

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

Vol. 27, No. 11, p. 275-320

October 23, 1987

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EARLY EOCENE BATS (MAMMALIA, CHIROPTERA) AND OTHER VERTEBRATES IN FRESHWATER LIMESTONES OF THE WILLWOOD FORMATION, CLARK'S FORK BASIN, WYOMING

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Abstract.—Fossil vertebrates are preserved in a variety of freshwater limestones in the Willwood Formation of the Clark's Fork Basin, Wyoming. Six limestones are described in detail. Three are interpreted to represent still water environments including the centers of hollow trees, flooded remnants of tree stumps or burrows, and shallow vegetated pans. The remaining three limestones represent a spectrum of moving water deposits ranging from a sizable perennial stream to an ephemeral stream or storm wash.

Fifteen limestone lenses are weathering from a single bed or narrow stratigraphic interval at the site where vertebrate fossils were first discovered in limestones. These lenses resemble trees in size and spacing, and concentration of fractured bone, isolated teeth, and fragmentary jaws of terrestrial vertebrates within one small lens suggests Joggins-like preservation in hollow trees. The vertebrate-bearing lens at the discovery site is late Clarkforkian in age, and it includes eight species of land snails (one prosobranch and seven pulmonates), one or more salamanders, a frog, three anguimorph lizards, the oldest known heron (new genus and species), and thirteen species of mammals (including a new genus and two new species of Nyctitheriidae, a new genus and species of Palaeochiropterygidae, and a new species of Viverravidae). The palaeochiropterygid is the oldest bat known to date.

INTRODUCTION

The Willwood Formation was named by F. B. Van Houten for "red-banded strata in the Big Horn Basin that in their normal position overlie the Polecat Bench, or 'Fort Union,' formation and underlie the Tatman" (Van Houten, 1944, p. 176). The "Big Horn Basin" of Van Houten included both the Clark's Fork and Bighorn drainage basins in northwestern Wyoming. These drainage basins appear to have had different histories of subsidence preceding Willwood deposition (Gingerich, 1983), and consequently the two are regarded as contiguous but distinct structural basins. The name of the formation is taken from the Willwood agricultural settlement at the base of McCullough Peaks in the northern Bighorn Basin.

Van Houten (1944, p. 178) wrote that the Willwood Formation generally consists of about 2500 feet (ca. 760 meters) of variegated shale, numerous beds of unsorted, occasionally arkosic, white and yellow sandstone, and locally abundant conglomerate lenses. He noted that small, irregular, rust-colored calcareous concretions (nodules) abound in shale layers. Development of red banding and abundant calcareous nodules are both attributed to soil-forming processes (Neasham and Vondra,

1972; Bown, 1979; Bown and Kraus, 1981a). Paleosol horizons developed in Willwood mudstones yield abundant remains of fossil vertebrates spanning the early Clarkforkian (latest Paleocene) and middle Clarkforkian (earliest Eocene) through early Bridgerian (middle Eocene) land-mammal ages (Bown, 1979; Gingerich et al., 1980; Winkler, 1980, 1983; Bown and Kraus, 1981b; Rose, 1981; Gingerich, 1982, 1983; Torres and Gingerich, 1983).

Paleocene Fort Union limestones often occur as more or less continuous beds 10–50 cm in thickness intercalated within mudstones (Gingerich, 1969; Hickey, 1980; see also Yuretich et al., 1984). Originally gray, these weather to brown, orange, and purple as they break up when exposed at the surface. In addition, extensive but discontinuous exposures of lenticular orange-weathering calcium carbonate occur in the Fort Union Formation; these are interpreted as mineralized remains of fossil trees (Kraus, 1985). Calcium carbonate soil nodules are rare in the Fort Union Formation. In contrast, Willwood limestones rarely occur as continuous beds. More often they appear as discontinuous lenses or pods, some, again, plausibly representing mineralized remains of fossil trees. Calcium carbonate soil nodules are abundant in the Willwood Formation.

The Clark's Fork Basin is unusual in that aquatic mollusks (both bivalves and gastropods) and land snails are exceptionally common and well preserved, as are calcareous hackberry seeds (*Celtis* sp.). Hackberry seeds calcify during growth, and their abundance in latest Clarkforkian and Wasatchian sediments of the Clark's Fork Basin may reflect growth environments rich in calcium as well as depositional environments favoring preservation of the seeds. Evidence provided by soil nodules, mollusks, and hackberry seeds indicates that calcium carbonate was present in the early Eocene environment in unusual concentrations. Carbonate nodules, mollusks, and hackberry seeds are present but notably less common in adjacent parts of the northern Bighorn Basin.

Soil nodules have long been known to form around isolated bones and teeth of fossil vertebrates, but associated diverse vertebrate remains were first found in Willwood limestones of the Clark's Fork Basin in 1975. The initial discovery included a partial dentary of the plesiadapiform primate *Carpolestes*, a dentary of the small insectivore *Leptacodon*, a broken shearing premolar of the multituberculate *Ectypodus*, and fragmentary bird remains, all preserved in a small concentration of orange-weathering limestone rubble at University of Michigan locality SC-29 (late Clarkforkian). This site has now been studied in detail, and its lithology and fauna are described below.

Ongoing work in the Clark's Fork Basin indicates that early Eocene vertebrates are present in a wide variety of freshwater limestones of both Clarkforkian and Wasatchian age. The purpose of this report is, first, to describe unusual modes of preservation of fossil vertebrates in Willwood carbonates that may prove productive when investigated in detail here and elsewhere, and second, to describe the invertebrate and vertebrate fossils, including bats, found at the 1975 discovery site.

All specimen numbers prefaced by the acronym UM are in the fossil vertebrate collections of the University of Michigan Museum of Paleontology. UM(I) refers to molluscan specimens numbered separately in the invertebrate collection. Fossil localities prefaced by SC are in the Sand Coulee area of the Clark's Fork Basin in northwestern Wyoming. Specimens prefaced AMNH are in the American Museum of Natural History, New York; specimens prefaced UW are in the University of Wyoming Geological Museum, Laramie.

VERTEBRATE-BEARING LIMESTONES OF THE WILLWOOD FORMATION

Six different occurrences of freshwater limestones yielding remains of fossil mammals and other vertebrates are described here: (1) SC-29 Discovery Site, (2) SC-29 *Carpolestes* Skull Site, (3) SC-29 *Ectocion* Site, (4) SC-289 Unionid Coquina Site, (5) SC-133 Bird Quarry Site, and (6) SC-133 Calcirudite Site. The first four of these sites are late Clarkforkian in age (*Phenacodus-Ectocion* Zone

of Rose, 1980, 1981; zone Cf-3 of Gingerich, 1983), while the latter two are early Wasatchian in age (late Sandcouleean or zone Wa-2 of Gingerich, 1983). The geographic placement of University of Michigan localities prefaced SC is shown on the Clark's Fork Basin map published by Gingerich and Klitz (1985). The six sites described here represent only a small sample of the richness and variety of vertebrate-bearing early Eocene carbonates in the Willwood Formation. Middle Clarkforkian vertebrate-bearing limestones are also under study. One of these yielded specimens of *Ceutholestes dolosus* described by Rose and Gingerich (1987), and another limestone discovered in 1986 yielded a skull and partial skeleton of *Plesiadapis cookei* with associated microfauna. Other vertebrate-bearing limestones will be described as they are studied in coming years.

SC-29 Discovery Site

The first discovery of fossil vertebrates in Willwood Formation limestones of the Clark's Fork Basin was made by the author in 1975 when a partial dentary of *Carpolestes* was found in a piece of orange-weathering limestone at University of Michigan locality SC-29 (late Clarkforkian). This locality is at the head of Big Sand Coulee, and the discovery site itself (Fig. 1) is near the center of the NW1/4 of Section 36, T56N, R101W, Park County, Wyoming. Fragments of limestone concentrated at this site were collected and washed in an attempt to find more of the *Carpolestes* dentary. No additional remains of *Carpolestes* were found, but close examination yielded a dentary of *Leptacodon* in limestone and the site was marked for further investigation.

A map of the SC-29 Discovery Site is shown in Figure 2. Here erosion has excavated fifteen discrete orange-weathering masses of carbonate from the shallow slope of a low hill. These masses are hereafter called "lenses" because of their present lenslike shape. The present shape of a mass is not a sure indication of its original shape because all are weathered to some degree. The tops of lenses may be rounded secondarily by weathering, and the bases of lenses, where excavated, are rounded as well (even though they are not weathered)—hence the lenslike appearance of the limestone masses.

Lenses at the discovery site measure 0.3 to 1.0 m in diameter, with a mean diameter of 0.6 m (standard deviation = 0.2 m). The average distance between neighboring lenses is 2.9 m (standard deviation 1.7 m). As indicated in Figure 3, carbonate lenses at SC-29, including those at the discovery site, appear to be confined to discrete levels rather than being scattered at random through the stratigraphic section.

The vertebrate-bearing lens at the discovery site, lens J, is a mottled micritic muddy limestone (wackestone) including gastropod shell fragments, plant debris, and vertebrate bone (Fig. 4). This limestone is brown in unweathered hand specimen, and the micrite is brown in polished thin section. The orange color that appears on weathering seems to be due to the presence of finely divided oxides that stain the host rock when present in sufficient concentration. Etching in dilute hydrochloric acid leaves lines of clay mineral or oxide residue that adhere to acetate peels, residues that may reflect fine lamination or bedding at deposition. Dissolution of the limestone in dilute formic acid (10%) to recover vertebrate fossils leaves etched but insoluble, opaque, brown, angular flakes of iron-rich carbonate ranging up to 0.3 mm in diameter.

Lens J is fine grained. Some carbonate lenses at the discovery site (those without visible bone) are even finer-grained, almost porcelainlike in texture, while others are much more silty. Examination of lens J limestone in polished thin section reveals zones of mottled light and medium brown micrite, zones of microbrecciated micrite, and zones of greater porosity in the form of extension cracks. Sparry calcite fills interstices between microbrecciated micrite as well as extension cracks. Angular quartz grains 0.01–0.02 mm in diameter (fine to medium silt) are widely dispersed throughout the micritic

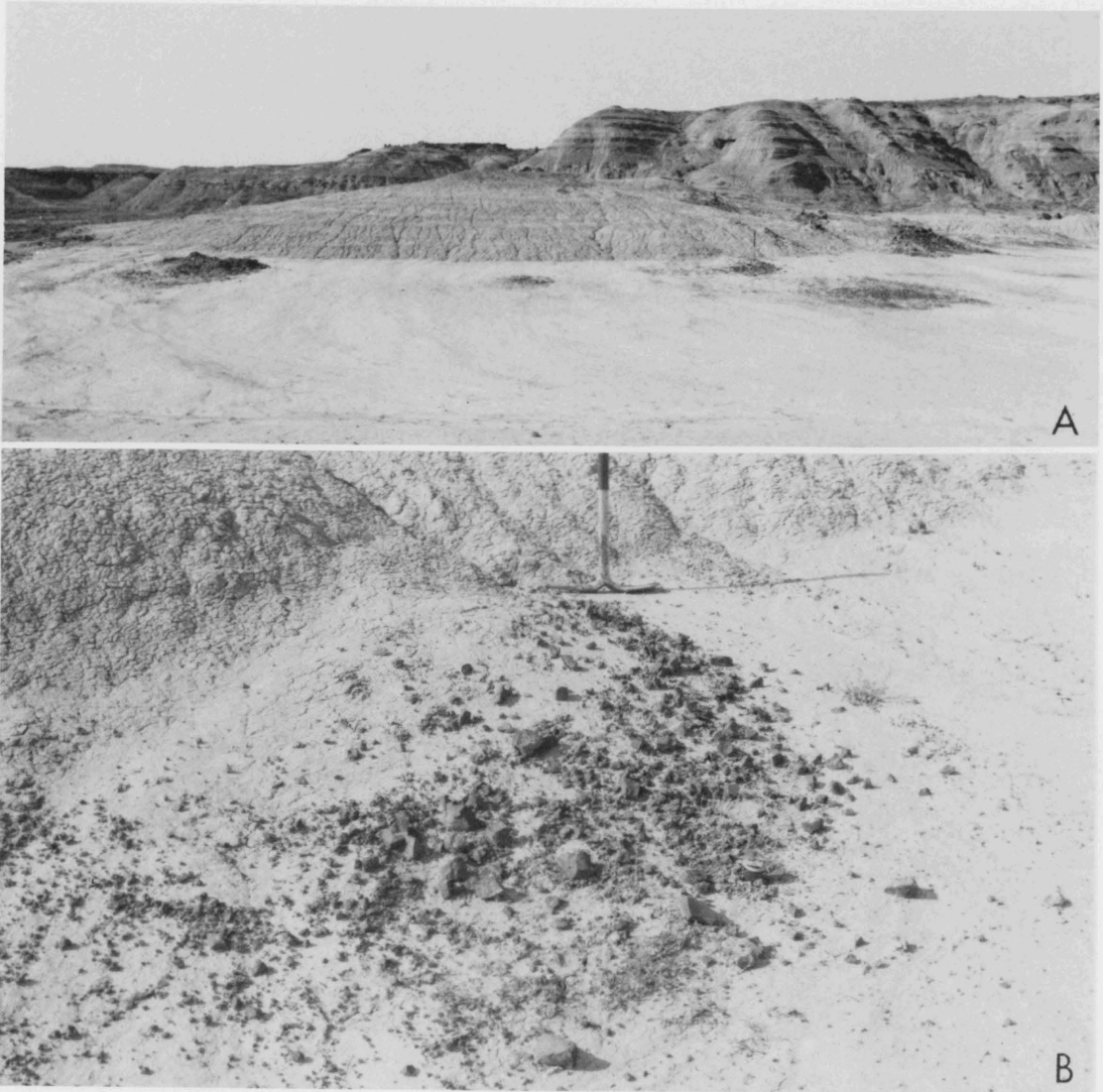


FIG. 1— Discovery site at University of Michigan locality SC-29 (late Clarkforkian), where fossil mammals were first found preserved in a limestone lens. Upper photograph (A) shows general setting at SC-29. Limestones interpreted as mineralized remains of fossil trees occur as scattered lenses on northern slope of shallow hill. View is to the south. Pick standing vertically near vertebrate-bearing lens J in right center of photograph is 0.65 m in length. Lower photograph (B) shows vertebrate-bearing lens J as it appeared when discovered. Scattered pieces preclude reliable estimate of original diameter. View as in A above. Head of pick measures 0.34 m from tip to tip. Photographs by George Junne.

matrix. Some small zones a millimeter or less in diameter have concentrations of angular quartz grains ranging up to 0.05 mm in diameter (coarse silt).

Gastropod shells and vertebrate bones are evident in hand samples of lens J, but organic remains as a whole constitute a relatively small component. Plant debris is finely divided and widely dispersed. Most gastropod shells are filled with sparry calcite, indicating that they were buried intact. Broken gastropod shell fragments are also present. Careful examination of intact shells in thin section usually

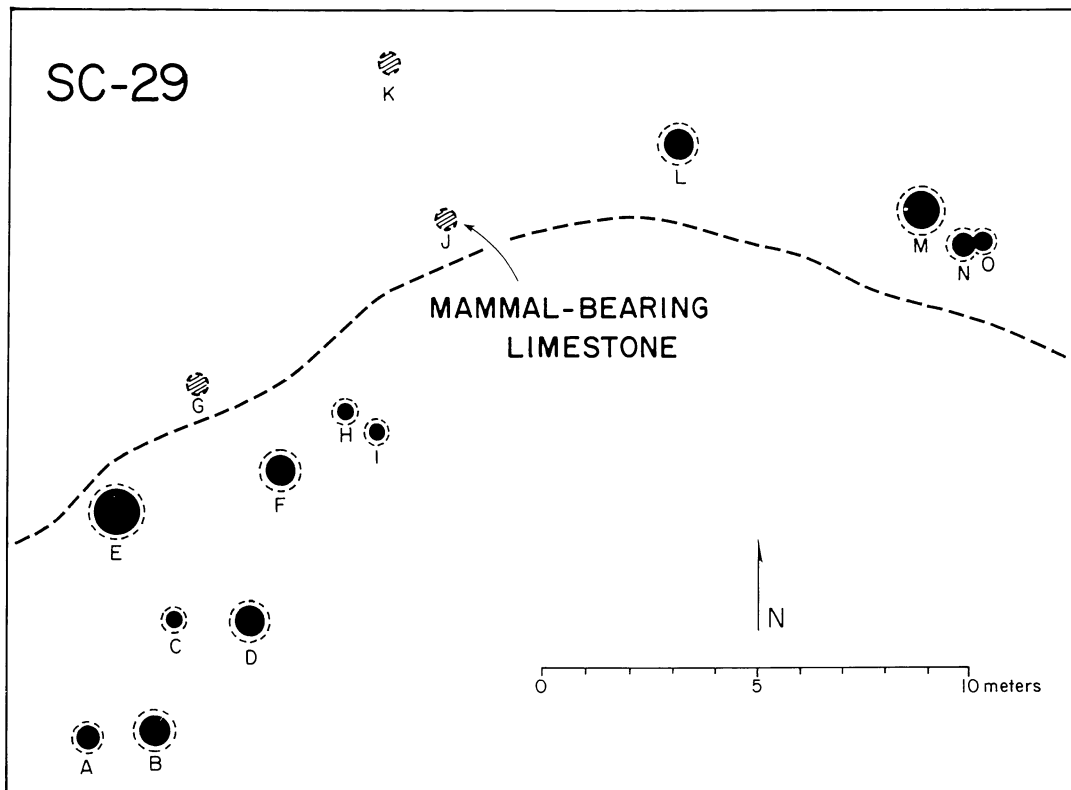


FIG. 2— Schematic map of discovery site at University of Michigan locality SC-29, showing the surface distribution of limestone lenses interpreted as mineralized remains of fossil trees. Lens J is the only lens to yield significant vertebrate remains. Diameter of each lens is drawn to scale where this could be estimated in the field (solid circles). Average diameter of lenses preserved here is 0.6 m, and average spacing between neighboring lenses (measured from the center of one lens to center of neighbor) is 2.9 m. Lenses A-F and H-I are weathering out of hill sloping gently to north and west (heavy dashed line marks edge of shallow slope shown in Fig. 1A).

reveals that some micritic matrix is present lining the lower, inner surfaces of outer whorls (“lower” here refers to present orientation in the rock, which does not necessarily correspond to the gastropod’s life orientation). This micritic lining grades upward from dark to light in color, which presumably reflects small differences in grain size and density. In some cases, dark and light layers of micrite within gastropod shells are contorted and fluidly deformed. Vertebrate bone is often broken and filled with micrite, although some voids in bone are filled with sparry calcite.

Interpretation of the depositional environment of SC-29 lens J requires careful consideration of its preserved fauna, described in a following section of this paper, and full interpretation is deferred to the general discussion. It is sufficient to note here that the distribution of limestone lenses and the fauna of lens J suggest accumulation in a hollow tree trunk.

SC-29 *Carpolestes* Skull Site

The *Carpolestes* skull site is approximately 500 meters WSW of the discovery site, near the center of the eastern edge of Section 35, T56N, R101W, Park County, Wyoming, and it is located a little

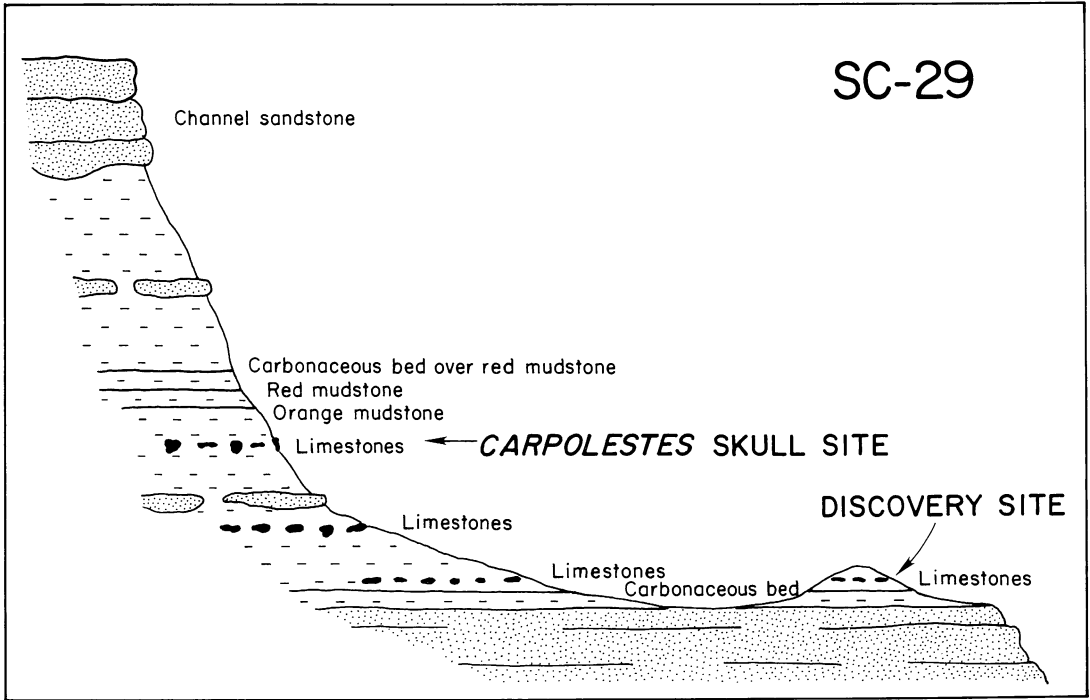


FIG. 3.— Diagrammatic cross section showing stratigraphic units comprising University of Michigan locality SC-29. This locality includes approximately 20 m of siltstone and mudstone between bounding channel sandstones. Sedimentary cycles on this scale (comprising channel sandstones overlain by channel margin and levee deposits, floodplain mudstones with weakly developed orange paleosol horizons, strongly developed red paleosol horizons, floodplain mudstones, levee deposits, and channel sandstones) are common in the Clark's Fork Basin (interpretation of cycles by M. J. Kraus, pers. comm.). Virtually all vertebrate fossils and all limestones found to date occur in the lower 10 m of such localities (e.g., *Carpolestes* skull site and discovery site shown here). This may reflect differing ground water conditions during deposition of strata overlying ancient channel sandstone aquifers, but it may also reflect greater accessibility of lower parts of localities because they are invariably exposed on gentler slopes. *Ectocion* site at SC-29 is at approximately the same stratigraphic level as *Carpolestes* skull site. Stratigraphic section between channel sandstones is approximately 20 m thick.

higher stratigraphically within locality SC-29 (see Fig. 3). Here William Ryan found the front of a skull of *Carpolestes* cf. *C. nigridentis* [UM 86273] projecting from the surface near the top of a vertical pillarlike limestone approximately 0.7–0.8 m high and 0.5 m in diameter (Figs. 5, 6). The bottom surface of the pillar is convex, resting on mudstone, but it is not rooted in the substrate in any way. The upper one-third of the limestone pillar, including the skull-bearing interval, was removed for acid preparation, and the bottom was sampled as well for textural comparison with the upper interval. Upper and lower intervals are compared in Figures 7 and 8.

The upper part of the *Carpolestes* skull site limestone (Fig. 7) consists of fine grained, horizontally bedded micrite with some evidence of microbrecciation and remineralization. In thin section, the micrite is brown in color, with some scattered and broken bone fragments, a few shell fragments, and lots of plant debris. There are very few detrital quartz grains, all about 0.05 mm in diameter. Spar-filled voids represent dessication cracks and, in some instances, burrows. The lower part of this limestone (Fig. 8) includes chips and blocks of fine grained siltstone, masses of calcarenite, and some mixed masses of siltstone, sandstone, and calcarenite, all deformed to some extent and juxtaposed as

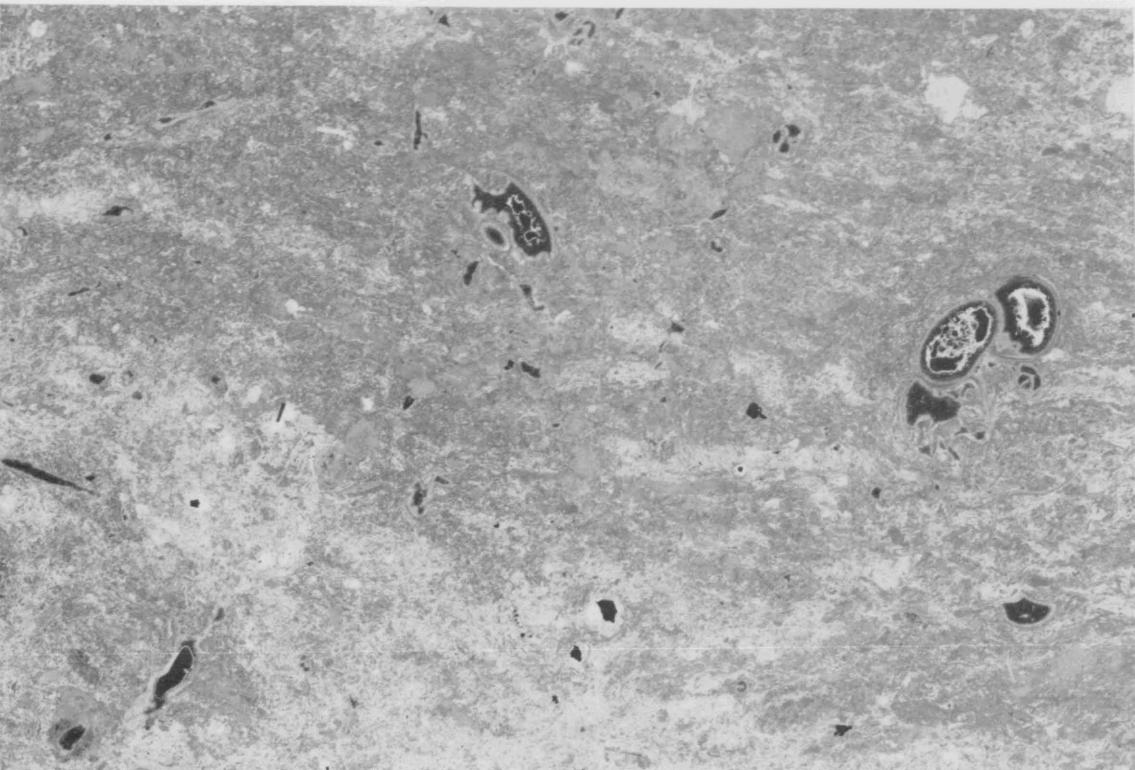


FIG. 4— Photograph printed from acetate peel of polished section of vertebrate bearing limestone, lens J, at SC-29 Discovery Site. Polished surface etched in dilute (5%) hydrochloric acid for five seconds. Note fine grained matrix and gastropods (*Discus ralstonensis*) partially filled with authigenic calcite spar (black in photographic print). Polished thin sections indicate matrix to be micritic, with sparry calcite filling interstices between microbrecciated fragments that are extension features. Gastropod shell fragments, plant debris, and bone are present, and angular quartz grains 0.02 mm in diameter are widely dispersed throughout sample. Judging from mottled texture, micrite has been thoroughly bioturbated. Very fine white lines visible here are insoluble residues of clay or iron-rich carbonate. Photograph enlarged to 5x natural size.

soft sediment before lithification. In thin section, distorted bedding is seen to include thin bands of angular quartz 0.1–0.2 mm in diameter. Gastropod fragments are rare, and there are a few ostracodes.

The *Carpolestes* skull site limestone has not been processed in acid, and the only vertebrate fossil recovered to date is the original *Carpolestes* skull itself. Inspection of broken surfaces of hand samples of limestone indicates that neither molluscan nor vertebrate remains are as common here as they are at the discovery site. Taken together, the stratigraphic setting of the *Carpolestes* limestone, its lithology, and its limited fauna suggest relatively rapid accumulation or precipitation in ponded water in a well defined hole or depression on a flood plane. The water table on a flood plain is normally near the surface, and it is likely that the original depression penetrated the water table. Interbedded chips and masses of silt, occasional beds of sorted fine quartz sand, and soft sediment deformation suggest small scale caving and slumping of silt walls into standing water. Dessiccation cracks suggest minor fluctuation in the water table. A flood plain hole or depression 0.5 m in diameter and 0.7 m or more in depth probably originated either as a large tree rotted away or possibly as a vertebrate burrow was flooded by a rising water table.



FIG. 5— *Carpolestes* skull site discovered by William J. Ryan at University of Michigan locality SC-29 (late Clarkforkian). Limestone mass here measured approximately 0.5 m in diameter and 0.7-0.8 m in height before *Carpolestes*-bearing block was removed (handle of Marsh pick at right is about 60 cm in length). *Carpolestes* skull was found in a 15 cm thick block that originally rested on top of limestone pedestal shown here. Excavation of base of limestone mass shows contact with underlying mudstone to be convexly rounded with little penetration into substrate. View looking to north. Photograph by George Junne.

SC-29 *Ectocion* Site

A third limestone at locality SC-29, found by Gregg Gunnell, yielded well preserved dental remains of the moderately large condylarth *Ectocion osbornianus* [UM86267], including both maxillae and parts of both dentaries (Fig. 9). The *Ectocion* site is at approximately the same stratigraphic level a few hundred meters north of the SC-29 *Carpolestes* skull site discussed above, near the southeastern corner of the NE1/4, NE1/4, Section 35, T56N, R101W, Park County, Wyoming. The *Ectocion* specimen was picked up on the surface as an isolated find within a small mass of surrounding fine sandstone-like matrix. Examination of other isolated masses of similar sandstone-like matrix here yielded the dentary of a medium-sized insectivore as well [UM 86268]. While it is more resistant to weathering than surrounding siltstone, the *Ectocion* limestone was not found in situ at SC-29 and it probably does not occur as a vertically or laterally extensive bed.

The matrix surrounding the *Ectocion* specimen looks like fine sandstone in hand sample, but examination under a microscope or in thin section reveals many angular grains of fine sand set in a groundmass of faintly bedded calcarenite. The relative proportions of quartz grains and calcarenite

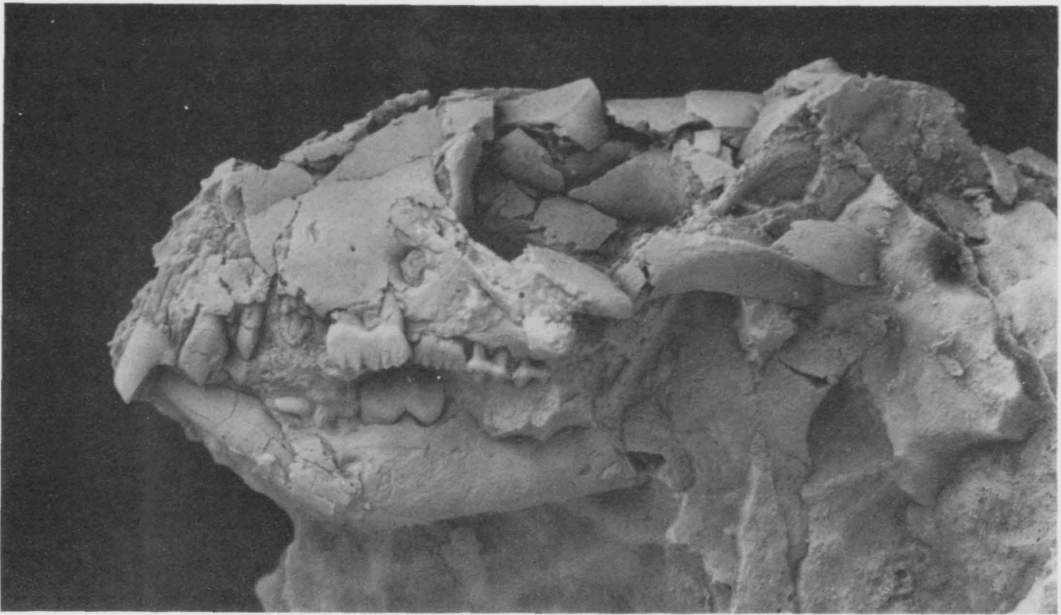


FIG. 6— Photograph of *Carpolestes* cf. *C. nigridentis* skull [UM 86273], as preserved in the rock after preliminary etching in dilute formic acid. Photograph by George Junne, 4x natural size.

differ sharply in different parts of the matrix as a result of differential sorting (probably current winnowing).

Ectocion osbornianus is the most common mammalian species found in late Clarkforkian sediments of the Clark's Fork Basin, and its presence in limestone is noteworthy in demonstrating that small mammals are not the only remains to have been entombed in limestone. The *Ectocion* limestone is likely to represent slow burial by fine quartz and carbonate sand in shallow water moved by gentle currents. Origin of the carbonate sand is at present unknown.

SC-289 Unionid Coquina Site

Locality SC-289 is a late Clarkforkian locality approximately eight kilometers northwest of SC-29 (north center of NE1/4, Section 20, T56N, R101W, Park County, Wyoming) and some 115 m higher stratigraphically. This locality is noteworthy in exhibiting a 10 cm thick carbonate-cemented bed densely packed with unionid bivalves and diverse aquatic gastropods (Fig. 10). A cross-section of this coquina is shown in Figure 11. The bed consists of broken, poorly sorted molluscan shells and shell fragments, detrital carbonate, quartz sand, carbonized wood, with occasional bone, scales, and teeth of vertebrates.

Vertebrate remains include gar scales (*Lepisosteus*), crocodilian teeth (*Allognathosuchus*), and mammalian teeth (*Phenacodus*, *Ectocion*, and *Didymictis*) [all catalogued as UM 86274]. One of the mammalian teeth lacks enamel, resembling enamel-less teeth Fisher (1981a,b) interpreted as having been demineralized during digestion by crocodilians.

Unionid bivalves require fresh, clean, oxygenated, shallow, calcium-rich, permanent water habitats with a current, pH greater than 7, stable substrate, ample food, and at least seasonally warm

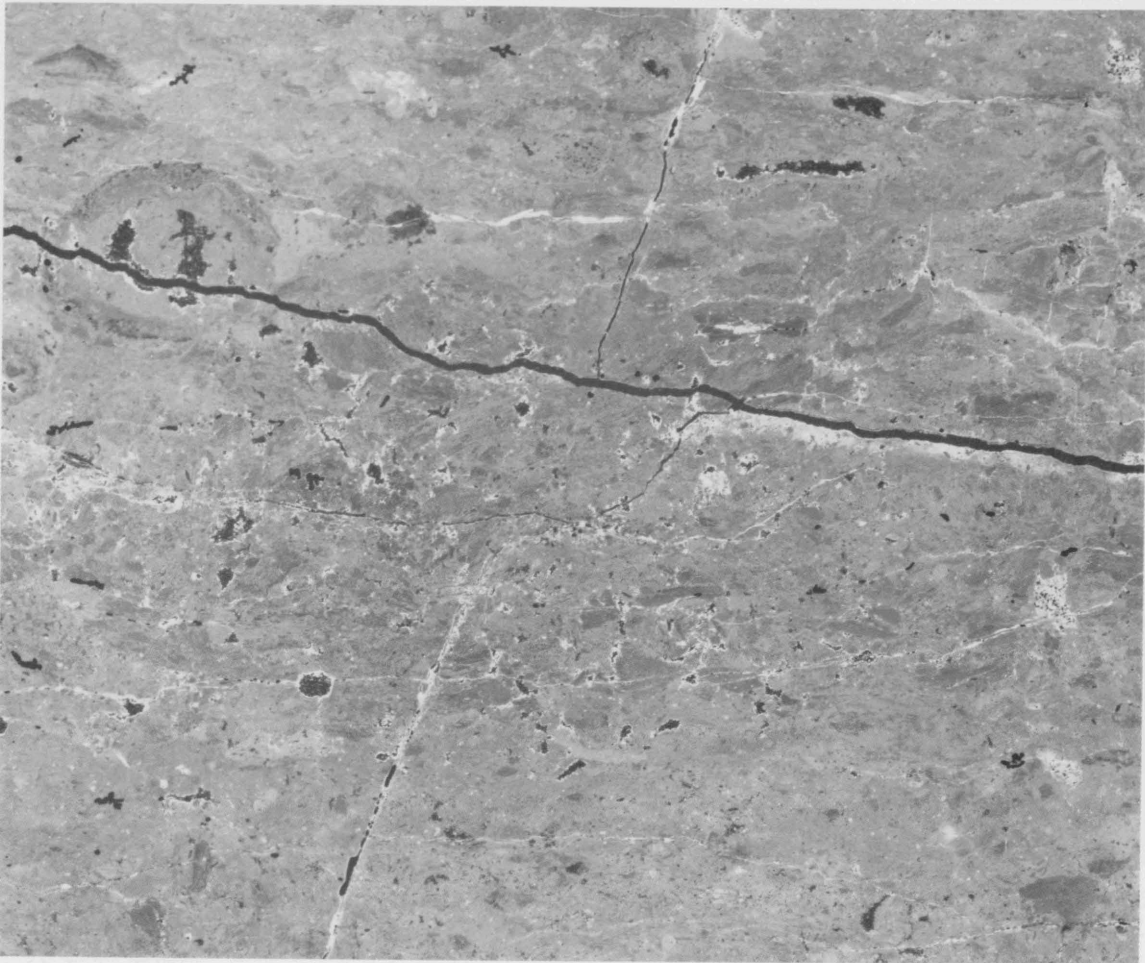


FIG. 7— Photograph printed from acetate peel of polished section from interval of *Carpolestes* skull in upper part of limestone at *Carpolestes* skull site, University of Michigan locality SC-29. Skull itself was found at level of heavy black line crossing photograph (epoxy holding upper and lower parts of block together). Note fine grained, horizontally bedded limestone matrix with some authigenic remineralization and microbrecciation. Photograph enlarged to 5x natural size.

temperatures (Hanley, 1976). The SC-289 unionid coquina site is interpreted to represent deposition in a stream meeting these environmental conditions.

SC-133 Bird Quarry Site

The largest concentration of avian and mammalian fossils found to date in a single limestone of the Willwood Formation is in a 2 m by 2 m lens of orange-weathering carbonate within locality SC-133 (Fig. 12). SC-133 is located in the northern half of the NE1/4, Section 1, T55N, R102W, Park County, Wyoming. This locality is early Wasatchian in age (zone Wa-2 of Gingerich, 1983), stratigraphically some 365 m higher than SC-29 and 250 m higher than SC-289. The lens varies from 10–20 cm in

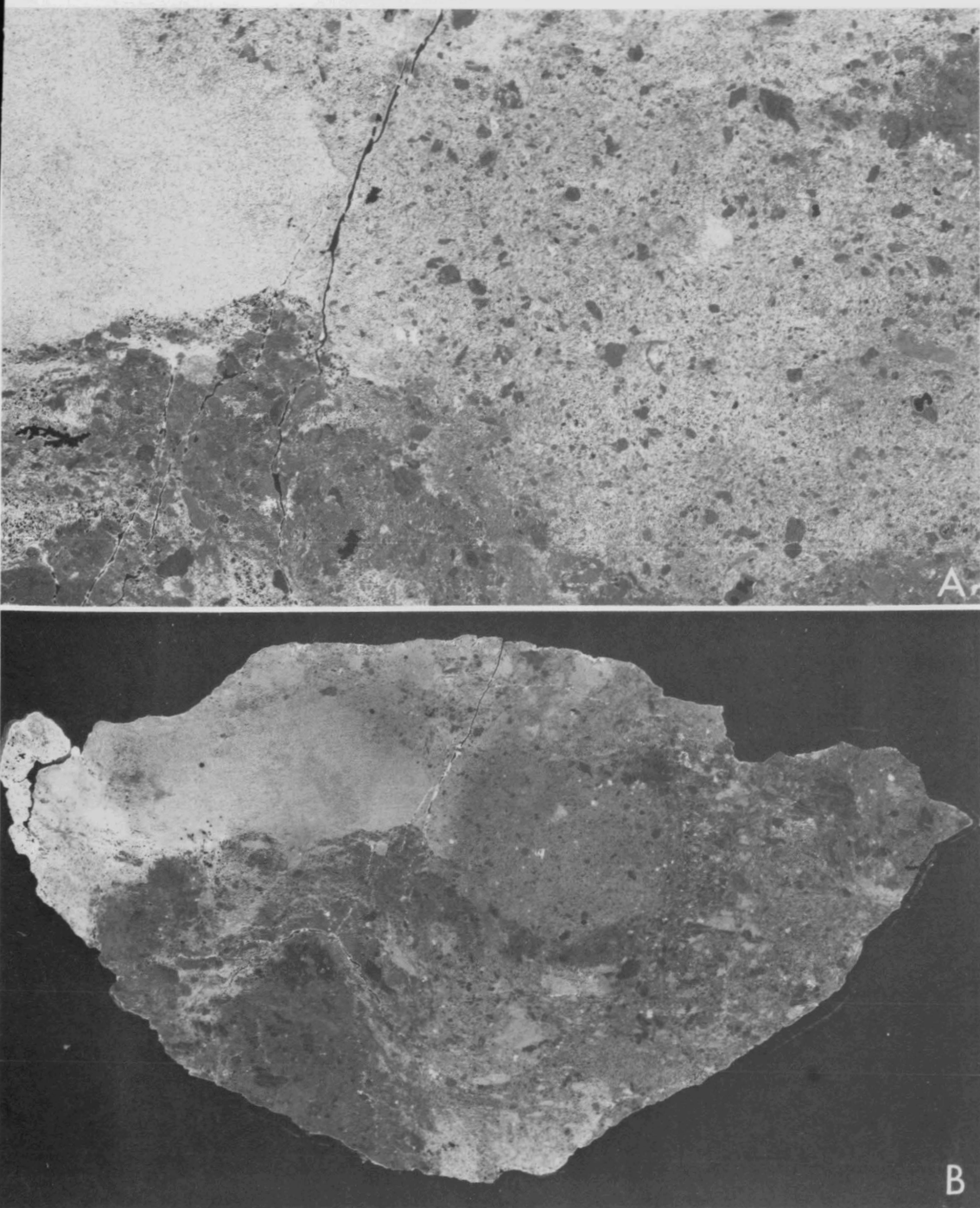


FIG. 8.— Photograph printed from acetate peel of polished section at base of *Carpolestes* skull site limestone, locality SC-29. Upper photograph (A) shows variety of lithologies enlarged to 5x natural size from center of hand sample shown in lower photograph (B, printed approximately 1.9x natural size). Note convex lower border of limestone where it contacted underlying mudstone, and postdepositional plastic deformation of bedding and lithologies. Lithology at upper left in A is fine grained siltstone, lithology at lower left is deformed calcarenite, and lithology at right is mixed siltstone, sandstone, and calcarenite.

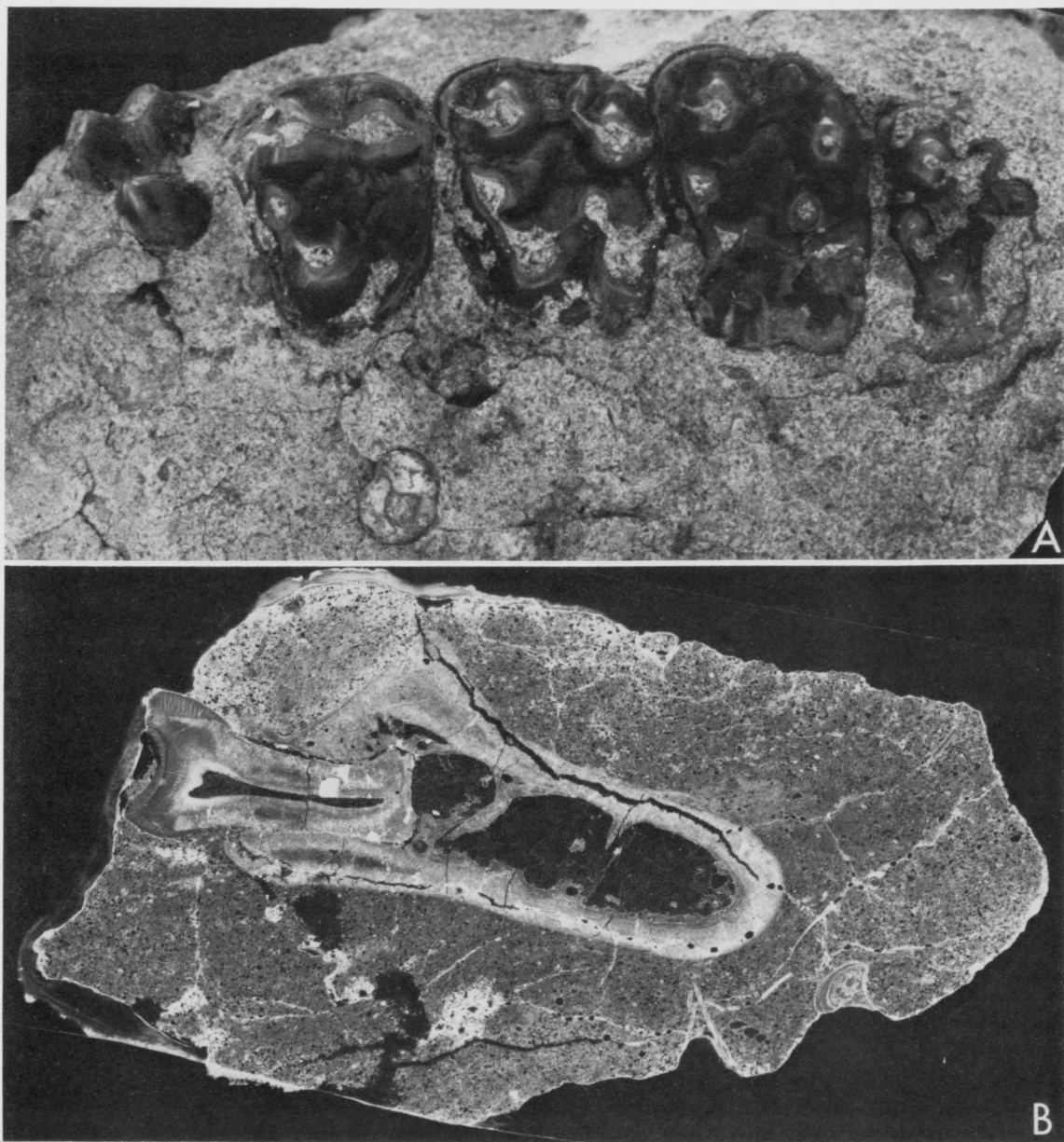


FIG. 9— *Ectocion osbornianus* from the *Ectocion* site at University of Michigan locality SC-29 (late Clarkforkian). Upper photograph (A) shows left part of palate with $P^{3-4}M^{1-3}$ [UM 86267] as exposed on the surface of a fine grained calcarenite. Note unidentified small gastropod. Lower photograph (B) printed from an acetate peel of a polished transverse section through dentary of the same specimen. Mandibular ramus is filled with calcite spar (black in photographic print). Small black grains scattered through sedimentary matrix are angular quartz grains. Very small, high-spired, sinistral gastropod below base of dentary is possibly the pupillid *Albertanella*. Note faintly developed horizontal bedding of calcarenite matrix. Both photographs enlarged to 5x natural size. Upper photograph by George Junne.

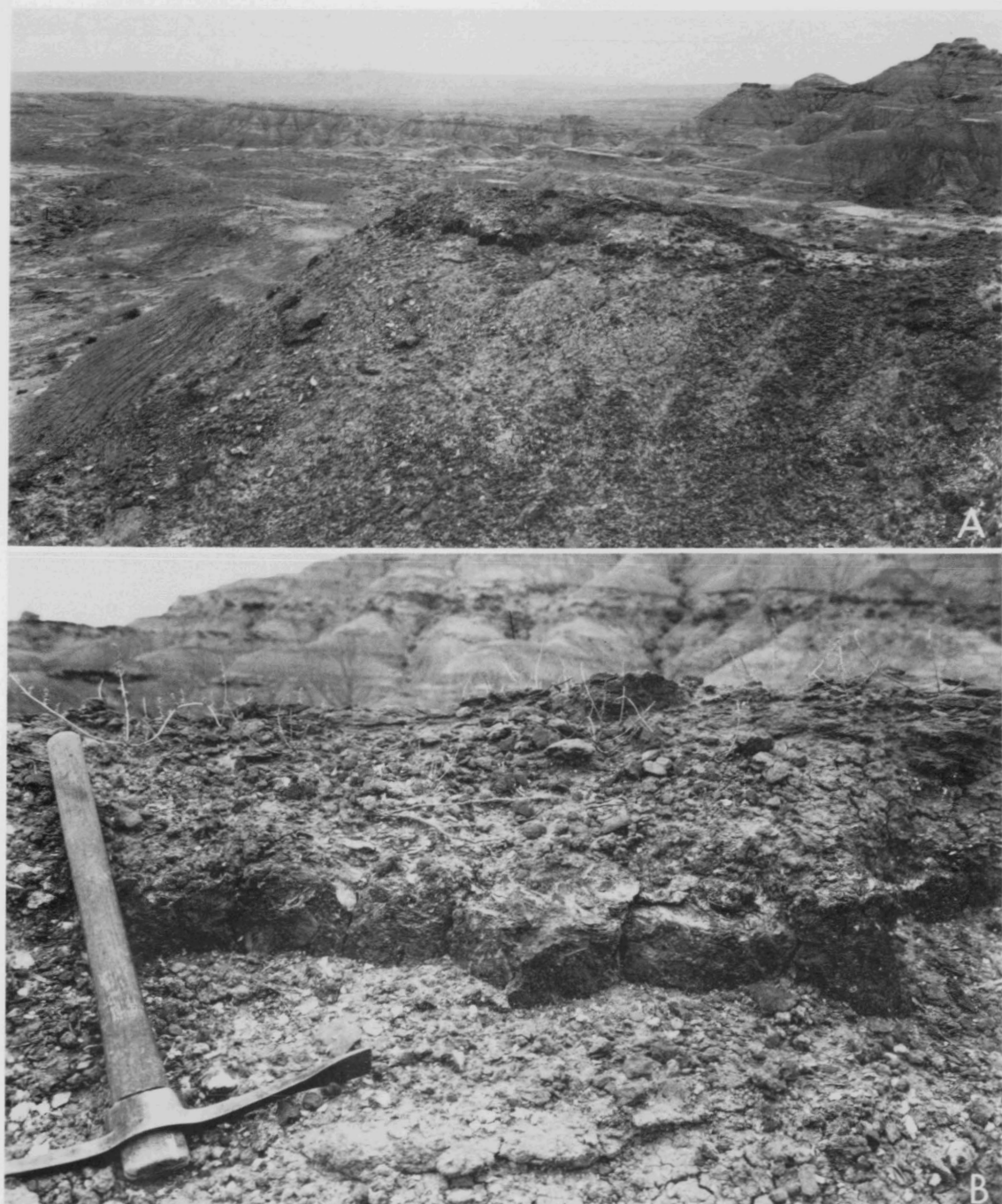


FIG. 10— Limestone cemented unionid coquina site at University of Michigan locality SC-289 (late Clarkforkian). Upper photograph (A) shows coquina capping ridge in foreground, with white shells of unionid bivalves littering slope. View is to southeast. Lower photograph (B) is closeup of same bed, showing closely packed freshwater gastropods and bivalves. Handle of Marsh pick is about 60 cm in length.

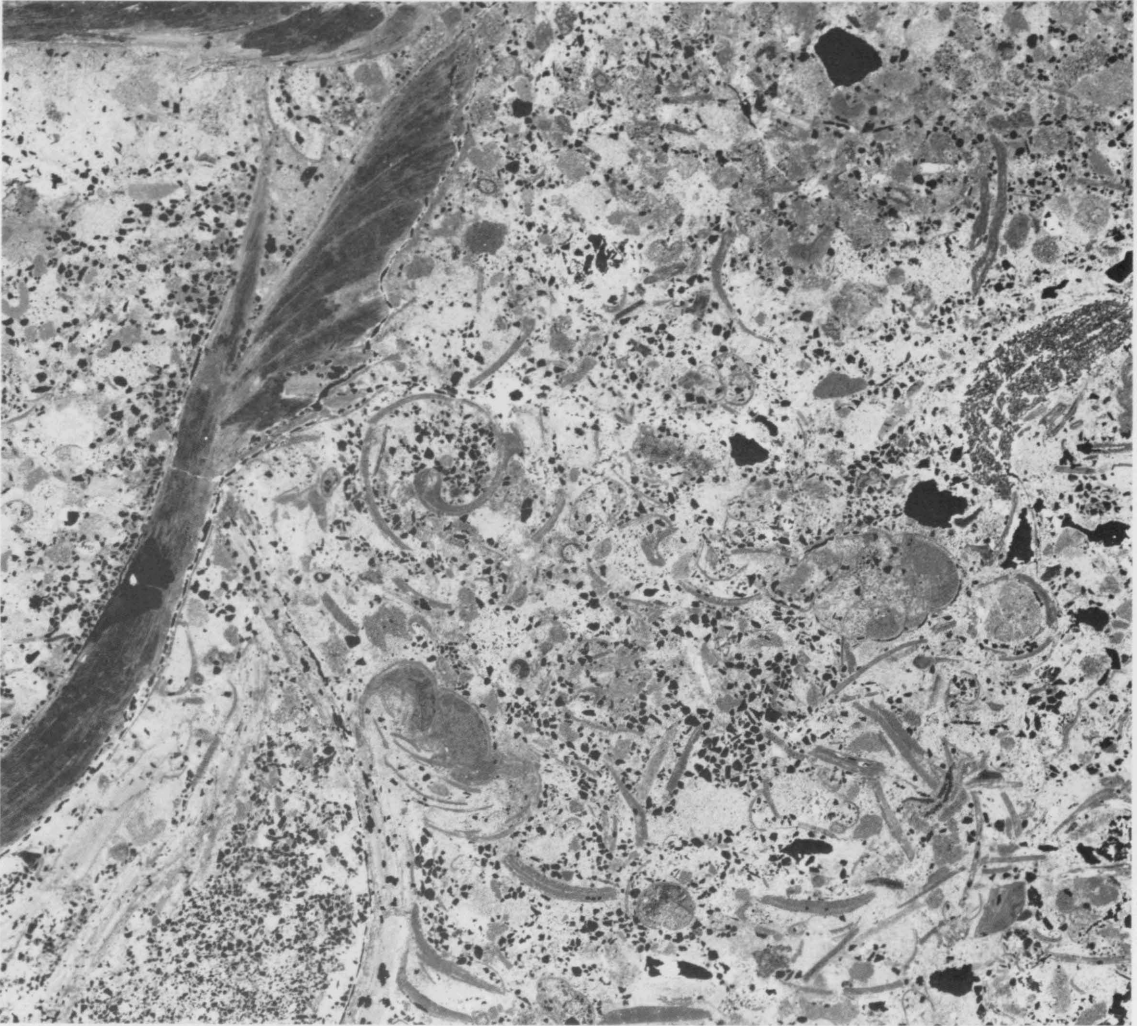


FIG. 11— Photograph printed from acetate peel of polished section through unionid coquina site at University of Michigan locality SC-289, showing abundant unionid pelecypods and freshwater gastropods in matrix of detrital carbonate and quartz sand. Unusual structure near middle right side of photograph appears to be carbonized wood. Mollusk shells are matrix-filled, and many are broken. Note angularity of quartz sand grains. Photograph enlarged to 5x natural size.

thickness, and it contains abundant bone. Bird Quarry is near the center of SC-133 both geographically and stratigraphically. It lies within a bed of gray mudstone in the middle of a series of alternating orange and gray beds.

The Bird Quarry limestone is a complex mass of brecciated, bioturbated micrite with some spar-filled dessication cracks and rare spar-filled gastropods (Fig. 13). Etching in dilute formic acid highlights burrows on the order of 5 mm in diameter, now filled with laminations of reworked micrite and silt (Fig. 14). Etching also reveals a complex network of anastomosing spar-filled voids up to 1 mm thick that are interpreted as plant rootlets. Lithologically the Bird Quarry limestone resembles that from the discovery site described above, but it differs in being a lens of very different shape (more tabular or sheet-like, being much broader than thick). It differs also in exhibiting distinct burrows and



FIG. 12— Bird Quarry site at University of Michigan locality SC-133 (early Wasatchian). Upper photograph (A) shows site as discovered, near dry stream bed in lower part of photograph (view is to southeast). Lower photograph (B) is closeup of site (view is to east). Marsh pick rests on productive limestone bed in both photographs (pick handle is about 60 cm in length).

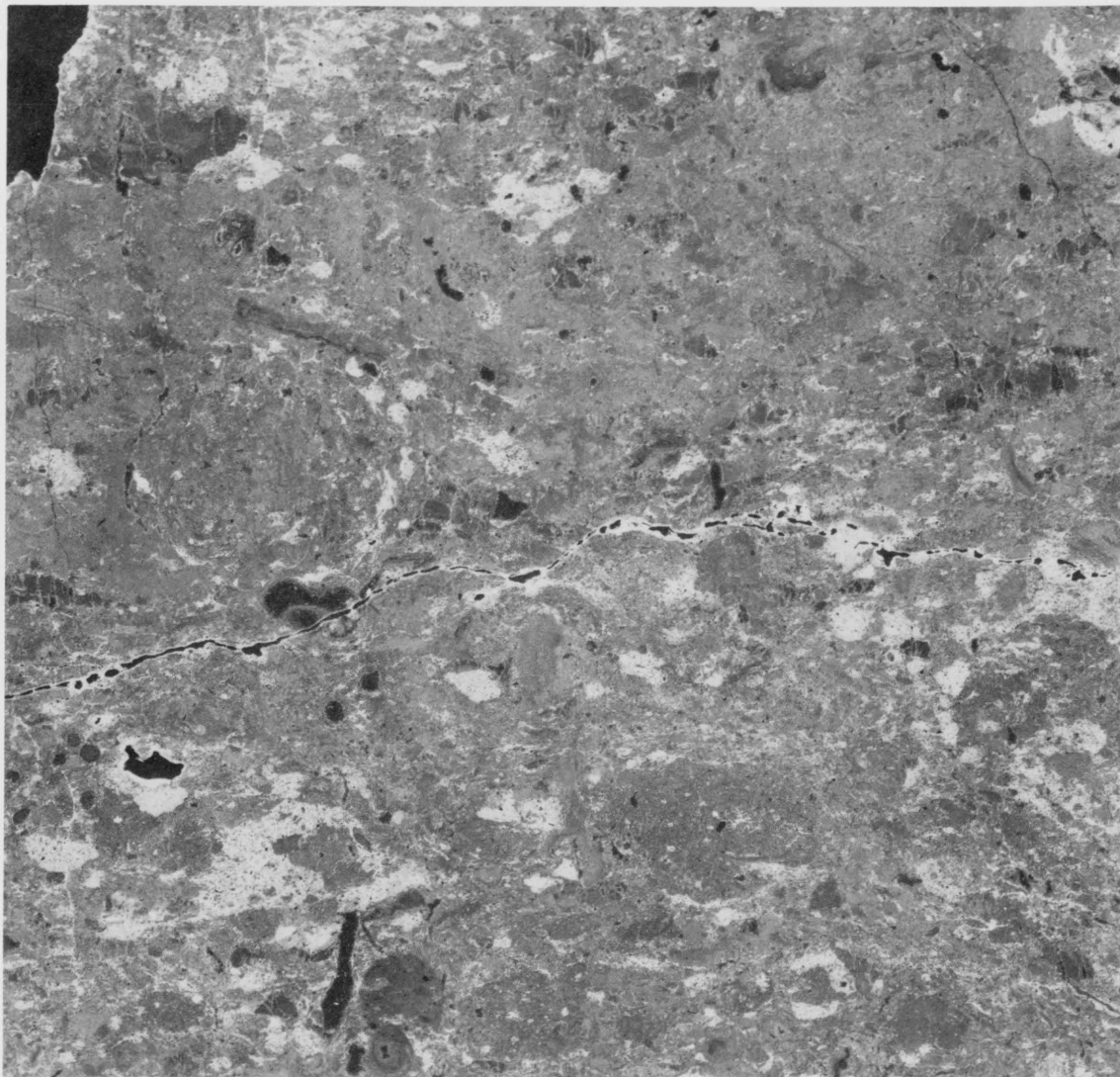


FIG. 13— Photograph printed from acetate peel of polished section through Bird Quarry site, University of Michigan locality SC-133, showing brecciated, bioturbated micritic matrix with some remnants of bedding. Bone fragments and spar-filled rootlets are visible throughout. Spar-filled gastropods (left center of photograph) are rare. Photograph enlarged to 5x natural size.

networks of plant rootlets not seen in the discovery site limestone. Parenthetically it may be noted that burrowers reworking the Bird Quarry limestone before lithification carried underlying silt into the limestone. These tubes of silt, now lithified, are softer than surrounding limestone. When excavated they serve today as solitary nesting sites for an insect, probably a bee or wasp.

The molluscan fauna from Bird Quarry is very limited, comprising one specimen each of *Discus ralstonensis* and *Grangerella* sp. Acid preparation of the vertebrate fauna from Bird Quarry is not yet complete and most remains are uncatalogued, but the fauna collected to date includes lizard jaws and vertebrae, numerous bird bones [UM 86343], and jaws or teeth of the following mammalian taxa: *Peradectes* sp., one or more insectivores, *Arctodontomys wilsoni*, *Apheliscus* sp., *Paramys* sp., and

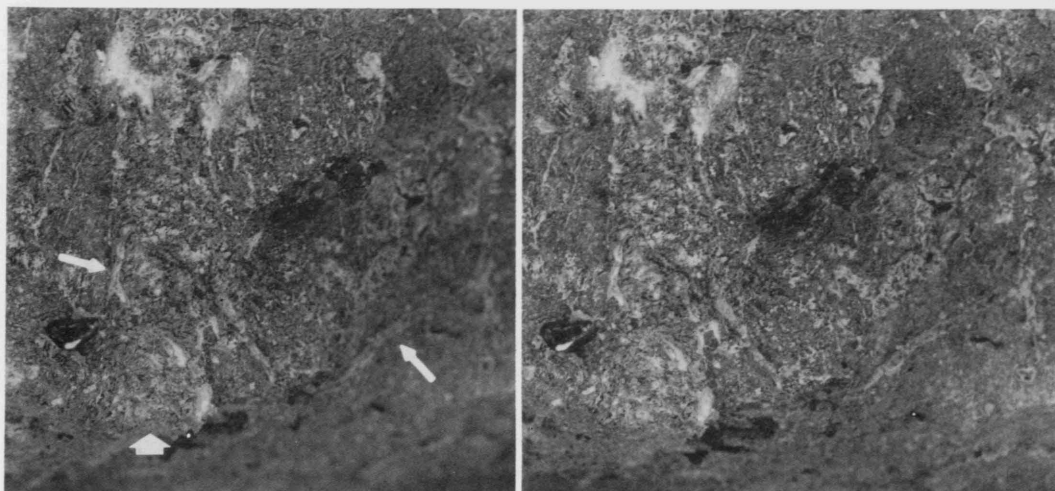


FIG. 14— Stereophotograph of etched surface of limestone from Bird Quarry site. Bone fragments are common. Note concentric laminations in vertical burrow traversing left center of photograph (large arrow), and presence of numerous anastomosing spar-filled plant rootlets (small arrows). Photograph enlarged to 2x natural size.

Diacodexis metsiacus [UM 86344, 86345]. Most long bones of vertebrate specimens are broken, and skeletal elements, if associated, are disarticulated.

Taken together, the shape of the lens, preservation of distinct borrows, presence of numerous anastomosing plant rootlets, rarity of gastropods (both terrestrial), and evident diversity of vertebrate remains, suggest a pedogenic origin involving accumulation or precipitation of calcium carbonate in a shallow intermittently flooded depression. Burrowing organisms inhabited the soil and terrestrial gastropods lived on the soil surface or on plants growing in the depression. The presence of abundant vertebrate bone, much of it broken, may indicate that the depression was an occasional source of water attracting lizards, birds, and mammals preyed upon by carnivorous mammals.

SC-133 Calcirudite Site

The final source of vertebrate fossils in Willwood limestones documented here is the SC-133 calcirudite site (Fig. 15), a bed of coarse clastic carbonate outcropping some 10 m higher stratigraphically than Bird Quarry. The bed, of unknown length (due to cover), is lenticular and 1–2 m wide in cross section. It lies in the southeastern part of the locality at the base of a sequence of red beds forming the upper levels of SC-133. The calcirudite bed is composed of rounded calcium carbonate nodules equivalent in grain size to coarse sand, with the bed reaching a maximum thickness in places of 30–40 cm. It is underlain by the lowest red bed in a complex of red mudstones exposed here, and it grades upward into a thin platy sandstone. Shrinkage cracks are well developed within carbonate clasts, and clast size fines upward within the bed. Most Eocene vertebrates known from Pakistan come from clastic carbonate beds like this one, which Wells (1983) interpreted as reworked soil nodules deposited by transient streams in semi-arid sand-poor environments.

The fauna preserved in the SC-133 calcirudite includes freshwater unionid bivalves, gastropods, and mammalian teeth and jaws, including a dentary of *Haplomyilus speirianus* [UM 86340] and a dentary of *Hyopsodus loomisi* [UM 86341]. Mammalian teeth and jaws are rare in the deposit, and

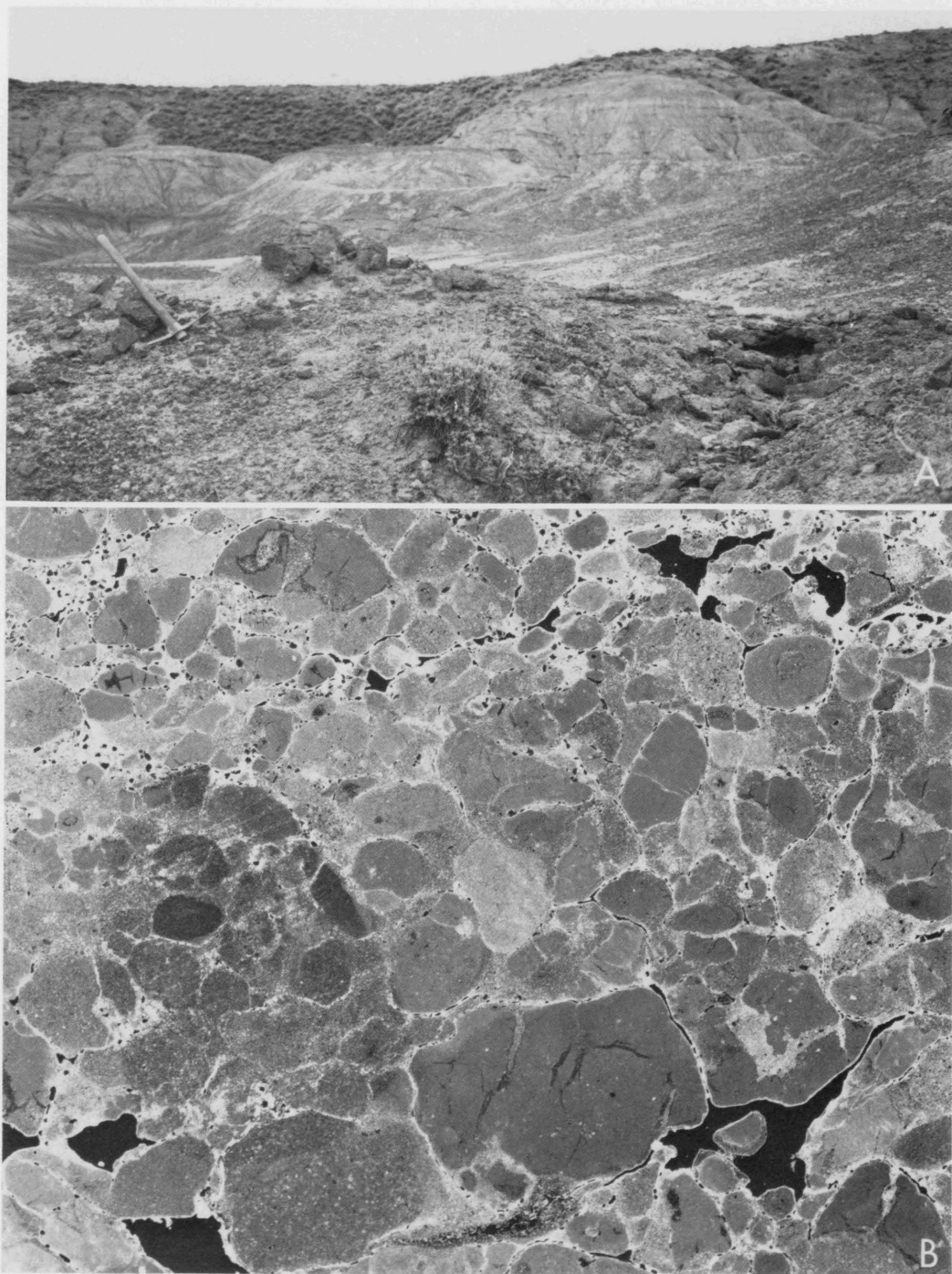


FIG. 15— Calcirudite site at University of Michigan locality SC-133 (early Wasatchian). Upper photograph (A) shows blocks of calcirudite weathering from ridge top in foreground (view is to south). Handle of Marsh pick is about 60 cm in length. Lower photograph (B) printed from acetate peel of polished section through calcirudite block showing fining upward change in grain size and shrinkage cracks developed within clasts. Lower photograph enlarged to 5x natural size.

they appear to have behaved as clasts like the soil nodules, having been swept from eroding surfaces and redeposited together. The mollusks are poorly preserved, and they too may have been transported.

SYSTEMATIC PALEONTOLOGY OF
FAUNA FROM LIMESTONE AT SC-29 DISCOVERY SITE

The fauna recovered from lens J at the discovery site, University of Michigan locality SC-29, is listed in Table 1. Estimated minimum numbers of individuals representing each species are given in the right hand column. Table 1 includes both molluscan and vertebrate taxa. The entire lens J fauna was recovered from a mass of freshwater limestone occupying a volume of approximately 2,000 cm³ and weighing an estimated 5 kg.

Phylum MOLLUSCA
Class GASTROPODA

All of the mollusks present in lens J at the discovery site are land snails, including one prosobranch and seven pulmonates (following classification of Solem, 1978). These were identified by comparison with figures and descriptions published in Cockerell and Henderson (1912), Cockerell (1914a,b, 1915a,b), Russell (1931a,b), Pilsbry (1939, 1940, 1946, 1948), La Rocque (1960), Hanley (1976), and Roth (1986). Representative pulmonates are illustrated in Figure 16.

Subclass PROSOBRANCHIA
Family Helicinidae
Hendersonia evanstonensis (White, 1878)
Fig. 16D

All specimens found in early collections from lens J were pulmonates. However, careful recollecting at the site in 1986 yielded several specimens of the helicinid prosobranch *Hendersonia evanstonensis* [UM(I) 65510]. This species has a dextrally coiled, operculum-bearing shell about 8–9 mm in diameter over five whorls. It is wider than high, with faint dorsal sculpturing, and it is imperforate, the umbilical region being occupied by a callous pad. None of the specimens collected to date from lens J preserve the operculum.

Subclass PULMONATA
Family Oreohelicidae
Oreohelix megarche Cockerell and Henderson, 1912

The largest pulmonate from lens J, the oreohelcid *Oreohelix megarche*, is represented by a single specimen [UM(I) 65404], an impression of the umbilical surface of a very large dextrally coiled shell (not illustrated). *Oreohelix* is the only discoidal gastropod of this size reported from the early Eocene.

TABLE 1 — Molluscan and vertebrate fauna from vertebrate-bearing carbonate lens (lens J) at SC-29 Discovery Site. Minimum numbers of individuals representing each species are noted in brackets at right.

MOLLUSCA	
Gastropoda	
PROSOBRANCHIATA	
<i>Hendersonia evanstonensis</i> (White, 1878); UM(I) 65510	[6]
PULMONATA	
<i>Oreohelix megarche</i> Cockerell and Henderson, 1912; UM(I) 65404	[1]
Cf. <i>Microphysula</i> sp.; UM(I) 65405	[1]
<i>Discus ralstonensis</i> (Cockerell, 1914a); UM(I) 65406, 65511	[ca. 200]
Cf. <i>Pupilla</i> sp.; UM(I) 65407	[ca. 100]
Cf. <i>Albertanella minuta</i> Russell, 1931a; UM(I) 65408	[2]
<i>Grangerella sinclairi</i> (Cockerell in Cock. and Hend., 1912); UM(I) 65512	[1]
Cf. <i>Grangerella</i> (?) <i>phenacodorum</i> (Cockerell, 1914b); UM(I) 65513	[2]
CHORDATA (VERTEBRATA)	
Amphibia	
URODELA (CAUDATA)	
Numerous vertebrae of small salamander; UM 76871(a-j)	[1]
ANURA (SALIENTIA)	
Distal humerus of small frog; UM 76883	[1]
Reptilia	
SQUAMATA	
Indeterminate anguimorph lizard (very small); UM 76872, 76873	[1]
Gerrhonotine lizard; UM 76874, 76875, 76878, 76879(?), 76881	[1]
Varanoid lizard; UM 76876, 76877	[1]
Aves	
ARDEIFORMES (CICONIIFORMES)	
<i>Calcardea junnei</i> n. gen., n. sp.; UM 76882	[1]
Mammalia	
MULTITUBERCULATA	
<i>Ectypodus powelli</i> Jepsen, 1940; UM 71553, 76884–76892	[2]
MARSUPIALIA	
<i>Peradectes</i> cf. <i>P. chesteri</i> (Gazin, 1952); UM 76893, 76894	[2]
INSECTIVORA	
<i>Leptacodon rosei</i> n. sp.; UM 65359, 76895–76905, 76907–76908, 76926(?)	[3]
Cf. <i>Leptacodon</i> sp.; UM 76909	[1]
"Cf. <i>Plagioctenodon krausae</i> Bown, 1979"; UM 76906, 76920	[1]
<i>Limaconyssus habrus</i> n. gen., n. sp.; UM 86724	[1]
CHIROPTERA	
<i>Wyonycteris chalice</i> n. gen., n. sp.; UM 76910–76919, 76923(?), 76926(?)	[3]
Cf. <i>Icaronycteris</i> sp.; UM 76921, 76922, 76925	[1]
DERMOPTERA	
Cf. <i>Worlandia</i> sp.; UM 76927, 86727	[1]
PRIMATES	
<i>Tinimomys graybullensis</i> Szalay, 1974; UM 76924	[1]
<i>Carpolestes</i> cf. <i>C. nigridens</i> Simpson, 1928; UM 65254	[1]
CARNIVORA	
<i>Viverravus boweni</i> , n. sp.; UM 76928–76930	[1]

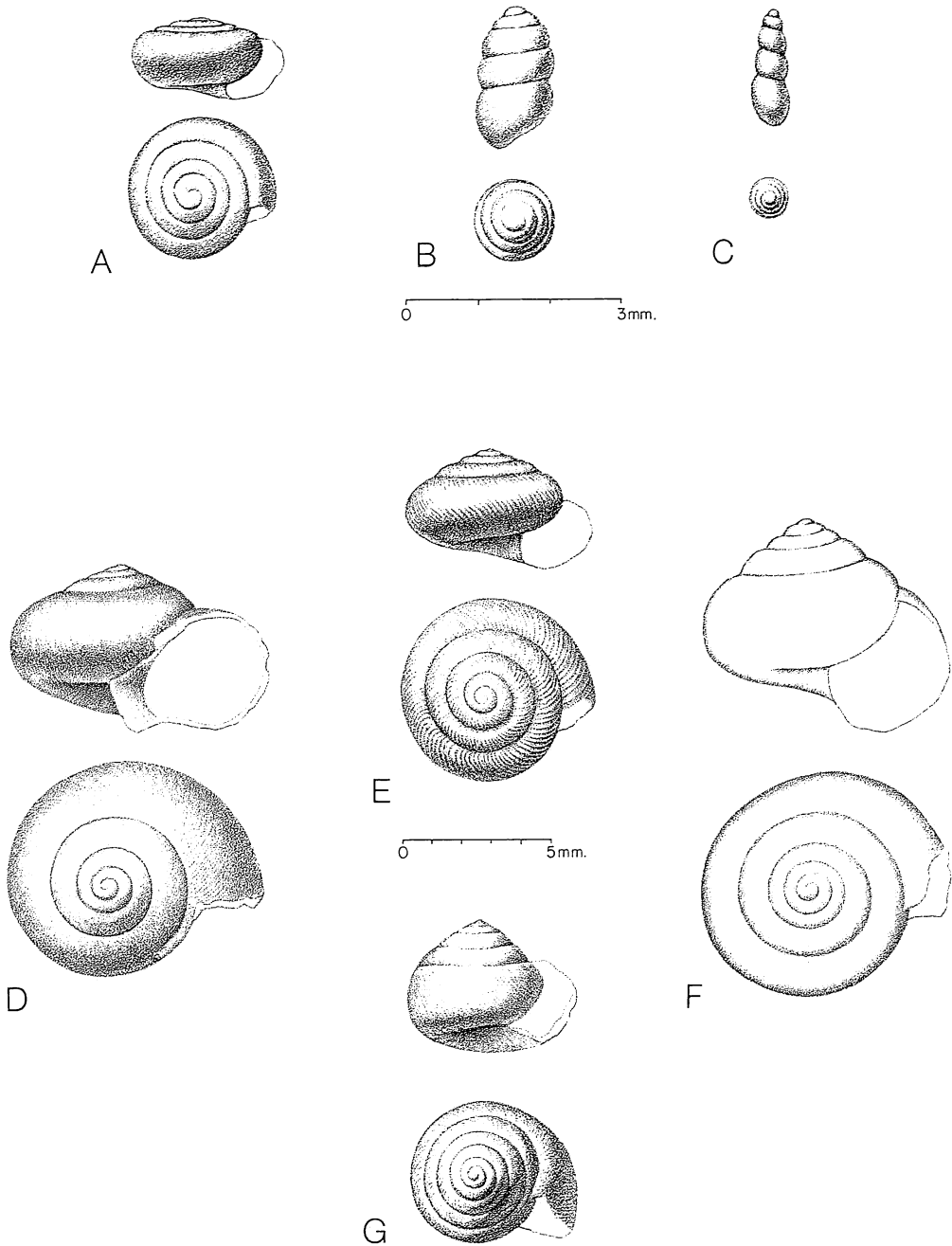


FIG. 16— Prosobranch and pulmonate gastropods preserved in limestone lens J at SC-29 Discovery Site. Each species is shown in lateral and apical view. A: Sagdid Cf. *Microphysula* sp. [UM(I) 65405], last whorl is incomplete. B: Dextral pupillid Cf. *Pupilla* sp. [UM(I) 65407], last whorl is incomplete. C: Sinistral pupillid(?) *Albertanella* cf. *A. minuta* [UM(I) 65408], final whorl(s) missing. D: Helicid *Hendersonia evanstonensis* [UM(I) 65510] with partially complete aperture. E: Partial shell of endodontid *Discus ralstonensis* showing first four of five whorls [UM(I) 65406]. F: Internal mold of grangerellid *Grangerella sinclairi* [UM(I) 65512] showing first five whorls. G: Grangerellid Cf. *Grangerella(?) phenacodorum* [UM(I) 65513] showing six whorls with seventh rising toward apex. Upper scale is for drawings A-C; lower scale is for drawings D-G.

The specimen is identified as *O. megarche* based on the size of the umbilical impression, indicating an umbilicus approaching 10 mm in diameter.

Family Sagdidae
Cf. *Microphysula* sp.
Fig. 16A

A second dextral discoidal species, much smaller, is represented by a single individual in the fauna from lens J [UM(I) 65405]. It is very low spired and smooth, with overlapping whorls and a relatively open umbilicus. It compares well with the sagdid *Microphysula oxyaenae* (Cockerell, 1914b), from which it differs in being only 2.2 mm in diameter (over four whorls).

Family Endodontidae
Discus ralstonensis (Cockerell, 1914a)
Fig. 16E

The most abundant gastropod in lens J is the endodontid *Discus ralstonensis*, represented by many individuals (including some juvenile specimens). *Discus ralstonensis* is a dextrally coiled, discoidal species measuring about 6 mm in diameter (5 whorls) with pronounced axial striae. The umbilicus is widely open. Early collections are catalogued as UM(I) 65406, and 1986 specimens are catalogued as UM(I) 65511.

Family Pupillidae
Cf. *Pupilla* sp.
Fig. 16B

Two species referred to Pupillidae are present. The first, dextral Cf. *Pupilla* sp., being very common [UM(I) 65407]. These specimens are typically pupillid in having subcylindrical shells measuring 2.0–2.2 mm high and 1.1–1.2 mm in diameter over five whorls. The umbilicus appears to have been small but open, and the mouth edge appears not to have been thickened. The presence or absence of teeth within the mouth of the shell cannot be determined.

Cf. *Albertanella minuta* Russell, 1931a
Fig. 16C

The second species from lens J referred (questionably) to Pupillidae is a rare high-spired sinistral species that may be compared with *Albertanella minuta* [UM(I) 65408], recognizing that *Albertanella* is at present little more than a form genus for high-spired sinistral species. The specimens measure about 1.6 mm high and 0.5 mm in diameter over five whorls. It is not clear whether more whorls were present or not, and nothing is preserved of the aperture. This species is so different in size and proportion that, whatever its affinities, it cannot be conspecific with Cf. *Pupilla* sp. described here.

Family Grangerellidae

Grangerella sinclairi (Cockerell in Cockerell and Henderson, 1912)

Fig. 16F

Recollecting the surface at the site of lens J in 1986 yielded a rather poor specimen of *Grangerella sinclairi* [UM(I) 65512]. The first five whorls are present, and the specimen measures 8.0 high and 8.8 mm in diameter as preserved. The obtuse shape of the spire, closely spaced whorls, slightly impressed sutures, and flat nearly closed umbilicus indicate that this is a *Grangerella*. Whorls six and seven are missing. The latter, also missing in Cockerell's slightly larger type specimen of "*Gastrodonta(?) evanstonensis* var. *sinclairi*," would have been directed upward toward the apex of the shell. The holotype of *Grangerella sinclairi* was collected in 1912 by W. J. Sinclair "about three miles north of Ralston, Wyoming," and it is thus probably late Clarkforkian in age. The holotype of Cockerell's (1915a) *Grangerella megastoma* is similar in size. It was collected in 1912 by Walter Granger in the "head of Big Sand Coulee, Clark's Fork Basin, Wyoming," and it too is probably late Clarkforkian in age. I regard these species as synonyms.

Cf. *Grangerella(?) phenacodorum* (Cockerell, 1914b)

Fig. 16G

Recollecting the surface at the site of lens J in 1986 also yielded two specimens initially referred to the grangerellid *Protoboysia complicata* [UM(I) 65513]. While undoubtedly representing a grangerellid, these specimens are larger and less high-spined than typical *Protoboysia complicata*, measuring 4.5 mm in apical height and 6.0 mm in diameter over seven whorls. The last whorl rises toward the apex of the shell, as is characteristic of grangerellids, but the aperture itself is not complete.

Note on mollusks from SC-29 lens E

In addition to work at lens J, careful examination of discovery site lens E in 1986 yielded several species of gastropods different from those in lens J: Cf. *Viviparus retusus* (Meek and Hayden), see Russell (1931b, p. 7) [UM(I) 65514]; *Radiocentrum grangeri* (Cockerell and Henderson, 1912—see also Roth, 1986, p. 248) [UM(I) 65515]; and a third indeterminate species [not catalogued]. Each of these three species is represented by a single specimen. *Discus ralstonensis* is represented in lens E by two specimens [UM(I) 65516] and *Hendersonia evanstonensis* is represented by ten specimens [UM(I) 65517]. Egg shell fragments are present in lens E, but vertebrate bone is very rare. The rarity of vertebrates, the abundance of *Hendersonia*, and the presence of a possible aquatic *Viviparus* suggest that lens E represents a different depositional environment than nearby lens J.

Phylum CHORDATA (VERTEBRATA)

No fish remains were found in material collected from SC-29 lens J, but remains of amphibians, reptiles, birds, and mammals are relatively common.

Class AMPHIBIA
Order URODELA (CAUDATA)

Numerous vertebrae of a small salamander are present. These are catalogued as UM 76871(a-j).

Order ANURA (SALIENTIA)

The distal end of the humerus of a small frog is catalogued as UM 76883.

Class REPTILIA
Order SQUAMATA

Reptiles in lens J are all anguimorph lizards. Two fragmentary dentaries represent a very small indeterminate anguid [UM 76872 and 76873]. Another dentary, a maxilla, a premaxilla (possibly two), and a frontal represent a gerrhonotine or diploglossine anguoid with slightly compressed pleurodont tooth crowns [UM 76874–76875, 76878–76879(?), and 76881]. The teeth are high-crowned and beveled, almost bicuspid, with a large posterior cusp and small anterior shoulder cusp or cuspule. Another dentary and maxilla represent one or possibly two *Parasaniwa* or *Provaranosaurus*-like varanoids (Bartels and Gautier, pers. comm.) [UM 76876 and 76877]. Teeth in these are also pleurodont, with compressed tooth crowns. One tooth is very well preserved in the dentary, and it has a single acute apical cusp. There are slight grooves defining anterior and posterior ribs on the medial surface of the tooth. Gautier (1982) described the oldest diploglossine from the early Wasatchian of southwestern Wyoming, and Bartels (1983) has previously reported both gerrhonotines and varanoids from localities of Clarkforkian age in the Clark's Fork Basin.

Class AVES
Order ARDEIFORMES (CICONIIFORMES)
Family Ardeidae

Postcranial elements of a moderately large bird are present in the discovery site collection. A fragment of sternum shows overlapping coracoidal sulci, the left above the right, as is characteristic of herons (Ardeidae) and, to a lesser degree, storks (Ciconiidae). The oldest heron-like bird recorded previously is from the London Clay, a formation in England spanning the latter part of the early Eocene. Richard Owen (1846) described and illustrated the anterior part of the sternum of a small wading bird, later named *Proherodius oweni* by Lydekker (1891). The oldest heron-like birds recorded previously from North America are *Botauroides parvus* and *Eoecornis ardetta* described by Schufeldt (1915) from the Bridgerian middle Eocene of southwestern Wyoming. The specimen described here is the oldest heron-like bird discovered to date.

Calcardea junnei, new genus and species

Fig. 17

Holotype.—UM 76882 (Fig. 17), anterior part of sternum, partial left coracoid, nearly complete right coracoid, partial left humerus, two nearly complete vertebrae, fragmentary left and right tarsometatarsi, and several phalanges, all probably representing a single individual bird.

Diagnosis.—Resembles *Eoceornis ardetta* in having similar coracoid overlap, but differs in being significantly larger and in having a much more pronounced ventral manubrial process. *Butauroides parvus* is a smaller bird, less than half the size of that described here. *Calcardea junnei* is the same size as *Proherodius oweni* but differs in having shallower, more rounded coracoidal sulci and, again, a more pronounced manubrial process. *Calcardea junnei* evidently differed from living herons and storks in having shorter cervical vertebrae, with a distinct condyle on the dorsal surface of the anterior surface of the centrum, and distinct dorsal processes rising above the postzygapophyses.

Description.—The sternal fragment of *Calcardea junnei* (Fig. 17A,B) is particularly important for comparison with previously described fossil material. It preserves a complete manubrial spine and overlapping coracoidal sulci, left above right, as is characteristic of herons and storks. The spine is intermediate in size (length ca. 5.5 mm) by comparison with extant herons (Payne and Risley, 1976). The coracoidal sulci are approximately 3.5 mm in depth, and they overlap by approximately 6 mm (ca. 3 mm on each side of midline).

The right coracoid is well preserved (Fig. 17C), and the sternal facet of the coracoid is appropriate in size and shape to articulate with the sternal fragment described here—the two fit together perfectly. The body of the coracoid is missing at midshaft, but its total length can be estimated by matching bone contours. As reconstructed, the coracoid measures approximately 58 mm in length from the center of the coracohumeral surface of the head to the center of the sternal facet. The furcular facet on the head is largely eroded away, and reconstruction might lengthen this estimate slightly. The tips of both the internal distal angle and sternocoracoidal process are broken, and the body of the coracoid is sheared and displaced just above the sternocoracoidal impression. This displacement affects the angle of attachment of the sternal end of the coracoid to the body, but it does not appear to affect the length of the coracoid. The procoracoid is missing (broken). The brachial tuberosity has a slight posterior overhang, the glenoid facet is almost flat, and the scapular facet is deep, round, and cup-shaped, all characteristic of ardeids.

The left humerus includes the complete head, much of the proximal half of the shaft, and the isolated external condyle with ectepicondylar prominence. Head and shaft are separated by crushing around the pneumatic foramen, and neither the pneumatic fossa nor the deltoid crest is preserved. The humerus appears to have been about 10.5 mm in maximum diameter at midshaft. A portion of the head of the right humerus is also preserved.

Parts of the distal shafts of both tarsometatarsi are preserved, the most complete being the right. The left preserves more of the distal end, including the outer extensor groove and part of the distal foramen. Neither preserves any part of the trochleae. At its narrowest point some 10 mm above the distal foramen, the tarsometatarsus measures 6.5 mm in maximum diameter and 4.3 mm in minimum diameter. The shaft of the tarsometatarsus is convex anteriorly and concave posteriorly at the point where the trochlear processes divide. Figure 17E is a composite drawing of the distal shaft of a left tarsometatarsus based on both left and right sides.

The most interesting cervical vertebra is illustrated in Figure 17G-I. By analogy with herons, it is probably the seventh cervical. The vertebra is intact except for the left prezygapophysis, which appears to be rotated a little out of position posteriorly, and the right prezygapophysis, which is missing. The centrum, like the rest of the vertebra, is relatively short for a heron, and even a little shorter than similar cervical vertebrae in storks of comparable size. Large lateral vertebral canals are

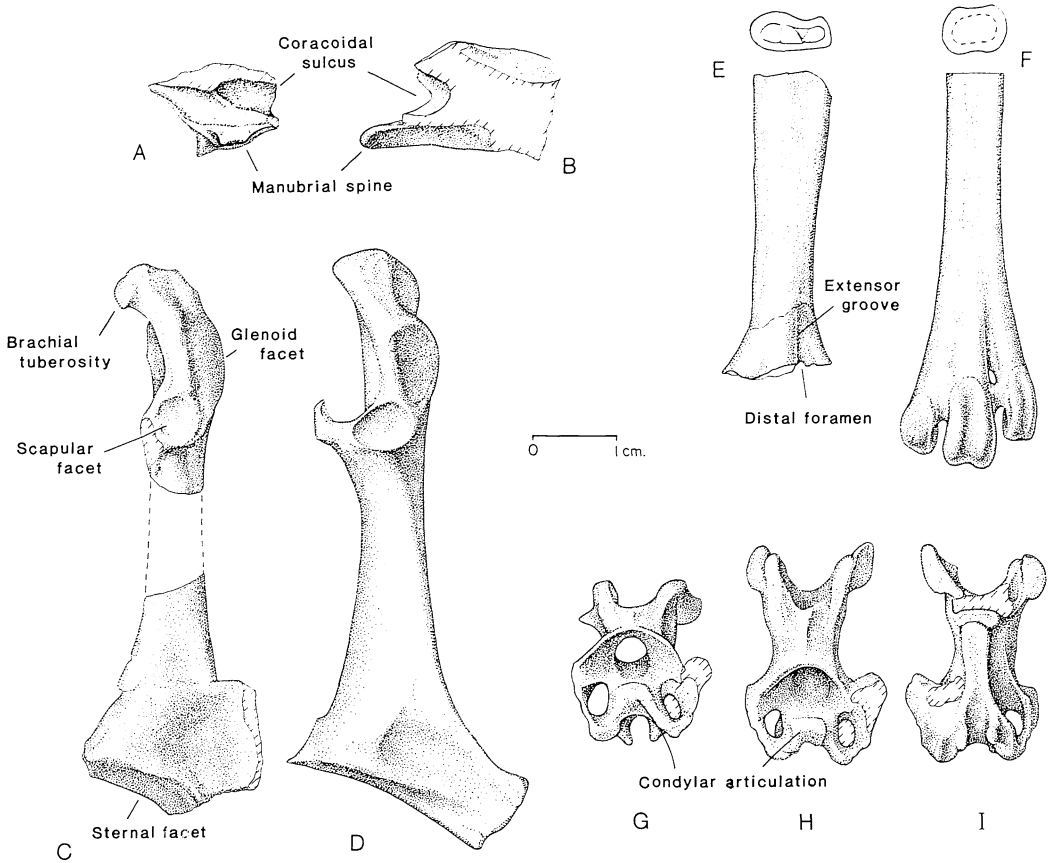


FIG. 17— Holotype of *Calcardea junnei* [UM 76882], new genus and species, from limestone lens J at SC-29 discovery site. *A, B*: Manubrium of sternum in anterior and left lateral views. Note overlapping coracoidal sucli characteristic of modern herons and storks. *C*: Right coracoid in dorsal view. Sternal facet articulates with coracoidal sulcus on sternum. Note round, cup-shaped scapular facet characteristic of ardeids. *D*: Right coracoid of modern ciconiid *Ciconia abdimii* for comparison (University of Michigan Museum of Zoology 152870). Note oval, cup-shaped scapular facet. *E*: Right distal tarsometatarsus in anterior view (composite based on fragments from both left and right sides). *F*: Right distal tarsometatarsus of modern ciconiid *Ciconia abdimii* for comparison (University of Michigan Museum of Zoology 152870). *G-I*: Cervical vertebra in anterior, dorsal, and ventral views. Note prominent condylar articulation indicating unusual flexibility in the cervical series at this point.

present, and each postzygapophysis bears a robust dorsal process. The most distinctive feature of this cervical vertebra is the presence of an enlarged condylar articulation on the dorsal surface of the centrum extending the centrum's anterior articular surface upward. The anterior opening of the neural canal is well behind the anterior articular surface of the centrum, facilitating sharp dorsal flexion of the neck like that seen in herons. The centrum measures 14.5 mm in length from anterior to posterior articular surfaces. The dorsal surface of each postzygapophysis rises 13.9 mm above the base of the centrum, and the vertebra appears to have been about 14.6 mm wide across the prezygapophyses.

Etymology.—Prefix latinized from Greek *chalix*, calcareous, in allusion to discovery of this bird in limestone, with *ardea*, L., heron. Species is named for George Junne in appreciation of his considerable assistance and encouragement in the field over the past five summers.

Discussion.—*Calcardea junnei* was about the size of a purple heron (*Ardea purpurea*) or the small Amdim's stork (*Ciconia abdimi*), with which it is compared in Figure 17. Damage to most preserved

bones resembles that described by Bickart (1984) and attributed to scavenging by mammalian carnivores.

The type specimen of *Calcardea junnei* includes a fragmentary sternum with a distinctively heron-like configuration of coracoidal sulci, an articulating right coracoid, and many associated parts of the skeleton. All appear to belong to a single individual bird, but in the event that these should prove to belong to more than one individual or species, the coracoid and articulating sternal fragment are here designated as the primary holotype.

There is some broken eggshell in the limestone matrix of lens J. This is possibly avian, but it appears to come from eggs too small to represent *Calcardea junnei*.

Class MAMMALIA

A minimum of eleven mammalian species are known from lens J at the discovery site, each represented by fragmentary dentaries, maxillae, or isolated cheek teeth. Specimen numbers are listed in Table 1.

Order MULTITUBERCULATA

Family Neoplagiaulacidae

Ectypodus powelli Jepsen, 1940

The multituberculate *Ectypodus powelli*, first described from SC-29 lens J by Krause (1980, p. 1169), is now represented by 10 teeth [UM 71553, 76884–76892], all isolated, indicating the presence of a minimum of two individuals.

Order MARSUPIALIA

Family Didelphidae

Peradectes cf. *P. chesteri* (Gazin, 1952)

Remains of the marsupial *Peradectes* cf. *P. chesteri* include two isolated teeth [UM 76893 and 76894]. These have the high paraconid, open trigonid, concave cristid obliqua, squared talonid, and twinned entoconid-hypoconulid characteristic of marsupials. The dentary [UM 65359] allocated to this species by Rose (1981, p. 34) appears, with better comparative material, to belong to *Leptacodon rosei*, new species (see below).

Order INSECTIVORA

Family Nyctitheriidae

There are four nyctitheriid insectivores present among specimens recovered from the discovery site. The first, described here as a new species of *Leptacodon*, is the most common.

Leptacodon rosei, new species

Fig. 18

Holotype.—UM 71650, left dentary with $P_{2-4}M_{1-3}$ from University of Michigan locality SC-188, SW 1/4, SW 1/4, Section 6, T56N, R101W, Park County, Wyoming. This specimen was illustrated by Rose (1981: fig. 11).

Age and locality.—Middle through late Clarkforkian land-mammal age, early Eocene. The holotype and largest sample come from a screen-washed site ("Holly's Microsite") within middle Clarkforkian locality SC-188. This species is also common in SC-29 lens J.

Diagnosis.—Relatively low-crowned nyctitheriid differing from late Tiffanian *Leptacodon tener* Matthew and Granger, 1921, and *L. packi* Jepsen, 1930, in having P_3 much smaller and lower-crowned than P_4 . Further differs from these species in having a broader talonid basin and a larger and higher paraconid on P_4 . Differs from Wasatchian *Leptacodon catulus* Krishtalka (1976) in retaining more prominent paraconids on P_4 and M_1 . Differs from Clarkforkian and Wasatchian specimens referred to *Pontifactor* in lacking prominent styler cusps on upper molars.

Description.—The lower dentition of *Leptacodon rosei* was described and illustrated by Rose (1981, pp. 39–41: fig. 11). The holotype dentary preserves two mental foramina, one beneath P_2 and the other beneath P_4 . Rose (1981: table 4) provides measurements of lower cheek teeth for the holotype and four additional middle Clarkforkian specimens from the type locality SC-188.

New specimens of *Leptacodon rosei* from SC-29 lens J include UM 76408 with alveoli for three procumbent incisors, an alveolus for a relatively large canine, alveoli for a single-rooted P_1 and double rooted P_2 and P_3 , and intact crowns of P_4 and M_1 . This specimen differs conspicuously from the holotype in having a single elongate mental foramen beneath P_3 , but the shape and size of preserved tooth crowns leaves little doubt that it belongs to *Leptacodon rosei*.

The most complete upper dentition of *Leptacodon rosei* is a specimen [UM 76895] preserving P^4M^{1-3} and supernumerary M^4 (Figure 18). This maxilla and similar isolated nyctitheriid upper molars are referred to *L. rosei* because they are the proper size and shape to occlude with lower teeth of this species and because *L. rosei* is the most common nyctitheriid found in lens J. Upper cheek teeth of *L. rosei* are relatively broader than those of *L. tener*, but otherwise differ little from comparable elements of that species (see McKenna, 1968).

Etymology.—Named for Dr. Kenneth D. Rose, who described the first specimens of this species, in recognition of his great contribution to the study of Clarkforkian mammals.

Discussion.—A long, straight partial metapodial [UM 76926] from SC-29 lens J was carefully studied as a possible metacarpal of a primitive chiropteran. This specimen is illustrated in Figure 19. However, comparison with more complete metapodials found in the 1986 *Plesiadapis cookei* limestone precludes this possibility. The new metapodials are virtually identical to the specimen described here, but one of the new bones preserves both proximal and distal articulations on a shaft only slightly longer than UM 76926. The specimens are clearly elongated metatarsals rather than metacarpals. They appear to be the right size to be metatarsals of *Leptacodon rosei* (a species common also in the *P. cookei* limestone). If this attribution is correct, it suggests that *Leptacodon* was certainly digitigrade and possibly saltatorial.

Hypodigm.—The type sample of *Leptacodon rosei* from SC-188 includes UM 68866, 71650 (holotype), 71661, 71662, 71841, 73682, 77023, 77030, and 77032. Other specimens include UM 66195 from SC-81 and UM 82389, 82601, 82609, 82610, 82675, and 82690 from SC-62.

Leptacodon rosei is represented in the lens J fauna by three dentaries, two maxillae, and several isolated teeth [UM 65359, 76895–76905, 76907–76908], and possibly by a single metatarsal [UM 76926], indicating the presence of a minimum of three individuals.

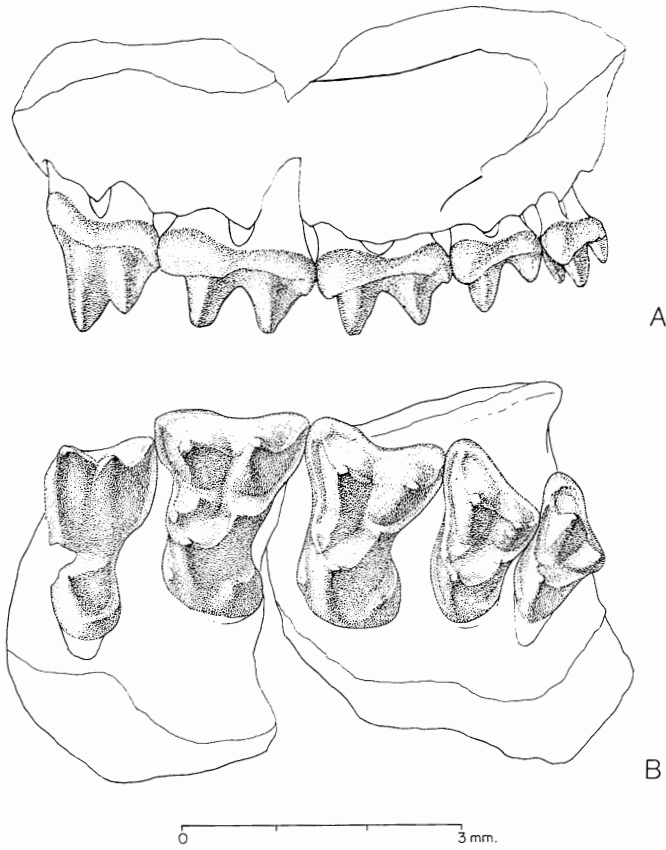


FIG. 18— Left maxilla of *Leptacodon rosei*, new species, from limestone lens J at SC-29 discovery site. Drawing shows P⁴ and M¹⁻⁴ [UM 76895] in lateral (A) and occlusal view (B). Note presence of supernumerary fourth upper molar in an otherwise normal maxillary dentition.

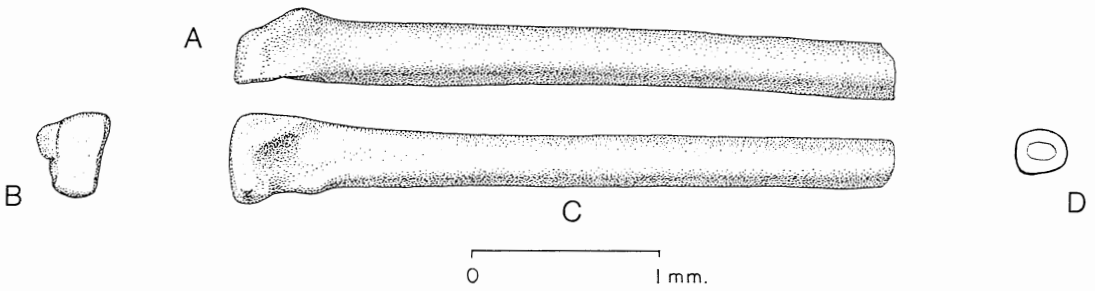


FIG. 19— Elongated metatarsal from limestone lens J at SC-29 discovery site. This specimen [UM 76926] is questionably referred to *Leptacodon rosei*. Comparison with similar specimens found elsewhere indicates that only a very short segment of distal shaft and the distal articulation are missing.

Cf. *Leptacodon* sp.

A second nyctitheriid species, Cf. *Leptacodon* sp., is represented by a single lower molar, M_1 , [UM 76909] that is too large to belong to *Leptacodon rosei*. It measures 1.9 mm in length, 1.3 mm in breadth across the talonid, and approximately 1.5 mm in trigonid height. M_1 in *Leptacodon rosei*, by comparison, measures 1.4 - 1.6 mm in length, 1.0 - 1.2 mm in breadth, and 1.3 - 1.5 mm in trigonid height.

“Cf. *Plagioctenodon krausae* Bown, 1979”

A third nyctitheriid, including Clarkforkian specimens that Rose (1981) attributed to Cf. *Plagioctenodon krausae* Bown, 1979, has M_1 measuring 1.15 mm in length and 0.75 mm in breadth across the trigonid (Rose, 1981, p. 41-42), and approximately 1.1 - 1.2 mm in trigonid height. This species is represented in the SC-29 lens J fauna by an isolated first or second lower incisor [UM 76906] and the buccal half of an upper molar [UM 76920]. The incisor is particularly interesting in having a procumbent cuspidate crown bearing five marginal denticles separated by fissures like I_2 in the European nyctitheriids *Saturninia* and *Amphidozotherium* (Sigé, 1976). The lens J incisor and upper molar are identified as “Cf. *Plagioctenodon krausae*” by comparison with an exceptionally complete nyctitheriid (UM 86725, found while preparing a partial skeleton from the 1986 *Plesiadapis cookei* limestone). This new specimen resembles *Leptacodon* as much as it does *Plagioctenodon*, and definitive placement of all of these specimens must await study of the new material.

***Limaconyssus habrus*, new genus and species**

Fig. 20

Holotype.—UM 86724, left dentary with P_4M_{1-3} .

Age and distribution.—Late Clarkforkian land-mammal age, early Eocene. The holotype and only specimen came from limestone lens J, locality SC-29, near center of NW1/4, S36, T56N, R101W, Park County, Wyoming.

Diagnosis.—Small insectivore differing from all other nyctitheriids in having unusually high-crowned cheek teeth. P_4 has a large but narrow trigonid with a prominent paraconid displaced anteriorly, the metaconid is high but lower than the protoconid, and the talonid is both short and narrow. Lower molars have acutely angled trigonid crests, making molar trigonids more triangular than quadrate in occlusal view.

Description.—The type and only specimen of *Limaconyssus habrus* is a left dentary with alveoli for a double-rooted P_2 , roots for P_3 , and intact crowns of P_4 and M_{1-3} . The mandibular ramus is shallow, measuring only 1.2 mm beneath M_1 . There are two mental foramina, an anterior one beneath P_2 and a posterior one just in front of the anterior root of P_4 .

Crowns of P_2 and P_3 are not preserved, but judging from alveoli and roots, they were long and narrow like P_4 . The crown of P_4 has a large trigonid and an exceptionally narrow talonid. The paraconid is moderately high and positioned well anterior of the protoconid and metaconid. The metaconid is also moderately high, but it is closely appressed to the protoconid. The talonid on P_4 is basined, but narrow, joining the trigonid at an oblique angle.

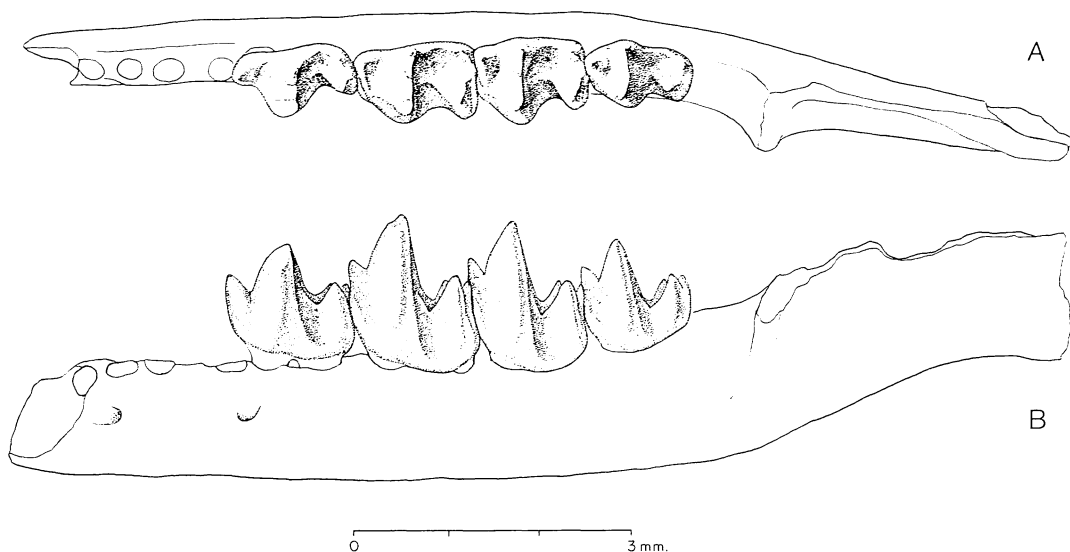


FIG. 20— Left dentary of *Limaconyssus habrus*, new genus and species, from limestone lens J at SC-29 discovery site. Drawing shows P_4 and M_{1-3} [UM 86724, holotype] in occlusal (A) and lateral view (B). Note narrow, high crowned cheek teeth characteristic of this very small nyctitherid.

Lower molars have high trigonids with sharply crested paraconids and high sharp protoconids and metaconids. The latter cusps are of equal height. The paracristid and protocristid on all three molars make acute angles when seen in occlusal view. The talonids of M_{1-3} are basined, each basin being surrounded by a distinct hypoconid, entoconid and small hypoconulid. The cristid obliqua runs up the back of the metaconid, creasing it to the apex. There are small but distinct precingulids on M_{1-3} and postcingulids on M_{1-2} . The acute angle formed by crests bordering both the protoconid and hypoconid on each molar gives each of these external cusps a pinched pillarlike appearance that makes them distinctly different from molars of *Leptacodon*.

M_1 is the largest tooth in the lower cheek tooth series, and teeth decrease in size anteriorly and posteriorly from M_1 . P_4 measures 1.3 mm in length, 0.7 mm in maximum breadth, and 1.3 mm in trigonid height. M_1 measures 1.3 mm in length, 1.0 mm in trigonid breadth, and 1.6 mm in trigonid height. M_2 measures 1.2 mm in length, 0.9 mm in trigonid breadth, and 1.6 mm in trigonid height. M_3 measures 1.1 mm in length, 0.8 mm in trigonid breadth, and 1.2 mm in trigonid height.

Etymology.—*Limax*, Gr., slug, and *nyssus* (m.), pierce or puncture. *Habrus*, delicate, graceful. Literally, delicate slug piercer.

Discussion.—*Limaconyssus habrus* is one of the smallest and most high-crowned insectivores described to date from the early Cenozoic. Preserved cheek teeth, while distinctive, share a general resemblance with those of nyctitheriid insectivores. Consequently, it appears easier to expand the concept of Nyctitheriidae than to erect a new monotypic family for this genus and species.

Order CHIROPTERA
Family Palaeochiropterygidae

A dentary and several isolated upper and lower molars from lens J indicate the presence of a small *Myotis*-sized chiropteran. This is the earliest evidence of bats in the fossil record, and it is one of the smallest Clarkforkian mammals known to date.

Wyonycteris chalice, new genus and species

Figs. 21–22

Holotype.—UM 76910, a right dentary with P₄, M₁ (part), and M₂.

Age and distribution.—Late Clarkforkian, early Eocene. The holotype and all referred specimens were found in lens J at the discovery site, locality SC-29, near the center of NW1/4, Section 36, T56N, R101W, Park County, Wyoming.

Diagnosis.—Differs from early Eocene chiropterans known to date (*Ageina*, *Archaeonycteris*, *Icaronycteris*, and *Palaeochiropteryx*), in possessing small but distinct mesostyles and prominent conules on upper molars. P₄ with a small metaconid and reduced talonid. Lower molars, especially M₂, set obliquely in the dentary, with strongly curved protoconids. Cristid obliqua extends up the posterior surface of the metaconid, separated from it by a distinct groove. Lower molars nyctalodont and lacking a labial cingulid.

Description.—The type specimen, UM 76910, is a right dentary with the posterior alveolus for P₃, a nearly complete crown of P₄, talonid of M₁, intact crown of M₂, and alveoli for M₃ (Fig. 21). The mandibular ramus is shallow (measuring 1.4 mm in depth beneath M₁), and there is a single small mental foramen directly beneath P₄. Crowns of anterior teeth, including anterior lower premolars and all upper premolars, and the crown of M₃ are all unknown. UM 76923 may be a broken dP⁴ of *Wyonycteris*, but this cannot be determined with certainty.

The crown of P₄, well preserved in the holotype, is moderately long and narrow. Most of a small anteriorly placed paraconid is missing, so one cannot determine how well developed this cusp may have been. The protoconid is the highest cusp, dominating a triangular wedge-shaped trigonid. There is a small but distinct metaconid medial and slightly posterior to the protoconid. Three very small cusps mark the posterior edge of the talonid, the largest being the hypoconid. A weak cristid obliqua runs forward from the hypoconid and up the back of the metaconid. The talonid as a whole is small by comparison with the trigonid. It is narrow and only weakly basined. The talonid depression is transverse to the long axis of the crown and opens medially.

The trigonid of M₁ is missing in the holotype and the talonid is partially broken. The only characteristic of importance is a nyctalodont relationship of the hypoconid, hypoconulid, and entoconid (nyctalodonty, according to Menu and Sigé, 1971, means that the hypoconid and hypoconulid are connected by a distinct crest, the postcristid, while the hypoconulid and entoconid are separated by a fissure). The most complete M₁ is an isolated tooth, UM 76912 (Fig. 22E,F), which is worn but nevertheless exhibits a number of important features. The paraconid, protoconid, and anterior part of the metaconid appear to have been approximately equal in size, forming, when viewed occlusally, an isosceles triangle narrowest on the lingual side (opposite the protoconid). The protoconid is high, rising and curving upward and then lingually from the base of the crown. The metaconid is almost doubled, being separated by a distinct groove paralleling and anterior to the cristid obliqua. As on P₄, the cristid obliqua joins the hypoconid and metaconid. The postcristid joins the hypoconid and hypoconulid, stopping short of the entoconid. The entoconid is the highest talonid cusp, and the whole crown appears skewed, with lingual cusps positioned much higher on the crown than labial cusps.

M₂ is well preserved in the holotype (Fig. 21) and, as an isolated tooth, in UM 76914. As in M₁, viewed occlusally, the tips of the paraconid, protoconid, and metaconid form an isosceles triangle narrowest lingually. Viewed anteriorly, the paracristid joining the paraconid and protoconid has a sharp right-angled bend midway between the two cusps. Viewed posteriorly, the protocristid joining the protoconid and metaconid also has a right-angled bend midway between cusps. The trigonid is deeply basined, with this basin opening medially. The cristid obliqua is a distinct crest joining the posterior part of the metaconid to the hypoconid. As on M₁, a groove parallels the cristid obliqua, running up the back of the trigonid and dividing the metaconid. The basined talonid on M₂ is again nyctalodont.



FIG. 21— Right dentary of *Wyonycteris chalice*, new genus and species, from limestone lens J at SC-29 discovery site. Drawing shows P₄, part of M₁, and intact M₂ [UM 76910, holotype], in occlusal (A) and lateral view (B). Note narrow P₄ with reduced metaconid, cristid obliqua rising to the metaconid on M₂, absence of labial cingulid, and nyctalodont relationship of talonid cusps.

In the upper dentition, M¹ is present in a maxillary fragment, UM 76917 (Fig. 22C,D), with alveoli for P⁴, and it is also represented by isolated tooth UM 76916. The crown of M¹ is distinctive in having an anteriorly projecting cusate parastyle, a small narrow stylar shelf, a crestlike mesostyle, and a labially expanded metastylar crest. The paracone is higher and sharper than either the protocone or metacone. The paraconule and metaconule and associated crests are well developed, and a small pericone and hypocone flank the protocone anteriorly and posteriorly. The premetaconulecrista runs from the metaconule up the lingual surface of the metacone rather than into the trigon basin as it does in most insectivores. Thus the trigon basin is a long, transverse, V-shaped groove obstructed only by the protocone at its lingual end.

M² is represented by a single isolated tooth, UM 76915 (Fig. 22G,H), that differs from M¹ in being more symmetrical anteroposteriorly. The parastyle projects less anteriorly, and the skewed metastylar crest is shorter. As in M¹, the mesostyle is distinct but small. M³ is represented by two specimens, UM 76918 and 76919 (Figs. 22A,B, and 22I,J). These are reduced in size by comparison with M¹ and M². The paracone remains the dominant cusp and the parastyle is strong, but all other cusps are reduced disproportionately.

Hypodigm and measurements.—Holotype and referred specimens include the following (measurements of upper molars are given as anteroposterior ectoloph length : protoconal length : transverse breadth; measurements of lower molars are given as anteroposterior length : trigonid breadth : talonid breadth; all measurements in mm):

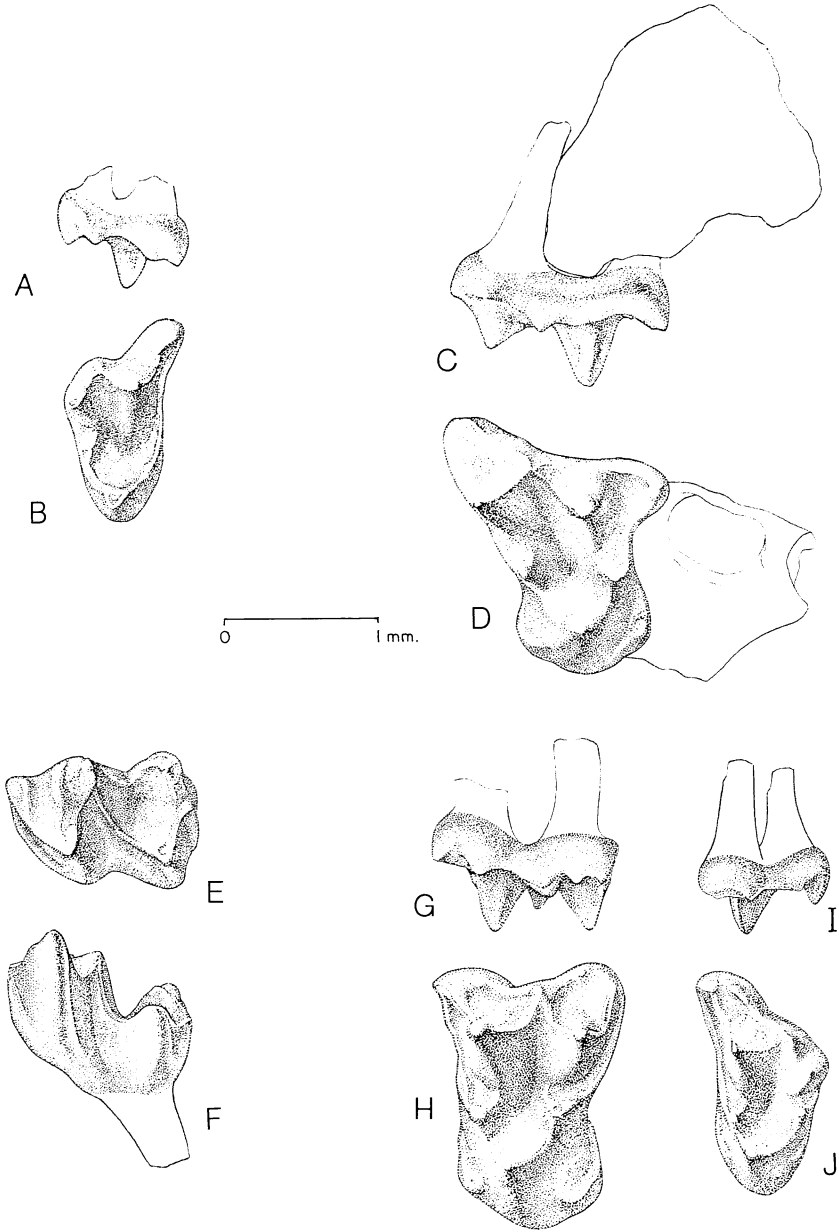


FIG. 22— Isolated teeth of *Wyonycteris chalice*, new genus and species, from limestone lens J at SC-29 discovery site. *A, B*: Right M^3 [UM 76919] in lateral and occlusal view. *C, D*: Right M^1 in maxillary fragment [UM 76917] in lateral and occlusal view. *E, F*: Left M^1 [UM 76912] in occlusal and lateral view. *G, H*: Left M^2 [UM 76915] in lateral and occlusal view. *I, J*: Left M^3 [UM 76918, possibly same individual as 76915] in lateral and occlusal view. Note W-shaped ectoloph, crested mesostyles, well developed conules, and pericones on upper molars. Note also absence of labial cingulid, and cristid obliqua with accompanying groove rising up posterior surface of metaconid on lower molar.

UM 76910, holotype, right P_4 measuring 1.1 in length, 0.6 in breadth; right M_1 measuring approximately 1.3 in length, 0.9 in talonid breadth; right M_2 measuring 1.3 : 0.9 : 0.9. Trigonid of M_2 is 1.0 high.

UM 76911, edentulous dentary measuring 1.4 in depth beneath M_2 .

UM 76912, left M_1 measuring 1.2 : 0.7 : 0.8.

UM 76913, trigonid of right M_2 measuring 0.9 in width.

UM 76914, right M_2 measuring 1.2 : 0.8 : 0.8.

UM 76915, left M^2 measuring 1.3 : 0.9 : 1.7.

UM 76916, right M^1 measuring 1.4 : 1.0 : 1.5.

UM 76917, right M^1 measuring 1.5 : 0.9 : 1.5.

UM 76918, left M^3 measuring 0.9 : 0.6 : 1.5.

UM 76919, right M^3 measuring 0.8 : 0.5 : 1.2.

Etymology.—*Wyoming*, anglicized contraction of Leni Lanape Indian word *Maughwauwama* or *Meche weaving*, meaning “large plains” or “alternating plains and mountains” (Urbanek, 1974), and *nykteris*, Gr. (f.), bat. Specific name *chalix*, Gr., limestone, in reference to discovery in limestone.

Discussion.—*Wyonycteris chalix* is the first bat to be recorded from transitional Paleocene-Eocene sediments of Clarkforkian age, and it is the oldest chiropteran to have been found anywhere. *Wyonycteris* is similar in size and general morphology to nyctitheriid insectivores, like small *Leptacodon* and *Limaconyssus*, but *Wyonycteris* differs in having low crowned cheek teeth, a narrower premolariform P_4 with a reduced talonid, and transversely skewed lower molars with high lingual cusps and low curved labial cusps. The combination of small size, W-shaped ectoloph on upper molars, simple P_4 , and skewed lower molars with high lingual cusps, low curved labial cusps, and small hypoconulid are characteristic of chiropterans.

Menu and Sigé (1971) first distinguished nyctalodonty (hypoconid-hypoconulid joined, entoconid separate) and myotodonty (hypoconid-entoconid joined, hypoconulid separate) in bats, and considered nyctalodonty to be the primitive condition among chiropterans. This was questioned by Van Valen (1979) who noted that while early Eocene *Icaronycteris* is nyctalodont, *Ageina* and *Archaeonycteris* are not. Now however, for what it is worth, the earliest chiropteran, *Wyonycteris*, is nyctalodont as predicted by Menu and Sigé. Given our limited knowledge of early chiropteran evolution, distinguishing nyctalodonty and myotodonty serves principally to emphasize the morphological diversity present in early Eocene bats.

Rose (1981, p. 39) suggested that some genera now classified as lipotyphlan insectivores may prove to be chiropterans, citing Matthew's (1918) referred specimen of “*Nyctitherium celatum*” as an example. This specimen, AMNH 15103, was collected by Walter Granger in the Bighorn Basin, Wyoming, from a locality “5 miles south of Otto” (Wasatch field catalogue for 1910 in the archives of the American Museum of Natural History). This is the locality published by Matthew (1915) as the type locality of *Cantius* (= “*Pelycodus trigonodus*”, a middle Wasatchian species. The appropriate entry in the field catalogue, field number 587, indicates: “Various small genera (including insectivore). Fragments of skull, jaws, and skeleton material from one place.” [Two specimens of *Hyopsodus* (AMNH 14976 and 15009) were subsequently removed from this field number and catalogued separately]. Describing AMNH 15103, Matthew (1918, p. 603) wrote:

A specimen referred to *Nyctitherium celatum* affords some additional evidence on the affinities of this species. It consists of portions of upper and lower jaws with which are associated three long slender bones, suitable in size and proportions for the shafts of chiropteran forelimb bones, and a few other small fragments not recognizable. Both the jaw parts and associated bones belong to an immature individual, the upper and lower premolars being in a corresponding stage of emergence, and all the remains were found within a few centimetres of each other, in the original matrix. No remains of any other animals were associated with them. The upper and lower jaws almost certainly belong to the same individual. It is highly probable, therefore, that the supposed limb bones

likewise pertain to it. Although the supposed limb bones are too incomplete for positive identification, the ends absent or unrecognizable, yet they show clearly an extremely slender, nearly straight shaft, unlike any bone of any terrestrial mammal with which I have compared them. If this identification is correct, as appears reasonably probable, it indicates that this species is a chiropteran; but whether the genus should be referred to that order is still doubtful in view of the form of the anterior portion of the jaw in some Bridger species (apparently also in this one), the absence of molar cingula, and the conditions of deposition of the Wasatch formation, these conditions making the preservation of an insectivore in its strata far more probable than of a chiropteran. Practically all the positively identified chiropteran fossils have come from cave or fissure formations; the Wasatch is a river-valley formation. For these reasons I have preferred not to transfer *Nyctitherium* to the Chiroptera, although its known remains are very suggestive of affinity to the bats.

West (1974) described *Pontifactor bestiola* from the middle Eocene of North America, based on upper cheek teeth. West compared *P. bestiola* with Matthew's referred specimen of *Nyctitherium celatum* (AMNH 15103) in referring *Pontifactor* to Nyctitheriidae. AMNH 15103 has subsequently been transferred from *Nyctitherium celatum* to *Pontifactor* sp. (Krishtalka, 1976; see also Bown, 1979, and Rose, 1981).

AMNH 15103 certainly does not belong in *Nyctitherium*, but I am not persuaded that it belongs in *Pontifactor* either. Matthew's (1918) and Krishtalka's (1976) illustrations show the upper molars of AMNH 15103 to be relatively short anteroposteriorly and broad labiolingually, while upper molar length and breadth are more nearly equal in *Pontifactor* (judging from West's illustrations—measurements appropriate for comparison have never been published). Both have a W-shaped ectoloph, but AMNH 15103 has much more strongly developed conules, a distinct pericone, and a lingually placed hypocone, characteristics resembling *Wyonycteris*. Cheek tooth morphology indicates that AMNH 15103 is more likely to represent *Wyonycteris* than *Pontifactor*, and Matthew may have been right in suggesting chiropteran affinities for this specimen (if better specimens demonstrate that AMNH 15103 is a nyctithere, then the "long slender bones" mentioned by Matthew, now lost, may have been metatarsals).

AMNH 15103 and UM 71032 (described from the middle Clarkforkian by Rose, 1981, p. 42) have more exaggerated hypoconulids on lower molars and mesostyles on upper molars, and neither appears to represent *Wyonycteris chalice*. Both are provisionally referred to Cf. *Wyonycteris* sp. The systematic position of *Pontifactor bestiola*, still known only from upper cheek teeth, remains uncertain. *Pontifactor* too may be a chiropteran (McKenna et al., 1962, described the lower jaw of a contemporary chiropteran with which it might be compared), but it differs in important ways from *Wyonycteris* (exaggerated mesostyle, weaker conules, no pericone).

Several characteristics distinguishing *Wyonycteris* from early Eocene *Ageina*, *Archaeonycteris*, *Icaronycteris*, and *Palaeochiropteryx* (nyctalodont lower molars without labial cingulids, and upper molars with well developed conules and small pericones and hypocones) are features of resemblance to *Placentidens lotus* described by Russell et al. (1973) from the early Eocene of Europe. Teeth of *Placentidens* are about the same size as those of *Wyonycteris*, and upper molars bear enlarged conules with a transverse V-shaped central groove on the trigon. Lower molars have a cristid obliqua with a parallel anterior groove rising to the apex of the metaconid, curved labial cusps, and no labial cingulid. *Placentidens* differs from *Wyonycteris* in lacking any real mesostyle and its lower molars are myotodont (if a hypoconulid is present at all), but discovery of *Wyonycteris* as a structural intermediate suggests that *Placentidens* should be included in Chiroptera rather than Dermoptera. *Placentidens* resembles early chiropterans, through newly discovered *Wyonycteris*, more closely than it does any dermopteran.

Cf. *Icaronycteris* sp.

Fig. 23

Three fragmentary specimens from SC-29 lens J represent a chiropteran different from *Wyonycteris* [UM 76921, 76922, and 76925]. These specimens lack the mesostyle and strong conules on upper molars, and the cristid obliqua connected to the metaconid on lower molars that are characteristic of *Wyonycteris*. Given the limited evidence at hand, this species compares most closely with *Icaronycteris* described by Jepsen (1966, 1970).

Order DERMOPTERA

Family Plagiomenidae

Cf. *Worlandia* sp.

Two isolated teeth of a small dermopteran are known from SC-29 lens J. These appear to be most similar to *Worlandia inusitata* described by Bown and Rose (1979), but differ somewhat in both form and size. Both teeth, lower premolars, differ from homologous teeth in *Plagiomene* in being lower crowned and less molarized. UM 86727 is a right P₃ measuring 2.3 mm in crown length and 1.6 mm in maximum breadth. This tooth is larger than P₃ in *Worlandia*, and it has a distinct metaconid and hypoconulid not seen on P₃ in *Worlandia*. The paraconid is more anteriorly placed and prominent than that of P₃ in *Planetetherium*. UM 76927 is a right P₄ measuring 2.5 mm in crown length and 1.6 mm in maximum (talonid) breadth. In comparison with P₄ of *Worlandia*, this tooth is larger and relatively narrower, with a more distinct hypoconulid. It is less massive than P₄ in *Planetetherium*.

Rose (1981, p. 48) mentioned a late Clarkforkian dermopteran dentary lacking tooth crowns [UM 68221] that is too large to be *Worlandia inusitata* and too small to be *Plagiomene accola*. This specimen may represent the same taxon as the two dermopteran teeth described here. There are five alveoli in front of double-rooted P₃ in UM 68221, the anteriormost being enlarged and procumbent like that of *Worlandia*. The following alveoli match those seen in *Worlandia* very closely, including a small single-rooted I₂, small single-rooted C₁, small single-rooted P₁, and larger single-rooted P₂. Thus the lower dental formula of UM 68221 was probably 2.1.4.3 as in *Worlandia inusitata* (Rose, 1982).

Order PRIMATES

Family Microsyopidae

Tinimomys graybullensis Szalay, 1974

This species is represented by the lingual half of a right upper molar [UM 76924], M¹ or M², matching the Clarkforkian specimen illustrated by Rose (1981, p. 54) very closely.

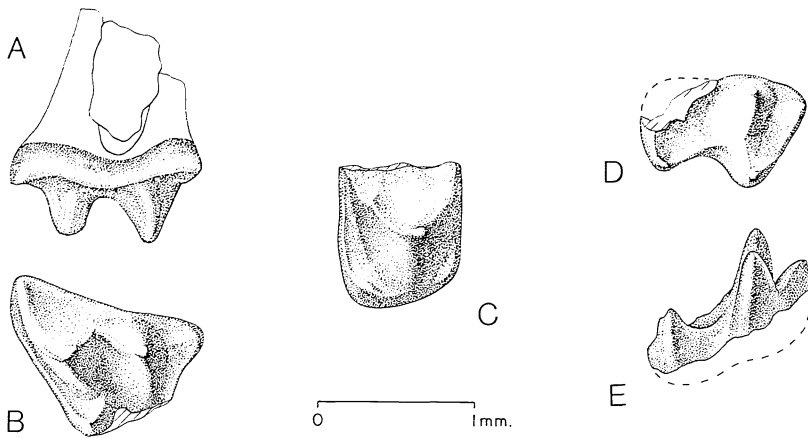


FIG. 23— Isolated teeth of Cf. *Icaronycteris* sp. from limestone lens J at SC-29 discovery site. A, B: Buccal half of right M² [UM 76921] in lateral and occlusal view. C, D: Lingual half of right M¹ or M² [UM 76922] in occlusal view. E, F: Partial crown of M₂ [UM 76925] in occlusal and lateral view. Note W-shaped ectoloph but absence of mesostyle, weakly developed conules, and absence of pericone on upper molars. Note anteroposteriorly short trigonid and cristid obliqua curving toward protoconid on lower molar.

Family Carpolestidae

Carpolestes cf. *C. nigridentis* Simpson, 1928

The plesiadapiform primate *Carpolestes* cf. *C. nigridentis* is known from SC-29 lens J only by a right dentary with P₄M₁-2 [UM 65254]. This is the original specimen found at the discovery site, and no additional specimens have been found.

Order Carnivora

Family Viverravidae

***Viverravus boweni*, new species**

Fig. 24

Holotype.—UM 76928, left dentary with impression of P₃ and crowns of M₁₋₂ from lens J at the discovery site, locality SC-29, near the center of NW1/4, Section 36, T56N, R101W, Park County, Wyoming. UM 76929 from this locality is probably part of the same individual as the holotype, and 76930 may be as well.

Age and distribution.—Middle Clarkforkian through early Wasatchian, early Eocene, of Bighorn and Clark's Fork basins, Wyoming.

Diagnosis.—Smaller than all described species of *Viverravus* except possibly middle Eocene *V. minutus* Wortman. Differs from *V. minutus* in having a shorter dentary with more crowded premolars and shorter talonids on M₁ and M₂. Very similar to *V. acutus* Matthew, but cheek teeth average 16-17% smaller in linear dimensions (16-17% is more than two standard deviation units in each case).

Description.—The holotype is a left dentary with the crown of the canine and part of the mandibular symphysis reflected along the medial side of the ramus (Fig. 24A). The canine measures about 1.9 mm in maximum anteroposterior diameter at the base of the crown. An impression of P₃ is preserved in

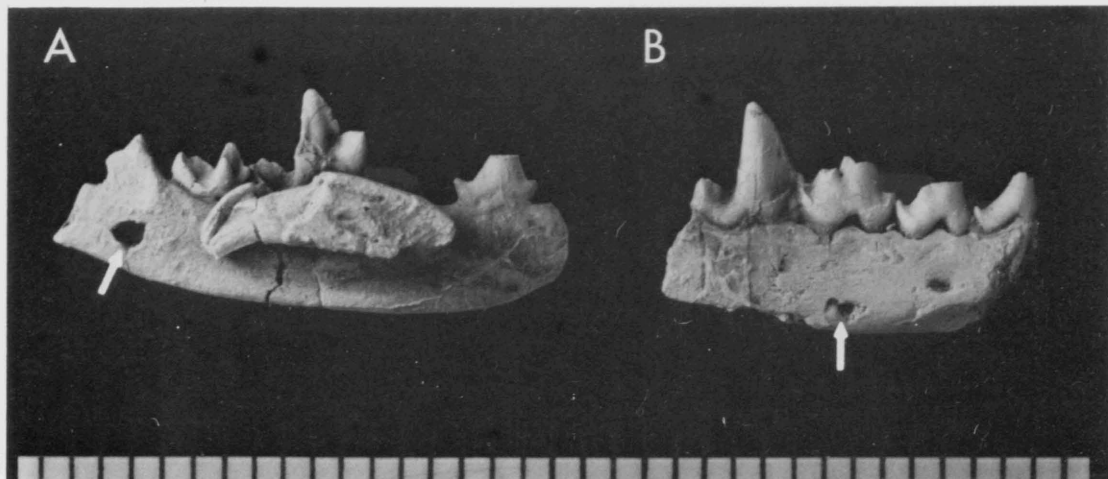


FIG. 24— Photographs of left and right dentaries of *Viverravus bowni*, new species, from limestone lens J at SC-29 discovery site. A: Left dentary with P₃, M_{1,2} [UM 76928, holotype] in medial view. B: Right dentary with P₂₋₄, M₁ [UM 76929] in lateral view. Anterior part of left dentary was broken before burial, reflected, and preserved adjacent to mandibular ramus. Note apparent bite marks (arrows) inferred to have been inflicted by canine teeth of a mammalian carnivore. Scale is in mm. Photographs by George Junne, 4x natural size.

epoxy (poured into a natural impression of this tooth before rock matrix was removed). The crowns of M₁ and M₂ are well preserved. M₁ has the high trigonid and low basined talonid characteristic of carnassials in this genus. The protoconid is the highest cusp, but the paraconid and metaconid (here broken) are well developed also. M₂ is much smaller than M₁ and the trigonid rises little above the talonid. M₁ in the holotype measures 4.1 mm in crown length, 2.4 mm in trigonid length (measured anteroposteriorly), 2.2 mm in trigonid breadth, 1.6 mm in talonid breadth, and 3.8 mm in protoconid height above the base of the crown. The dentary is 3.3 mm in depth beneath the carnassial. M₂ measures 2.6 mm in crown length, 1.5 mm in trigonid breadth, and 1.1 mm in talonid breadth.

UM 76929 is a right dentary, probably representing the same individual as the holotype (Fig. 24B). Lower premolars P₂₋₄ are preserved intact, and the labial half of M₁ is preserved as well. P₂₋₃ have simple crowns with a single large protoconid and a small posterior basal cusp. P₄ is more complex, with a small anterior basal cusp in front of the sectorial protoconid followed by distinct hypoconid and basal hypoconulid cusps. The crowns of the premolars are crowded together with no diastemata between them. P₂ measures 2.3 mm in crown length and 1.0 mm in breadth. P₃ measures 2.6 mm in length and 1.1 mm in breadth. P₄ measures 3.4 mm in length and 1.4 mm in breadth.

The two dentaries exhibit several sharp puncture marks, suggesting that the skull to which they belonged may have been eaten by a mammalian predator.

UM 76930 preserves partial crowns (lacking bases) of P²⁻³ together with a small portion of the palate. This specimen too may be part of the same individual as UM 76928 and 76929.

Hypodigm.—Specimens here referred to *Viverravus bowni* were first described from the early Wasatchian of the Bighorn Basin, Wyoming, by Bown (1979, p. 94, fig. 54a; UW 9832), and later from the middle and late Clarkforkian of the Clark's Fork Basin, Wyoming, by Rose (1981, p. 101; UM 64713, 71578, 71579). Additional specimens from the Wasatchian of the Clark's Fork Basin include UM 75058, 75117, 75603, 75961, 75977, 79681, 80546, 83081, 83087, 86125, 86203, and 86532.

Etymology.—Named for Dr. Thomas M. Bown, who first illustrated a specimen of this species, in recognition of his many contributions to the systematics of early Eocene mammals.

Discussion.—Work in progress suggests that there are as many as eight lineages of viverravid carnivores present in the early Eocene of Wyoming. Four (possibly five) of these lineages comprise large, medium, small, and very small species of *Viverravus*. The large species is *V. politus*, the medium species is *V. acutus*, the small species is *V. bowni*, and the very small species remains to be described. *Viverravus bowni* and *V. acutus* are close in size and virtually indistinguishable in any feature other than size. These might be interpreted as different sexes of a single dimorphic species except for the fact that *V. bowni* and *V. acutus* each exhibit the variability in tooth size characteristic of *V. politus*. In addition, *V. bowni* is common in the Clarkforkian and early Wasatchian but virtually absent from the middle Wasatchian, while *V. acutus* remains common from the Clarkforkian through at least the middle Wasatchian. It would be exceptional for one sex to flourish in the absence of the other through all of middle Wasatchian time.

DISCUSSION

Charles Lyell made many contributions to paleontology. One of the least known, and most important for vertebrate paleontology, was discovery of terrestrial fossil vertebrates within the erect trunks of petrified Paleozoic trees (*Sigillaria*). "Lyell's tree," discovered in 1851 at South Joggins, Nova Scotia, was the first of many Joggins trees to yield evidence of the earliest reptiles. J. W. Dawson (1863, 1878, 1882) reported that Joggins trees ranging from one to three feet in diameter, growing on underclays and wet soils, appear to have been flooded and partially buried in argillaceous sandstone. The trees, killed by surrounding sediment, began to decompose. Tree tops above the level of surrounding sediment broke off, exposing hollow vertical cylindrical cavities at the level of the new soil surface. These vertical cavities entrapped both sediment and, occasionally, terrestrial animals including land snails ("*Pupa vetusta*"), labyrinthodonts (e.g., *Dendrerpeton*), and primitive reptiles (*Hylonomus*). Entrapment ended when the vertical cavities became full or a new flood buried all and initiated the process again. Of 25 erect tree trunks studied by Dawson (1882), ten were unproductive. The remaining fifteen trees yielded remains of land animals, fragmentary plant material, and occasional seeds or fruits. No remains of aquatic animals were found in any of the trees. Most vertebrate remains from Joggins are disarticulated, and these are often dissociated (Carroll, 1967).

Preservation of land animals in standing hollow tree trunks requires episodic flooding in a subsiding basin. Major floods must stand long enough or deposit enough sediment to kill standing trees, and major floods must be spaced in time at intervals sufficient to allow new forests to replace old ones. When one tree dies as a result of burial during episodic flooding, many of its neighbors should die as well.

Combining evidence of the shape and spacing of limestone lenses at the discovery site, evidence of the texture and fabric of lens J, and evidence of the fauna preserved in this lens, Kraus' (1985) interpretation that carbonate lenses of this type represent mineralized remains of fossil trees appears largely corroborated. There is no macroscopic evidence of petrified wood remaining in any lens at the discovery site, and it seems unlikely that woody parts of trees were involved or preserved. Limestone lenses at the discovery site are interpreted, rather, as mineralized infillings of hollow tree trunks, the trunks themselves having later decomposed without being mineralized. Macroscopic plant debris is visible in some lenses, and finely divided plant tissue is scattered throughout lens J. This is interpreted as wood and other plant tissue that fell into hollow tree trunks and survived intense bioturbation (see below).

None of the limestone lenses at the discovery site appear to be rooted in any way, lying directly over a shaly mudstone and siltstone with no intergradation nor significant penetration into this substrate. This too suggests that the lenses are probably best viewed as carbonate masses filling the hollows of

trees rather than mineralized remains of the trees themselves. A pattern of distribution like that shown in Figure 2 might result if limestone lenses formed in depressions at the site of rotting tree stumps, rather than hollow tree trunks, but there is so little silt or other detrital sediment present in lens J that this interpretation appears to be ruled out, at least in the case of vertebrate-bearing lens J.

Three problems with formation of lens J concern (1) the source of calcium carbonate composing the lens, (2) transport and deposition of the calcium carbonate, and (3) concentration of vertebrate remains. The Puercan and Torrejonian land-mammal ages (early and middle Paleocene) together comprise about 100 m of stratigraphic section in the Clark's Fork and northern Bighorn Basins. The Tiffanian (late Paleocene) is about 850 m thick, the Clarkforkian (transitional Paleocene-Eocene) is about 570 m thick, and the first half of the Wasatchian (early Eocene) is about 500 m thick. These thicknesses correspond to net rates of sediment accumulation of 20 m/my through the Puercan and Torrejonian, 130 m/my in the early Tiffanian, 280 m/my in the late Tiffanian, 280 m/my in the Clarkforkian, and 250 m/my in the early Wasatchian (Gingerich, 1983). Rates of accumulation provide some indication of basin subsidence relative to uplift of surrounding highlands, and a high rate of late Tiffanian and Clarkforkian sediment accumulation in the Clark's Fork Basin can safely be assumed to correspond to an interval of exposure and erosion of thick Paleozoic limestones in the Bighorn Range some 100 km or more to the east and the Beartooth Mountains some 30 km or more to the west. Some 700 m of a 1100 m thick Paleozoic section is limestone in the eastern Beartooths (Foose et al., 1961). Much of this was exposed to erosion during the late Tiffanian and Clarkforkian, providing a likely source of calcium carbonate in the Clark's Fork Basin.

Micritic limestones preserve little distinctive structure permitting one to distinguish calcium carbonate originating as a precipitate in carbonate-rich ground water from detrital calcium carbonate, and neither of these two possibilities can be eliminated at present. If limestone lenses at the discovery site are correctly interpreted as remnants of tree trunks and if local ground water was heavily saturated with calcium carbonate, one might expect more woody tissue to have been preserved by carbonate mineralization.

Calcium may have been transported fluvially from surrounding highlands as a component of detrital clays. Willwood mudstones include smectite-rich mixed-layer illite smectites as dominant clay minerals, which would yield calcium on weathering (Bown, 1979; Bown and Kraus, 1981a).

Alternatively, fine grained calcium carbonate filling the hollows of tree trunks at SC-29 might be eolian rather than aquatic in origin. Leeder (1975) states that a major source of carbonate needed for calccrete formation is now thought to be eolian dusts, which are often calcareous. Janecek and Rea (1983) postulated atmospheric circulation of unusually high intensity during the latest Cretaceous and Paleocene, with a significant reduction in intensity during the Paleocene-Eocene transition, all based on the median grain size of eolian sediment in deep sea cores. Intersection of high global intensity of atmospheric circulation during the Paleocene with extensive limestone exposure in the Beartooths and adjoining mountains during the latest Paleocene and early Eocene makes eolian transport of calcium carbonate from the Beartooth Mountains to the Clark's Fork Basin a possibility. This might explain why limestones appear to be common in Clarkforkian strata near the Beartooths, but rare elsewhere.

Nonfossiliferous silty limestone lenses at the discovery site contain significant contamination from windblown and/or waterlain ground sediment, with little precipitation from ground water, and these may represent hollow trees that filled rapidly, with little opportunity for accumulation of fossils. Porcelainlike lenses, on the other hand, may reflect carbonate precipitation from ground water with little or no influx of ground sediment. These may have been largely inaccessible to animals of any kind. Lens J is intermediate in preserving abundant invertebrate and vertebrate remains in a matrix of coarser, intensely bioturbated micrite that may reflect carbonate transport by both wind and ground water. The relative proportions of carbonate and detrital sand and silt filling hollow trees may reflect how high each open tree trunk stood above ground level. Trees that were not hollow probably decomposed without leaving any trace in the sedimentary record.

The fauna contributes to this interpretation in that all of the gastropods in lens J are land snails, most air-breathing pulmonates, able to live independently of perennial water. Extant *Hendersonia* are operculate helicoid prosobranchs inhabiting midcontinent North America and characterized by Shimek (1919) as “strictly a deep-woods form . . . its presence is conclusive evidence of well-developed forest conditions.” *Oreohelix*, known today as the “mountain snail,” are calciphilous, restricted to North American Western Interior habitats rich in lime, generally limestone outcrops, but also extending to loess substrates of eastern Iowa (Pilsbry, 1939: 413–415). *Microphysula* is another mountain snail of the Western Interior, preferring, in this case, humid environments (Pilsbry, 1940: 991). Extant *Discus* are holarctic in distribution, living in humid forest, under dead wood, and among rotting leaves or grass in rather wet situations (Pilsbry, 1948: 604). Extant *Pupilla* are ground snails, worldwide in distribution, living under wood and stones and among leaves in moderately humid situations (Pilsbry, 1948: 927). *Albertanella* is an extinct pupillid presumed to resemble *Pupilla* in preferred habitat. *Grangerella* and the family Grangerellidae to which it belongs are extinct. Habitats of living representatives of gastropod genera found in lens J suggest a humid microenvironment including decaying wood or leaves.

Gastropod shells are scattered randomly through lens J, and they are randomly oriented as well. Most shells are complete and filled with secondarily deposited sparry calcite rather than surrounding micritic limestone matrix. The completeness of shells precludes some forms of predation and makes it unlikely that shells were moved by predators—snails must have been living essentially where they were buried. Limited infilling with micritic matrix indicates that shells may have been occupied when buried (pulmonates do not have an operculum that might close the shell long after death). Micritic limestone matrix fills part of the outer shell whorl in some cases, and limited infilling might be explained by failure of sediment to migrate upward into higher whorls. However, this would require a uniform orientation of snails in sediment that is not observed. Limited infilling is more likely to have occurred when mobile sediment invaded the living chamber as the enclosed snail began to decompose. Taken together, these observations suggest that snails fell into the accumulating deposit or were disturbed on the surface before they were buried, yet burial followed closely after or coincided with death.

Amphibians preserved in lens J include many vertebrae of a small salamander or salamanders, and a single isolated distal humerus of a frog. Reptiles found here contribute little to understanding the origin of the deposit—anguimorph lizards are generally small, cryptic, slow moving, stalk-and-leap predators. Many modern anguids are shortlimbed and skinklike, living in forest leaf litter, which is consistent with the habitat indicated by gastropods.

Avian remains in lens J are all disarticulated, and virtually all are fractured like bones described by Bickart (1984) that were scavenged by mammalian carnivores. Long bones present here are fragmentary and filled with sedimentary matrix, indicating that they were broken before burial.

Mammalian specimens in lens J are all fragmentary, and they were so on burial. Most are lower jaws, dentaries, but several specimens include upper teeth (possibly representing the same individual animals as those known from dentaries). The multituberculate, marsupial, insectivores, bats, dermopteran, and primates preserved in lens J are all small mammals weighing 100 grams or less. The carnivore *Viverravus bowni* is larger, being about the size of a long-tailed weasel, *Mustela frenata*, and weighing 100–200 g. *V. bowni* is known from left and right dentaries and possibly a maxilla as well (all possibly, even probably, representing a single individual). Interestingly, the left dentary of *V. bowni* was broken before burial, and the anterior part of the dentary was reflected and buried adjacent to the rest of the mandibular ramus. As preserved in the rock, a freshly fractured fragment of the dentary of cf. *Leptacodon packi* lay reflected alongside the mandibular ramus, suggesting that it too was bound to the ramus by connective tissue when positioned for burial. Given the low energy, fine grained deposit in which both dentaries were found, breakage at or shortly after death (while enveloped in connective tissue) is required to explain reflection without disassociation, suggesting

mastication by predators or scavengers. Punctures preserved on both *Viverravus* dentaries, and on some other remains, are plausibly interpreted as bite marks, providing positive evidence implicating one or more small mammalian predators or scavengers. Location of a predator or scavenger's habitual feeding site above an open tree trunk would explain the concentration of vertebrate remains found within lens J.

Evidence at the SC-29 discovery site (lens J) and the *Carpolestes* skull site (described above) suggests that preservation of fossil vertebrates and land snails in some Willwood carbonates may conform to a Joggins model of accumulation in hollow tree trunks. There are differences, in that little evidence of wood or even woody plant debris is preserved in the SC-29 carbonate lenses yielding animal remains, and none of the lenses show evidence of any rooted connection to an underclay or underlying soil, but similarities appear to outweigh the differences. Walker et al. (1986) describe a Miocene fossil vertebrate locality on Rusinga Island in Kenya that they interpret as having accumulated in the hole left when a large tree rotted away, so there is at least one other precedent for the interpretation offered here.

Fossil vertebrates are found in other Willwood Formation limestones as well, representing a broad range of depositional models. Bird Quarry is similar in some respects, but different in the shape of the whole deposit, the rarity of snails, the size and freshness of burrows, and the presence of an extensive network of rootlets. The remaining three limestones described above were all deposited in moving water: the *Ectocion* limestone involved slow burial in current winnowed quartz and carbonate sand, the unionid coquina involved deposition in a larger perennial stream, and the calcirudite probably involved reworking of soil nodules by a more ephemeral transient stream.

ACKNOWLEDGMENTS

I thank W. S. Bartels and J. A. Gauthier for help in identifying lizards, K. E. Campbell and R. W. Storer for examining avian material, and B. H. Wilkinson for comments on thin sections. M. C. McKenna (American Museum of Natural History, New York) and J. A. Lillegraven (University of Wyoming Geological Museum, Laramie) provided access to comparative material, and D. E. Russell (Muséum National d'Histoire Naturelle, Paris) provided casts of early Eocene chiropterans. I am indebted to T. M. Bown, G. F. Gunnell, K. D. Rose, and J. G. M. Thewissen for thorough reading of the manuscript. I also thank W. J. Ryan for preparing specimens, George Junne for photography, and Karen Klitz for artwork. This research was completed during tenure of National Science Foundation grant BSR 86-07841.

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