: **ang,** angular; cl, cleithrum; **dent,** dentary; **dsp,** dermosphenotic; fr, frontal; mx, maxillary; **na,** nasal; **op,** operculum; **pa,** parietal; **pcl,** postcleithrum; **pm,** pineal macula; **pmx,** premaxillary; **pop,** preoperculum; **pros,** postrostral; **pt,** **posttemporal;** **scl,** subcleithrum; **tf,** temporal fenestrae; **ros,** rostral.

of the temporal fenestrae and are deeply embayed for reception of the posttemporals. The frontoparietal suture is not apparent. The posttemporals are disturbed, but consist of two rectangular elements immediately adjacent to the rear margin of the parietals. As a result of this disarticulation, the small, presumably ovoid extrascapulars are not preserved.

The right dermosphenotic is damaged. Unlike in other species, the front margin is situated behind the anteromesial margin of the frontals to accommodate slightly enlarged nasals. The rostrum consists of the rostral, postrostral, paired nasals, and premaxillaries. The right nasal, premaxillary, and the rostral and postrostral are visible. The square postrostral is moved slightly out of position in contact with the frontals. It is smaller than in *P. sculptus* and is ornamented with four well defined transverse ridges. The rostral is small, compact, and in contact with the anterior margin of the postrostral. It is poorly preserved in the phosphatized part as a single groove, while in the counterpart it is a faint oval impression. Though previously noted only by Štamberg (1978) for *P. sculptus,* I suspect this arrangement of the rostrum is characteristic for the genus because it is also visible in a topotype of *Pyritocephalus lineatus* (PU 17181). The remaining bones of the rostrum include the right nasal, which is enlarged and ornamented with semiconcentric swirling rugae, and the right premaxillary. The latter element is triangular and rapidly narrows toward the tip of the snout, which is not well preserved.

The preoperculum is dorsoventrally elongate and ventrally wider than in other species. It is bordered by a small, triangular antoperculum and more ventrally by the suboperculum. At least two suborbitals contact the anterior margin of the preoperculum but are largely obscured due to compression. The operculum is ovate, twice as large as the suboperculum, and lies directly above it. The right maxillary displays an expanded base typical of the Parahaplolepinae and, like in *Haplolepis,* considerably narrows under the orbit. The left maxillary is also preserved as an overturned, disarticulated element beneath the dentary. Proportionally, it is more similar to *P. sculptus* than to other species; it lacks the more uniform width of *P. lineatus* (e.g. PU 17181) and *P. gracilis* (e.g. YPM 3259), but is nonetheless dorsally larger than in those species. No teeth are visible. The dentary is adjacent to the ventral base of the maxillary expansion and extends to the snout. It is ornamented by at least four parallel grooves and has a gently upward-curving ventral margin just below the premaxillary. The angular is preserved in the counterpart as a distinct groove forming the posteroventral portion of the dentary. The quadratojugal is a small, poorly preserved element lying between the ventral extension of the preoperculum and the base of the maxillary expansion. The cleithrum and postcleithrum are very pronounced. The cleithrum is broad and ventrally larger than in *P. sculptus* or *P. lineatus,* and the postcleithrum is also wider than in other species of the genus. The subcleithrum narrows ventrally and is notched for reception of the cleithrum along the anterolateral margin. The right clavicle is in the normal position but is not well shown. Because the specimen is preserved in dorsolateral aspect, the ventral skull elements are not visible. They are presumed to consist of a modified branchiostegal series with a median and paired posterior and lateral gulars which typify *Pyritocephalus* and other haplolepids.

The pectoral fin has 10-11 completely segmented fin rays bounded anteriorly by fringing fulcra which extend four-fifths the length of the fin rays. The pelvic fin contains seven fin rays in similar arrangement, but the fulcra are not well displayed. The dorsal fin is situated posteriorly of the anal fin and originates at the 21st vertical scale row (counting along the main lateral line). It has at least 10 fin rays and the dorsal flank scales at the fin's point of origin are ovoid. The base of the anal fin begins at the 14th vertical scale row and, like the dorsal and paired fins, is anteriorly bordered by fringing fulcra for most of the fin-ray length. The caudal inversion comprises five lateral rows of cycloid-shaped scales which become reduced in number and size toward the terminus of the caudal lobe. The caudal web contains 12 completely segmented fin rays which extend nearly the entire length of the upper, scaled lobe. Unlike *P. comptus, P. gracilis,* and *P. lineatus,* the fin rays of the paired and median fins do not bifurcate distally.

The squamation is composed of thin scales which display peg-and-socket articulation and are arranged in 28 vertical scale rows. The scales are rhomboid over most of the body, but become progressively deeper than wide behind the dorsal fin. The anterolateral area of the trunk differs from other species in mostly lacking the ornamentation of fine parallel ridges, which is otherwise characteristic for the genus. Development of parallel ridges is found only adjacent to the cleithrum and pectoral fin and is not very pronounced. The dorsal midline behind the skull shows an unpaired row of broadly triangular scales which possess an anteriorly directed process. Other species also display unpaired dorsal-ridge scales, but these are usually deeply rectangular. The histology of *Pyritocephalus* scales has never been investigated. It is reasonable to assume that the scale microstructure is similar to that of *Parahaplolepis,* which was discussed by Westoll (1944) and Cavender (1963). These authors agreed that scales of this genus include the same components of bone, dentine, and ganoin as in all other actinopterygians, but Cavender (1963) noted that the relative proportions of these elements differed in *Parahaplolepis,* which has very thin bone and ganoin layers. In contrast, the dentine layer is very well developed and thicker than that found in any of the paleoniscids studied by Aldinger (1937) or in primitive neopterygians such as *Semionotus* (Thomson & Mc Cune, 1984).

Discussion

Specimens referable to *Pyritocephalus* were first described by Newberry (1856) as one *(P. lineatus)* of eight species of a new genus, *Mecolepis,* all from Linton, Ohio. Later, Newberry (1857) found *Mecolepis* preoccupied and applied the new name *Eurylepis* to these species. Subsequently, Newberry (1888) transferred *Eurylepis lineatus* to the fusiform paleoniscid genus *Rhadinichthys.* Eastman (1917) briefly described and figured *a Pyritocephalus* from Mazon Creek and followed Newberry by referring it to *Rhadinichthys gracilis.* It was upon this specimen (USNM 4401) that Berg (1936) founded the family Teleopterinidae to include *Teleopterina improvisa ("Rhadinichthys gracilis")* as the type genus and species. The name *Pyritocephalus* was first coined by Fritsch (1895) for material previously described as *Palaeoniscus sculptus* (Fritsch, 1883) from the Plzen Basin, Czechoslovakia. Our current understanding of the genus is based on Westoll's (1944) thorough revision of the Haplolepidae. He synonymized *Rhadinichthys gracilis* and *R. lineatus* with *Pyritocephalus* Fritsch, and described *P. rudis* (the only other European species) from Newsham, England, and *P. comptus* from Mazon Creek, Illinois. More recent studies of haplolepids (e.g. Baird, 1962, 1978; Lowney, 1980, 1983) have concentrated largely on other genera or interfamilial relationships, and with the exception of Štamberg (1978) and Hook & Baird (in press) have largely ignored *Pyritocephalus.*

Six species of *Pyritocephalus* (including *P. lowneyae) are* recognized. The oldest (Westphalian B) is *P. rudis* from Newsham, Northumberland, which Westoll (1944) founded on a single skull roof. The specimen (Westoll, 1944: 59-60) is clearly referable to the genus and displays much wider frontoparietals with resultant shallow temporal fenestrations. Westoll regarded *P. rudis* as primitive on the basis of the broad skull roof and concluded that this species is closely related to *Parahaplolepis.* Mazon Creek (early Westphalian D) *Pyritocephalus* comprises two species, *P. gracilis* and *P. comptus.* The former is distinguished by a slender frontoparietal, deeper fenestrations, maxilla with a "taller" expansion, smaller preoperculum, and a smaller number of fin rays than in *P. lineatus* or *P. sculptus* (Westoll, 1944). Examination of YPM 3259 (YPM 440 of Westoll, 1944: 5657) confirms this diagnosis, and it should be noted that the original label for this specimen, signed by Eastman, indicates that it is the counterpart of the holotype of *P. gracilis* figured by Newberry & Worthen (1870: pl. 3/4). The other YPM specimen of *P. gracilis* mentioned by Westoll, YPM 1234, cannot be presently located (M. Turner, pers. comm. 1990). *P. comptus* includes but a single specimen (USNM 4310) with a poorly preserved skull. Westoll (1944) recognized it as a somewhat anomalous species displaying more posterior insertions of the paired and median fins and a higher number of vertical scale rows (32) to the origin of the caudal inversion.

The only species of *Pyritocephalus* which are represented by large samples (20 or more specimens) are *P. lineatus* from Linton and Five Points, Ohio, and *P. sculptus* from Bohemia, Czechoslovakia. The Ohio species is defined by a broader cleithrum, shorter and deeper maxillary expansion, and a slender head displaying a more vertical suspensorium (Westoll, 1944). *P. lineatus* is similar to the Mazon Creek species in possessing fin rays with distal bifurcations. *P. sculptus* is the type and best known species of the genus. Westoll (1944) revised the original description of Fritsch (1895), and tamberg (1978) provided additional comments on the dermal-skull morphology and established the range of meristic variation for this species. *P. sculptus* and *P. lowneyae* are similar in possessing fin rays which lack distal bifurcations and have fulcra extending four-fifths the length of the fin rays. They are differentiated by the dimensions of certain dermal elements (e.g. cleithrum, preoperculum), squamation, body depth, and number of rays in the paired and median fins.

Pending further study, I tentatively regard all the above-mentioned species as valid. Some forms are quite distinct (compare *P. rudis* and *P. sculptus),* while others exhibit only minor differences. Because early Westphalian D species *(P. gracilis* and *P. comptus)* are represented by a very small sample from a single locality, it is difficult to assess the range of dermal-skull and meristic variation. Defining taxa on meristic data alone is questionable, as such a taxonomy may result in recognition of a plethora of otherwise ill-defined species (e.g. McCune, 1987). *P. comptus* is problematic in this regard because a larger sample from Mazon Creek may demonstrate a wider range of intraspecific variation and suggest synomony of *P. comptus* with *P. gracilis.*

Three evolutionary grades of *Pyritocephalus* are evident. The first (oldest) is represented by *P. rudis* with its broad frontoparietal, symmetrical lateral and anterior sutures, and shallow fenestrations. The second complex includes *P. gracilis, P. comptus,* and *P. lineatus* which show dimensional variation in dermal-skull morphology but are united by the presence of distally branching fin rays and fulcra which extend one-half to two-thirds the length of the fin rays. *P. sculptus* and *P. lowneyae* comprise the third grade with fringing fulcra extending almost the entire fin length and fin rays which lack distal bifurcations. Comparison of fin rays in *P. gracilis, P. lineatus, P. sculptus,* and *P. lowneyae* indicates that reduction and eventual loss of the distal bifurcations were accompanied by a decrease in number of segmented lepidotrichia and the appearance of stouter individual rays. The loss of the former character over time within a single genus has not been before clearly demonstrated for any actinopterygian family; it appears to indicate that *Pyritocephalus* could not have been derived from *Parahaplolepis,* as suggested by Lowney (1983).

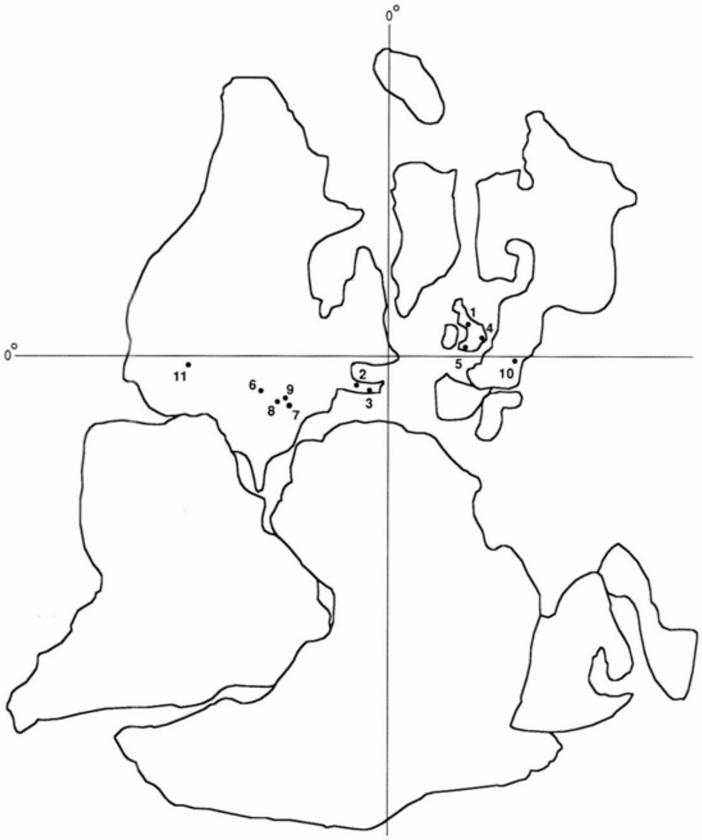
The genus may have evolved from *Blairolepis* (Lowney, 1983) or possibly *Haplolepis.* These genera appear well before *Pyritocephalus* and display skull roofs which with successive modification could have evolved into the *Pyritocephalus* pattern. While *Haplolepis* maintains distally branching lepidotrichia, this condition is unknown for *Blairolepis* which is based on a single skull roof. Because haplolepid endocrania are virtually unknown, it is not possible to determine the origin and functional significance of the temporal fenestrations which typify *Pyritocephalus.* These qualities are pivotal in establishing an ancestor for the genus and/or developing a general phylogenetic classification of the Parahaplolepinae as defined by Lowney (1983). Westoll (1944) thought that the fenestrae resulted from extension of endocranial musculature toward the fossae bridgei or are related to reduction of the circumorbital series which accommodates an enlarged eye socket. He concluded that either or both would contribute to inhibition of bone development along the frontoparietal margin, with correlative modification of the laterosensory canals.

Hook & Baird (in press) identify a thin layer of "tympani" covering the vacuities which are "formed in the substance of the dermopterotic." This condition is also present in Linton *Pyritocephalus* (PU 17181) and the type specimen of *P. sculptus* (D. Baird, pers. comm. 1991). It is tempting to view the tympani-covered fenestrations as a specialized sensory apparatus. An auditory function may be ruled out as the inner ear in osteichthyans does not have an open endolymphatic duct as in chondrichthyans and placoderms. What is clear is that the progressive development of the fenestrae over time (compare *P. rudis* to *P. gracilis* to *P. lineatus)* parallels gradual reduction of the dermal skull roof, which is exemplified by the narrow frontoparietal and variable absence of frontoparietal and sagittal sutures in the latter species. Until more informative material is collected, the significance of the temporal fenestrae will remain enigmatic.

Haplolepids have been found in Great Britain, Czechoslovakia, and North America (Fig. 3) where they usually occur in Late Carboniferous coal-swamp environments. According to Lowney (1983), haplolepids originated in Great Britain during the Early to Middle Carboniferous and rapidly dispersed to North America and central Europe. The dispersal resulting in the two evolutionary pathways evident within the family (Haplolepinae and Parahaplolepinae; Lowney, 1983) occurred early and probably predates the Westphalian stage. Subsequent radiation began during Westphalian A—B, with haplolepids present in the vertebrate faunas of Parrsboro and Joggins, Nova Scotia (Baird, 1962, 1978). Westphalian C taxa are known only from the Coal Measures of Great Britain, where the earliest *Pyritocephalus* is found. The radiation peaked during the Westphalian D and both subfamilies are well represented by the diversity of species found at Mazon Creek, Cannelton, Linton, and Five Points in eastern North America. The last documented European species is *Pyritocephalus sculptus* from the Plzen Basin of Czechoslovakia (late Westphalian D). Thus, *Pyritocephalus lowneyae* from the Kinney Quarry is the youngest haplolepid (early Stephanian) of late Missourian or early Virgilian age. It is interesting to note that this species also represents the western limit of haplolepid radiation.

Acknowledgments

I wish to express gratitude to Bob Jurgena, President of the Kinney Brick Company, for allowing access to the quarry. NMMNH provided preparation facilities, Pete Reser made casts of the specimen, and Jiri Zidek and Spencer G. Lucas



1. **Loanhead, Midlothian**
   (Namurian A)
   Blairolepis loanheadensis
   Protohaplolepis scotica
   Pyritocephalus comptus
   Parahaplolepis cf. *tuberculata*
   Microhaplolepis cf. *ovoidea*
2. **Parrsboro, Nova Scotia**
   (Westphalian A)
   Parahaplolepis canadensis
3. **Joggins, Nova Scotia**
   (Westphalian B)
   Parahaplolepis cf. *canadensis*
   Haplolepis cf. *corrugata*
4. **Newsham, Northumberland**
   (Westphalian B)
   Pyritocephalus rudis
   Parahaplolepis aff. *anglica*
   Parahaplolepis westolli
   Haplolepis attheyi
5. **Longton, Staffordshire**
   (Westphalian C)
   Parahaplolepis anglica
6. **Mazon Creek, Illinois**
   (early Westphalian D)
   Pyritocephalus gracilis
7. **Cannelton, Pennsylvania**
   (middle Westphalian D)
   Microhaplolepis serrata
8. **Five Points, Ohio**
   (late Westphalian D)
   Pyritocephalus sp.
   Haplolepis sp.
9. **Linton, Ohio**
   (late Westphalian D)
   Pyritocephalus lineatus
   Parahaplolepis tuberculata
   Haplolepis corrugata
   Microhaplolepis ovoidea
   Microhaplolepis serrata
10. **Nyrany, Bohemia**
    (late Westphalian D)
    Pyritocephalus sculptus
11. **Kinney Quarry, New Mexico**
    (= Stephanian ?A)
    Pyritocephalus lowneyae

FIGURE 3—Distribution of the Haplolepidae. Numbers of localities in paleogeographic reconstruction correspond to those in distribution list. Map after Scotese et al. (1979); distribution data from Lowney (1983) and Hook & Baird (in press).

supplied photographs. Stanislav Štamberg sent peels of *Pyritocephalus sculptus* and Donald Baird a photo of *Pyritocephalus lineatus* (PU 17181). Mary Ann Turner provided access to YPM 3259 and Ron Rukstela drafted Fig. 3. I am especially thankful to Donald Baird, David Bardack, and Jiri Zidek for their helpful reviews of this paper and comments which substantially improved it.

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A new deep-scaled "palaeoniscoid" from the Kinney Quarry, Late Pennsylvanian of New Mexico

Michael D. Gottfried

Calvert Marine Museum, P.O. Box 97, Solomons, Maryland 20688

Abstract—Lower actinopterygian fishes (platysomoids and "palaeoniscoids") are the most common vertebrates at the well-known Late Pennsylvanian (Virgilian) Kinney Brick Quarry, Bernalillo County, north-central New Mexico. Among the palaeoniscoid-grade actinoptergyians is a distinctive new genus and species characterized by dorsoventrally deepened scales in the midbody region combined with a fusiform-body morphology. The squamation of this new taxon makes a transition from deepened to more typical rhomboid scales posteriorly and toward the dorsal margin of the body. The combination of deepened body scales and a fusiform body is convergent with the pattern seen in a number of more phylogenetically derived Triassic and younger actinopterygians.

Introduction

The Kinney Brick Quarry in Bernalillo County, north-central New Mexico, has produced a diverse Upper Pennsylvanian (Virgilian) biota from the Pine Shadow Member of the Wild Cow Formation (Madera Group). The locality has been collected since 1961 by private individuals and by parties from several museums and universities (see Kues & Lucas, this volume, for a history of collecting activities). The most common vertebrate remains from the quarry are primitive actinopterygians (platysomoids and "palaeoniscoids") along with numerous specimens of the acanthodian *Acanthodes* (Zidek, 1975, this volume; Gottfried, 1987a, b). The vertebrate fauna also includes smaller numbers of primitive chondrichthyans, the dipnoan *Proceratodus hlavini,* and a coelacanth (Zidek, 1975, this volume; Schultze, this volume). Tetrapods include the trimerorhachid amphibian *Lafonius lehmani* (Berman, 1973) and two other primitive amphibians currently under study (D. Berman, pers. comm.).

Previous published reports on actinopterygians from Kinney have dealt with the first record of an aeduelliiform actinopterygian from outside of Europe (Gottfried, 1987a) and the description of a new genus and species of primitive long-snouted, palaeoniscoid-grade actinopterygian (Gottfried, 1987b). This paper is concerned with the description of an additional new palaeoniscoid-grade actinopterygian from the Kinney Brick Quarry. The new form is characterized by dorsoventrally deepened body scales coupled with an otherwise typically fusiform-body morphology, a squamation pattern that is convergent with that seen in a number of more phylogenetically derived Triassic and younger actinopterygians.

Systematic paleontology

Class OSTEICHTHYES Huxley 1880
Subclass ACTINOPTERYGII Woodward 1891
Infraclass ACTINOPTERI Cope 1871
Order "PALAEONISCIFORMES" Hay 1902
Suborder "PALAEONISCOIDEA" Goodrich 1909
Family indet.

SCHIZOLEPIS n. gen.

Diagnosis—Scales in anterior midbody region three to four times deeper than wide, in two bands. Peg-and-socket articulation of deepened scales located near their posterior border. Ornamentation of deepened scales consists of smooth ganoine surface with shallow, irregular, intersecting furrows that form mosaic pattern. Scales on posterior and dorsal portions of body are diamond-shaped rhomboids which are much finer and narrower along the ventral margin. Body fusiform and slightly elongate, with head comprising approximately 25% of overall length and maximum body depth 20% of overall length. Dorsal fin posteriorly positioned, low in profile, and small relative to anal fin. Pectoral fin lobate at base, with ca. 12 slightly rounded scales covering fleshy lobe. Triangular suborbital present, contacts both preoperculum and maxilla. Separate intertemporal and supratemporal bones present. Dermosphenotic relatively large and T-shaped, forming major portion of dorsal border of orbital opening and contacting nasal.

Etymology—From the Latin *schizos* (split) and *lepis* (scale), in reference to the combination of unusually deepened and more typically proportioned scales on the body.

Type *species—Schizolepis manzanitaensis* n. sp.

SCHIZOLEPIS MANZANITAENSIS n. sp.

Diagnosis—As for genus.

Holotype—Nearly complete articulated specimen (Figs. 1A, 2A) deposited in the Vertebrate Paleontology collection of the University of Kansas Museum of Natural History (KUVP 83501). The specimen was donated to KUVP by Spencer Lucas (then of the University of New Mexico) in 1984, and was probably collected by one of the student groups from the University of New Mexico that excavated at the Kinney Brick Quarry between 1977 and 1984.

Paratypes—KUVP 83502, KUVP 104197; New Mexico Museum of Natural History NMMNH P-14359, NMMNH P-14365, NMMNH P-14366; and Carnegie Museum of Natural History CM 47851, CM 47852, CM 47853, CM 47854.

Etymology—Named for the Manzanita Mountains of north-central New Mexico, where the type locality is located.

Locality and geologic setting—The Kinney Brick Quarry is located in the Manzanita Mountains, Bernalillo County, north-central New Mexico, 12.6 km south of the town of Tijeras (NW^1/4 SW^1/4 SE1/4 sec. 18, T9N, R6E). Quarrying operations at the site expose sediments of the Pine Shadow Member of the Wild Cow Formation (Madera Group), which consists of interbedded limestone, limey shale, and sandstone layers. The Pine Shadow Member is generally considered to be Late Pennsylvanian (Virgilian). The principal fish-bearing horizon consists of 0.4 m of calcareous shale near the base of the exposed section. This horizon, which contains articulated fish, immediately overlies a dark-gray, laminar to massive, micritic limestone that forms the floor of the quarry (see geologic sections in Gottfried, 1987b, and Kues & Lucas, this volume).

Depositional environment—The paleoenvironment of the Kinney Brick Quarry "fish bed" has been a subject of discussion by most of the authors who have dealt with the Kinney biota. Opinions include a protected estuary or lagoon with relatively low salinity, a very active tidal environment with varying salinity, and nearshore marine (see summary in Kues & Lucas, this volume). There is a general consensus that the Kinney section in its entirety represents a marine regressive sequence (perhaps associated with a prograding clastic delta, according to Kues & Lucas). The presence of palaeoniscoid-grade actinopterygians at Kinney does not bear on the question of paleosalinity levels because "palaeoniscoids" have been found elsewhere in deposits ranging from fresh to marine water (Gottfried, 1989a). The relatively common occurrence of articulated fishes in the fish horizon (Zidek, 1975; Gottfried, 1987a, b; Kues & Lucas, this volume) is suggestive of either a low-energy environment that favored preservation of nearly complete fishes, or very rapid burying of undisturbed carcasses by fine sediments.

Description

This description includes information derived from the holotype KUVP 83501, a nearly complete articulated fish preserved in internal left lateral view, and the paratypes which include five partial articulated fishes that preserve some cranial features (NMMNH P-14359, P-14365; CM 47852, 47853, 47854); three articulated but headless specimens (NMMNH P-14366; KUVP 80352, KUVP 104197); and a patch of scales from the dorsal region of the body (CM 47851).

General features—The skull is typically palaeoniscoid in its overall morphology and the general shape and arrangement of the individual elements (Figs. 1-3). The snout is rounded and projecting, the orbital opening is large and anteriorly placed, and the mouth is subterminal, with a relatively long gape. The individual dermal bones of the cranium are tightly sutured to one another. The teeth are simple, slightly recurved, and conical. Ornamentation of the cranial bones is best represented in CM 47853 (Fig. 2B) and consists of ovoid to elongated subparallel ridges and islands of ganoine.

The arrangement of the skull-roof bones is typical for a primitive actinopterygian, with an unpaired rostral, large nasals, relatively elongate parietals, shorter postparietals, intertemporals, and supratemporals, and large, T-shaped dermosphenotics. The posterior region of the skull roof is not well preserved in any of the specimens.

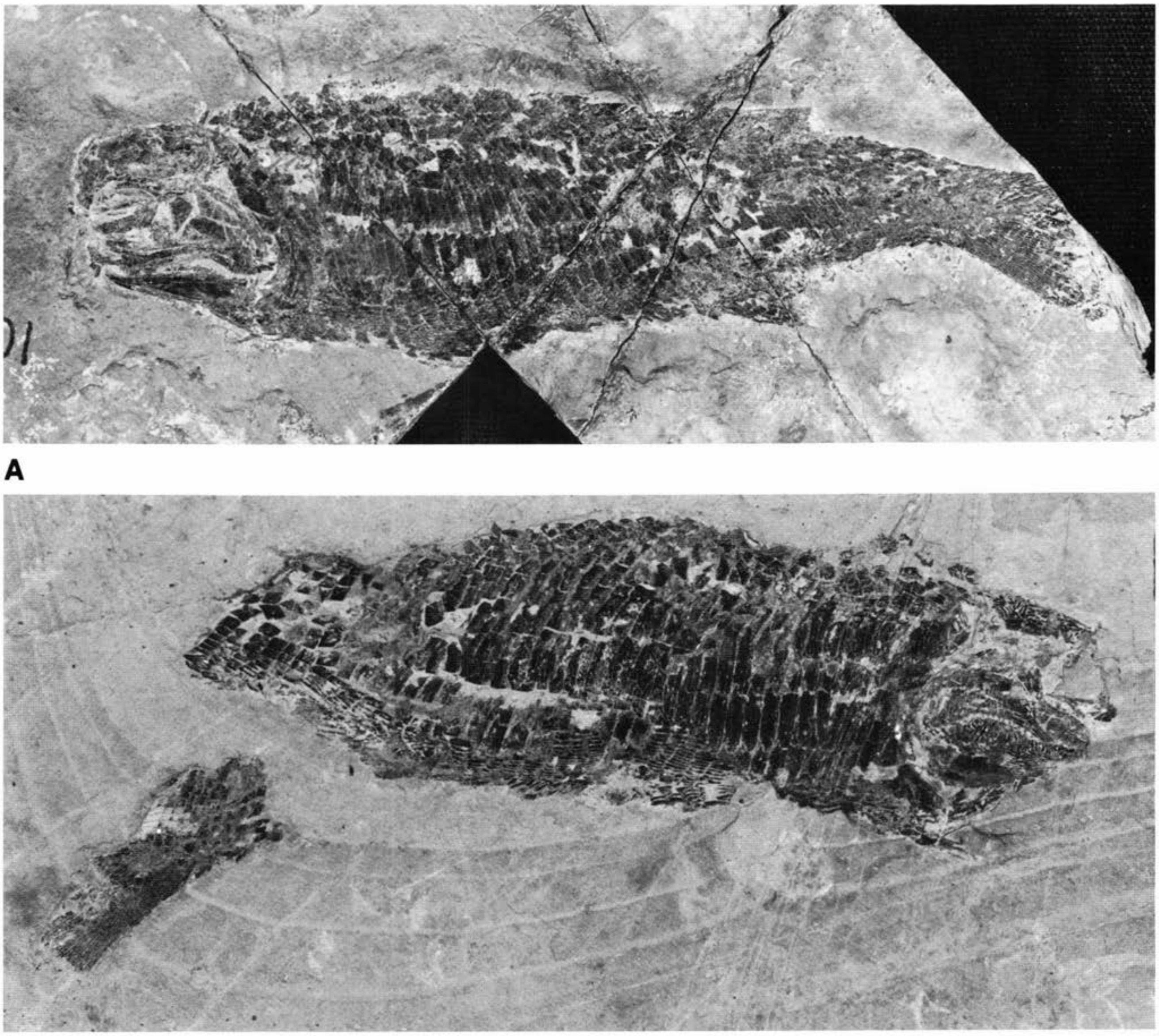

FIGURE 1—**A,** Holotype of *Schizolepis manzanitaensis,* KUVP 83501, ×1.4. **B,** *Schizolepis manzanitaensis,* paratype CM 47853, ×1.7.

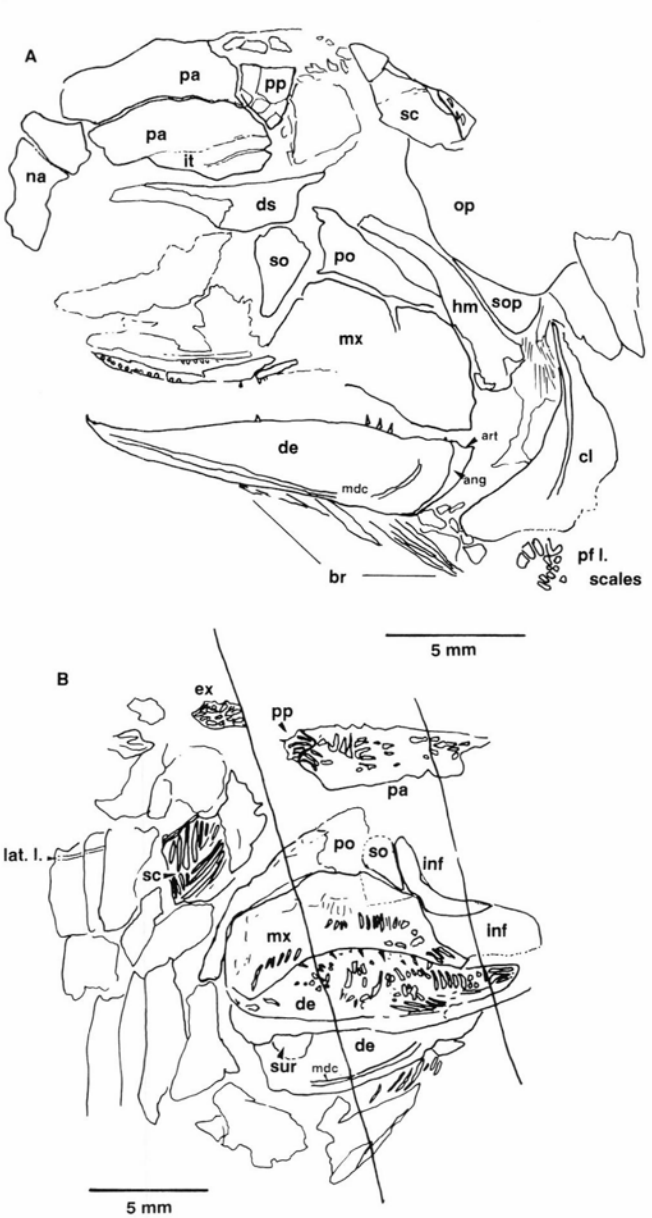

FIGURE 2—**A**, Cranial region of holotype of *Schizolepis manzanitaensis*, KUVP 83501. **B**, Cranial region of *Schizolepis manzanitaensis*, paratype CM 47853. Abbreviations: **ang**, angular; **art**, articular; **br**, branchiostegal rays; **cl**, cleithrum; **de**, dentary; **ds**, dermosphenotic; **ex**, extrascapular; **hm**, hyomandibular; **inf**, infraorbital; **it**, intertemporal; **lat. l.**, lateral line; **mdc**, mandibular sensory canal; **mx**, maxilla; **na**, nasal; **op**, operculum; **pa**, parietal; **pf l.**, pectoral-fin lobe; **po**, preoperculum; **pp**, postparietal; **sc**, supracleithrum; **so**, suborbital; **sop**, suboperculum; **sur**, surangular.

The cheek region includes a suborbital, which is of significance in assessing the phylogenetic position of this taxon (discussed below). The maxilla has an expanded postorbital portion and a narrow infraorbital process as is typical in "paleoniscoids," and is dorsally joined to a sharply angled preoperculum that has distinct dorsal and ventral limbs. The hyomandibular is also obliquely angled, which indicates an oblique rather than vertical suspensorium. Two infraorbital bones form the posterior and ventral margins of the orbital opening. The lower jaw is relatively deep and of a typical lower-actinopterygian construction, with a large dentary and smaller surangular and angular bones comprising the external dermal investing elements. The course of the mandibular sensory canal is visible, passing through the dentary.

The opercular series consists of an ovoid and relatively large operculum, a smaller suboperculum, and an estimated 20 branchiostegal rays. The operculogular elements form a curving series posterior to the preoperculum, maxilla, and lower jaw, with the branchiostegalia extending ventral to the lower jaw.

The shoulder girdle is not completely preserved, but the cleithrum is well represented. It is a crescent-shaped element posterior to the branchiostegal rays, which contacts a median clavicle anteroventrally. A small patch of slightly rounded scales just behind the posteroventral border of the cleithrum provides evidence for a lobate pectoral fin.

The unpaired fins include a relatively small and low-profile dorsal fin, a larger anal fin which has an insertion anterior to that of the dorsal fin, and a heterocercal caudal fin. The pelvic fin is present but not well preserved in any of the available specimens.

The squamation consists of two bands of markedly deepened scales in the anterior midbody region, which grade into more typically rhombic scales posteriorly and dorsally, and into narrow scales along the ventral margin of the body. This distinctive squamation is discussed in detail below.

Cranial morphology—A median rostral element typically forms a major portion of the snout region in palaeoniscoids; its reconstruction in *S. manzanitaensis* (Fig. 3) is conjectural because it is not well preserved in any of the specimens.

The nasal (Figs. 2A, 3) is a relatively large element that lies lateral to the presumed position of the rostral and forms the anterodorsal margin of the orbital opening. Two invaginations, one along the lateral and another on the medial margin of the nasal, mark the position of the paired narial openings. The ventral border of the nasal apparently reaches the premaxilla, although that region is poorly preserved and the exact nature of the nasal/premaxilla contact is unclear. Posteriorly, the nasal reaches the anterolateral corner of the parietal and the anterior end of the dermosphenotic. Ornamentation of the nasal consists of small, closely spaced, rounded tubercles of ganoine.

The dermosphenotic (Figs. 2A, 3) is a relatively large Tor tau-shaped element that forms the dorsal and postero-

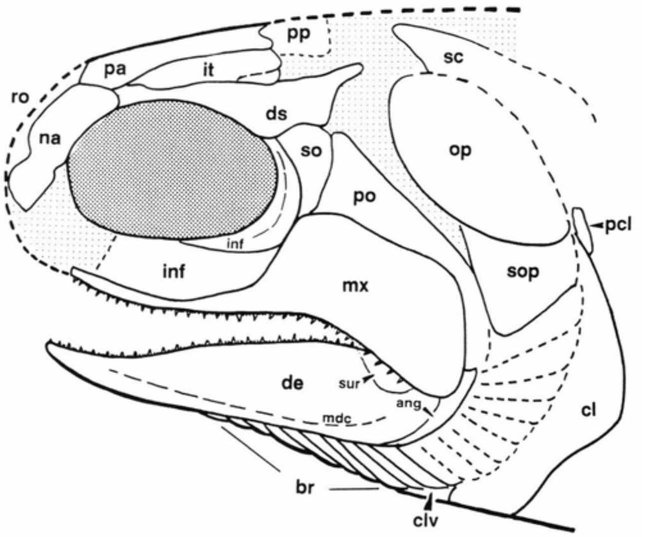

FIGURE 3—Composite restoration of skull of *Schizolepis manzanitaensis* in left lateral view. Light stippling indicates areas of nonpreservation, dashed lines indicate uncertainty as to exact shape of bones. Abbreviations: **ang**, angular; **br**, branchiostegal rays; **cl**, cleithrum; **clv**, clavicle; **de**, dentary; **ds**, dermosphenotic; **inf**, infraorbital; **it**, intertemporal; **mdc**, mandibular sensory canal; **mx**, maxilla; **na**, nasal; **op**, operculum; **pa**, parietal; **pcl**, postcleithrum; **po**, preoperculum; **pp**, postparietal; **ro**, rostral; **sc**, supracleithrum; **so**, suborbital; **sop**, suboperculum; **sur**, surangular.

dorsal border of the orbital opening. It lies lateral to the parietal from which it is largely separated by the intertemporal; it does appear that the anteriormost part of the dermosphenotic contacts the anterolateral corner of the parietal. The middle region of the dermosphenotic is wider and extends farther ventrally than do either the long anterior or shorter posterior arms of the bone. The dermosphenotic reaches relatively far anteriorly, and probably contacted the posterior border of the nasal. A slender piece of bone displaced into the orbital opening anterior to the dermosphenotic in the holotype may be a broken piece of the dermosphenotic or a displaced circumorbital bone, but this is unclear and the paratypes are not helpful in establishing the precise structure of this region.

A somewhat wedge-shaped intertemporal occupies most of the area between the parietal and dermosphenotic; it does not appear that the inter temporal reached the nasal (Figs. 2A, 3). A V-shaped notch along the posterior border of the intertemporal marks the entrance of the lateral-line canal, which can be traced anteriorly a short distance through the bone.

The large, approximately rectangular parietals (Figs. 2A, B, 3) form a major portion of the skull roof. Each parietal reaches the rostral anteriorly and lies medial to the dermosphenotic and intertemporal. Although the postparietal is represented only by fragments, it is clear that the parietal is approximately twice the length of the postparietal. Schultze (in press) considers this to be the derived condition relative to basal actinopterygians such as *Cheirolepis,* in which the parietal and postparietal are of approximately equal length, and *Dialipina* (from the Lower Devonian of Siberia) in which the postparietal is longer than the parietal. The ornamentation of one isolated parietal (CM 47853; Fig. 2B) consists of elongated ovoid to linear ridges of ganoine. The ganoine ridges on the anterior portion of the parietal are horizontally aligned relative to the long axis of the bone, whereas those nearer the posterior end are nearly vertical or steeply angled and more curved. The posterior margin of the parietal is formed into a sinusoidal curve and is contacted along this suture by the anterior end of the postparietal in CM 47853 (Fig. 2B). The pineal opening is not preserved, or may have been absent.

The parietal/postparietal terminology is used here, rather than frontal/parietal, in accordance with Romer (1945) and Jollie (1962, 1987) who argued persuasively that those names best reflect the homologies of the elements involved. Other recent authors, including Gardiner (1984) and Gardiner & Schaeffer (1989), continue using the frontal/parietal nomenclature.

The skull roof posterior to the parietal—postparietal contact is not well preserved in any of the specimens. Paired postparietals and extrascapulars are present, but their exact relationships are unclear. A relatively small isolated subrectangular bone in CM 47853 (Fig. 2B) is probably an extrascapular; it is ornamented with elongated ovals of ganoine similar to those on the parietal.

The cheek region includes a small, nearly triangular suborbital bone posterior to the orbit and anterior to the preoperculum and maxilla (Figs. 2A, B, 3). According to Gardiner (1984) and Gardiner & Schaeffer (1989), the presence of one or, more suborbitals is an important feature in assessing the phylogenetic position of primitive actinopterygians (discussed below).

Two infraorbitals (the jugal and lachrymal of Gardiner, 1984, and Gardiner & Schaeffer, 1989) are present in CM 47853 (Fig. 2B). The more dorsal of the two infraorbitals is a relatively slender lunate element that tapers ventrally to a point and is slightly broader at its dorsal extremity. It forms the posteroventral border of the orbit and contacts the ventralmost part of the dermosphenotic and the anterior edge of the suborbital. It also meets the anterior border of the postorbital process of the maxilla. The course of the infraorbital sensory line is indicated by a canal that runs through the middle portion of the bone. The more ventral infraorbital is not as completely preserved but appears to be larger and more plate-like than the dorsal infraorbital. It forms the ventral border of the orbit and is joined to the dorsal edge of the infraorbital process of the maxilla. The orbital opening itself (Figs. 2A, 3) is large, ovoid, and anteriorly positioned, as is typical for palaeoniscoids.

The maxilla (Figs. 2A, B, 3) is a large, prominent bone which, as in other palaeoniscoids, consists of an expanded plate-like postorbital portion and a narrow infraorbital process. The postorbital portion bears closely spaced, linear, vertical ridges of ganoine, which are somewhat rounded and less elongate in the anterior portion of the postorbital expansion. The posteroventral extremity projects ventrally, overlapping the posterior end of the lower jaw. The laniary teeth are slightly recurved, sharply pointed, and conical with swollen bases. These teeth are fairly regularly spaced along the ventral margin of the maxilla on a lamina of bone that projects medially from the internal surface of the maxilla, and become more dense anteriorly. Approximately 30 laniary teeth appear to have been present. Smaller marginal teeth are positioned lateral to the laniaries, with three to four of them between each larger laniary tooth. The infraorbital process is narrow and upwardly curved at its tip, and reaches as far anteriorly as the anterior margin of the orbital opening. The maxilla/premaxilla contact is not clear, and the premaxilla is represented only by fragments so that its precise shape and relationships to surrounding bones are not obvious.

The preoperculum (Figs. 2A, B, 3) is a narrow and sharply angled element with distinct dorsal and ventral limbs that lie along the dorsal and posterior margins of the maxilla, respectively. The anterior margin of the preoperculum is shallowly concave and contacts the posterodorsal margin of the suborbital.

The operculum (Figs. 2A, 3) lies posterior and dorsal to the preoperculum. It is a large, ovoid element with long curving ridges of ganoine. The ganoine ridges curve in such a way that they reflect the anterior and posterior margins of the operculum and meet in its middle part, forming a distinctive pattern. The smaller plate-like suboperculum lies ventral to the operculum and posterior to the ventral limb of the preoperculum. It comes to a rounded point ventrally and contacts the dorsalmost branchiostegal ray. There are an estimated 20 branchiostegalia (Fig. 3), which lie ventral to the suboperculum and lower jaw.

The lower jaw (Figs. 2A, B, 3) is slipper-shaped and relatively deep. The dorsal toothed margin is gently curved and flares slightly dorsally at its anterior tip. The largest of the dermal bones comprising the mandible is the dentary, which contains the mandibular sensory canal in its ventral region. The teeth on the dentary are similar to those on the maxilla, with each slightly recurved laniary separated by several smaller and more laterally disposed marginal teeth. Ornamentation of the mandible consists of ridges of ganoine which are linear and vertically arranged anteriorly and become more irregular in the posterior half. The ornamentation tends to consist of more rounded, smaller islands of ganoine near the toothed margin. CM 47853 preserves the external dermal elements of the left mandible in internal view and allows for an interpretation of the nature of the surangular, which is a wedge-shaped triangular element located just anterior to the lower-jaw articulation (Figs. 2B, 3). A relatively small and narrow angular forms the posterior portion of the mandible. The holotype includes the posterior end of the right mandible in internal view, where the cup-like cotyle of the articular is clearly visible posterior to the dentary and immediately ventral to the slightly displaced posteroventral corner of the maxilla.

Some elements of the suspensorium and palate are visible in the holotype (Fig. 2A). The hyomandibular is an angled element that lies medial to the preoperculum and mirrors the preoperculum's orientation, indicating an oblique jaw suspension as is typical for primitive actinopterygians. The rounded knob on the dorsal end of the hyomandibular would have articulated with the lateral wall of the braincase (not preserved). The relatively broad ventral end of the hyomandibular suggests articulation with an interhyal. No opercular process is present on the hyomandibular.

Part of the palatoquadrate can be seen just dorsal to the infraorbital process of the maxilla in the holotype (Fig. 2A). Although poorly preserved, this appears to be the anterior portion of the right palatoquadrate. It somewhat mirrors the shape of the overlying maxilla, being broader posteriorly and coming to a tapered point anteriorly, but its anterior region is broader than the maxilla. A large invagination near the anterior end of this element probably represents the position of the basipterygoid foramen. The entopterygoid is present as a narrow strip of bone that is closely appressed to the ventral extremity of the palatoquadrate and bears a row of densely arranged, small, rounded teeth along its ventral margin.

The narrow anterior portion of the parasphenoid can be seen in lateral view within the orbital opening of CM 47853 and in NMMNH P-14359. It appears that there are small, tubercle-like teeth on the ventral surface of the parasphenoid in CM 47853, but they are not clearly visible.

Shoulder girdle—The supracleithrum (Figs. 2A, B, 3) is not completely preserved in any of the specimens. It appears to be an elongate and slightly ovoid element lying dorsal to the cleithrum and posterior and dorsal to the operculum. The precise nature of its articulation with the posterior skull roof is not readily discernible from the material at hand. The lateral-line canal can be seen entering the posterior part of the supracleithrum in CM 47853.

The cleithrum (Figs. 2A, 3, 4A, B) is a large, crescentic bone lying posterior to the branchiostegal rays and extending dorsally to the posterior border of the suboperculum. The posterior border of the cleithrum is rounded and broad in its midsection, becoming narrower both ventrally and dorsally. The dorsal tip of the cleithrum ends in a distinct point, while the bone's ventral end is more broadly rounded. A thickened ridge runs from the dorsal end into the midregion of the cleithrum on the medial surface of the bone. The posteroventral border of the cleithrum is formed into a relatively shallow invagination or embayment which marks the position of the pectoral-fin insertion. This curving embayment is not as pronounced or as deep as that typically seen in palaeoniscoid cleithra. The ornamentation of the cleithrum consists of long, parallel, slightly curving ganoine ridges that follow the shape of the bone; these ridges are finer along the anterior edge of the cleithrum in CM 47854.

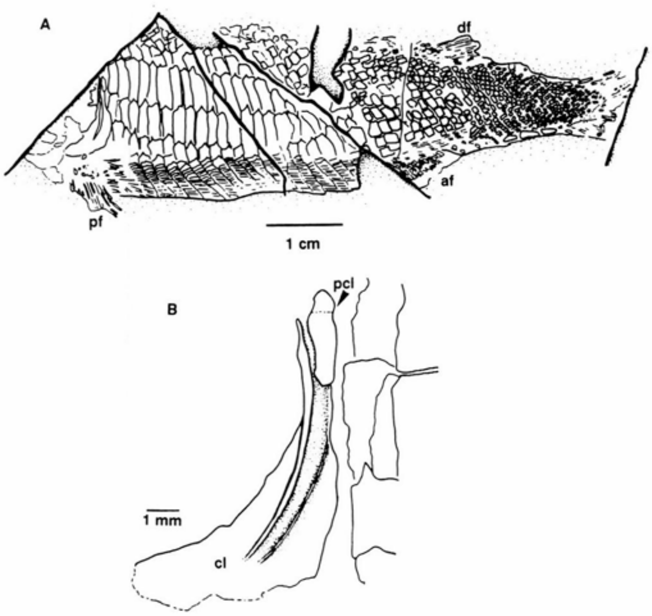

FIGURE 4—**A,** Articulated *Schizolepis manzanitaensis,* paratype KUVP 83502; note deepened scales in anterior midbody region. **B,** Close-up view of pectoral-girdle region of KUVP 83502. Abbreviations: **af,** anal fin; **cl,** cleithrum; **df,** dorsal fin; **pcl,** postcleithrum; **pf,** pectoral fin.

The clavicle is present but not well preserved. Its restoration in Fig. 3 is based on the typical size and location of clavicles in other "paleoniscoids."

A single elongately rectangular postcleithrum is present near the dorsal tip of the deithrum (the primitive condition for actinopterygians; Gottfried, 1989b). The major portion of the postcleithrum is immediately posterior to the dorsal tip of the cleithrum and slightly underlies that part of the cleithrum in KUVP 83502 (Fig. 4B). The position of this element, its smaller size relative to the deepened scales of the anterior region of the body, and its lack of a peg-and-socket indicate that it is a postcleithrum and not a scale from the first scale row.

Paired fins—The pectoral fin is relatively long and tapering, with between 20 and 30 rows of segmented lepidotrichia. It cannot be determined if the fin rays bifurcate to form secondary lepidotrichia on the distal part of the fin. A small patch of about 12 slightly rounded scales posterior to the cleithrum in the holotype (Fig. 2A) and KUVP 83502 (Fig. 4A) provides evidence for the presence of a scale-covered lobe at the base of the pectoral fin (as shown in Fig. 5). The lobe scales are distinct from the scales on the anterior part of the body in being slightly rounded rather than rhombic and shaped differently than the narrow ventral scales on the anteroventral region of the body. A fleshy pectoral lobe is also present in the basal Devonian actinopterygian *Cheirolepis* (Pearson & Westoll, 1979, and references therein), the Carboniferous genera *Cornuboniscus* (White, 1939) and *Tarrasius* (Moy-Thomas, 1934), and extant cladistians.

The pelvic fin is not well preserved in any of the specimens. It is located approximately midway along the total length of the body and closer to the anal than the pectoral fin. The pelvic lepidotrichia are segmented, and it appears that approximately 12 rows of lepidotrichia are present in CM 47853 and NMMNH P-14359.

Median fins—The single dorsal fin (Figs. 1A, 4A, 5) is relatively small, of low profile, and occupies a more posterior position than usual in fusiform palaeoniscoids, with its insertion posterior to that of the anal fin. It appears that there are approximately 15 to 20 rows of primary lepidotrichia, with the most anterior lepidotrichium shorter and stouter than the others in order to form a strengthened leading edge of the fin.

The anal fin (Figs. 1A, 4A, 5) is large relative to the dorsal fin, with a long base on the posteroventral margin of the body and (as noted above) an insertion anterior to that of the dorsal fin. It is acuminate in shape, with ca. 30 rows of primary, segmented lepidotrichia; the segments are relatively broad and stout.

The caudal fin (Figs. 1A, 5, 6) is strongly heterocercal and slightly inequilobate, with a moderately cleft posterior margin. The dorsal lobe bears several rows of caudal inversion scales. Approximately 45 rows of lepidotrichia appear to be present, with the individual segments in each row being somewhat longer than broad. The more dorsal lepidotrichia

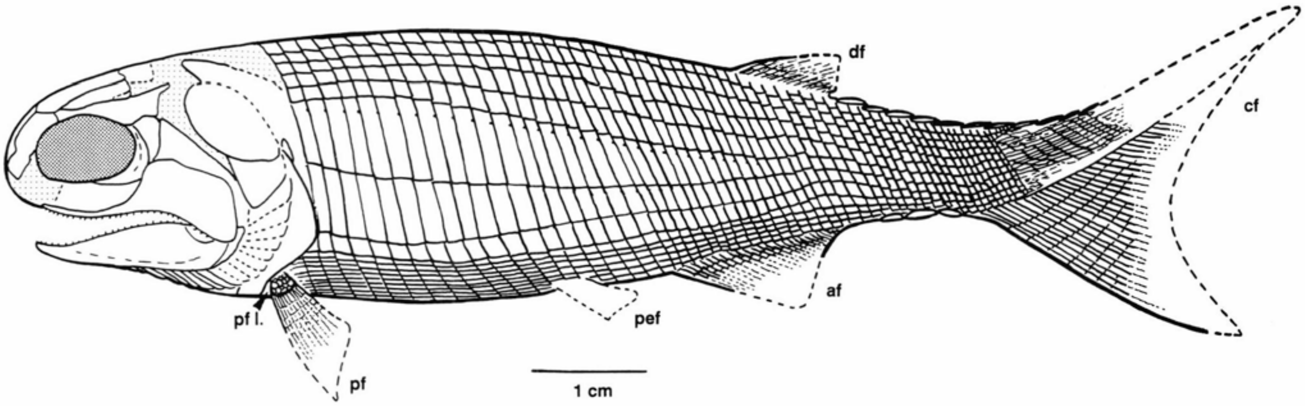

FIGURE 5—Composite reconstruction of *Schizolepis manzanitaensis* in left lateral view. Note deepened scales, small size and posterior position of dorsal fin, and lobate pectoral fin. Abbreviations: **af,** anal fin; **cf,** caudal fin; **df,** dorsal fin; **pef,** pelvic fin; **pf,** pectoral fin; **pf l.,** pectoral-fin lobe.

are stouter and shorter than those closer to the ventral margin of the fin.

Squamation—The most distinctive and immediately obvious feature of S. *manzanitaensis* is the unusual squamation. The scales in the anterior midbody region are three to four times as deep as they are wide, from the first to about the 30th scale row (out of a total of ca. 60 scale rows), forming two distinct lateral bands of deep scales that run from just behind the head to the midbody region (Figs. 1A, B, 4A, 5, 7). These deepened scales grade into more typical diamond-shaped rhombic scales in the posterior half and along the dorsal part of the body. The squamation along the ventral margin consists of numerous very fine, narrow, rhombic scales. Three large basal fulcral scales are present along the ventral margin of the body between the anal and caudal fins. A series of overlapping dorsal fulcral scales extends along the dorsal midline between the dorsal and caudal fins, grading into narrower overlapping caudal fulcra along the dorsal margin of the caudal fin itself. There is no indication of denticulate or serrate posterior margins on any of the scales.

Each of the deepened scales (Fig. 7) bears a strongly developed peg for articulation with the V-shaped socket of the dorsally adjacent scale in the row. The pegs are triangular and relatively elongate and, along with the sockets, are located near the posterior edges of the deep scales. The anterodorsal process of these deep scales is rounded and not strongly developed. The more dorsal of the two bands of deep scales contains the deepest scales, with maximum depth at about the eighth or ninth scale row where the scales are four times deeper than wide. The course of the lateral line is visible in CM 47853, passing through the dorsal portion of the upper band of deep scales. The anterior margin of these scales has a distinct rounded opening where the canal enters, while the posterior margin has a small invagination that marks the exit point of the lateral-line canal. The course of the lateral line is indicated in the reconstruction (Fig. 5). The external ganoine-covered surface of the deep scales is smooth, with shallow furrows that form a network on the free-field surface of the scales. This unusual ornamentation gives an irregular mosaic appearance (Fig. 7B). The normally shaped rhombic scales have a more typical ornamentation, which consists of several prominent ridges that run anterodorsally-posterventrally across the surface.

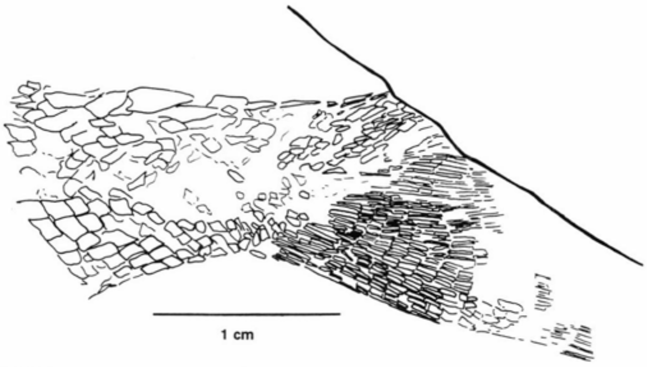

FIGURE 6—Heterocercal caudal fin in **holotype** (KUVP 83501) of *Schizolepis manzanitaensis*.

Discussion

Systematic *affinities—Schizolepis manzanitaensis* is demonstrably a member of the Actinopterygii based on its possession of the following features, considered actinopterygian synapomorphies or features that evolved at a very primitive level within actinopterygians: presence of ganoine, single dorsal fin, mandibular sensory canal enclosed within the

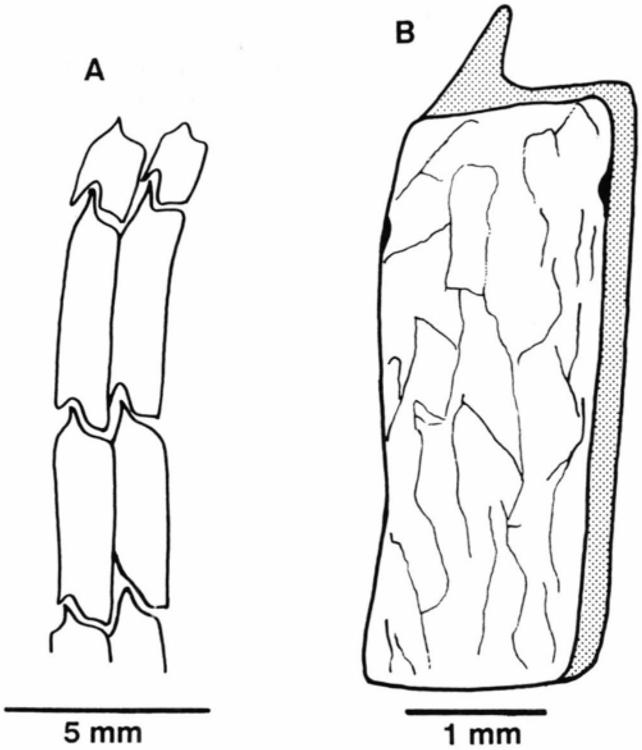

FIGURE 7—**A,** Articulated deep scales from 10th and 11th scale rows of paratype (CM 47853) of *Schizolepis manzanitaensis;* medial view, anterior to the right. **B,** Composite reconstruction of deepened lateral-line scale of *Schizolepis manzanitaensis;* external view, anterior to the right.

dentary, rhomboid scales with a narrow-based peg, and caudal fulcral scales bordering upper lobe of caudal fin (Lauder & Liem, 1983; Gardiner, 1984; Gardiner & Schaeffer, 1989).

S. manzanitaensis possesses several autapomorphic features which serve to distinguish it from other Palaeozoic actinopterygians. Principal among these is the unusual squamation, with the deepened scales in the anterior mid-body region. Another late Paleozoic actinopterygian with a somewhat similar squamation pattern is *Eurylepidoides socialis* described by Case (1935) from the Early Permian of Texas. *Eurylepidoides,* however, has only a single row of deepened scales, which run almost all the way back to the caudal fin. In addition, the shape and structure of the fins are far different in *Eurylepidoides,* and the skull-roof bones are unornamented and differ in proportions from those of *Schizolepis.* Finally, the teeth of *Eurylepidoides* are minute and very slender in comparison to the conical and well-developed teeth on *Schizolepis.* The similarity in squamation pattern between the two forms is therefore interpreted as convergent and not indicative of a close phylogenetic relationship.

The unusual mosaic-like ornamentation pattern on the deep scales is also interpreted as an autapomorphy. Some Paleozoic lower actinopterygians, including aeduelliforms (Heyler, 1969), have smooth, unornamented scales, but a pattern of shallow intersecting furrows forming an irregular mosaic appears to be unique.

The presence of a fleshy lobe at the base of the pectoral fin has been considered a primitive condition in actinopterygians (Pearson, 1982; White, 1939). This interpretation relies heavily on the fact that a lobate pectoral fin occurs in *Cheirolepis* and cladistians (the extant genera *Polypterus* and *Calamoichthys),* thereby implying that this is the primitive condition because *Cheirolepis* and cladistians are very primitive taxa within the Actinopterygii according to Gardiner & Schaeffer (1989) and others. However, the very infrequent occurrence of lobate pectoral fins in other primitive fossil actinopterygians *(Cornuboniscus,* White, 1939; and *Tarrasius,* Moy-Thomas, 1934) and the absence of lobate pectoral fins in basal sarcopterygians (i.e. onychodontiforms) suggest that the presence of a pectoral-fin lobe in primitive actinopterygians is better and more parsimoniously interpreted as independently derived where it occurs. Therefore, the lobate pectoral fin of *Schizolepis* is regarded as an autapomorphy for the genus.

The small size and posterior position of the dorsal fin is also considered derived for *S. manzanitaensis.* The primitive situation in lower actinopterygians is for a relatively prominent single dorsal fin to have its insertion even with, or slightly anterior to, that of the anal fin, as seen in such basal-level forms as *Howqualepis* (Long, 1988), *Moythomasia* (Jessen, 1968), and *Mimia* (Gardiner, 1984).

Identifying *Schizolepis manzanitaensis as* a primitive actinopterygian and diagnosing it as a distinct new taxon is relatively straightforward. It is more difficult to assess its interrelationships with other palaeoniscoid-grade actinopterygians. Incomplete preservation of the cranial region and lack of preservation of neurocranial details mean that many features considered to be useful in lower actinopterygian phylogenetic studies are not available for analysis in S. *manzanitaensis.*

One feature of S. *manzanitaensis* with possible phylogenetic significance is the presence of a suborbital. Anamestic suborbitals situated between the preoperculum/maxilla and infraorbital series occur in the majority of lower actinopterygians, but are absent in the basal forms *Cheirolepis, Mimia,* and *Moythomasia.* Gardiner & Schaeffer (1989) maintained that the presence of suborbitals is a synapomorphy of actinopterygians above the basal-level taxa, but allowed that some genera above that level lack suborbitals (in their view secondarily), including *Mesopoma, Cleithrolepis, Bobasatrania,* chondrosteans, *Australosomus,* and *Luganoia* (which is the sister taxon to neopterygians in their analysis).

The presence of a suborbital in *Schizolepis manzanitaensis* provides a synapomorphy that provisionally unites the taxon with other lower actinoptergyians above the basal level in actinopterygian phylogeny. Furthermore, the mandible of *S. manzanitaensis* includes a surangular, a bone that is primitively absent in *Cheirolepis* and *Mimia.* It appears that the surangular disappeared several times independently, including in chondrosteans and teleosts, but its presence at this level in actinopterygian phylogeny is interpreted as derived.

The cranium of *S. manzanitaensis* includes both an intertemporal and (by interpretation) supratemporal along the lateral edge of the skull roof; these two bones would have been of approximately the same size. The presence of separate intertemporal and supratemporal bones is the primitive condition in actinopterygians. The derived condition is for a single bone, the dermopterotic, to occupy the position of the inter-plus-supratemporal of primitive forms (Gardiner & Schaeffer, 1989). Basal-level actinopterygians *(Cheirolepis, Mimia, Howqualepis,* and *Moythomasia)* have separate inter- and supratemporals, but in those forms the intertemporal is markedly smaller than the supratemporal, while in "lower" palaeoaniscoids above the basal level these two bones are of subequal to roughly equal size. This pattern suggests the following transformation series: separate inter- and supratemporals with a small intertemporal --> separate bones approximately equal in size —› fusion of the two bones to form a dermopterotic (in "higher" palaeoniscoids and neopterygians). The extent of the intertemporal in *S. manzanitaensis* relative to the other bones of the skull roof suggests that the supratemporal (which is not preserved) in this form would have been approximately the same size as the intertemporal.

The lack of detail on portions of the skull and absence of preserved endocranial features make it difficult to construct a rigorous hypothesis of this form's phylogenetic interrelationships with other lower actinopterygians. Fig. 8 represents an attempt to use a small subset of several unambiguous cranial characters for which *S. manzanitaensis* can be scored and compared with other primitive actinopterygians. The resulting cladogram suggests that it is a "lower" palaeoniscoid, more derived than the basal-level taxa but more primitive than "higher" palaeoniscoids and neopterygians.

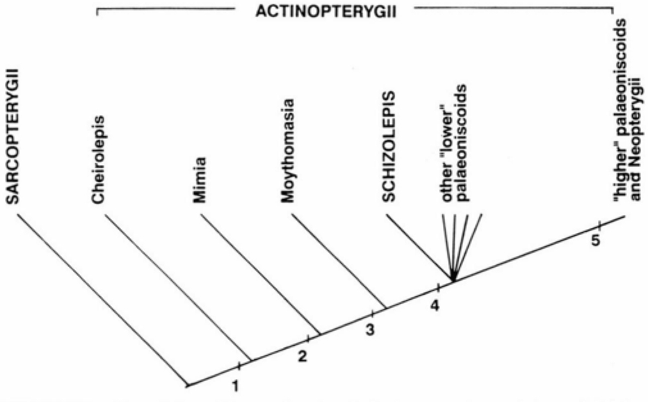

FIGURE 8—Provisional hypothesis of phylogenetic position of *Schizolepis manzanitaensis* relative to other primitive palaeoniscoid-grade actinopterygians. Characters at nodes: **1,** actinopterygian synapomorphies (see text); **2,** postparietal shorter than parietal; **3,** surangular bone present in lower jaw; **4,** suborbital(s) present; **5,** dermopterotic present (rather than separate inter- and supratemporals).

Functional implications—The squamation pattern of *S. manzanitaensis* leads to some speculation on the functional significance of a stiff jacket of deepened scales running along the sides of a fusiform body. A convergent pattern has been described in *Eurylepidoides* (Case, 1935) from the Permian of Texas and *Tanyrhinichthys* from the Late Pennsylvanian of New Mexico (Gottfried, 1987b), and in a number of relatively derived Mesozoic actinopterygians including *Peltopleurus, Habroichthys, Luganoia, Besania, Thoracopterus, Australosomus, Placopleurus, Cephaloxenus, Aspidorhynchus, Pleuropholis,* and *Ichthyokentema* (Brough, 1939; Burgin, 1990, and references therein).

One possible functional correlation of this squamation pattern is that the stiffened jacket of scales contributed to locomotory stability. The reduced flexure resulting from stiffening in the anterior part of the body of a fish with deepened flank scales would reduce axial body torsion during swimming, allowing for faster and more efficient locomotion (although probably at some cost to fine] movements). Reducing axial body torsion allows for the body to remain in a transverse plane during locomotion and results in a more efficient action of the caudal fin as the main source of locomotory power. Pearson (1981) speculated on this with regard to the extant cladistian *Polypterus*, which also has a stiff external jacket of rhombic scales (although they are not markedly deepened).

The need for increased efficiency of locomotion in very primitive actinopterygians could be connected with the absence in these forms of a hypochordal longitudinalis muscle in the caudal fin. Lauder (1989) maintained that this muscle, which has a line of action at an angle to the body axis, became well developed at the halecomorph level in actinopterygian phylogeny, and that presence of a hypochordal longitudinalis muscle was a major refinement in that it allowed for a greater control of the caudal fin during locomotion. The squamation on *Schizolepis* and other lower actinopterygians with convergent scale-morphology patterns may have helped to provide for more effective locomotion in the absence of a hypochordal longitudinalis muscle.

A second possible functional explanation for the squamation in *S. manzanitaensis* is that it aided in respiration. Brainerd et al. (1989) demonstrated that the extant cladistian *Polypterus senegalus* uses energy produced by the deformation and recoil of its bony-scaled integument to effect lung ventilation by aspiration. Recoil aspiration differs from buccal pulse pumping, in which air is brought into the mouth cavity and the mouth then closes, compressing the mouth cavity and forcing the air into the lungs (as in *Amia calva;* Brainerd et al., 1989). In contrast, recoil aspiration in *Polypterus* involves air being brought into a lung that is already expanding before the mouth closes. In the absence of a diaphragm or movable ribs, the negative inspiratory pressure needed to accomplish this is created by passive recoil of the body scales (the energy is loaded into the scales during exhalation). A somewhat comparable ventilation method is utilized by lampreys which, after compression of the branchial basket, use the subsequent recoil to draw in water and ventilate their gills (Randall, 1972). It is possible that the stiff integument of bony scales in *S. manzanitaensis* functioned in a similar way; the tightly sutured, relatively akinetic cranium would have rendered effective respiration via orobranchial expansion difficult in this form and in other palaeoniscoid-grade actinopterygians.

Acknowledgments

I thank S. G. Lucas for donating the holotype to the KUVP collection. Discussion and many helpful comments and criticisms were provided by H.-P. Schultze and G. Arratia. Additional helpful information and critical input were provided by **J.** Zidek. Preliminary work on this paper was done under the guidance of H.-P. Schultze while a graduate student at the University of Kansas. W. R. Jurgena, Kinney Brick Company, graciously allowed access to the quarry by the Kansas field crew and other field parties. The loan of specimens from the Carnegie Museum was facilitated by D. Berman. Field work at Kinney by the University of Kansas field party was supported by a grant from the New Mexico Bureau of Mines & Mineral Resources.

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Late Pennsylvanian palaeonisciform fish from the Kinney Quarry, New Mexico

David Bardack

Department of Biological Sciences, University of Illinois at Chicago, Chicago, Illinois 60680

Abstract—Six ?new palaeonisciform fish are present in the Kinney Brick Quarry (Late Pennsylvanian: Virgilian) in addition to those described elsewhere. They are represented by about 50 poorly preserved specimens which are not formally described but can be placed in six informal groups: (1) Type 1 is distinguished by shape of scales and a general lack of surface sculpture; (2) type 2 is distinguished by the possession of ossified centra; (3) type 3 is distinguished by the positions of the dorsal and anal fins; (4) type 4 is distinguished by overall body proportions and a relatively short head; (5) type 5 is distinguished by the form and sculpture of scales; and (6) type 6 is distinguished by the shape, ornamentation and distribution of scales. There are 12 actinopterygian genera present at Kinney, which is more than at other Mississippian/Pennsylvanian localities. Some taxa show similarities with the Bear Gulch (Mississippian) fauna.

Introduction

The actinopterygian fish assemblage from the Kinney Quarry presents an unusual diversity for such a limited geographic area. Six genera have been described and most of these are based on a small number of specimens. These six genera are: cf. *Bourbonnella*, an aeduellid (Gottfried, 1987b); *Tanyrhinichthys*, family undetermined (Gottfried, 1987a); *Schizolepis*, family undetermined (Gottfried, this volume); *Pyritocephalus*, a haplolepid (Huber, this volume); *Amphicentrum*, an amphicentrid (Zidek, this volume); and *Platysomus*, a bobasatraniid (Zidek, this volume), probably with two species.

In addition to these, another six actinopterygii, broadly grouped as palaeonisciforms, can be recognized among fossil fishes from the Kinney Quarry. These are identified from a sample of about 50 specimens in the collections of the New Mexico Museum of Natural History (NMMNH), the University of Kansas Museum of Natural History (KU), the Carnegie Museum (CM), the Black Hills Institute of Geological Research (BHI), the Museum of Natural History, and the Smithsonian Institution (SI). Of these six new fishes, half are represented by only one individual. The preservation of the new fishes is generally poorer than those heretofore described. These six species are represented, primarily, by incompletely preserved specimens. In most cases the bodies are split so as to show internal views of the scales. In some the matrix shows impressions of the lateral surface of the scales, but in most specimens the matrix is rather soft and the scales are friable so that it is difficult to remove them to obtain impressions of their outer surfaces. Heads are generally not preserved but in cases where they are, the bone is thin and there are many incomplete elements and these are often broken into a bony flour. Few individuals preserve features of the external bone surface and few impressions of these surfaces are left on the matrix. Fins are often missing or incompletely preserved.

Despite these limitations, some specimens, especially those from the denser gray shales, in contrast to the tan to yellowish limestones, show relatively well preserved structures. In view of these limitations and of the early stage of collection of Kinney Quarry fossils, it seems appropriate here only to provide preliminary accounts of these specimens and not to try to formally describe them. Many of the critical features needed to characterize and compare palaeonisciform fishes are not preserved in this material.

Some of the new fossils are unlike any known palaeonisciforms but several resemble fishes from the Mississippian Bear Gulch fauna. If better preserved material becomes available, the Kinney Quarry palaeonisciform fishes could contribute to our knowledge of palaeonisciform evolution during the Carboniferous.

Systematic paleontology

Class OSTEICHTHYES Huxley 1880
Subclass ACTINOPTERGII Woodward 1891
Infraclass ACTINOPTERI Cope 1871
Order "PALAEONISCIFORMES" Hay 1902
Family indet.

TYPE 1

Material—KU 104418, an almost intact fish (Fig. 1).

Description—This individual (Fig. 1) is about 9 cm long and 1.8 cm in maximum depth. The incomplete dorsal fin arises about 4 cm behind the incompletely preserved front of the head. The anal fin, with about 50 rays, arises below the posterior end of the dorsal fin. The pelvic fin originates in front of the dorsal and has about 15 rays and the pectoral fin has about 35. The pectoral fin appears to arise from a lobed base. All fin rays are segmented, but not branched. The body is entirely covered by scales with perhaps 33 in the linear distance between the posterior of the head and the caudal inversion. At midbody, there are 14-15 vertical scale-rows. The scales are generally rhombic with a smooth surface (Fig. 2). A few curved ridge lines appear on anterior, midbody scales. There are no peg-like processes for connection to grooves in the scales above. Scales on the upper

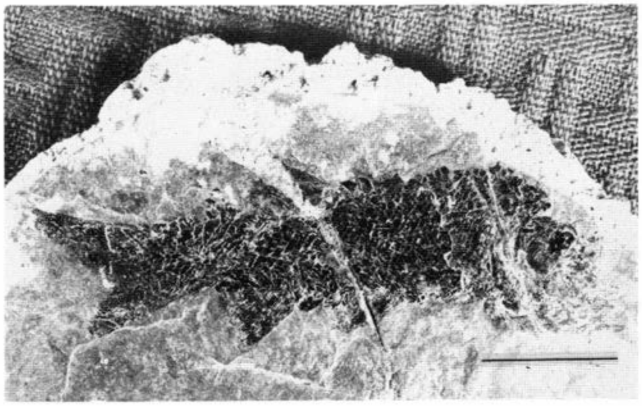

FIGURE 1—Articulated palaeonisciform, Kinney Quarry, type 1 (KU 104418). Scale bar is 2 cm.

FIGURE 2—Scale from below dorsal fin of palaeonisciform, Kinney Quarry, type 1 (KU 104418). Anterior to right. Scale bar is 1 mm.

lobe of the caudal fin are slender, rhomboidal and at least twice as long as high.

Discussion—Without being able to examine bones of the head, the scales provide the only basis for comparison with other palaeonisciforms. Based on the shape of the scales and the general lack of surface sculpture, this fish appears to differ from known palaeonisciforms. *Sphaerolepis,* of the Bohemian Carboniferous basins (Stamberg, 1989), is usually considered to have smooth scales, but on that fish the scales are basically cycloid in outline and younger specimens show concentric growth lines while older specimens have multiple, posteriorly directed denticulations.

TYPE 2

Material—CM 47874, almost entire specimen lacking anterior two-thirds of head (Fig. 3). Tail and anterior part of head are in part and counterpart.

Description—The single specimen measures about 8.5 cm from the middle of the head to the end of the upper lobe of the caudal fin. Perhaps 1 cm of the head is missing but enough is preserved to determine that the hyomandibula is oriented strongly obliquely. The body is slender (Fig. 3) and about 1.3 cm in maximum depth. Midbody margins are difficult to ascertain due to the lack of scales. The dorsal fin has 29 rays and begins only 1.5 cm anterior to the caudal fin. The rays are segmented but not divided. The anal fin has 24 rays and begins below the middle of the dorsal fin and it is preceded by some fulcral scales. There is a broad pelvic fin with perhaps 15 rays in the midbody region. The pectoral fin arises from the side of the body. The elongate, heterocercal, caudal fin shows a lower lobe almost as long as the upper. This fin is deeply cleft and preceded by about 10 short fulcral scales.

Bones of the preserved part of the head and shoulder girdle are not individually distinguishable. The most striking features of this specimen are the almost complete absence of scale cover and the preservation of ossified centra. While ossification of centra in palaeoniscoid fishes has been noted (Fritsch, 1895; Schultze & Chorn, 1986), such centra have been reported principally on the basis of isolated specimens. 40-45 compressed centra extend from the head at least to the level of the dorsal fin in the Kinney Quarry specimen. In addition to centra, neural arches, neural spines and transverse processes appear as densely ossified elements. Due to the compression and small size of the centra, it will be difficult to determine their structure histologically. It is not clear whether ossification is limited to a peripheral chordal sheath or if the entire centrum is ossified, but the latter is likely because of the thickness of the preserved material. The neural spines and transverse processes are short and stout. Impressions of a few ventral ribs are seen in midbody.

Few scales are developed on the body. A row of scales appears along the area of the lateral line. There are also small, square-shaped scales (about 0.5 mm in length) along the body lobe supporting the caudal fin. These are smooth-surfaced scales without evident denticulation. Finally, some scales are seen just behind the head and above the vertebral column. These are barely 1 mm high and about 0.75 mm long. Impressions of their external surface show a series of perhaps 4-5 anteroposteriorly elongate ridges and the posterior margins are characterized by 5-7 stout, elongate denticulations.

The lack of scales on large sections of the body is probably not due to loss of the scales since they are uniformly missing below the vertebral column and along much of the upper

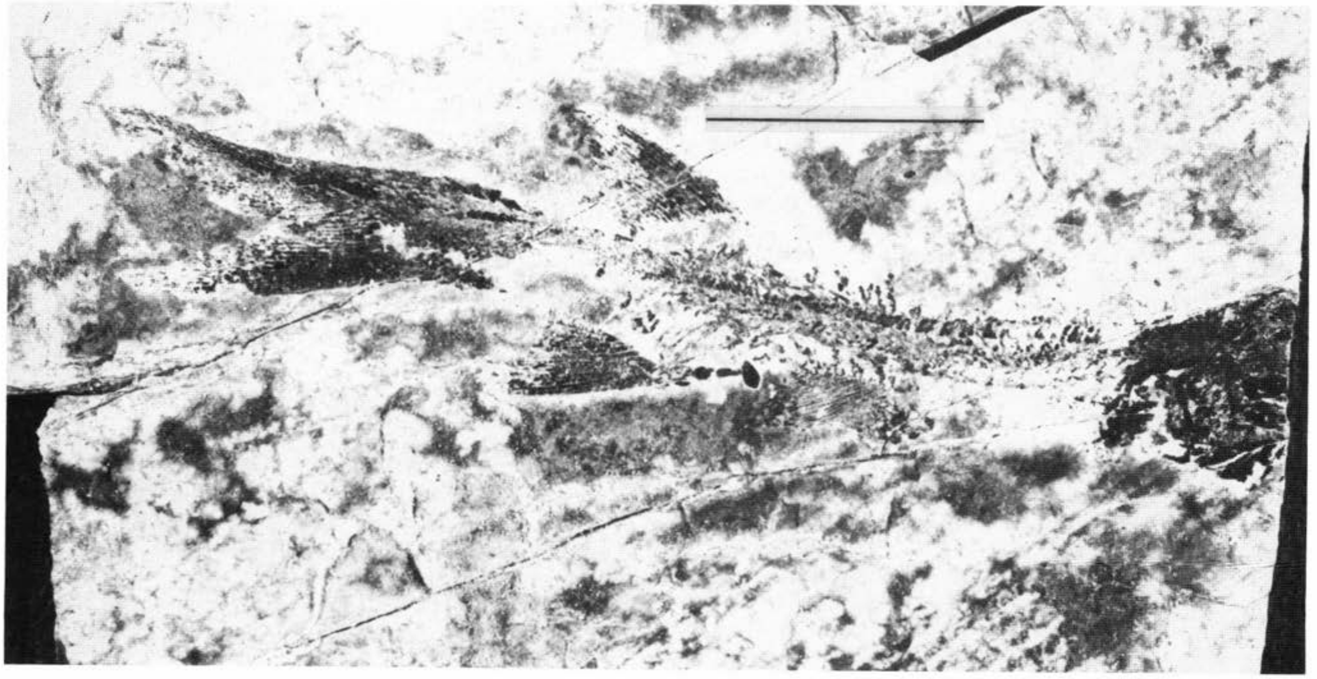

FIGURE 3—Articulated palaeonisciform, Kinney Quarry, type 2 (CM 47874). Scale bar is 2 cm.

body. There is no indication that missing scales were broken off from the remaining scales during fossilization. The well-ossified centra suggest that this is a mature individual on which scalation should have already developed.

Discussion—As in the case of the first fish described, this single specimen appears to be unique to the Kinney Quarry. It is broadly speaking a palaeonisciform because it exhibits an oblique hyomandibula, fewer anal fin pterygiophores than fin rays, a strongly heterocercal tail, and, where present, rhomboidal, ganoine covered scales. The ossified centra are quite unusual and hopefully additional material may clarify their structure. Fritsch (1895) described ossified centra preserved *in situ* in *Sceletophorus* but the scales of this fish are quite different from those of the Kinney Quarry fish. Similarly, *in situ* centra have been reported from several Bear Gulch (Namurian A) actinopterygii (Lowney, 1980) and in haplolepids (Baum & Lund, 1974) from the Pennsylvanian of Ohio, but these fishes also differ in many details from those from the Kinney Quarry.

TYPE 3

Material—NMMNH P-14371 part and counterpart, posterior three-quarters of body; CM 47875 complete specimen (Fig. 4); CM 47876 more or less complete specimen, in part and counterpart.

Description—CM 47875 (Fig. 4) is about 8.5 cm in total length and 1.5 cm in maximum depth. The dorsal margin of the body forms a long, straight line and the dorsal fin, with perhaps 15 branched rays, arises 4.5 cm from the front of the head. The anal fin is incompletely preserved but it can be seen to arise just posterior to the dorsal fin. The caudal fin is probably equilobate (CM 47876). The pelvic fin, with about 10 rays, arises anteror to the dorsal fin at about midbody.

The head measures about one-quarter the length of the body (excluding the caudal fin). Bones of the roof of the head show a pattern of elongate rugose lines while bones toward the front of the head show a more pustulate pattern. The hyomandibular is angled steeply posteriorly.

The body is entirely covered by small, rectangular scales almost all of which are seen in medial view. About 70 scales are in place from the area of the shoulder girdle to the caudal scale inversion and a single vertical row contains about 30 scales. A low, vertical ridge characterizes the inner surface of the scales. The lateral surface of a few scales from different parts of the body exhibit a few anteroposterior ridges. Each scale ends posteriorly in 3-5 spike-like processes. These processes are greater in number on midbody scales and fewer in number on scales lying dorsally just behind the head or low on the peduncle. The posterior scale border is deeply deft between these processes, especially where there are fewer of them (Fig. 5).

Discussion—Within the Kinney Quarry groups, type 3 palaeonisciforms are distinguished by the remote positions of the dorsal and anal fins and the small number of dorsal rays. The numerous scales are quite small and characterized by stout, deeply cleft posterior processes. Skull surface rugosity is found on many palaeoniscoids but the elongate, broadly rounded quality of the pattern along the roof in contrast to the shorter, more pustulate pattern on anterior skull bones appears to be characteristic.

TYPE 4

Material—NMMNH P-14368, almost entire fish (Fig. 6).

Description—The single specimen is about 9 cm in length from the anterior end of the head to the caudal inversion and about 3.8 cm in maximum depth (Fig. 6). Thus, it is relatively deeper than the other types described above. About 1.5 cm of the forked tail is probably missing. The dorsal fin has about 14 articulated rays, of which the anterior 8 show flattened, proximal segments. This fin arises about 4.5 cm behind the front of the head. The anal fin, with perhaps 16 rays, arises behind the dorsal fin. The pectoral fin emerges

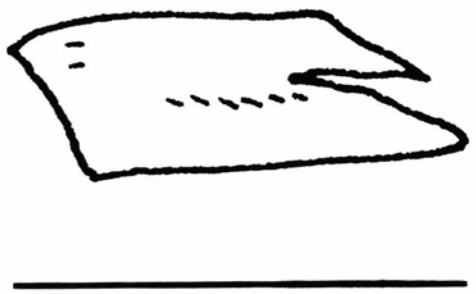

FIGURE 5—Scale from above anal fin of palaeonisciform, Kinney Quarry, type 3 (CM 47876). Anterior to left. Scale bar is 1 mm.

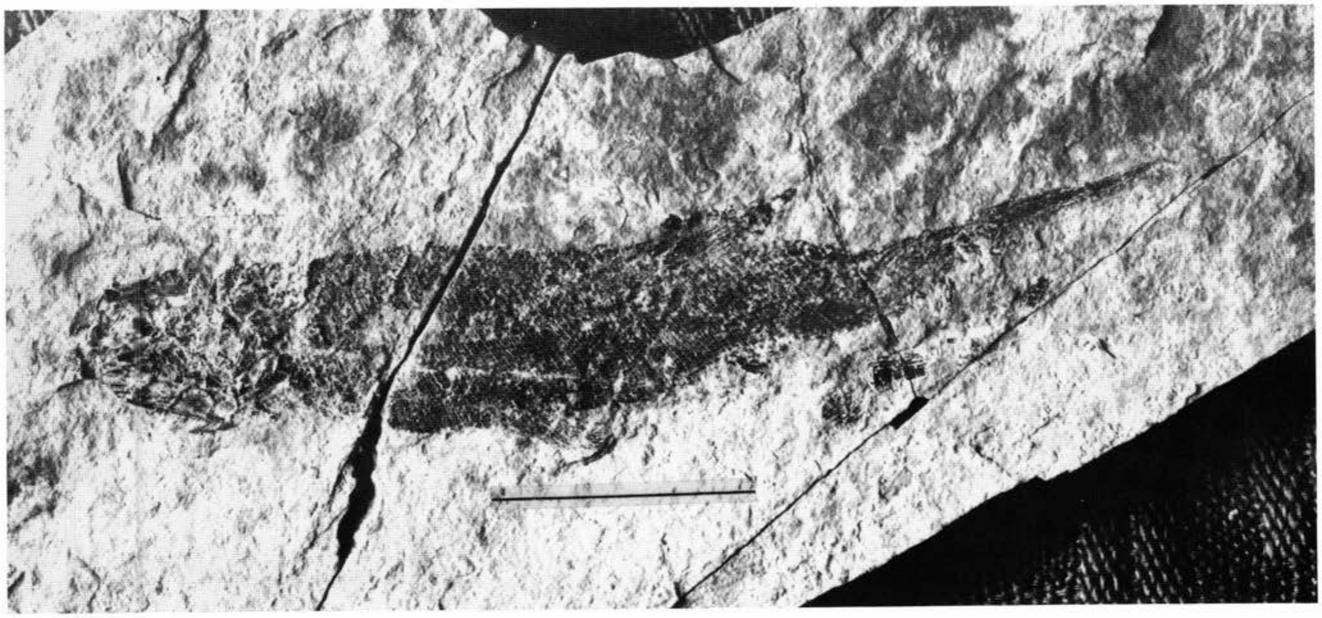

FIGURE 4—Articulated palaeonisciform, Kinney Quarry, type 3 (CM 47875). Scale bar is 2 cm.

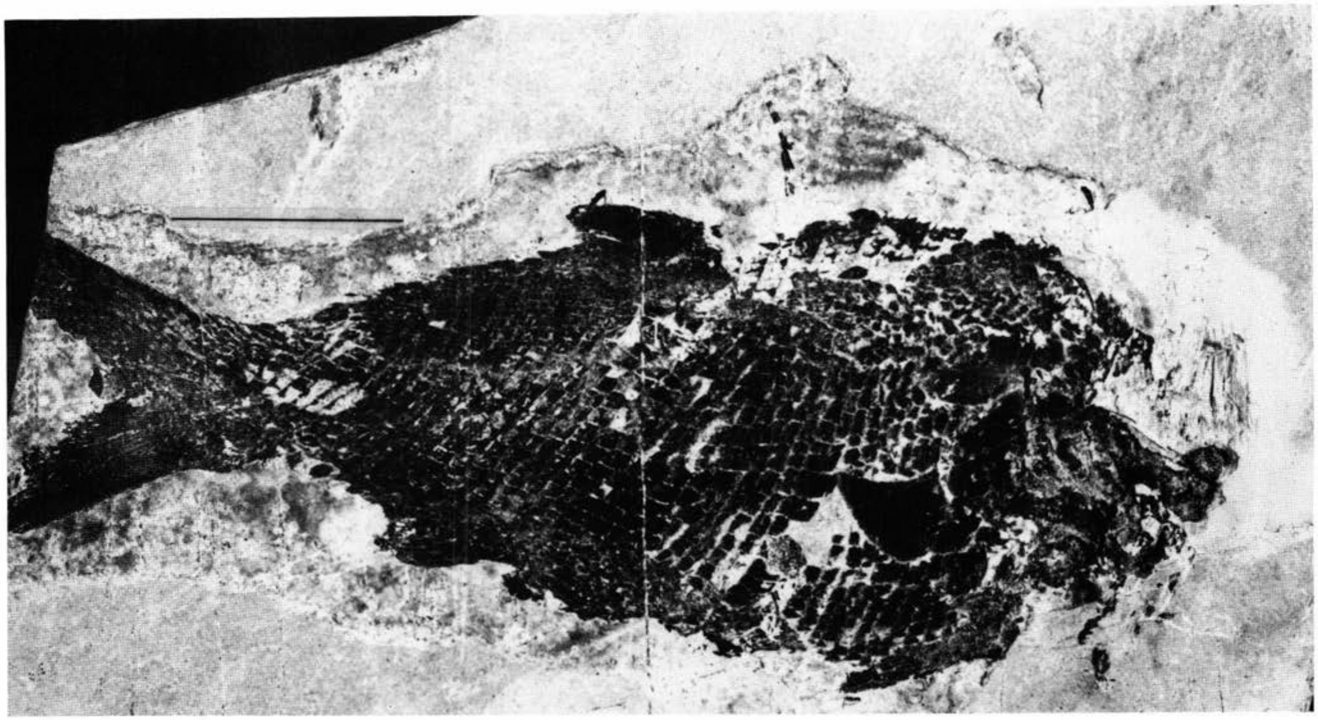

FIGURE 6—Articulated palaeonisciform, Kinney Quarry, type 4 (NMMNH P-14368). Scale bar is 2 cm.

low on the body. The head is contained about three and a half times in the body length. Unfortunately, the bones of the head are fragmentary. It appears that the hyomandibula is oriented more vertically than in the forms described above.

Along the midbody, an anteroposterior row of about 33 scales is present. There are about 24 scales in a vertical row with those toward the dorsal border being somewhat smaller than those located more ventrally. Most scales are seen in interior view. Scales of the midbody are about one and a half times longer than high and are crossed by a vertical ridge one-half to two-thirds of the way behind the anterior border. External surfaces of these scales, or their impressions, show a series of about 6 horizontal to posteroventrally directed ridges tapering into short posterior spines. About 12 fulcural scales precede the upper lobe of the caudal fin and fewer lie before the anal fin. These scales bear elongate ridges.

Discussion—Within the Kinney Quarry fish groups, this type differs in its body proportions, and in possessing a relatively short head with, presumably, a short gape, and ridged scales. The single specimen preserves few cranial or scale features and is thus difficult to compare with palaeonisciforms from other localities. In body proportion it is somewhat like aeduellids from France (Heyler, 1969) but not like the specimen of cf. *Bourbonnella* described by Gottfried (1987a) from the Kinney Quarry.

TYPE 5

Materials—BHI 2034, complete fish except for caudal peduncle and fin, preserved in a gray-black shale (Fig. 7); NMMNH uncataloged, whole fish shown in outline by disorganized scales and head bones and preserved in a grayish tan limestone; NMMNH P-14373, body twisted and poorly preserved; NMMNH P-14367, whole fish in part and counterpart (Fig. 8); KU 104414, nearly whole fish in part and counterpart; CM 47877, poor head and part of body; CM 47878, fragments of body and head.

Description—Among these specimens are the largest actinopterygians of the Kinney Quarry (Fig. 7). Measurements of the 3 best preserved and least distorted individuals show total lengths of 12 to 22 cm and standard lengths of 9 to 15 cm. Body depths range from 2.5 cm to 6 cm. The bodies of these fishes are not as deep (Fig. 8) as that of type 4 (Fig. 6). The dorsal fins on the larger specimens arise about 10 cm behind the front of the head and the anal fin just before the end of the dorsal. The triangular dorsal fin rises at an obtuse angle from the upper body margin and has a height of about 4 cm, and a basal length of about 4 cm. There are about 40 dorsal fin rays. The anterior rays of this fin are heavily coated with ganoine. Except for the most distal anterior rays, there seems to be no branching. The anal fin is more triangular with a shorter base and 36-38 fin rays. BHI 2034 shows a midbody pelvic fin with about 12 segmented and distally dividing rays. A large, broad-based, pectoral fin with 30 rays arises low on the body of this specimen. The first ray is thickened and composed of a series (about 5 per mm) of irregularly transverse segments which are fused. The anterior margin of this fin ray bears fine denticulations. Some of these features are probably due to the large size of this fish.

The head is contained two to two and a half times in the body length. The lower jaw (BHI 2034) is 4.5 cm long and supported by the most strongly angled suspensorium of the palaeonisciforms discussed here. Along the upper and lower jaw, about 10 tall teeth are separated by 3-4 smaller, spike-like teeth. The jaw bones are characterized by an elongate rugose lateral surface grading into a more pustulose pattern anteriorly and along the dental margin.

A complete scale count cannot be obtained from any specimen. BHI 2034 shows 50 scales along the body length to a point probably close to the caudal inversion. All seven specimens share a strongly rugose scale pattern. The bony bases of the scales are thick and probably proportionately more so than in the other Kinney fishes described here. Scales above the midbody are elongate and rhomboidal in outline with a dorsoanterior projection. A broad surface rugosity runs generally anteroposteriorly and the ridges are often divided. Posteriorly, they end in a set of 5-7 processes which do not appear to project beyond the articulating ends of the scales (Fig. 9). These processes are usually thicker on

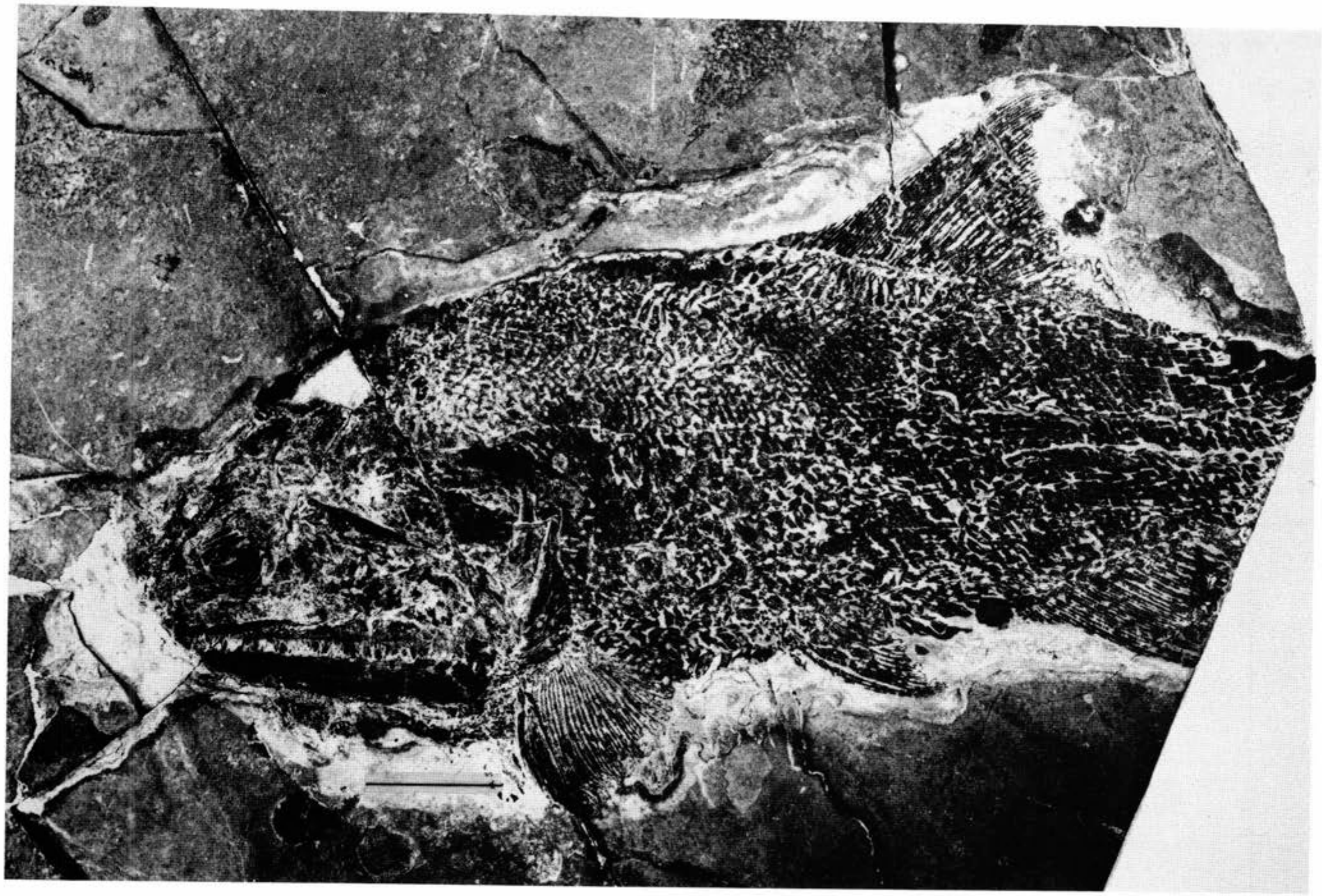

FIGURE 7—Articulated palaeonisciform, Kinney Quarry, type 5 (BHI 2034). Scale bar is 2 cm.

midbody than more ventral scales. Scale ridges are thickly covered with ganoine. Broad, ridged scales characterize the middorsal line and probably are continuous with fulcral scales which are heavily ridged.

Discussion—This type of fish is distinguished by its scale form and sculpture and includes the largest of the Kinney Quarry palaeonisciforms. Similar rugose scales occur on many palaeonisciform fishes including *Elonichthys* (Schultze & Bardack, 1987) and *Rhadinichthys*.

TYPE 6

Material—KU 104411, part and counterpart of body; KU 104412, part and counterpart of body; KU 104413, part and counterpart of body and rear of head; KU 104415, part and counterpart of whole fish (Fig. 10); KU 104417, distorted body; NMMNH P-14374, head and anterior part of body; NMMNH P-14375, part and counterpart of body; CM 47879, part of head and body; CM 47880, head and body; CM 47881, part of body; CM 47883, body; CM 47884 body; SI

FIGURE 8—Articulated palaeonisciform, Kinney Quarry, type 5 (NMMNH P-14367). Scale bar is 2 cm.

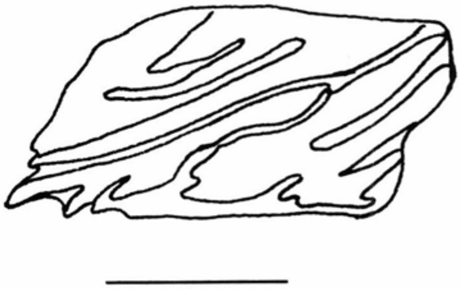

FIGURE 9—Scale from above anal fin of palaeonisciform, Kinney Quarry, type 5 (BHI 2034).

446288 part and counterpart of body; SI 446289 part and counterpart of body. Possible representatives of this taxon are: CM 47885, body viewed ventrally; NMMNH P-14362, almost complete fish.

Description—Based on the five to six complete specimens, this type ranges from about 7-12 cm in standard length and 1.7 to 2.5 cm in depth. These are elongate, more slender fishes (Fig. 10) than those of type 4 (Fig. 6). The snout is projecting (KU 104415). Fins are poorly preserved. The dorsal fin is preserved in NMMNH P-14375. It has more than 15 rays and originates at a point three-quarters of the way between the front of the head and base of the caudal fin. The anal fin has about a dozen rays and begins just behind the start of the dorsal fin. Cranial elements are poorly preserved. The eye is large and is about one-half the length of the head (KU 104415). Some specimens show broadly rugose sculpture on the skull roof while the surface of the lower jaw is characterized by linear rugosity. The lower jaws bear a band of minute teeth (KU 104417).

The shape and pattern of the scales and their distribution distinguish this fish. The count of scales from behind the shoulder girdle to the caudal inversion ranges from 37-41. Dorsoventrally, at midbody, there are 27-30 scales. Scales on the lower abdomen are compressed, three to four times longer than high, and comprise at least a dozen of the scales in a vertical column. The transition from these elongate scales to the more rhombic scales of the central part of the body is rapid and occurs over only 2-3 scales. Toward the middorsal surface, scales again become somewhat shallower and longer. Scales along the midbody are generally rhombic in outline from the caudal inversion to the level of the pelvic fin, where they gradually become more elongate dorsoventrally with their height attaining twice their length. Viewed internally, a broad process rises from the dorsal margin to articulate with a groove on the scale above. These processes emerge from a vertical ridge running across each scale. The surface features of these scales also distinguish this group of fishes. Basically the scales (Fig. 11), regardless of size or position, show 1-7 thin ridges along the anterolateral surface. These curve anteriorly onto the ventrolateral surface. These ridges are more numerous on the midbody scales. The ventral abdominal scales terminate in two posterior, stout processes. Scales of midbody are more rectangular to about twice as high as long and end in 5-7 thinner denticulations. Scales along the peduncle are more elongate and terminate in perhaps 3 stout processes.

Discussion—Overall scale pattern and surface structure distinguish this Kinney Quarry fish. In some respects these specimens are similar to *Rhadinichthys* with which they share a pointed snout and *Mesopoma* which has a more rounded snout. *Rhadinichthys* from the Bear Gulch limestone also shows somewhat enlarged anterior midbody scales like the Kinney Quarry fishes. If better cranial material is found, comparisons with these genera would be worthwhile, for they appear not only somewhat morphologically similar, but also occur (Montana) in relatively close geographic proximity to the Kinney Quarry.

Conclusions

The Kinney Quarry actinopterygians may provide a different perspective on the evolution and diversification of

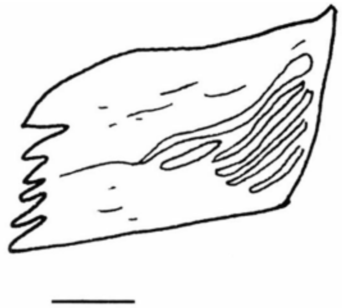

FIGURE 11—Scale from midbody of palaeonisciform, Kinney Quarry, type 6 (KU 104417). Anterior to right. Scale bar is 1 mm.

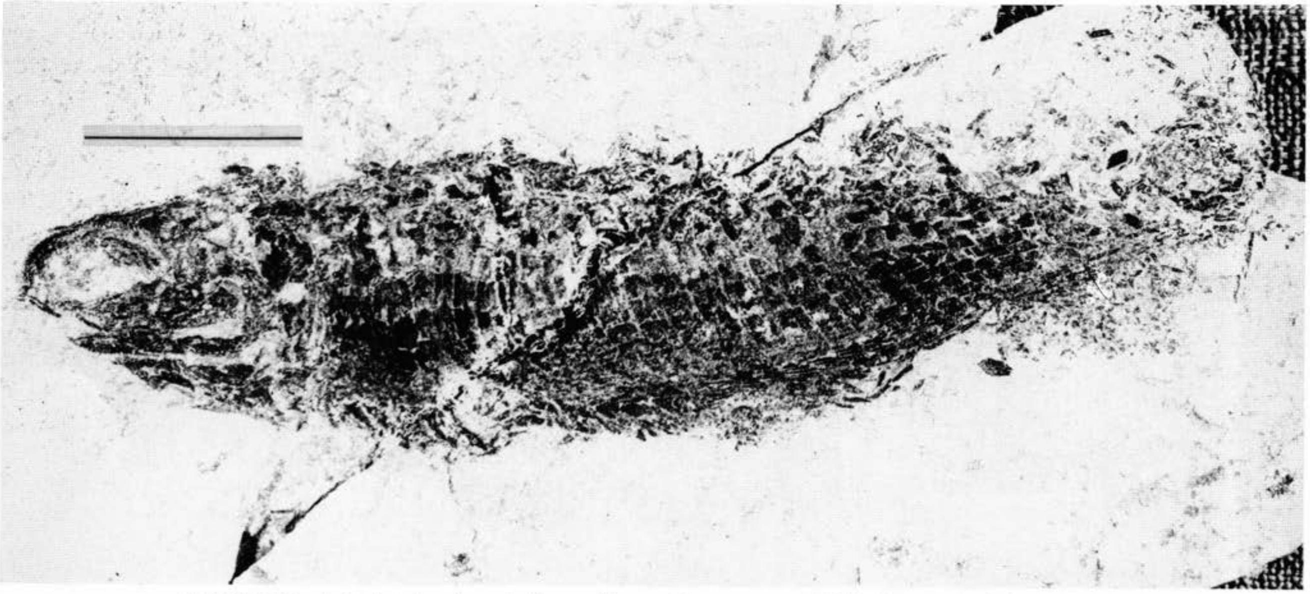

FIGURE 10—Articulated palaeonisciform, Kinney Quarry, type 6 (KU 104415). Scale bar is 2 cm.

these fishes than we now have from the better known sites in Europe and the eastern United States. Efforts to collect fossil fishes from the Kinney Quarry have been relatively limited compared to work at several other late Paleozoic sites in Europe and North America. Also, exposures yielding fishes at the Kinney Quarry are limited in extent. Nevertheless, these efforts appear to have yielded about a dozen actinopterygian genera. It is difficult, for many reasons, to compare faunas from different localities. However, a recent generic level survey of five United States and two European Pennsylvanian localities which represent different paleoenvironments shows about 6 actinopterygian genera, at most, at any one of these 7 sites (Maples & Schultze, 1988). Had these authors included some British Mississippian sites, the number of actinopterygian genera would have been closer to that at Kinney. The still incompletely described diversity of actinopterygians from the Mississippian (Namurian A) Bear Gulch fauna appears to have more than 10 such genera (Lowney, 1980), which is comparable to Kinney. However, in total numbers Kinney is distinctive. Several genera from Kinney are more similar to those from the older Bear Gulch fauna or some late Carboniferous (Pennsylvanian) European sites rather than those from other, more or less contemporaneous, deposits in the eastern part of North America. Further study of the Kinney palaeonisciform actinopterygians, and hopefully the discovery of better preserved fossils, should provide evidence to test these comparisons with due regard to taxonomic and ecological factors.

Acknowledgments

I thank Jiri Zidek, Phillip Huber, Hans-Peter Schultze, Peter Larson and Michael Gottfried for assistance at various stages of this project.

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Coelacanth fish (Actinistia, Sarcopterygii) from Late Pennsylvanian of Kinney Brick Company Quarry, New Mexico

Hans-Peter Schultze

Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045-2106

Abstract—The coelacanth from the Late Pennsylvanian of Kinney Brick Company Quarry is redescribed based on new material. Postcranial features place the new form within the family Coelacanthidae, above the phylogenetic level of *Rhabdoderma.* The postcranial features are distinct from all other actinistians, but are not sufficient for defining a new genus and species.

Introduction

Coelacanth specimens are rare in the exposed (Pine Shadow Member) part of the Wild Cow Formation at the Kinney Brick Company Quarry (in the Manzanita Mountains east of Albuquerque). Remains (scales, fin spines, neural arches, and pelvic girdle) of two specimens (USNM 187143 and 187149) were described by Zidek (1975) as Coelacanthidae g. et sp. indet. Additional material has been collected by members of the Black Hills Institute from the shaly limestone in the lower part of the section (units 2-4 of Lucas & Huber, 1991), and by a six-man field crew of the University of Kansas in June 1984, including one specimen (KUVP 82702) from the underlying massive limestone. Thus, six coelacanth specimens are known from the locality, and of those only one (BHI 1581) is nearly complete and shows the typical actinistian diphycercal tail with a supplementary lobe.

Abbreviations: BHI = Black Hills Institute, Hill City, South Dakota; KUVP = University of Kansas, Museum of Natural History, Division of Vertebrate Paleontology; USNM = U.S. National Museum, Smithsonian Institution, Washington, D. C .

Systematic paleontology

Class OSTEICHTHYES Huxley 1880
Subclass SARCOPTERYGII Romer 1955
Order ACTINISTIA Cope 1871
Family COELACANTHIDAE Agassiz 1843

UNIDENTIFIED GENUS AND SPECIES

1975. Coelacanthidae g. et sp. indet., Zidek, pp. 18, 20, fig. 4A, B.
1991. Unidentified coelacanth: Lucas & Huber, table 1.
1991. Coelacanthidae gen. et sp. indet. of Zidek 1975: Cloutier & Forey, table 1.

Material—USNM 187143 (counterparts: fin rays and scattered scales; Zidek, 1975: fig. 4A), USNM 187149 (neural arches, fin rays, pelvic girdle, impressions of scales: Zidek, 1975: fig. 4B), KUVP 82700 (urohyal and clavicle, part and counterpart), KUVP 82701 (parasphenoid, part and counterpart), KUVP 82702a-c (disarticulated head with gular, gill arches, scales, fin rays), BHI 1581 (nearly complete specimen, part and counterpart).

Locality and horizon—Kinney Brick Company Quarry, NW1/4 NW1/4 SE1/4 *sec.* 18, T9N, R6E, Bernalillo County, New Mexico; Pine Shadow Member, Wild Cow Formation, Madera Group, Virgilian, Upper Pennsylvanian. All specimens except KUVP 82702 are from the lower units 2-4 which are rich in fish (Lucas & Huber, 1991); specimen KUVP 82702 has been found by A. Mebrate in the massive dark-gray limestone of unit 1.

Description—The nearly complete specimen BHI 1581 (Fig. 1) is 18 cm long. The head comprises 25% of the total length. The body is dorsoventrally compressed. The head is split obliquely so that the arrangement of the head bones cannot be seen. The impressions of parts of bones show an ornament of round or elongated tubercles. Individual bones of the head are not discernible except for the operculum and the postparietal, both seen from the inside. The straight dorsal margin and the concave anterior margin of the right operculum meet in a pointed anterodorsal corner and are connected by a convex posterior margin. The inner side of the right postparietal is seen dorsal to the operculum. The width of the anterior part of the right postparietal comprises 65% of the width of the posterior part. Below the opercu-

FIGURE 1—Coelacanth from Kinney Brick Company Quarry, specimen BHI 1587.

lum, the right clavicle is preserved, the anterior part of it only as an impression. Parts of right and left cleithrum are visible. The counterpart shows angular, parts of one gular from the inside, anterior skull roofing bones from the inside, gill arches, and toothed parts of the pterygoid. The parasphenoid (Fig. 2A) can be reconstructed to a large extent from part and counterpart of specimen KUVP 82701. It is a dumb-bell-shaped bone with a broad anterior portion and the middle part bearing small, slender teeth. Specimen KUVP 82700 consists of an urohyal and a clavicle. The ossified part of the urohyal (Fig. 2B) forms a long anterior shaft which diverges posteriorly into two processes. Specimen KUVP 82702 from horizon 1 represents an assemblage of skull bones, gill arches, fin rays, and scales. There is one plate whose shape is very similar to the "pelvic plate" figured by Zidek (1975: fig. 4B). The plate carries a lateral-line canal from which numerous tubules branch off into each of the wavy elevations on the margin of the plate. It is a plate of the cheek, possibly a preoperculum.

The postcranial skeleton is known from specimen BHI 1581 and isolated elements such as scales. The first dorsal fin lies opposite to the pelvic fins, as are the basal plate of the first dorsal fin and that of the pelvic girdle. The first dorsal fin carries 8-9 robust fin rays, whereas the fin rays of the second dorsal and anal fins are delicate. The second dorsal and anal fins are opposite each other, whereas the basal plate of the second dorsal fin lies anterior to that of the anal fin. The ossified lung is seen in two parts, one just behind the shoulder girdle and the other in front of the anal fin. That may represent a situation comparable to *Coelacanthus granulatus* (Schaumberg, 1978: fig. 21), where the anterior part is separated from the posterior part by a narrow passage (isthmus) above the pelvic fins. The basal plate of the first dorsal fin (Fig. 3A) has an antero-posteriorly elongated oval shape; its length is more than double its depth. The basal plate of the second dorsal fin (Fig. 3B) has the shape of a two-pronged fork with the anterodorsal prong about three times deeper than the anteroventral one and the anterodorsal prong one-quarter shorter than the anteroventral one. The posterior part where the two prongs join is as long as the anterodorsal prong. The basal plate of the anal fin (Fig. 3D) has a straight posterior margin and a convex lower anterior margin; it is narrow at its preserved dorsal end. The dorsal end is not smooth, and it thus cannot be decided whether the plate bore a dorsal narrow extension as in *Hadronector* (Lund & Lund, 1985: fig. 35), *Polysteorhynchus* (Lund & Lund, 1985, fig. 46), *Allenypterus* (Lund & Lund, 1985: fig. 57), *Rhabdoderma (Dumfregia) huxleyi* (MoyThomas, 1937: fig. 12), or *Rhabdoderma elegans* (Forey, 1981: fig. 9). The basal plate is preserved in vertical position and forms an oblique angle with the radials which lie on the posterior part of the ossified lung. It seems therefore more likely that the preserved shape is real; it is similar to that of *Coelacanthus granulatus* (Moy-Thomas, 1935: fig. 11b).

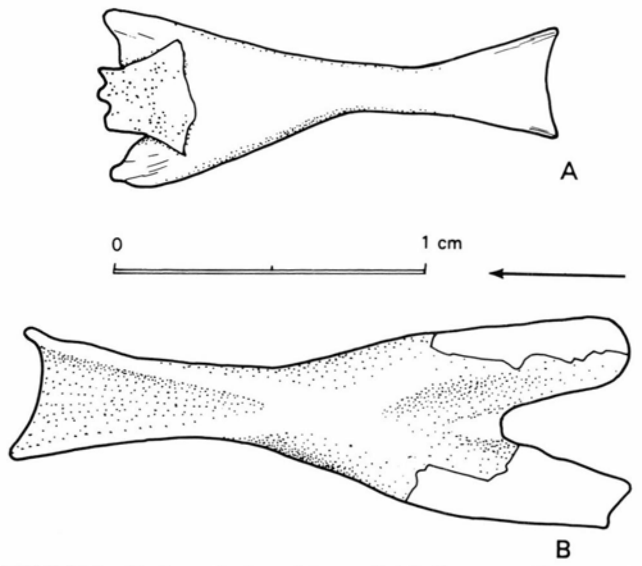

FIGURE 2—Coelacanth from Kinney Brick Company Quarry. **A,** Parasphenoid, specimen KUVP 82701; **B,** urohyal, specimen KUVP 82700. Anterior to the left.

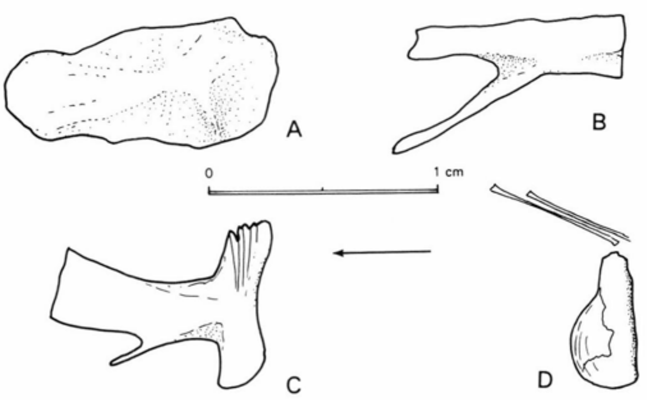

FIGURE 3—Coelacanth from Kinney Brick Company Quarry, specimen BHI 1587. **A,** Basal plate of first dorsal fin; **B,** basal plate of second dorsal fin; **C,** pelvic girdle; **D,** basal plate of anal fin. Anterior to the left.

Both pelvic girdles are preserved in specimen BHI 1581. The reconstruction from part and counterpart shows a small T-shaped plate (Fig. 3C; smaller than the basal plate of the first dorsal fm). A prong-like process branches off from the anterior part of the plate. The crossbar is half as long as the anterior part. It ends rounded laterally and in small finger-like processes medially. The plate identified as a pelvic basal plate by Zidek (1975: fig. 4B) does not have this shape and may be a head plate in association with gular (or angular) plates. The anal plate is a vertically oriented, elongated plate with a convex anterior margin and a nearly straight posterior margin; a long dorsal process is not visible. The caudal fin has the diphycercal tail with a supplementary lobe typical of coelacanths; it is dorso-ventrally compressed in specimen BHI 1581, which is a preservational artifact. The dorsal lobe has 15 radials and fin rays, and the ventral lobe has 12.

All scales in specimen BHI 1581 show only the free field with parallel ridges; tubercles appear anterior to the ridges in one or two scales. The latter feature is very well seen in an isolated scale (Fig. 4); the whole posterior, free field is covered with round to elongate tubercles. This is a very primitive feature according to Cloutier (1991) and is known to occur only in Devonian actinistians. Zidek (1975: fig. 4A) described tubercles in the transitional zone between the free and the covered field of the scale. **I** could not see the wrinkles (herringbone pattern) on the ridges described by Zidek (1975).

Comparison—It is obvious from the description of the material that only postcranial features are available for comparison of the Kinney coelacanth with other coelacanth genera. The ornament of the scales and the shape of the basal plates of the fins are distinct enough to be used for comparison.

The Kinney coelacanth does not show the special arrangement of converging ridges on the free field of the scales of *Rhabdoderma* (Forey, 1981: fig. 10) or *Synaptotylus* (KUVP 59079); the ridges run more or less parallel as in most coelacanths. The tubercles are present only in post-Devonian coelacanths (Cloutier, 1991); however, Moy-

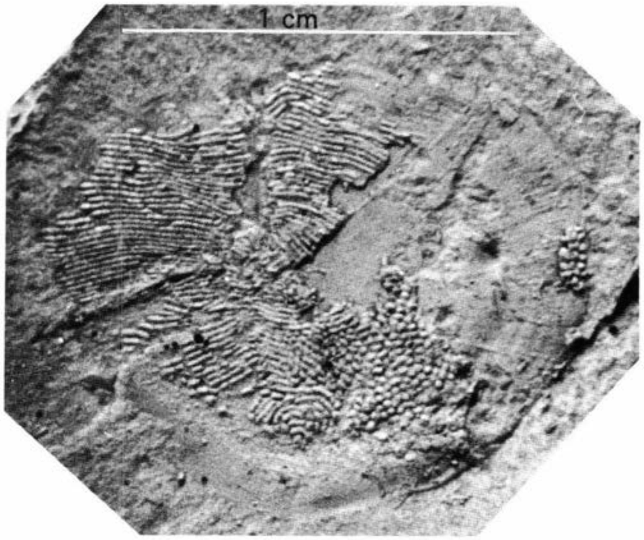

FIGURE 4—Coelacanth from Kinney Brick Company Quarry, specimen USNM 187149, scale (photograph of latex peel). Anterior to the left.

Thomas & Westoll (1935: fig. 12) described tubercles on the free field of scales of *Coelacanthus granulatus.*

The urohyal has the typical coelacanthid shape; it is more robust than in *Rhabdoderma* (Forey, 1981: fig. 3B), but not as broad posteriorly as in *Synaptotylus.* It is very similar to the urohyal of *Coelacanthus granulatus* (Moy-Thomas & Westoll, 1935: fig. 5).

The parasphenoid shows a similarity with that of *Synaptotylus* (Echols, 1963: fig. 2) in having one median and two lateral extensions on its anterior margin, but differs in the overall shape.

The basal plate of the first dorsal fin (Fig. 5) lacks the ventral processes which occur in the plate of *Rhabdoderma elegans* (Moy-Thomas, 1937: fig. 11; Forey, 1981: fig. 9), *Caridosuctor* (Lund & Lund, 1985: fig. 19), *Lochmocercus* (Lund & Lund, 1985: fig. 68), and *Polyosteorhynchus* (Lund & Lund, 1985: fig. 46). The plate is as uncharacteristic in its shape as that of *Allenypterus* (Lund & Lund, 1975: fig. 57), *Hadronector* (Lund & Lund, 1985: fig. 35), or *Coelacanthus granulatus* (Moy-Thomas & Westoll, 1935: fig. 10). The basal plate of the second dorsal fin (Fig. 6) matches that of *Coelacanthus granulatus* (Moy-Thomas & Westoll, 1935: fig. 11a) in all features, and differs completely from all Bear Gulch coelacanths (Lund & Lund, 1985: figs. 19, 35, 46, 57, 68). The basal plate of the second dorsal fin of *Rhabdoderma elegans* (Forey, 1981: fig. 9) has anterior processes like the Kinney coelacanth, but the anterodorsal process is twice as long as that of the posterior part and is as narrow as the anteroventral process.

The pelvic girdle (Fig. 7) has a characteristic shape which does not compare with the more elaborate pelvic girdles of *Caridosuctor* (Lund & Lund, 1985: fig. 30), *Rhabdoderma* (MoyThomas, 1937: fig. 10A; Lund & Lund, 1985: fig. 73A), or *Synaptotylus* (Echols, 1963: fig. 6B), nor the simple pelvic girdle of *Dumfregia* (Lund & Lund, 1985: fig. 15), *Allenypterus* (Lund & Lund, 1985: fig. 57), *Lochmocercus* (Lund & Lund, 1985: fig. 68), or *Polyosteorhynchus* (Lund & Lund, 1985: fig. 46). *Hadronector* (Lund & Lund, 1985: fig. 35) has a long anterior bar and a crossbar like the pelvic girdle in specimen BHI 1581, but it lacks the prong-like process and possesses a posterior process. There are slight similarities with the pelvic girdle of *Coelacanthus granulatus* (Moy-Thomas & Westoll, 1935: fig. 9) and with that of *Diplurus* (Schaeffer, 1952: fig. 11C). The pelvic girdles of *Coelacanthus* and *Diplurus* have the same number of parts and processes; in *Coelacanthus* the lateral process is not separated from the anterior part, whereas in *Diplurus* it is longer than the anterior part of the pelvic girdle, corresponding to the small prong-like process in specimen BHI 1581. Of all known coelacanths, the pelvic girdles of *Coelacanthus* and *Diplurus* are the closest to the Kinney coelacanth, but they do not match.

The basal plate of the anal fin (Fig. 8) in the Kinney coelacanth can only be compared with that of *Coelacanthus granulatus* (Moy-Thomas & Westoll, 1935: fig. 11b).

In conclusion, the coelacanth from Kinney Brick Company Quarry shows no matching features to any known Paleozoic coelacanth genus. All features indicate that we are dealing with a new genus and species. However, the available features are not sufficient for defining a new species or genus.

Placing it in the two recently published cladograms of coelacanths (Cloutier, 1991; Forey, 1991) cannot be done satisfactorily because most of the characters used by both

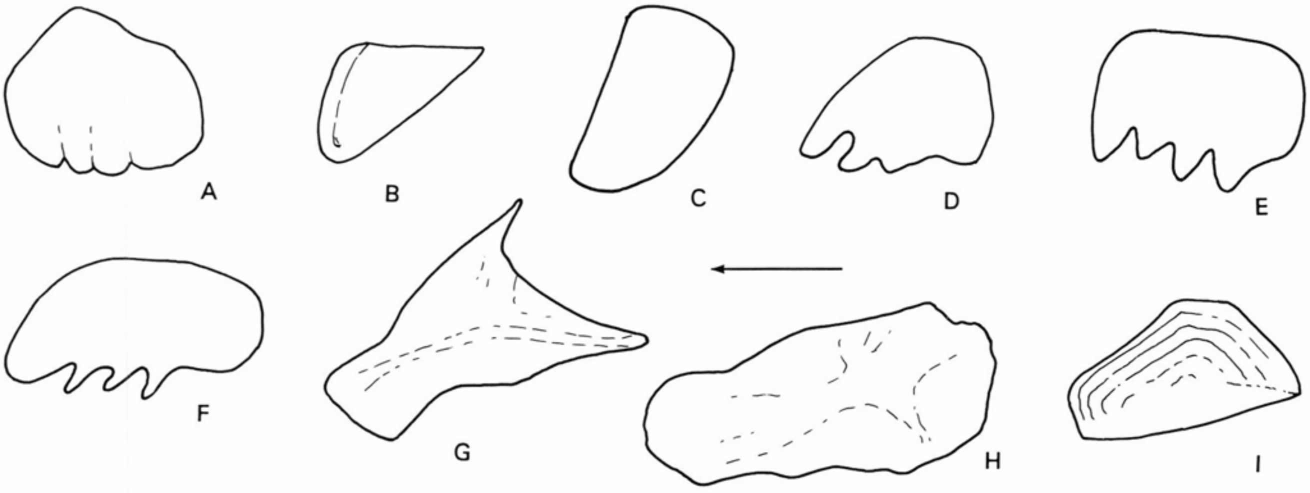

FIGURE 5—Basal plate of first dorsal fin of Paleozoic actinistians. **A,** *Polyosteorhynchus simplex* (after Lund & Lund, 1985: fig. 46); **B,** *Hadronector donbairdi* (after Lund & Lund, 1985; fig. 35); **C,** *Allenypterus montanus* (after Lund & Lund, 1985: fig. 57); **C,** *Lochmocerus aciculodontus* (after Lund & Lund, 1985: fig. 68); **E,** *Caridosuctor populosum* (after Lund & Lund, 1985: fig. 19); **F,** *Rhabdoderma elegans* (after Moy-Thomas, 1937: fig. 11); **G,** *Synaptotylus newelli* (after Echols, 1963: fig. 7A); **H,** Kinney coelacanth; **I,** *Coelacanthus granulatus* (after Moy-Thomas & Westoll, 1935: fig. 10). Anterior to the left.

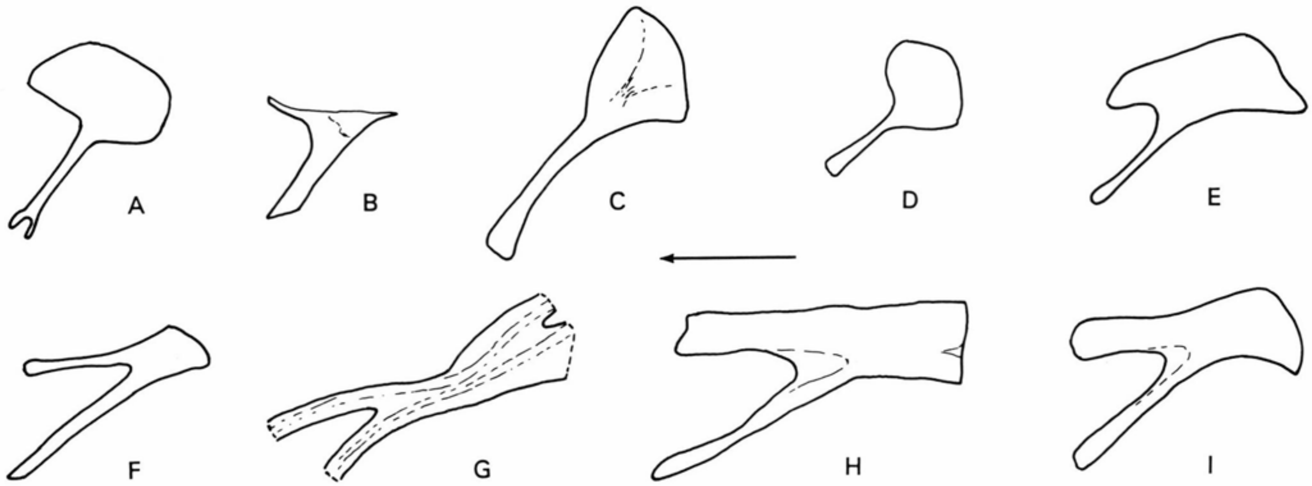

FIGURE 6—Basal plate of second dorsal fin of Paleozoic actinistians. **A,** *Polyosteorhynchus simplex* (after Lund & Lund, 1985: fig. 46); **B,** *Hadronector donbairdi* (after Lund & Lund, 1985: fig. 35); **C,** *Allenypterus montanus* (after Lund & Lund, 1985: fig. 57); **D,** *Lochmocerus aciculodontus* (after Lund & Lund, 1985: fig. 68); **E,** *Caridosuctor populosum* (after Lund & Lund, 1985: fig. 19); **F,** *Rhabdoderma elegans* (after Forey, 1981: fig. 9); **G,** *Synaptotylus newelli* (after Echols, 1963: fig. 7B); **H,** Kinney coelacanth; **I,** *Coelacanthus granulatus* (after Moy-Thomas & Westoll, 1935: fig. 11a). Anterior to the left.

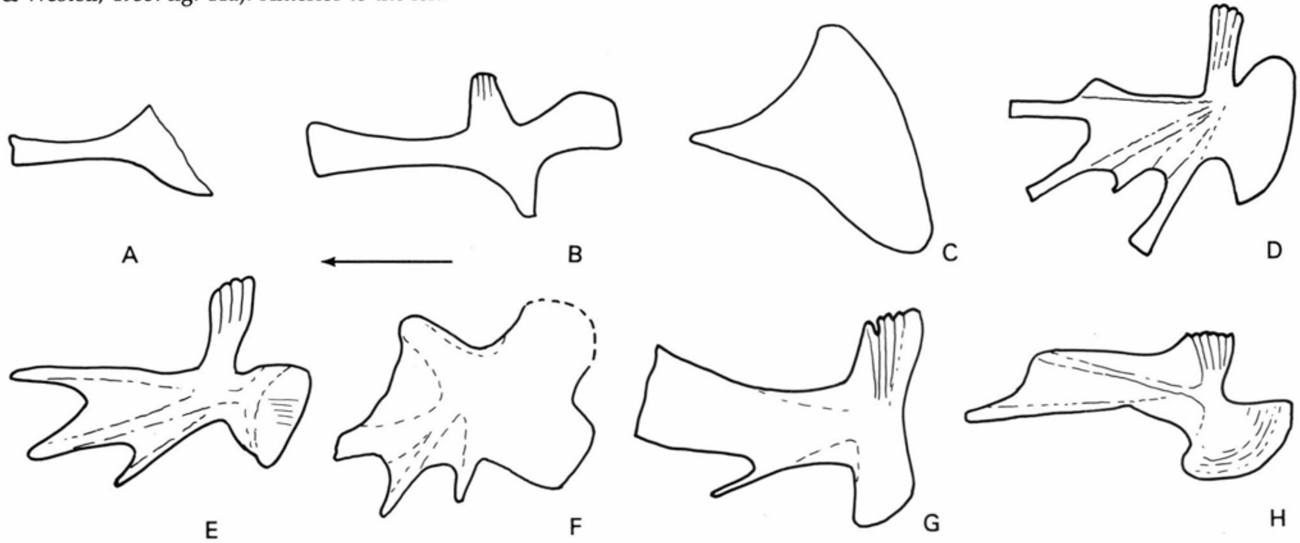

FIGURE 7—Pelvic girdle of Paleozoic actinistians. **A,** *Polyosteorhynchus simplex* (after Lund & Lund,1985: fig. 46); **B,** *Hadronector donbairdi* (after Lund & Lund, 1985: fig. 35); **C,** *Allenypterus montanus* (after Lund & Lund, 1985: fig. 57); **D,** *Caridosuctor populosum* (after Lund & Lund, 1985: fig. 30); **F,** *Synaptotylus newelli* (after Echols, 1963: fig. 6B); **G,** Kinney coelacanth; **H,** *Coelacanthus granulatus* (after Moy-Thomas & Westoll, 1935: fig. 9). Anterior to the left.

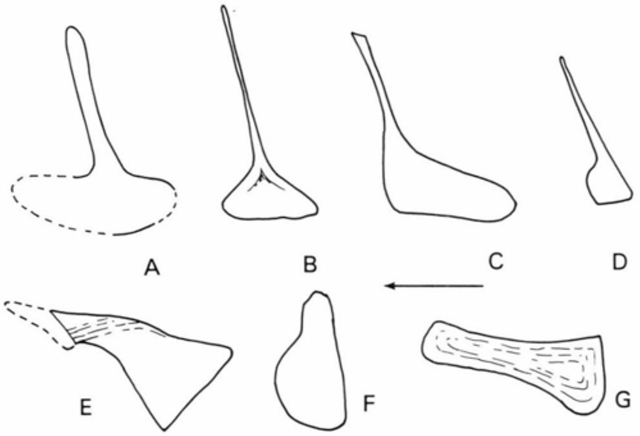

FIGURE 8—Basal plate of anal fin of Paleozoic actinistians. **A,** *Polyosteorhynchus simplex* (after Lund & Lund, 1985: fig. 46); **B,** *Hadronector donbairdi* (after Lund & Lund, 1985: fig. 35); **C,** *Allenypterus montanus* (after Lund & Lund, 1985: fig. 57); **D,** *Rhabdoderma elegans* (after Forey, 1981: fig. 9); **E,** *Synaptotylus newelli* (after Echols, 1963: fig. 6C); **F,** Kinney coelacanth; **G,** *Coelacanthus granulatus* (after Moy-Thomas & Westoll, 1935: fig. 11b). Anterior to the left.

authors are not known for the Kinney coelacanth. In Forey's scheme, the coelacanth from Kinney Quarry can only be placed above *Hadronector* on the basis of equal number of fin rays and radials in the caudal fin and the "asymmetrical" caudal fin (more fin rays in the dorsal lobe than in the ventral lobe). The later character shows a reversal in *Rhabdoderma* with symmetrical tail; that is another feature in which the Kinney coelacanth differs from *Rhabdoderma*. In Cloutier's scheme, the coelacanth from Kinney Quarry has to be placed above *Rhabdoderma madagascariense* on the basis of a smooth ventral margin of the basal plate of the first dorsal fin and the 1:1 relationship between lepidotrichia and radialia in the caudal fin. It would be placed above *Synaptotylus* if the number of lepidotrichia of the first dorsal fin is nine. In the first case the Kinney coelacanth could be placed in the family Laugiidae Berg 1940, and in the second case in the Coelacanthidae Agassiz 1843. Many similarities with *Coelacanthus granulatus*, although undiagnostic, indicate that the Kinney coelacanth more likely belongs in the Coelacanthidae than in the Laugiidae. The basal plates and the pelvic girdle of *Laugia* and *Synaptotylus*, both members of the family Laugiidae, show no similarities with the corresponding plates of the Kinney coelacanth. In any case, the new material confirms Zidek's (1975) conclusion that the coelacanth from the Kinney Brick Company Quarry is more advanced than *Rhabdoderma*. It belongs to another suborder, the Coelacanthoidei Berg 1937 (Schultze, 1992), and Zidek (1975) may have been correct in placing it in the Coelacanthidae.

Acknowledgments

I would like to thank the New Mexico Bureau of Mines & Mineral Resources and its former director Dr. F. E. Kottlowski for funding the excavation at Kinney Brick Company Quarry by a group of six people from the University of Kansas in June 1984. M. Gottfried, J. McAllister, A. Mebrate, G. Ostrander, and X. Wang joined me at the excavation. W. R. Jurgena, President of the Kinney Brick Company, kindly allowed us to collect and camp in the quarry. Peter Larson, Black Hills Institute, Hill City, South Dakota, loaned the specimen collected by his group in 1978. Finally I would like to thank Dr. J. Zidek for improving the English of the manuscript.

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The Late Pennsylvanian amphibian fauna of the Kinney Quarry, central New Mexico

Adrian P. Hunt[1], Spencer G. Lucas[1], and David S Berman[2]

[1] New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, New Mexico 87104;
[2] Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213

Abstract—Four specimens of amphibians have been collected from the Pine Shadow Member of the Wild Cow Formation (Late Pennsylvanian: early Virgilian) at the Kinney Brick Company Quarry, Manzanita Mountains, Bernalillo County, New Mexico. An amphibamid is distinguished from other members of the family by deep embayments of the occipital borders of the skull so that the midline portion of the postparietals projects posteriorly beyond the rest of the skull table, and by postparietals with a midline length greater than half that of the parietals. The other specimens include the holotype of *Lafonius lehmani* Berman 1973, an indeterminate saurerpetontid, and an unprepared skeleton of unknown affinity. These are among the oldest tetrapod fossils from New Mexico.

Introduction

Since the 1880's, New Mexico has been well known for Early Permian (Wolfcampian) amphibians from the Abo and Cutler red beds, principally from northern New Mexico (e.g. Case et al., 1913; Langston, 1953; Berman & Reisz, 1980; Berman et al.,1981). During this century it has become increasingly evident that one of the most famous red-bed faunas, that from the Cutler Formation of El Cobre Canyon in Rio Arriba County, is actually Late Pennsylvanian in age (Williston & Case, 1912; Fracasso, 1980; Hunt, 1983; Berman et al., 1987). El Cobre Canyon was the only Pennsylvanian tetrapod locality in New Mexico until Berman (1973) described the trimerorhachid amphibian *Lafonius lehmani* from Upper Pennsylvanian (Virgilian) strata in the Manzanita Mountains of central New Mexico. This locality lies within the Pine Shadow Member of the Wild Cow Formation in the Kinney Brick Company Quarry (Lucas & Huber, 1991). Berman collected another amphibian skeleton from this locality in 1977 for the Carnegie Museum of Natural History, and P. Huber collected two additional skeletons in 1988 and 1989 for the New Mexico Museum of Natural History. The purpose of this paper is to describe these new specimens, to assess their relationships, and to speculate briefly on their paleoecological significance.

Abbreviations are: CM, Carnegie Museum of Natural History; NMMNH, New Mexico Museum of Natural History; USNM, United States National Museum.

Geological context

About 28 m of the upper part of the Pine Shadow Member of the Wild Cow Formation are exposed at the Kinney Brick Company Quarry (5E^{1}14 sec. 18, T9N, R6E, Bernalillo County, New Mexico), hereafter referred to as the Kinney Quarry. However, most fossils discovered and reported from the quarry are from the lowermost 0.5 m of shale and shaly limestone above the micritic limestone that floors the quarry (Lucas & Huber, 1991). The amphibians described here are from this interval (unit 3 of the measured section of Lucas & Huber, 1991). Based on fusulinids, Myers (1988) assigned the Pine Shadow Member to the Late Pennsylvanian (early Virgilian).

Systematic paleontology

Class AMPHIBIA Linnaeus 1758
Order TEMNOSPONDYLI Zittel 1895
Superfamily DISSOROPHOIDEA Bolt 1969
Family AMPHIBAMIDAE Moodie 1910

AMPHIBAMID NMMNH P-3696
Figs. 1, 2, 3B, D

Trimerorhachid: Hunt et al., 1989: 26A.

Description—NMMNH P-3696 consists of a partial skeleton preserved on two blocks (Figs. 1, 2). The posterior half of the skull is preserved as bone in ventral view on the principal block, whereas the entire skull is preserved in ventral view as a faint impression on the counterpart. The skull is approximately 11 mm wide and 7.5 mm long, with a short postorbital area and very large orbits (Fig. 1). Details of the cranial structure can be discerned only in the posterior half of the skull preserved on the principal block, which also includes the posterior portions of both jaws. The description of the skull roof on the principal block is hampered by the overlying lower jaws and parasphenoid, numerous fractures, and loss of bone. It is also important to note that the sutural pattern on the dorsal surface of the skull roof is likely to be different from that of the ventral surface due to overlapping at sutural contacts.

Only the posterior portions of the paired frontals are preserved, but they appear to be narrow and rectangular. Each frontal contacts the parietal in a sinuous but simple suture. The paired parietals are the largest of the posterior skull-roof elements and are nearly intact. The parietals are broadly rectangular bones that become somewhat narrower anteriorly as they extend between the orbits, but still occupy almost 90% of the interorbital width. The large pineal foramen is partially hidden by the cultriform process of the parasphenoid and lies at the level of the posterior margin of the orbits, at about one-third the midline length of the parietals from their anterior margin. The postparietals are partially covered by the parasphenoid and are relatively very large, with an exceptionally long antero-posterior length that is greater than half that of the parietals. Together, the postparietals have a nearly square outline except for their lateral margins which curve strongly anterolaterally to form a broad, wing-like process that laterally contacts the tabular.

The only evidence of the prefrontal is an impression on the principal block of a small portion of the narrow posterior end of the right prefrontal. Its narrow contact with the postfrontal excludes the frontal from the orbital margin. The postfrontals are long, narrow, arcuate bones that border the posteromedial margin of the orbit, gradually widening posteriorly from a splint-like anterior end to a bluntly rounded posterior end. The ventral surface forms a thick, broadly rounded ridge. The posterior end of the left postfrontal is missing, revealing more fully the extent of the postorbital. The postorbital has a typically triangular outline, with a posteriorly directed apex that wedges between the anterior ends of the supratemporal and squamosal. The right postorbital appears as a small, rectangular, flat and featureless element in ventral view.

Although it appears that both supratemporals are present, only the left is well enough exposed to permit descrip-

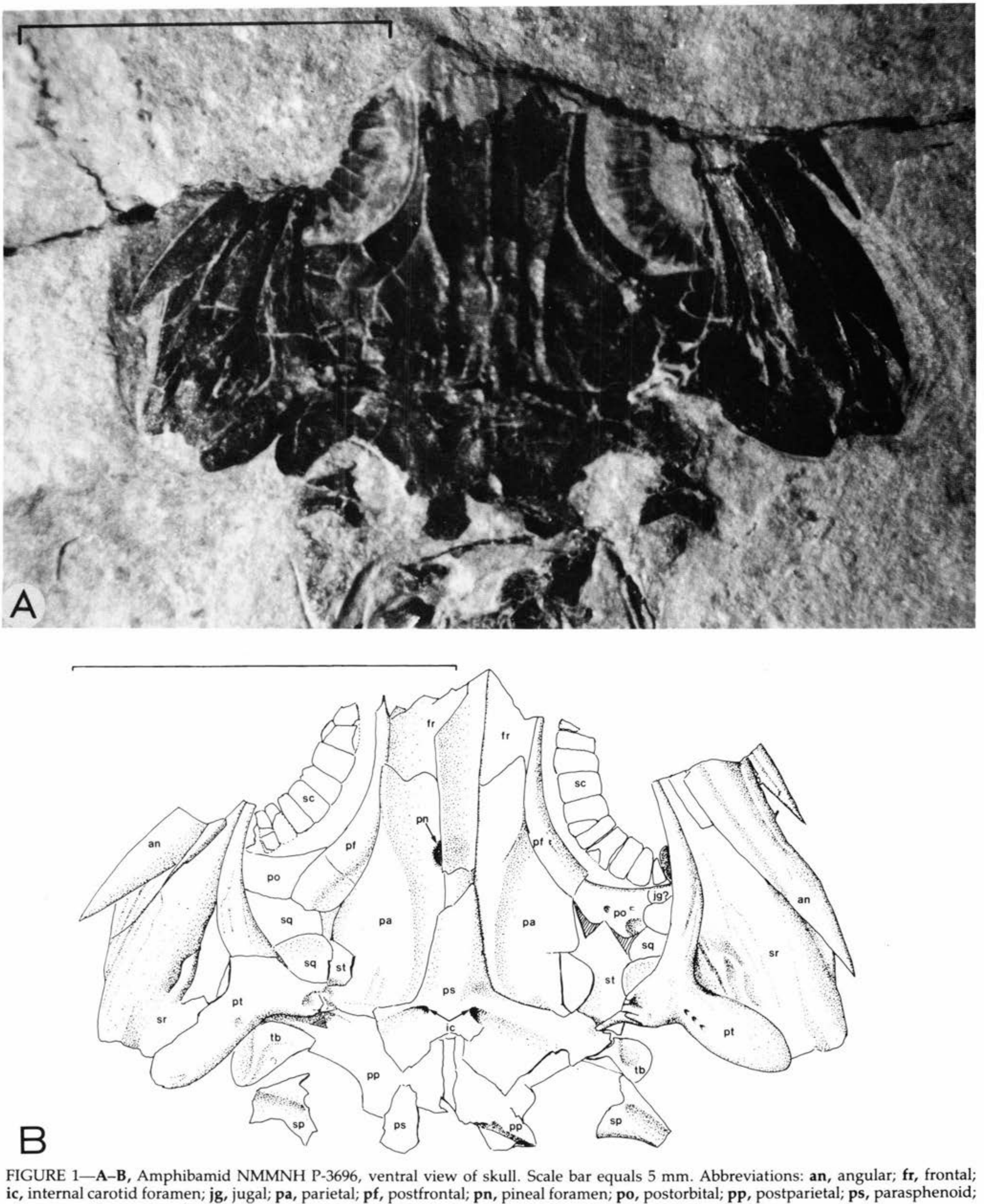

FIGURE 1—**A–B,** Amphibamid NMMNH P-3696, ventral view of skull. Scale bar equals 5 mm. Abbreviations: **an,** angular; **fr,** frontal; **ic,** internal carotid foramen; **jg,** jugal; **pa,** parietal; **pf,** postfrontal; **pn,** pineal foramen; **po,** postorbital; **pp,** postparietal; **ps,** parasphenoid; **pt,** pterygoid; **sc,** sclerotic plates; **sp,** stapes; **sq,** squamosal; **sr,** surangular; **st,** supratemporal; **tb,** tabular.

tion. It is large and long, and laterally borders the postorbital portion of the parietal. Anteriorly, the supratemporal wedges between the parietal and postfrontal and, although not visible in this specimen, obviously posteriorly contacted the postparietal and tabular.

There is no indication of the presence of intertemporals. Both tabulars are visible, but only the right is almost entirely exposed. The tabular is suboval in outline and appears to be much thicker than adjacent margins of the postparietal. The anterolateral portion of its ventral margin has a shallow excavation. Deep, concave, bilateral embayments of the occipital border of the skull table are bordered by the tabular and the anterolateral, wing-like process of the postparietal, and give the false impression that the midline portion of the paired postparietals projects unusually far posteriorly. Partially exposed elements lying lateral to the supratem-

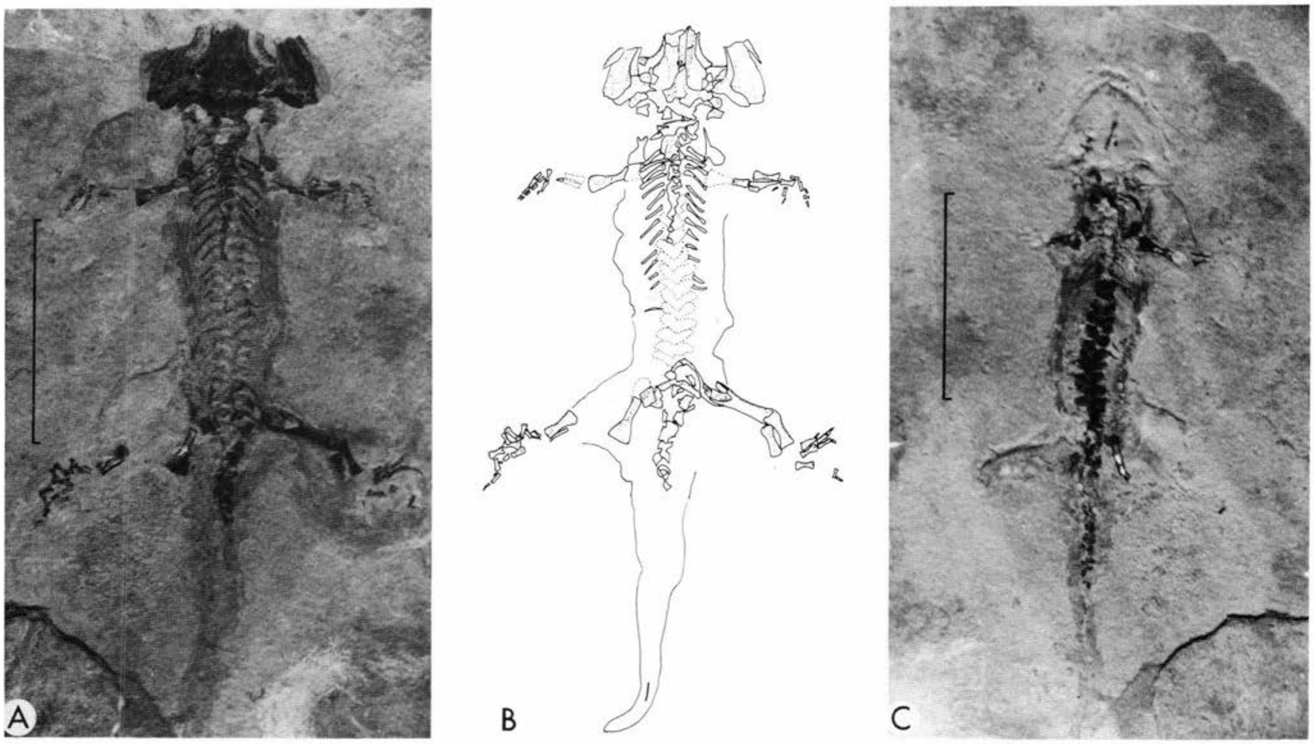

FIGURE 2—Amphibamid NMMNH P-3696. **A,** Skeleton in ventral view on the main block. **B,** Illustration of skeleton as preserved on the main block. **C,** Skeleton in ventral view on the counterpart block. Scale bars equal 1 cm.

porals and contacting the postfrontal and postorbital anteriorly are tentatively identified as squamosals. The lateral margins of the squamosals are hidden by the pterygoids. On the posterior half of the exposed ventral surfaces of both squamosals is a cup-shaped depression bordered by a pronounced ridge that may mark the point of articulation with the quadrate.

The only palatal elements that are preserved are the paired pterygoids and the parasphenoid. All three portions of the triradiate pterygoid are well preserved. The narrow anterior process tapers gradually anteriorly and is strongly bowed laterally, indicating that it bordered a greatly expanded interpterygoid vacuity. The much shorter and broader, posterolaterally directed quadrate process is oval in outline. The short, stout, medially directed basal process exhibits a very small cup-shaped excavation at its distal end for articulation with the braincase. Several small protuberances surround the cotylus. The parasphenoid, which is flattened against the ventral surface of the skull roof, is incomplete, but most of its structure can be determined. The cultriform process is relatively wide and flat. It gradually narrows anteriorly to about the level of the midlength of the parietal, then gradually widens to almost its proximal width at its distally incomplete end. The main body, or corpus, of the parasphenoid is a large, apparently pentangular plate. The anterior margins angle slightly posterolaterally, and the lateral margins appear to have angled strongly posteromedially. At the base of the cultriform process are two large, prominent foramina for the carotid arteries. Each lies at the end of a steadily deepening, anteromedially directed groove. There are no palatal teeth on either the pterygoid or the parasphenoid.

The tips of a few teeth are preserved on the right anterolateral margin of the impression of the skull roof on the counterpart block. These have the form of thin-walled tubes with no evidence of labyrinthine structure. As many as eleven, mainly rectangular, sclerotic plates are preserved in the posteromedial portion of the left orbit, and eight are preserved in the right orbit. What appears to be the greater portions of both stapes in posterior view are preserved just posterior to the tabulars. The notch in the expanded footplate of the left stapes may represent the stapedial foramen.

Only the posterior halves of the lower jaws are preserved, and they are collapsed inward beneath the skull roof so as to expose their lateral surfaces. The surangular obviously dominated this region of the jaw. The wedge-shaped posterior end of the angular extended along the ventral margin of the surangular to within a short distance of the end of the jaw. There is no evidence of a retroarticular process. With the exception of faint, minute, longitudinal striations, the lateral surface of the jaws lacks ornamentation.

Branchial dentides occur in roughly antero-posterior rows behind the stapes, along the external margins of the pectoral girdles. They are short, needle-like elements averaging 0.16 mm in length. In the counterpart there is a small fragment of ?bone, indistinguishable from that which comprises the sclerotic plates, that appears to preserve the denticles in-situ as parallel rows. On the counterpart slab there is an elongate rod of bone located below the cultriform process of the parasphenoid that possibly represents the basihyal.

The essentially complete vertebral column is preserved as a series of paired neural-arch halves and associated ribs. There is no evidence of central elements, and apparently only the neural arches of the vertebrae were ossified. The neural arches are preserved as bone and are most easily studied on the principal block. Except for the neural arches of the cervical and caudal regions being jumbled, each pair of arches has been flattened into a horizontal plane so that the dorsal margins of the right and left halves of each arch meet on the axial midline. There are approximately 22-24 presacral-arch pairs in a length of about 16 mm, but preservation allows only a general account of their morphology.

The neural spines are very low and broadly convex. The pre- and postzygapophyses are weakly developed. As preserved, the neural-arch halves are oriented so that the shelf-like anterior zygapophysis is anterolateral and the posteriorly directed, spike-like posterior zygapophysis is adjacent to the midline of the column. The neural-arch halves continue below the levels of the pre- and postzygapophyses the entire length of the arch as a narrow band that expands somewhat anteriorly. There is no indication of a facet for the rib. The sacral vertebrae cannot be distinguished, and the caudal neural arches are too disturbed to count or describe, except to say that in general they appear to be like those of the presacral region.

The ribs are best preserved on the principal block, where about the first 17 can be clearly seen. They are short and straight and become moderately dilated at both ends, with the proximal end being wider. There is no division of the rib head into separate articular facets. The largest rib in the series is about the fifth. Anterior to the fifth rib, the ribs are shorter and wider, whereas posteriorly they gradually decrease in length.

The clavicles are preserved in anterior view on the counterpart block. At about midlength along their anterior margin they curve abruptly medially to form an internal angle of about 120°, so as to be divisible into a dorsal stem and a ventral plate. The anterior margin of the ventral plate is turned sharply inward in a lip-like structure. The dorsal stem is strongly bowed to form a narrow, posteriorly facing, trough-like groove that received the ventral end of the cleithrum. Only portions of the thin anterior edges of the cleithra can be seen in articulation with the clavicles on the principal block. What appear to be portions of the interclavicle in anterior view are seen between the ventral ends of the clavicles. Both scapular blades are preserved, but incompletely ossified, on the counterpart block, with the left being the more complete but slightly displaced from the rest of the shoulder girdles. They are narrowly rectangular, with their long axes oriented dorsoventrally, and expand moderately toward their dorsal and ventral ends.

The humerus is a relatively elongated bone about 3.5 mm long and deeply waisted at midlength to a diameter of about 0.5 mm. As in the other upper limb bones, it is thin-walled and had suffered considerable post-mortem crushing. The radius and ulna are subequal in length (about 1.7 mm) and strongly waisted at midlength. The greater parts of three digits are preserved in the right forelimb and four are present in the left. Disarticulation prevents determination of the serial positions of the digits or their phalangeal counts. There are no ossified carpal elements. The phalanges are elongate, and the unguals are both elongate and recurved.

Only the left pelvis on the principal block is partially preserved as bone. The ilium consists only of the dorsal blade in lateral view, with the portion contributing to the acetabulum broken away. Much of the distal end of the blade is covered by the head of the left femur. Extending anteriorly from near the base of the iliac blade is a narrow, partially exposed blade with a smooth rounded margin that may be the anterolateral edge of the pubis. A flat, rectangular piece of bone a few millimeters posteromedial to the iliac blade may be a portion of the ischium.

The hindlimb is more stoutly constructed that the forelimb (Fig. 3D). The femur is about 4.2 mm long. The anteroposterior width of the proximal head is much narrower (about 1 mm) than that of the distal head (about 1.4 mm), and the shaft is strongly waisted, with a diameter of about 0.5 mm. The dorsal surface of the proximal head is moderately convex and smooth, whereas ventrally a moderately deep intertrochanteric fossa occupies about one-third of the length of the femur. The tibia and fibula are about 2.3 and 2.0 mm long, respectively. Their shafts are moderately waisted, though the lateral margin of the tibia and the medial margin of the fibula are more concave, giving the appearance that the two bones bow slightly away from one another. There are no ossified tarsal elements. Four digits can be recognized in the left hindlimb and five are questionably identified in the right, but in neither can the serial position of the digits or their phalangeal counts be determined.

The body outline is preserved throughout most of the length of the skeleton as irregular, subparallel, minute ridges that are spaced about 10/mm and generally oriented anteromedially (Fig. 3B). Judging mainly by the body impression, the tail was approximately 23 mm long, but only the proximal half contains vertebral elements. There are no scales preserved.

Discussion—If NMMNH P-3696 had been found at the beginning of the century, it would have been unquestionably placed in the family Branchiosauridae of the "Order" Phyllospondyli, because it is a small labyrinthodont of neotenic aspect, with unossified vertebral centra. However, it has long been known that this order represents an artificial assemblage of juvenile temnospondyls (Romer, 1939; Gregory, 1950; Milner, 1982), although Boy (1971, 1972, 1974, 1978, 1987) has demonstrated that Branchiosauridae sensu stricto should be preserved for a few taxa. Lack of the anterior portion of the skull and the covering of the lateral margins of the remaining skull by the mandibles hinders assessment of the relationships of NMMNH P-3696. However, preservation of the remainder of the skull and skeleton allows for detailed comparisons.

NMMNH P-3696 is recognized as a temnospondyl on the basis of distinct interpterygoid vacuities bordered by triradiate pterygoids, strut-like parasphenoid with a long cultriform process and a broad, flat basal plate, and straight ribs (Milner, 1990). NMMNH P-3696 belongs to the Eryopoidea–Dissorophoidea clade because it has a short, broad skull table with an abbreviated postorbital not wedged between the supratemporal and squamosal, semicircular interpterygoid vacuities, small, rounded interclavicles, and narrow-bladed clavicles (Milner, 1990). This specimen represents a post-trematopid dissorophoid as it possesses a humerus that lacks a supinator process (Milner, 1990). NMMNH P-3696 differs from members of the Micromelerpetontidae in having less that 26 presacral vertebrae, not having a secondarily elongated skull table with long parietals and supratemporals, and in having a more elongate humerus (Werneburg, 1989). Within the Dissorophoidea the elongate humerus is characteristic of the Dissorophidae, Amphibamidae (= Peliontidae), and Branchiosauridae (A. R. Milner, pers. comm. 1991). It is hard to eliminate the possibility that NMMNH P-3696 represents the larva of an armored dissorophid because there are no known larval specimens (A. R. Milner, pers. comm. 1991). However, small dermal scutes from Fort Sill (Bolt, 1974) suggest that metamorphosis occurred at a small size (A. R. Milner, pers. comm. 1991). NMMNH P-3696 possesses several shared, derived characters of the Amphibamidae and Branchiosauridae, including extreme abbreviation of the skull table, greatly reduced ectopterygoid (evidenced by pterygoid shape in NMMNH P-3696), interclavicle reduced to poorly ossified disc, and ribs reduced in size (Milner, 1990). The presence of 24 presacral vertebrae is suggestive but not indicative of this clade (A. R. Milner, pers. comm. 1991).

NMMNH P-3696 most likely represents a new taxon because it possesses (1) a prominent bilateral embayment of the occipital margin of the skull table that results in the midline portion of the paired postparietals projecting posteriorly well beyond the rest of the skull table, and (2) post-parietals with a midline length greater than half that of the parietals (Moodie, 1916; Bulman & Whittard, 1926; Gregory, 1950; Carroll, 1964; Boy, 1971, 1972, 1978; Daly, 1981, 1988; Milner, 1982, 1986).

It is difficult to evaluate to which family NMMNH P-3696 belongs on the basis of this juvenile specimen. Characters that favor assignment to the Amphibamidae are: (1) anterior ribs very slender, which is more similar to amphibamids

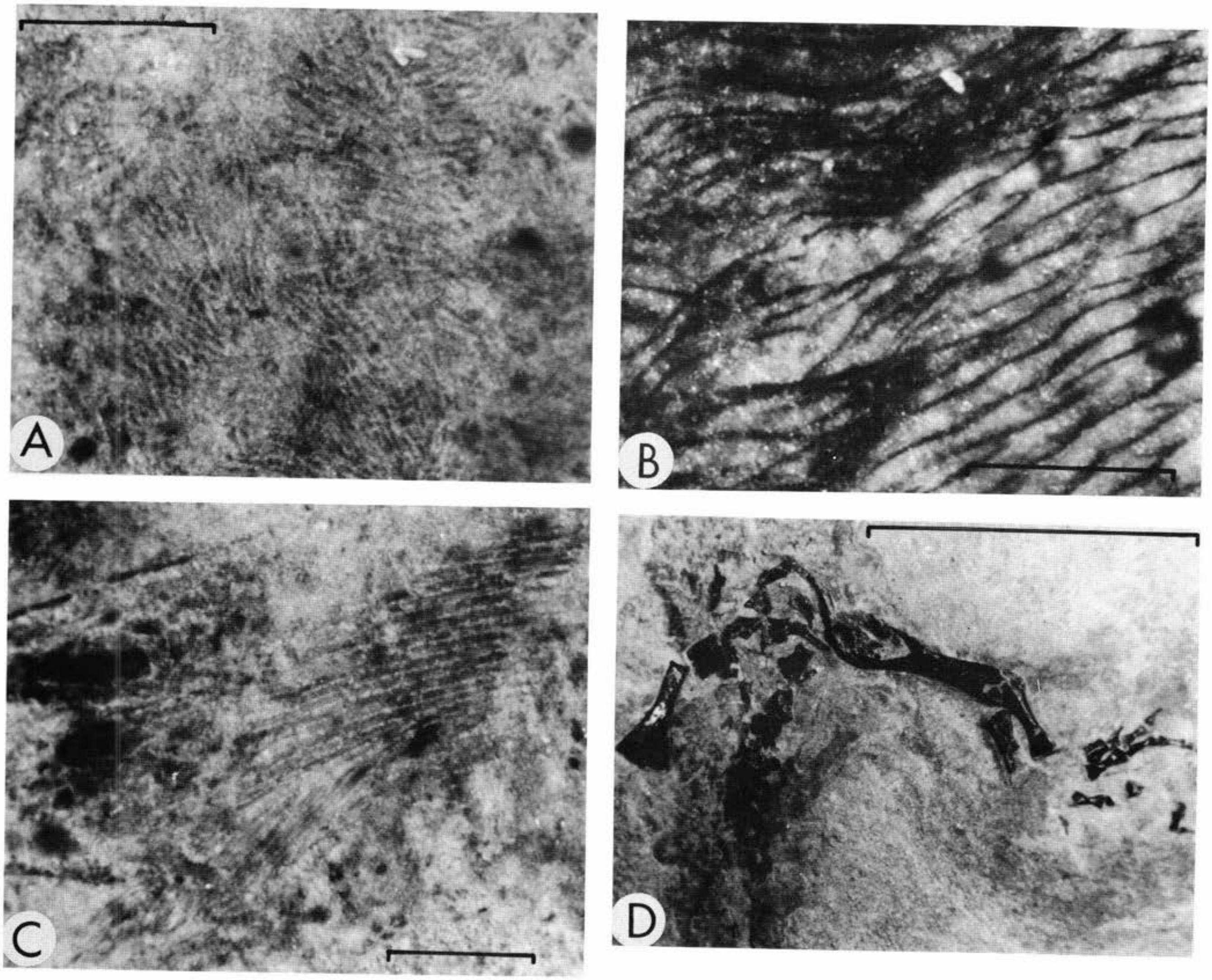

FIGURE 3—Temnospondyls from the Late Pennsylvanian of Kinney Brick Quarry, central New Mexico. **A,** CM 41708, Saurerpetontidae indet., close-up of scalation. **B,** Amphibamid NMMNH P-3696, close-up of skin texture. **C,** CM 41708, Saurerpetontidae indet., close-up of branchial elements. **D,** Amphibamid NMMNH P-3696, left hindlimb. Scale bars equal 0.5 mm in A and B, and 5 mm in C and D.

than branchiosaurids (cf. Carroll, 1964: fig. 24, and Boy, 1978: fig 10); (2) the presence of prominent ridges on the underside of the parietals indicating the outline of the unossified sphenethmoid (A. R. Milner, pers. comm. 1991); and (3) sphenethmoid Hairs anteriorly as indicated by ridges on ventral side of parietals (A. R. Milner, pers. comm. 1991). In contrast, characters that indicate a branchiosaurid relationship are: (1) absence of denticles on the anterior portion of the main body or corpus of the parasphenoid (cf. Daly, 1981: fig. 6, and Boy, 1978: fig. 20b); (2) position and prominence of carotid foramina (cf. Milner, 1982: fig. 3d, and Boy, 1978: fig. 13); (3) the robust stapes (A. R. Milner, pers. comm. 1991); and (4) the presence of branchial ossicles in a specimen of this size (A. R. Milner, pers. comm. 1991). In conclusion, it is difficult to determine whether NMMNH P-3696 is a late-metamorphosing amphibamid or a branchiosaurid. We think it probable that this specimen is an amphibamid because the characters which it shares with this family are more fundamentally important than those which it shares with branchiosaurids (A. R. Milner, pers. comm. 1991).

There is no direct evidence that NMMNH P-3696 had external gills. However, this may not be significant because even in branchiosaurid assemblages that preserve body out lines external gills are visible in only about 20% of specimens (A. R. Milner, pers. comm. 1991). The rows of branchial denticles likely functioned as gill-rakers for internal gills or gill slits (Boy, 1972; Berman, 1973). The gill-rakers in NMMNH P-3696 are associated, but are not robustly conjoined by bone as in *Micromelerpeton* (Boy, 1974: fig. 12). Gill-rakers are indicative of a pre-metamorphosis condition (Boy, 1974). Other juvenile (pre-metamorphosis) characters of NMMNH P-3696 are large orbits, abbreviated snout (A. R. Milner, pers. comm. 1991), anteriorly placed parietal foramen, lack of endocranial ossification, fairly straight sutural lines, lack of spinous processes on the vertebrae (Boy, 1974), and an elongate tail. The degree of ossification of the cranial and postcranial skeleton, including carpal and tarsal elements, indicates a post-middle-larval stage of development (sensu Boy, 1974). The presence of sclerotic rings suggests a post-metamorphosis condition, although these elements questionably occur in very late larvae (Boy, 1974: table 1). The beginning of ossification of the branchial skeleton in the region of the copula suggests an early post-metamorphic stage of development (Boy, 1974). However, the presence of gill-rakers suggests pre-metamorphosis (Boy, 1974). It is probably most parsimonious to conclude that NMMNH P-3696 represents a late larval form.

Superfamily TRIMERORHACHOIDEA Romer 1947
Family SAURERPETONTIDAE Chase 1965
SAURERPETONTIDAE gen. et sp. indet.
Figs. 4, 5A

Referred specimen—CM 41708, nearly complete skeleton on part and counterpart slabs (Figs. 4, 5A).

Description—CM 41708 consists essentially of a skull and postcranial skeleton of a small labyrinthodont preserved on part and counterpart blocks. This specimen is difficult to interpret because of disarticulation, numerous fractures, and loss of bone.

The principal block (Figs. 4, 5A) contains the skull in ventral view and the right lower jaw. The skull is missing most of the left side lateral to the mid-orbit. The palate is incomplete, and the cultriform process of the parasphenoid lies along the medial portion of the right orbit. The elements of the anterior portion of the skull are disassociated slightly so that, for example, the incomplete left maxilla lies on its outer side anterior and to the right of its original position.

Also present are part of the pectoral girdle, the right humerus preserved mainly as an impression, right-manus digits, and a very poor impression of the left humerus. Posterior to the pectoral girdle the axial skeleton is exposed in left lateral view. Most of the presacral and postcervical vertebrae are very poorly preserved and/or exposed. In contrast, most of the ribs are well preserved as bone or impressions. The right side of the pelvis is partially preserved, as is most of the right hindlimb.

The counterpart block contains part of the right mandible and right margin of the palate, most of the pectoral girdle and left humerus, and impressions of many ribs. Skin impressions are well preserved in the caudal region and anterior to the humerus in the counterpart. Skin impressions also occur over scattered areas of the counterpart and on the main slab.

The skull is short and broad, with a length of 11 mm and a width of 14.5 mm (Fig. 4). Few sutures are discernible on the ventral skull roof. The parietal is a wide bone that narrows as it extends anterior and medial to the orbit and the postfrontal. The postfrontal is a long, narrow, arcuate bone that thins anteriorly. The suture between the parietal and the frontal is strongly concave posteriorly. The large pineal foramen lies anterior to the level of the posterior margins of the orbits. It is uncertain if intertemporals are present. The fragment of left maxilla on the main block is low and elongate, decreasing in height posteriorly. The maxillary and premaxillary teeth are simple, elongate cones with no evidence of labyrinthodont structure. There are a few sclerotic elements in both orbits.

The palate is poorly preserved. The cultriform process of the parasphenoid is relatively wide and flat to slightly concave. The pterygoid, preserved on the right side only, is very narrow and is missing the quadratic process. The anterior process of the pterygoid extends forward nearly to the level of the anterior margin of the orbit. There are no denticles on either the parasphenoid or the pterygoid.

A long, thin, arcuate strap of bone bearing a row of small teeth lies near the anterolateral margin of the orbit. Near its anterior end is a thickened process that extends posteromedially. This process appears to separate the margins of two fenestrae. It is probable that these fenestrae are the internal naris and the anterior palatine fenestra. A non-labyrinthine tusk lies between the fenestrae. This entire

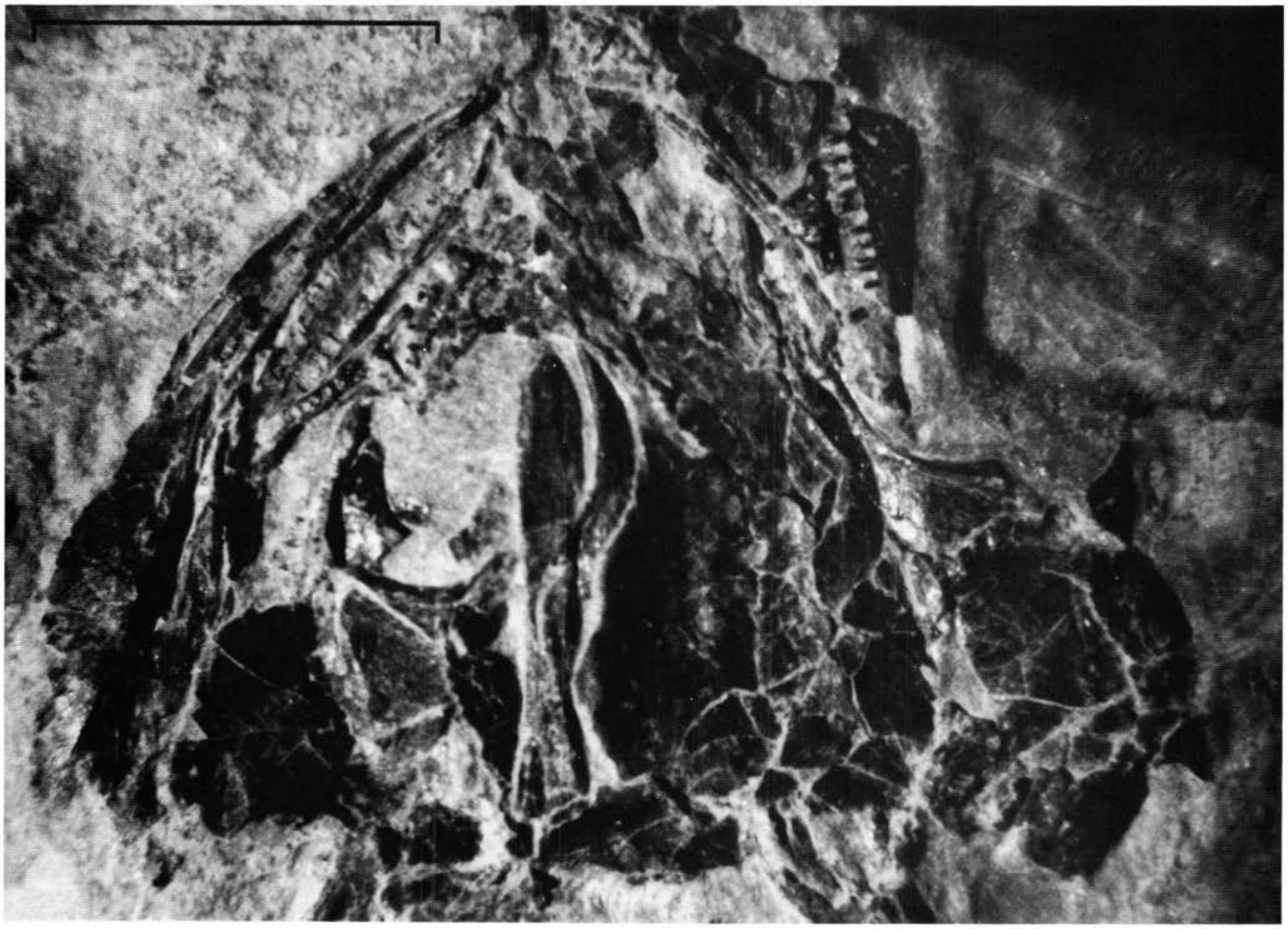

FIGURE 4—CM 41708, Saurerpetontidae indet., skull in ventral view. Scale bar equals 5 mm.

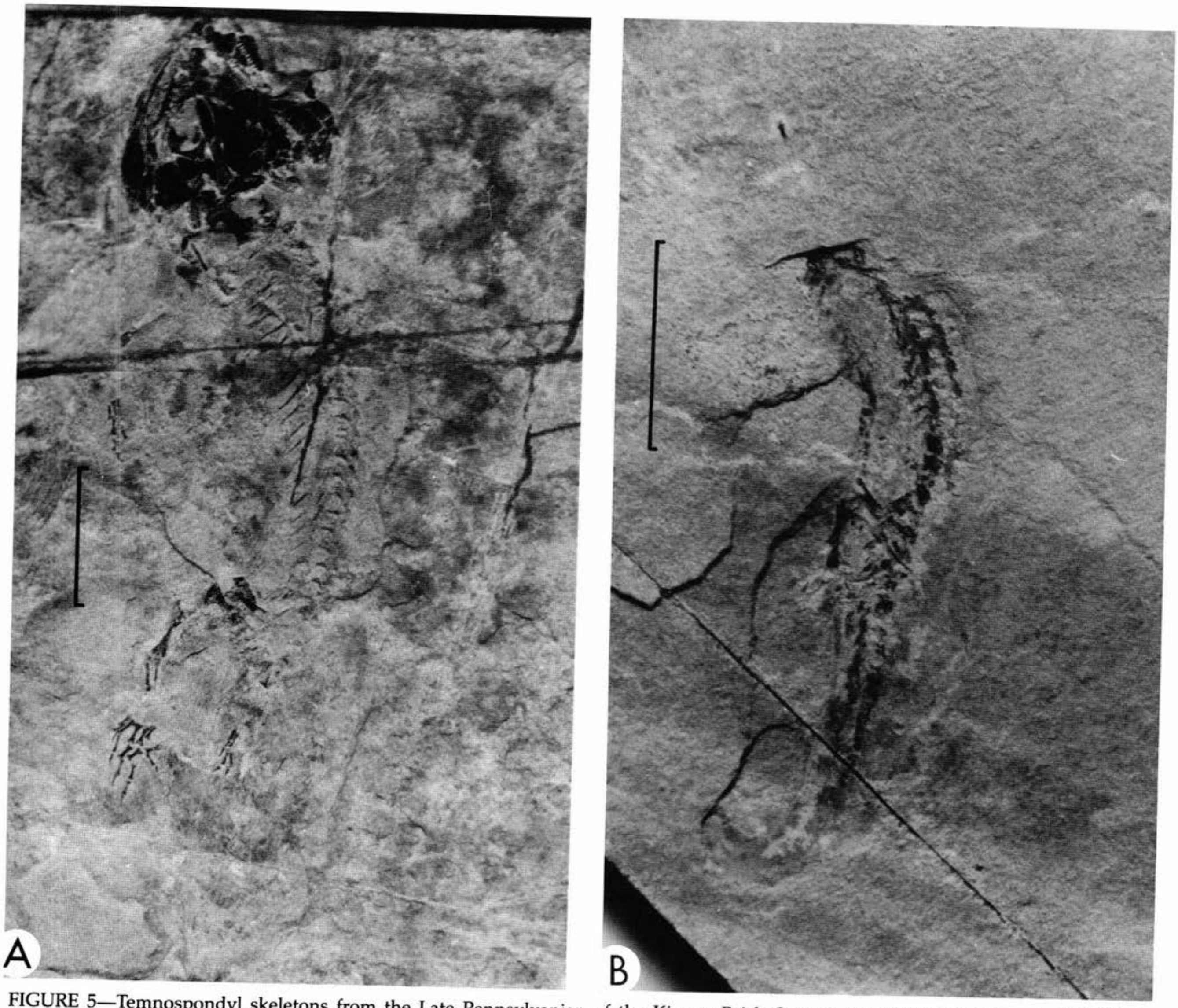

FIGURE 5—Temnospondyl skeletons from the Late Pennsylvanian of the Kinney Brick Quarry, central New Mexico. **A**, CM 41708, Saurerpetontidae indet., skeleton in ventral view. **B**, NMMNH P-15019, ?temnospondyl, skeleton in left lateral view. Scale bars equal 1 cm.

tooth-bearing fragment of bone probably represents the vomer.

The lower jaws were collapsed inward against the ventral surface of the skull, so that only their unsculptured lateral faces are visible. A thin, elongate bone preserved near the location of the cultriform process, on the counterpart, is possibly the basihyal.

The vertebrae are very difficult to discern, but there appear to have been about 22-24 presacral vertebrae based on the number of ribs. There are no apparent ossified centra, and the neural spines are very thin. The ribs are elongate, with markedly flared proximal ends, and they become shorter and broader near the pectoral girdle. It is possible that the anteriormost ribs are double-headed. The presacral length of the vertebral column is about 28 mm, and the truncated tail is 26 mm long. No caudal vertebrae are preserved.

The pectoral girdle is robustly constructed. The interclavicle is a transversely broad, elongate bone which widens anteriorly from a rounded posterior margin to a blunt anterior end. The ventral plate portion of the clavicles is broadly leaf-shaped. The poorly preserved right scapula is broad. The displaced cleithrum is narrow and elongate, extending anteriorly from the scapular. The humerus is elongate, as are the carpal digits. The unguals are long and recurved. Just posterior to the right humerus is a series (1 mm wide) of arcuate and parallel needles of bone, each about 1.5 mm long, which functioned as gill-rakers (Fig. 3C).

The proximal end of the ilium is boot-shaped and has a broad shaft. The femur is elongate and about two to three times the length of the tibia and fibula. Five elongate tarsal digits are preserved. There are no ossified carpals or tarsals.

The skin consists of broad, U-shaped, cycloid scales (Fig. 3A), broadly similar to other Pennsylvanian temnospondyls (e.g. Berman, 1973: fig. 5f), that have an ornamentation of fine longitudinal ridges. There are large patches of scales preserved, but their original arrangement is unclear.

Discussion—CM 41708 is less well preserved that NMMNH P-3696, but enough features are present to assess its relationships. First, it is clear that this specimen does not represent either of the other taxa from the Kinney Quarry. It differs from NMMNH P-3696 in many respects, notably in possessing an elongate interclavicle and broad clavicles (primitive condition), large, longitudinally striated scales, smaller orbits, a wider iliac blade, and more elongate digits. CM 41708 differs from *Lafonius* in having much larger orbits (in a skull of similar size), much shorter postorbital area, much more elongate humerus and femur, and different construction of the gill-rakers (denticles elongate as opposed to short). The scalation is very similar to *Lafonius* (Berman, 1973), but branchiosaurids also have broadly similar scales (Boy, 1972: fig. 53a-b).

CM 41708 is a temnospondyl because it possesses large interpterygoid vacuities (evidenced by the shape of the cultriform process of the parasphenoid), and it is a member of the Trimerorhachoidea because of: (1) the presence of anterior palatal fenestrae (Godfrey et al., 1987), although this character is also present in colosteids (Hook, 1983), which are not temnospondyls (Milner, 1990), and other primitive groups (R. W. Hook, pers. comm. 1991); (2) shallow otic notch (Milner, 1990); and (3) the shape of the pterygoid suggests that it was partly withdrawn down the sides of the interpterygoid vacuities (Milner, 1990). Other characters of the Trimerorhachoidea, such as a short facial region and a relatively broad cultriform process (Godfrey et al., 1987; Foreman, 1990), are present also in some dissorophoids (e.g. *Branchiosaurus).*

Within the Trimerorhachoidea, CM 41708 is assignable to the Saurerpetontidae because: (1) the skull is short and broad; (2) there are no denticles on the parasphenoid or pterygoid (Case, 1935; Chase, 1%5; Godfrey et al., 1987; Foreman, 1990); (3) the presacral vertebral count (22-24) is close to that of the only saurerpetontid with a complete column (24 in *Saurerpeton:* A. R. Milner, pers. comm. 1991) and unlike the count (31-35) of trimerorhachids (e.g. *Trimerorhachis:* Case, 1935; *Neldasaurus:* Chase, 1965); and (4) the slender phalanges and elongate ribs are like in small specimens of *Saurerpeton,* which has unusually slender forelimbs for a trimerorhachoid (e.g. USNM 4471; A. R. Milner, pers. comm. 1991).

CM 41708 is broadly similar to juvenile specimens of the saurerpetontid *Saurerpeton* from the Pennsylvanian of Illinois (Milner, 1982: figs. 1-2, pl. 64). The skull of CM 41708 differs from juvenile *Saurerpeton* in having a more acutely angled snout, a proportionally narrower cultriform process, lacking external gills, and having much more elongate limb bones. The more pointed snout of CM 41708 gives it a greater similarity to the holotypic snout of *S. latithorax* (Romer, 1930: fig. 4) and other adult saurerpetontids such as *Acroplous* (Foreman, 1990: fig. 1A-B). CM 41708 differs from *Saurerpeton* in possessing a wide iliac blade, as opposed to a long and slender blade (A. R. Milner, pers. comm. 1991).

The family Saurerpetontidae, within the superfamily Trimerorhachoidea, was erected by Chase (1965) to include *Saurerpeton, Isodectes (Eobrachyops),* and *Acroplous.* Subsequently, Coldiron (1978) suggested that the family was paraphyletic, but Foreman (1990) has recently demonstrated that the Saurerpetontidae is monophyletic. Unfortunately, poor preservation prevents determining whether CM 41708 possesses the diagnostic characters of this taxon (Foreman, 1990: 396). However, CM 41708 more closely resembles members of this family than those of other temnospondyl families. Thus, in conclusion, we tentatively assign CM 41708 to the Saurerpetontidae. Within this family, CM 41708 most closely resembles *Acroplous* because of the relative shortness of the posterior region of the skull.

Interestingly, CM 41708 has exactly the same mosaic of pre- and post-metamorphic characters as both the amphibamid described above and *Lafonius,* including the presence of sclerotic rings and branchial ossicles, and absence of evidence for external gills. Thus, CM 41708 is probably also a late larval form.

Family TRIMERORHACHIDAE Cope 1882
LAFONIUS LEHMANI Berman 1973

Lafonius lehmani was the first amphibian skeleton described from the Kinney Quarry (Berman, 1973) and is currently only known from the holotype (CM 25474). Taxonomically, this is the least controversial of the Kinney Quarry amphibians. This taxon has been universally accepted as a trimerorhachid (e.g. Foreman, 1990). The holotype of *Lafonius is* at about the same stage of ontogenetic development as NMMNH P-3696 and CM 41708, and is best regarded as a late larval form.

A FOURTH AMPHIBIAN SKELETON
Fig. 5B

NMMNH P-15019 is a 45 mm long body segment of a small labyrinthodont exposed in left lateral view on part and counterpart blocks. This specimen has not been prepared, and most of the skeleton anterior to the front limb is covered with matrix. The skin impressions in this specimen are similar to those of NMMNH P-3696. It appears that the anterior centra may be ossified, but the degree of ossification decreases posteriorly. The left front limb is present but lacks most of the digits. Most of the left pelvis and hindlimb are preserved. The body outline is preserved and indicates a deep tail below the axis of the vertebral column. The length of the tail is about 21 mm, as compared to an intergirdle length of 22 mm. This specimen requires further preparation before its taxonomic affinities can be properly determined.

Paleoenvironmental significance of the Kinney Quarry amphibians

The environment of deposition of the vertebrate-bearing strata at the Kinney Quarry has been the subject of much debate (e.g. Lucas & Huber, 1991; Kues & Lucas, this volume; Lorenz et al., this volume), as is also the case at the nearly contemporaneous Hamilton Quarry in Kansas (Maples & Schultze, 1988). In both cases there is paleontological evidence for both fresh- and saline-water environments. In both cases the ultimate answer is probably that the environment was periodically both saline and fresh water. How do the amphibians help in reconstructing the paleoenvironment?

Berman (1973) speculated that the *Lafonius* skeleton had been washed into the saline Kinney lagoon during a period of peak runoff from a stream. Now, there are three other amphibian skeletons from the Kinney Quarry, but these only represent about 1% of vertebrate specimens from the site which has otherwise produced a diverse fish fauna (Lucas & Huber, 1991; see also papers by Bardack, Huber, Gottfried, Schultze, and Zidek in this volume).

Several authors have suggested that both trimerorhachoids and some dissorophoids, which were undoubtedly aquatic in habit, were tolerant of saline waters (Parrish, 1978; Schultze, 1985; Milner, 1987). This view has been challenged by Hook and coworkers (Hook & Baird, 1986, 1988; Hook & Ferm, 1985; Hook & Hower, 1988).

We note two features of the amphibian assemblage at the Kinney Brick Quarry which may be important in assessing the paleoenvironment: (1) all of the amphibian skeletons from the Kinney Quarry, representing at least three taxa in separate families, are at the same stage of ontogenetic development (late larval); (2) three of the amphibian specimens include gill-rakers, which indicate planktonic feeding (Milner, 1982). These two features suggest a specialized environment which either existed in the lagoon or which was "washed into" the lagoon.

In conclusion, although both trimerorhachids and dissorophoids may have been tolerant of high-salinity waters, we believe that the extreme rarity of amphibians at Kinney suggests that they were washed into a saline lagoon as originally suggested by Berman (1973). We note, however, that the only modern brackish-water amphibians (e.g. *Rana cancrivora—the* mangrove or crab-eating frog) have brackish-tolerant larvae, and that Tertiary fresh-water frogs and salamanders are never found in lagoonal environments (A. R. Milner, pers. comm. 1991).

Acknowledgments

We thank the Kinney Brick Company for access to the quarry and D. Baird, R. W. Hook, A. R. Milner, and M. A. Shiskin for reviews. APH and SGL thank Phillip Huber for collecting and donating NMMNH P-3696 and P-15019, and NMMNH for support. DSB thanks Albert Kollar, who assisted him in the field at the time that CM 41708 was collected, and the M. Graham Netting Research Fund for support.

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Late Pennsylvanian coprolites from the Kinney Brick Quarry, central New Mexico, with notes on the classification and utility of coprolites

Adrian P. Hunt

New Mexico Museum of Natural History, 1801 Mountain Rd. NW, Albuquerque, New Mexico 87104

Abstract—Bromalite is a new term to encompass coprolites, cololites, and regurgitalites (a new term for vomit balls, gastric residues, etc. of previous authors). Coprolites are distinguished by a number of characteristics. The presence of fish regurgitalites in Paleozoic rocks is unproven. Cololite is restricted to in-situ intestinal fillings. The Late Pennsylvanian strata of the Kinney Quarry preserve intact coprolites which indicate a lack of benthic scavengers and no effect of current on the substrate. Sedimentation was probably rapid. Bromalites have numerous uses in biochronology, biostratigraphy, sedimentology, paleoecology, taphonomy, and economic geology.

Introduction

The Kinney Brick Quarry in the Manzanita Mountains of central New Mexico is a Lagerstätten that has yielded a diverse fish fauna (Zidek, 1975, 1991, this volume; Gottfried, 1987a, b, 1991, this volume; Lucas & Huber, 1991) of Late Pennsylvanian age. Among the fish remains are a number of accumulations of disarticulated fish material and other organic debris (Fig. 1) which are similar to specimens from elsewhere that have been referred to as coprolites, cololites/ enterospirae, or regurgitations (e.g. Zangerl & Richardson, 1963; Williams, 1972; Duffin, 1979; McAllister, 1988). This paper has four objectives: to review the terminology of the above-mentioned types of fossils; to clarify criteria by which these types of fossils can be distinguished; to present a preliminary description of the Kinney specimens in the light of these criteria; and to discuss briefly the importance of coprolites, cololites, and regurgitations. Abbreviations are: NMMNH, New Mexico Museum of Natural History, Albuquerque; MNA, Museum of Northern Arizona, Flagstaff; UMMP, University of Michigan Museum of Paleontology, Ann Arbor.

Classification of coprolites, cololites, and regurgitations

There are three main types of fossil specimens that comprise fossilized food items that have been ingested, and often evacuated, prior to fossilization. These three types represent fossilized feces, vomit, and intestinal-tract fillings (e.g. McAllister, 1988: fig. 1). Many authors have discussed the terminology to be applied to these fossils (Amstutz, 1958; Bronniman & Norton, 1960; El-Baz, 1968; Häntzschel et al., 1968; Williams, 1972; Duffin, 1979; McAllister 1985, 1988), but with limited agreement. Unfortunately, there is no term to encompass all these types of fossils. McAllister (1988) used the term coprolitic matter to apply to coprolites, cololites, and regurgitations. However, coprolite is a well-established name that all agree should be restricted to matter extruded past the anus (e.g. Häntzschel et al., 1968). Therefore, it is very confusing to refer to intestinal residues and regurgitated matter as coprolitic. However, there is a need for a term to apply to all these categories as there is often confusion as to which of these categories a particular specimen should be assigned (Williams, 1972; McAllister, 1985, 1988) and thus the option of assignment to a more inclusive category is essential. I propose the term bromalite (from the Greek *broma,* food) to apply to anally or orally derived ejecta and in-situ intestinal matter. Within bromalites, there are three main subdivisions: coprolites, cololites, and regurgitalites.

The term coprolite was proposed by Buckland (1829), who demonstrated in a very elegant paper that they were of fecal origin. Buckland (1835), who can be considered the father of bromalite studies, injected Roman cement into the intestines of sharks to demonstrate the similarity of the coprates that he was studying to the intestinal passage of sharks. As noted above, the term coprolite is almost universally recognized as referring to fecal matter. I believe that this term should be used for all fecal matter regardless of its size or composition (contra Bates & Johnson, 1980).

The term cololite was proposed by Agassiz (1833) to refer to preserved intestines or intestinal contents of fish (e.g. *Lumbricaria).* Fritsch (1907) suggested the name enterospirae for preserved spiral-valve intestines filled with fecal matter. Subsequently, the specimens on which both these terms were based have been demonstrated to represent other kinds of fossils (M. Williams, pers. comm. 1991), but this does not affect the meaning or utility of these terms. Although the morphology of the specimens to which these terms are referred to by their original authors is different, the meaning of the two terms is the same. Williams (1972) used the two terms as synonyms. McAllister (1985) used cololite to refer to fecal matter preserved in the intestine and enterospira to refer to fossilized valvular intestines. This distinction between the preservation of an infilling (cololite) as opposed to the preservation of a structure whether it is infilled or not (enterospira) is inconsistent with Fritsch's (1907) definition of enterospira as "the entire spiral-valved intestines filled with fecal matter" (translation of Fritsch, 1907, *in* Häntzschel et al., 1968). Enterospirae are a particular kind of cololite. I will use cololite in preference to enterospira since it is a much older term, since enterospira implies a spiral morphology which is not always the case (e.g. Pollard, 1990: fig. 2), and since it is more similar in verbal construction to the term coprolite. The latest AGI Glossary (Bates & Johnson, 1980) lists cololite as being a trace fossil of the genus *Lumbricaria.* However, such a use of the term is obviously contrary to the intent of Agassiz who meant the term to describe "intestinal tracts of fishes, more or less filled" (translation of Agassiz, 1833, *in* Häntzschel et al., 1968: 676). Note that the term applies both to the intestine and to its contents. Cololite should not be restricted to fish specimens and should be applied to all intestinal contents which are known from many types of organisms including myriapods, insects, ammonites, ichthyosaurs, and bats (Pollard, 1990). Cololite as used here refers to all material preserved within the gastrointestinal tract.

The terms vomit ball, ejecta, ejected prey, gastric residue,

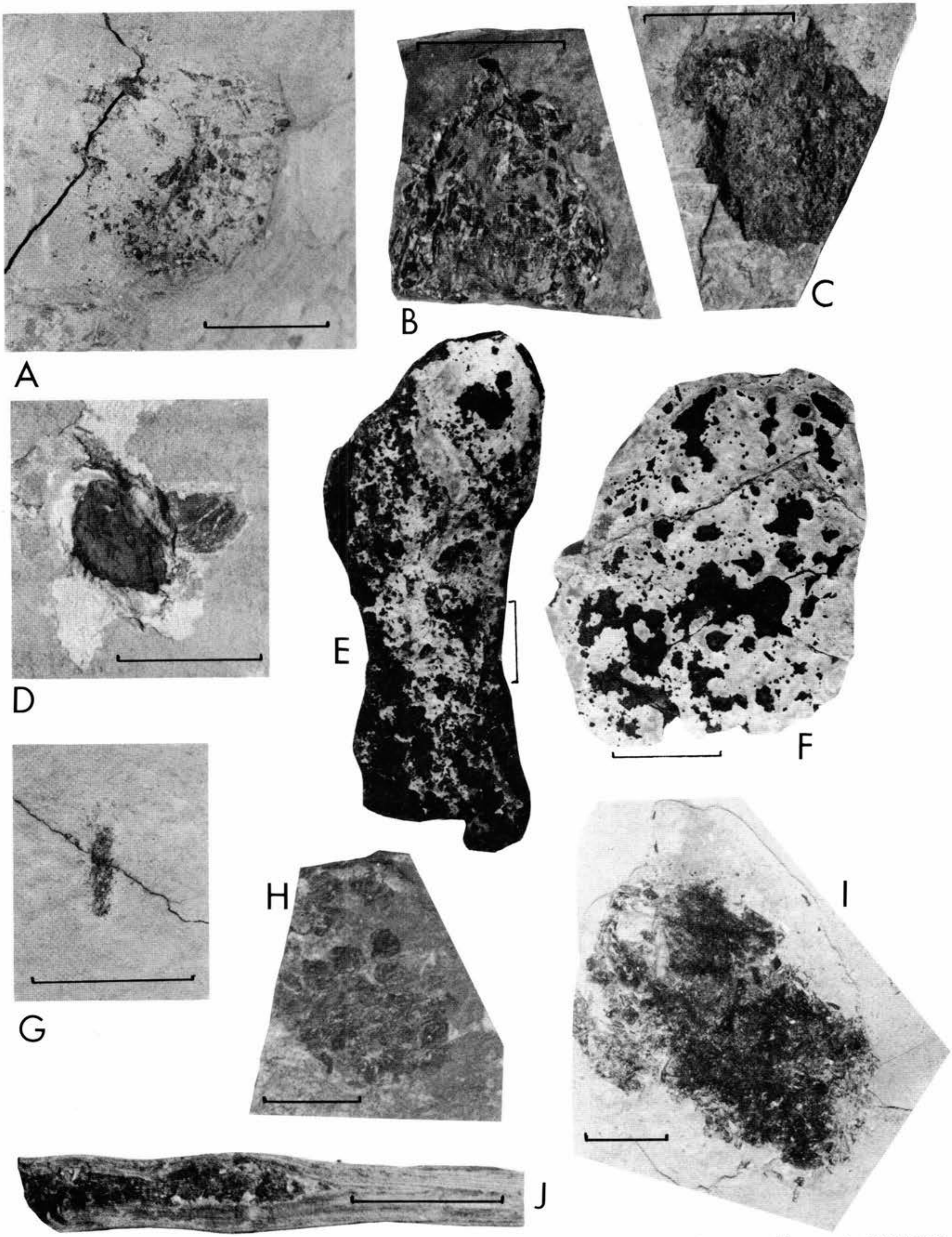

FIGURE 1—Coprolites from the Kinney Quarry. All scale bars equal 1 cm. **A,** Unprepared coprolite covered by matrix, NMMNH P-19168. **B,** Coprolite composed primarily of palaeoniscoid scales, NMMNH P-19160. **C,** Coprolite composed primarily of calcified shark cartilage, NMMNH P-19164. **D,** Small coprolite containing palaeoniscoid scales and small ?acanthodian spines, NMMNH P-19155. **E,** Spiral coprolite after preliminary acid etching, NMMNH P-19163. **F,** Oval coprolite that contains xenacanth(?) teeth and palaeoniscoid and acanthodian scales, after preliminary acid etching, NMMNH P-19172. **G,** Small, rod-shaped coprolite with microdebris preferentially distributed at the top end, indicating the influence of a weak current, NMMNH P-19162. **H,** ?Coprolite containing conchostracans, NMMNH P-19157. **I,** ?Coprolite with no fine-grained groundmass, NMMNH P-19165. **J,** Cross section through coprolite, NMMNH P-19153.

regurgitation, regurgitate, and pellet have been applied, among others, to matter orally ejected from the gastrointestinal tract (McAllister, 1988; Pollard, 1990). However, there is no term to apply to all types of regurgitated matter. Here, regurgitalite is proposed as a term, consonant with coprolite and cololite, to refer to regurgitated material.

Recognition of bromalites

Coprolites are most likely to be confused with concretions. However, coprolites can be distinguished by a combination of some or all of the following: (1) extrusive external morphology, e.g. spiral (Amstutz, 1958); (2) internal structure is ordered, e.g. spiral or with longitudinal canals; (3) longitudinal or spiral striations (Amstutz, 1958); (4) narrow range of linear dimensions in a population (Amstutz, 1958); (5) similarity of morphology to animal guts (Amstutz, 1958); (6) morphology reflecting ranges of viscosity in modern fecal matter (Amstutz, 1958); (7) flattening of ventral side (Amstutz, 1958); (8) inclusions of organic matter (McAllister, 1988); (9) presence of evidence for gas bubbles or gas-escape structures (McAllister, 1988); (10) composition of calcium phosphate; (11) very fine-grained matrix; (12) marked vertical relief even in finely laminated shales; and (13) presence in sedimentary rocks or unconsolidated sediment.

Cololites can only be unequivocally recognized when they are found within the intestinal tract of a fossilized animal. A good example of an incontrovertible cololite is within the Devonian shark specimen illustrated by Woodward (1917: fig. 1). Williams (1972) hypothesized, in an influential paper, that Lower Permian bromalites from Kansas were fossilized valvular intestines, although they were not found within body cavities, on the basis of detailed microscopic and comparative-anatomical studies. However, McAllister (1985) was able to demonstrate that these specimens were indistinguishable from fecal pellets produced by a modern shark. Thus, at our present stage of knowledge, it is apparent that the term cololite should be restricted to intestinal fillings preserved within body cavities.

Regurgitalites are the most difficult bromalites to recognize in the fossil record. Only owl regurgitalites in Neogene and Quaternary deposits are easy to identify on the basis of element representation, breakage patterns, and relative lack of digestive erosion (Korth, 1979; Kusmer, 1990). Fish regurgitalites are particularly difficult to interpret. Zangerl & Richardson (1963) conducted a classic study of the paleoecology of two Pennsylvanian-age black shales in Indiana. Among the large number of fish fossils discussed in their study, they recognized many fragmented or/and fragmentary fish as regurgitalites (their gastric residues and ejected prey). These specimens often include more than one individual and are associated with "material resembling coprolitic groundmass" (Zangerl & Richardson, 1963: 140). Zangerl & Richardson (1963) also noted that some modern sharks regurgitate indigestible remains.

There appear to be three broad categories of specimens that Zangerl & Richardson attributed to regurgitalites. First, some specimens consist of a wide scatter, usually under 0.1 m^2, which consists of fragmentary fish debris (Zangerl & Richardson, 1963: pl. 41A), to which they refer as a "gastric residue spatter." There is no evidence to suggest that these represent other than fish that have undergone natural decay and have been dissociated by floating in a bloated state or have been scavenged. There is no evidence of "coprolitic groundmass." Second, there are whole fish which show slight disarticulation (Zangerl & Richardson, 1963: pl. 41C). Again, there is no "coprolitic groundmass," and it is more parsimonious to assume normal decay with dissociation caused by a slight current. Third, there are discrete ovoid masses of "coprolitic groundmass" containing many fish bones (Zangerl & Richardson, 1963: pls. 43-45, 46C, 49, 5013-C). Apparently, the authors considered these specimens to be regurgitalites because they have rather large amounts of bone material relative to groundmass and show more scattering than specimens regarded as true coprolites. However, there is no reason to believe that these specimens are not coprolites and that the more scattered ones represent further degrees of decay.

Elder (1985) criticized Zangerl & Richardson's (1963) interpretation of large numbers of regurgitalites because: (1) regurgitation is a maladaptive behavior; (2) the "regurgitalites" (I presume she means Zangerl & Richardson's third type) possess no characteristics to distinguish them from coprolites; and (3) because no other gastric residues have been recognized in the fossil record. The strongest of these arguments is that the supposed regurgitalites cannot be distinguished from coprolites (or in some cases naturally decayed fish). Undoubtedly, some modern sharks do regurgitate some indigestible elements, but this is no justification for assigning most of the specimens described by Zangerl & Richardson (1963) to that category.

More recently, McAllister (1988) has referred to specimens from the Pennsylvanian of Kansas as regurgitalites. He also followed Zangerl & Richardson (1963) in dividing regurgitalites into gastric residues (from the stomach) and ejecta from the oral cavity), with the former indicated by a greater degree of disarticulation, more groundmass, and more advanced digestive etching. To judge from his descriptions and illustrations (e.g. McAllister, 1988: fig. 5A), there is no indication that these specimens are not coprolites in varying stages of decay or of different viscosities. In conclusion, modern sharks do regurgitate food matter, but current assignments of Paleozoic specimens to regurgitalites should be treated with caution pending studies of criteria which can be used to adequately distinguish this type of bromalite. Most specimens that are currently considered to represent regurgitalites are more parsimoniously interpreted as decayed fish or coprolites.

The Kinney Brick Quarry bromalites

Geologic setting

The strata exposed in the Kinney Brick Quarry pertain to the Pine Shadow Member of the Wild Cow Formation which is early Virgilian (Late Pennsylvanian) in age (Myers, 1988). The specimens described here are from a 0.5 m thick sequence of calcareous shales (units 2-4 of Lucas & Huber, 1991) overlying a micritic limestone (unit 1 of Lucas & Huber, 1991) that floors the quarry.

Methods

Most of the bromalites were discovered during the splitting of shale (Fig. 1B-D, G-J) and thus are now visible in cross section. A few coprolites were discovered as bulges in the shale laminae (Fig. 1A). Some of these specimens were prepared mechanically or by the use of glacial acetic and muriatic acids (Fig. 1H-I). No specimens easily separated from the surrounding matrix. As a result, the external morphology of most of the coprolites was not visible and most of the interpretations are based on internal features (cf. McAllister, 1988). Coprolites were found on the same laminae as fish specimens.

Coprolites

There are 12 undoubted coprolites in the NMMNH collection (Fig. 1A-F, J; Table 1). These are recognized on the basis of the presence of disarticulated fish material within a fine groundmass in an ovoid or rod-like shape. The groundmass differs from the surrounding rock matrix, but both are calcareous and react strongly to acid. All these coprolites have a greater thickness than any of the articu-

TABLE 1—Dimensions and composition of Kinney Quarry coprolites. Measurements are in millimeters. Abbreviations: acanth, acanthodian; e, estimated; palaeo, palaeoniscoid; xena, xenacanth.

NMMNH No.	length	width	thickness	content	comments
19153	33e	?	4	palaeo scales	
19154	?	23	2	palaeo scales	
19155	9	5	2	palaeo scales/ ?small acanth spines	groundmass gray/surrounding matrix olive, dark outer rind
19158	19	11	0.8	palaeo scales	
19160	20e	16	1.5	palaeo scales	
19161	10	2	0.5	palaeo scales/acanth scales	no groundmass
19162	5	1	0.5	?palaeo debris	no groundmass, pattern of decay indicates slight unidirectional current
19163	65	28	12	acanth scales/rare palaeo scales	locally calcite rind
19164	20e	14	2.5	shark	calcified cartilage
19168	20e	18	2	palaeo scales	
19172	55	43	6.5	acanth scales/palaeo scales/xena(?) teeth	
19177	19	14	2	palaeo scales/acanth scales	

lated fish specimens from the quarry and all show a high degree of flattening relative to their presumed original (round) cross section. The largest coprolite (NMMNH P-19163) is 65 mm long, 28 mm wide, and 12 mm thick. The majority of coprolites contain the remains of palaeoniscoid fish (10 of 12) and three contain visible evidence of more than one taxon of fish. The only shark remains are teeth in one coprolite and portions of calcified cartilage in another (Table 1).

Because most of the coprolites are visible in cross section, it is difficult to determine their external morphology. Only one of them appears to be spiral. NMMNH P-19163 appears to be weakly heteropolar (Fig. 1E). Most of the coprolites are ovoid, with only the largest (NMMNH P-19163; Fig. 1E) and smallest (NMMNH P-19161 and P-19162; Fig. 1G) being rod-like.

NMMNH P-19161 and 19162 (Fig. 1G) are not only by far the smallest coprolites but also the only ones that lack a fine-grained groundmass. They are nevertheless considered to represent coprolites because they preserve finely macerated fish debris in a sharply delimited area of rod-like shape.

Cololites

One of the most interesting specimens of bromalite is preserved within the body of a symmoriid shark (Fig. 2; NMMNH P-19182) described elsewhere (Zidek, this volume). This cololite is 28 mm long (fish length 52.5 cm) and lies between the neural and haemal arches of the vertebral column (Fig. 2B). The cololite is broadly ovoid in cross section, but is asymmetrical, with a wider, rounded posterior end and an acutely pointed and more diffuse anterior end. The cololite contains finely macerated fish debris which appears to be acanthodian. Whether this cololite represents material in the intestine or the colon is not clear because the position itself is not diagnostic, as some of the posterior intestinal tract may recede posteriorly and even extrude through the anus in modem sharks (Williams, 1972). The presence of an apparently hardened cololite within the body cavity is reminiscent of similar findings in recent sharks (McAllister, 1985).

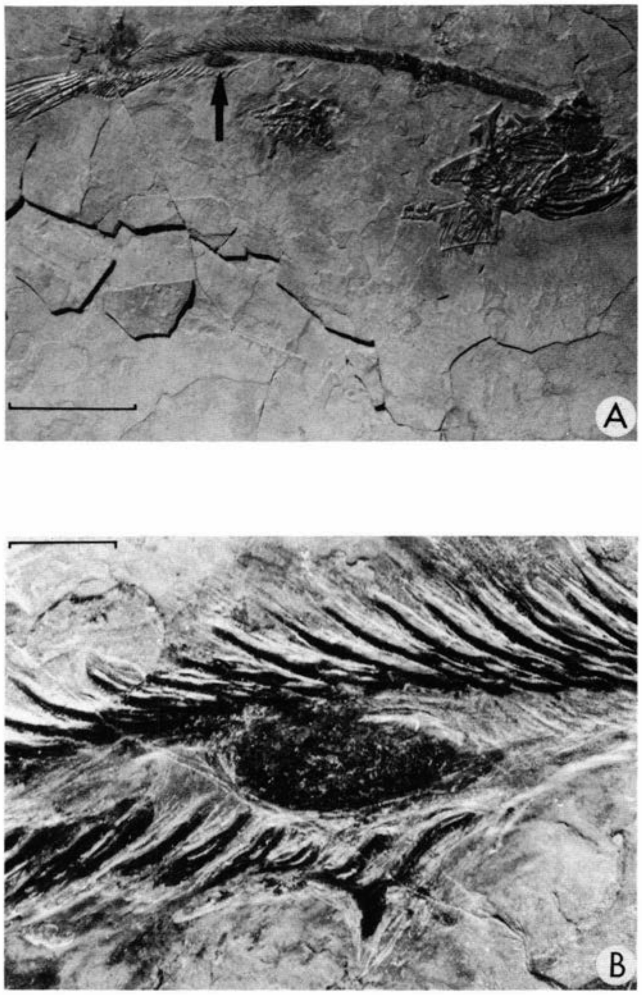

FIGURE 2—Cololite within the body cavity of a symmoriid shark. **A,** Skeleton with coprolite in posterior region, NMMNH P-19182, scale bar equals 10 cm. **B,** Close-up of cololite, scale bar equals 1 cm.

?Coprolites

Nine specimens from the Kinney Brick Quarry are tentatively regarded as coprolites (Table 2). These specimens consist of three-dimensionally jumbled fish debris or overlapping conchostracan valves preserved in a discrete ovoid area, and are not associated with any coprolitic groundmass (Fig. 1H—I). Some authors might regard these features as indicative of regurgitalites (e.g. McAllister, 1988). However, since there is no evidence of anything characteristic of modern regurgitated material, I consider it more parsimonious to regard these specimens as a different kind of coprolite which lacks groundmass. The reasons for a lack of ground-mass could include coprolite production by an animal in which the "groundmass" is more fluid (e.g. most modern sharks; Williams, 1972), routinely or depending on diet.

The conchostracan *(Pseudestheria)* accumulations do not have as well defined margins as the other representatives of this group of coprolites, and valves are often entire (Fig. 1H). The completeness of the valves suggests that these putative coprolites were not produced by fish, as arthropods ingested by modern fish are excreted in a very fragmentary condition (J. Zidek, pers. comm. 1991). However, M. Williams (pers. comm. 1991) has found well-preserved valves in Devonian coprolites. There is no evidence for current influence on the substrate which could account for the accumulations of conchostracans. K. Kietzke (pers. comm. 1991) noted that many ostracodes at the Kinney Quarry are also found in coprolite-like accumulations consisting of dissociated, and often fragmented, valves of a single taxon. Similar accumulations are found in concretions from the Pennsylvanian Mazon Creek, Illinois (K. Kietzke, pers. comm. 1991).

Discussion

The Kinney Brick Quarry coprolites are most comparable with those of the Hamilton Quarry in Kansas (McAllister, 1988; Maples & Schultze, 1988). Similarities are: (1) The coprolites and surrounding marix are calcareous; (2) coprolite contents are dominated by palaeoniscoid and acanthodian scales, with rare coprolites containing shark or invertebrate specimens; and (3) spiral coprolites are uncommon. Such similarities are to be expected at two localities which are close in age (both Virgilian), paleoecology (both contain nonmarine and marine elements), and fauna (associated fish in each case include acanthodians, palaeoniscoids, and sharks, although in different proportions).

All the coprolites, except those containing conchostracans, are attributed to fish on the basis of their large size, number of included fish elements, and similarity to coprolites undoubtedly associated with fish (e.g. Zidek, 1980). There is no evidence at the Kinney Brick Quarry for invertebrates large enough to ingest the majority of the fish (although they could have scavenged them) or to have produced such large coprolites as are preserved. The conchostracan ?coprolites may have been produced by invertebrates despite their large size. There are enigmatic invertebrates of fairly large size known from the quarry (Kues, this volume).

The Kinney Brick Quarry coprolites and decayed fish, which earlier authors might have considered regurgitalites, give clues to the paleoecology and environment of deposition of the strata exposed in the quarry. First, coprolites are uncommon at Kinney; there are only 21 coprolites in the NMMNH collection. The Hamilton Quarry sample is also small relative to the number of fish. McAllister (1988) indicated that there was a collecting bias in favor of more complete specimens. However, unlike the Hamilton Quarry collection, the Kinney Brick Quarry collection was made essentially by one person (Phillip Huber), who collected all possible coprolites (P. Huber, pers. comm. 1990); therefore, the paucity of coprolites is real. One would not expect to find many fish coprolites in any assemblage because it is obvious that most modern fish produce feces which are not viscous enough to be preserved as fossils (e.g. sharks; Williams, 1972). Therefore, the paucity of coprolites relative to the number of complete fish suggests that the fish sample obtained from the quarry may be reasonably unbiased.

Second, some of the coprolites exhibit signs of decay and movement of fish inclusions, with formation of a partial halo of fragments around the main body of the coprolite. However, only in NMMNH P-19162 is there an asymmetry to the halo. Obviously, if there was any marked effect of current on the substrate where the decaying coprolite lay, the coprolite decay products would show a preferred displacement direction (cf. decaying fish; Elder, 1985). We can thus conclude that there was virtually no effect of current on the substrate where the coprolites came to rest.

Third, the number of severely decayed fish (regurgitalites of previous authors) is small (less than 15) (Fig. 3). The majority (ca. 80%) of fish are complete or very slightly disarticulated, with no preferential dispersal direction. These factors indicate: (1) that the majority of fish did not bloat, float, and decay (Elder, 1985); (2) that there were few scavengers on the sediment surface; and (3) that little or no current affected the sediment surface. Experiments by Elder (1985) indicate that fish do not float, hence are usually preserved whole, if the water is cooler than 15°C or more than 8-10 m deep. Even if the water was deep, the rarity of floated (disarticulated) fish would suggest cool temperatures, as warm waters, even at depth, often result in partial flotation and decay (Elder, 1985). The small number of disarticulated fish skeletons indicates that there were few

TABLE 2—Dimensions and compositions of Kinney ?coprolites. Measurements are in millimeters. Abbreviations: conch, conchostracans; e, estimated; palaeo, palaeoniscoid.

NMMNH No.	length	width	thickness	content	comments
19156	12	9	0.1	conch	superimposed on plant frond, overlapping valves
19157	22e	15	0.1	conch	overlapping valves
19165	41	24	1.5	palaeo scales	no groundmass
19166	18e	10e	0.1	conch	overlapping valves
19171	?	25	2	palaeo scales	
19178	?	17	1	palaeo scales	
19179	18	5	0.1	conch	overlapping valves
19183	?	25	1.5	palaeo scales +	
19184	23e	17	2	palaeo scales	

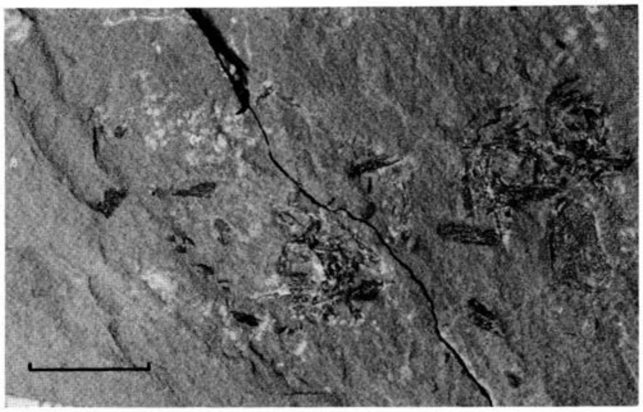

FIGURE 3—Disarticulated palaeoniscoid fish, NMMNH P-19175. Scale bar equals 1 cm.

predators on the substrate and that there was essentially no current to affect the bottom. Fish preservation is incompatible with a tidal-flat model of deposition for the Kinney strata (Archer & Clark, 1991; Feldman et al., 1991), as tidal flats maintain large communities of invertebrate scavengers which would have undoubtedly disrupted the majority of fish skeletons in a characteristic way (Elder, 1985).

In conclusion, according to Elder's (1985) data the manner of preservation of coprolites and decayed fish in the Kinney Quarry indicates that the laminae on which they are preserved were formed in cool (<15°C) water more than 8-10 m deep. However, the paleolatitude and the fossil flora and fauna of the quarry indicate that temperatures were not cool. Furthermore, the cyclic sedimentation evident in the Kinney strata is apparently of tidal origin (Archer & Clark, 1991; Feldman et al., 1991), suggesting shallow water. An explanation for the fish and coprolite preservation, and for shallow, warm water conditions is to assume very rapid rates of sedimentation. Tidally influenced, cyclic sedimentation suggests high rates of sedimentation. In such conditions, fish would be buried before they bloated or were scavenged, and there would be little time for in-situ decay and the effect of currents. However, the details of the taphonomy of the quarry are more complex and require further study. For example, to understand why some laminae preserve nonmarine organisms (e.g. amphibians; Hunt et al., this volume) and others do not.

Importance of bromalites

Introduction

Bromalites are geologically important trace fossils whose diverse uses have been overlooked. The following is a brief consideration of the many contributions that bromalites (chiefly coprolites) can and do make to various subdisciplines of geology.

Biochronology

Coprolites have an unrealized potential for use in biochronology, particularly in nonmarine red beds. A case in point concerns the Late Triassic Chinle Group (sensu Lucas, in press) of the American Southwest. The Chinle Group yields thousands of coprolites, but most museum collections which preserve large numbers of vertebrate fossils from these strata include only a handful of coprolites (e.g. University of Michigan Museum of Paleontology; Texas Memorial Museum; University of California at Berkeley, Museum of Paleontology). During the last six years, I have made a special effort to collect thousands of coprolites at several particularly rich sites and also as isolated finds. These samples cover much of the late Carnian, Norian, and Rhaetian (Hunt, in press). Preliminary analysis of these samples, together with examination of all pertinent museum collections, indicates that coprolites are of biochronological utility in the Chinle Group.

Two morphologies of coprolites are restricted to late Carnian strata in samples of the Chinle Group from Wyoming to west Texas (Fig. 4). The first of these types is a heteropolar spiral coprolite (sensu Neumayer, 1904) usually less than 3 cm long, which tapers to a blunt point and usually has four to six spirals at the wider end (Fig. 4A—B; Case, 1922: fig. 33A—B; Ash, 1978: fig. 2h). It is also known from late Carnian strata in India (Jain, 1983: fig. 2A, pl. 82/1-6, 9-11). This type of heteropolar coprolite is absent from all Norian coprofaunas in the Chinle Group. The second type of coprolite averages 6-9 cm in length and thus is at least twice the length of typical Chinle coprolites (Fig. 4C). These coprolites are broad and preserve no external features except for rare longitudinal striations which are discontinuous. They are always dark gray, in contrast to most Chinle coprolites which

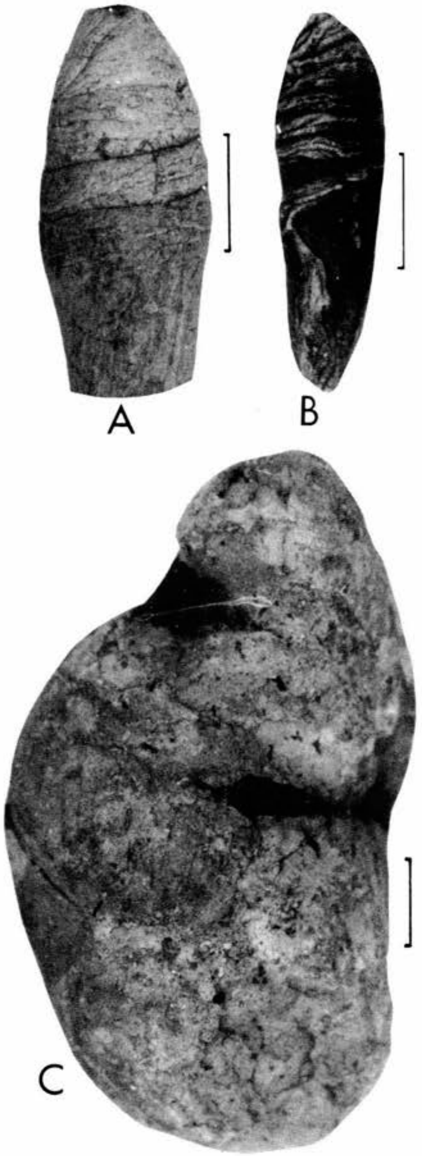

FIGURE 4—Coprolites from the Chinle Group of the American Southwest. Scale bars equal 1 cm. **A,** Heteropolar spiral coprolite from the Tecovas Formation of west Texas, UMMP 7283. **B,** Heteropolar spiral coprolite from the Tecovas Formation of west Texas, UMMP 7283. **C,** Dicynodont coprolite from the *Placerias* quarry of northeastern Arizona, MNA 2720.

are red, and contain large amounts of fine- to coarsely macerated plant debris. This type of coprolite is currently known only from late Carnian strata in west Texas (UMMP 7255) and Arizona (e.g. MNA 2720-2723).

The first type of coprolite is similar to heteropolar coprates from the late Paleozoic (e.g. Williams, 1972: pl. 1). Because of their spiral nature, this form of coprolite has generally been attributed to a fish with a spiral valve, usually a dipnoan (e.g. Case, 1922), a shark, or another primitive fish (e.g. McAllister, 1985). The xenacanth sharks become locally extinct at the Carnian-Norian boundary in the Chinle Group (Huber et al., in press), and lungfish show a marked reduction in abundance at this boundary and are only very locally abundant thereafter (e.g. the Lungfish Locality of Murry, 1989) in Norian strata of the American Southwest. It is thus unclear what organism produced this type of coprolite, although it is tempting to attribute them to xenacanths because of similar stratigraphic ranges and because this kind of coprolite has previously been assigned, albeit tentatively, to xenacanth sharks (Williams, 1972).

The second type of coprolite obviously represents a large herbivore. There is fairly strong circumstantial evidence to suggest that these coprolites derive from dicynodonts, because (1) this type of coprolite is only abundant at the *Placerias* quarry in northeastern Arizona, which is characterized by a mass accumulation of dicynodont bones (Camp & Welles, 1956); and (2) dicynodonts are the only very large-bodied herbivore in the Chinle Group, and they have the same stratigraphic distribution as this type of coprolite, dicynodonts becoming extinct at the Carnian-Norian boundary. Aetosaurs are the only other large herbivores in the Chinle Group, but they are present throughout the Carnian and Norian, and their distribution suggests that they are not responsible for this type of coprolite.

Thus, coprolites are of great biochronologic utility in the Chinle Group, particularly because they are often more common than biochronologically significant tetrapod fossils. This biochronology is only locally significant, as there are undoubtedly coprolites of similar morphology which occur in strata of different ages, but possibly with more detailed work this "coprochronology" will have broader applications.

Biostratigraphy

In some cases coprolites have utility for correlation which is not related to absolute age (i.e. not biochronologic) but to the correlation of strata by their included fossils (i.e. biostratigraphy). One example of the biostratigraphic utility of coprolites is the coprolite horizon of the upper Weber Formation (Pennsylvanian) of Colorado. Johnson (1934) demonstrated that a coprolite horizon, with an assemblage of amphipolar and heteropolar spiral coprolites, could be correlated through Chaffee and Park Counties, Colorado, in the upper Weber Formation. Price (1927) demonstrated a similar utility of coprolites in the Pennsylvanian of West Virginia. It is apparent that coprolites, or more particularly beds rich in coprolites, have a demonstrated potential for biostratigraphic correlation.

Paleoecology and taphonomy

Coprolites have a number of uses in paleoecology, namely in indicating 'the presence of organisms not known from body fossils and in recognizing different fades. Ideally, all organisms which produce excreta could be recognized on the basis of coprolites. In reality only invertebrate coprolites can be identified with any certainty and this is principally because of the large amount of work on modern invertebrate feces (e.g. Moore, 1939; Schafer, 1972). Thus, invertebrate coprolites can be very useful in paleoecology by inferring the presence of organisms not recognized on the basis of body fossils (e.g. Bronnimann & Norton, 1960). Hopefully, increased work on modern vertebrate feces will produce similar results (e.g. Kusmer, 1990).

Ideally, not only could the coprolite producer be identified, but also conclusions could be drawn about the feeding behavior of the animal in question. However, such studies are fraught with difficulties. For example, McAllister (1988) used the size of acanthodian scales in coprolites from Kansas to estimate the size of the ingested prey, using data from Zidek (1976), and from this he inferred that very small and very large acanthodians were not preyed upon. However, he failed to note that the scales visible in the coprolites might not be the largest scales of the ingested prey (J. Zidek, pers. comm. 1991) and that the smaller scales, with their larger surface area/volume ratio would be preferentially destroyed by stomach acids (Dodson, 1973). Nevertheless, it might be possible, in the light of greater knowledge, to infer food preferences of organisms (or certain morphs of coprolite) from coprolite contents.

K. Kietzke (pers. comm. 1991) notes an interesting use of coprolites in paleoecology. In the Oligocene Brule Formation of South Dakota, coprolites containing bone material, and thus inferred to have been produced by carnivores, are commonly associated with skeletons of partially scavenged herbivores. K. Kietzke suggests that this may represent marking of food areas by predators or scavengers (probably *Hyaenodon* based on size).

There has been little work on "coprofacies," but it is evident that coprolites characterize different facies at various scales. On a large scale it is apparent that red-bed sequences, such as are common in the Permian and Triassic of Laurasia, preserve abundant and diverse coprofaunas. This is in marked contrast to non-red-bed sequences of the **Jurassic** and Cretaceous of North America, where coprolites are rare in comparable fluvial and lacustrine strata (e.g. Hunt, in press). There must be taphonomiddiagenetic explanations for these patterns of occurrence. Within a red-bed sequence various coprofacies can be recognized. If we again consider the late Carnian portion of the Chinle Group, preliminary analysis suggests that at least three coprofacies are presently distinguished by different assemblages of coprolites: (1) dominated by ?dicynodont coprolites (see above); (2) a typical red-bed fluvial assemblage (e.g. Case, 1922: fig. 33); and (3) a lacustrine assemblage (e.g. Ash, 1978). Further work on the distribution and morphology of these assemblages will eventually aid in the recognition of coprofacies, which will in turn aid in paleoecological reconstruction.

Microvertebrate assemblages in nonmarine strata are accumulations of small, disarticulated bones and teeth which are virtually the only source of information in the Mesozoic on animals with body weights less than 5 kg, and are also important in the understanding of small animals in the Tertiary and Quaternary (Mellett, 1974; Fisher, 1981). A coprolite or regurgitalite origin has long been suspected for microvertebrate assemblages (e.g. Simpson, 1937; McGrew, 1963; Mellett, 1974; Korth, 1979; Kusmer, 1990). It now seems clear that some microvertebrate assemblages are of coprolite origin, but these are restricted to Tertiary and Quaternary strata (Hunt, 1984, 1987, in press). Mesozoic microvertebrate assemblages all are of hydrodynamic origin, probably because digestive systems of theropod dinosaurs destroyed most bone before defecation, as do modern crocodiles (Hunt, 1984, 1987, in press). Thus, bromalites are important in the formation of microvertebrate assemblages in post-Mesozoic rocks and hence in our understanding of evolution of small vertebrates.

Sedimentology

There are numerous uses of coprolites in sedimentology, as indicators of current direction (Hakes, 1976), for estimating rates of deposition (Zangerl & Richardson, 1963), degree of compaction, and current velocity, and as evidence of periods of nondeposition, among others. The very preservation of coprolites in some environments, such as in nonmarine red beds, is indicative of a certain set of sedimentological conditions which bear study. In conclusion, coprolites can be quite important in sedimentology, although this is not widely appreciated. For example, Potter et al. (1980) have only one entry for coprolites in the subject index of their book on sedimentology of shale. It should be noted that many trace fossils are wholly or in part of bromalitic (usually invertebrate) origin (K. Kietzke, pers. comm. 1991).

Structural geology

Bromalites are potentially useful for determining structural attitude and degree of deformation in structurally distorted rocks.

Economic geology

Bromalites are economically important in several ways. Most importantly, coprolites are a major source of phosphates. Bat and bird guano (ornithocoprus of Buckland, 1835) is the most obvious bromalite source of phosphate. Guano varies from unaltered bat feces to bird coprolites on oceanic islands that has been leached to form an insoluble residue of calcium phosphate. Guano has been mined, for example at U-Bar Cave in southwestern New Mexico (Harris, 1986). Marine phosphatic rocks are a much more important source of sedimentary phosphates. There is no widely accepted scheme for classifying these deposits, but they include bedded phosphorites, bioclastic phosphorites, nodular phosphorites, and pebble-bed phosphorites. Although these deposits are not just "submarine guano," coprolites appear to have been a component in the formation of several of these types of deposits (Pettijohn, 1976: 432). At the very least the coprolites contribute to the high organic content of strata that, together with an 0_2 minimum zone, is necessary for phosphogenesis (Trappe & Vondra, 1991), and at most coprolites may be the source of phosphorus.

In a more negative way, coprolites can diminish the economic importance of otherwise important deposits. The Whitemud Formation (Late Cretaceous) of Saskatchewan, Canada, is a potential source of ceramic clay, but it is rendered uneconomic by the presence of numerous iron-rich coprolites (Broughton et al., 1978).

In summary, coprolites are of economic importance and increased study of their formation and preservation can only help our understanding of these trace fossils.

Acknowledgments

I wish to thank K. K. Kietzke, S. G. Lucas, and **J.** Zidek for useful discussions, K. K. Kietzke, S. G. Lucas, J. A. McAllister, and M. E. Williams for thoughtful reviews of this paper, J. Zidek for bringing to my attention the cololite within the symmoriid skeleton, P. Huber and D. D'Andrea for donation of specimens, and NMMNH for support.

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Comparison of the Late Pennsylvanian faunal assemblage of Kinney Brick Company Quarry, New Mexico, with other Late Pennsylvanian Lagerstatten

Hans-Peter Schultze[1] and Christopher G. Maples[2]

'Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045; 'Kansas Geological Survey, University of Kansas, Lawrence, Kansas 66047

Abstract—The fauna of the Pine Shadow Member of the Wild Cow Formation in the Kinney Brick Company Quarry is compared with eight other Pennsylvanian faunas from Lagerstätten in Kansas, Illinois, Ohio, France, and Czechoslovakia. The Kinney fauna is most similar to the geographically and stratigraphically nearest Kansas localities of Hamilton and Robinson; it represents a nearshore marine assemblage. The terrestrial faunas, both invertebrates and vertebrates, result in more robust clusters than the aquatic faunas, which we judge to reflect preferential collecting of unusually well preserved vertebrates and insects at these Lagerstätten.

Introduction

In 1989, we compared eight Pennsylvanian-age vertebrate localities and arranged them in a sequence from more marine to more fresh-water-influenced (Maples & Schultze, 1989). That preliminary study was done by comparing the faunas of the eight localities in a table without using cluster analysis or any other statistical method. Nevertheless, a clear picture emerged that was obvious for both vertebrates and invertebrates. A continuum from more marine-influenced localities such as Hamilton and Robinson, Kansas, to more fresh-water-influenced localities such as Montceaules-Mines, France, and Nýrany, Czechoslovakia, appeared. The purpose of this paper is to perform cluster analyses on these data and compare the results with data obtained from the Kinney Brick Company Quarry, New Mexico. These nine localities were situated within 10° of the Late Pennsylvanian paleoequator (Fig. 1). All nine Lagerstätten are Middle to Late Pennsylvanian in age, although they are not exactly contemporaneous (Fig. 2).

Limitations of cluster analysis

We do not repeat here the general limitations connected with Lagerstätten analyses (see Maples & Schultze, 1989, for discussion of faunal mixing, collecting bias, taphonomic bias, amphidromy, etc.), but refer only to limitations of cluster analysis as both mathematics and art. As a multivariate technique, cluster analysis is so commonly used by paleontologists that a section on its limitations may seem a bit superfluous. However, over the years it has become obvious that many users of cluster analysis suffer from the all-too-common "black-box syndrome." In cluster analysis, we define black-box syndrome as a tendency to assume that a dendrogram is the absolute answer because it was constructed using mathematical procedures. We feel that nothing could be further from the truth. However, lest we "throw the baby out with the bathwater," we judge cluster analysis to be a simple but powerful and useful method for visually conveying relative similarities and differences. Some of the following discussion has been paraphrased from a series of

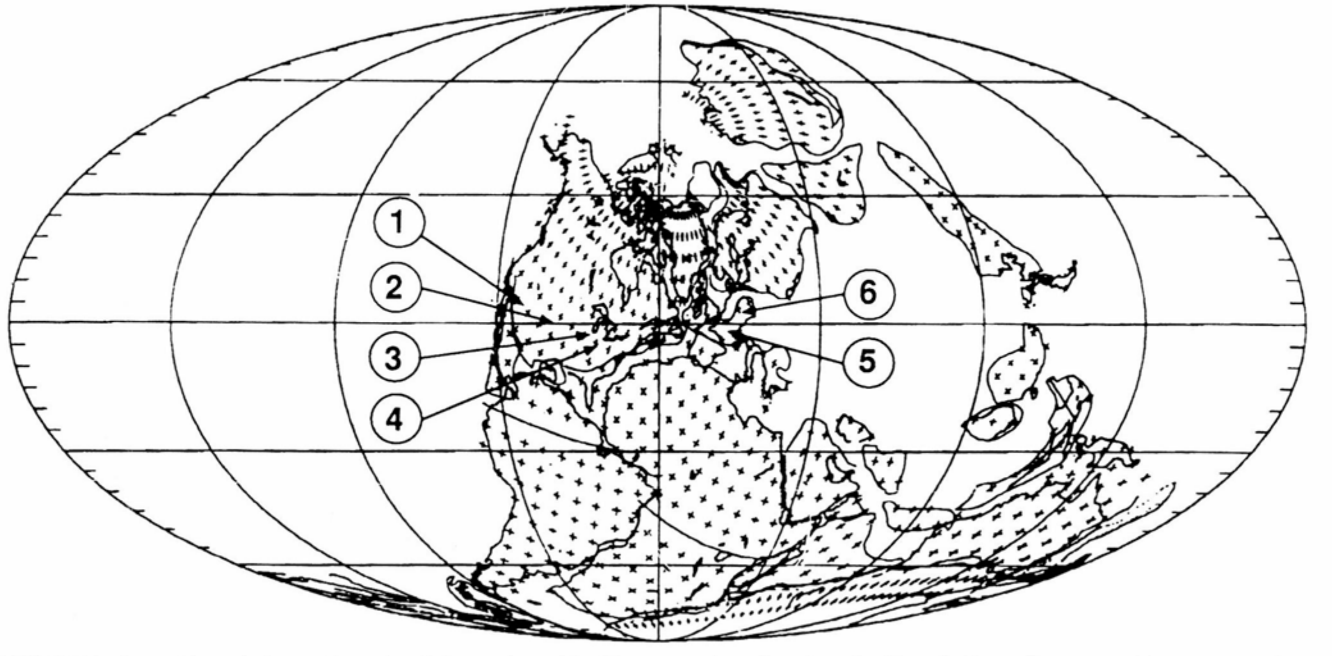

FIGURE 1—Late Paleozoic Lagerstätten localities evaluated in this paper, plotted against the Westphalian paleogeographic reconstruction of Scotese & McKerrow (1990). 1 = Kinney Brick Company Quarry, New Mexico; 2 = Hamilton, Robinson, and Garnett, Kansas; 3 = Essex and Braidwood (= Mazon Creek), Illinois; 4 = Linton, Ohio; 4 = Montceau-les-Mines, France; 6 = Nýřany, Czechoslovakia.

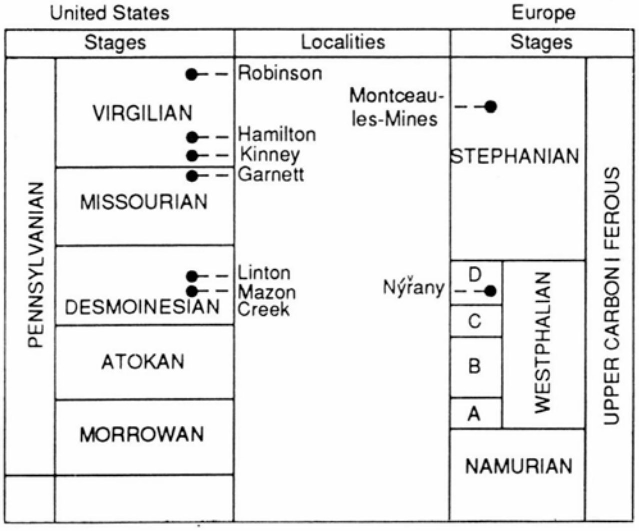

FIGURE 2—Approximate stratigraphic positions of the nine Lagerstätten evaluated in this paper. The relative position of Kinney is estimated from age assignments for associated strata (modified from Maples & Schultze, 1989).

papers addressing cluster analysis (Archer & Maples, 1987, 1989a, b; Maples & Archer, 1988). Other parts of the discussion are from our experiences using data familiar to us.

Sparseness

Many paleontological data sets are sparse (i.e. many zeros or missing data; for example, see data sets of Mills & Langenheim, 1987, and Wilson, 1982) and comparative Lagerstätten data of the type we present herein are particularly susceptible to sparseness. Maples & Archer (1988) and Archer & Maples (1989b) noted that most cluster coefficients do not respond well to large numbers of zeros in the data matrix. This is because many coefficients use "D" (mutual absences; see Fig. 3) as positive correlation indicators in the numerator. Because of the poor response of cluster coefficients to zeros, we have culled our data to include only those taxa that occur in at least two of the nine localities (see Appendix 1). Culling data does, however, have its disadvantages. Archer & Maples (1987) suggested that, given 50% ones and 50% zeros, most coefficients required at least 20 variables to be interpreted with confidence. Later, Maples & Archer (1988) noted that sparse matrices required even more variables to provide adequate results. Culling data reduces the number of variables. Clearly, we are in the fringe of acceptable number of variables in these data sets (especially the terrestrial data).

		Sample 1	
		Present	Absent
Sample 2	Present	A	B
	Absent	C	D

FIGURE 3—2 × 2 contingency table used as the basis for assignment of values in coefficient formulae. The Jaccard coefficient [A/(A+B+C)] ignores mutual absences (the "D" cell), whereas Euclidean distance [(B+C)/(A+B+C+D)] de-emphasizes mutual absences.

This brings us to a fundamental question involving the art of selecting cluster coefficients: Are mutual absences important? For comparative Lagerstätten data, we would have to answer "not very." We feel this way in part because the sedimentological and taxonomical evaluation of each Lagerstätte has been different. For some Lagerstätten (Hamilton and Kinney) we have bed-by-bed data. Data from other Lagerstätten are derived from one locality with little regard to microstratigraphic placement (Robinson, Garnett, Linton). Worse still, some data are microstratigraphic amalgams from several localities over relatively large areas (Essex, Braidwood, Nýrany, Montceau-les-Mines). Objective comparison of these varied data sets is difficult.

Moreover, it is unclear whether these Lagerstätten have even remotely similar taphonomic histories. Clearly, different Lagerstätten exhibit different degrees of preservational quality, but quantifying these differences is a problem at this time. Thus, taxa that occur in well-preserved, well-studied Lagerstätten, such as Mazon Creek, do not compare favorably with taxa that occur in less well preserved and/ or less well known Lagerstätten, such as Robinson, Kansas, or Nýrany, Czechoslovakia. For these reasons, we have based our interpretations more heavily on those coefficients that de-emphasize the "D" (e.g. Euclidean distance: Sokal & Sneath, 1963) or ignore the "D" altogether (e.g. Jaccard: **Jaccard,** 1908).

Dendrograms

As two-dimensional representations of multidimensional relationships, dendrograms have their own peculiar characteristics. The dendrograms that we present herein are derived from data in which each of the nine localities is compared with the other eight. In theory, this would require eight dimensions of space to accurately depict all of these relationships simultaneously. The larger the dendrogram, the more this becomes a problem. Most computer cluster programs begin at row one of the input matrix and search in order through the matrix for high linkage levels. In case of a tie, the first one encountered is used. Thus, shapes of dendrograms can be subtly affected by input order of the original matrix. For this reason, and because we are most concerned with the relationship of the Kinney Brick Company Quarry to other Lagerstätten, we purposely put it first in the data matrix. We are concerned only with a total of nine Lagerstätten localities, therefore multidimensional dendrogram permutation is not a significant problem in our analyses. Nonetheless, we present in Appendix 2 the output-matrix values derived using Euclidean distance (a dissimilarity coefficient) and Jaccard (a similarity coefficient).

Interpretations of cluster analyses

To do cluster analyses of Lagerstätten data is very difficult because the data are so sparse and because rare taxa comprise so much of the taxonomic diversity in Lagerstätten that little overlap exists from locality to locality. This is reflected in the high coefficient values generated using Euclidean distance (a dissimilarity coefficient; Appendix 2.AbGb) and the low values generated using the Jaccard coefficient (Appendix 2.Aa—Ga). Although some general trends persist, we must caution readers that these general trends have little, if any, mathematical viability (see discussion in Archer & Maples, 1989b). We have broken our data into subsets, each of which is evaluated separately below.

Aquatic invertebrates

Aquatic invertebrates have little overlap among the Lagerstätten evaluated here (Appendix 2.Aa and 2.Ab). However, two pairs of localities have general similarities and consistently fall out as pairs: Hamilton with Robinson, and Essex with Braidwood (Fig. 4). Furthermore, the Essex-

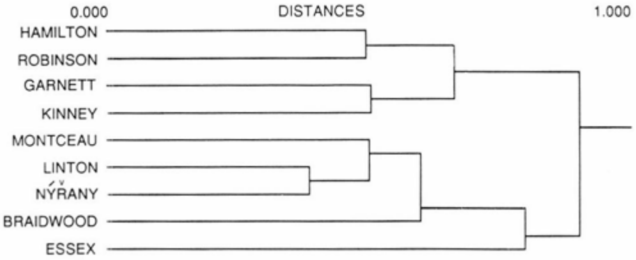

FIGURE 4—Dendrogram of aquatic invertebrates derived using presence–absence data presented in Appendix 1 and constructed using Euclidean distance dissimilarity coefficient values (Appendix 2.Ab) and Ward's linkage method (Ward, 1963).

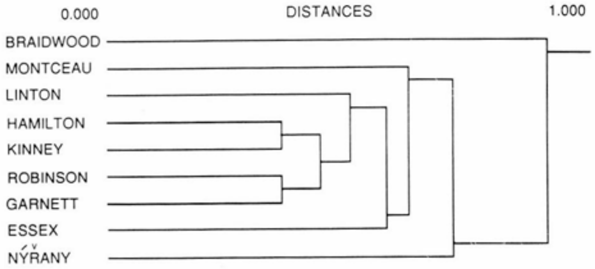

FIGURE 6—Dendrogram of terrestrial invertebrates derived using presence–absence data presented in Appendix 1 and constructed using Euclidean distance dissimilarity coefficient values (Appendix 2.Cb) and Ward's linkage method (Ward, 1963).

Braidwood pair is accentuated by its overall dissimilarity with almost all other localities. The relatively high (and certainly consistent) correlation of Essex and Braidwood, and their comparative dissimilarity with other Lagerstätten, is a direct result of the large number of shared arthropod taxa, many of which are not known from anywhere else.

The Kinney aquatic invertebrates are more similar to Robinson, Hamilton, and Essex (see Appendix 2.Aa) than to other localities (the more marine-influenced Lagerstätten of Maples & Schultze, 1989), but we note this similarity with some degree of trepidation. Non-arthropodan invertebrates are responsible for this similarity, however two of the three arthropod groups (branchiopods and *Adelophthalmus)* reported from Kinney also occur at Essex, which is regarded as the more marine of the Essex—Braidwood (Mazon Creek) pair (Baird et al., 1985a, b).

Aquatic vertebrates

The same two pairs of localities noted using aquatic-invertebrate data (Essex with Braidwood, Hamilton with Robinson) are also present using aquatic-vertebrate data (see Appendix 2.Ba and 2.Bb). Kinney has the closest similarities with Braidwood and Essex (Appendix 2.Ba), but it clusters with Montceau-les-Mines, the third least dissimilar locality (Fig. 5). Gottfried (1987a) argued for connection of Kinney with the region of Montceau-les-Mines based on the occurrence of a bourbonellid fish. Kinney has only three genera *(Acanthodes, "Elonichthys," Bourbonella)* in common with Montceau-les-Mines, but five in common with Essex and Braidwood (see Appendix 1). Garnett is in a similar situation, with closest similarities to Hamilton and Robinson, but clustering with Nýrany. In general, few taxonomic similarities occur among the nine localities, with exception of the Essex—Braidwood and Hamilton—Robinson pairs.

Terrestrial invertebrates

The terrestrial-invertebrate data suffer from two major problems, sparseness and low number of variables (16 versus 51 taxa for aquatic invertebrates). The most closely related group of terrestrial-invertebrate localities (see Appendix 2.Ca) is Hamilton, Montceau-les-Mines, and Kinney. Kinney has its closest similarities with the terrestrial invertebrates of Hamilton, followed by Garnett and Montceau-lesMines. The terrestrial invertebrates of Montceau-les-Mines are most similar to those of Hamilton, followed by Braid-wood and Kinney. Some relationships, even in this small, sparse data set, are both clear and striking. Every terrestrial invertebrate in the data occurs at Braidwood, whereas none occurs at Robinson. Braidwood compares best with Montceau-les-Mines and Nýrany (Fig. 6), and is dissimilar to all other localities (Appendix 2.Cb). As was the case with the aquatic invertebrates, the terrestrial invertebrates generally segregate these Lagerstätten into more marine-influenced (Kinney, Hamilton, Robinson, Garnett, Essex) and less marine-influenced (Braidwood, Linton, Montceau-les-Mines, Nýrany) localities (Fig. 6), which generally conforms to the pattern recognized by Maples & Schultze (1989).

Terrestrial vertebrates

The two recorded tetrapod occurrences in the Kinney Brick Company Quarry place the locality closest to Hamilton and Robinson, Kansas (see Appendix 2.Da; Fig. 7). Two close pairs of localities also occur using terrestrial vertebrates: Linton with Nýrany, and (again) Essex with Braidwood. Other than this terrestrial-vertebrate association with Linton, Nýrany is quite distinct from all other localities based on terrestrial vertebrates (Appendix 2.Db). The association of Garnett with Montceau-les-Mines is misleading because it is based in large part on the presence of unspecified vertebrate trackways.

All terrestrial taxa

Braidwood shows closest similarities to Nýrany, Montceau-les-Mines, and Linton in terrestrial forms (Appendix 2.Fa) and the total data set (Appendix 2.Ga). These are the most terrestrially influenced localities of our sample. The

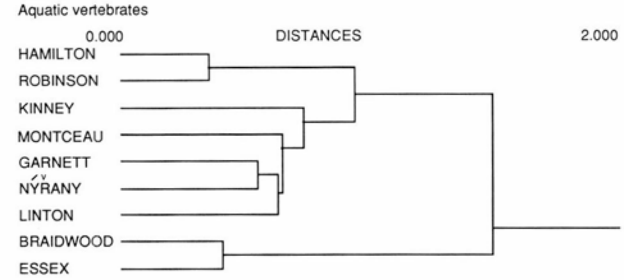

FIGURE 5—Dendrogram of aquatic vertebrates derived using presence–absence data presented in Appendix 1 and constructed using Euclidean distance dissimilarity coefficient values (Appendix 2.Bb) and Ward's linkage method (Ward, 1963).

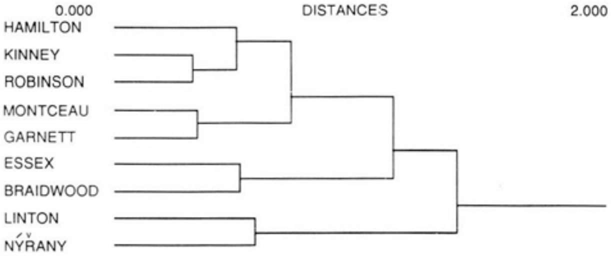

FIGURE 7—Dendrogram of terrestrial vertebrates derived using presence–absence data presented in Appendix 1 and constructed using Euclidean distance dissimilarity coefficient values (Appendix 2.Db) and Ward's linkage method (Ward, 1963).

vertebrate faunas of Linton and Nýrany are more similar to each other than either is to Braidwood (Appendix 2.Fa). They share one polychaete, one branchiopod, three fish, eight amphibian, and one reptilian genera. As a result, Braidwood and Essex, and Linton and Nýrany, appear as two pairs of localities in the dendrogram of all terrestrial taxa (Fig. 8), whereas the remaining localities are not so well constrained. Except for Linton, the terrestrial fauna of Nýrany is dissimilar to all other terrestrial data sets (Appendix 2.Fb). Montceau-les-Mines has its closest affinity to Braidwood in all terrestrial forms and the total data set (see Appendix 2.Fa, Ga). The vertebrate fauna of Garnett is not really similar to any of the other eight localities that we evaluated, although there is a slight similarity with Hamilton (hybodont sharks and pelycosaur reptiles).

Total data set

Of all the localities evaluated, Hamilton and Robinson, Kansas, and Braidwood and Essex, Illinois, always form two distinct pairs using data sets consisting of all aquatic forms or the total data set (Appendix 2.Ea, Ga; Fig. 8). Hamilton and Robinson share occurrences of fusulinids, bryozoans, brachiopods *(Neochonetes, Punctospirifer),* bivalves *(Permophorus, Phestia),* gastropods *(Euphemites),* ostracodes, crinoids, echinoids, elasmobranchs *(Orthacanthus,* hybodontids), acanthodians *(Acanthodes),* palaeonisciforms, actinistians, dipnoans *(Sagenodus),* megalichthyids, rhipidistians, trimerorhachoid amphibians, and protorothyrid reptiles—clearly a marine assemblage. The number of co-occurring taxa between Essex and Braidwood is even higher (bivalves: *Permophorus;* polychaetes: *Spirorbis;* branchiopods; eocarids: *Belotelson;* pygocephalomorphs: *Anthracaris;* syncarids: *Acanthotelson, Palaeocaris;* eurypterids: *Adelophthalmus;* scorpions: *Eoctonus, Mazonia, Titanoscorpio;* chilopods: *Latzelia, Mazoscolopendra;* insects: Diaphanopterodea; xiphosures: *Euproops;* incertae sedis: *Halicyne;* elasmobranchs: *Xenacanthus, Bandringa, Dabasacanthus;* acanthodians: *Acanthodes;* palaeonisciforms: *"Elonichthys";* platysomids: *Platysomus, Amphicentrum;* haplolepiforms: *Haplolepis, Pyritocephalus;* actinistians: *Rhabdoderma;* rhipidistians: *Rhizodopsis;* dipnoans: *Ctenodus;* amphibians: *Aornerpeton, Amphibamus).* The faunas of Essex and Braidwood have been collected over a wide geographic area and are not clearly separated from each other, which may explain some of the overlap.

Kinney Brick Company Quarry

The fauna of the Kinney Brick Company Quarry is most similar to the Kansas (Hamilton and Robinson) localities (Appendix 2.Ga). It has bryozoans, gastropods, ostracodes, myriapods, blattarians, and eight vertebrate genera *(Acanthodes, "Elonichthys,"* actinistians, dissorophoids, and trimerorhachoids) in common with Hamilton, and bryozoans, gastropods, ostracodes, *Lingula, Aviculopecten,* and four vertebrate genera *(Acanthodes, "Elonichthys,"* actinistians, and trimerorhachoids) in common with Robinson. The next closest locality to Kinney is Essex (Appendix 2.Ea, Ga), with eight invertebrate (brachiopods: *Lingula;* bivalves: *Aviculopecten, Dunbarella, Myalina;* cephalopods; polychaetes: *Spirorbis;* branchiopods; eurypterids: *Adelophthalmus)* and five vertebrate (acanthodians: *Acanthodes:* palaeonisciforms: *"Elonichthys";* platysomids: *Platysomus, Amphicentrum;* haplolepids: *Pyritocephalus)* taxa in common; shared terrestrial forms are lacking. The fauna of Kinney has only four invertebrate and two vertebrate genera in common with Linton and Montceau-les-Mines, and no vertebrate genera (only four invertebrate forms) in common with Garnett, nevertheless the locality clusters sometimes (Fig. 9) with Garnett using some coefficients (see discussion about coefficients that use "zero" data above and in Maples & Archer, 1988).

Paleoenvironmental interpretation

We are dealing here with aquatic localities with a terrestrial faunal influx. Nevertheless, comparisons of the aquatic data sets result in very low similarities (Appendix 2.Aa, Ca, Ea) and high dissimilarities (Appendix 2.Ab, Cb, Eb) among the nine localities, except for two recurring pairs: Essex with Braidwood, and Hamilton with Robinson. These two pairs of localities each share a relatively high number of aquatic vertebrates and invertebrates, which may be explained in two ways. First, localities rich in vertebrates commonly are poor in invertebrates because of preferential preservation of phosphatic remains. The invertebrates are poorly preserved, flattened, or occur as shadows or impressions at these localities. Second, collectors of vertebrate localities preferentially select vertebrates (and exceptional invertebrates such as insects) and discard most invertebrates and plants. Many famous Lagerstätten continue to be collected in this way—a practice we hope will end. Thus, we conclude that the aquatic-invertebrate data sets probably are not representative for Garnett, Linton, Montceau-les-Mines, and Nýrany.

We are dealing here with localities at the interface between marine and fresh water from tidally influenced coastal or estuarine localities (Essex, Braidwood, Hamilton, Robinson, Garnett) to less marine influenced (Linton) and even to completely fresh water (at least according to the literature) localities (Montceau-les-Mines and Nýrany). The fauna of the Kinney Brick Company Quarry compares with localities of the first group, especially with Hamilton, Robinson, and Essex. Marine invertebrates (bryozoans, brachiopods, conodonts) are in common among Kinney and the Kansas localities. The bivalves *(Aviculopecten, Dunbarella, Myalina),* cephalopods, and platysomids *(Amphicentrum* and *Platysomus)* that occur at Kinney and the Illinois localities are marine forms, whereas other taxa *(Lingula, Spirorbis,* branchiopods, *Adelophthalmus,* and other fish genera) present at both Kinney and Essex are reported from both marine and fresh-water environments.

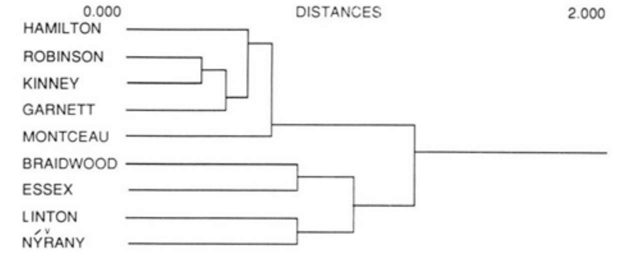

FIGURE 8—Dendrogram of all terrestrial fauna derived using presence–absence data presented in Appendix 1 and constructed using Euclidean distance dissimilarity coefficient values (Appendix 2.Fb) and Ward's linkage method (Ward, 1963).

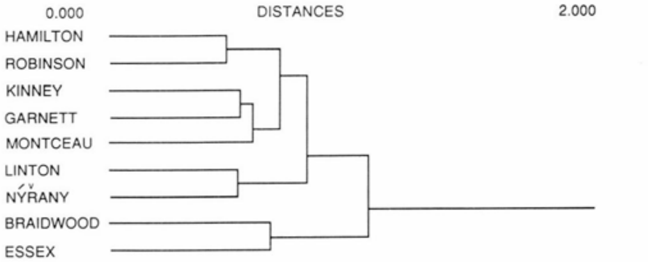

FIGURE 9—Dendrogram of all fauna derived using presence–absence data presented in Appendix 1 and constructed using Euclidean distance dissimilarity coefficient values (Appendix 2.Gb) and Ward's linkage method (Ward, 1963).

Another Pennsylvanian vertebrate locality (group of localities), the Mecca Quarry Shale, fits in the group of more marine faunas with cephalopods and conodonts. The vertebrate fauna of the Kinney Brick Company Quarry shows additional similarities to these black-shale faunas with the occurrence of specific black-shale elasmobranchs (symmoriids, *Listracanthus)* and long-snouted actinopterygians (Poplin, 1978; Gottfried, 1987b). The faunal comparisons indicate a nearshore-marine paleoenvironment for the Kinney Brick Company Quarry. At the same time, the geographically and stratigraphically nearest localities, in Kansas, show the closest similarities with the Kinney Brick Company Quarry. Geographically more distant localities, e.g. Montceau-les-Mines, show similarities with Kinney in ubiquitous taxa such as *Acanthodes* and *"Elonichthys,"* and only rarely co-occurrence of unique forms such as a bourbonellid fish.

Acknowledgments

This research constitutes part of an overall program of Lagerstatten evaluation (coordinated at the Kansas Geological Survey and Department of Systematics and Ecology, University of Kansas, and Department of Geology, Kansas State University) that either has been, or currently is being, conducted by A. W. Archer, C. Cunningham, H. R. Feldman, E. K. Franseen, R. Gastaldo, G. K. Mapes, C. G. Maples, H.-P. Schultze, and R. R. West. We acknowledge the valuable discussions with all of these people. This research was supported by National Science Foundation grants EAR-8903792 (to HPS and CGM), EAR-9018079 (to HRF, AWA, CGM, HPS, and RRW), and National Geographic Society grant 4041-89 (to CGM and HPS). R. R. West reviewed a preliminary version of this manuscript. Many thanks go to R. Hensiek, who provided last-minute (again) drafting help. Thanks go to the owners of the Kinney Brick Company for allowing access to the quarry and to the New Mexico Museum of Natural History for organizing the symposium on the Kinney Brick Company Quarry at the GSA Rocky Mountain—South-Central Sections meeting in April 1991. Special thanks go to Phillip Huber for providing data on the Kinney Brick Company Quarry biota.

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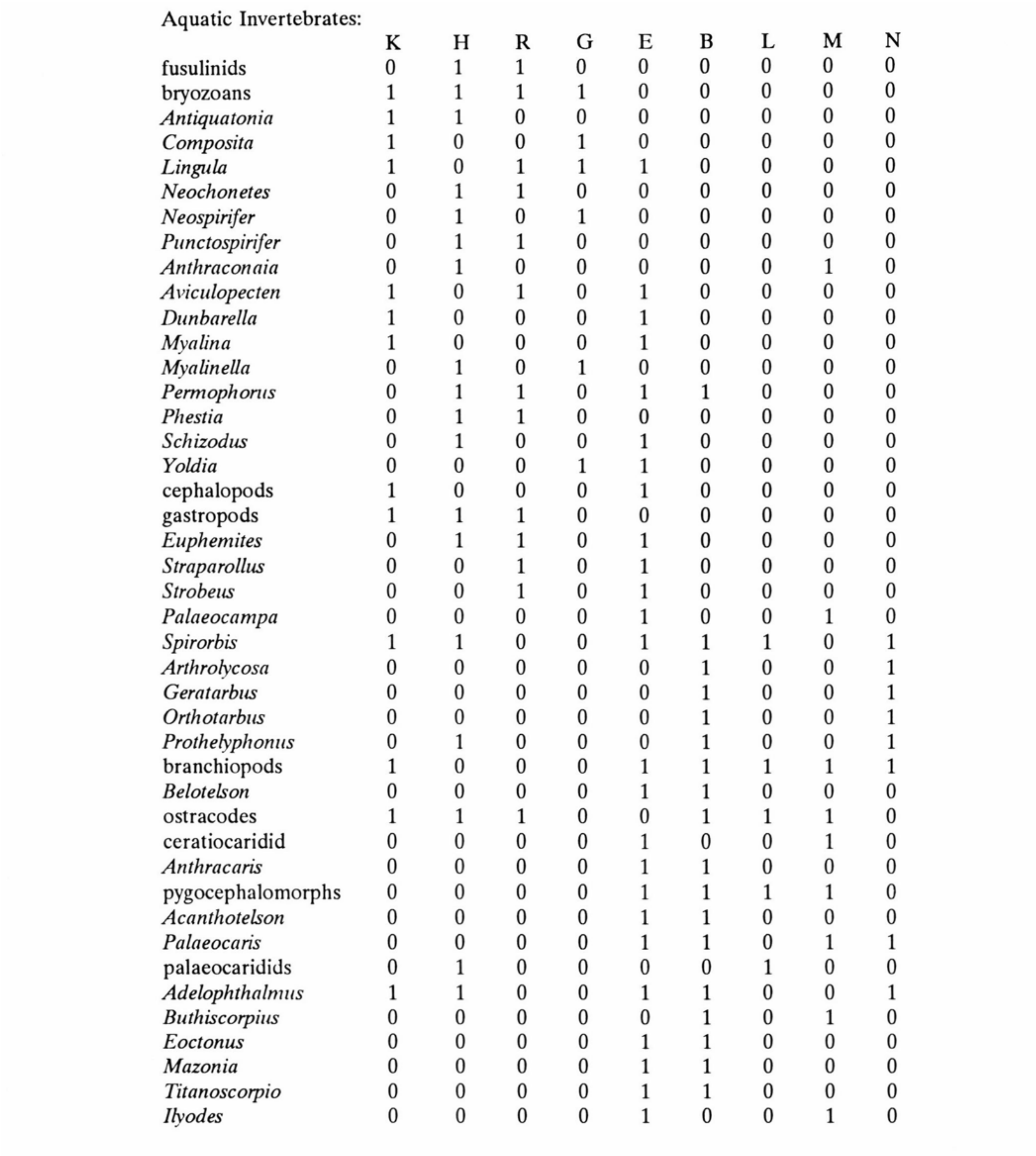
Appendix 1 starts on next page

Appendix 1

Presence/Absence (1/0) data used in cluster analyses of the nine Lagerstätten localities compared in this paper: K=Kinney Brick Company Quarry, New Mexico; H=Hamilton, Kansas; R=Robinson, Kansas; G=Garnett, Kansas; E=Essex, Illinois; B=Braidwood, Illinois; L=Linton, Ohio; M=Montceau-les-Mines, France; N=Nyrany, Czechoslovakia (sources listed in Maples & Schultze, 1989; Lucas & Huber, 1991). Kinney Brick Company Quarry data supplemented by P. Huber (written comm. 1991).



Aquatic Invertebrates:

	K	H	R	G	E	B	L	M	N
fusulinids	0	1	1	0	0	0	0	0	0
bryozoans	1	1	1	1	0	0	0	0	0
Antiquatonia	1	1	0	0	0	0	0	0	0
Composita	1	0	0	1	0	0	0	0	0
Lingula	1	0	1	1	1	0	0	0	0
Neochonetes	0	1	1	0	0	0	0	0	0
Neospirifer	0	1	0	1	0	0	0	0	0
Punctospirifer	0	1	1	0	0	0	0	0	0
Anthraconaia	0	1	0	0	0	0	0	1	0
Aviculopecten	1	0	1	0	1	0	0	0	0
Dunbarella	1	0	0	0	1	0	0	0	0
Myalina	1	0	0	0	1	0	0	0	0
Myalinella	0	1	0	1	0	0	0	0	0
Permophorus	0	1	1	0	1	1	0	0	0
Phestia	0	1	1	0	0	0	0	0	0
Schizodus	0	1	0	0	1	0	0	0	0
Yoldia	0	0	0	1	1	0	0	0	0
cephalopods	1	0	0	0	1	0	0	0	0
gastropods	1	1	1	0	0	0	0	0	0
Euphemites	0	1	1	0	1	0	0	0	0
Straparollus	0	0	1	0	1	0	0	0	0
Strobeus	0	0	1	0	1	0	0	0	0
Palaeocampa	0	0	0	0	1	0	0	1	0
Spirorbis	1	1	0	0	1	1	1	0	1
Arthrolycosa	0	0	0	0	0	1	0	0	1
Geratarbus	0	0	0	0	0	1	0	0	1
Orthotarbus	0	0	0	0	0	1	0	0	1
Prothelyphonus	0	1	0	0	0	1	0	0	1
branchiopods	1	0	0	0	1	1	1	1	1
Belotelson	0	0	0	0	1	1	0	0	0
ostracodes	1	1	1	0	0	1	1	1	0
ceratiocaridid	0	0	0	0	1	0	0	1	0
Anthracaris	0	0	0	0	1	1	0	0	0
pygocephalomorphs	0	0	0	0	1	1	1	1	0
Acanthotelson	0	0	0	0	1	1	0	0	0
Palaeocaris	0	0	0	0	1	1	0	1	1
palaeocaridids	0	1	0	0	0	0	1	0	0
Adelophthalmus	1	1	0	0	1	1	0	0	1
Buthiscorpius	0	0	0	0	0	1	0	1	0
Eoctonus	0	0	0	0	1	1	0	0	0
Mazonia	0	0	0	0	1	1	0	0	0
Titanoscorpio	0	0	0	0	1	1	0	0	0
Ilyodes	0	0	0	0	1	0	0	1	0

Aquatic Invertebrates:

	K	H	R	G	E	B	L	M	N
Kottixerxes	0	0	0	0	1	0	0	1	0
Sottyxerxes	0	0	0	0	1	0	0	1	0
Euproops	0	0	0	0	1	1	0	0	0
Pringlia	0	0	0	0	0	1	0	1	0
Halicyne	0	0	0	0	1	1	0	0	0
crinoids	0	1	1	1	1	0	0	0	0
echinoids	0	1	1	0	0	0	0	0	0
conodonts	1	0	1	0	0	0	0	0	0

Terrestrial Invertebrates:

	K	H	R	G	E	B	L	M	N
Acantherpestes	0	0	0	0	0	1	0	0	1
Amynilyspes	0	0	0	0	0	1	0	0	1
Archiulus	0	0	0	0	0	1	0	0	1
Euphoberia	0	0	0	0	0	1	0	0	1
Xyloiulus	0	0	0	0	0	1	1	0	1
Latzelia	0	0	0	0	1	1	0	0	0
Mazoscolopendra	0	0	0	0	1	1	0	0	0
myriapods	1	1	0	0	0	1	1	1	0
Arthropleura	0	0	0	0	0	1	1	1	0
Blattaria	1	1	0	1	0	1	0	1	1
Caloneurodea	0	0	0	0	0	1	0	1	0
Diaphanopterodea	0	0	0	0	1	1	0	0	0
Megasecoptera	0	0	0	1	0	1	0	0	0
Palaeodictyoptera	0	1	0	0	0	1	0	1	0
Protorthoptera	0	1	0	0	0	1	0	1	0
Thysanura	0	0	0	0	0	1	0	1	0

Aquatic Vertebrates:

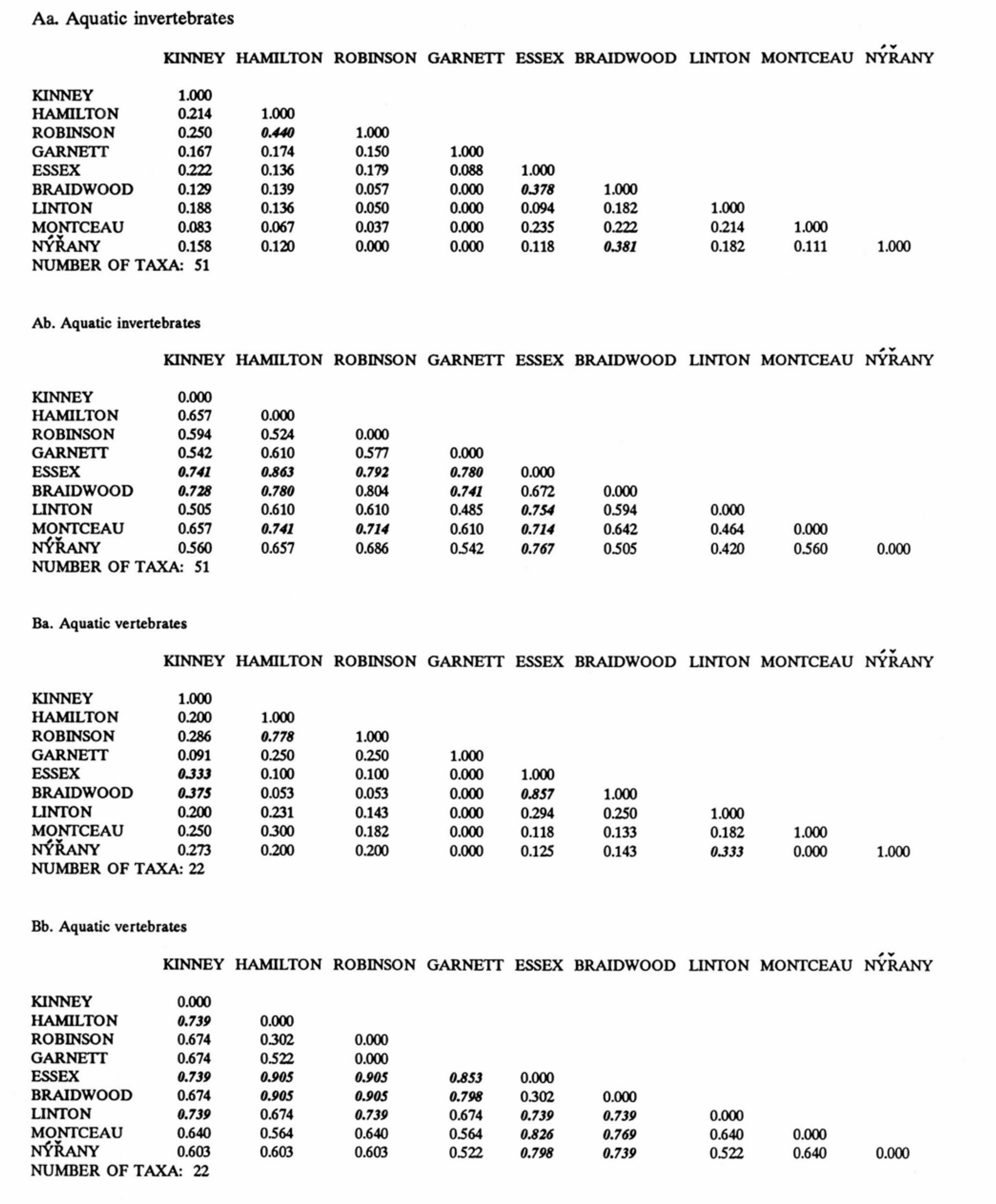
	K	H	R	G	E	B	L	M	N
Expleuracanthus	0	1	0	0	0	0	1	1	0
Orthacanthus	1	1	1	0	0	0	1	0	1
Xenacanthus	1	0	0	0	1	1	0	0	1
Bandringa	0	0	0	0	1	1	0	0	0
Dabasacanthus	0	0	0	0	1	1	0	0	0
hybodont	0	1	1	1	0	0	0	0	0
cladodont	1	0	1	0	0	0	0	0	0
Acanthodes	1	1	1	0	1	1	0	1	0
"*Elonichthys*"	1	0	0	0	1	1	1	1	0
palaeonisciform	0	1	1	0	0	0	0	1	0
Amphicentrum	1	0	0	0	1	1	0	0	0
Platysomus	1	0	0	0	1	1	0	0	0
Haplolepis	0	0	0	0	1	1	1	0	0
Pyritocephalus	1	0	0	0	1	1	1	0	1
Rhabdoderma	0	0	0	0	1	1	1	0	0
actinistian	1	1	1	1	0	0	0	0	0
megalichthyid	0	1	1	0	0	0	0	0	0
Rhizodopsis	0	0	0	0	1	1	0	0	0
Conchopoma	0	0	0	0	1	0	1	0	0
Ctenodus	0	0	0	0	1	1	0	0	0
Sagenodus	0	1	1	0	0	0	1	0	1
Bourbonella	1	0	0	0	0	0	0	1	0

Terrestrial Vertebrates:

	K	H	R	G	E	B	L	M	N
Aonerpeton	0	0	0	0	1	1	0	0	0
Ophiderpeton	0	0	0	0	0	1	1	0	1
Phlegethontia	0	0	0	0	0	0	1	0	1
Ptyonius	0	0	0	0	0	1	1	0	0
Sauropleura	0	0	0	0	0	0	1	0	1
Odonterpeton	0	0	0	0	1	1	0	0	0
Spharodus	0	0	0	0	0	1	0	0	1
Amphibamus	0	0	0	0	1	1	1	0	1
Baphetes	0	0	0	0	0	0	1	0	1
branchiosaur	0	0	0	0	0	1	0	1	1
dissorophoid	1	1	0	0	0	0	0	0	0
eryopoid	0	1	0	0	0	0	0	0	1
Gaudrya	0	0	0	0	0	0	1	0	1
Megalocephalus	0	0	0	0	0	0	1	0	1
Saurerpeton	0	0	0	0	1	1	0	0	0
trimerorhachoid	1	1	1	0	0	0	0	0	0
Cephalerpeton	0	0	0	0	1	1	0	0	0
protorothyrid	0	1	1	0	0	0	0	0	0
indet. reptile	0	1	0	0	0	0	0	0	1
Archaeothyris	0	0	0	0	0	0	1	0	1
ophiacodont	0	1	0	1	0	0	0	0	0
trackways	0	0	0	1	0	0	0	1	0

Appendix 2

Output-matrix values for each of the data sets clustered (Appendix 1). The dendrograms presented in Figs. 4-9 are derived from these matrices. Aa, Ba, Ca, Da, Ea, Fa, and Ga data were derived using the Jaccard similarity coefficient (most similar data given in boldface italics); Ab, Bb, Cb, Db, Eb, Fb, and Gb data were derived using the Euclidean distance dissimilarity coefficient (most dissimilar data given in boldface italics).



Aa. Aquatic invertebrates

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	1.000								
HAMILTON	0.214	1.000							
ROBINSON	0.250	***0.440***	1.000						
GARNETT	0.167	0.174	0.150	1.000					
ESSEX	0.222	0.136	0.179	0.088	1.000				
BRAIDWOOD	0.129	0.139	0.057	0.000	***0.378***	1.000			
LINTON	0.188	0.136	0.050	0.000	0.094	0.182	1.000		
MONTCEAU	0.083	0.067	0.037	0.000	0.235	0.222	0.214	1.000	
NÝŘANY	0.158	0.120	0.000	0.000	0.118	***0.381***	0.182	0.111	1.000

NUMBER OF TAXA: 51

Ab. Aquatic invertebrates

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	0.000								
HAMILTON	0.657	0.000							
ROBINSON	0.594	0.524	0.000						
GARNETT	0.542	0.610	0.577	0.000					
ESSEX	***0.741***	***0.863***	***0.792***	***0.780***	0.000				
BRAIDWOOD	***0.728***	***0.780***	0.804	***0.741***	0.672	0.000			
LINTON	0.505	0.610	0.610	0.485	***0.754***	0.594	0.000		
MONTCEAU	0.657	***0.741***	***0.714***	0.610	***0.714***	0.642	0.464	0.000	
NÝŘANY	0.560	0.657	0.686	0.542	***0.767***	0.505	0.420	0.560	0.000

NUMBER OF TAXA: 51

Ba. Aquatic vertebrates

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	1.000								
HAMILTON	0.200	1.000							
ROBINSON	0.286	***0.778***	1.000						
GARNETT	0.091	0.250	0.250	1.000					
ESSEX	***0.333***	0.100	0.100	0.000	1.000				
BRAIDWOOD	***0.375***	0.053	0.053	0.000	***0.857***	1.000			
LINTON	0.200	0.231	0.143	0.000	0.294	0.250	1.000		
MONTCEAU	0.250	0.300	0.182	0.000	0.118	0.133	0.182	1.000	
NÝŘANY	0.273	0.200	0.200	0.000	0.125	0.143	***0.333***	0.000	1.000

NUMBER OF TAXA: 22

Bb. Aquatic vertebrates

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	0.000								
HAMILTON	***0.739***	0.000							
ROBINSON	0.674	0.302	0.000						
GARNETT	0.674	0.522	0.000						
ESSEX	***0.739***	***0.905***	***0.905***	***0.853***	0.000				
BRAIDWOOD	0.674	***0.905***	***0.905***	***0.798***	0.302	0.000			
LINTON	***0.739***	0.674	***0.739***	0.674	***0.739***	***0.739***	0.000		
MONTCEAU	0.640	0.564	0.640	0.564	***0.826***	***0.769***	0.640	0.000	
NÝŘANY	0.603	0.603	0.603	0.522	***0.798***	***0.739***	0.522	0.640	0.000

NUMBER OF TAXA: 22

Ca. Terrestrial invertebrates

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	1.000								
HAMILTON	***0.500***	1.000							
ROBINSON	0.000	0.000	1.000						
GARNETT	***0.333***	0.200	0.000	1.000					
ESSEX	0.000	0.000	0.000	0.000	1.000				
BRAIDWOOD	0.125	0.250	0.000	0.125	0.188	1.000			
LINTON	0.250	0.167	0.000	0.000	0.000	0.188	1.000		
MONTCEAU	0.286	***0.571***	0.000	0.125	0.000	***0.438***	0.250	1.000	
NÝŘANY	0.143	0.111	0.000	0.143	0.000	***0.375***	0.125	0.083	1.000

NUMBER OF TAXA: 16

Cb. Terrestrial invertebrates

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	0.000								
HAMILTON	0.354	0.000							
ROBINSON	0.354	0.500	0.000						
GARNETT	0.354	0.500	0.354	0.000					
ESSEX	0.559	0.661	0.433	0.559	0.000				
BRAIDWOOD	***0.935***	***0.866***	1.000	***0.935***	***0.901***	0.000			
LINTON	0.433	0.559	0.433	0.559	0.612	***0.901***	0.000		
MONTCEAU	0.559	0.433	0.661	0.661	***0.791***	***0.750***	0.612	0.000	
NÝŘANY	0.612	***0.707***	0.612	0.612	***0.750***	***0.791***	0.661	***0.829***	0.000

NUMBER OF TAXA: 16

Da. Terrestrial vertebrates

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	1.000								
HAMILTON	***0.333***	1.000							
ROBINSON	***0.333***	***0.333***	1.000						
GARNETT	0.000	0.143	0.000	1.000					
ESSEX	0.000	0.000	0.000	0.000	1.000				
BRAIDWOOD	0.000	0.000	0.000	0.000	***0.556***	1.000			
LINTON	0.000	0.000	0.000	0.000	0.077	0.200	1.000		
MONTCEAU	0.000	0.000	0.000	***0.333***	0.000	0.100	0.000	1.000	
NÝŘANY	0.000	0.125	0.000	0.000	0.063	0.235	***0.615***	0.077	1.000

NUMBER OF TAXA: 22

Db. Terrestrial vertebrates

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	0.000								
HAMILTON	0.426	0.000							
ROBINSON	0.302	0.426	0.000						
GARNETT	0.426	0.522	0.426	0.000					
ESSEX	0.564	***0.707***	0.564	0.564	0.000				
BRAIDWOOD	***0.707***	***0.826***	***0.707***	***0.707***	0.426	0.000			
LINTON	***0.707***	***0.826***	***0.707***	***0.707***	***0.739***	***0.739***	0.000		
MONTCEAU	0.426	0.603	0.426	0.302	0.564	0.640	***0.707***	0.000	
NÝŘANY	***0.798***	***0.798***	***0.798***	***0.798***	***0.826***	***0.769***	0.477	***0.739***	0.000

NUMBER OF TAXA: 22

Ea. All aquatic forms

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	1.000								
HAMILTON	0.186	1.000							
ROBINSON	0.237	***0.529***	1.000						
GARNETT	0.143	0.194	0.179	1.000					
ESSEX	0.264	0.125	0.153	0.060	1.000				
BRAIDWOOD	0.217	0.109	0.056	0.000	***0.510***	1.000			
LINTON	0.161	0.171	0.088	0.000	0.163	0.211	1.000		
MONTCEAU	0.143	0.125	0.079	0.000	0.196	0.190	0.200	1.000	
NÝŘANY	0.167	0.143	0.059	0.000	0.120	0.286	0.250	0.074	1.000

NUMBER OF TAXA: 73

Eb. All aquatic forms

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	0.000								
HAMILTON	0.692	0.000							
ROBINSON	0.630	0.468	0.000						
GARNETT	0.573	0.585	0.561	0.000					
ESSEX	***0.731***	***0.876***	***0.828***	***0.802***	0.000				
BRAIDWOOD	***0.702***	***0.819***	***0.836***	***0.759***	0.585	0.000			
LINTON	0.597	0.630	0.652	0.549	***0.749***	0.641	0.000		
MONTCEAU	0.641	0.692	0.692	0.597	***0.749***	0.682	0.523	0.000	
NÝŘANY	0.585	0.641	0.662	0.536	***0.776***	0.585	0.453	0.585	0.000

NUMBER OF TAXA: 73

Fa. All terrestrial forms

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	1.000								
HAMILTON	***0.400***	1.000							
ROBINSON	0.200	0.200	1.000						
GARNETT	0.143	0.167	0.000	1.000					
ESSEX	0.000	0.000	0.000	0.000	1.000				
BRAIDWOOD	0.074	0.129	0.000	0.074	***0.320***	1.000			
LINTON	0.067	0.048	0.000	0.000	0.053	0.194	1.000		
MONTCEAU	0.182	0.267	0.000	0.182	0.000	***0.308***	0.105	1.000	
NÝŘANY	0.048	0.120	0.000	0.048	0.040	***0.303***	***0.429***	0.080	1.000

NUMBER OF TAXA: 38

Fb. All terrestrial forms

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	0.000								
HAMILTON	0.397	0.000							
ROBINSON	0.324	0.459	0.000						
GARNETT	0.397	0.513	0.397	0.000					
ESSEX	0.562	0.688	0.513	0.562	0.000				
BRAIDWOOD	***0.811***	***0.843***	***0.843***	***0.811***	0.669	0.000			
LINTON	0.607	***0.725***	0.607	0.649	0.688	***0.811***	0.000		
MONTCEAU	0.487	0.538	0.538	0.487	0.669	0.688	0.669	0.000	
NÝŘANY	***0.725***	***0.761***	***0.725***	***0.725***	***0.795***	***0.778***	0.562	***0.778***	0.000

NUMBER OF TAXA: 38

Ga. Total data set

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	1.000								
HAMILTON	0.250	1.000							
ROBINSON	0.262	***0.455***	1.000						
GARNETT	0.143	0.186	0.147	1.000					
ESSEX	0.234	0.125	0.164	0.066	1.000				
BRAIDWOOD	0.181	0.143	0.063	0.044	***0.447***	1.000			
LINTON	0.156	0.167	0.109	0.027	0.132	0.203	1.000		
MONTCEAU	0.156	0.167	0.063	0.056	0.149	0.239	0.163	1.000	
NÝŘANY	0.118	0.133	0.037	0.024	0.093	0.294	***0.341***	0.078	1.000

NUMBER OF TAXA: 109

Gb. Total data set

	KINNEY	HAMILTON	ROBINSON	GARNETT	ESSEX	BRAIDWOOD	LINTON	MONTCEAU	NÝŘANY
KINNEY	0.000								
HAMILTON	0.598	0.000							
ROBINSON	0.533	0.469	0.000						
GARNETT	0.525	0.567	0.516	0.000					
ESSEX	0.670	***0.801***	***0.717***	***0.723***	0.000				
BRAIDWOOD	***0.736***	***0.813***	***0.824***	***0.772***	0.621	0.000			
LINTON	0.590	0.643	0.613	0.575	***0.736***	***0.710***	0.000		
MONTCEAU	0.590	0.643	0.643	0.559	***0.723***	0.684	0.575	0.000	
NÝŘANY	0.643	0.691	0.691	0.613	***0.790***	0.664	0.498	0.657	0.000

NUMBER OF TAXA: 109

Selected conversion factors*

TO CONVERT	MULTIPLY BY	TO OBTAIN
Length		
inches, in	2.540	centimeters, cm
feet, ft	3.048×10^{-1}	meters, m
yards, yds	9.144×10^{-1}	m
statute miles, mi	1.609	kilometers, km
fathoms	1.829	m
angstroms, Å	1.0×10^{-8}	cm
Å	1.0×10^{-4}	micrometers, μm
Area		
in^2	6.452	cm^2
ft^2	9.29×10^{-2}	m^2
yds^2	8.361×10^{-1}	m^2
mi^2	2.590	km^2
acres	4.047×10^{3}	m^2
acres	4.047×10^{-1}	hectares, ha
Volume (wet and dry)		
in^3	1.639×10^{1}	cm^3
ft^3	2.832×10^{-2}	m^3
yds^3	7.646×10^{-1}	m^3
fluid ounces	2.957×10^{-2}	liters, l *or* L
quarts	9.463×10^{-1}	l
U.S. gallons, gal	3.785	l
U.S. gal	3.785×10^{-3}	m^3
acre-ft	1.234×10^{3}	m^3
barrels (oil), bbl	1.589×10^{-1}	m^3
Weight, mass		
ounces avoirdupois, avdp	2.8349×10^{1}	grams, gr
troy ounces, oz	3.1103×10^{1}	gr
pounds, lb	4.536×10^{-1}	kilograms, kg
long tons	1.016	metric tons, mt
short tons	9.078×10^{-1}	mt
oz mt^{-1}	3.43×10^{1}	parts per million, ppm
Velocity		
ft sec^{-1} (= ft/sec)	3.048×10^{-1}	m sec^{-1} (= m/sec)
mi hr^{-1}	1.6093	km hr^{-1}
mi hr^{-1}	4.470×10^{-1}	m sec^{-1}

TO CONVERT	MULTIPLY BY	TO OBTAIN
Pressure, stress		
lb in^{-2} (= lb/in^2), psi	7.03×10^{-2}	kg cm^{-2} (= kg/cm^2)
lb in^{-2}	6.804×10^{-2}	atmospheres, atm
lb in^{-2}	6.895×10^{3}	newtons (N)/m^2, N m^{-2}
atm	1.0333	kg cm^{-2}
atm	7.6×10^{2}	mm of Hg (at 0° C)
inches of Hg (at 0° C)	3.453×10^{-2}	kg cm^{-2}
bars, b	1.020	kg cm^{-2}
b	1.0×10^{6}	dynes cm^{-2}
b	9.869×10^{-1}	atm
b	1.0×10^{-1}	megapascals, MPa
Density		
lb in^{-3} (= lb/in^3)	2.768×10^{1}	gr cm^{-3} (= gr/cm^3)
Viscosity		
poises	1.0	gr cm^{-1} sec^{-1} *or* dynes cm^{-2}
Discharge		
U.S. gal min^{-1}, gpm	6.308×10^{-2}	l sec^{-1}
gpm	6.308×10^{-5}	m^3 sec^{-1}
ft^3 sec^{-1}	2.832×10^{-2}	m^3 sec^{-1}
Hydraulic conductivity		
U.S. gal day^{-1} ft^{-2}	4.720×10^{-7}	m sec^{-1}
Permeability		
darcies	9.870×10^{-13}	m^2
Transmissivity		
U.S. gal day^{-1} ft^{-1}	1.438×10^{-7}	m^2 sec^{-1}
U.S. gal min^{-1} ft^{-1}	2.072×10^{-1}	l sec^{-1} m^{-1}
Magnetic field intensity		
gausses	1.0×10^{5}	gammas
Energy, heat		
British thermal units, BTU	2.52×10^{-1}	calories, cal
BTU	1.0758×10^{2}	kilogram-meters, kgm
BTU lb^{-1}	5.56×10^{-1}	cal kg^{-1}
Temperature		
°C + 273	1.0	°K (Kelvin)
°C + 17.78	1.8	°F (Fahrenheit)
°F − 32	5/9	°C (Celsius)

**Divide by* the factor number to reverse conversions.
Exponents: for example 4.047×10^{3} (see acres) = 4,047; 9.29×10^{-2} (see ft^2) = 0.0929.

Editor: *Jiri Zidek*

Typeface: Palatino

Presswork: Miehle Single Color Offset
Harris Single Color Offset

Binding: Saddlestitch

Paper: Cover on Hollistone Lexotone
Text on 80-lb Patina Matte

Ink: Cover—PMS 430 (silkscreen)
Text—Black

Quantity: 1,000