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PALEOECOLOGY AND PALEONTOLOGY OF THE LOWER CRETACEOUS KIOWA FORMATION, KANSAS

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ABSTRACT

The Lower Cretaceous (Comanchean) Kiowa Formation at most places in central and southern Kansas overlies Permian rocks unconformably, and underlies the Dakota Formation with apparent unconformity. Four fossil zones—***Venezoliceras kiowanum*** Zone, ***Adkinsites bravoensis*** Zone, ***Inoceramus comancheanus*** Zone, and ***Inoceramus bellvuensis*** Zone—verify correlation of the lower Kiowa with the Goodland through Denison Formations in Texas. Six lithofacies contain fossils: dark-gray shale; tan mudstone; thin-laminated sandstone; thin-bedded sandstone; mottled sandstone; and shell conglomerate.

Kiowa fossil assemblages are preserved 1) in place or in the neighborhood where the fossils lived or 2) as transported assemblages. Mixed assemblages contain species representing several substrates.

Relative abundance data, accurate stratigraphic and geographic distribution data, and the Jaccard coefficient define ten recurring associations of abundant or unique species. The fossil associations are named: *Nuculana;* corbulid-breviarcid; *Trachycardium-Turritella;* pteriid-mytilid; *Gryphaea; Cyprimeria; Crassostrea; Lopho quadriplicata; Brachidontes;* and trace fossil associations. Each comprises species distinguished by similar feeding and dwelling habits and substrate preferences. Because the assemblages have paleoecologic consistency, they represent parts of ancient communities and can be compared with modern marine benthic communities. Interspecific relationships of predation, trophic levels, competition, and commensalism were not unlike those of present-day marine communities. The climate during transgression and regression of the Kiowa sea was humid, tropical to subtropical. The sea in the nearshore, central Kansas area was shallower and less saline than in the offshore southern Kansas region.

INTRODUCTION

LOCATION AND GEOLOGIC SETTING

The Kiowa Formation, of Early Cretaceous (Comanchean) age, crops out in central and southern Kansas on the eastern edge of the Dissected High Plains physiographic province. Two extensive outcrop areas are separated by 80 miles of Quaternary deposits that conceal the unit. The larger one, in central Kansas, is discontinuous and trends northeast-southwest; several outliers lie to the east. The southern Kansas belt trends east-west (Fig. 1).

In central Kansas the Kiowa is 100 to 125 feet thick, and dominant lithologies are dark-gray shale and brown sandstone. The Kiowa disconformably overlies Permian rocks and at least locally is disconformable beneath the Dakota Formation. Northward the outcrop narrows and in Washington County the Kiowa is overlapped by the Dakota.

Shale generally underlies hummocky, grassy slopes, and sandstone forms more resistant ledges that cap part of the Smoky Hills region. Good exposures generally are incomplete and widely separated. Only one complete section of the Kiowa was found in central Kansas. Outcrops at some localities consist of float from resistant strata. Best exposures were seen on banks of streams and lakes.

In southern Kansas the Kiowa Formation is more than 250 feet thick in drill holes (Latta, 1946). But exposures consist only of partial sections. Dominant lithologies are dark-gray shale with intercalated, thin, shell conglomerates and sandstones. The upper part of the sequence consists of brown sandstone. In Kiowa County, the type area, the Kiowa is generally conformable on the underlying Cheyenne Sandstone; and in Clark and Comanche counties it is disconformable over Permian rocks. The relation between the Kiowa and the overlying Dakota is not clear because the contact is known only from one locality in Kiowa County. In most places Tertiary or Pleistocene rocks disconformably overlie the eroded Kiowa.

The formation records an onlap-offlap sequence. The Early Cretaceous sea advanced from south to north, progressively overlapping older Permian rocks. At many localities a very thin silty or sandy basal zone marks the initial Cretaceous deposition. Retreat of the sea is indicated by development of sublittoral, nearshore sandstones and claystones in the upper part of the section. The continental Dakota Formation overlies the Kiowa with apparent unconformity.

The central Kansas outcrop area lies on the southeastern edge of the buried Central Kansas Uplift and

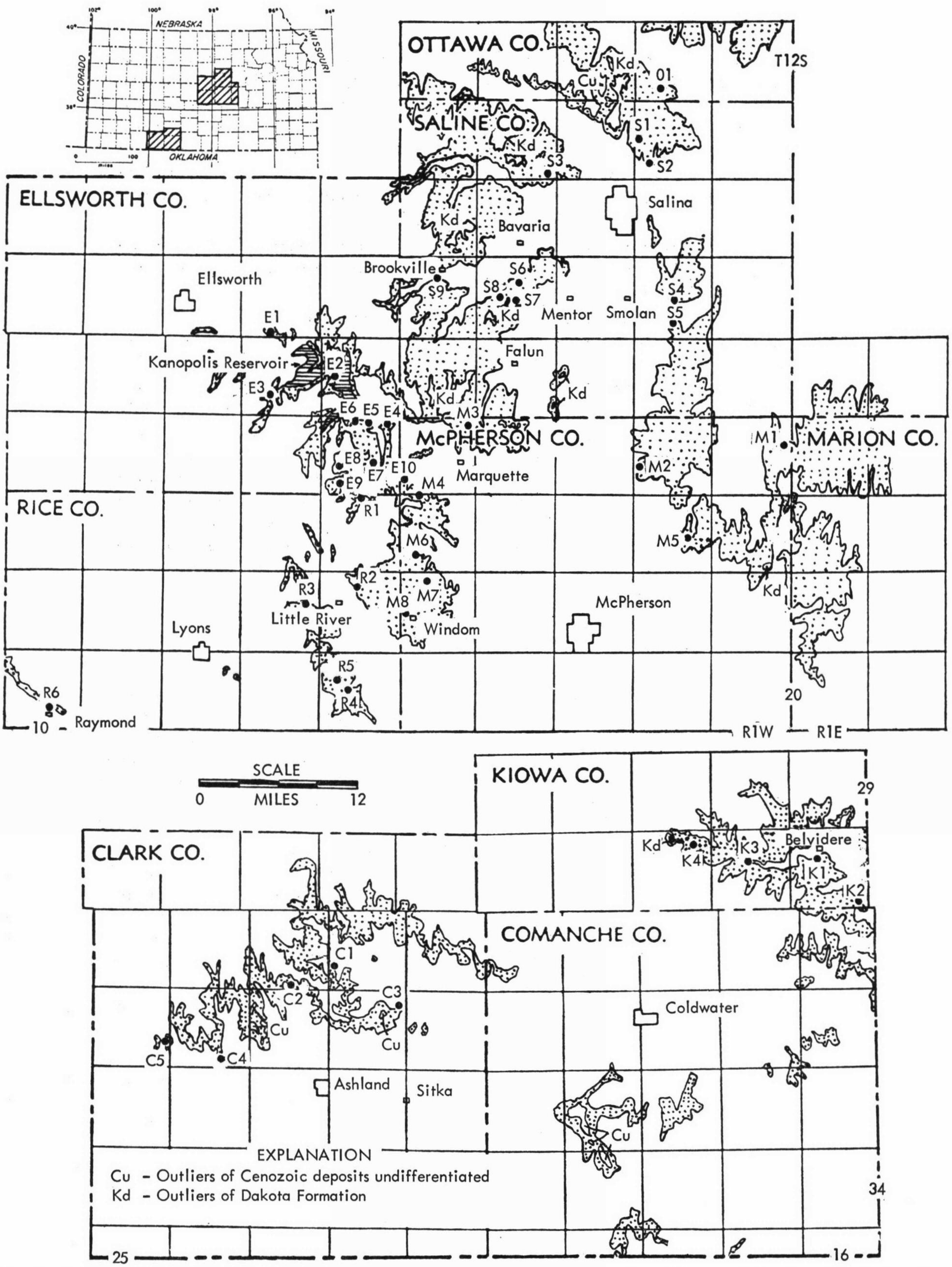


FIG. 1. Outcrops of the Kiowa Formation (stippled pattern) in parts of central and southern Kansas and location of studied sections.

trends northeastward into the area underlain by the Salina Basin. Regional dip on the top of the Dakota Formation is to the north about 7 feet per mile (MERRIAM, 1963). Minor folds and faults have been mapped by FRANKS (1966). The Kiowa outcrop in southern Kansas lies on the eastern margin of the Western Kansas Basin, and the gentle regional dip is to the northwest.

PREVIOUS WORK

CRAGIN (1894b) named the dark- and light-colored shale overlying the Cheyenne Sandstone or Permian rocks in southern Kansas the Kiowa shales. By 1900 the stratigraphy and paleontology of these Lower Cretaceous rocks were relatively well known. The history of discovery of the Kiowa fauna was reviewed by TWENHOFEL (1924). Suffice it to mention the major contributions. CRAGIN (1894b, 1895a,b) summarized stratigraphy (Fig. 2), lithology, and paleontology of the Kiowa Formation. He correlated "Mentor beds" in central Kansas with the upper Kiowa of southern Kansas. The "Champion shell bed" in southern Kansas was correlated with the middle part of the Fredericksburg Group in Texas; the lower Kiowa shales were correlated with the Kiamichi Formation; and the upper Kiowa ("Tucumcari shale") was correlated approximately with the Duck Creek Formation of the Washita Group.

HILL (1895) compared the Kiowa fauna with the Comanchean fauna of Texas and concluded that the Kiowa "represents the modified attenuated northern extension of the Washita division and probably a portion of the Fredericksburg division" (p. 234). He suggested that many of the 23 species found only in the Kiowa and not in the Texas equivalent represent "the naturally denser [more diverse?] population of the more northern shallower littoral" waters (p. 225).

PROSSER (1897) described most of the outcrops of the Kiowa and thoroughly reviewed the previous literature.

The next major synthesis of Kiowa studies with new petrologic and paleontologic data was by TWENHOFEL (1924). He followed GOULD's (1898) stratigraphic classification (Fig. 2) in southern Kansas and established three new members for the central Kansas section. He judged the reddish sandstone with fossil plants, stratigraphically below marine Kiowa strata, to be continental "Dakota" equivalents. In this interpretation the Kiowa and "Dakota" Formations were considered to be in part lateral facies equivalents and in part vertical facies successions. TWENHOFEL correlated the Kiowa with the Washita, while acknowledging the "Fredericksburg aspect" of the fauna. Sixteen new species were described and many of CRAGIN's (1894b), MEEK's (1871), and WHITE's (1880) Kiowa species were redescribed. TWENHOFEL concluded that the lower Kiowa was deposited in a shallow, restricted, marine basin with intermittent connections to the south; "tidal action was probably insignificant" (p. 41). During a southward retreat of the sea, deltaic and lagoonal deposits in central Kansas extended over the marine sediments; the upper Kiowa "Mentor beds" were deposited during a second marine transgression. Final regression was followed by continental deposition of the post-Kiowa "Dakota." All of this occurred in an arid or semiarid climate.

These interpretations were largely accepted by REESIDE (1957), who emphasized the periodic influx of normal marine waters with a Kiamichi fauna and a subsequent killing of the fauna by stagnant waters. This alternation of oxygenated and stagnant waters was postulated to explain the alternation of shell conglomerates and dark-gray shale. He interpreted the climate to be mild and perhaps subtropical.

Stratigraphic nomenclature of the Kiowa and related rocks in southern Kansas was completely reviewed by LATTA (1946). He redefined the Kiowa and suppressed all member names (Fig. 2) because these units could not be recognized outside of their type localities.

The latest review of stratigraphic nomenclature was published by FRANKS (1966), who changed the name from Kiowa Shale to Kiowa Formation in recognition of its lithologic heterogeneity. He mapped the Kiowa and studied in detail the petrology and stratigraphy of its rock units.

Foraminifera from Kiowa shales in southern Kansas have been described by LOEBLICH & TAPPAN (1950). None were found in the Cheyenne Sandstone or in the Dakota ("Kirby clays"). The fauna contains 27 species, among which the 14 arenaceous forms are far more abundant than the calcareous ones. *Ammobaculites* and *Trochammina* are the most abundant genera; the 7 species of Lagenidae are rare; one planktonic species is common in some samples; and most calcareous species are very small. LOEBLICH & TAPPAN concluded that this assemblage was adaptable to a wide range of conditions and that it represents a brackish marine environment. The few stratigraphically restricted species in the fauna are characteristic of the Goodland and Kiamichi Formations in Texas. Unfortunately, exact local ranges in Kansas cannot be determined because stratigraphic positions of the samples were not reported.

APPROACHES AND STUDY OBJECTIVES

Because the Kiowa Formation is thick, widely distributed, and relatively well known, it is suited for an integrated paleoecologic study. Three approaches were combined with the hope of achieving this synthesis. First, the lithology and mode of fossil occurrence of each sampled unit were described in order to interpret the mode of origin of the fossil assemblage. Second, fossil associations were defined on the basis of their geographic and stratigraphic distribution and the relative abundance of each species. Third, the feeding and dwelling habits and substrate preferences of the fossil species were interpreted by comparing them with modern and fossil relatives. Then, if associated species had similar or related habitats, the fossil associations would represent parts of ancient communities. The associations are compared with modern marine communities for additional environmental implications. This integrated approach leads to reconstruction of the ancient communities of a given area and stratigraphic unit.

Major objectives of the study were to review and update the systematics and nomenclature of the fauna, to obtain accurate geographic and stratigraphic distributional data, to describe the mode of occurrence and relative abundance of the taxa, and to synthesize the literature on the flora and vertebrate fauna. Techniques such as use of the Jaccard coefficient of association and SIMPSON's diversity coefficient were applied to this study. These data are the bases for revised paleoecological interpretations of the Kiowa Formation in Kansas.

VERTEBRATE PALEONTOLOGY

The Kiowa Formation contains a relatively large and varied vertebrate fauna which has been reported in many scattered publications. A synthesis of this literature is presented in Table 1. No attempt was made by me to evaluate quality of the paleontologic work, but the validity of some generic names was confirmed by DAVID H. DUNKLE at the U.S. National Museum. Additional information about Kiowa vertebrates was kindly provided by THEODORE EATON, JR., vertebrate paleontologist at the University of Kansas, and by MYRL WALKER and ORVILLE BONNER, vertebrate paleontologists at Fort Hays Kansas State College, where my collection of vertebrates has been deposited.

In general, the taxonomic diversity of plesiosaurs, sharks, and fishes is moderate, and reptile species other than plesiosaurs are few. Rocks in southern Kansas have yielded the greatest number of specimens and species; central Kansas has yielded only a few species of crocodiles and sharks. Fish scales are relatively common in shale in both areas. Plesiosaur remains are more common, weathering out of dark-gray shale in the lower Kiowa of southern Kansas; shark teeth were seen commonly in shell conglomerate and sandstone. The paleoecologic significance of these vertebrates is discussed in a later section.

PALEOBOTANY

Reports of fossil plants from what is now called the Kiowa Formation are few and difficult to separate from reports of the "Dakota" flora. CRAGIN (1890) and GOULD (1900) reported fossil leaves associated with shark teeth and fish vertebrae from upper Kiowa sandstones 12 miles northwest of Ashland, Clark County. The locality is at the head of West Bear Creek about 3 to 4 miles northwest of Locality C2. SWINEFORD (oral communication, 1966) mapped this area as Kiowa and did not recognize Dakota Formation strata in Clark County. A "Dakota-type" flora consisting of three species of *Eucalyptus,* one laurel, and unidentified specimens of poplar, oak, willow, and fig, among others, were reported from Chatman Creek in the same area (GOULD, 1900; TWENHOFEL, 1924). In McPherson County at the Natural Corral locality (M4), GOULD (1900) and TWENHOFEL (1924) found dicotyledon leaves in sandstone 47 feet above the base of the Kiowa and 45 feet below the uppermost fossiliferous sandstone ("Mentor bed"). PROSSER (1897, p. 187) reported leaves from Kiowa sandstone capping a butte southwest of Falun, sec. 9, T. 16 S., R. 4 W.

LESQUEREUX (1892) monographed the flora from the Dakota Formation in Kansas, and only one of his localities could possibly be from the Kiowa Formation. This is described simply as being 8 miles north of the Salina railroad station and 8 miles above the mouth of the Saline River and is in an area in which both Kiowa and Dakota are present (FRANKS, 1966). O. S. FENT (oral communication, 1965) has seen plants in this area in what he calls Kiowa sandstone. LESQUEREUX reported one conifer and 12 dicotyledons from this area.

Two new plant fossil localities were found by me in the Kiowa. At Locality S7 in the middle Kiowa a few incomplete leaves that could not be identified were associated with bivalves and a vertebra. In Ellsworth County, NW SE sec. 14, T. 16 S., R. 6 W., FRANKS collected several nearly complete dicotyledon leaves from the uppermost part of the Kiowa. Amber was reported from the upper Kiowa in sec. 18, T. 16 S., R. 6 W., Ellsworth County (LANGENHEIM, BUDDHUE, & JELINEK, 1965).

The more abundant flora of the Cheyenne Sandstone in Kiowa County contains 23 species: four ferns, one cycadeoid, four coniferophytes, and 11 angiosperms (BERRY, 1922). The climate represented by this flora was "warm and more or less arid," and deposition was on "a wide sandy coastal plain or fluctuating beaches backed by dunes, and . . . farther inland a more varied and normal flora existed" (BERRY, 1922, p. 203). He concluded that the age of the Cheyenne flora was Late Cretaceous but older than the Dakota and Woodbine floras.

STRATIGRAPHY AND CORRELATION

On the basis of the section at the Natural Corral area (Loc. M4) TWENHOFEL (1924) divided the Kiowa in central Kansas into four members (Fig. 2) to "designate the occurrence of fossils and the stratigraphic posi-

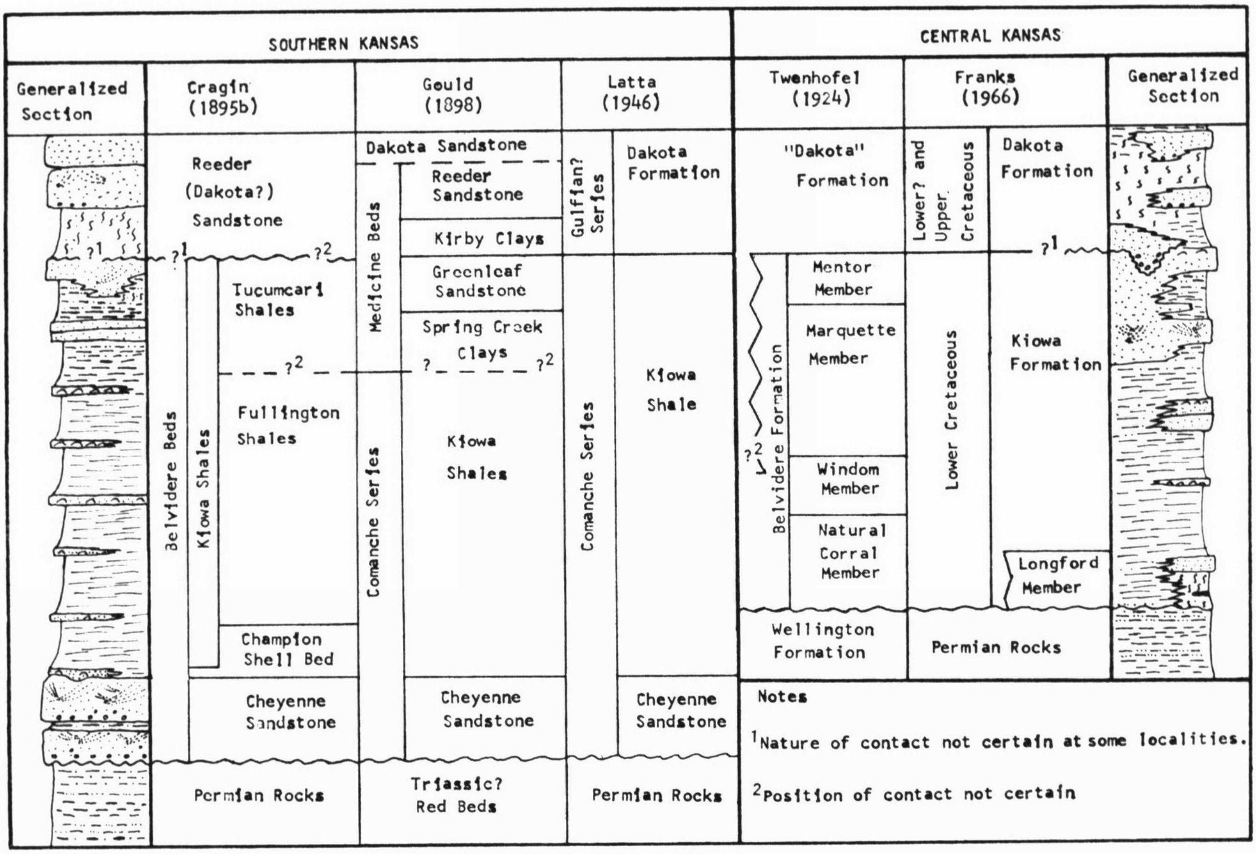


FIG. 2. Generalized columnar sections and stratigraphic nomenclature of Lower Cretaceous rocks in Kansas.

tion of exposures" (p. 31). The names have been abandoned because the units do not occupy the same stratigraphic position elsewhere, and in fact may occur in several parts of the same section, and because fossils are found elsewhere in the section. Frank's (1966) classification is adopted here, although his Longford Member does not occur in any of the studied sections and is not known to contain fossil shells.

St. John (1887) and Cragin (1889a) first recognized that the Kiowa fauna was similar to that of the Comanchean Series in Texas. Most recently Cobban & Reeside (1952a) correlated the Kiowa with uppermost Fredericksburg and lowermost Washita strata.

New detailed information on the stratigraphic distribution of species in the Kiowa and the discovery of *Inoceramus bellvuensis* permit the development of a faunal zonation resulting in a more precise correlation of the Kiowa with the Texas section (Fig. 3).

Previously I have defined three zones in the Kiowa of Kansas (Scott, 1967a, b). Additional collecting in Kansas and new materials from Oklahoma, New Mexico, and Colorado have led to redefinition of these zones and recognition of an additional zone. The four concurrent range zones, now being described (Scott, in press), in ascending order are the *Venezoliceras kiowanum* Zone, *Adkinsites bravoensis* Zone, *Inoceramus comacheanus* Zone, and *Inoceramus bellvuensis* Zone. The ranges of stratigraphically useful fossils and their occurrence in each of the zones are given in Figure 3.

The *Venezoliceras kiowanum* Zone is limited to the basal few feet of the Kiowa in southern Kansas. It ranges from a featheredge to 1.5 feet thick in Kiowa County, thickens southward, and is not recognized north and west of Kiowa County. This zone is time equivalent with the upper part of the *Manuaniceras powelli* Zone of Young (1966) in north Texas. The *M. powelli* zone occurs in the lower Duck Creek, and the zone is probably Goodland Limestones. Recognition of the *V. kiowanum* Zone clarifies Cragin's (1895b) attempt to establish the "Champion Shell Bed" as a separate stratigraphic unit because of its faunal relations with the Fredericksburg Group.

The *Adkinsites bravoensis* Zone is about 60 to 70 feet thick in southern Kansas. Young (1966) identified this zone in Kansas by the presence of *A. bravoensis* and *Manuaniceras descernae;* this zone occurs in the Kiamichi of Texas.

TABLE 1. *Species of Vertebrata Reported from the Kiowa Formation.*

[Taxonomic classification after ROMER (1945, 1966). Range in feet above base of the Kiowa given where known.]

SPECIES; AUTHOR OF REPORT	MATERIAL	LOCALITY	RANGE	PALEOECOLOGY
Class REPTILIA Subclass ANASPIDA Order CHELONIA (Cope, 1894; Williston, 1894; Gould, 1929)	Bone fragments; scapula-precoracoid of a large species	Bluff Ck., Clark Co.; Belvidere; Ft. Supply, Okla.	0-100	Amphibious scavenger or herbivore
Subclass EURYAPSIDA Order SAUROPTERYGIA Suborder PLESIOSAURIA Family PLIOSAURIDAE				
?Brachauchenius sp. (Williston, 1903)	Jaw fragment collected by M. Walker & O. Bonner, Ft. Hays College	12 mi. No. of Sitka, Clark Co.	Uncertain	Carnivore
Family POLYCOTYLIDAE				
Cimoliasaurus sp. (Williston, 1894; Gould, 1929)	Few disassociated vertebrae	Bluff and Sand Ck., Clark Co.	0-100	Carnivore
Trinacromerum sp.	Complete humerus collected by M. Walker & O. Bonner, Ft. Hays College	Clark Co.	Uncertain	Same
Family PLESIOSAURIDAE				
Plesiosaurus? mudgei (Cragin, 1894c; Williston, 1897; Gould, 1929; Williston, 1903)	Several vertebrae, KUMVP 1305	Bluff Ck., Clark Co., Belvidere	Uncertain	Same
P.? gouldii (Williston, 1897; Gould, 1929)	Several vertebrae; larger than *P.? mudgei*	Clark Co.	Uncertain	Same
Plesiosaur fragments (Cope, 1894)	A vertebra	Ft. Supply	0-30±	Same
Subclass ARCHOSAURIA Order CROCODILIA Suborder MESOSUCHIA Family GONIOPHOLIDAE				
Goniopholis [*Hyposaurus*] *vebii* (Cope, 1872)	Vertebra from well	Brookville	0-50±	Amphibious carnivore
Dakotasuchus kingi (Mehl, 1941)	Incomplete articulated skeleton in concretion, partly weathered, 10-12 feet long	Exact locality unknown, SE of Salina, near Kipp (O. S. Fent, oral com., 1966)	Uncertain	Amphibious carnivore
D. sp. cf. *D. kingi* (Vaughn, 1956)	Dorsal scute (KUMVP 9971)	18-16S-6W, Smoky Hill R.	Upper Kiowa	Same
Crocodile fragments (Cope, 1894; Williston, 1894; Gould, 1929)	Vertebrae and femur	Ft. Supply; Ashland	Lower Kiowa	Same
Reptilian vertebra (Hill, 1895)		Kiowa Co., 36-30S-16W	70-90	
Dinosaur fragments (Lane, 1946)		Clark Co.	Uncertain	
Class CHONDRICHTHYES Subclass ELASMOBRANCHII Order SELACHIA Suborder GALEOIDEA Family CARCHARIIDAE				
Scapanorhynchus? sp. (Lane, 1944)	Teeth of "goblin shark"	Clark Co.	Uncertain	Carnivore on fish, mollusks, crustaceans
Family ISURIDAE (LAMNIDAE)				
Lamna quinquelateralis (Cragin, 1894c)	A single vertebra that Williston (1900) thought may go with some teeth	Belvidere	0-20	Carnivore on fish
Lamna? occidentalis (Williston, 1894)	A single tooth	Bluff and Sand Ck., Clark Co.	0-100	Same

TABLE 1. *(Continued.)*

SPECIES; AUTHOR OF REPORT	MATERIAL	LOCALITY	RANGE	PALEOECOLOGY
Lamna sp. (Cope, 1894; Hill, 1895; Williston, 1900)	Two types of teeth; several teeth	Ft. Supply; Clark Co.; 36-30S-16W	Lower Kiowa	Same
"Probable Isuroid affinity" (Dunkle, written communication, 1965)				
Leptostyrax bicuspidatus (Williston, 1900)	Two teeth (USNM 1979)	SW of Marquette 4½ miles	Uncertain	Carnivore on fish
Family SCYLIORHINIDAE				
Scyliorhinus [*Scyllium*] *rugosum* (Williston, 1900)	Several teeth	Greenleaf Ranch, Kiowa Co.	"Greenleaf sandstone," Upper Kiowa	Carnivore on mollusks and crustaceans
S. planidens (Williston, 1900)	Same	Same	Same	Same
S. [*Lamna?*] *gracilis* (Williston, 1900)	Same	Same	Same	Same
Shark teeth; Gould, 1900		Kiowa and Clark Co.	"Greenleaf" Upper Kiowa	
Suborder HYBODONTOIDEA				
Family HYBODONTIDAE				
Hybodus clarkensis (Cragin, 1895b)	Undescribed teeth	So. Kansas	0-150	Carnivore
Class OSTEICHTHYES				
Subclass ACTINOPTERYGII				
Infraclass HOLOSTEI				
Order SEMIONOTIFORMES				
Family SEMIONOTIDAE				
Lepidotes sp. (Cope, 1894; Williston, 1900)	Scales, teeth, scute (USNM 1063)	Ft. Supply; Central Kansas	Uncertain	Carnivore on mollusks; or herbivore
Order PYCNODONTOIDEA				
Family PYCNODONTIDAE				
Coelodus brownii (Cope, 1895; Williston, 1900; Lane, 1944)	Part of mandibular ramus with teeth	Ft. Supply; Belvidere	Uncertain	Carnivore on mollusks
C. stantonii (Williston, 1900; Lane, 1944)	Fragment of lower jaw with teeth	Belvidere	Uncertain	Same
Gyroconchus [*Mesodon*] *abrasus* (Cragin, 1894b)	Several teeth; Williston (1900) thought it was *Coelodus* or *Lepidotes*	Belvidere	15-60	Probably same
Uranoplosus? arctatus (Cope, 1895)	Teeth; generically undeterminable pycnodont teeth (Dunkle, written communication, 1965)	Ft. Supply	Lower Kiowa	Probably same
U.? flectidens (Cope, 1895)	Teeth and palate	Ft. Supply	Lower Kiowa	Probably same
Infraclass TELEOSTEI				
Superorder OSTEOGLOSSOMORPHA				
Order OSTEOGLOSSIFORMES				
Suborder ICHTHYODECTOIDEI				
Family ICHTHYODECTIDAE				
Xiphactinus? [*Portheus*] sp. (Williston, 1894)	A single chirocentrid vertebra	Bluff Ck., Clark Co.	0-100	Carnivore on fish

The overlying *Inoceramus comancheanus* Zone is distinguished by the overlapping ranges of *Engonoceras belviderense, Lopha quadriplicata,* and *Pteria salinensis,* and by the top of the *Gryphaea corrugata* range. The zone is 40 to 50 feet thick in southern and central Kansas. It is not recognized in Texas, but *I. comancheanus* occurs in the lower Duck Creek, and the zone is probably equivalent to part of the Duck Creek.

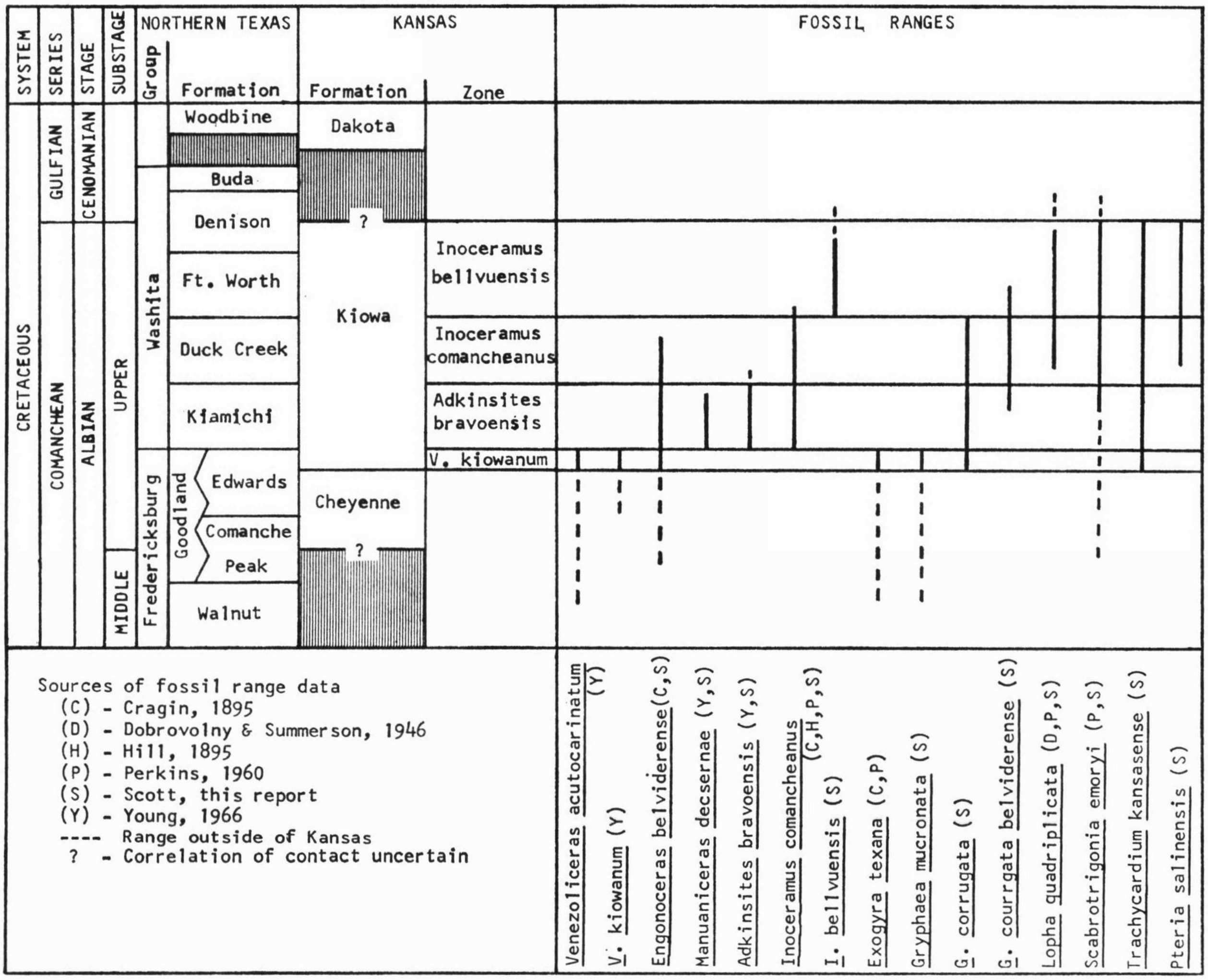


FIG. 3. Faunal zones and correlation of Kiowa with the Texas Lower Cretaceous section.

The uppermost Kiowa zone is the *Inoceramus bellvuensis* Zone, which extends to the top of the Kiowa in southern and central Kansas. Its thickness ranges from 60 to 150 feet. Correlation of the zone in Kansas with the Texas sequence is uncertain because of the lack of guide fossils. However, the presence of *Lopha quadriplicata* suggests that the zone is equivalent to the lower Denison Formation. In the Front Range Kauffman (written communication, December, 1967) reports that *I. bellvuensis* ranges into the lowermost part of the Cenomanian. In Kansas it is likely that the Albian-Cenomanian boundary belongs within the erosional vacuity between the Kiowa and Dakota Formations.

ACKNOWLEDGMENTS

I am very grateful to Curt Teichert, Department of Geology, University of Kansas, for his encouragement and stimulating ideas. During the summer of 1966 this study was helped greatly by award of a traineeship from National Science Foundation grant GB-4446X to the University of Kansas and by a grant in support of field expenses from the same source. The Kansas State Geological Survey through W. W. Hambleton generously provided much of the field expense, and helped in many other ways. Roger L. Kaesler kindly wrote the computer program for colculating the Simpson diversity coefficient and loaned his program for the Jaccard coefficient. I thank Norman F. Sohl, of the U.S. Geological Survey, for patiently looking at most of the fauna, for identifying many gastropod specimens, for reviewing the systematic descriptions of the Gastropoda and Ostreidae, and for many stimulating ideas. Paul C. Franks gave me an insight into the stratigraphy and petrology of the Kiowa and offered many suggestions and ideas.

KIOWA FOSSIL ASSEMBLAGES AND ASSOCIATIONS

The group of fossil specimens that occurs in particular strata at a given locality makes up a fossil assemblage (Fagerstrom, 1964). Its mode of occurrence is the basis for interpreting the mode of origin of each assemblage. Distinct from the modes of occurrence and origin of any assemblage of specimens is its taxonomic composition, which serves to define fossil associations. Fossil associations are defined by relative abundance data and in this way are similar to Petersen's statistical communities (Thorson, 1957) and to the assemblage zones of Waage (1964).

MODES OF OCCURRENCE OF KIOWA FOSSIL ASSEMBLAGES

The mode of occurrence of a fossil assemblage includes the kind of preservation of the fossils, their orientation, and their relations with other specimens in the rock. This description logically precedes interpretation of the origin of the assemblage. Johnson (1960) evaluated 11 descriptive properties of fossil assemblages as they relate to the origin of those assemblages. Eight of these properties proved meaningful in describing fossil assemblages in the Kiowa and served to distinguish four modes of origin (Table 2). The properties are discussed in an order that might be followed in describing an outcrop.

TEXTURE, STRUCTURE, AND SHAPE OF SEDIMENTARY BODY

Purdy (1964) related grain size of sediments to faunal communities and dwelling habits, concluding that deposit-feeders are dominant in clayey to silty substrates, and that suspension-feeders are dominant in sandy substrates. McKee (1964) reviewed the environmental significance of stratification, and his definitions of various types of stratification are followed here. The section on lithofacies presents in detail the rock types and their relations.

DISPERSAL OF FOSSILS

The dispersal patterns of fossils in rocks are described as random, uniform, or clumped. These patterns have limited interpretative value in paleoecology (Johnson, 1960; Fagerstrom, 1964); they are convenient descriptive categories, however, that provide some picture of the three-dimensional disposition of fossils in the rock.

DENSITY OF FOSSILS

Density of fossils in the assemblages has been described by Johnson (1960) and Fagerstrom (1964). It is a descriptive property that rarely has the ecologic signicance it does in Recent communities. Relative terms based on visual estimation are used, "many" being employed where fossils cover more than 50 percent of unit outcrop areas, "some" where they cover 10 to 50 percent, and "few" where they cover less than 10 percent. Where dispersal in the rock is clumped, density of both the aggregates within the rock unit and of the fossils within the aggregates are indicated.

ORIENTATION OF FOSSILS

Attitudes of the commissural plane of nearly equilateral bivalves and of the spiral axis of turreted gastropods in relation to stratification surfaces of beds containing fossil specimens define their orientation surfaces. Johnson (1960) and Ager (1963, p. 81) concluded that most preferred orientations result from current action, and that deviations from the norm may be caused by interference of adjacent particles. Nagle (1967) experimentally showed that orientation of shells by waves is characterized by two maxima parallel to the wave front, that the long direction of most shells points into the direction of wave progression, and that current-oriented shells show single or multiple maxima. Toots (1965) demonstrated on theoretical grounds that most truly random orientations "can be attributed to the activity of burrowing organisms."

The azimuthal orientation of *Turritella* was measured at several Kiowa localities on one or several bedding planes, and data were plotted on circular histograms (Fig. 4). Most of these show a pair of dominant maxima and one or two secondary maxima at nearly right angles to the dominant pair. Such patterns suggest the influence of wave action. Figure 4 shows multiple maxima, some of which are paired, suggesting effects of complex currents.

DISSOCIATION OF HARD PARTS

The percentages of articulated and disarticulated valves, and of right and left inequilateral valves among Kiowa fossils were calculated. Articulated specimens were counted as two valves. Johnson (1960) and Fagerstrom (1964) have pointed out various complications in using such data to interpret energy conditions. On the other hand Boucot, Brace, & DeMar (1958) employed the disarticulation ratio to interpret relative distances of transport. Many bivalves become disarticulated soon after death even without buffeting, so that proportions of articulated valves would be a function of rate of burial, amount of post-mortem disturbance, and nature of shell articulation. An additional factor affecting this ratio is the selective destruction of the less robust valve of inequivalved species. The left to right valve ratio of inequilateral species, however, should indicate whether current sorting and selective transportation occurred (Kornicker, Wise, & Wise, 1963).

TABLE 2. *Modes of Occurrence and Origin of Fossil Assemblages in the Kiowa Formation and Their Descriptive Criteria.*

Modes of origin Modes of occurrence		IN-PLACE ASSEMBLAGE	DISTURBED-NEIGHBORHOOD ASSEMBLAGE	TRANSPORTED ASSEMBLAGE	MIXED ASSEMBLAGE OF ANY TYPE
Lithologic characteristics		shale, sandstone; stratification indistinct	sh., ss., shell cgl.; stratification and minor structures variable	sandstone, shell cgl.; regular and current stratification	criteria characteristic of particular mode of origin
Dispersion and density of fossils		uniform-random; some-many	uniform, random or clumped; few, some, many	uniform-random some, many	as above
Orientation of fossils	Convex up	commonly	commonly	not commonly	as above
	Convex dn	commonly	commonly	commonly	
	To bedding	attached as in life	subparallel-random	subparallel	
	Vector	not commonly	not commonly	commonly	
Dissociation of hard parts	Art:dis	nearly equal	most disarticulated	disarticulated	as above
	L:R	nearly equal	nearly equal	not equal	
Fragmentation of remains		many whole shells and some fragments	many whole shells and some gragments	many fragments	as above
Size-sorting of abundant species or of entire assemblage		poor-moderate	poor-moderate	poor-well	as above
Interpreted ecologic consistency of fauna		homogeneous	homogeneous	homogeneous	heterogeneous

FRAGMENTATION OF REMAINS

Fragmentation refers to the breaking of shells and separation of the fragments by physical processes or by organisms. JOHNSON (1960) showed that fragmentation is characteristic of most assemblages transported or disturbed by current action. An accurate ratio of fragments to whole shells is difficult to determine in the Kiowa assemblages because weathering and collecting have caused additional breakage. A qualitative statement of the ratio of fragments to whole specimens of each species is useful (*see* Table 2). "Many" as applied to fragments indicates that more than 30 percent of the specimens are broken, and "some" indicates less than 30 percent; in various assemblages no distinction between breakage by currents or by weathering and collecting is possible.

SIZE-SORTING OF ABUNDANT SPECIES

Unless an assemblage is preserved undisturbed in its habitat, size-frequency distribution tells very little about the living populations (OLSON, 1957). Because of many factors affecting size-frequency distribution, it cannot be a criterion basic to interpretation of the mode of origin of the assemblage. However, the relative degree of size-sorting of each abundant species and of the entire assemblage is a descriptive property, and may suggest post-mortem factors affecting an assemblage, as does the sorting of other sedimentary particles. If an assemblage is obviously not in life position and is well sorted, it may have been transported; a poorly sorted assemblage not in place may not have been moved far from its life habitat. Thus this parameter may support an interpretation based on other characters. A well-sorted assemblage contains mainly almost equal-sized specimens of each species; a moderately sorted assemblage contains some specimens of different sizes; and a poorly sorted assemblage contains a wide range in size of specimens.

FAUNAL COMPOSITION

Fossil species that preferred the same type of substrate and general overall habitat (i.e., set of physical conditions; KENDEIGH, 1961) and are preserved together in that substrate probably lived in the area or neighborhood where they are preserved. Generally they are not in life position and have been reoriented by currents or by organisms. This is an ecologically homogeneous assemblage. Species perserved together and suggestive of different substrates form an ecologically heterogeneous assemblage.

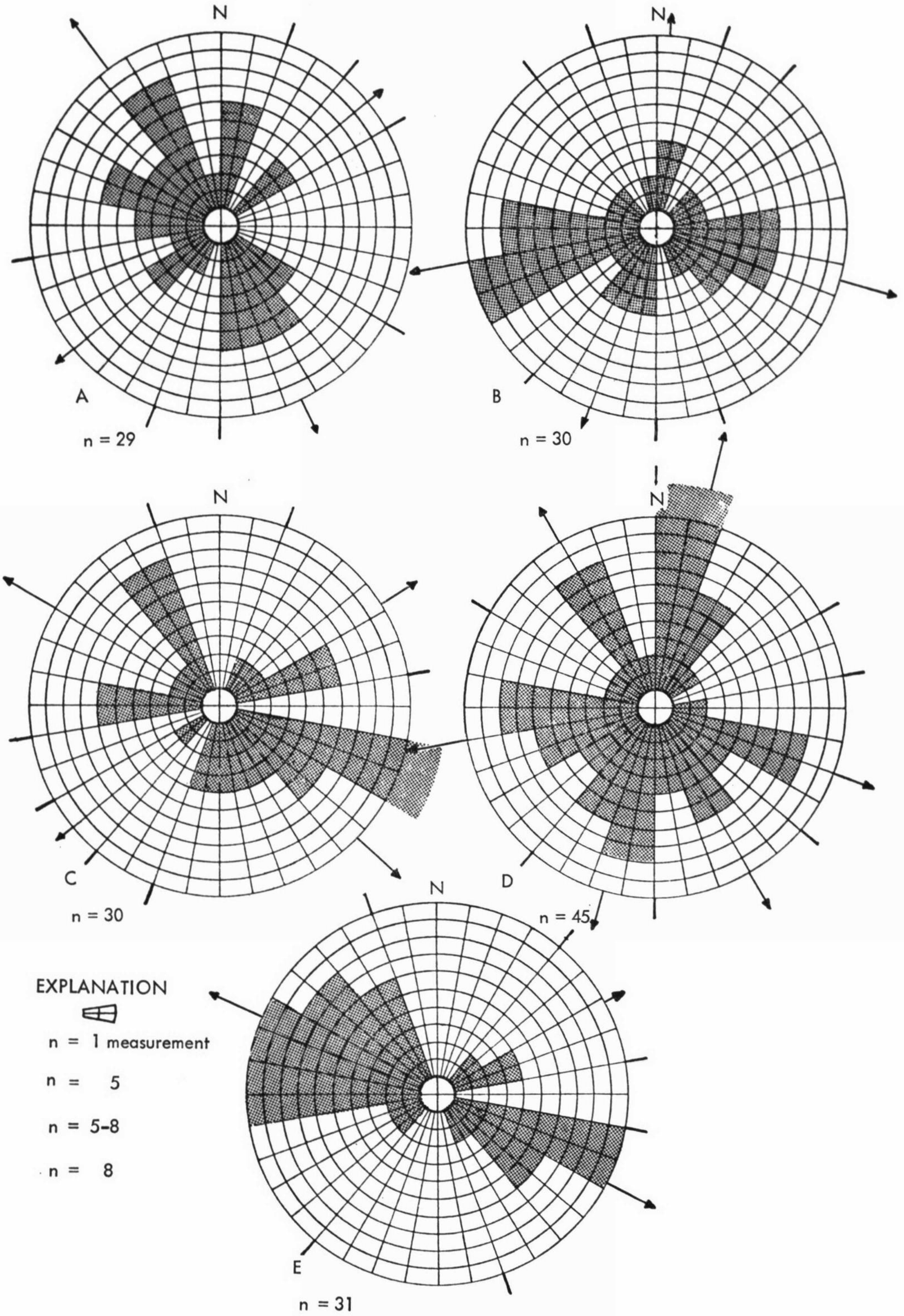


FIG. 4. Circular histograms showing apical orientations of *Turritella* plotted in 20° sectors. Two radius segments beginning at innermost circle equal one measurement. Arrows on edge of histograms indicate modes based on visual estimates; bars indicate the range of measurements in the modes. See SCOTT (1967a) for measurements.

MODES OF ORIGIN OF KIOWA FOSSIL ASSEMBLAGES

Fagerstrom (1964) distinguished four modes of origin for fossil assemblages: 1) fossil communities, 2) residual fossil communities, 3) transported fossil asemblages, and 4) mixed fossil assemblages, based on many of the properties used by Johnson (1960). Interpretation of the mode of origin of the Kiowa assemblages at each locality was reached by posing the following questions: Are the fossils in life position or natural death position, or in a disturbed position? If disturbed, are they preserved in the substrate or neighborhood thought to be preferred, or in a foreign substrate? The categories "in-place," "disturbed-neighborhood," and "transported" are conclusions for these questions and in general are equivalent to Johnson's (1960) three models. The next question is whether the assemblages are ecologically homogeneous or heterogeneous, the latter equivalent to Fagerstrom's (1964) mixed category. If the assemblage is heterogeneous, the adjective "mixed" is placed before the appropriate category. Finally, were the assemblages disturbed or transported by organisms or by physical processes? The modes of origin of Kiowa assemblages and their descriptive criteria are shown in Table 2.

DEFINITION OF KIOWA FOSSIL ASSOCIATIONS

The recurring suite of species that comprise Johnson's (1962) fossil association differs in concept from the traditional biofacies, which is an area or rock unit characterized by certain species. Biofacies refers to a specific stratigraphic unit, whereas fossil association may be found in any place and is simply a statistical concept. In this way, too, fossil association differs from the concept of biotic community, if community is applied to groups of living organisms (MacGinitie, 1939).

The Kiowa fossil associations were defined empirically after an inspection of the measured sections and relative abundance data. The degree of association of each taxon was then tested by the Jaccard coefficient (Fig. 5,6), which sorts species, lithofacies, and modes of origin of fossil assemblages into groups based on the number of times each item occurs with any other item (Kaesler, 1966, Appendix A). Kaesler has shown that this is an adequate measure of association for definition of modern ostracode biofacies and Mello & Buzas (1968) have used the Jaccard coefficient to define foraminiferal biofacies.

Most Kiowa fossil associations are found at several localities at slightly different stratigraphic levels and may even be repeated in a given section. The associations do not necessarily have paleoecologic significance, and none have stratigraphic value. Associations in given units may include a few specimens of a few species which do not commonly occur with the given association and which may even characterize other associations. Generally these species are interpreted as transported if they represent a substrate different from that of the abundant species. Other species are simply noncharacteristic.

Eight Kiowa fossil associations are defined (Fig. 5): *Gryphaea,* trace fossil, *Crassostrea, Trachycardium-Turritella,* corbulid-breviarcid, *Cyprimeria, Nuculana,* and pteriid-mytilid. Two other associations, *Lopha quadriplicata* and *Brachidontes,* were found only at one or two localities, and therefore are not shown on the dendrograms. They are considered as associations because they are clearly the dominant fossils at those localities. A dendrogram (Fig. 6) shows that most commonly the *Gryphaea* association occurs as a mixed-transported assemblage in shell conglomerate; that the *Trachycardium-Turritella,* corbulid-breviarcid, and trace-fossil associations are found as disturbed-neighborhood assemblages in laminated sandstone; that the *Nuculana* association occurs in dark-gray shale and claystone (mudstone); and that the pteriid-mytilid association is most common in thin-bedded sandstone as a mixed-disturbed-neighborhood assemblage. These associations are further described in the following section on lithofacies.

Certain discrepancies in comparing empirical fossil associations with those shown by the dendrograms need to be explained. Four species occur so infrequently with other species (Fig. 5-6) that they were grouped together at the bottom of the dendrogram. Furthermore, *Lingula, Flaventia,* and *Drepanochilus* have not been included in the adjacent associations on the dendrogram because their mode of life allies them more closely with other associations. Their anomalous position on the dendogram probably reflects their occurrence in many mixed transported assemblages of shell conglomerate together with *Trachycardium.* The *Trachycardium-Turritella* and corbulid-breviarcid associations are more closely allied with shell conglomerate than with thin-bedded sandstone because they occur about as commonly in both rock types. Note that the coefficient of association of these taxa with mottled sandstone is only a little less than with shell conglomerate.

The corbulid-breviarcid association is not clearly defined on the dendrograms because *Trachycardium* and *Turritella* are common elements in this association, and at three localities these latter genera form their own association exclusive of *Corbula?*. The *Cyprimeria* association also is closely allied to *Trachycardium* and *Corbula?* because these latter are common species in shell conglomerates. Kaesler (1966) pointed out that species occurring at very many localities have high coefficients of association, even though they may not always occur in the same associations.

The diversity of associations in each unit (Table 3) is indicated by Simpson's diversity coefficient (Simpson, 1949; see Appendix A for explanation).

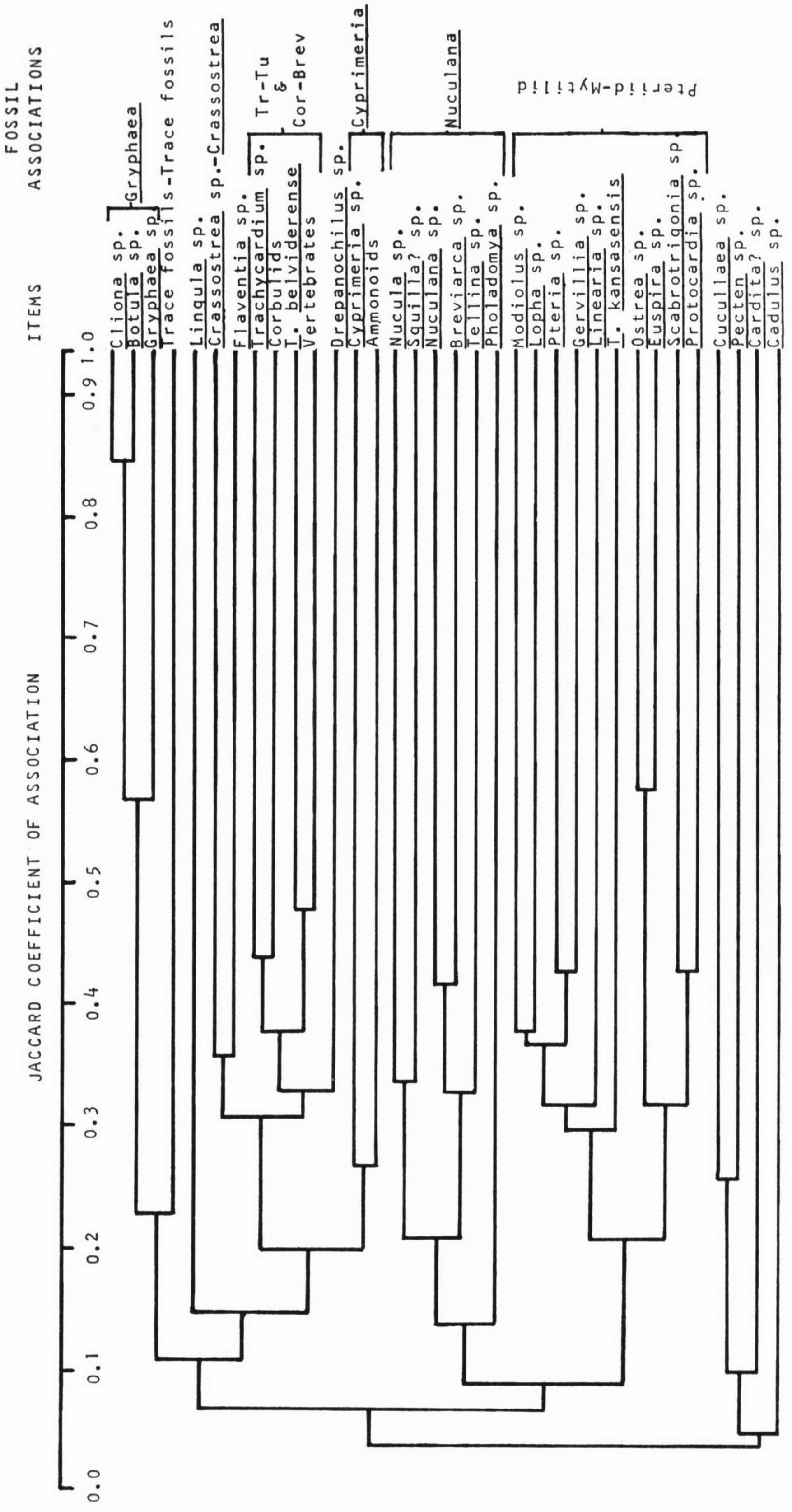


FIG. 5. Dendogram of Kiowa taxa found at more than three localities each; data from Table 5; using weighted pair-group method of clustering with arithmetic averages.

TABLE 3. *Distribution of the More Common Taxa of the Kiowa Fauna; Localities Containing Only Trace Fossils of Plants Omitted.*

[Left number in each column is number of specimens per species; right number is relative abundance of the species in the indicated unit in percentage. Percentages are rounded to the nearest whole number, or to 0.5 if between 0.3 and 0.7, or to trace (*tr*) if less than 0.3. A ? before the left number questions the taxonomic assignment of the specimens. Rare, few, common, and abundant are relative terms having no numerical significance. Abbreviations are from MITCHELL & MAHER (1957); *Cor*=Corbulid, *Brev*=*Breviarca*, *Trach*=*Trachycardium*, *Turrit*=*Turritella*, *Nuc*=*Nuculana*, *Gryph*=*Gryphaea*, *Cypri*=*Cyprimeria*, *Crass*=*Crassostrea*. Categories 23, 31, 46 and 64 include poorly preserved specimens that could not be assigned to a species; each category is counted as one species.]

COUNTY	Clark											
LOCALITY	C1								C2			
SAMPLED UNIT	4	5	7	9	10	12	13-14	16	3-4	6	8	10
1. Cliona sp.							few			few	few	
2. Lingula subspatulata?		?2, 10	?1									
3. Nucula sp. cf. N. rivulana												
4. N.? catherina												
5. Nuculana mutata				15, 63	?2							
6. Yoldia microdonta		1, 5		4, 17								
7. Breviarca habita		7, 35										
8. B. angulata				1, 4								
9. B. subovata												
10. B. salinaensis?												
11. Cucullaea recedens						2, 7						
12. C. ?herculea												
13. Modiolus sp. A												
14. M. sp. B												
15. Brachidontes nonbifurcus												
16. Botula carolinensis?							abnt			abnt	com	
17. Pteria salinensis												
18. Gervillia mudgeana												
19. Pecten occidentalis												
20. P. inconspicuus				1, 4		2, 7						
21. Ostrea arcuata & O. rugosa												
22. Crassostrea kiowana							12, 15					
23. Ostreidae sp. indet.			2	rare	3	1, 4	abnt					
24. Lopha quadriplicata												
25. L. subovata												
26. Gryphaea corrugata							3, 4			abnt	few	
27. G. corrugata var. belviderensis							16, 21				few	
28. G. hilli												
29. G. mucronata												
30. G. navia							2, 3					
31. Gryphaea sp. indet.							32, 41					rare
32. Scabrotrigonia emoryi		1, 5					3, 4					
33. Cardita? belviderensis	?rare											

34. Crassatellina oblonga												
35. Crassinella semicostata		1, 5		1, 4	4	9, 32		11, 5				
36. Trachycardium kansasense		?5, 25				4, 14	7, 9			com	abnt	
37. Protocardia texana				?1, 4	?1	2, 7	2, 3	?1, 5			com	com
38. Leptosolen otterensis												
39. Tellina? sp. indet.						1, 4						
40. Linearia kansasensis												
41. Arcopagella mactroides?												
42. Cyprimeria kiowana												rare
43. Flaventia belviderensis						1, 4						abnt
44. Corbula? smolanensis				1, 4								abnt
45. Corbula? fenti												
46. Corbulids								6, 27				
47. Pholadomya? belviderensis		?1, 5					1, 1					
48. Cadulus praetenuis												
49. Turritella belviderei					3			13, 59				
50. T. kansasensis												
51. Drepanochilus kiowanus		2, 10						1, 5				
52. Aporrhaidae												
53. Euspira smolanensis												
54. Engonoceras belviderense												
55. Adkinsites sp.									rare			
56. Ammonoidea sp. indet.												
57. Squilla? kiowana												
58. Arenicolites sp.												
59. Domichnia												
60. Chondrites sp.												
61. Rhizocorallium sp.			rare									
62. Scolicia sp.						rare						
63. Repichnia	com		com			abnt	rare	com	com	com	com	com
64. Vertebrata (fragments)		rare		rare		rare		rare	rare			
65. Other species						Anomia 2, 7 Cytheridea? 4, 14	Membranipora ? few					Anomia rare
66. Total number specimens		20	3	24	13	28	78	22				
67. Total number species, N	2	9	4	9	5	13	14	7	3	5	7	8
68. Dominant lithology	Ss, lam;	Sh, dk-gy	Ss, mot	Sh, dk-gy	mud st	Ss, lam	Shell cgl	Ss, lam	Ss, mot	Ss, lam	Ss, lam	Ss, lam
69. Mode of origin of fossil assemblage	In-place	Mix dist-neigh	Mix dist-neigh	Mix dist-neigh	Mix dist-neigh	Mix-transp	Mix-transp	Dist-neigh?	Mix dist-neigh	Mix-transp	Mix-transp	Mix-transp
70. Simpson's Diversity Coefficient		5.76	1.50	2.48	6.00	7.26	4.22	2.04				
71. Fossil Association	Trace fossil	Nuc	Trace fossil	Nuc	Cor-Brev-Turrit	Cor-Brev-Trachy	Gryph	Cor-Brev-Turrit	Trace fossil	Gryph	Gryph	Cypri

TABLE 3. *(Continued.)*

	Clark (continued)									Kiowa						
	C2	C3						C4		K1						
	12	2	3	4	6	7	8	2-5	6	1	2	3	4	6A	6B	7A
1.										rare						
2.			2	?1		?2						?1				1, 0.5
3.					1, 1			?rare	1, 5							
4.																
5.		?6			6, 6	3			1, 5							
6.					1, 1											
7.					1, 1				3, 14							
8.																
9.					11, 11											
10.																
11.																
12.																
13.																
14.									2, 8							
15.					1, 1											
16.	com									rare						
17.																
18.																
19.										1, 0.3						
20.																
21.																
22.	rare															
23.								com	1, 5							
24.																
25.																
26.										188, 61					3, 3	23, 10
27.	com															2, 1
28.										40, 13						
29.										51, 17						
30.																
31.					com		20, 69	com	4, 18	12, 4					64, 67	136, 62
32.																
33.										11, 4					?2, 2	
34.												abnt				
35.					3, 3				6, 27							
36.		?3		?4	11, 11	?4	7, 24	rare			27, 21		3, 13			5, 2
37.									?1, 5							
38.																
39.					4, 4	1								?3, 9		

40.																	
41.													?5, 22				
42.															5, 5	7, 3	
43.													3, 13			2, 1	
44.		5			20, 19	3				1, 0.3	abnt			3, 9			
45.											abnt			28, 80			
46.				1					?1, 5		98, 78		7, 30	rare	1, 1	1, 0.5	
47.		?1			8, 8												
48.											1, 1		3, 13	1, 3			
49.		3			16, 16								?2, 9		?20, 21	39, 17	
50.																	
51.					20, 19	2										7, 3	
52.																	
53.																	
54.																	
55.				1			2, 7									1, 0.5	
56.									2, 8								
57.																	
58.																	
59.																	
60.									rare								
61.							rare										
62.																	
63.	com		com				few	com	rare								
64.			few		rare	rare			few							rare	
65.										Serpula rare Plicatula 3, 1		Mesogastropoda com					
66.		18	2	7	103	15	29		22	307	126		23	35	95	217	
67.	5	5	3	4	15	7	5	5	13	11	4	3	6	5	6	12	
68.	Ss, lam	Sh, dk-gy	Sh, dk-gy	Sh, dk-gy	Sh, dk-gy; mudst	Sh, dk-gy; mudst	Ss, mot	Sh, dk-brn	Ss, lam mudst	Shell cgl	Ss, lam	Sh, dk-gy	Ss, lam	Ss, lam	Shell cgl	Shell cgl	
69.	Mix-transp	Mix dist-neigh	Dist-neigh	Mix dist-neigh	Mix dist-neigh	Mix? dist-neigh	Mix dist-neigh	In-place; transp?	Mix dist-neigh	Dist-neigh	Dist-neigh	Dist-neigh	Dist-neigh	Dist-neigh	Mix-transp	Mix-transp	
70.		4.94	1.00	3.50	7.92	7.50	1.92		8.88	2.38	1.54		6.17	1.64	2.01	2.44	
71.	Gryph	Nuc	Nuc	Nuc	Nuc; Cor-Brev-Trachy	Nuc; Cor-Brev-Trachy	Gryph; Trachy	Trace fossil; Gryph	Cor-Brev	Gryph	Cor-Brev-Trachy	Nuc	Cor-Brev-Trachy	Cor-Brev-Trachy	Gryph	Gryph	

TABLE 3. (*Continued.*)

	Kiowa (continued)													Rice			McPher-son
	K1				K2					K3				R2	R3	R6	M3
	8	10	12	13	1	2	8	10	12	1	3, 5	7	9	5	5		1
1.	com		com		com				rare	rare		rare					
2.		4, 3											?1	?1, 1		17	
3.	?1,0.5																1
4.	2, 1							1, 1									
5.						?1		?1, 1									2
6.																	
7.																	
8.	4, 2																
9.																	
10.																	
11.																	
12.																	
13.																	
14.																	
15.																	
16.	com		com		com				rare	rare		rare			rare		
17.																	
18.																	
19.																	
20.																	
21.																	
22.		7, 6		5			?2, 3			53, 95		53, 49		5, 11	24, 34		
23.		abnt		abnt			36, 53	28, 20			abnt			21, 48	36, 51		
24.										?1, 2				1, 2			
25.														1, 2	1, 1		
26.			14, 24		31, 35				2	?2, 4		2, 2					
27.			13, 22		22, 25				4			21, 19					
28.					22, 25												
29.																	
30.	2, 1		5, 8														
31.	31, 11		26, 44		13, 15				abnt			33, 30					
32.														?2, 4			
33.		1, 1															
34.																	
35.			1, 2					3, 2					8	2, 4			
36.	19, 7	6, 5				2	1, 1	25, 19								?1	
37.													3				
38.																	
39.						1											?2

40.																	
41.															?1, 1		
42.	5, 2	22, .19					7, 11	9, 7					2				
43.	6, 2	1, 1				2	?1, 1	5, 4						?2, 4			
44.																	
45.		1, 1															
46.	3, 1					4											
47.						1											
48.		13, 11						1, 1									
49.	156, 58	26, 23					17, 25	?41, 30						8, 18	?7, 10		?1
50.														1, 2			
51.	36, 13	30, 26					4, 6	20, 15							1, 1		
52.																	
53.																	
54.																	
55.	2, 1	3, 3															
56.																	
57.																	rare
58.																	
59.																	
60.			com										rare				
61.																few	
62.																	
63.						com							com	com		com	
64.		rare					com	com					rare				rare
65.	Neo-gastropoda 1, 0.5	Membranipora? rare Trochid 1, 1												Lopha? kansasensis 1, 2			
66.	268	115	59	5	88	11	68	134	6	56		109	14	45	70	18	6
67.	15	16	8	2	6	7	8	11	5	5	1	6	7	12	7	4	6
68.	Shell cgl	Shell cgl	Shell cgl	Shell cgl	Shell cgl	Ss, lam	Shell cgl	Shell cgl	Shell cgl	Shell cgl	Shell cgl	Shell cgl	Ss, lam	Ss, mot	Shell cgl	Ss, thn-bdd	Sh, dk-gy
69.	Mix-transp	Mix-transp	Transp?	Transp	Dist-neigh	Dist-neigh	Mix-transp	Mix-transp	Transp	Mix-transp	Transp	Mix-transp	Dist-neigh	Mix dist-neigh	Transp	Transp	Dist-neigh
70.	2.67	5.89	3.39	1.00	3.81	6.87	2.87	5.13	2.14	1.12		2.78	2.84	3.94	2.61	1.13	7.50
71.	Gryph	Cypri	Gryph	Crass	Gryph	Cor-Brev-Trachy	Cypri	Cypri	Gryph	Crass	Crass	Gryph	Cypri	Crass	Crass	Trace fossil	Nuc

TABLE 3. (*Continued.*)

	McPherson (continued)										Ellsworth					
	M3		M4			M6			M7	M8	E2	E3		E4		E6
	2	3	6-7	8-9	15	5	10	16			1	2	4	4	6	2
1.													rare			
2.				1												
3.					?1, 0.5						?3					3, 5
4.																
5.	?3, 3	5, 3	3					?1, 2			?2					?14, 22
6.		1, 0.5														?1, 1
7.																
8.																
9.	?1, 1	19, 13											?1, 1			1, 1
10.								?1, 2								
11.					7, 5											
12.					1, 0.5											
13.												?1, 2				
14.											2					
15.																
16.													rare			
17.																
18.					1, 0.5											
19.																
20.																
21.					2, 1	7, 35										
22.									43, 63	80, 49		2, 5	com	11, 37	11, 10	
23.	2, 2				?1, 0.5							33, 81	79, 84		16, 15	
24.					1, 0.5		47, 98					2, 5	com		11, 10	
25.												1, 2				
26.																
27.																
28.																
29.																
30.																
31.																
32.					1, 0.5											
33.																
34.					1, 0.5											
35.	55, 55						1, 2			7, 4					com	
36.					42, 27	4, 20		?1, 2	8, 12	19, 12			?2, 2		3, 3	
37.					13, 8											
38.											1					3, 5
39.	?4, 4	?2, 1									?1					

40.								2, 4								
41.																
42.										1, 0.5						
43.										?1, 0.5	?1					
44.	9, 9														com	
45.																
46.		20, 13			?4, 3	7, 35				12, 7					30, 27	3, 5
47.																
48.		5, 3								?1, 0.5					?7, 6	
49.	25, 25	92, 62		rare	?75, 48	2, 10		49, 91	16, 24	43, 26	?2	1, 2	?12, 13	19, 63	?32, 29	39, 60
50.																
51.												1, 2				
52.		?1, 0.5			2, 1											
53.		?4, 3			1, 0.5											
54.																
55.																
56.																
57.											2					com
58.																
59.																
60.																
61.																
62.																
63.												rare				
64.	rare	rare	rare	rare					rare	rare	com		few		rare	com
65.	?Cytheridea? 1, 1	"Ampullina" 2, 1			"Ampullina" 1, 0.5				Amberleya 1, 1							?Cytheridea? 1, 1
66.	100	151	3	1	155	20	48	54	68	164	14	41	94	30	110	65
67.	9	11	2	3	17	4	2	5	5	9	9	8	9	2	10	10
68.	Mudst	Shell cgl; mudst	Sh, dk-gy	Sh, dk-gy	Ss, Thn-bdd	Ss, lam	Ss, lam	Ss, thn-bdd	Shell cgl	Shell cgl	Sh, dk-gy	Ss, lam	Shell cgl	Shell cgl	Shell cgl	Sh, dk-gy
69.	Dist-neigh	Mix dist-neigh?	Dist-neigh	Dist-neigh	Mix dist-neigh	Dist-neigh	Dist-neigh	Mix dist-neigh	Mix-transp	Mix-transp	Mix? dist-neigh	Dist-neigh	Mix trans-	Transp	Mix-transp	Dist-neigh
70.	2.70	2.48	1.00		3.19	3.88	1.04	1.22	2.17	3.09	1.30	1.55	1.39	1.93	5.06	2.47
71.	Cor-Brev-Turrit	Cor-Brev-Turrit	Nuc	Nuc	Trachy-Turrit	Pteriid-Mytilid?	Lopha quad	Trachy-Turrit	Crass	Crass	Nuc	Crass	Crass	Crass	Crass	Nuc

TABLE 3. *(Continued.)*

	Ellsworth (continued)				Saline										
	E6		E8	E10	S2	S4	S5		S6	S7	S8		S9		
	3A	3B					1	2			1	9	3	4	9
1.															
2.						12, 2									2
3.															
4.															
5.	?4, 12						1, 2					1, tr		3	
6.															
7.							?12, 18								
8.															
9.	1, 3				5, 2										
10.															
11.															
12.															
13.						1, tr			7, 12	1, 0.5	7, 7	7, 2	75, 28		
14.															
15.					?103, 47										
16.															
17.							?2, 3		2, 3	1, 0.5		2, 0.5	3, 1		
18.									25, 42		2, 2	15, 3	15, 6		
19.															
20.															
21.						73, 9	1, 2					1, tr			
22.						4, 0.5	?5, 7	abnt				1, tr	6, 2		
23.						7, 1				?3, 1	10, 10	26, 6	12, 4		
24.									2, 3	2, 1	4, 4	10, 2	11, 4		
25.															
26.															
27.															
28.															
29.															
30.															
31.															
32.			1	2		1, tr	1, 2			23, 10	6, 6	20, 4	20, 7		
33.			1												
34.															
35.	com	54, 46										1, tr		1	
36.				2		78, 10	3, 4		10, 17	18, 8	16, 16	48, 10	64, 24		
37.				7		15, 2	9, 13			3, 1	5, 5	9, 2			
38.														1	
39.		?1, 1					?5, 7							?1	

40.					?1, 0.5					4, 2		25, 5	2, 1		
41.															
42.													?2, 1		
43.		?1, 1		1		2, tr	?1, 2			8, 4	8, 8	?9, 2	23, 9		
44.	few						21, 31			2, 1		24, 5	4, 1		
45.					?9, 4	591, 74									
46.	14, 44	35, 30				9, 1									
47.												2, 0.5		?1	
48.		?1, 1													
49.	12, 38	?25, 21		?5		?1, tr			2, 3			?3, 05	14, 5	2	
50.										158, 70	41, 41	260, 56			
51.						2, tr	2, 3		6, 10	1, 0.5			10, 4		
52.															
53.						4, 0.5	2, 3				1, 1	1, tr			
54.									5, 9				6, 2		
55.															
56.	1, 3														
57.														1	
58.															
59.															
60.															
61.													rare		
62.															
63.			com			rare			rare						rare
64.	rare	com							rare			rare		com	
65.		Gegania 1, 1			Homomya sp. A 22, 10 Pyramidellidae 80, 36	Otostoma 1, tr Pirsila? 1, tr	Mathilda 2, 3			Amberleya 1, 0.5 Strepteneura 1, 0.5		Ophiura 1, tr	Homomya sp. B 2, 1 Cassiope 1, 0.5		
66.	32	117	2	17	220	803	67		59	226	100	466	270	10	2
67.	8	7	3	5	6	18	14	1	11	14	10	21	18	8	2
68.	Sh, dk-gy	Shell cgl	Ss, mot	Ss, thn-bdd	Ss, lam	Ss, thn-bdd	Ss, lam	Shell cgl	Ss, thn-bdd	Ss, thn-bdd	Ss, thn-bdd	Ss, thn-bdd	Ss, mot	Sh, dk-gy	Sh, dk-gy
69.	Dist-neigh	Mix-transp	Dist-neigh	Dist-neigh	Dist-neigh	Mix dist-neigh	Mix dist-neigh	Dist-neigh?	Mix dist-neigh	Mix dist-neigh	Mix? dist-neigh	Mix dist-neigh	Dist-neigh; in-place?	Dist-neigh	Dist-neigh
70.	3.04	2.92		4.12	2.77	1.79	6.52	1.00	4.34	1.98	4,83	2.97	6.44	1.13	1.00
71.	Cor-Brev-Turrit	Cor-Brev-Turrit	Trace fossil	Trachy-Turrit	Brachidontes	Pteriid-Mytilid	Cor-Brev-Trachy	Crass	Pteriid-Mytilid	Pteriid-Mytilid	Pteriid-Mytilid	Pteriid-Mytilid	Pteriid-Mytilid	Nuc	Nuc

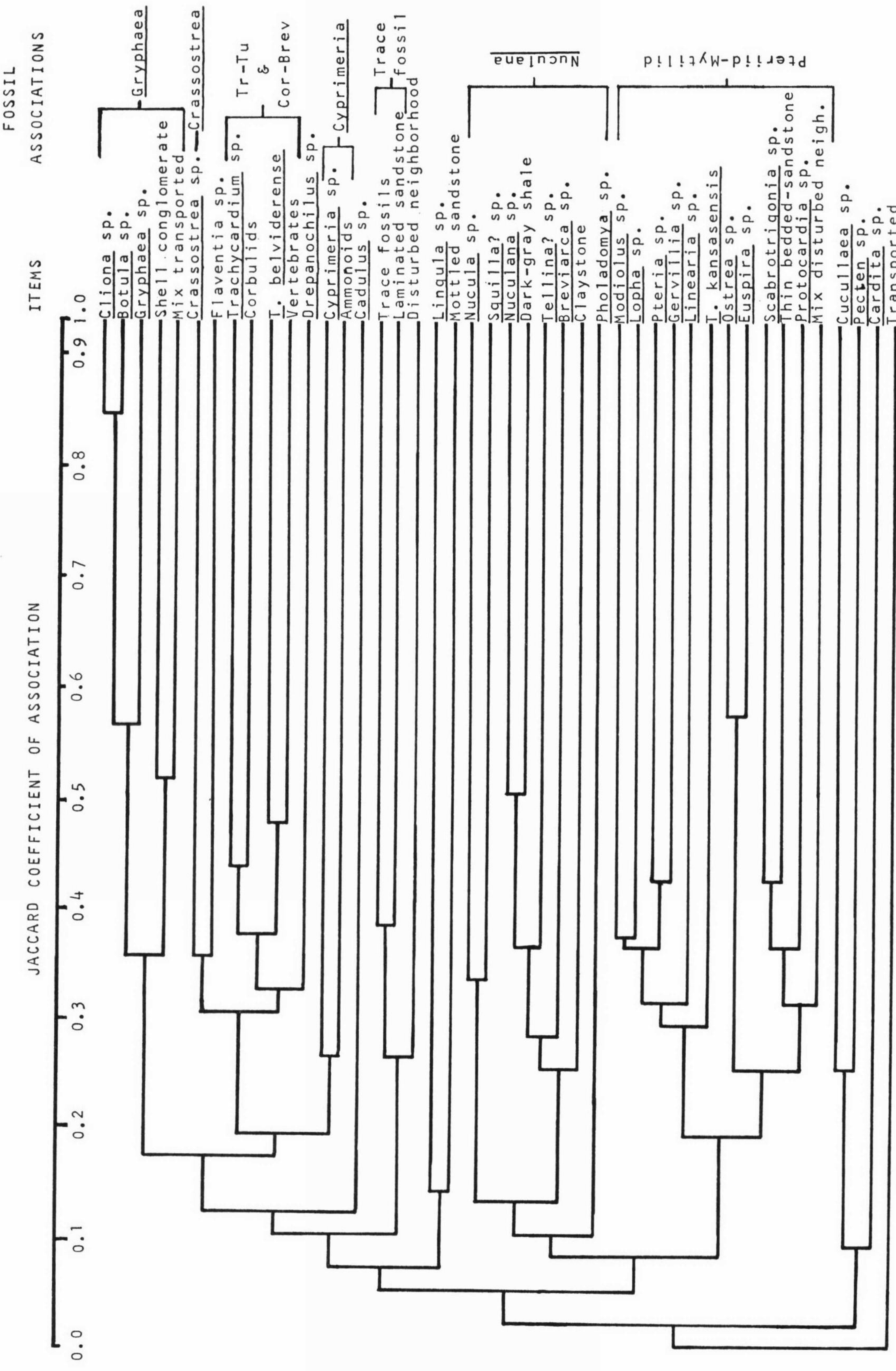


FIG. 6. Dendrogram of taxa, lithofacies, and modes of origin of fossil assemblages of taxa in Figure 5; data from Table 3.

LITHOFACIES AND FOSSIL ASSOCIATIONS

The various lithologies comprising the Kiowa Formation are grouped into lithofacies or descriptive categories that summarize their lithologic properties (Teichert, 1958). Lithofacies in the Kiowa are laterally and vertically discontinuous, interfingering bodies that recur in stratigraphic succession. The lithofacies are defined by grain size and sedimentary structures, which reflect depositional processes. The characteristic properties of the facies are summarized in Table 4. Stratification terminology follows McKee and Weir (1953). Only those rock types in the measured sections (*see* Fig. 10-13) are described (*see* Franks, 1966, for descriptions of other lithologies).

Generalized environmental interpretations are made for each lithofacies based on lithologic and paleontologic features. The feeding and dwelling habits and substrate preferences of the characteristic species, then, provide some paleoecologic significance to the association (Imbrie, 1964; Purdy, 1964; Sohl, oral communication, 1966). The paleoecology of each taxon is discussed in the Systematic Descriptions.

DARK-GRAY SHALE LITHOFACIES

LITHOLOGY

Dark-gray to medium dark-gray, fissile, thin-laminated shale is the dominant lithology in the sampled sections of Kiowa. It encloses many units of the other facies. In some sections of the upper Kiowa this facies is overlain by and grades into mudstone and thin-laminated to thin-bedded sandstone.

The color of shale varies somewhat and less commonly it is medium light-gray or light-gray depending partly on the degree of weathering. Minor sedimentary structures are poorly developed. Silt and very fine-grained sand mottles (Moore & Scruton, 1957, p. 2727) are very common in the less fissile shale; less common are very thin (0.1 mm.), discontinuous laminae and nodules 3 to 6 cm. long. Besides quartz, the mottles locally contain fish scales and other chitinous fragments.

The dominant minerals of the shale are illite, montmorillonite, and kaolinite, in various proportions; kaolin percentage increases towards the top of the Kiowa (Franks, 1966). Primary accessory material observed are: silt-size to very fine-grained quartz, locally rounded and frosted; muscovite flakes; glauconite pellets, which are common in sand mottles; carbon flecks; phosphatic pebbles, grains, and fragments; and very rare calcitic shell fragments. Diagenetic minerals are pyrite cubes, nodules, and fossil casts; siderite concretions ranging in diameter from about 1 to 50 cm. or more; calcite cone-in-cone concretions and laminae; and chertlike nodules. Weathering products are gypsum veinlets in fractures, and beautiful euhedra in slope wash; limonite staining in some gypsum veinlets; yellow jarosite stain along fractures; and iron oxide stain on siderite concretions.

PALEONTOLOGY

Fossil molds and casts are very sparse and locally common. Many replicas are broken but fragments are not displaced, indicating that probably during compaction the shells were fractured before being dissolved. The fossils occur as disturbed-neighborhood assemblages, and several are mixed assemblages.

The most common genera are *Nuculana, Yoldia, Nucula, Breviarca, Pholadomya?, Turritella, Drepanochilus,* and *Lingula,* which together constitute 18 to 84 percent of the *Nuculana* association (Fig. 7); *Corbula?* makes up the remainder. *Tellina, Leptosolen,* and *Squilla?* are common only in central Kansas. Plesiosaur fragments and fish scales are present at many localities. A unique assemblage of articulated *Crassatellina oblonga, Lingula subspatulata?,* and small, indeterminate species of Mesogastropoda characterize the chertlike nodules in unit 3, Loc. K1. The diversity coefficient ranges from 1.00 to 7.92, and averages 3.61. The greatest diversity is in units of interbedded claystone and shale.

Many specimens of the more abundant species are small; however the species themselves are small. Pyritized specimens of *Turritella belviderei* at Loc. E2 are no smaller than specimens from any of the other facies. Some specimens may be immature, such as *Lingula subspatulata?* (*see* Systematic Descriptions). Most specimens of *Trachycardium, Protocardia, Gryphaea,* and ostreids are transported fragments.

INTERPRETATIONS

The shale was formed by compaction of mud derived from land areas. Currents were strong enough, at least occasionally, to transport some fine-grained quartz and shell fragments. The bottom in many places was firm enough to support animal burrows that are preserved as mottles of silt- and sand-sized grains. That bottom waters were oxygenated is indicated by the limited presence of burrowing detritus-feeders and some filter-feeders that preferred a mud substrate. The dark sediment contained abundant organic matter which may have been rich in bacteria. This in turn probably caused the reducing conditions below the sediment-water interface, which subsequently led to the dissolution of calcite and the precipitation of pyrite and siderite (ZoBell, 1946).

This interpretation differs from that of Twenhofel (1924, p. 39) who compared the Kiowa "black shales" to Recent deposits in stagnant basins of the Baltic Sea. His interpretation was based on the presence of pyrite, which probably was formed after deposition and below the sediment-water interface.

TABLE 4. *Summary of Lithologic and Paleontologic Properties of the Kiowa Lithofacies.*
[See Table 3 for explanation of abbreviations.]

Lithofacies Properties	Dark-gray shale	Mudstone	Thin-Laminated sandstone	Thin-bedded sandstone	Mottled sandstone	Shell conglomerate
Color	dark-gray to med dark-gray	medium-brown to yellow-brown	light-gray to yellow-brown	grayish-orange to red-brown	gray-brown to orange-brown	brown-gray to gray-brown
Strat-ification	thin-lam. to laminated	thin-lam. to laminated	thin-lam. to thin-bedded	thin-bedded	thin- to thick-bedded	laminated
Grain size	clay-size	clay-size	silt to very fine sand	very fine to fine sand	very fine to fine sand	silt to cobble-size
Dominant minerals	illite, montmorillonite, kaolin	kaolin, illite, montmorillonite	quartz	quartz	quartz	quartz and shall fragments
Accessory minerals	quartz, mica, glauconite, carbon	quartz, mica, carbon	clay, mica, carbon	clay, mica, carbon	clay, mica, carbon	phosphate, glauconite
Sedimentary structures	homogeneous to mottled	homogeneous to mottled	homogeneous	ripple marks, cross bedded	mottled	ripple marks, graded-type bedding
Origin of fossil assem	disturbed-neighborhood	disturbed-neighborhood	dist-neigh, mix-transp	mix dist-neighborhood	disturbed-neighborhood	mixed-transported
Fossil associations	Nuculana	Corbula?-Breviarca	Trace fossil, Cor-Brev, Lopha, Brachid	Trace fossil, Trach-Turrit, Pter-Mytilid	Trace fossil, Trachy, Crass, Pter-Mytilid	Gryphaea Crassostrea Cyprimeria

MUDSTONE LITHOFACIES

LITHOLOGY

Brownish, blocky, laminated mudstone is not common in the Kiowa and forms units 0.2 to 15 feet thick or more.

The facies generally overlies the dark-gray shale and grades into it by alternation of strata. In some sections it is present only as interbeds in dark-gray shale. Generally mudstone is overlain by and in abrupt contact with the thin-bedded or the laminated sandstone facies. In some sections very thin beds or laminae of mudstone alternate with very thin beds of siltstone.

The color of the mudstone ranges from medium brown to light-yellow brown to medium gray. It is plastic and locally laminated to thin-laminated. Dominant minerals are kaolin, "degraded" illite, and montmorillonite (FRANKS, 1966). Silt mottles are common, and silt is disseminated throughout. The rock becomes claystone where silt is absent. Less common accessory materials are mica, carbon flecks, wood and plant fragments, and calcitic shell fragments, which are partly leached. Small siderite concretions and cone-in-cone laminae (Loc. M3) are very rare. At Loc. E1 grayish-black lignitic claystone is interbedded with brownish-gray claystone, all of which is unfossiliferous except for carbonized wood fragments.

PALEONTOLOGY

In this facies fossil molds and casts are very rare to common, forming disturbed-neighborhood assemblages and several mixed assemblages. Calcitic shells are rare, and where present they are partly leached, suggesting that most shell material was removed by weathering. The most common and abundant genus is *Corbula?* (including *Crassinella*) with a relative abundance of 13 to 76 percent; *Breviarca* and *Turritella* are the next most common forms, together making up 14 to 75 percent of the corbulid-breviarcid-*Turritella* association (Fig. 7). Nuculanids are present but usually constitute not more than 10 percent. Ostreid and *Gryphaea* fragments are present in many assemblages but were probably transported. The diversity coefficient ranges from 2.48 to 8.88 and averages 5.91. Strata having the greatest faunal diversity consist of interbedded mudstone and dark-gray shale or siltstone. An exceptional occurrence of the corbulid-*Turritella* association is as a mixed transported assemblage in calcite-cemented shell conglomerate (unit 3b, Loc. E6). The unit overlies dark-gray shale and underlies a cone-in-cone zone.

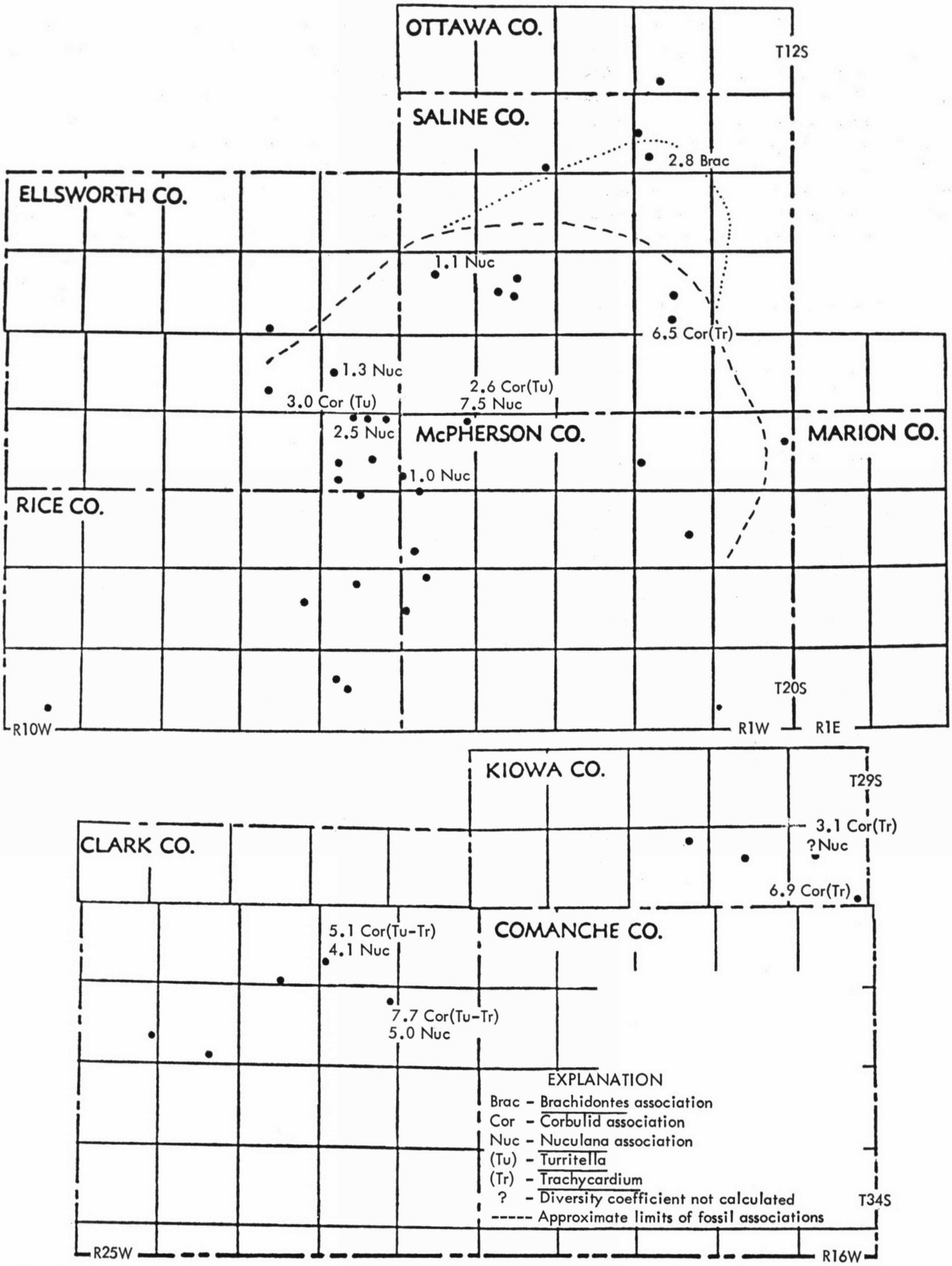


FIG. 7. Maps showing distribution and diversity of *Brachidontes,* corbulid-breviarcid, and *Nuculana* associations. In Figs. 7-9 the Simpson diversity coefficient at each locality is the average of all assemblages of the particular association at that locality. See Fig. 1 for index map of Kansas and scale.

INTERPRETATIONS

This facies represents an environment in which oxidizing conditions persisted even after deposition. Oxidation may have been caused either by a low amount of organic matter or by flushing the sediment with oxygenated waters. The preserved fauna is no less abundant in this facies than in the dark-shale facies and would have contributed as much organic matter. *Corbula?*, a shallow-burrowing filter-feeder, and *Breviarca*, an epifaunal filter-feeder, apparently were adapted to a firm mud substrate.

THIN-LAMINATED SANDSTONE LITHOFACIES

LITHOLOGY

Light-gray to medium-gray to yellow-brown, thin-laminated to very thin-bedded siltstone and sandstone occur throughout the Kiowa but are most common in the middle portion. Generally the laterally discontinuous sets of laminae are 0.5 foot thick and alternate with dark-gray shale or mudstone, forming interbedded units less than 1 foot to more than 15 feet, most commonly 5 feet thick. These units overlie the dark-gray shale facies and underlie thin-bedded sandstone or rarely mudstone. At Loc. S5 laminated sandstone underlies *Crassostrea* shell conglomerate. Contacts are gradational. Where overlain by the thin-bedded sandstone facies this lithofacies merges with it through a transition zone of alternating strata which shows an increase in thickness of beds and in sand percentage. Contacts are gradational. Where the shell conglomerate facies is present in the sequence, laminated sandstone merges with it by an increase in the percentage of shells relative to inorganic detritus. At Loc. K1 laminated sandstone unit 6 can be traced laterally into a shell conglomerate.

Quartz is the dominant mineral; common accessory materials are clay minerals, mica, carbon, and rarely glauconite pellets; less common are chert grains, feldspar, zircon, and calcitic shell fragments. Secondary cements are calcite and marcasite(?), and the latter is partly weathered to iron oxide, resulting in a medium yellow-brown to grayish-orange color. Locally, cone-in-cone concretions are developed directly above or below the siltstone strata. Secondary gypsum is common within the siltstone.

The rock as seen in thin section consists mainly of silty to very fine-grained, moderately to well-sorted, angular to subrounded quartz; elongate grains are subparallel to stratification. The matrix consists of fine to coarse crystalline (0.1-5 mm.), secondary calcite; less common are gypsum and marcasite(?). Weathering products are iron oxide, limonite, and gypsum.

PALEONTOLOGY

Molds and casts of fossils are absent to common in this facies. Sand in most replicas is cemented by secondary iron oxide. Shells occur in disturbed-neighborhood assemblages and, more rarely, in mixed or transported assemblages.

Trace fossils occur as in-place assemblages. Four faunal associations are distinguished by different dominant species: 1) the trace-fossil association with abundant small and large-diameter Repichnia, and less common *Chondrites* and Domichnia; 2) the corbulid-breviarcid-*Trachycardium* association; 3) the *Lopha quadriplicata* association; and 4) the *Brachidontes nonbifurcus-Homomya* sp. B-Pyramidellidae association. Assemblages in laminated sandstone at Loc. C2 are like assemblages in shell conglomerate and are discussed in that section.

The trace-fossil association is the most common in this facies in both southern and central Kansas (Fig. 8). Trace fossils are found either alone or with shells or fish vertebrae and scales. Generally the units containing trace fossils are intercalated with claystone or dark-gray shale and underlie thin-bedded sandstone; less commonly units with trace fossils are intercalated within the dark-gray shale facies alone.

The corbulid-breviarcid-*Trachycardium* association generally occurs as a disturbed-neighborhood assemblage, and these genera make up 32 to 99 percent of the fauna. Diversity of this association (Fig. 7) is increased by the presence of a small percentage either of species that preferred other habitats and probably are transported, such as *Drepanochilus* and *Nuculana*, or of species uncommon in this facies, such as *Protocardia*, *Turritella*, and *Cadulus*. The diversity coefficient ranges from 1.04 to 8.88 and averages 4.76. This association differs from the corbulid association in mudstone only by the substitution of *Trachycardium* for *Turritella*.

The *Lopha quadriplicata* association occurs as a disturbed-neighborhood assemblage and is found in unit 10, Loc. M6, where it constitutes 98 percent of the fauna and *Crassinella semicostata* constitutes 2 percent. In unit 2, Loc. E3, *L. quadriplicata* occurs with other oysters, *Turritella*, and *Drepanochilus*. The average diversity coefficient for the two localities is 1.29. The facies is intercalated in dark-gray shale.

The *Brachidontes* association (Fig. 7) occurs as a disturbed-neighborhood assemblage and is found only in unit 2, Loc. S2. *Brachidontes* is 46 percent of the fauna; *Homomya* sp. B is 10 percent; and a species of Pyramidellidae is 39 percent. The diversity coefficient is 2.77. Unit 2 consists of hematitic siltstone intercalated with medium dark-gray shale. This unit precedes thin-bedded, cross-stratified sandstone.

INTERPRETATIONS

The different units and fossil associations probably represent somewhat different environments. The siltstone and sandstone strata intercalated in dark-gray shale and containing trace fossils, the corbulid, or the *Lopha* associations were derived from currents, perhaps storm-

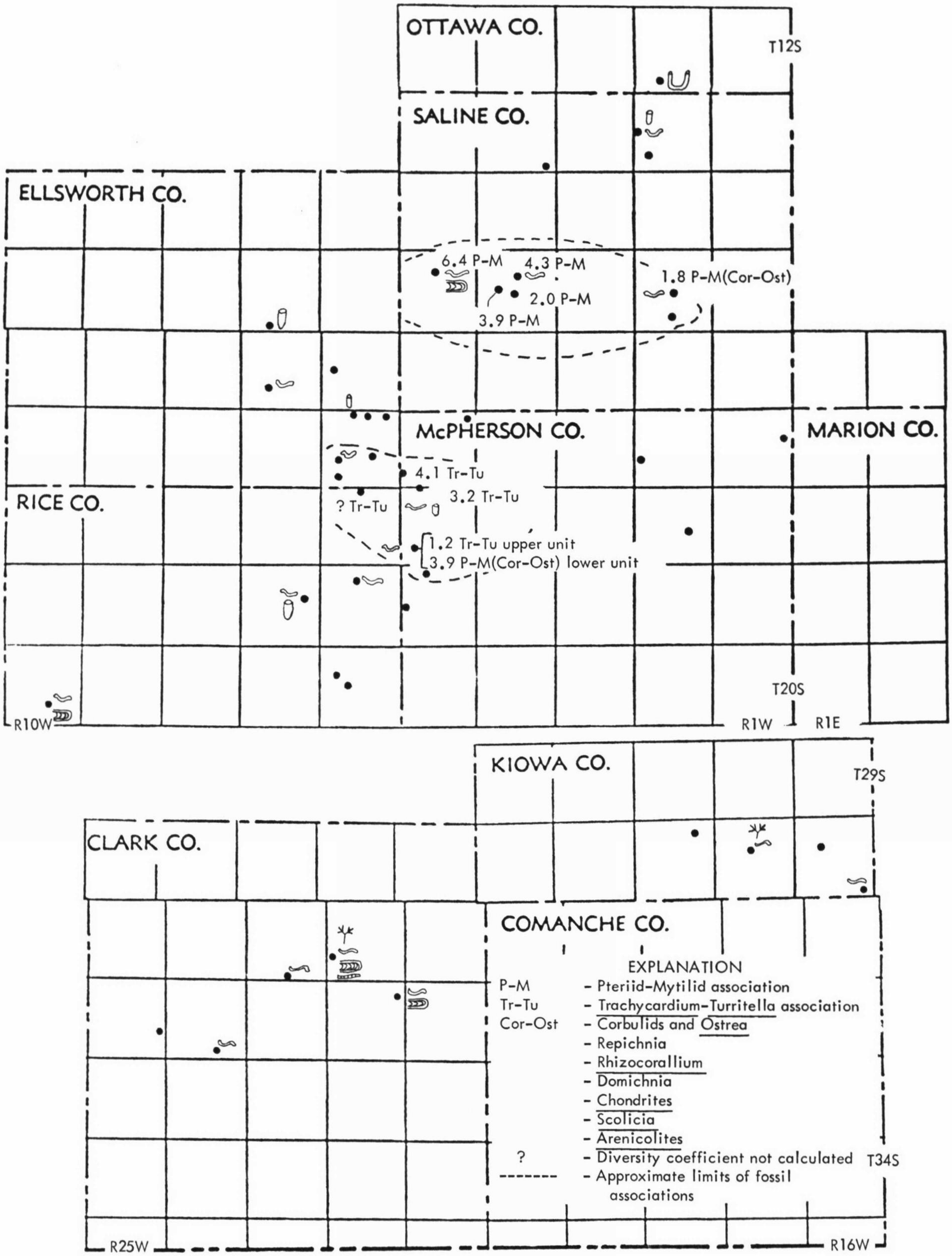


FIG. 8. Maps showing distribution and diversity of pteriid-mytilid, *Trachycardium-Turritella,* and trace fossil associations.

generated. The shallow-burrowing and epifaunal filter-feeders preferred a fine-grained, sandy substrate and may have migrated into the area after deposition of sand, and formed short-lived communities, or the shells may have been transported along with the sand.

The laminated siltstone and sandstone strata that underlie thin-bedded sandstone and contain trace fossils or locally the *Brachidontes* association may represent gradually shoaling conditions, and perhaps locally a lowered salinity.

THIN-BEDDED SANDSTONE LITHOFACIES

LITHOLOGY

Grayish-orange to moderate reddish-brown, thin-bedded sandstone is common in the middle and upper parts of the Kiowa. The strata are tabular in shape, rarely lenticular, and form units 2 to 20 feet thick. They generally overlie a transition zone of intercalated, thin-laminated sandstone and dark-gray shale or mudstone, and more rarely dark-gray shale alone. Thin-bedded sandstone underlies dark-gray shale or mudstone, or it is the uppermost unit in the Kiowa. No transition zone is present and the contact is abrupt.

Strata are regularly bedded and generally cross-stratified in thin-bedded sets. Cross-stratification is small- to medium-scale, tabular, planar, and trough. Strata sets commonly are separated by shaly partings, and bounding surfaces are marked with both transverse and interference ripples. The grand vector resultant of cross strata in the Kiowa of central Kansas is S. 7 E., with a range of about 130 degrees (Franks, 1966).

Grain size is very fine to fine. Detrital minerals are generally the same as in the thin-laminated sandstone facies. Marcasite(?) nodules and concretions are rare, and generally are weathered to iron oxide. The sandstone varies from friable to highly indurated. Most common cements are iron oxide, calcite, and siderite; other cements described by Swineford (1947) are dolomite, silica, and celestite. Swineford maintained that calcite cementation was early diagenetic and was related to the marine environment of the Kiowa. Some silica cement replaced calcite early, and some very late; celestite probably was early diagenetic. Much of the iron oxide is a weathering product. Cementation and its environmental significance is discussed to a greater extent in the section on shell conglomerates.

PALEONTOLOGY

Fossil molds and casts are absent to abundant in this facies. The replicas generally are highly cemented with iron oxide. Three faunal associations are distinguished by different dominant species: 1) Trace fossil association with common small and large Repichnia and rare Domichnia; 2) *Trachycardium - Protocardia - Turritella belviderei* association; 3) Pteriid-mytilid association characterized by the presence of *Gervillia, Pteria, Flaventia, Modiolus,* and *Ostrea,* and the most abundant genera being *Trachycardium, Scabrotrigonia, Linearia,* and *Corbula?.*

The uppermost thin-bedded sandstone units in southern Kansas are apparently unfossiliferous except for fish fragments. However, Gould (1900) reported sparse fossils from the "Greenleaf sandstone" ten miles west of Belvidere, including *Lingula, Pholadomya, Cyprimeria kiowana, Turritella,* and shark teeth. Twelve miles northwest of Ashland fossil leaves are associated with fish fragments in this facies (Gould, 1900). In central Kansas this facies is locally barren except for plant fragments. Leaves are preserved in the uppermost sandstone in NW SE sec. 14, T. 16 S., R. 6 W.

The in-place trace fossil association consists of Repichnia and Domichnia of various sizes, including rare *Rhizocorallium* (Fig. 8). It occurs in both the middle and the uppermost Kiowa in central Kansas. Locality R6 is unique and contains a few fragments of *Lingula subspatulata?* as a transported assemblage, besides Repichnia and *Rhizocorallium.*

In the mixed, disturbed-neighborhood assemblages of the *Trachycardium-Turritella* association, *Trachycardium kansasense* constitutes 27 percent of the fauna, and includes *Protocardia texana* (8 percent), *Turritella belviderei* (48 to 91 percent), and *Scabrotrigonia emoryi* (1 percent). Faunal diversity is low, ranging from 1.22 to 4.12, and averaging 2.84. The assemblage is restricted to the uppermost Kiowa in central Kansas (Fig. 8).

In the mixed, disturbed-neighborhood assemblages of the pteriid-mytilid association, *Gervillia mudgeana* constitutes 3 to 42 percent of the fauna, *Pteria salinensis,* 1 to 3 percent, *Modiolus,* 1 to 12 percent, *Linearia,* 2 to 5 percent, and *Ostrea,* 1 to 9 percent. However, the most abundant genera are *Trachycardium,* 8 to 17 percent, *Scabrotrigonia,* 1 to 10 percent, *Corbula?,* 1 to 74 percent, and *Turritella kansasensis,* 41 to 70 percent. Faunal diversity is limited, the coefficient ranging from 1.79 to 4.83 and averaging 3.18, which is not greatly different from the previous association. Some genera, such as *Lingula* and *Drepanochilus,* probably are transported from other habitats. This association is restricted to several horizons in the middle Kiowa in Saline County (Fig. 8).

INTERPRETATIONS

This facies is dominated by shallow-burrowing and byssate filter-feeders that preferred a firm, sandy substrate. The lithologic and paleontologic data suggest that most thin-bedded sandstone units, including the barren units, may have been deposited in a nearshore, sublittoral, slightly brackish environment within the zone of current activity. Local habitat differences probably caused the faunal differences.

The *Trachycardium* - *Turritella* and pteriid-mytilid associations make up part of CRAGIN's (1895a) "Mentor beds," which TWENHOFEL (1924) defined as a fossiliferous marine unit supposedly at the top of the Kiowa. The measured sections on Figs 10-13, especially Loc. S8 where two "Mentor beds" are in succession, show that this thin-bedded sandstone facies occupies several stratigraphic positions, not only the uppermost part. As TWENHOFEL recognized, the fauna of the two combined associations contain many species, a few of which are abundant, and the abundant species are not always the same at different localities. TWENHOFEL interpreted the unfossiliferous units of this lithofacies to be "fluvial deposits on a coastal plain," and fossiliferous units to be marine, nearshore deposits (1924, p. 40).

MOTTLED SANDSTONE LITHOFACIES

LITHOLOGY

Light grayish-brown to light orange-brown, thin-bedded to thick-bedded mottled sandstone is not common in the Kiowa and generally occurs as tabular units 1 to 5 feet thick. These strata overlie dark-gray shale or mudstone interbedded with laminated sandstone. Contacts are gradational to abrupt. Mottled sandstone generally underlies dark-gray shale with an abrupt contact. Strata are irregular, thin- to very thin-bedded sets that are mottled, or the unit is unstratified and mottled (see unit 3, Loc. S9). Mottles are formed by dark-gray clay that fills burrows and by unevenly distributed aggregates of sand grains and matrix, resulting in an irregular weathered surface. Some clay-filled burrows are long and relatively straight; most are irregular blotches.

Detrital materials are generally the same as in the thin-laminated sandstone facies with the addition of phosphatic fragments. Calcite is the most common cement, forming medium-crystalline (1-5 mm.) patches that enclose several sand grains. Large siderite concretions in unit 3, Loc. S9, have microcrystalline ($<$0.1 mm.) to fine-crystalline (0.1-1 mm.) cement that contains minor amounts of Ca, Mn, or Mg (X-ray analysis by P. C. FRANKS, 1966).

Petrographic examination shows that the rock consists of very fine- to fine-grained, poorly to moderately sorted, angular to subrounded quartz grains; calcite or siderite cement is nearly half of the rock. The rock is poorly to moderately packed with few grains touching. Mottles are formed either by areas of undisturbed sand grains surrounded by irregular ribbons of illite, calcite, and gypsum, or by the aggregation of quartz grains into areas of greater and lesser abundance associated with variations in siderite grain size. The poor packing and the mottling suggest that cementation took place during deposition and that the force of crystallization may have pushed some grains apart and slightly increased the volume of the rock (SWINEFORD, 1947).

PALEONTOLOGY

Fossil molds and casts are sparse to abundant in this facies which contains fossil associations of several other facies. Repichnia and *Rhizocorallium* are the only fossils present at most localities.

The three Clark County localities contain sparse, mixed, disturbed-neighborhood assemblages of trace fossils, *Trachycardium, Gryphaea,* ostreids, *Adkinsites,* and *Lingula. Trachycardium* may be preserved in the area of its habitat. In Clark County this unit may prove to be a useful local stratigraphic datum because it is present in several measured sections 40 to 60 feet above the base of the Kiowa (seen also in sec. 35, T. 30 S., R. 23 W.).

In Rice County, Loc. R2, mottled sandstone has two fossil associations, a lower in-place trace fossil association, and an upper mixed, disturbed-neighborhood assemblage of the *Crassostrea* association. The sand is cemented by calcite that locally forms concretions and locally is absent. The *Crassostrea* association is diverse, with four species of oysters, which make up 65 percent of the fauna, a total of twelve species, and a diversity coefficient of 3.94.

Mottled sandstone at Loc. S9 contains a faunal assemblage similar to the pteriid-mytilid association of the thin-bedded sandstone facies. This assemblage can be divided into two local zones characterized by different modes of formation and by different dominant species. The lower disturbed-neighborhood assemblage has *Trachycardium, Scabrotrigonia,* and *Flaventia* as the dominant genera, constituting 75 percent of the fauna. Fossils are concentrated in siderite concretions and are very rare outside of them. Within the concretions the shells are in apparent random orientation, many being perpendicular or oblique to the bedding.

The upper zone contains an in-place assemblage characterized by *Modiolus* and *Gervillia,* which make up 72 percent of the fauna. Their articulated shells are concentrated along obscure stratification planes with the plane of commissure horizontal.

Concretions are rare and fossils serve as loci of iron oxide concentration, probably a weathering product of siderite nodules. The upper surface of this unit at the contact with the overlying dark-gray shale has sparse *Rhizocorallium* burrows and *Homomya* sp. A in life position with its anterior portion buried in sand.

The fauna of both units together is quite diverse with 18 species and a diversity coefficient of 6.66. These two zones are developed only locally and could not be distinguished a quarter of a mile along the continuous outcrop.

The only mottled-sandstone unit seen in the upper part of the Kiowa is at Loc. E8 and contains a sparse assemblage of Repichnia, *Scabrotrigonia,* and *Cardita?*. The assemblage is probably of a disturbed-neighborhood origin.

INTERPRETATIONS

The mottled-sandstone lithofacies differs from the thin-bedded sandstone lithofacies mainly in its minor sedimentary structures. This facies probably represents a similar type of primary environment: a sublittoral, sandy bottom that has been modified by secondary processes. The texture of the facies indicates that burrowing organisms disturbed the sand after deposition and before cementation (Moore and Scruton, 1957). Trace fossils support this conclusion. However, shell fossils are different from locality to locality indicating that local environments varied; and at many localities of mottled sandstone, mollusks were absent or not important.

More specific conclusions can be stated about unit 3, Loc. S9. The lower *Trachycardium* zone consists mainly of shallow burrowing filter-feeders that prefer a clean sand substrate. The aggregation and apparent random orientation of shells probably was accomplished by burrowing activity. Toots (1965) discussed three processes that may cause random orientation, and concluded that "most occurrences of random orientation can be explained by activity of burrowing organisms." The burrowed and mottled texture of the rock strongly supports this hypothesis. It is possible at this locality that the force of crystallization of siderite cement caused some further reorientation of shells as of mineral grains (Swineford, 1947). However, no evidence at this locality suggests this. Probably siderite was precipitated soon after deposition and burial and did force sand grains slightly apart to form the poorly packed texture. The common glauconite pellets probably were derived from fecal matter in a slightly reducing environment (Burst, 1958); such an environment is also indicated by the siderite.

The upper pteriid-mytilid zone consists mainly of byssate filter-feeders and is extensively burrowed. The zone probably represents a slight difference in environment or a change in source of derivation of mollusk shells. Siderite nodules are developed only around the fossils, suggesting that decay of organic matter locally lowered the oxidation potential.

SHELL CONGLOMERATE LITHOFACIES

LITHOLOGY

Moderate brownish-gray to light grayish-brown, laminated to thin-bedded shell conglomerate is rare to common in the lower and middle parts of the Kiowa. These strata are thin, tabular, and laterally discontinuous, pinching out into the dark-gray shale facies. Individual units are no more than 0.5 to 1 foot thick, and contacts are relatively sharp. Stratification normally is poorly developed and obscured by the large number of shells, which are subparallel and horizontal. Where the abundance of shells decreases to less than about 40 percent of the rock, this facies grades into the thin-laminated sandstone facies, and commonly the upper surfaces of these units are marked by interference ripples.

In some shell conglomerates, notably unit 13, Loc. C1 and unit 6B, Loc. K1, shells are concentrated in the lower half of the unit; and the upper half is calcareous, clayey, laminated sandstone, resulting in a type of graded bedding.

Two lithologic types of shell conglomerates are distinguished in thin section by differences in the amount of inorganic detritus. Up to 95 percent of the relatively clean shell conglomerate consists of a shell-fragment framework and carbonate cement. Detrital material other than shells is less than 15 percent of the rock. Silt to very fine-grained quartz, phosphate pebbles and fragments, and glauconite pellets are common. Locally shells are recrystallized to coarse-crystalline calcite. Cement is either microcrystalline to fine-crystalline siderite or medium- to coarse-crystalline calcite with a trace of intermixed carbon. Local areas of coarse-crystalline calcite appear to be void fillings. Locally, marcasite(?) and gypsum replace carbonate and shells. Brown iron oxide is disseminated throughout and occurs as irregular grains in the matrix.

Sandy shell conglomerate consists mainly of shells and carbonate cement which together constitute 60 to 85 percent of the rock. The remaining 15 to 40 percent of the rock is comprised of the above detrital minerals. Additional minerals present in trace amounts are mica and feldspar. The matrix consists of microcrystalline to fine-crystalline carbonate that locally is recrystallized to spherules of radiating carbonate prisms. Much iron oxide stain and irregular grains and illite are disseminated throughout. Some voids between shells and inside of shells contain coarsely-crystalline calcite which is in contact with the matrix of microcrystalline carbonate. This suggests that the matrix was formed before void-filling calcite was precipitated. In general, the microcrystalline carbonate was formed first, locally recrystallized, and later was partly replaced by marcasite(?), gypsum, and iron oxide.

PALEONTOLOGY

Calcitic shells are common to very abundant in this facies. Most commonly, the fossils occur as mixed-transported assemblages. Three fossil associations can be distinguished: 1) *Gryphaea* association; 2) *Crassostrea* association; 3) *Cyprimeria* association. Other characteristic species are present, and the relative abundances vary from unit to unit.

The mixed-transported and disturbed-neighborhood assemblages of the *Gryphaea* association are characterized by 51 to 100 percent of one or several species of *Gryphaea*. As the percentages of *Cyprimeria, Flaventia,* and *Turritella* increase this association grades into the *Cyprimeria* association; and as the percentage of *Crasso-*

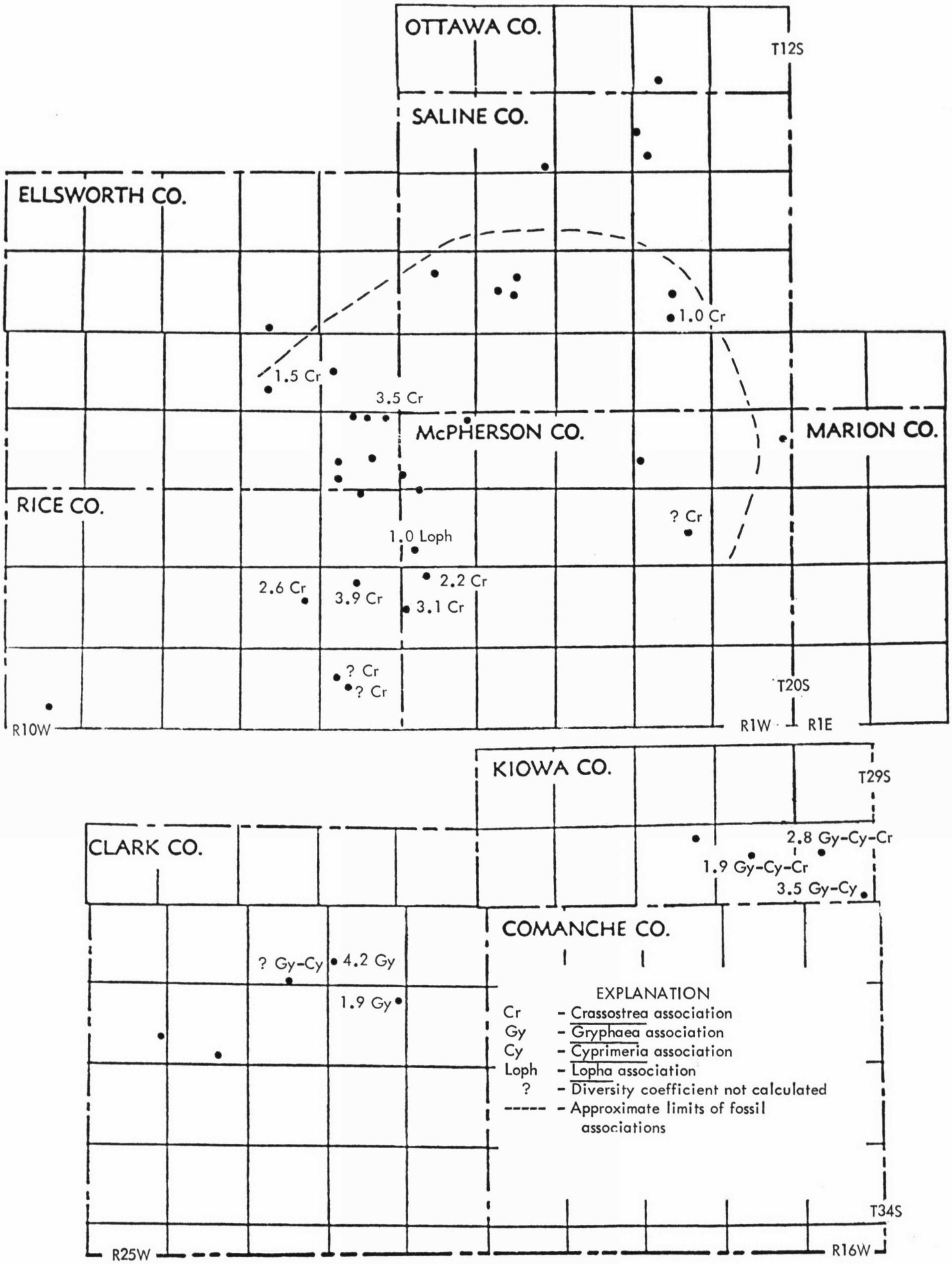


FIG. 9. Maps showing distribution and diversity of *Crassostrea, Gryphaea, Cyprimeria,* and *Lopha* associations.

strea increases, it grades into that association. Various other species are present locally and in small amounts. The diversity coefficient ranges from 2.01 to 4.22 and averages 2.90. The *Gryphaea* association occurs in sandy shell conglomerate in southern Kansas (Fig. 9).

The *Crassostrea* association occurs as transported, mixed-transported, and locally, disturbed-neighborhood assemblages. This association is composed of 35 to 100 percent of shells of that oyster. Other abundant species are *Turritella belviderei* and *Corbula?* or *Crassinella,* which together may constitute as much as 63 percent of the fauna. The diversity coefficient ranges from 1.00 to 5.06 and averages 2.04. This association occurs generally in clean shell conglomerate in central and southern Kansas (Fig. 9).

Cyprimeria makes up 2 to 19 percent of the *Cyprimeria* association which occurs in mixed-transported assemblages; ostreids constitute less than 35 percent of the fauna. Other characteristic or abundant species are *Flaventia belviderensis, Turritella belviderei, Drepanochilus kiowanus,* and *Trachycardium kansasense.* The diversity coefficient ranges from 2.67 to 5.89 and averages 4.12. This association occurs in middle Kiowa sandy shell conglomerates in southern Kansas (Fig. 9).

INTERPRETATIONS

Most of the shell conglomerate units were probably deposited by storm-generated currents. The extreme fragmentation of fossils, the abundance of sand, the ripple marks, the oriented *Turritella* shells, the concave-down, subparallel orientation of bivalve shells, and the local graded-type bedding suggest this hypothesis. If it is correct, the fossil assemblages would reflect environments of the source areas, not of the shell conglomerate lithofacies. Thus, the sandy *Gryphaea* association might have been derived from a firm sand substrate favorable to epifaunal filter-feeders. The sandy *Cyprimeria* association probably was derived from several habitats with epifaunal and shallow, infaunal communities on sandy substrates. The less sandy *Crassostrea* association probably was derived from oyster beds where there was little sand.

The geographic distribution of the various fossil associations in the shell-conglomerate facies suggests regional environmental differences. The *Gryphaea* and *Cyprimeria* associations are restricted to southern Kansas, although most species in the latter association are found rarely in central Kansas. The *Crassostrea* association is present in both areas, and in southern Kansas a small percentage of *Gryphaea* usually is associated. If *Gryphaea* is less tolerant of lowered salinities than *Crassostrea,* as suggested by Bergquist and Cobban (1957), salinity probably was greater in southern Kansas than in central Kansas.

Included in the *Gryphaea* shell-conglomerate facies is the "Champion shell bed" (Cragin, 1895b). This basal Kiowa sandy shell conglomerate is present only in the vicinity of Belvidere, where it overlies the Cheyenne Sandstone. Fossils occur as a disturbed-neighborhood assemblage and probably are preserved in the habitat in which they lived. The diversity coefficient at two localities is 2.38 and 3.81, with a total of eleven species found in this study. This mode of formation and the reported diversity (Cragin listed 36 species) distinguish this basal unit from shell conglomerates higher in the sequence. Most of the species are represented by one or two specimens found by Cragin or Twenhofel. Cragin defined this unit as a formation because 14 species were restricted to it and because its fauna was more similar to the Fredericksburg fauna; whereas the overlying faunas were similar to the Washita fauna. Twenhofel (1924) emphasized that the faunas of the "Champion shell bed" and the Kiowa were not essentially different.

The fauna of this basal unit, characterized by *Gryphaea hilli, G. mucronata,* and *G. corrugata,* is distinct from other associations and has ecologic significance. The unit probably represents the first sublittoral sand substrate of a transgressing sea. Some of the sand may have been derived from the underlying Cheyenne Sandstone. The extreme diversity of species and the dominance of a few suggests that the environment was nearly fully marine and similar to the open sea to the south (Texas), but that some factor or factors were near the limiting tolerance level for most stenohaline marine animals (*Actinastrea, Salenia, Exogyra, Pecten,* and *Serpula*). Salinity may have been one of these factors. When the new habitat was opened by transgression, many species migrated into the area. But conditions were not favorable for the establishment of populations of most of these species, and only a *Gryphaea* community could flourish.

The *Crassostrea* shell-conglomerate facies in central Kansas was called the "Windom Member" by Twenhofel (1924). This unit was characterized by abundant *Crassostrea kiowana* and *Turritella belviderei,* five other less common species, and by cone-in-cone layers. Generally the fauna varied from place to place (Twenhofel & Tester, 1926), and the unit was used as a marker bed within the Kiowa. But the unit does not have the correlative value they stated, because it occurs at several stratigraphic levels in some sections (Fig. 10-13). Also, other fossil associations and lithologies, such as the Corbulid association and siltstone, are associated with cone-in-cone, which even also occurs without fossils. Cone-in-cone has environmental significance (Franks, 1966) but not stratigraphic value. Franks interprets cone-in-cone in the Kiowa as representing localized reducing conditions within the sediment resulting in calcite precipitation prior to compaction.

GEOGRAPHIC AND STRATIGRAPHIC VARIATIONS

Some geographic variations in the distribution of fossils have already been mentioned and are here summarized. A count of known Kiowa megainvertebrate species shows that 49 are restricted to southern Kansas, 36 to central Kansas, and 35 occur in both areas. Of these 120 species, 28 are gastropods, and 73 are bivalves. Mesogastropod species outnumber the other three gastropod orders 21 to 7. Bivalves include four species of Protobranchia (*Nucula, Nuculana,* and *Yoldia*) and 69 species of Polysyringia, which includes all the other species in the Kiowa (classification of Purchon, 1963). This distribution of bivalve groups compares favorably with the general survey by Nicol & Gavenda (1964). They concluded that Polysyringia are by far the most abundant group in warm, shallow seas, and that Protobranchia and Septibranchia are abundant in deeper, colder waters.

The *Gryphaea* and *Cyprimeria* associations are restricted to southern Kansas (Fig. 9); the *Brachidontes* association is known only in central Kansas (Fig. 7). The *Trachycardium-Turritella* and pteriid-mytilid associations are likewise restricted to central Kansas (Fig. 8); however, some species from these groups are abundant in the shell-conglomerate facies in southern Kansas as transported assemblages.

Postulation of a salinity gradient between southern and central Kansas is based on the virtual restriction of *Gryphaea, Cliona, Membranipora?, Salenia, Actinastrea,* and *Serpula* to southern Kansas. Environmental significance of other restricted species is not known.

The stratigraphic distribution of ammonoids and *Inoceramus bellvuensis* was discussed under the heading of "Stratigraphy and Correlation." A few additional generalizations on stratigraphic distribution of lithofacies and fossils can be made tentatively. In both central and southern Kansas, the dark-gray shale facies commonly is replaced upwards in the section by the mudstone facies, and sandstones make up a greater part of the uppermost Kiowa. Distribution of the coarser clastic interbeds is more complex, and no generalization can be made. In southern Kansas the thin-laminated sandstone facies is common in the basal part of the sequence; shell conglomerate is present somewhat higher; commonly thin-laminated sandstone replaces the shell conglomerates in the upper part; and the uppermost Kiowa consists of thin- to massive-bedded sandstone. In central Kansas shell conglomerates are less common and generally underlie thin-laminated sandstone, which gives way to thin-bedded sandstone in the upper part. As lithofacies succeed one another in stratigraphic succession, so do fossil associations. Variations in each section are complex, but generally the offshore *Nuculana* association is replaced by the corbulid-breviarcid association, which is replaced by the nearshore *Trachycardium-Turritella* association. Stratigraphic variation in diversity is likewise irregular, but generally the variations are summarized by this pattern: relatively low diversity in the lower part of the Kiowa; somewhat higher diversity in the middle Kiowa; and lower diversity again in the upper part.

COMPARISON OF KIOWA FOSSIL ASSOCIATIONS WITH ANALOGOUS RECENT MARINE COMMUNITIES

INTRODUCTION

Associations of fossil species having similar responses to hydrographic conditions and substrates probably represent parts of ancient communities. Johnson (1962, p. 32) stated "if we assume that recurring associations of species existed at a given time in the past, then some recurring combinations of fossils must represent life assemblages."

The graphs in Figure 14 show that most Kiowa associations consist of species having similar or complementary feeding and dwelling habits and substrate preferences. The *Cyprimeria* association contains representatives of two or three habitats. This association occurs as a mixed-transported assemblage and reflects paleoecologic conditions within the source areas.

A comparison of these fossil assemblages with modern marine communities is based on two generalizations: 1), that benthic communities consist of a very few abundant species which occur "together because of similar responses to the physical environment" (Johnson, 1964); and 2), that "parallel communities" inhabit "the same type of bottom at similar depths and are characterized by different species of the same genera but replace each other in accordance with the geographical region" (Thorson, 1957, p. 521). If the characterizing species are replaced in space, they can be replaced in time, so that Thorson's "parallel communities" should be represented by fossil associations in the geologic record. In fact, Waage (1964) mentioned several Upper Cretaceous associations that recur in stratigraphic succession. On the other hand, the Kiowa fossil associations are not fossil communities (Fagerstrom, 1964), if a community is considered to be an assemblage of living organisms (MacGinitie, 1939), for such terminology is contradictory. But the fossils once were part of an ancient community and, thus, do represent a part of that deceased community.

Johnson (1964) summarized and analyzed several problems raised by the suggestion that fossil associations

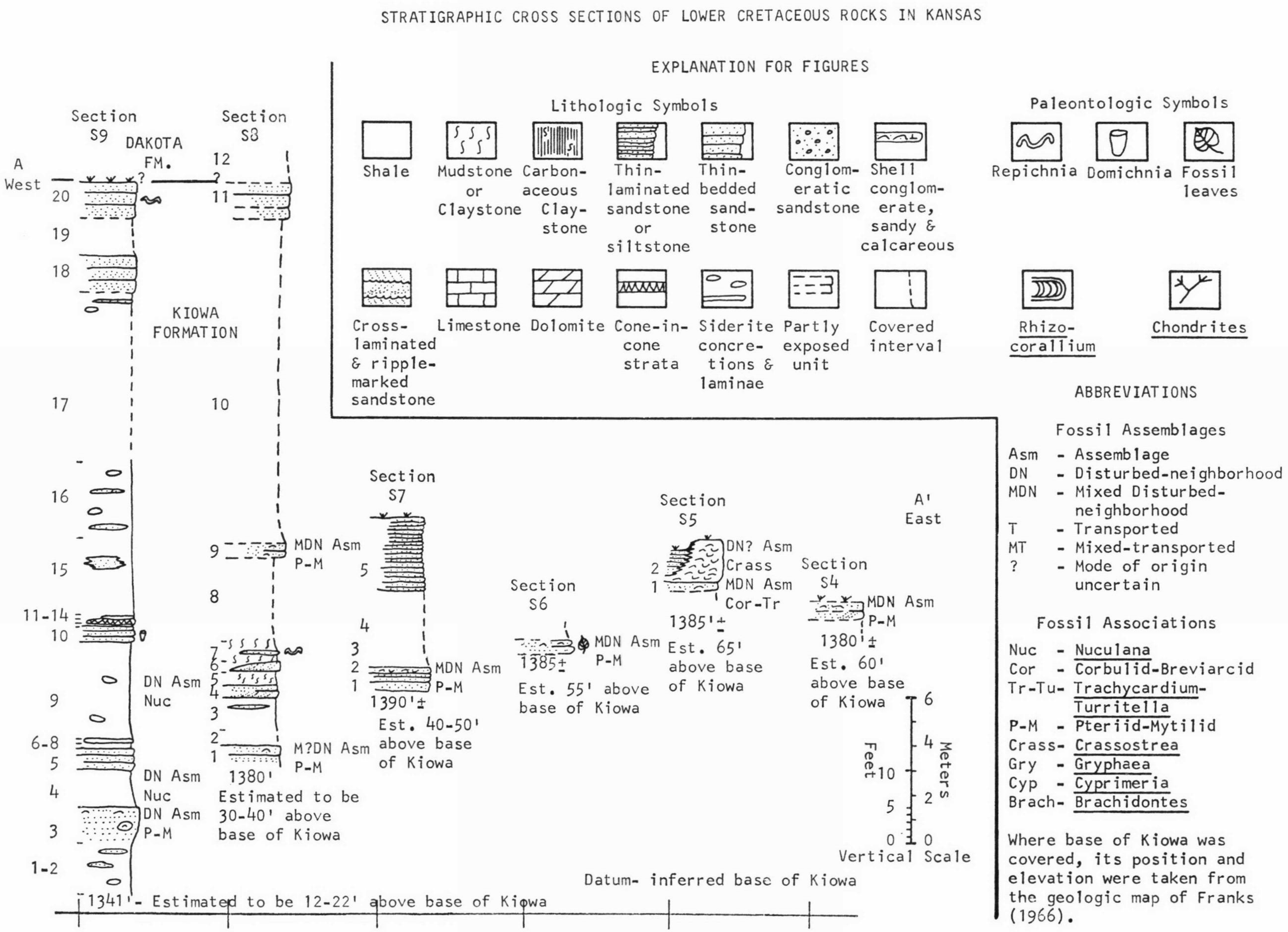
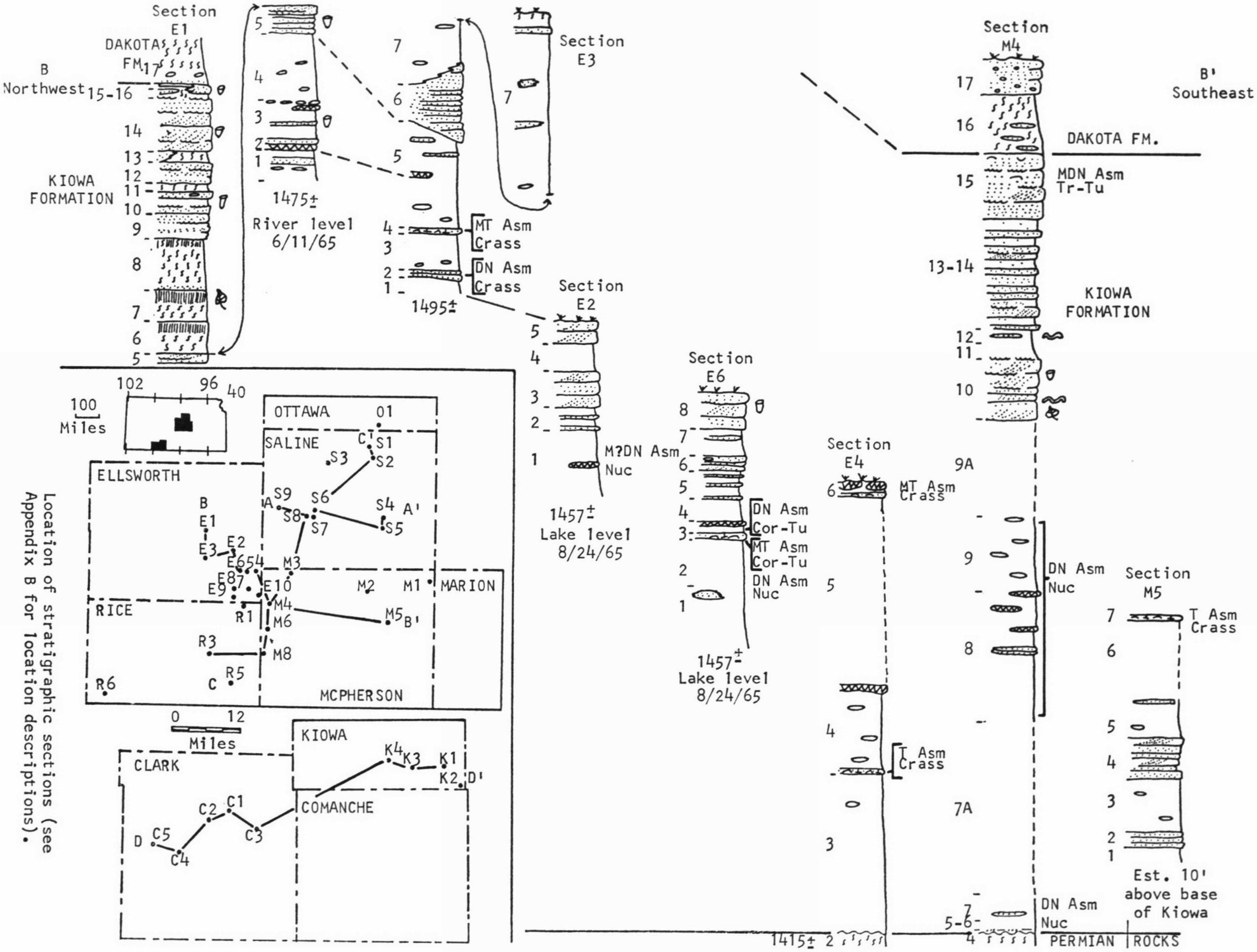


FIG. 10. Stratigraphic cross section A-A' of the Kiowa Formation in central Kansas (for location see Fig. 11). Descriptions of measured sections in Figs. 10-13 are in SCOTT (1967a), FRANKS (1966), LATTA (1946), and TWENHOFEL (1924).



Location of stratigraphic sections (see Appendix B for location descriptions).

FIG. 11. Stratigraphic cross section B-B' of the Kiowa Formation in central Kansas. For symbols and abbreviations see Fig. 10. Sections E1-E3 and E6 were correlated with section E4 by assuming a northward dip of 7 feet per mile (MERRIAM, 1963).

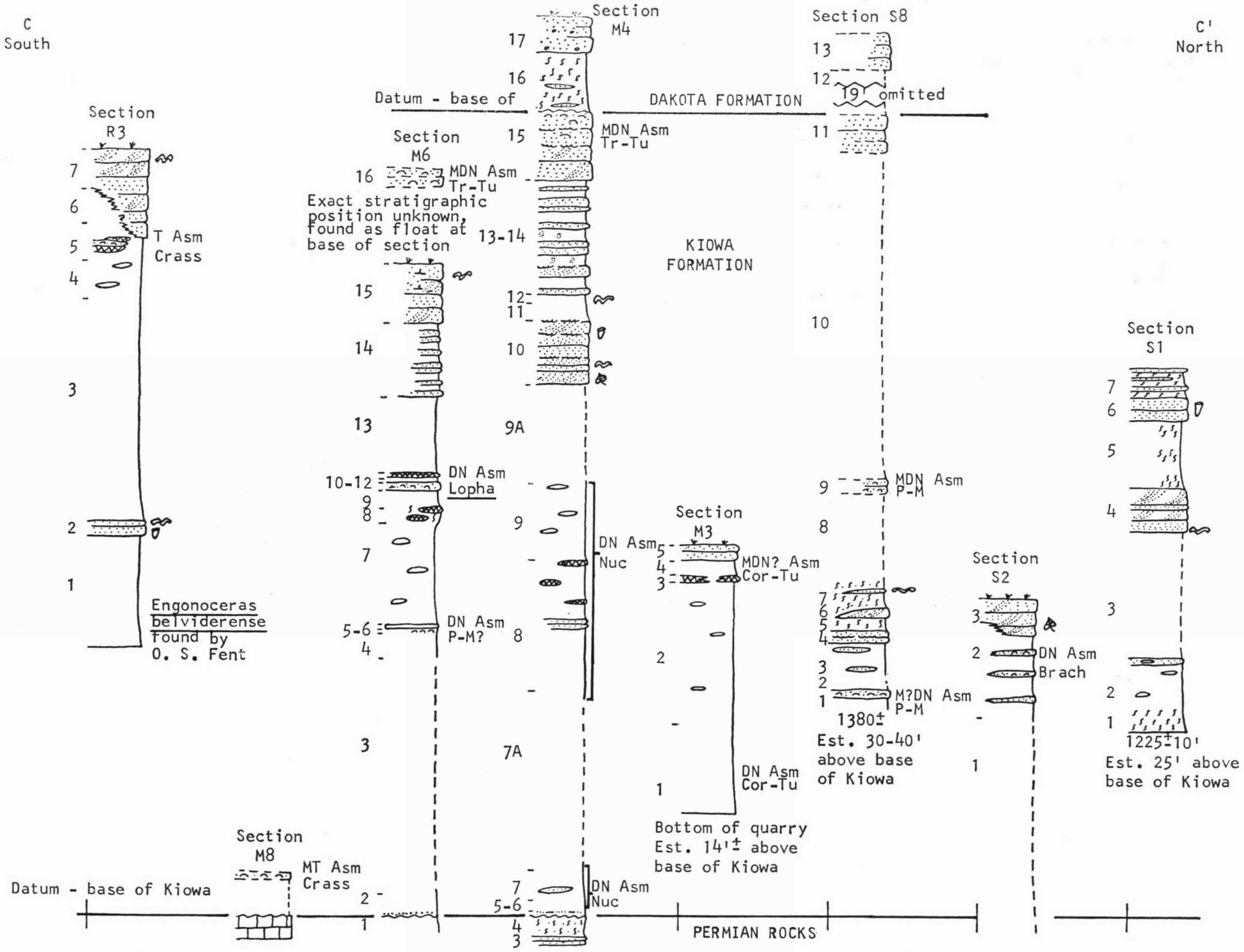


FIG. 12. Stratigraphic cross section C-C′ of the Kiowa Formation in central Kansas. For symbols and abbreviations see Fig. 10; for location see Fig. 11.

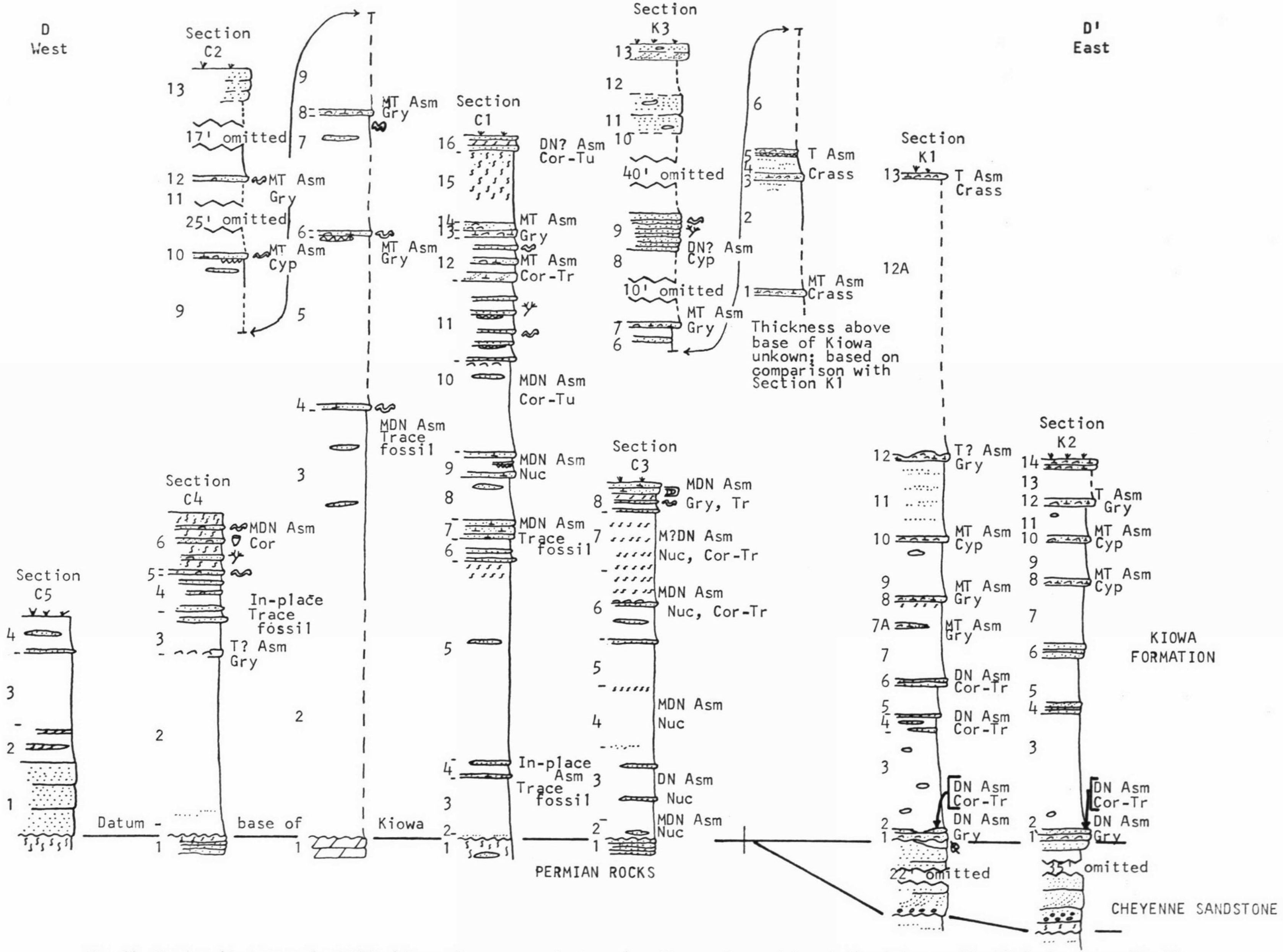


FIG. 13. Stratigraphic cross section D-D' of Lower Cretaceous rocks in southern Kansas. For symbols and abbreviations see Fig. 10; for location see Fig. 11.

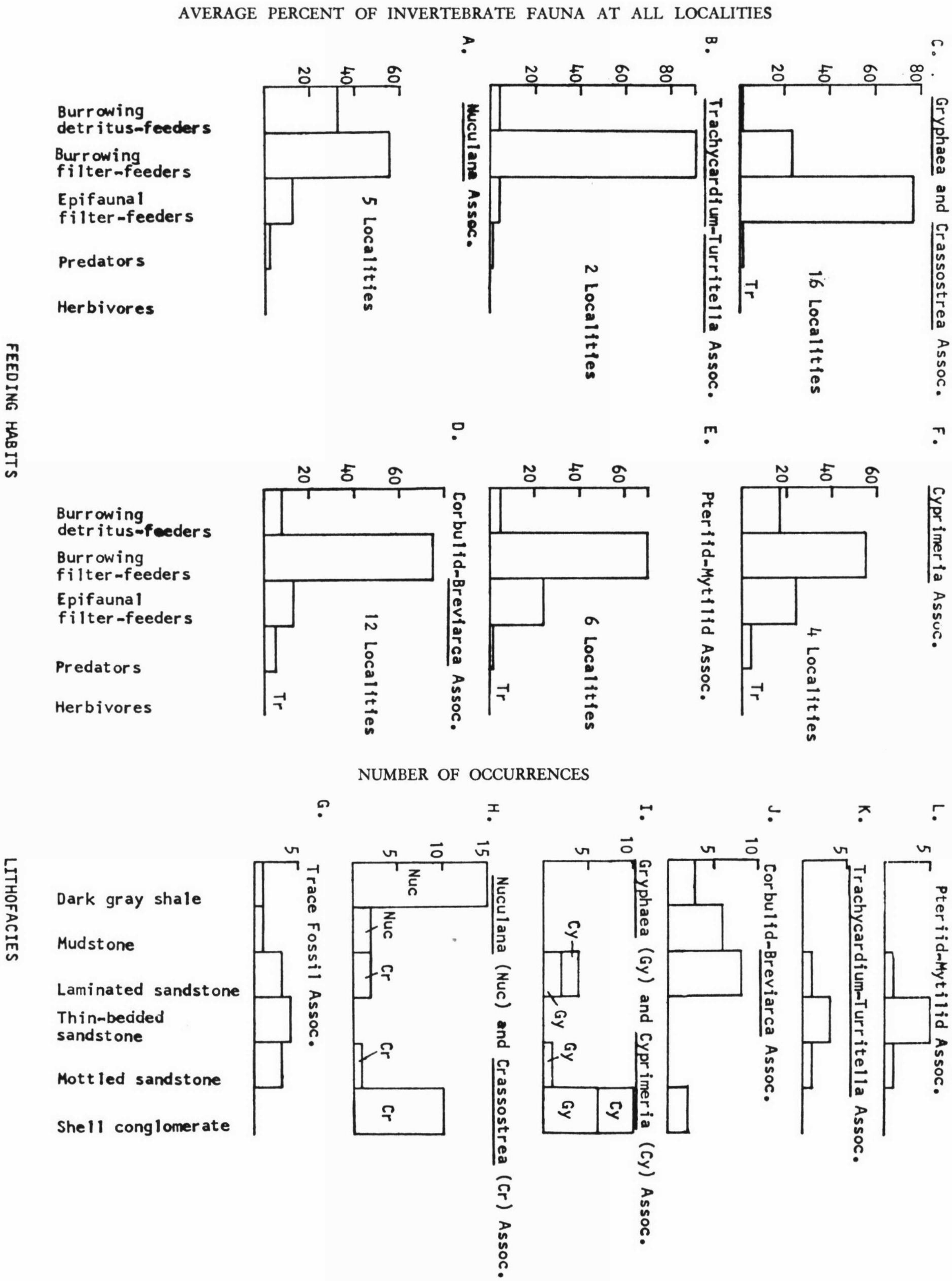


FIG. 14. Histograms A-F showing average relative abundance of species in each feeding-habit category in the various fossil associations. Histograms G-L showing the frequency of each fossil association with each lithofacies *(see facing page)*.

represent ancient communities. First, many specimens are not preserved where they lived. Second, fossil assemblages differ from the ancient communities because many of the species are not preserved. Therefore, some important modern communities of polychaetes and other soft-bodied organisms will be represented in the geologic record only by indirect evidence, if at all. "Parallel communities" dominated by animals with hard parts, however, should be represented by fossils.

Third, most level-bottom communities are defined without including the deep burrowing forms, which may be more abundant and characteristic than the other animals. These communities of epifaunal and shallow burrowing animals are not permanently confined to one area and may move to other favorable areas during a period of years (MacGinitie, 1939). MacGinitie concluded that "the surface and subsurface communities are separate entities, having but little influence upon one another" (1939, p. 44). That these two communities do not interrelate remains to be proven as a widely valid generalization.

A fourth problem is more serious. Different species within a family may dominate very different habitats. *Macoma* and *Abra* (Tellinidae) form estuarine communities on muddy substrates, and *Tellina* forms an open marine community on a firm sand substrate (Thorson, 1957). Of the many species of cardiids, some are narrowly restricted by the environment, and others, like *Cardium edule,* adapt to many different habitats. This variation of habitat adaptation within a family is the weakest link in comparing fossil associations with modern communities. Generally, feeding and dwelling habits of molluscan species are grossly similar within families, and direct geologic evidence of substrate preference may support the comparison. The consistent recurrence of associations of certain dominant species strongly suggests that the Kiowa associations reflect the ancient communities to some degree.

In the following section the Kiowa fossil associations are compared to analogous modern benthic marine communities. Certain paleoecological inferences will be drawn and used as working hypotheses to interpret environmental changes during deposition of the Kiowa Formation.

NUCULANA ASSOCIATION

This fossil association is characterized by burrowing detritus-feeders and filter-feeders that prefer muddy substrates (Fig. 14,*A,H*): *Nuculana, Yoldia, Nucula, Pholadomya?, Leptosolen, Turritella, Drepanochilus, Lingula,* and *Squilla?*. Most commonly it occurs in the dark-gray shale lithofacies.

Nuculana and *Squilla?* are not dominant members of any described Gulf Coast community; but they are present in at least two different environments, the lower sound-prodelta slope area and the deeper shelf area (Parker, 1956). In the lower sound-prodelta slope environment the community is dominated by the mactrid, *Mulinia,* and by *Nassarius,* a carnivorous snail. The substrate is silty clay to clayey silt; salinity is about 28 to 36‰, depth ranges from 2 to 15 m., and the water is very turbid. The deeper shelf community is not completely known, but *Nuculana, Yoldia, Nucula, Squilla,* and *Cadulus* are among the more common genera represented. Depth ranges from about 27 to 92 m., the substrate generally is silty clay, and salinity is about 36‰.

The *Pandora-Yoldia* community in restricted bays among the San Juan Islands in Puget Sound prefers a soft, muddy bottom, 2 to 73 m. deep (Shelford and others, 1935). Currents are weak, plankton is abundant, and oxygen content and salinity are lower than in the other areas of Puget Sound. Several polychaetes and starfish are also important members of this community. This community is commonly associated with the nearshore *Macoma-Paphia* community, which apparently is not represented in the Kiowa.

In Greenwich Bay, Rhode Island, *Nucula proxima* and *Squilla empusa* are characteristic species of the *Ampelisca* community, which is dominated by that amphipod (Stickney & Stringer, 1957). Other common animals are *Macoma, Pitar, Mulinia,* and polychaetes. The community inhabits a muddy substrate at depths of 2 to 5 m. Summer salinities range from 27 to 30‰; tidal currents are weak.

The Kiowa *Nuculana* association probably inhabited a muddy bottom in a large epicontinental sea rather than in a small, restricted bay, because the dark-gray shale lithofacies has wide geographic distribution. Population densities of this and all other associations varied from place to place and locally were relatively high; the overall distribution is clumped. Clustering of individuals is somewhat common in benthic communities, and the causes are many and complex (Waage, 1964). The mottled structure of the shale suggests that burrowing organisms were common in parts of the basin, and their distribution coincided with an abundance of bivalves. Elsewhere the infauna was sparse, inhibited perhaps by a lower oxygen content of the sediment and bottom waters. Turbidity may have been great, and currents washed in sand-sized detritus and shell fragments. The salinity and depth ranges are indeterminate, but probably in most places the depth was greater than depth of normal wave base.

CORBULID-BREVIARCID ASSOCIATION

This association is characterized by shallow-burrowing filter-feeders that preferred sandy mud or muddy sand substrates (Fig. 14,*D,J*): *Corbula?, Breviarca,* and *Turritella.* As the sandy substrate becomes cleaner *Trachycardium* replaces *Turritella.* The association is most common in the laminated sandstone facies and the claystone facies.

Corbula is one of the characteristic genera in the *Syndosmya* community, which also consists of *Cultellus* and *Nucula* (THORSON, 1957, p. 510). It populates estuaries and other sheltered areas, commonly in a "somewhat reduced salinity," and on sandy mud to muddy sand bottoms. Depth range is 5 to 29 m.

Cardium and *Turritella* communities are discussed on pages 46-47. *Corbula, Venus,* and the polychaete *Nerinides* form a community on fine-grained sand in the Black Sea (CASPERS, 1957). *Cardium* and *Mytilus* are among the many other reported genera. Depth ranges from 0 to 15 m., and salinity is generally less than 15‰.

The corbulid-breviarcid-*Trachycardium* association in thin-laminated sandstone represents a habitat different from the corbulid-breviarcid-*Turritella* association in mudstone. Generally sandstone or siltstone occurs as a thin bed within the dark-gray shale lithofacies and probably represents a sand sheet perhaps deposited by storm-generated currents. In southern Kansas these units are replaced upwards in the sequence by shell conglomerate. *Corbula?* and *Trachycardium* represent a community on a sand substrate in a well-aerated sea. Two explanations are possible. The association may have been displaced along with the sand by wave action and would reflect the environment in the source area. Or the association colonized the sand sheet soon after its deposition and was ultimately killed, perhaps by renewed mud deposition. The associations have been interpreted to be in their life neighborhood because the association is in its preferred substrate. Field data on mode of occurrence are not conclusive evidence for or against either hypothesis.

The corbulid-breviarcid-*Turritella* association probably inhabited a muddy bottom. The Eh of the sediment probably was oxidizing, as indicated by its lighter color, and perhaps the sediment was bathed by more regular and constant currents. Salinity probably was less than normal marine (36‰). The intercalation of this association with the *Nuculana* association suggests that they occupied closely related habitats and that hydrographic conditions of each habitat alternated for a short period.

The corbulid-*Turritella* shell conglomerates (unit 3, Loc. M3; unit 3B, Loc. E6) probably represent local current accumulations of animals living within the area. The units are closely associated with dark-gray shale and claystone, where the animals probably lived. Cone-in-cone concretions directly overlie the shell beds and indicate alkaline and less reducing post-depositional conditions than in the dark-gray shale (FRANKS, 1966).

TRACHYCARDIUM-TURRITELLA ASSOCIATION

This association is characterized by shallow-burrowing filter-feeders that prefer sandy substrates (Fig. 14, *B,K*): *Trachycardium kansasense, Protocardia texana,* and *Turritella belviderei.* It is most common in the thin-bedded sandstone lithofacies.

Species of *Cardium* are characteristic of the Recent *Macoma* community, along with *Macoma, Mya,* and *Arenicola* (THORSON, 1957, p. 505). This shallow-water community is common in brackish tidal flats and estuaries from the intertidal zone to a depth of 60 m. or more. On sandy bottoms *Cardium* is more abundant than *Macoma* and *Arenicola,* and in the Mediterranean Sea *Cardium edule* is the only member of this "reduced" community. In deeper water the community is transitional with the *Venus* community.

Species of *Turritella* together with *Echinocardium* and *Aporrhais pes pelecani* dominate the *Amphiura* community on sandy mud bottoms at depths from 15 to 100 m. *Turritella* and *Cerithium* communities in New Zealand and Japan populate substrates of sandy mud to muddy sand and coarse shell debris at depths from 4 to 40 m. (THORSON, 1957, p. 514).

VAN STRAATEN (1956) considered *Turritella tricarinata communis* and three species of *Cardium* found in beach deposits typical open-ocean and tidal-inlet forms. *Cardium edule* apparently is abundant in many environments from open-sea beaches to tidal flats.

The dominant members of the *Trachycardium-Turritella* association apparently represent diverse substrates. *Trachycardium* probably inhabited a sandy bottom within the zone of wave action; whereas *Turritella belviderei* probably inhabited both muddy and sandy bottoms. Recent *Turritella* seems to adapt to a variety of substrates, and flourishes on mud. Either the Kiowa *Turritella* was likewise adaptable, or it was transported onto the sandy substrate occupied by *Trachycardium.* However, the widespread and abundant occurrence of *Turritella* and the absence or very small representation of other muddy bottom species suggests that *Turritella* was adaptable to a sandy substrate as well as to a muddy bottom.

This association probably occupied a nearshore, infralittoral, sandy substrate. Salinity was probably less than 30‰ because no high-salinity animals are found in the association. Depth was as shallow as depth of wave action. The clumped distribution of specimens may be due in part to a gregarious tendency of the species and in part to post-mortem distribution by currents, or other unknown factors.

PTERIID-MYTILID ASSOCIATION

This association is characterized by epifaunal filter-feeders and an abundance of shallow-burrowing filter-feeders that prefer sandy substrates (Fig. 14,*E,L*): *Gervillia mudgeana, Pteria salinensis, Modiolus* sp. A, *Ostrea rugosa, Linearia kansasensis, Trachycardium, Corbula?,* and *Turritella kansasensis.* At different localities one or the other of the four epifaunal species may be the most abundant or even the only epifaunal species. This association, too, is most common in the thin-bedded sandstone facies.

The *Tellina* community is a shallow-water community (intertidal zone to 9 m. deep) characterized by *Tellina, Donax,* and *Dosinia* (THORSON, 1957, p. 507). This community flourishes on hard, clean sandy substrates. At depth this community is transitional with the *Venus* community. On the Gulf Coast the *Tellina* community consists also of the sand dollar, *Mellita,* and the sea pansy, *Renilla.* It exists on hard, sandy bottoms near barrier islands where salinity ranges from about 25 to 34‰. *Dinocardium* is a common member of this community (PARKER, 1956).

Mytilus forms banks together with *Ostrea edulis* and *Modiola* [sic] *adriatica* in the Black Sea (CASPERS, 1957). The banks grow in areas of relatively weak currents, at very shallow depths down to 64 m. The substrate between banks consists of soft mud. Salinity ranges from 15 to 17‰.

The Upper Cretaceous *Protocardia-Oxytoma* assemblage zone in the Fox Hills Formation, South Dakota (WAAGE, 1964), is similar in faunal composition to this Kiowa association. *Protocardia* and *Oxytoma* occur in sandy limestone concretions.

The most abundant members of the pteriid-mytilid associations, *Trachycardium* and *Turritella kansasensis,* seem to represent a sandy substrate, while the characteristic members, *Gervillia, Pteria, Modiolus,* and *Ostrea rugosa,* seem to reflect a rocky substrate or shell bank habitat. The restricted distribution of individual species suggests that the general habitat varied locally. The occurrence of *Modiolus* sp. A and *Gervillia mudgeana* in apparent life position at Loc. S9 suggests that these species could attach to a firm sand substrate. *Linearia* may be analogous to Recent *Tellina* in occupying a firm, sandy bottom. *Ostrea rugosa* may have formed beds or banks near the sandy substrate in which it is preserved. The variability of the association suggests a mixing of several nearshore communities and deposition on an infralittoral, sandy bottom. The preserved habitat probably was similar to that of the *Trachycardium-Turritella* association near the top of the Kiowa.

GRYPHAEA ASSOCIATION

This association is characterized by the epifaunal filter-feeder, *Gryphaea,* which may have adapted to a sandy substrate. It is most common in the transported assemblages in sandy shell conglomerate (Fig. 14,*C,I*).

Although *Gryphaea* is extinct, its paleoecology can be interpreted by analogy with its occurrence in other fossil assemblages. In the Blue Lias of southwestern England *Gryphaea* occurs in thin shell beds in the offshore limestone facies (HALLAM, 1960). The shell beds are interpreted to be mixed, disturbed-neighborhood assemblages. HALLAM (1960, p. 38) concluded that "probably the shallow, well-aerated water was the most important factor controlling distribution, but *Gryphaea* was apparently well adapted to high rates of sedimentation."

Gryphaea washitaensis in the limestone and marl Denton Formation, northern Texas, is thought to be preserved where it lived (LAUGHBAUM, 1960). *Gryphaea* represents somewhat deeper, less turbid waters relative to the oysters farther north. Salinity was inferred to be normal marine, and climate was tropical to subtropical.

The basal, sandy *Gryphaea* shell conglomerate exposed in Kiowa County probably represents the preferred substrate of *Gryphaea* and was a nearshore, infralittoral, sandy bottom. Currents were active; water depth was shallower than depth of wave base; and salinity may have been nearly normal marine. Most of the other *Gryphaea* shell conglomerates probably were derived from such an area by storm-generated currents, and were deposited in the offshore part of the basin, where dark-gray mud was being deposited.

CYPRIMERIA ASSOCIATION

This association is characterized by *Cyprimeria kiowana* and occurs with genera representing associations of several living habits and substrate preferences (Fig. 14, *F,I*): *Flaventia belviderensis,* and *Trachycardium kansasense* were shallow-burrowing filter-feeders in a clean, sandy substrate; *Turritella belviderei* was adaptable to several substrates; and *Drepanochilus kiowanus* was a shallow-burrowing detritus-feeder on muddy substrates; *Gryphaea* was an epifaunal filter-feeder. This mixed association is most common in shell conglomerate as a transported assemblage.

The Recent *Venus* community may be analogous to part of the *Cyprimeria* association. This community is common in the open sea on a loose, clean, sandy substrate at depths from 7 to 40 m. (THORSON, 1957, p. 508). As the substrate becomes silty the tellinid, *Syndosmya,* or the brittle-star, *Amphiura,* will dominate; and as the substrate becomes hard, *Tellina* dominates.

Venus mercenaria characterizes Greenwich Bay, Rhode Island, but is not restricted to any of the local communities (STICKNEY & STRINGER, 1957). The environment is described under the *Nuculana* association; *Venus* occupied sandy to muddy substrates from the intertidal zone to the bay center.

The other associations have already been interpreted. *Cyprimeria kiowana* may have formed a community on a sandy substrate somewhat deeper and farther offshore than the *Trachycardium-Turritella* association. Other hydrographic conditions would not have differed greatly. *Flaventia belviderensis* probably was a member of the *Trachycardium-Turritella* association, although it may have lived with *Cyprimeria* also.

Thus, fossils in the middle Kiowa shell conglomerates were derived from several source areas: the nearshore, infralittoral, sandy substrate; a perhaps deeper, sandy substrate; and the muddy bottom with *Nuculana* and *Drepanochilus.*

CRASSOSTREA ASSOCIATION

This association is characterized by the epifaunal filter-feeder, *Crassostrea,* which prefers a firm, stable substrate. It too, is most common in the transported assemblages in shell conglomerate (Fig. 14,*C,H*). The *Lopha quadriplicata* association can be considered here, because its food and substrate requirements probably were similar.

Crassostrea virginica forms banks east of the Mississippi River Delta in the delta front and lower distributaries environment (PARKER, 1956). The substrate is clayey silt; salinity is about 4 to 18‰; temperature and depth of the shallow water cover are quite variable. Associated bivalves are *Macoma* and *Rangia.* Elsewhere in bays and lagoons of the Texas Gulf Coast, *Crassostrea* banks support many encrusting bryozoans, boring sponges, serpulids, annelids, mollusks, and various crustaceans (PUFFER & EMERSON, 1953). The substrate surrounding the banks is mud, and water depth ranges from 1 to 4 m. Salinity is variable and ranges from 3 to 42‰, but generally is less than 36‰.

In Apalachicola Bay, Florida, *Crassostrea* banks occur across the mouths of inlets on a sandy clay substrate (DAWSON, 1955). Water depth over the banks ranges from 1 to 5 m., salinity ranges from about 10 to 34‰ and is very unstable at most places during the year. Few other bivalves are associated, but a wide variety of other animals is found.

The *Crassostrea* association probably was derived from banks along the shoreline of the Kiowa sea. The major requirements are a firm substrate, such as other shells, and a steady current to supply food; the lack of *Cliona* borings suggests that the water was very brackish; turbidity could have been relatively great. At most localities *Crassostrea* occurs as a transported shell conglomerate mixed with species of other associations, such as *Turritella* and *Trachycardium,* suggesting that the oyster banks were near the shallow, sandy habitat. The *Crassostrea* shell conglomerate at Loc. S5 is unique in that it has an elongate, mound shape and overlies a thin-laminated sandstone with *Corbula?* and *Breviarca.* The oyster shells generally are disarticulated and in apparent random orientation. Perhaps this accumulation is a preserved bank rather than a current accumulation. Convincing evidence for either interpretation is lacking.

Lopha quadriplicata appears to have been a gregarious species (unit 10, Loc. M6) favoring a sandy substrate. It commonly occurs with the Pteriid-Mytilid association and probably occupied a closely related habitat.

BRACHIDONTES ASSOCIATION

This association is characterized by epifaunal and shallow-burrowing filter-feeders that prefer a hard sand or muddy sand substrate: *Brachidontes nonbifurcus, Homomya* sp. B, and Pyramidellidae. This association occurs at Loc. S2 in the thin-laminated sandstone facies.

Brachidontes recurvus and *B. exustus* are characteristic of the upper sound environment east of the Mississippi River Delta (PARKER, 1956). This bay area has salinities ranging from 18 to 34‰; the substrate is sandy silt and silty sand; and depth ranges from 2 to 4 m. Other common species are *Tagelus divisus, Abra aequalis,* and *Amphiopodia limbata,* a brittle star. *Brachidontes exustus* is abundant and commonly attaches to oyster shells on the *Crassostrea* banks in many bays on the Texas Gulf Coast (PUFFER & EMERSON, 1953).

Because the occurrence of this association is unique in the Kiowa Formation, it is difficult to interpret. Its presence on the northward limit of fossil distributions in the Kiowa (Fig. 7) suggests that it inhabited a nearshore embayment, perhaps associated with *Crassostrea* banks. However, the oyster has not yet been found so far north. *Brachidontes* may have attached to other firm objects, and nearby *Homomya* probably burrowed in a soft muddy or sandy substrate.

TRACE FOSSIL ASSOCIATION

This association consists of a variety of Repichnia, Domichnia, *Rhizocorallium, Chondrites,* and *Scolicia* and is most common in the three sandstone facies: laminated, thin-bedded, and mottled. Domichnia of filter-feeders and *Rhizocorallium* are members of the trace fossil *Cruziana* facies (SEILACHER, 1964); *Chondrites* and *Scolicia* can occur in any assemblage of trace fossils. The *Cruziana* facies generally is associated with oscillation ripple marks and well-stratified and well-sorted sandstone and shale. It suggests a littoral to sublittoral environment above wave base (SEILACHER, 1964).

Many of the soft-bodied annelids and crustaceans and others that could leave trace fossils are present in most of the modern benthic communities already discussed. *Chondrites* probably are tunnels excavated by sediment-feeding animals, possibly sipunculoid annelids (SIMPSON, 1957); *Rhizocorallium* probably was formed by sediment-feeding animals such as worms or crustaceans (SEILACHER, personal communication *in* HALLAM, 1960). Both occur in the offshore facies of the Blue Lias, which was deposited in relatively shallow, marine waters in a zone of weak currents (HALLAM, 1960).

The common occurrence of Domichnia in central Kansas suggests that the area was very near shore. The occurrence of *Chondrites* in southern Kansas with *Gryphaea* suggests that this animal, too, may have been limited by brackish salinities.

INTERSPECIFIC RELATIONSHIPS

Certain interspecific relationships recognized in the Kiowa fauna suggest possible community relationships. The fossil associations are not fossil communities, but

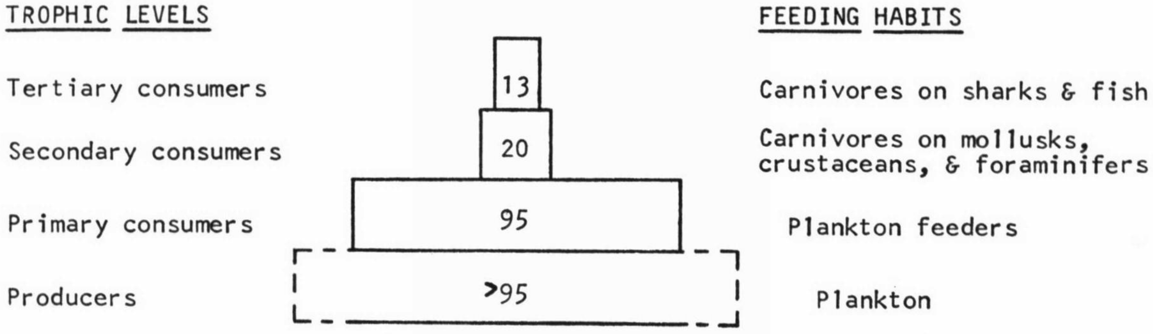


FIG. 15. Graph showing the number of species in each feeding habit and probable trophic level.

they do reflect or represent part of this community that did exist in Albian time (see p. 39). The interpretation of symbiotic relationships (in the broad sense of AGER, 1963) is a clue to which species lived together in these ancient communities.

PREDATION

Most species of the dominantly molluscan fauna were filter-feeders. A few species may have been predators and herbivores, as suggested by the habits of their Recent relatives. *Acmaea,* Trochidae, *Otostoma marcouana,* and *Amberleya mudgeana* are related to predominantly herbivorous groups. *Cadulus praetenuis* and *Pirsila?* may have preyed on Foraminifera and ostracodes on the sea floor and directly below the sediment-water interface. *Squilla?* probably preyed on a variety of small animals. *Euspira smolanensis* is closely related to the carnivore, *Natica,* which bores into other molluscan shells to feed. However, bored shells were not found, suggesting that *Euspira* fed in another way and on other foods. *Ophiura* probably was a carnivore.

Recent species of Pyramidellidae are parasites on echinoderms, but the Kiowa species probably had a different host and even a different feeding habit, although unknown. Its great abundance at Loc. S2 suggests that it was not directly dependent on another species. The other species in the association are filter-feeders, and perhaps this species of Pyramidellidae was a filter-feeder or detritus-feeder. The ammonoids probably preyed on a variety of species.

Most of the vertebrates were carnivores; thirteen probably preyed on fish and sharks, eleven on mollusks and crustaceans, and two (turtles and *Lepidotus*) may have been herbivores or scavengers. Some species may have preyed on more than one of these groups.

The Kiowa species can be classified according to their feeding habits: filter-feeders and detritus-feeders upon plankton and planktonic detritus; carnivores preying upon mollusks, crustaceans, and Foraminifera; and carnivores preying upon sharks and fish. Some species may be preyed upon by other species in the same category, and thus these categories obscure the more detailed food chain relations. Figure 15 shows the number of species in each feeding habit category, which is roughly proportional to the number of individuals in each category (see Table 3). This graph differs from the standard trophic level pyramid of the ecologist, which is based upon either the number of individuals, the dry biomass weight, or the gross productivity. The graph does not present the rate of production, it presents diversity. But "a characteristic of trophic levels in most communities is that the nearer a level is to the source of energy, the greater the diversity of species involved" (KENDEIGH, 1961, p. 196). The graph is analogous to a trophic level pyramid because the feeding habit categories represent the various producer and consumer trophic levels of the ancient Kiowa communities.

Plankton made up the primary producing trophic level and probably consisted of algae, eggs, larvae, juveniles of benthos and nekton, and permanently pelagic invertebrates as it does in modern seas (JOHNSON, 1957). Plankton was the major source of organic detritus. The number of species in the plankton can not be estimated but it was at least as great as the number of species having planktonic larvae, which is nearly the entire invertebrate fauna. Filter-feeders, detritus-feeders, and herbivores depended upon plankton and constituted a part of a very generalized primary consumer trophic level. A secondary consumer level consisted of fishes, sharks, and some invertebrates that preyed upon the filter- and detritus-feeders. These in turn were preyed upon by sharks, fishes, plesiosaurs, and crocodiles which constituted a third consumer level. The food chains and productivity of the Kiowa sea were probably similar in structure to those in modern seas.

A unique occurrence in dark-gray shale from unit 5, Loc. C1, provides indirect evidence of predation on mollusks. Nine shell fragments of *Breviarca habita* and other unidentifiable bivalves are cleanly broken and strewn about on the bedding plane in a 2 cm.^{2} area. The fragments obviously can be fitted together to make whole valves. The most likely explanation is that an unidentified predator broke the valves and ejected them either as fecal material or as rejected food.

COMPETITION

Direct evidence of competition among species of the Kiowa fauna is lacking, but mutually exclusive distributions of some species might be explained by competition eliminating one or the other (Ager, 1963, p. 257).

Turritella belviderei is the most abundant gastropod in all the lithofacies in both southern and central Kansas, except at two localities in Saline County. There, *Turritella kansasensis* is a member of the pteriid-mytilid association in thin-bedded sandstone facies in the middle Kiowa, and *T. belviderei* is absent. *T. belviderei* is very rare at other localities of this same fossil association even though *T. kansasensis* is absent. Perhaps some other factor besides competition between the species was more important in restricting *T. belviderei*. Environmental factors are not apparent.

At most localities where one of the following species is very abundant, *Ostrea rugosa, Crassostrea kiowana,* or *Lopha quadriplicata,* the others are absent or much less common. *Crassostrea* is most abundant in transported assemblages of the shell-conglomerate facies, and the other two species are abundant in any of the three sandstone facies as disturbed-neighborhood assemblages. This distribution suggests that *L. quadriplicata* and *Ostrea rugosa* preferred firm sandy substrates and usually were associated with a more diverse fauna (in terms of numbers of species) than were *C. kiowana*. The abundant occurrence of *C. kiowana* in less diverse transported assemblages suggests that it may have formed oyster beds or banks as the genus does today. As already discussed (p. 38), *C. kiowana* probably flourished at lower salinities than *Gryphaea*.

The various species of *Gryphaea* may be ecophenotypic variants of one species as suggested in the Systematic Descriptions. Each species may reflect local differences in substrate or some other environmental factor such as competition for space resulting from crowding of individuals. Little more can be said without a statistical analysis of the group.

Habitat or niche requirements should be different for the three corbulid species, but their distribution shows no consistent pattern, except that at a few localities one or the other species is more abundant. The ecology of Recent corbulids is poorly known.

COMMENSALISM

A type of commensalism that Ager (1963) considered under "other relationships" is represented by boring and attached species. *Cliona, Membranipora?,* and *Serpula* are most common on the exterior and interior of *Gryphaea* valves in southern Kansas, and *Serpula* also encrusts other firm objects. Obviously most encrustation and boring occurred after death of the host and probably before transportation, which is suggested by their presence on shells in the disturbed-neighborhood assemblage in unit 1, Loc. K1. *Botula* is found on both *Gryphaea* and *Lopha subovata* valves in southern and central Kansas. *Botula* and *Cliona* are essentially restricted to thick-shelled species because the borings are for protection not predation. *Cliona, Membranipora?,* and *Serpula* probably were restricted to southern Kansas by the salinity gradient postulated between the two areas (p. 38).

DEPOSITIONAL ENVIRONMENT AND PALEOECOLOGIC SYNTHESIS

CLIMATE AND PALEOGEOGRAPHY

The preceding data and tentative interpretations can be combined into a unified picture of the environmental conditions during deposition of the Kiowa Formation. Such an interpretation is necessarily limited by the narrow geographic scope of this study, and conclusions that apply to the Kansas outcrop area may not apply to time-equivalent rocks elsewhere in the Western Interior or Gulf Coast.

The regional climate in the Kansas area probably was humid, tropical to subtropical (Reeside, 1957), and near a temperate region as suggested by the plant fossils in the Kiowa and Cheyenne Sandstone. Sassafras, laurel, magnolia, eucalyptus, fig, and *Cycadoidea* are most abundant in humid, tropical to subtropical regions; poplar, oak, and willow trees are found in subtropical and temperate regions. In general the flora is similar to a lowland, coastal-plain flora in a humid, subtropical climate, not unlike parts of the present-day Gulf Coast.

The Kiowa in Kansas was deposited near the eastern margin of the Comanchean epicontinental sea, which transgressed from the south (Reeside, 1957). The central Kansas area probably was closer to shore than the southern area, as suggested by the northward thinning of the Kiowa and by the generally greater abundance of sandstone in central Kansas. That the sea floor was within the sublittoral zone (0 to 184 m.) is suggested by the dominance of polysyringid bivalves (Nicol & Gavenda, 1964), by the thick, lenticular sandstone bodies in central Kansas (Franks, 1966), and by the low- to moderate-angle cross stratification and mottled structures of the sandstone units (McKee, 1964). In comparing southern and central Kansas, no precise interpretations of depth can be made; but at the time of maximum transgression the offshore southern area may have been somewhat deeper than the nearshore central area because of that geographic relationship. If so, the sea floor sloped gently southward.

SUCCESSION OF THE ANCIENT COMMUNITIES

The most common substrates were dark-gray and light-brown muds, very fine-grained sands, and shell banks. Generally each substrate supported a distinctive community of mollusks and nonpreservable animals, which is represented in part by the fossil associations. As the habitat at any one place changed through time, one community would replace another so that each community was a sere (KENDEIGH, 1961) in the succession of marine communities during the transgression and regression of the Kiowa sea in Kansas. The succession of seres was different in southern and central Kansas, and individuals of some seres were removed from their dwelling area and preserved in transported-shell conglomerates.

In the southern Kansas portion of the Kiowa sea the initial nearshore sand substrate was developed locally ("Champion shell bed") and was occupied by a large *Gryphaea* population. A host of other marine invertebrates from the south migrated into this area but apparently could not repopulate the habitat (p. 38). A more limited corbulid-*Trachycardium* community (represented by unit 2, Loc. K1) followed the initial sere but was killed off, perhaps by increased turbidity and development of a dark-gray, muddy bottom. Elsewhere in southern Kansas the muddy bottom, rich in organic detritus, formed very soon after transgression. The sediment Eh was highly reducing and locally, perhaps, affected the Eh of the sea water directly above the bottom. But in many places individuals of the *Nuculana* community burrowed in the mud feeding on organic detritus. Part of the nektonic community was also preserved in this mud. Plesiosaurs, sharks, fishes, and marine turtles were relatively common and fed on each other or on the abundant molluscan and crustacean faunas (see p. 49).

Locally, better circulation between the sediment and the water resulted in better aerated and lighter colored muds (the claystone facies). Here the corbulid-breviarcid-*Turritella* community became established.

Occasional storm-generated currents (hurricanes?) swept in many shells, shell and fish fragments, and sand from the nearby nearshore areas. These sheets of debris were discontinuous but covered relatively large areas of the sea floor; their composition varied laterally and the sheets pinched out into the dark muds (unit 7A, Loc. K1).

The stratigraphic change in mineralogy and taxonomic composition of these shell beds indicates change through time in the kinds of substrates and communities occupying the nearby source areas. These changes probably accompanied the gradual transgression and regression of the sea. Measured sections at Loc. K1 and C2 provide most of the evidence for the following interpretations. The earlier deposits consisted of sand and supported the corbulid-breviarcid-*Trachycardium* community. These species either inhabited a sandy substrate in the source area or they migrated to the site of sand deposition (see p. 32, 34).

The next several shell beds in the sequence were sandy and contained many species and many specimens of *Gryphaea, Cyprimeria, Trachycardium,* and *Turritella.* Presence of these genera suggests that several habitats supplied shells to the deposit. By this time the *Gryphaea* and *Trachycardium* communities occupied the nearshore, sandy bottoms and perhaps *Cyprimeria* and *Flaventia* formed a community on the slightly deeper, sandy substrates. These last genera were abundant during the maximum transgression, presumably when the shoreline was displaced farthest from the southern Kansas area. However, the factors that controlled the *Cyprimeria* populations are unknown. The presence of *Drepanochilus, Lingula, Nucula,* and *Turritella* suggests that the dark-gray muddy substrate was also a source of shell material.

The shell beds above became less sandy and contained fewer species but greater numbers of *Gryphaea* and *Crassostrea.* This suggests that in the marginal source areas *Gryphaea* and *Crassostrea* banks flourished and that the other nearshore communities were not close by.

The last community represented in this area contained *Cyprimeria, Flaventia, Corbula?, Crassinella,* and soft-bodied, burrowing animals and inhabited a sandy substrate. The final substrates available in the regressing Kiowa sea were sands and brownish muds that apparently were not occupied by animals that left hard parts.

In the nearshore central Kansas area the succession of communities followed a slightly different pattern which varied from place to place. Commonly the *Nuculana* community was the initial sere occupying the dark-gray, muddy bottom. This community generally had a very sparse population but consisted of many of the same species as in southern Kansas. The nektonic community left remains of sharks, fishes, and crocodiles. A few *Crassostrea* shell conglomerates were intercalated in this dark-gray shale facies indicating the presence of marginal oyster banks. These shell conglomerates probably were storm-current deposits.

The local sands inhabited by *Trachycardium, Turritella,* and the pteriids probably were infralittoral (<92 m.) sandy bottoms in the zone of wave action. The mytilids may have formed a shoreline community either on solid objects or on a stable, sandy bottom. Elsewhere, dark muds and brownish, silty clays and siltstones were alternately deposited prior to the local deposition of a thicker bed of very fine-grained sand which supported only a sparse(?) population of soft-bodied animals that formed vertical dwelling burrows and feeding trails. Perhaps these were very shallow-water deposits.

Generally these middle Kiowa sandstones were followed by renewed deposition of dark mud inhabited by a very sparse *Nuculana* community.

The last deposits were alternating thin-bedded sands and clays that locally supported an abundant *Trachycardium-Turritella* community or a community of soft-bodied animals. The absence of mytilids suggests that perhaps no stable substrate was available. In some places no animals were preserved in this last sandy bottom.

In summary, the succession of the Kiowa marine communities was dependent largely upon the type of substrate available, provided that other physical, biological, and chemical conditions were tolerable. The variability of these other conditions is suggested in part by the variable development of the associations in different units of the same lithofacies. Other factors such as post-mortem aggregation and winnowing by currents and differential preservation may have partly caused the clumped distribution.

SUMMARY OF OTHER ENVIRONMENTAL FACTORS

The terrestrial flora suggests that the climate was warm. A significant temperature gradient in sea water between southern and central Kansas is unlikely because the distance is short. Modern temperature gradients are developed along both coasts of North America over distances of several hundred miles.

A salinity gradient between the southern and central areas has been postulated on the basis of the distribution of more or less stenohaline species and of *Gryphaea* (p. 38). The near absence of the boring sponge *Cliona* and of bryozoans from central Kansas and the smaller total number of species can be explained most readily by lowered salinities, perhaps in the range of 20‰ or less. The salinity in the southern area probably was less than 36‰ because corals and echinoderms are rare. Salinity changes through time are more difficult to interpret. However, salinity could have been one factor in the reduction and local exclusion of species from some late Kiowa sandy substrates in both areas. Other factors, however, may have been more important.

Oxygen content of the water probably was relatively high in most places, as suggested by the presence of a bottom fauna preserved in its preferred substrate. On the other hand, the post-depositional Eh of nearly all the Kiowa sediments was reducing. Locally, bottom waters could have been reducing, but barren sands probably were not deposited in stagnant waters, so other factors excluded preservable animals.

Plankton food supply probably was adequate throughout most of the area, because suspension-feeders are locally abundant in many places in the Kiowa. Possibly water circulation was so poor locally that food was scarce; however this rarely occurs in modern, open seas. The wide distribution of suspension-feeders and the interpreted plankton suggest that water circulation in the Kiowa sea generally was good and that connections to the south probably were open throughout most of Kiowa time. This interpretation contrasts with that of TWENHOFEL (1924), who postulated intermittent connections to the south to explain the periods of stagnation in which dark-gray muds were deposited. However, it is evident that the muds supported a characteristic fauna and that reducing conditions developed within the sediment after deposition.

The deposition of the different substrates was a function of currents, shoreline configuration, and source areas. Generally, a greater thickness of sand was deposited in central Kansas and apparently closer to shore. FRANKS (1966) compared the thick, lenticular sandstone bodies in central Kansas to offshore bars. A greater thickness of muds was deposited in southern Kansas farther from the postulated shoreline.

Turbidity and turbulence in each habitat depended on the kind of currents. Only qualitative comparisons can be made between lithofacies. Probably turbulence was greater across the sandy substrates than across the muddy bottoms. The local shell conglomerates suggest relatively strong and short-lived currents. Turbidity may have been greater in areas of mud deposition than where sand was being deposited. Locally abundant clays could have been winnowed from the sands resulting in very turbid waters.

CONCLUSIONS

1. Four ammonite-bivalve zones afford satisfactorily precise correlation of the Kiowa Formation of Kansas with the Texas section. The *Venezoliceras kiowanum* Zone is equivalent to the upper *Manuaniceras powelli* Zone in the Goodland-Comanche Peak. The *Adkinsites bravoensis* Zone is in the lower Kiowa and the Kiamichi. The *Inoceramus comancheanus* Zone of the middle Kiowa is equivalent to the Duck Creek zones. The uppermost *Inoveramus bellvuensis* Zone is approximately equivalent to zones in the Fort Worth and lower Denison.

2. Kiowa fossil assemblages were formed in one of three ways: very few are in-place assemblages; many are preserved in the substrate where they lived, but not in place, i.e., disturbed-neighborhood assemblages; many are transported assemblages; and in addition, species from different substrates may be mixed together in either of the last two kinds of assemblages.

3. Kiowa fossil associations consist of recurring suites of abundant and unique species. Ten associations are recognized: 1) *Nuculana;* 2) Corbulid-breviarcid; 3) *Trachycardium-Turritella;* 4) Pteriid-mytilid; 5) *Gry-*

phaea; 6) *Crassostrea;* 7) *Lopha quadriplicata;* 8) *Cyprimeria;* 9) *Brachidontes;* 10) Trace fossil. These associations are based upon relative abundance data and the Jaccard coefficient of association.

4. Six lithofacies are recognized in the Kiowa: dark-gray shale; mudstone; thin-laminated sandstone; thin-bedded sandstone; mottled sandstone; and shell conglomerate.

5. The feeding habits and probable substrate preferences of the mollusks are closely related to the lithofacies so that most species are preserved in the preferred substrate.

6. The Kiowa fossil associations consisting of species having similar or related feeding and dwelling habits and substrate preferences represent parts of ancient communities. These associations are compared with modern marine benthic communities that have closely related genera and species.

7. The *Nuculana* association is analogous to modern communities on the deeper shelf of the Gulf Coast and to the *Ampelisca* community in shallow bays. Probably the *Nuculana* association inhabited muddy bottoms in a large epicontinental sea.

8. The corbulid-breviarcid association may be analogous to the modern *Syndosmya* community in bays and estuaries on sandy mud bottoms. The corbulid-breviarcid-*Turritella* association probably inhabited a muddy bottom in the epicontinental sea; and the corbulid-breviarcid-*Trachycardium* association probably inhabited a sandy bottom in either the nearshore or the offshore areas.

9. The *Trachycardium-Turritella* association is analogous to parts of two modern communities: the *Macoma-Cardium* and the *Amphiura-Turritella* communities. *Turritella* in Cretaceous time probably was adaptable to muddy and sandy substrates, and this association may have inhabited a nearshore, sandy bottom within the zone of wave activity.

10. The pteriid-mytilid association is analogous to parts of modern communities of *Cardium, Turritella, Mytilus,* and *Tellina,* all of which inhabit firm sandy or shelly substrates. Probably this association represents two ancient communities in close proximity to one another: one consisting in part of *Trachycardium, Turritella,* and locally *Linearia* or *Corbula?* inhabiting an infralittoral sandy bottom; and the other consisting of *Modiolus, Gervillia, Pteria,* and *Ostrea rugosa* inhabiting shell banks or firm, sandy substrates, perhaps locally at shoreline.

11. The *Gryphaea* association is extinct, but its stratigraphic recurrence suggests that it represents part of an ancient community adaptable to several habitats. In the Kiowa it occupied nearshore, sandy substrates.

12. The *Cyprimeria* association generally occurs in transported assemblages with representatives from several associations. It may be somewhat analogous to the modern *Venus* community, and perhaps inhabited sandy substrates at depths somewhat greater than *Trachycardium-Turritella.*

13. The *Crassostrea* and the *Lopha quadriplicata* associations are analogous in part to the modern *Crassostrea* community, and probably formed shell beds and banks in nearshore, brackish waters.

14. The *Brachidontes* association is not well known but may be analogous to parts of modern communities containing this genus. It may have occupied a very nearshore, firm sand or muddy sand substrate.

15. The trace fossil association represents several ancient communities of predominantly soft-bodied animals. *Chondrites* occurs in offshore sands; *Rhizocorallium* is found in both offshore and nearshore sands; Domichnia are common in nearshore sands; and Repichnia occur in nearly all lithofacies and environments.

16. Plankton was the producing level of the food chain in the ancient Kiowa sea. Filter-feeding and detritus-feeding mollusks and Foraminifera formed the primary consumer level, carnivores on mollusks, crustaceans, and Foraminifera formed the secondary, and carnivores on sharks and fishes the tertiary level.

17. Competition resulting in mutual exclusion may have existed between species of *Turritella* and some oysters. Presumed species of *Gryphaea* probably were ecophenotypes. A type of commensalism is represented by boring and encrusting species on *Gryphaea* and *Crassostrea* valves.

18. The small terrestrial flora in the Kiowa suggests humid, tropical to subtropical, conditions near a coastal plain.

19. The Kiowa Formation in Kansas was deposited near the eastern margin of the Comanchean epicontinental sea; the central Kansas area probably was closer to shore than the southern Kansas area.

20. A decreasing salinity gradient from southern to central Kansas is suggested by the virtual restriction of more or less stenohaline species to southern Kansas.

21. The dark-gray shale facies probably was deposited in relatively oxygenated waters in offshore areas and in nearshore bays.

22. The tan mudstone facies may represent better circulation between the sediment and the water, so that a reducing environment did not develop; some units were deposited offshore and some nearshore.

23. Most shell conglomerates and some thinly laminated sandstones may have been deposited by storm-generated currents. The fauna of these lithofacies generally represent several habitats, and stratigraphic faunal variations reflect a succession of ancient communities in the source areas.

24. Thin-bedded sandstones were deposited very near the shore. Mottled sandstones indicate that extensive burrowing activity during and after deposition was common in these nearshore sands.

25. Oxygen content of the water probably was high in most places; but reducing conditions developed within most sediments.

26. The stratigraphic relationships of the lithofacies and fossil associations suggest that the nearshore environments were succeeded by offshore environments as the sea transgressed, and nearshore environments later recurred as the sea regressed.

27. This study shows that parts of ancient communities can be recognized in fossil assemblages and that a synthesis of the mode of origin of fossil assemblages, the paleoecology of fossil associations, and the depositional environment of lithofacies provides a relatively detailed and accurate interpretation of ancient environments.

SYSTEMATIC DESCRIPTIONS AND PALEOECOLOGIC DISCUSSIONS

INTRODUCTION

A major purpose of this study is to update the nomenclature of the Kiowa fauna, to determine synonymies, to provide more complete descriptions of some species, and to describe new species. Descriptions of species are omitted where the new material adds nothing; and a discussion section is omitted where nothing original can be added.

Principal sources used for most of the information leading to generic reassignment of many species are Adkins & Winton (1920), Stanton (1947), and Stephenson (1941, 1952). Other sources are indicated in the discussion of particular species. The suprageneric classification of Bivalvia follows Newell (1965); classification of the Gastropoda is that of Taylor & Sohl (1962); the classification of other groups follows the *Treatise on Invertebrate Paleontology*. In preparing the synonymy of each species no exhaustive literature search has been attempted.

The type specimens of species described by Cragin (1889a,b; 1894a,b; 1900) appear to be lost (Twenhofel, 1924, p. 50), and few of Twenhofel's types were found. In an attempt to find them I made inquiries of the Museum of Invertebrate Paleontology at the University of Kansas, William S. Twenhofel, son of W. H. Twenhofel, the Museum at the University of Wisconsin, Peabody Museum of Natural History at Yale, and the U.S. National Museum. Karl M. Waage kindly loaned Yale's collection of paratypes of 18 species named by Twenhofel. The original collection of holotypes deposited at the University of Kansas has not been found. Neotypes have been designated only where syntype material was thoroughly reviewed. The term *plesiotype* is applied only to specimens so designated by Stanton (1947). Erle G. Kauffman and Frederick J. Collier generously furnished catalog numbers of Meek's and White's types at the U.S. National Museum (USNM) and loaned certain type specimens.

All type specimens for new species, all figured material, and, with Dr. Waage's permission, Twenhofel's collection of paratypes have been deposited in the University of Kansas Museum of Invertebrate Paleontology (catalog-prefix KU). Included is a set of representative specimens of all species found in this study.

The number of specimens of rare species available for study is indicated in the systematic description. The number of specimens and relative abundance of abundant species found at each locality is given in Table 3. Species not found in this study but reported from the Kiowa are listed in Table 5.

To indicate the approximate ranges of species in the Kiowa Formation, where precise stratigraphic position is unknown, the informal subdivisions of lower, middle, and upper Kiowa refer to the estimated thickness above the base of the Kiowa at the specified locality. Total thickness is taken as 100 to 125 feet in central Kansas and 200 to 300 feet in southern Kansas.

Stratigraphic ranges of species outside of Kansas are derived from Adkins (1928) or Perkins (1960). Ecologic information was gleaned from Parker (1956), Thorson (1957), Keen (1958), and N. F. Sohl (oral communication, 1966).

Phylum PORIFERA Grant, 1872—Class DEMOSPONGIA Sollas, 1875—Order HADROMERIDA Topsent, 1898—Family CLIONIDAE Gray, 1867

Genus CLIONA Grant, 1826

CLIONA sp. indet.

Description.—Boring apertures small, circular or nearly circular; some connected by branching tubes; some tubes bottle-shaped. Opening diameter ranges from 0.2 to 0.75 mm.

Discussion.—These borings are very similar to casts in shells in the Woodbine Formation of Texas that Stephenson (1952) called *Cliona retiformis*. However, spicules, if they could be found, would furnish more reliable characters for the species.

Occurrence.—Common on *Gryphaea* valves in shell conglomerates in southern Kansas. Valves with borings KU 500029-500031a-c.

Paleoecology.—Recent *Cliona* species are marine filter-feeders that bore into oysters for a place of attachment. Commonly, the invasion of a very great number of individuals will force the oysters to expend excessive energy in repairing the shell and eventually to expire. Generally, *Cliona* is thought to tolerate salinities not much less than normal marine. However, WELLS (1961) has reported that some species thrive at salinities as low as 25‰.

Cliona borings are most common on the exterior of left valves, less common on the interior or on right valves. This suggests that most *Gryphaea* valves were abandoned and free on the substrate, perhaps not even in the vicinity where the oysters lived. Scarcity of *Cliona* borings suggests that perhaps some limiting factor, such as low salinity, was near the minimum tolerance level for the species.

Phylum COELENTERATA Frey & Leuckart, 1847—Class ANTHOZOA Ehrenberg 1834—Subclass ZOANTHARIA de Blainville, 1830—Order SCLERACTINIA Bourne, 1900—Family ASTROCOENIIDAE Koby, 1890

Genus ACTINASTREA d'Orbigny, 1849

ACTINASTREA NIDIFORMIS (Cragin, 1894)

Astrocoenia nidiformis CRAGIN, 1894b, p. 50.——TWENHOFEL, 1924, p. 51, pl. 10, fig. 4.——WELLS, 1933, p. 73, pl. 6, fig. 4.

DESCRIPTION.—Corallum cerioid, incrusting, or massive, 35 x 45 mm., about 4 mm. thick; corallites small, 1.56-1.30 mm. diameter; walls of corallites septothecal, 0.2 mm. thick; 6 primary septa, 6 secondary septa, 12 tertiary septa, septal structure unknown; columella small, generally poorly preserved, styliform, according to WELLS (1933). For a more complete description of the species see WELLS (1933).

DISCUSSION.—The species is placed in the genus *Actinastrea* because it possesses a styliform columella, which is absent in *Astrocoenia* (WELLS, 1956, p. *F*370).

TYPES.—Original material lost; TWENHOFEL's specimen KU 61525. WELLS' material is in the U.S. National Museum.

OCCURRENCE AND MATERIAL.—CRAGIN collected two colonies; TWENHOFEL one, which is partly recrystallized and abraded, from the "Champion shell bed" south of Belvidere. WELLS (1933) collected two colonies from the Comanche Peak Formation in Bell County, Texas.

PALEOECOLOGY.—Species of the family Astrocoeniidae have been hermatypic reef-builders at least since Early Cretaceous (WELLS, 1956, p. *F*356). Modern species of *Actinastrea* live in the infralittoral zone in relatively clear and well-circulated waters warmer than 18°C that have a salinity of 27-40‰.

The incrusting to massive form of *A. nidiformis* suggests adaptation to relatively highly agitated waters. TWENHOFEL's specimen encrusts a firm substrate of very fine-grained quartz sand and *Gryphaea* shells. The sparsity of *A. nidiformis* (three colonies) and its occurrence with one specimen of *Salenia kansasensis* suggest that both species lived near their tolerance limit for one or more factors, one of which may have been low salinity.

Phylum BRYOZOA Ehrenberg, 1831—Order CHEILOSTOMATA Busk, 1852—Suborder ANASCA Levinsen, 1909—Family MEMBRANIPORIDAE Busk, 1854

Genus MEMBRANIPORA de Blainville, 1830

MEMBRANIPORA? KIOWANA Scott, n. sp.

Plate 1, figures 2, 9

DESCRIPTION.—Zoarium pluriserial, or uniserial to pluriserial, budding from ancestrula or from early generation zooecia; ancestrula budding two, four, or six times; first-generation zooecia budding one, two, three, or four times from distal and proximal-lateral areas. Two or four main branches originating from first-generation zooecia; zooecia budding either distally or bilaterally into three zooecia or main branches, or distally and at irregular intervals unilaterally into one or two zooecia on minor branches.

Ancestrula circular to elongate-oval; length 0.08-0.30 mm., width 0.08-0.20 mm. Immature and uniserial zooecia longitudinally oval, tapering proximally; lateral and distal walls convex, sloping steeply; proximal gymnocyst convex, sloping steeply laterally, and gently proximally. Caudae gently tapered proximally to one-half of width of zooecium, generally shorter than rest of zooecium. Aperture elongate-oval, mural rim poorly defined, length 0.13-0.27 mm., width 0.11-0.15 mm.

Mature zooecia in pluriserial zooaria subhexagonal, more narrow distally than proximally; lateral and distal walls vertical; proximal gymnocyst short, convex, sloping equally steeply proximally and proximal-laterally. Aperture elongate-oval, mural rim sharply defined, smooth. Basal wall not calcified, basal edges of zooecial walls attached to substrate. No spines, ovicells, or other heterozoecia known.

DISCUSSION.—This species is tentatively assigned to the genus *Membranipora,* which currently is being revised under the direction of RICHARD S. BOARDMAN for the *Treatise on Invertebrate Paleontology*. The species has some features of *Pyripora* D'ORBIGNY (1849, emend. THOMAS & LARWOOD, 1956). The uniserial habit is developed during some growth stage in some zooaria; zooecia in uniserial zooaria are pyriform; budding pattern is similar to *Pyripora;* apertures of immature zooecia are oval, although in mature stage apertures are not; gymnocyst is well developed.

This species differs from *Pyripora texana,* from the Comanchean of Texas, by lateral budding of all zooecia

TABLE 5. *Species Reported from the Kiowa Formation but Not Found or Recognized in This Study.*

[Data from Cragin (1895a,b), Hill (1895), Twenhofel (1924), and Stanton (1947). Range in feet above base of the Kiowa given, where known. "Champion shell bed" is shortened to "Champ," and "Mentor beds" to "Ment."]

Species; Author of Report	Locality	Range	Remarks
COELENTERATA			
Actinastera (Astrocoenia) nidiformis (Cragin, 1894b)	Belvidere	"Champ"	See discussion on page 55
ANNELIDA			
Neries? incognita Cragin, 1894a	So. Kansas	0-100	May be Repichnia
BIVALVIA			
Astarte pikensis Hill, 1888 in Cragin, 1895b	Belvidere	"Champ"	Glen Rose Fm.
Modiolus pedernales Roemer, 1849 in Cragin, 1895a	Saline Co.	"Ment"	
Cardium? (Nemocardium) bisolare Cragin, 1894a	Belvidere	"Champ"	Variant? of *T. kansasense* or *P. texana*
Corbicula? nucalis Meek, 1871	Saline Co.	"Ment"	Pallial sinus is more like that in Veneridae
C.? subtrigonalis Meek, 1871	Saline Co.	"Ment"	
C.? elongata Meek, 1871	Saline Co.	"Ment"	
Corbula crassicostata Cragin, 1894b	So. Kansas	0-100	
Exogyra texana Roemer, 1852 in Cragin, 1889a	So. Kansas	0-35	Fredericksburg Gp.; KU 500233
Homomya alta Roemer, 1849 in Cragin, 1890	So. Kansas	0-150	
Inoceramus comancheanus Cragin, 1894b	So. Kansas	0-150	
Leptosolen canradi Meek, 1871	Saline Co.	"Ment"	
Lima semilaevis Cragin, 1893	Belvidere	"Champ"	Denton Fm.
Limopsis subimbricatus Cragin, 1894a	Belvidere	"Champ"	May be a *Breviarca*
Mactra antiqua Cragin, 1894a	Belvidere	15-30	
Modiolus concentrice-costellata Roemer, 1849 in Cragin, 1895b	So. Kansas	0-150	
Ostrea welleri Logan, 1899	Ellsworth Co.	"Ment"	Probably *L. quadriplicata*
Pecten texanus Roemer?, 1852 in Twenhofel, 1924	Belvidere	"Champ"	Fredericksburg-Washita Gp.
Pinna comancheana Cragin, 1894a	Belvidere	"Champ"	Fredericksburg Gp.
Barbatia parallela Meek, 1871	Saline Co.	"Ment"	
Roudaria quadrans Cragin, 1893	Belvidere	15-60	Variant? of *P. texana;* Comanche Peak Fm.
Avicula belviderensis Cragin, 1894a	Belvidere	0-60	Variant? of *P. salinensis*
Remondia ferrissi Cragin, 1889b	Belvidere	15-60	A crassatellid
Siliqua mentorensis Twenhofel, 1924	Saline Co.	"Ment"	KU 500234, 500235a,b
Tellina subscitula Meek, 1871	Saline Co.	"Ment"	
GASTROPODA			
"Anisomyon cragini" Twenhofel, 1924	Kiowa & Saline Co.	0-60	Vertebrae fragments (Stanton, 1925); KU 500315

TABLE 5. *(Continued.)*

SPECIES; AUTHOR OF REPORT	LOCALITY	RANGE	REMARKS
Calliostoma cragini Stanton, 1947 (=*Trochus texanus* Roemer, 1888)	So. Kansas	Lower Kiowa	Kiamichi Fm.
Cancellaria (Petersia) medicenensis (Cragin, 1894a)	Kiowa Co.	0-60	See Stanton (1947) for synonymy
Cerithium kansasense Stanton, 1947	Clark Co.	Mid Kiowa	
Lunatia? cragini Stanton, 1947 (=*Natica? cassatotensis* Hill, 1888)	Kiowa Co.	Lower Kiowa	
Margarita ornata Twenhofel, 1924	Saline Co.	"Ment"	May be *Hillites* KU 500419
Turbo? belviderensis Stanton, 1947	Kiowa Co.	Lower Kiowa	
T.? gouldi Stanton, 1947	McPherson Co.	"Ment"	Top Kiowa
T.? (Margarita) newberryi (Cragin, 1894a)	Belvidere	"Champ"	Washita Gp., Purgatoire Fm. Synonymy after Stanton (1947)
Tylostoma elevata (Shumard, 1854)?	Belvidere	"Champ"	Fredericksburg & Washita Gp.; may be *"Ampullina"* sp.
CEPHALOPODA			
Venezoliceras kiowanum (Twenhofel, 1924)	Kiowa Co.	0-60	Comanche Peak Ls. & Goodland Ls.
Manuaniceras decsernae Young, 1966 (=*Schloenbachia peruviana* von Buch in Twenhofel, 1924)	Kiowa Co.	0-60	Kiamichi Fm.
ECHINODERMATA			
Enallaster sp. in Hill, 1895; Cragin, 1895b	So. Kansas	0-150	Fragments
Holectypus plantanus Roemer, 1852 in Cragin, 1895b	Kiowa Co.	"Champ"	May be *Salenia*
Salenia kansasensis Twenhofel, 1924	Belvidere	"Champ"	KU 500425

on main branches, by less pyriform shape of closely packed zooecia, and by absence of a cryptocyst.

TYPES.—Holotype: KU 50029; paratypes: KU 50030, 500031a-c.

OCCURRENCE AND MATERIAL.—The few calcitic colonies encrusting exterior and interior surfaces of three *Gryphaea* valves are from shell conglomerate unit 13-14, Loc. C1, KU 500029, 500030, 500031a-c. Poorly preserved specimens were seen in unit 10, Loc. K1.

PALEOECOLOGY.—Recent Bryozoa are attached filter-feeders. Optimum salinity of most of them is 36‰; as salinity decreases to 12‰, the number of species is greatly reduced, although some may be quite prolific (OSBOURN, 1957). The relative scarcity of Bryozoa in the Kiowa suggests that the minimum tolerance level of one or more limiting factors, such as salinity, may have been approached.

Phylum BRACHIOPODA Duméril, 1806—Class INARTICULATA Huxley, 1869—Order LINGULIDA Waagen, 1885—Superfamily LINGULACEA Menke, 1828—Family LINGULIDAE Menke, 1828

Genus LINGULA Bruguière, 1797

LINGULA SUBSPATULATA Hall & Meek, 1855?

Plate 1, figures 1, 8

Lingula subspatulata HALL & MEEK, 1855, p. 380, pl. 1, fig. 2a, b. STEPHENSON, 1952, p. 54, pl. 10, fig. 1-3. Provides prior synonymy.

DISCUSSION.—Mature specimens, as noted by STEPHENSON (1941), have a subtruncate anterior end, whereas the immature shell has "a broadly rounded" anterior end. This is the basis for interpreting shells in shale as immature forms rather than as different species. No "very fine, obscure radial lines" were seen on these specimens. The absence of radial sculpture might provide a basis for placing these specimens in a new species.

TYPES.—Holotype: American Museum of Natural History, New York, 9341/1. Representative specimens: KU 500032, 500033a-b.

OCCURRENCE AND MATERIAL.—TWENHOFEL (1924) reported *Lingula* fragments in shale and in "Mentor beds." Additional molds and chitino-phosphatic shells are rare in shale, sandstone, and shell conglomerates in central and southern Kansas ranging throughout nearly the entire thickness of the Kiowa. The species ranges from Cenomanian to Maastrichtian in the Western Interior and Gulf Coast.

PALEOECOLOGY.—Recent *Lingula,* a sedentary burrowing filter-feeder, is common in tropical to subtropical seas from the intertidal zone to a depth of about 42 m.; it can tolerate marine to brackish salinities and is most abundant in a muddy substrate (FERGUSON, 1963).

In the Kiowa, mature specimens are found in transported assemblages in sandstone and shell conglomerate; most specimens in shale are immature; none are in place.

Phylum ANNELIDA Lamarck, 1809—Class POLYCHAETIA Grube, 1850—Order SEDENTARIDA Lamarck, 1818—Family SERPULIDAE Burmeister, 1837

Genus SERPULA Linné, 1768

SERPULA CRAGINI Twenhofel, 1924

Serpula cragini TWENHOFEL, 1924, p. 52, pl. 7, fig. 1. Provides prior synonymy.

DISCUSSION.—These specimens differ from *Serpula* as described by HOWELL (1962, p. *W*156) by apparent lack of "small concentric ridges." The lack of ornamentation need not exclude this material from the genus, because the character may be of significance only on the species level and serve to distinguish this species from others.

TYPES.—Holotype lost; syntypes: KU 500034-500036.

OCCURRENCE AND MATERIAL.—Calcareous tubes in sandstone are from the basal shell conglomerate, unit 1, Loc. K1.

PALEOECOLOGY.—*Serpula* is an attached, marine filter-feeder.

Phylum MOLLUSCA Linné, 1758—Class BIVALVIA Linné, 1758—Subclass PALAEOTAXODONTA Korobkov, 1954—Order NUCULOIDA Morton, 1963—Superfamily NUCULACEA Gray, 1824—Family NUCULIDAE Gray, 1824

Genus NUCULA Lamarck, 1799

PALEOECOLOGY.—Recent *Nucula* is an active burrower and sediment-detritus-feeder that lives at depths from 2 to at least 7900 m. It is abundant in silty muds and can tolerate salinities at least as low as 27‰ (STICKNEY & STRINGER, 1957). *N. proxima* is a member of the deep Gulf Coast assemblage (PARKER, 1956).

NUCULA sp. cf. N. RIVULANA Stephenson, 1952

Plate 1, figures 13, 14

Nucula rivulana STEPHENSON, 1952, p. 54, pl. 10, fig. 4-6.

DESCRIPTION.—Shell small, thin trigonal ovate, inequilateral, equivalved. Beak small, opisthogyrate, somewhat inflated; umbo broadly, gently arched; posterior umbonal ridge more inflated than anterior ridge. Dorsal margins forming a 90°-95° angle around beak; anterior dorsal margin slightly convex, gently sloping; anterior margin narrowly rounded; ventral margin gently convex; posterior margin moderately curved, merging with slightly convex and steeply sloping dorsal margin. Ornamented by thin growth lines. Hinge line with small denticles along the greater length of dorsal margins. Other interior features unknown.

DISCUSSION.—This may be the same species as *Nucula rivulana* (STEPHENSON, 1952) from the Woodbine of Texas, but it is not as wide nor as thick-shelled. However, this may be due to poor preservation.

OCCURRENCE AND MATERIAL.—Internal and external molds and casts are rare in dark-gray shale, lower Kiowa, central and southern Kansas. Internal cast in sandstone: KU 500037a (unit 15, Loc. M4); latex casts: KU 500037b-c.

NUCULA? CATHERINA Cragin, 1894

Plate 1, figure 15

Nucula catherina CRAGIN, 1894a, p. 4.

Nucula catharina CRAGIN. TWENHOFEL, 1924, p. 77.

Nucula? catherina CRAGIN. ADKINS, 1928, p. 86.

DISCUSSION.—This distinctive species is tentatively retained in the genus pending study of more complete material showing interior features. The shape certainly is nuculid; however, the ornamentation is somewhat stronger than usual in *Nucula,* and is not divaricate as in *Acila.*

TYPES.—Original material lost. Representative specimens: KU 500038, 500039.

OCCURRENCE AND MATERIAL.—CRAGIN (1894a, 1895b) described three specimens from an interval 15 to 60 ft. above the base of the Kiowa near Belvidere, and from "Mentor beds" in central Kansas. Two incomplete calcitic shells were found in shell conglomerate, unit 8A, Loc. K1.

Superfamily NUCULANACEA Meek, 1864—Family NUCULANIDAE Meek, 1864

Genus NUCULANA Link, 1807

NUCULANA MUTATA Stephenson, 1952

Plate 1, figure 10

Nuculana mutata STEPHENSON, 1952, p. 57, pl. 10, fig. 10-12.

DESCRIPTION.—Shell small, thin, elongate, inequilateral, equivalved. Beak, small, just anterior of mid-line. Dorsal margins slope gently from beak, anterior slope straight, posterior slope slightly concave. Anterior margin narrowly rounded, curving backward to join dorsal margin; ventral margin smoothly flattened arc; posterior margin narrowly rounded, joining dorsal margin at nearly a 95° angle. Ornamented by thin, closely spaced growth lines. Hinge margin containing many small, narrow denticles separated by wider interspaces; denticles somewhat cuneate . Size of LV's and RV's: height 4.6 mm., length 8.3 mm., width of single valve 0.9 mm.

DISCUSSION.—Valve thickness of these specimens is less than the average thickness of *Nuculana mutata* from the Woodbine Formation in Texas. Outline of valve is somewhat variable. The most common form is narrow elongate; less common is more oval shaped with a less angular posterior; least common is an elongate form with very angular posterior margin making an acute angle with the dorsal margin.

The species is similar in outline to *Nuculana bisulcata* (MEEK & HAYDEN, 1861) but differs by absence of a dorsoposterior sulcus, and by finer concentric sculpture.

TYPES.—Holotype: USNM 105115; paratypes: USNM 105116, 105117. Representative specimens: KU 500040a-b.

OCCURRENCE AND MATERIAL.—External casts and molds are found in dark-gray shale in the lower Kiowa, central and southern Kansas. The species occurs in the Woodbine in Texas.

PALEOECOLOGY.—Recent *Nuculana* is a burrowing detritus-feeder in muddy substrates. *N. acuta* is a member of several Gulf Coast assemblages: lower- and upper-sound, and deep-shelf assemblages; *N. eborea* is characteristic of the lower sound and prodelta assemblages (PARKER, 1956).

Genus YOLDIA Möller, 1842

YOLDIA MICRODONTA Meek, 1871

Plate 1, figure 5

Yoldia microdonta MEEK, 1871, p. 304.——TWENHOFEL, 1924, p. 86, pl. 15, fig. 11, 12; provides prior synonymy.——ADKINS, 1928, p. 87.

TYPES.—Holotype: USNM 12419; representative specimen: KU500041.

OCCURRENCES AND MATERIAL.—MEEK (1871) and TWENHOFEL (1924) found the species in "Mentor beds" west of Smolan and at Natural Corral. Internal and external casts and molds are rare in dark-gray shale in the lower Kiowa, central and southern Kansas. It is found in the Denison Formation in Texas (ADKINS, 1928).

PALEOECOLOGY.—Recent *Yoldia solenoides* is a member of the deep-shelf Gulf Coast assemblage (PARKER, 1956), and lives in about the same manner as *Nuculana*. It is most abundant in subarctic waters, where it forms a community from 4-7 m. deep (THORSON, 1957).

Subclass PTERIOMORPHIA Beurlen, 1944—Order ARCOIDA Stoliczka, 1871—Superfamily ARCACEA Goldfuss, 1820—Family ARCIDAE Goldfuss, 1820

Genus BREVIARCA Conrad, 1872

PALEOECOLOGY.—The genus is extinct, but the family is wide-ranging and represented by free and byssate filter-feeders. On the Gulf Coast *Noetia* is part of the shallow-shelf assemblage, and *Anadara* is in the deep-shelf assemblage (PARKER, 1956). *Breviarca* appears to have favored muddy substrates in the Kiowa sea.

BREVIARCA HABITA Stephenson, 1952

Plate 1, figures 11, 12

Breviarca habita STEPHENSON, 1952, p. 60, pl. 10, fig. 19, 20.

DISCUSSION.—Specimens in hand are incomplete and together show the features of the species. The hinge consists of small denticles nearly parallel to length of shell and slightly oblique to hinge line. The characteristic features are the posterior umbonal ridge and the finely cancellate ornamentation. The longest specimen is about 10 mm., which is somewhat larger than STEPHENSON'S specimens.

TYPES.—Holotype: USNM 105131; paratypes: USNM 105132, 105133. Representative specimens: KU 500042-500044, 500051, 500197.

OCCURRENCE AND MATERIAL.—Partial internal and external molds and casts were collected from shale and claystone, about 40 ft. above the base of the Kiowa in Clark County. Several casts and molds in sandstone (Loc. S5) are similar in outline and form to this species, but the ornamentation does not have radial striae, which may be a matter of preservation, or they may represent a different species. STEPHENSON (1952) found the species in the Woodbine Formation in Texas.

BREVIARCA ANGULATA Scott, n. sp.

Plate 1, figures 6, 7

DESCRIPTION.—Shell small, subquadrate in outline, nearly equilateral, equivalved. Beak moderate size, projecting slightly beyond hinge line. Dorsal margin long, straight; dorsal-anterior broadly rounded; ventral-anterior sharply rounded; ventral margin gently convex; ventral-posterior corner angular; posterior straight, sloping toward beak. Anterior umbonal ridge gently rounded; posterior umbonal ridge sharply rounded. Ornamented by thin shallow growth lines.

Dentition taxodont, otherwise unknown. Ligament external, narrow, markings unknown. Measurements of largest shell: length incomplete, 9 mm., height 7.4 mm., thickness of articulated specimen 4.5 mm.

DISCUSSION.—This species differs from *Breviarca habita* by the noncancellate ornamentation, by the less produced posterior, and by the less angular posterior umbonal ridge. The trivial name, ***angulata,*** refers to the distinctive angular ventral-posterior corner.

TYPE.—Holotype: KU 500048; paratypes: KU 500045-500047.

OCCURRENCE AND MATERIAL.—Casts in shale were found at Locs. C1 and C3; articulated calcite shells were found in unit 8, Loc. K1. Ranges 35-50 ft. above the Kiowa base in southern Kansas. Articulated calcite shells: KU 500045 (unit 8A, Loc. K1): KU 500046-500048.

BREVIARCA SUBOVATA Scott, n. sp.

Plate 1, figures 3, 4

DESCRIPTION.—Shell small, subovate, nearly equilateral, equivalved. Beak inflated, projecting beyond hinge line. Dorsal margin moderate length, straight; anterior margin broadly, smoothly curved; ventral margin slightly convex; posterior margin broadly curved, somewhat truncate dorsally. Umbo smoothly rounded anteriorly and posteriorly. Ornament of faint growth lines.

Hinge line gently arched; denticles small, closely spaced, oblique to hinge line, strongest on dorsal corners, weakest directly under beak. External ligament narrow, lined with faint grooves normal to hinge line. Interior shell features unknown. Measurements of holotype, an incomplete RV: length 4.5 mm., height 4.8 mm., width 2.3 mm.; complete RV: length 4.5 mm., height 3.9 mm., width 2.1 mm.

DISCUSSION.—This species differs from *Breviarca habita* by its noncancellate sculpture and subovate form; from *B. angulata* by its less angular posterior outline, more smoothly rounded umbonal ridges; from *B. salinaensis* (MEEK) by its less prominent beaks, more elongate form, and longer hinge line; and from *B. siouxensis* (HALL & MEEK, 1854) by its more rounded posterior. Three specimens from Loc. C3, unit 6, are similar to *B. subovata* but differ by less expanded umbo. They do not appear to be specifically distinct.

TYPES.—Holotype: KU 500049; paratype: KU 500050.

OCCURRENCE AND MATERIAL.—Calcitic shells and casts were found in claystone and cone-in-cone zone at Loc. M3, in shale unit 3, Loc. E6, and in sandstone at Loc. S2. Range is approximately mid-Kiowa, central Kansas. KU 500049 (unit 3, Loc. M3); KU 500050.

BREVIARCA SALINAENSIS (Meek, 1876)?

Trigonarca (Breviarca) salinaensis MEEK, 1876, p. 92, pl. 2, fig. 1a-c.——TWENHOFEL, 1924, p. 85, pl. 15, fig. 9.

DISCUSSION.—A single internal cast in sandstone is tentatively placed in this species because the hinge line is strongly arched and short. The external outline is incomplete, but tends to be similar to this species.

TYPES.—Disposition of type material unknown. Representative specimen: KU 500304.

OCCURRENCE AND MATERIAL.—MEEK (1876) and TWENHOFEL (1924) had specimens from "Mentor beds" west of Smolan. The single mold was collected from the float at Loc. M6. Ranges from middle to uppermost Kiowa, central Kansas.

Family CUCULLAEIDAE Stewart, 1930

Genus CUCULLAEA Conrad, 1862

PALEOECOLOGY.—Little is known of the ecology of this extinct genus other than it was a shallow-water, epifaunal, filter-feeder.

CUCULLAEA RECEDENS Cragin, 1894

Cucullaea terminalis CRAGIN (in part), 1893, p. 174.——STEPHENSON, 1952, p. 63.

Cucullaea terminalis var. *recedens* CRAGIN, 1894a, p. 3, pl. 1, fig. 19.

Cucullaea recedens CRAGIN. TWENHOFEL, 1924, p. 66, pl. 15, fig. 14; pl. 16, fig. 1-3; pl. 17, fig. 3, 4.——ADKINS, 1928, p. 88.

DISCUSSION.—According to TWENHOFEL (1924) and ADKINS (1928) this species differs from *Cucullaea terminalis* by its more centrally located beaks. STEPHENSON treated the species as a synonym of *C. terminalis* and noted its similarity to *Idonearca blanpiedi* STEPHENSON, which has a longer hinge line and lacks a dorsal sulcus on the posterior slope. PERKINS (1960) treated *C. recedens* as a valid species. I tentatively accept it as a distinct species until an adequate review of the genus is made.

TYPES.—Original material lost. Representative specimens: KU 500052-500056.

OCCURRENCE AND MATERIALS.—CRAGIN (1895b) and TWENHOFEL (1924) reported the species to be abundant in the "Champion shell bed" near Belvidere, and rare in the overlying shell conglomerates in Kiowa and Clark Counties. TWENHOFEL found it also in "Mentor beds" west of Smolan and at Natural Corral in central Kansas. It ranges throughout the Kiowa. In Texas it ranges from Walnut Marl to Kiamichi Formation (PERKINS, 1960).

CUCULLAEA? HERCULEA Twenhofel & Tester, 1926

Cucullaea? gigantea TWENHOFEL, 1924, p. 66, pl. 18, fig. 8.——STANTON, 1925, p. 340.

Cucullaea? herculea TWENHOFEL & TESTER, 1926, p. 561.

DESCRIPTION.—Shell large, thick, oval to subtrapezohedral, complete outline unknown. Beak and umbo greatly inflated, incurved, moderately arched. Posterior umbonal ridge sharp, sulcus not developed on posterior-dorsal slope. Ornamented by thin growth lines. Hinge line short, dentition unknown.

DISCUSSION.—TWENHOFEL questionably referred the species to ***Cucullaea*** because "the shape is so like that of ***Cucullaea recedens***." Because the specific name had been preoccupied, TWENHOFEL & TESTER (1926) renamed the species. STANTON (1925) suggested that it is related to ***Crassatella.***

TYPES.—Original specimens lost. Syntype: KU 500057; representative specimen: KU 500058a-c.

OCCURRENCE AND MATERIAL.—TWENHOFEL (1924) collected internal casts of the species from the uppermost Kiowa at Loc. M4, where an additional specimen has been found; central Kansas.

Order MYTILOIDEA Férussac, 1822—Superfamily MYTILACEA Rafinesque, 1815—Family MYTILIDAE Rafinesque, 1815

Genus BRACHIDONTES Swainson, 1840

BRACHIDONTES NONBIFURCUS Scott, n. sp.

Figure 16; Plate 2, figures 1-4

DESCRIPTION.—A species of *Brachidontes* characterized by small size, straight anterior margin, and by nonbifurcating costae.

Shell small, mytiliform, very inequilateral, nearly equivalved. Beaks on extreme anterior of valve, strongly prosogyrate; umbo narrowly curved, elongate arch; umbonal ridge gently curving to anteroventral corner, concave anteriorly. Anterodorsal margin below beak sharply rounded; anterior margin straight in early growth stages, slightly concave in later stages; ventral margin evenly and smoothly rounded, anterior corner arc having a smaller radius than posterior corner arc; posteroventral margin broadly rounded, joining straight to slightly convex dorsal hinge margin in about 135° angle. Angle between anterior margin and hinge margin around beak is about 42°. Valve surface anterior to umbonal ridge very steep; surface posterior to umbonal ridge steep below umbo, becoming broadly convex ventrally, and concave toward posteroventral corner of hinge line.

Ornamented by faint, closely spaced concentric growth lines and radial costae. Growth lines more pronounced on steep anterior surface than on rest of valve; spacing closer toward beak than ventral margin. Costae rounded, extending to beaks; costae and shallow interspaces becoming wider from umbo to ventral margin resulting in divergence of costae. Costae pronounced on ventral and posterior portions of valve, faint on umbo and steep anterior surface, where cancellate pattern results from intersection of costae and growth lines. Costa bifurcation or insertion within a wide interspace very rare on a specimen and among specimens; number of costae on margin generally the same as on umbo.

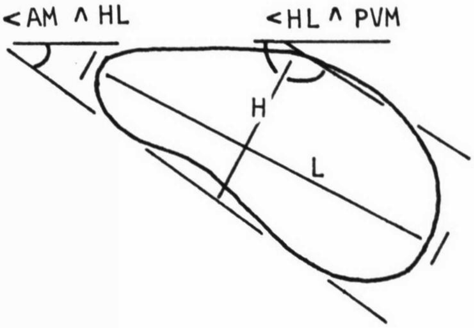


FIG. 16. Measured parameters of *Brachidontes nonbifurcus* SCOTT, n. sp. (*H*, height; *L*, length; *AMΛPVM*, angle between anterior margin and hinge line; *<HLΛPVM*, angle between hinge line and posteroventral margin).

No interior features shown by the collected specimens.

TABLE 6. *Measurements of Brachidontes nonbifurcus Scott, n. sp.*

Specimens	Length (mm.)	Height (mm.)	Width (mm.)	Angle between anterior margin and hinge line (degrees)	Angle between postero-ventral margin and hinge line (degrees)
Holotype KU 500067					
LV	15.3	8.2	4.6	45	
RV	15.0	7.3	4.6	42	
Paratype KU 500461					
RV	13.5	7.6	3.0	36	
LV	13.4	7.7	3.0	38	135
Other Specimens					
RV			3.0	48	133
LV			3.0	49	
LV		6.5	2.7	41	
RV			2.7	47	
RV			3.2	38	
LV			3.2		
LV	12.5	6.5	2.9		
Mean (mm.)	13.9	7.3	3.3	42.6	

See Table 6 for measurements of holotype, paratype, and other specimens. Figure 16 shows parameters measured.

DISCUSSION.—*Brachidontes nonbifurcus* SCOTT, n. sp., differs in form from *B. fulpensis* by its average smaller size, by its nearly straight, rather than concave anterior margin; by its smaller angle around beak: about 43° compared with 70° on holotype of *B. fulpensis;* and by its greater angle between the hinge and posteroventral margin: about 135° compared with about 100° on *B. fulpensis. B. fulpensis* generates many costae by bifurcation or insertion, but in *B. nonbifurcus* most costae are generated early in growth and very few, if any, arise later.

Brachidontes filisculptus Stephenson differs from the new species by possessing a "broad radial depression in front of and below the umbonal ridge extending from the beak to the ventral margin" (Stephenson, 1952), and by presence of beads on the costae.

A specimen of *Brachidontes filisculptus microcostae* from the Dakota Formation in Kansas (Hattin, 1965, fig. 3-2) appears to be intermediate in many ways to *B. nonbifurcus* and *B. filiscuptus*.

Types.—Holotype: KU 500067; paratype: KU 500461.

Occurrence and Material.—Type specimens are external casts of iron oxide collected from a concretionary siltstone at Loc. S3; an internal mold is from dark-gray shale at Loc. C3. Ranges about 30 to 50 ft. above the Kiowa base in central and southern Kansas.

Paleoecology.—Recent *Brachidontes* are byssate filter-feeders, and one species is common in the upper sound Gulf Coast assemblage (Parker, 1956).

Genus MODIOLUS Lamarck, 1799

[=*Volsella* Scopoli, 1777]

Paleoecology.—Recent species of *Modiolus* attach to a firm substrate by a byssus and filter food from the water. They are most common from the intertidal zone to sublittoral depths in waters of marine to brackish (27‰) salinities (Stickney & Stringer, 1957).

MODIOLUS sp. A

Plate 1, figure 16

Description.—Shell of moderate size, elongate-oval, inequilateral, equivalved; greatly inflated, maximum point of inflation one-third to one-half the distance from the anterior end, posterior area flattened. Beak not prominent, nearly terminal, prosogyrate, incurved. Umbonal ridge long, gently curved along length, cross section strongly curved at mid-length, asymmetrical, dying out toward posterior. Shallow sulcus directly ventral to ridge, beginning at umbo and continuing to ventral margin. Anterior margin sharply rounded; ventral margin concave and gently curved; posterior-ventral margin sharply rounded; posterodorsal margin broadly rounded; dorsal margin gently curved. Ornamented by thin closely spaced growth lines.

Apparently edentulous; ligament groove long and moderately deep, continuous with pallial line on dorsal posterior margin; pallial line becoming lightly impressed towards ventral margin. Muscle scars unknown. Measurements of complete articulated specimen (KU 500059): length 28.7 mm., height approximately 16.5 mm., width 15.5 mm.

Discussion.—Meek (1876), Cragin (1893), and Stephenson (1941, 1952) have described several Cretaceous species of *Modiolus*, to one of which these Kiowa specimens might be assigned. A monographic study of the group is needed to determine the range of variability within each species.

Occurrence and Material.—Cragin (1890) reported *Modiolus burlingtonensis* Whitfield (=*M. stonewallensis* Cragin) from the "Champion shell bed" in Kiowa County; Cragin (1895b) reported *M. concentrice-costellata* (Roemer, 1849) (=*M. stonewallensis*) ranging from the base to about 125 ft. above in southern Kansas, and from shale underlying "Mentor beds" in central Kansas (Cragin, 1895a).

New internal casts and external molds were collected from sandstone in Saline and Ellsworth Counties. Ranges through the lower half of the Kiowa in central Kansas. KU 500059 (unit 3, Loc. S9); KU 500060-500064.

MODIOLUS sp. B

Plate 1, figure 17

Description.—Shell very small, elongate oval, inequilateral, equivalved, slightly inflated, maximum point of inflation somewhat anterior to midline, posterior area slightly arched. Beak not prominent, prosogyrate, about one-fourth the length from the anterior end. Umbonal ridge low, broad, nearly straight, merging with posterior arch. Anterior margin narrowly curved; ventral margin gently convex; posterior margin asymmetrically curved, gradually merging with short dorsal margin. Ornamented by thin, shallowly to moderately impressed growth lines. Length of KU 500065a-b 9.0 mm., height 5.1 mm., width 0.7 mm.

Occurrence and Material.—Two external casts in shale are about 40-50 ft. above the Kiowa base in central and southern Kansas. Larger specimen, RV: KU 500065a-b (unit 6, Loc. C4); KU 500066 (unit 1, Loc. E2).

Genus BOTULA Mörch, 1853

BOTULA CAROLINENSIS (Conrad, 1875)?

Plate 1, figure 18

Arcoperna carolinensis Conrad, 1875, App. A, p. 5, pl. 1, fig. 6.
Lithophagus interrogatum Twenhofel, 1924, p. 74, pl. 7, fig. 5.
Botula carolinensis (Conrad). Stephenson, 1952, p. 87, pl. 21, fig. 18. Provides prior synonymy.

Discussion.—The single Kiowa specimen is slightly shorter than specimens from the Upper Cretaceous, but corresponds otherwise to the revised species description of Stephenson (1952). Approximate measurements: length 6.0 mm., height 4.0 mm., width of right valve 2.4 mm.

Presumably this is the same species that made the borings called *Lithophagus interrogatum* by Twenhofel (1924). Semielliptical borings on *Gryphaea* range in diameter from somewhat less than 0.5 mm. to about 8 mm., and are rarely up to 10 mm. deep.

Types.—Disposition of original specimens unknown. Stephenson's topotypes: USNM 31713-31715; Twen-

HOFEL's syntype: KU 500069; articulated specimen in *Gryphaea* valve: KU 500068.

OCCURRENCE AND MATERIAL.—CRAGIN (1897) reported borings in "*Serpula* knots" in the "Champion shell bed." TWENHOFEL found the species at all localities of *Gryphaea* shell conglomerates. An additional boring was found on *Lopha subovata* (unit 5, Loc. R3). On the Texas and North Carolina coastal plains the species ranges from Cenomanian to Maastrichtian.

PALEOECOLOGY.—Recent lithophagids are filter-feeders, and tolerate depths from high tidal level to several fathoms, and marine to brackish salinities. In the Kiowa the species is commensal with *Gryphaea* and *Lopha subovata,* which have borings on both valves and more commonly on the exterior. In some specimens the orientation of the boring suggests that the host shell was unoccupied at the time.

Order PTERIOIDA Newell, 1960—Suborder PTERIINA Newell, 1965—Superfamily PTERIACEA Gray, 1847—Family PTERIIDAE Gray, 1847

Genus PTERIA Scopoli, 1777

PTERIA SALINENSIS White, 1880

Plate 3, figure 4

Pteria (Oxytoma) salinensis WHITE, 1880, p. 296, pl. 5, fig. 1, 2. ——WHITE, 1883, p. 15, pl. 16, fig. 2a, b.——STEPHENSON, 1952, p. 69.

Pteria? salinensis WHITE. CRAGIN, 1893, p. 211.

Pteria salinensis WHITE. REESIDE, 1923, p. 203, pl. 47, figs. 1-5. ——TWENHOFEL, 1924, p. 82, pl. 18, fig. 1, pl. 22, fig. 4.—— ADKINS, 1928, p. 98.

DESCRIPTION.—Species as described by WHITE (1880) with the following additions: ligament groove multivincular, pits very shallow, anterior and posterior to beak; resilifer a larger, shallow pit. Byssal notch not developed. Adductor muscle scar slightly impressed, arcuate or "comma-shaped," placed about midway between beak and ventral margin, on anterior side of umbonal ridge.

DISCUSSION.—Some features of *Pteria salinensis* are similar to those of the genus *Phelopteria* STEPHENSON (1952), who based the genus on presence of a multivincular ligament in young forms of *Pteria dalli* STEPHENSON (1936). An apparent ontogenetic series shows the step-by-step loss of the ligament pits and in the adult stage only a single, long, shallow pit remains. Smaller specimens of *P. salinensis* from the Kiowa have a multivincular ligament groove. In addition, both genera are characterized by a single small anterior cardinal tooth, and a long posterior lateral tooth (MEEK, 1876, p. 28-29). However, *Phelopteria dalli* possesses two small muscle scars just below the beak, which are not recognized in species of *Pteria.* The pallial line of *P. dalli* consists of a row of small muscle pits. These small features are not seen in internal casts of *P. salinensis.* Because of these differences and because of the possibility that the ontogenetic change from multivincular to alivincular may be present in both genera, WHITE's species is retained in the genus *Pteria.*

TYPES.—Holotype: USNM 8025. Representative specimen: KU 500072a-c.

OCCURRENCE AND MATERIAL.—WHITE's (1880) and TWENHOFEL's (1924) specimens came from "Mentor beds" in Saline and McPherson counties. New internal casts and molds in sandstone are from Saline County. Ranges from middle to uppermost Kiowa in central Kansas.

PALEOECOLOGY.—Recent Pteriidae are epifaunal filter-feeders.

Family BAKEVELIIDAE King, 1850

Genus GERVILLIA Defrance, 1820

GERVILLIA MUDGEANA White, 1880

Plate 3, figure 6

Gervillia mudgeana WHITE, 1880, p. 295, pl. 5, fig. 3, 4.—— TWENHOFEL, 1924, p. 69, pl. 17, fig. 1, 2. Provides prior synonymy.

DISCUSSION.—TWENHOFEL (1924) stated that "fine radial lines from 0.5 to 1 mm. apart" are a feature of the sculpture, together with growth lines. None of the external molds in hand, including TWENHOFEL's specimen (1924, pl. 17, fig. 2) (KU 500070) show radial lines. Lack of radial striae separates this species from *Gervillia (Avicula) leveretti* CRAGIN (1893), which occurs in the Kiamichi.

TYPES.—Holotype: USNM 8023; representative specimens: KU 500070, 500071a-c.

OCCURRENCE AND MATERIAL.—TWENHOFEL reported the species from "Mentor beds" west of Smolan and at Natural Corral, and from my unit 8 at Loc. K1. CRAGIN (1895b) and HILL (1895) reported *Gervillia leveretti* from the Kiowa in Kiowa County. It is not certain that *G. leveretti* from southern Kansas is distinct from *G. mudgeana,* although CRAGIN (1895a) knew of this latter species from the "Mentor beds."

Internal casts and external molds are common in sandstone in central Kansas. Ranges throughout the Kiowa in central and southern Kansas.

PALEOECOLOGY.—Shell form suggests that the species was a byssate filter-feeder. At Loc. S9 it is common with *Modiolus* sp. A, and is oriented with LV down.

Family INOCERAMIDAE Giebel, 1852

Genus INOCERAMUS Sowerby, 1814

INOCERAMUS BELLVUENSIS Reeside, 1923

Plate 4, figure 1

Inoceramus bellvuensis REESIDE, 1923, p. 203, pl. 46, fig. 1-3.

DISCUSSION.—Specimens in hand were assigned to the species by ERLE G. KAUFFMAN, U.S. National Museum. The species is very similar to *Inoceramus comancheanus* (CRAGIN, 1894b) and perhaps specimens previously reported from the Kiowa (CRAGIN, 1895b; HILL, 1895) would be better assigned to this species. Judging from CRAGIN's (1894b) and REESIDE's (1923) descriptions, *I. bellvuensis* differs from *I. comancheanus* by a broader and more quadrate outline, by the hinge line and anterior margin forming a greater angle, and by a less convex valve. Concentric ribs of *I. bellvuensis* are angular and flattened, asymmetrical, and unevenly spaced.

TYPES.—Presumed in USNM; representative specimens: KU 500380a-b.

OCCURRENCE AND MATERIAL.—External molds in calcareous sandstone were found at one spot along the outcrop of unit 10, Loc. C2, 123 ft. above base of Kiowa, and 63 ft. above the highest occurrence of *Adkinsites,* southern Kansas. Occurrence of these specimens marks the base of the *I. bellvuensis* range zone in southern Kansas (SCOTT, in press).

PALEOECOLOGY.—*Inoceramus* probably was a free or cemented epifaunal filter-feeder. Its localized abundance in Cretaceous rocks suggests that it was gregarious.

Superfamily PECTINACEA Rafinesque, 1815—Family PECTINIDAE Rafinesque, 1815

Genus PECTEN Müller, 1776

PALEOECOLOGY.—Recent *Pecten* is a vagrant, epifaunal filter-feeder that lives in marine to slightly brackish waters on a sandy substrate. On the Gulf Coast it is very abundant in the infralittoral zone in brackish to normal marine water.

Subgenus PECTEN (NEITHEA) Drouet, 1825

PECTEN (NEITHEA) OCCIDENTALIS (Conrad, 1855)

Neithea occidentalis CONRAD, 1855, p. 269.

Pecten (Neithea) occidentalis (CONRAD). STANTON, 1947, p. 43, pl. 27, fig. 1-4. Provides prior synonymy.

DISCUSSION.—STANTON (1947) questioned without explanation TWENHOFEL's report of fragments of *Pecten texanus* ROEMER from the "Champion shell bed" at Belvidere. The ornamentation of the latter species is similar to that of *P. occidentalis,* and perhaps the fragments were misidentified.

TYPES.—Paratype: USNM 9872; plesiotypes: USNM 103227, 103228, 103229; representative specimen: KU 500073.

OCCURRENCE AND MATERIAL.—CRAGIN (1895b), TWENHOFEL (1924), and STANTON (1947) reported the species ranging from the basal shell conglomerate upwards about 100 ft. above the base of the Kiowa at Belvidere. In Texas it ranges from Walnut to Kiamichi formations. A single calcareous shell was collected from shell conglomerate (unit 1, Loc. K1). Lower Kiowa, southern Kansas.

Subgenus PECTEN (SYNCYCLONEMA) Meek, 1864

PECTEN (SYNCYCLONEMA) INCONSPICUUS Cragin, 1894

Pecten inconspicuus CRAGIN, 1894b, p. 51.

Pecten (Syncyclonema) inconspicuus CRAGIN. STANTON, 1947, p. 40, pl. 15, fig. 1-9. Provides prior synonymy.

TYPES.—Three syntypes: USNM 32684; plesiotypes: USNM 103214a-c, 103215a-b; representative specimens: KU 500074 and 500075.

OCCURRENCE AND MATERIAL.—CRAGIN (1895b) and STANTON (1947) reported the species to be rare in the lower 100 ft. of the Kiowa in southern Kansas. Two additional specimens, one a nearly complete, calcareous shell, and the other a complete internal cast, are from sandstone units 9 and 12, Loc. C1. The species also occurs in the Denison Formation in Texas.

Family PLICATULIDAE Watson, 1930

Genus PLICATULA Lamarck, 1801

PLICATULA SENESCENS Cragin, 1894?

?*Plicatula senescens* CRAGIN, 1894a, p. 2, pl. 1, fig. 17, 18——TWENHOFEL, 1924, p. 80, pl. 14, fig. 14, 15.

DISCUSSION.—Several specimens are tentatively placed in this species. They differ from CRAGIN's (1894a) description in having nearly continuous plications that merge into the umbo and die out at or just before the ventral margin. No punctations were seen.

CRAGIN (1895b) lists *Plicatula incongrua* CONRAD? from shell conglomerates in the Kiowa County. *P. senescens* may be a synonym of this species, and a comparison of specimens of the two species is needed.

TYPES.—Original material lost. Representative specimens: KU 500188a-c.

OCCURRENCE AND MATERIAL.—CRAGIN collected "two or three specimens" 20 to 60 ft. above the base of the Kiowa, presumably from shell conglomerates at Belvidere. Three specimens, molds and shells, were collected from the basal shell conglomerate at the same locality. Ranges from the base of the Kiowa to 50 ft. above base; Kiowa County. *Plicatula incongrua* ranges from Fredericksburg to Washita groups.

Superfamily ANOMIACEA Rafinesque, 1815—Family ANOMIIDAE Rafinesque, 1815

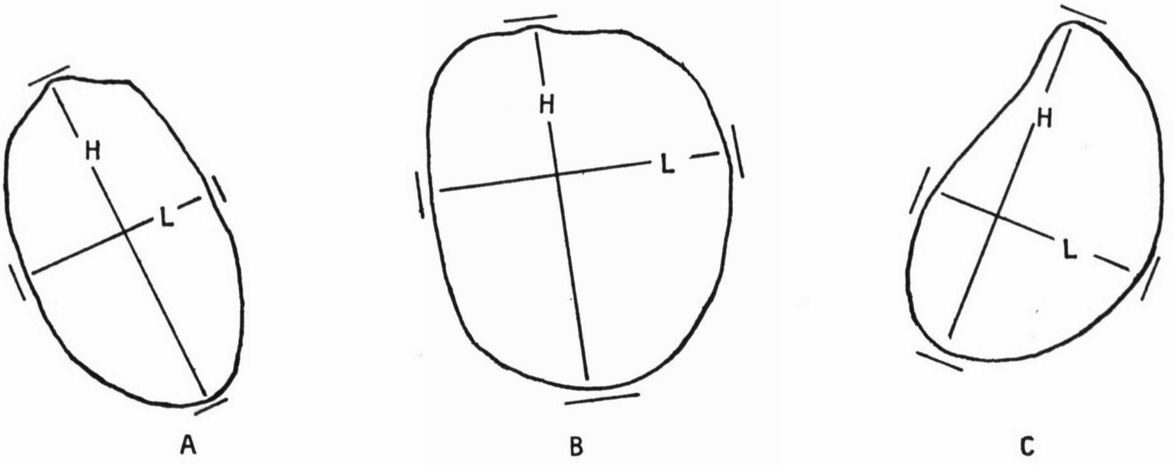


FIG. 17. Measured parameters, height *(H)* and length *(L)*, of *Ostrea arcuata* SCOTT, n. sp. (*A*, RV) and of *Ostrea rugosa* SCOTT, n. sp. *B*, RV; *C*, LV).

Genus ANOMIA Linné, 1758

ANOMIA sp. indet.

Plate 3, figure 3

DESCRIPTION.—Shell of moderate size, thin, oval, slightly inequilateral. Beak below margin, not prominent. Umbo slightly inflated, ellipsoidal, dying out towards ventral margin. Dorsal margin nearly flat, short; shell margins subcircular. Ornamented by thick growth lines. Length of KU 500076 21 mm., height 19 mm., width about 4-5 mm.

DISCUSSION.—CRAGIN (1895b) listed *Anomia* sp. from the Kiowa in southern Kansas, but no species was described from Kansas nor from equivalent rocks in Texas. This species is similar in form to *A. argentaria* in the Taylor and Navarro groups, but lacks radial striae.

OCCURRENCE AND MATERIAL.—CRAGIN (1895a,b) found *Anomia* in the "Champion shell bed" and shell conglomerates in the overlying 100 ft. of the Kiowa, and in "Mentor beds" in central Kansas. The only specimen collected in this study (KU 500076) is from sandstone in southern Kansas (unit 12, Loc. C1), others were seen in unit 10, Loc. C2.

PALEOECOLOGY.—Recent *Anomia* is a byssate filter-feeder. It is very common in the upper sound Gulf Coast assemblage (PARKER, 1956).

Suborder OSTREINA Férussac, 1822—Superfamily OSTREACEA Rafinesque, 1815—Family OSTREIDAE Rafinesque, 1815

Genus OSTREA Linné, 1758

PALEOECOLOGY.—Recent *Ostrea* is a free or cemented filter-feeder common in relatively clear waters at salinities greater than 15‰. The restricted occurrence of *Ostrea rugosa* SCOTT, n. sp. suggests that it would not tolerate as wide a range of conditions as *Crassostrea kiowana.*

OSTREA ARCUATA Scott, n. sp.

Figure 17,*A;* Plate 2, figures 6-8

DESCRIPTION.—Ostreid species distinguished by a very concave shell, very convex anterior margin, very arcuate inclined median longitudinal axis, and by faint concentric ornamentation.

Shell of small to moderate size, elongate rhombic, extremely inequilateral, height greater than length, inequivalved, strongly prosocline. Beak opisthogyrate, umbo greatly inflated, prosocline median longitudinal axis concave posteriorly.

Short hinge line extended posteriorly to form small auricle on LV. Anterior dorsal margin sloping gently from beak; anterior margin curving strongly posteriorly to form ventral arc; posterior margin not completely preserved; posterodorsal margin sharply angular around auricle; posterior margin descending steeply below auricle in concave arc. Form of RV not known.

Convexity of LV very great in umbonal region, less so in marginal areas. No marginal sulci present. Commissure planar, shell margins straight. Auricle on LV a small angular corner on posterodorsal margin; auricular sulcus absent.

Beak very small, projecting slightly beyond hinge line, continuous with umbonal surface. Ornamented by lightly impressed, widely spaced concentric grooves and growth lines.

Cardinal area simple, resilifer on LV a very shallow groove on a narrow plate beneath beak. Subcardinal cavity very deep. Posterior marginal denticles small and closely spaced; limited to about dorsal fourth of posterior margin length.

Pallial line lightly impressed; no grooves or scars. Adductor muscle scar subcentral, just posterior of midline, semicircular with straight dorsal margin. Measurements in Table 7; Fig. 17,*A* shows measured parameters.

TABLE 7. *Measurements of specimens of Ostrea arcuata Scott, n. sp., and Ostrea rugosa Scott, n. sp.*

Specimens	Length mm.	Height mm.	Width mm.
Ostrea arcuata			
Holotype:			
KU 500105a LV	20±	25	4.5
Paratype:			
KU 500104a LV	16±	22±	4±
Ostrea rugosa			
Holotype:			
KU 500097a LV	27.7	30.4	3±
KU 500098 RV	20	28	3±
KU 500101b RV	14	20	1±
KU 500101c RV	20	29	3±
KU 500102 LV	32	50±	4
KU 500100a LV	23	23	3
KU 500047a LV	19	21	2

DISCUSSION.—Specimens assigned to this species were originally considered a variant form of *Ostrea* n. sp. A (SCOTT, 1967a; here named *Ostrea rugosa*). It is here separated as a distinct species because the overall form, as well as ornamentation, are strikingly different. *Ostrea arcuata* has no anterior auricle and the posterior auricle is a small corner rather than a wide, flaring surface as it is in *O. rugosa*. *O. arcuata* has a much more concave and consequently thicker valve than *O. rugosa*. Concentric ornamentation of *O. arcuata* is much less pronounced than in *O. rugosa*. Generally the median longitudinal axis of *O. arcuata* is more greatly arched than that of *O. rugosa*, to which feature the trivial name refers.

TYPES.—Holotype: KU 500105a; paratype: KU 500104 a-b.

OCCURRENCE AND MATERIAL.—Molds and casts in laminated sandstone were found at Loc. M6, unit 5 in about the middle of the Kiowa of central Kansas.

OSTREA RUGOSA Scott, n. sp.

Figure 17, *B,C;* Plate 2, figure 5; Plate 3, figure 1, 2, 5, 7

Ostrea sp. MEEK, 1876, p. 12, pl. 2, fig. 8a, b.——TWENHOFEL, 1924, p. 77, pl. 21, fig. 1, 2.

DESCRIPTION.—A species of *Ostrea* characterized by concentric wrinkled ornamentation, by a gently curved prosocline median longitudinal axis concave posteriorly, and by nearly flat valves.

Shell of moderate size, rhombic-ovate, inequilateral, height greater than length, inequivalved, prosocline. Beak opisthogyrate; umbo moderately inflated, median longitudinal axis a gentle prosocline arc, concave posteriorly. Hinge line of LV extended posteriorly and anteriorly by auricles continuous in outline with lateral margins; anterior auricle narrower than posterior auricle. Dorsal margins of LV sloping gently from beak; anterior margin descending abruptly in broad, gentle convex curve; ventral margin more narrowly rounded; posterior margin broadly rounded. RV narrowly elongate, hinge line short, anterior margin steeply sloping broad arc, ventral-anterior margin moderately rounded; posteroventral margin sharply rounded; posterior margin gently curved, very slightly convex.

Convexity of LV greater than of RV; convexity greatest in umbonal region, shell distinctly flatter in ventral lateral regions. Attachment scar of immature stage a small flat area on beak.

Auricles developed only on LV, posterior generally the larger and broader. Auricle medium-sized sharply round, flattened salient of dorsolateral margin, anterior auricular sulcus faint.

Beaks on both valves small, opisthogyrate, continuous with convex umbonal region. Umbo on both valves commonly separated from flat margins by very shallow longitudinal sulci parallel to margin, anterior sulcus longer than posterior sulcus.

Ornamented by low, asymmetrically rounded, laterally discontinuous, concentric wrinkles, superimposed thin, closely spaced growth lines. Shell thin, wrinkles expressed interiorly more strongly on LV, less so on RV.

Cardinal area poorly developed; resilifer on LV a narrow, shallow trough bounded by narrow lateral plates. Surface marked by closely spaced grooves formed

EXPLANATION OF PLATE 1

FIGURE

1,8. Lingula subspatulata HALL & MEEK?——*1.* Mature valve, ×4, Loc. R6, KU 500032.——*8.* Immature valve, ×4, unit 9, Loc. M4, KU 500033a (p. 57).

2,9. Membranipora? kiowana SCOTT, n. sp.——*2.* Encrusting exterior of *Gryphaea* valve, ×18, unit 13-14, Loc. C1, KU 500031a.——*9.* Encrusting interior of *Gryphaea* valve, ×5, same loc., KU 500029 (p. 55).

3,4. Breviarca subovata SCOTT, n. sp.; *3,* exterior, and *4,* interior of RV, both ×4, unit 3, Loc. M3, KU 500049 (p. 60).

5. Yoldia microdonta MEEK, interior mold of LV in shale, ×2.7, unit 5, Loc. C1, KU 500041 (p. 59).

6,7. Breviarca angulata SCOTT, n. sp.; 6, exterior view of LV, and *7,* exterior view of RV of articulated specimen, both ×4, unit 8, Loc. K1, KU 500048 (p. 59).

10. Nuculana mutata STEPHENSON; opposed valves rotated before solution of shell material, casts in shale, ×3.3, unit 9, Loc. C1, KU 500040a,b (p. 59).

11,12. Breviarca habita STEPHENSON; *11,* exterior cast of LV in shale, ×4, and *12,* exterior cast of RV, ×6, unit 6, Loc. C4, KU 500043, KU 500042, respectively (p. 59).

13,14. Nucula sp. cf. *N. rivulana* STEPHENSON; *13,* external latex cast and *14,* internal sandstone mold, both ×4, unit 15, Loc. M4, KU 500037a,b (p. 58).

15. Nucula? catherina CRAGIN; external view ?LV, ×2.5, unit 8, Loc. K1, KU 500038 (p. 58).

16. Modiolus sp. A; internal sandstone cast of LV of articulated specimen, ×2, unit 3, Loc. S9, KU 500059 (p. 62).

17. Modiolus sp. B; external cast of RV in shale, ×4, unit 6, Loc. C4, KU 500065a (p. 62).

18. Botula carolinensis (CONRAD)?; exterior view of RV of articulated specimen in boring on *Gryphaea* valve; boring artificially enl., ×4, unit 7, Loc. K3, KU 500068 (p. 62).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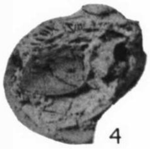
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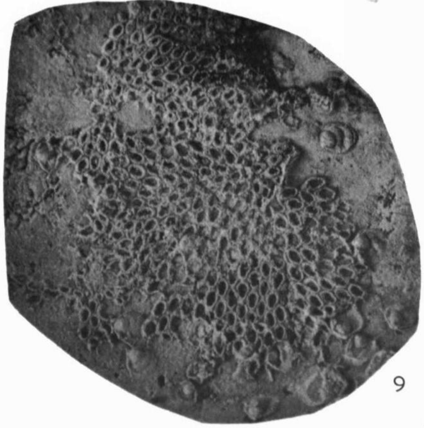
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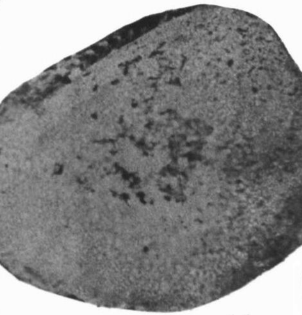
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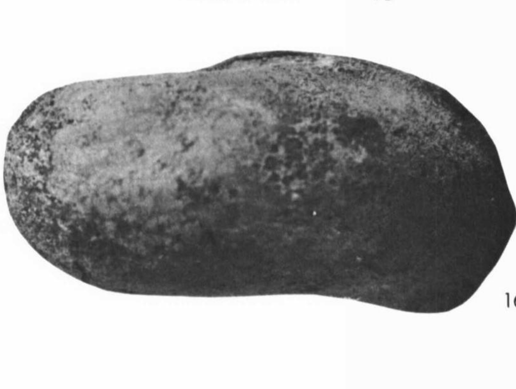
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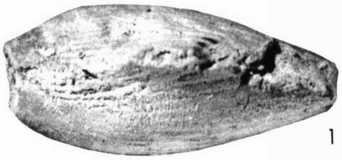
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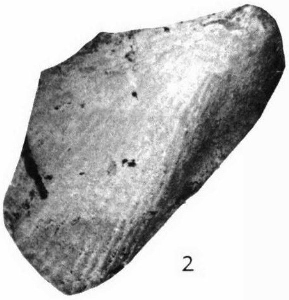
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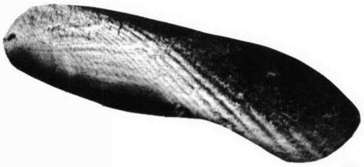
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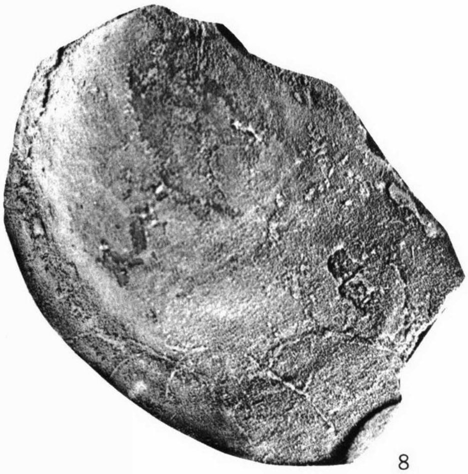
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by shell layers. Subcardinal cavity on LV shallow. Low cardinal fold of RV oblique to anterior margin, becoming flat towards beak and merging with lateral plates. Posterior marginal cardinal trough shallow ventrally and flattening towards beak.

Marginal denticles near beak of RV; present on posterior margin of LV, though rarely preserved. Commissure nearly a flat plane, not plicated. Pallial line commonly lightly impressed, approximately located along longitudinal sulci. Pallial or vascular grooves, shallow, short to long, impressed on ventrolateral margins.

Adductor muscle scar subcentral, slightly posterior of mid-line; scar on LV semi-circular with concave dorsal margin to "comma-shaped"; scar on RV semi-circular with straight dorsal margin. Scar shallowly impressed and part of surface marked by very faint concentric lines. Measurements given in Table 7; parameters shown in Fig. 17B,C.

Discussion.—The form described by Meek (1876) has an outline and ornamentation similar to this species, which is distinguished by the wrinkled ornamentation (indicated by the trivial name *rugosa*), the poorly developed resilifer-beak area, and the "comma-shaped" adductor muscle scar on LV. This scar shape is more similar to the muscle scar of both *Lopha* and *Crassostrea.* The planar commissure excludes it from *Lopha,* and the sub-central position of the muscle scar and more regular growth form from *Crassostrea.*

A variant form from unit 15, Loc. M4, is slightly larger, has no subcardinal cavity, and has a more strongly impressed pallial line. Auricles are smaller. Ornamentation is unknown. Other features are similar.

Types.—Holotype: KU 500097a, left valve (Loc. M4); paratypes: KU 500098, 500099a-b, 500100a-b, 500101a-c, 500102, 500103a-b, 500104a-b, 500105a-b, 500426a-b, 500427a-b.

Occurrence and Material.—Meek's specimens came from "12 miles southwest of Salina" near Loc. S6, S7, and S8. Generally complete internal and external molds and casts in sandstone are from Loc. S4, S5, and M4. Ranges from middle to uppermost Kiowa Formation in central Kansas.

Genus CRASSOSTREA Sacco, 1897 (emend. Sohl & Kauffman, 1964)

CRASSOSTREA KIOWANA (Twenhofel, 1924)

Plate 4, figures 5, 6

Ostrea franklini Coquand. Cragin, 1895b, p. 372.

Ostrea sp. Stanton in Hill, 1895, p. 216.

Ostrea kiowana Twenhofel, 1924, p. 77, pl. 21, fig. 6, 7; not fig. 1, 2.——Stanton, 1947, p. 22.

Description.—Shell of medium size, ovate-elongate or spatulate, inequilateral, inequivalved; width moderate; convexity of LV variable, shallow to moderately deep; RV flat to very shallowly convex. Beaks narrowly to broadly rounded, commonly opisthogyrate, erect or slightly incurved. Anterior margin gently convex to straight; ventral margin broadly rounded; posterodorsal margin of LV generally convex, rarely straight or slightly concave for a short distance. Ornamented by thin, rarely coarse, lamellar growth lines.

Resilifer on LV an elongate and slightly arcuate, triangular trough; subcardinal cavity variably developed. Mid-cardinal fold on RV low, gently sloping dorsally. Very short, straight denticles common on dorsolateral margins of both valves. Adductor muscle scar posteroventral, shallowly to deeply impressed, ventral edge semicircular, dorsal margin concave and sloping anteroventrally. Length of LV, KU 500077, 28 mm., height 44.6 mm., width 9.3 mm.

Discussion.—This species is placed in *Crassostrea* because it shows the following features considered characteristic of the genus by Sohl & Kauffman (1964): 1) denticulation of the dorsolateral margins; 2) posteroventral position of muscle scar; 3) arcuate outline of muscle scar; and 4) variable shell outline from elongate to ovate.

Cragin (1895b) assigned specimens of this species to *Ostrea franklini* because of the similarities of beaks, ligament grooves, and muscle scars. Stanton (in Hill, 1895) judged that "the beaks and the cartilage pit were sufficient for specific separation." In 1947 he acknowledged that the two species were "difficult to separate"; but "the beaks of *O. kiowana* are generally not so narrow and pointed, and some specimens have the margin near the beaks crenulated on the interior" (p. 22). Stanton's figured specimens of *O. franklini* show that the posterodorsal margin generally is slightly concave, and that the muscle scar is more ovate than arcuate, and is centrally located.

Twenhofel (1924) compared two of Meek's specimens of *Ostrea* sp. (1876, pl. 2, fig. 8a-b) with *Crassostrea kiowana.* I have not seen the original specimens; however, the figured specimens appear to belong to *Ostrea rugosa* Scott, n. sp.

EXPLANATION OF PLATE 2

Figure

1-4. Brachidontes nonbifurcus Scott, n. sp., ×3.4, Loc. S2.——*1.* Posterior view of external cast, paratype KU 500461.——*2.* External cast of RV, KU 500461.——*3.* Anterior view of external cast of LV, holotype KU 500067.——*4.* External cast of LV, KU 500067 (p. 61).

5. Ostrea rugosa Scott, n. sp., ×2.7, Loc. S4; internal latex cast of RV, paratype KU 500101c (p. 66).

6-8. Ostrea arcuata Scott, n. sp., ×2.7, Loc. M6.——*6.* Internal mold of LV, paratype KU 500104a.——*7.* Internal latex cast of LV, holotype KU 500105b.——*8.* Internal mold of LV, KU 500105a (p. 65).

Types.—Original specimens lost. Representative specimens: KU 500077, 500078 (unit 7, Loc. K3), 500079-500096.

Occurrence and Material.—Well-preserved calcareous valves and many partial valves and fragments are abundant in some shell conglomerates and sandstones, and rare in claystone. The species ranges through middle and upper Kiowa, central and southern Kansas.

Paleoecology.—Recent *Crassostrea* can tolerate a wide range of environmental conditions. Under optimum conditions, it may form banks or mounds that generally are perpendicular to prevailing current directions. The spat set on firm or soft bottoms, in warm to cool, brackish waters, and can survive a relatively high amount of turbidity.

None of the Kiowa *Crassostrea* are found in place, but their abundance in shell conglomerates suggests that they were gregarious, shallow-water inhabitants. The variety in shell shape from elongate narrow to nearly oval suggests that some lived in areas of strong currents, as elongate forms do today, and that others grew in quiet waters, where the ovate form is common today. This species may not have tolerated such a wide range of conditions as does Recent *Crassostrea,* but apparently it occupied a shallow-water, nearshore niche.

Genus LOPHA Bolten, 1798 (emend. Kauffman, 1965)

LOPHA QUADRIPLICATA (Shumard, 1860)

Ostrea quadriplicata Shumard, 1860, p. 608.

Ostrea (Lopha) quadriplicata Shumard. Stanton, 1947, p. 23, pl. 7, fig. 1, 2, 5-7. Provides prior synonymy.

Discussion.—This species is placed in *Lopha* as redefined by Kauffman (1965) because the species is quite inequivalve, the muscle scar is "comma-shaped," the dorsolateral margins are denticulate, and the commissure is plicate. However, the plications do not extend to the umbonal area as is more common in *Lopha.*

Lopha quadriplicata is generally restricted to the Denison Formation in Texas (Perkins, 1960), although Stanton (1947, p. 24) records that Adkins found it in the Kiamichi Shale in southwest Texas. Stanton pointed out that specimens of the species "from Denison and Ft. Worth generally have the radiating lines of the lower valve better developed than those from other regions" (p. 24). Stanton (p. 23) suspected that most specimens from the Kiowa in central Kansas assigned to *L. quadriplicata* really belonged to *L. kansasensis* (Logan, 1899), which is very similar. He judged that the latter species has a "somewhat broader form," "less prominent development of digitations ribs," and lacked "radiating lines on the umbonal region." A comparison of my specimens with published figures of *L. quadriplicata* (Cragin, 1893; Adkins & Winton, 1920; Stanton, 1947) show the latter two differences, but the outline of Denison specimens is variable and overlaps the Kiowa forms. On the other hand, my specimens differ from Stanton's figures of *L. kansasensis* by having a more arcuate or subfalcate form, and by having digitations expressed in growth lines for a greater distance towards the umbonal region. Only one specimen shows the radial striae on the margins. Perhaps Stanton's opinion is correct; however, a thorough restudy of type material and of large collections is needed.

Types.—Plesiotypes: USNM 8077, 103180, 103181a-b, 103182.

Occurrence and Material.—Cragin (1895b) reported the species from "the upper part of the Kiowa shales of Clark County and in the Mentor beds of Saline and Ellsworth Counties" (p. 374). Stanton reported it from "the Kiowa Shale near Belvidere, and the Mentor Formation at Brookville" (p. 24). Twenhofel (1924) found it common in "Mentor beds" west of Smolan and south of Marquette.

Internal and external molds are common in sandstone. Calcareous shells, generally partly broken, occur in sandstones and shell conglomerates in central Kansas, where the species ranges from about 50 ft. above the base to the top of the Kiowa. At two localities (Loc. S6 and S9) *L. quadriplicata* occurs with *Engonoceras belviderense.* In Texas it is found throughout the Washita Group.

Paleoecology.—Recent species of *Lopha* are widely distributed in warm waters (Stenzel, 1959). This Kiowa species apparently preferred a firm substrate for attachment because the scar on one specimen reflects ornamentation of *Corbula?;* other scars are indeterminate. It is most abundant at Loc. M6 in a thin sandstone, where one other species is represented by a single specimen. It is much less common at other localities where the faunal diversity is greater, and where perhaps it is a transported element. This suggests that *L. quadriplicata* tended to be gregarious and thrived under conditions somewhat restrictive to other species.

LOPHA? KANSASENSIS (Logan, 1899)

Ostrea kansasensis Logan, 1899, p. 88, pl. 20, fig. 9-11.——Stanton, 1947, p. 22, pl. 6, fig. 1, 2, 11, 12. Provides prior synonymy.

Description.—Stanton's (1947) description is complete and based on a study of type material.

Discussion.—Apparently this is a quite variable species and difficult to distinguish from *Lopha quadriplicata* as already discussed. I have assigned one nearly complete specimen to this species because of its subovate outline and poorly developed marginal digitations. The study of a larger collection will clarify the validity of this species.

Types.—Holotype disposition unknown. Representative specimen: KU 500313.

Occurrence and Material.—Logan (1899) found this species in "Mentor-type" sandstone near Kanopolis and Coal Cañon in Ellsworth County, precise localities unknown. Stanton reported the species from the uppermost sandstone at Loc. M5, and in the middle sandstone at Loc. S6. The single calcite shell found by me is from sandstone at Loc. R2. Range is lower or middle to uppermost Kiowa.

Paleoecology.—This species was an epifaunal filter-feeder that preferred a firm substrate.

LOPHA SUBOVATA (Shumard, 1854)

Ostrea subovata Shumard, *in* R. B. Marcy, 1854, p. 193, pl. 5, fig. 2.
Ostrea (Lopha) subovata Shumard. Stanton, 1947, p. 24, pl. 8, fig. 1; pl. 9, fig. 1, 2. Provides prior synonymy.

Description.—Shell large, subovate to trigonal, thick; rounded to angular ribs radiate from longitudinal carina, number of ribs variable; margin crenulate; interior lateral margins bearing many short denticles; adductor muscle scar posterior, large, semielliptical; dorsal margin convex.

Stanton (1947) provided a thorough description of this species including size measurements.

Types.—Plesiotypes: USNM 19108, 103184.

Occurrence and Material—Cragin (1895b) reported this species from the Kiowa in southern Kansas ranging from the basal "Champion shell bed" to 100 feet above the base. Three partial calcareous shells were found in the lower part of the Kiowa in central Kansas (unit 2, Loc. E3; Loc. R2; unit 5, Loc. R3). Stanton (1947) reported a range in Texas from Comanche Peak to Grayson Formations.

Paleoecology.—The habitat of this species probably was similar to that of *Lopha kansasensis.*

Genus GRYPHAEA Lamarck, 1801

Subgenus GRYPHAEA (TEXIGRYPHAEA) Stenzel, 1959

GRYPHAEA (TEXIGRYPHAEA) CORRUGATA CORRUGATA Say, 1823

Gryphaea corrugata Say, 1823, p. 410.——Stanton, 1947, p. 26, pl. 10, fig. 3-6; pl. 11, fig. 1, 3, 4. Provides prior synonymy.

Description.—Hill & Vaughan (1898) gave an adequate description of this species. Twenhofel (1924) characterized it by the absence of both a strong keel and posterior projection, by the oval shape, and by the smooth growth lines. Hill & Vaughan stated that the size of the posterior wing is variable. I have assigned to this species forms that are elongate-oval in outline, and that have a rounded keel.

Discussion.—The basal shell conglomerate in Kiowa County ("Champion shell bed") contains a gradational series of shell forms that vary from the type of *Gryphaea corrugata,* to *G. hilli,* and to *G. mucronata.* This series needs to be analyzed statistically, but its reality is shown by the arbitrary species assignment of some specimens. The entire assemblage appears to consist of all growth stages with the intermediate stages most abundant.

Types.—Plesiotypes: USNM 28769-71, 28773; representative specimens: KU 500106-500134, 500185-500187.

Occurrence and Material.—Twenhofel found *Gryphaea corrugata* in all shell conglomerates from the basal unit to the highest beds in Kiowa County. Shells were collected in most shell conglomerates containing identifiable *Gryphaea,* ranging from the base of the Kiowa at Loc. K1 to its upper half at Loc. K3, and also in Clark County. All *Gryphaea* species are represented by whole and fragmental calcitic shells. The range of this species in Texas is Kiamichi to Duck Creek (Adkins, 1928).

Paleoecology.—*Gryphaea* was a free or cemented epifaunal filter-feeder, and probably preferred a greater salinity and depth than did *Ostrea* (Bergquist & Cobban, 1957). Of the many ecological factors affecting the shape of *Gryphaea* shells, the firmness of the substrate may have been one of the more influential. Accordingly, each of the following species is interpreted as an ecophenotype that reflects substrate firmness. However, the taxonomy of previous workers is retained because a statistical analysis has not been made to test this hypothesis.

The deep dish-shape of *Gryphaea corrugata* suggests a substrate less firm than the substrate to which *G. navia* and *G. (T.) belviderensis* were adapted. The attachment scar of one immature individual reflects *Turritella* ornamentation.

GRYPHAEA (TEXIGRYPHAEA) CORRUGATA BELVIDERENSIS Hill & Vaughan, 1898

Gryphaea corrugata var. *belviderensis* Hill & Vaughan, 1898, p. 56, pl. 9, 10.——Stanton, 1947, p. 26, pl. 13, fig. 1, 2. Provides prior synonymy.
Gryphaea (Texigryphaea) belviderensis Hill & Vaughan. Stenzel, 1959, p. 28.

Description.—The subspecies is distinguished from *Gryphaea corrugata* "by its larger size, more triangular outline, and flatter form" (Stanton, 1947, p. 26). Twenhofel (1924) added that no keel is developed. I have included in this group forms having a somewhat narrowly rounded keel, intermediate to the sharply rounded keel of *G. navia.* This form grades into both *G. corrugata* and *G. navia,* and is more appropriately considered a subspecies.

Discussion.—On a few specimens a circular, flat to slightly concave attachment scar of variable size deforms the beak and umbo. The oval, cup shape of the early shell is not unlike *Gryphaea wardi,* but a posterior wing develops early. On one specimen from unit 7, Loc. K3, the surface of attachment reflects *Gryphaea*-like ornamentation. On the same specimen *Botula caroli-*

nesis? has bored into the scar at an angle, suggesting that the *Gryphaea* shell was concave down on the substrate, thus boring occurred after the animal died (Pl. 1, fig. 18). On a few valves the attachment area is gently convex and bordered by a posterior keel that merges into the umbo, suggesting that the keel was used to stabilize the immature shell on the substrate.

TYPES.—Syntypes: USNM 28774; TWENHOFEL's specimen: KU 500179a-b; representative specimens: KU 500176-500178.

OCCURRENCE.—TWENHOFEL found this subspecies in all shell conglomerates except the "Champion shell bed" in southern Kansas. It usually occurs together with either *G. corrugata* or *G. navia,* or both.

PALEOECOLOGY.—The larger, triangular posterior area of the left valve may have been adapted to lying on a relatively firmer substrate than *G. corrugata.*

GRYPHAEA (TEXIGRYPHAEA) HILLI Cragin, 1891

Gryphaea pitcheri var. *hilli* CRAGIN (in part), 1891, p. 181.
Gryphaea hilli CRAGIN. STANTON, 1947, p. 26, pl. 17, fig. 1-4, 6-9. Provides prior synonymy.

DESCRIPTION.—STANTON (1947) characterized this species by its small, slender form, beaks "strongly incurved, slightly deflected," dorsal furrow distinct and narrow, "inconspicuous dorsal wing." It differs from *Gryphaea corrugata* by its narrow form and smaller posterior wing; it differs from *G. mucronata* by its smaller form, smoother surface, and by the weaker dorsal furrow and wing.

DISCUSSION.—HILL & VAUGHAN (1898) and STANTON (1947) considered this form intermediate between *G. mucronata* and *G. corrugata.* TWENHOFEL (1924, p. 71) suggested that it may be a "dwarfed form of *G. corrugata* developed by adverse conditions of environment."

TYPES.—Plesiotypes: USNM 28772, 103186, 103187; representative specimens: KU 500135-500154.

OCCURRENCE.—CRAGIN (1895b) and TWENHOFEL reported the species only from the "Champion shell bed," in Kiowa County, where I also have found it.

PALEOECOLOGY.—Perhaps the narrow, deeply concave form was an adaptation to a relatively soft substrate, probably accompanied by crowding of neighboring individuals.

GRYPHAEA (TEXIGRYPHAEA) MUCRONATA Gabb, 1869

Gryphaea mucronata GABB (in part), 1869, p. 274.——STANTON, 1947, p. 28, pl. 18, fig. 1-26. Provides prior synonymy.

DESCRIPTION.—STANTON (1947) separated this species from *Gryphaea hilli* by its larger size, and by a stronger dorsal sinus and wing. The beak is generally strongly incurved, and low radial plications are on the umbonal region.

Two shells have attachment scars reflecting ornamentation of *Corbula?,* and one is attached to a right valve of *Gryphaea.*

TYPES.—Syntypes: Philadelphia Academy of Natural Science 4773; plesiotypes: USNM 28776 to 28778; representative specimens: KU 500155-500175.

OCCURRENCE.—In Kansas the species is in the basal shell conglomerate at Locs. K1 and K2. In Texas it ranges from Walnut to Goodland Formations; its highest occurrence is in the *Manuaniceras powelli* Zone.

GRYPHAEA (TEXIGRYPHAEA) NAVIA Hall, 1856

Gryphaea pitcheri var. *navia* HALL, 1856, p. 100, pl. 1, fig. 7-10.
Gryphaea navia HALL. STANTON, 1947, p. 27, pl. 19, fig. 1, 2. Provides prior synonymy.

DESCRIPTION.—HILL & VAUGHAN (1898) characterized the species by the sharp keel, the depressed dorsoposterior area, and the strongly curved umbo and beak. The valve outline generally is more compressed than *Gryphaea corrugata belviderensis,* and more triangular than *G. corrugata.*

TYPES.—Plesiotypes: USNM 28780, 28781, 8022; representative specimens: KU 500180-500184.

OCCURRENCE.—TWENHOFEL (1924) found this species in the middle shell conglomerates in southern Kansas, and not ranging to the base nor to the top. Shells were found in unit 13-14, Loc. C1; units 8 and 12, Loc. K1. It always is found with *Gryphaea corrugata belviderensis* or *G. corrugata* or both and is less abundant, although TWENHOFEL stated that in unit 12 it was twice as abundant as *G. corrugata.* In Texas and Oklahoma it is restricted to the Kiamichi.

PALEOECOLOGY.—The relatively flat, arcuate form of the posterior area of the LV may have been adapted to lying on substrate intermediate in firmness to that for which *G. corrugata* and *G. corrugata belviderensis* were adapted.

Subclass PALAEOHETERODONTA Newell, 1960—Order TRIGONIOIDA Dall, 1884—Superfamily TRIGONIACEA Lamarck, 1819—Family TRIGONIIDAE Lamarck, 1819

Genus SCABROTRIGONIA Deecke, 1925

SCABROTRIGONIA EMORYI (Conrad, 1857)

Trigonia emoryi CONRAD, 1857, p. 148, pl. 3, figs. 2a-c.——CRAGIN, 1895b, p. 376, not *Trigonia clavigera* CRAGIN.——ADKINS & WINTON, 1920, p. 73, pl. 17, fig. 4-6.——TWENHOFEL, 1924, p. 85, pl. 13, fig. 1-3.——ADKINS, 1928, p. 131.

DISCUSSION.—This species belongs in the *scabrae* group as summarized by STOYANOW (1949). CRAGIN (1895b) distinguished *Scabrotrigonia emoryi* from *S. clavigera* by the ridgelike radial costae of the former species having "low, narrowly compressed tubercles." Distinct ridges are lacking on the latter species and the costae are rows of "short, erect, triangularly stalked, clavate or tubercular-ended" nodes. CRAGIN noted that specimens from "Mentor beds" in Saline County seemed to have ornamentation of an intermediate character. I have not found unweathered molds having an "intermediate type" of ornamentation, but weathered specimens do appear so.

TYPES.—Original specimens lost. Representative specimens: KU 500189, 500190.

OCCURRENCE AND MATERIAL.—CRAGIN (1895a,b) and TWENHOFEL (1924) found the species in "Mentor beds" in central Kansas and in shell conglomerates in southern Kansas. New molds, casts, and iron oxide-replaced valves were found in sandstone and shale in both areas. Ranges from lower to uppermost Kiowa. In Texas it ranges from the Goodland to the Denison formations (PERKINS, 1960).

PALEOECOLOGY.—Recent *Neotrigonia* is a shallow-burrowing filter-feeder on sandy mud substrates at depths from 11 to 80 meters (MCALESTER, 1965).

Subclass HETERODONTA Neumayr, 1884—Order VENEROIDA H. Adams & A. Adams, 1858—Suborder LUCININA Dall, 1889—Superfamily CARDITACEA Fleming, 1828—Family CARDITIDAE Fleming, 1828

Genus CARDITA Bruguière, 1792

CARDITA? BELVIDERENSIS Cragin, 1894

Cardita belviderensis CRAGIN, 1894a, p. 5, pl. 1, fig. 9-11.——TWENHOFEL, 1924, p. 62, pl. 13, fig. 4-6.

DISCUSSION.—The outline and ornamentation of this species is similar to that of *Venericardia*, but until the dentition is fully known it is tentatively retained in *Cardita*.

TYPES.—Unknown. Representative specimens: KU 500191-500195.

OCCURRENCE AND MATERIAL.—CRAGIN (1894a) and TWENHOFEL (1924) found the species in the "Champion shell bed" and ranging upwards to about 50 to 60 ft. above the Kiowa base in southern Kansas. Additional partially incomplete calcitic shells and casts were collected from shell conglomerate, shale, and sandstone in southern Kansas and one specimen questionably assigned to the species in central Kansas.

PALEOECOLOGY.—Recent *Cardita* is a filter-feeder in shallow marine waters attached to a firm substrate by a byssus (KEEN, 1958).

Superfamily CRASSATELLACEA Menke, 1830—Family CRASSATELLIDAE Menke, 1830

Genus CRASSATELLINA Meek, 1871

CRASSATELLINA OBLONGA Meek, 1871

Figure 18

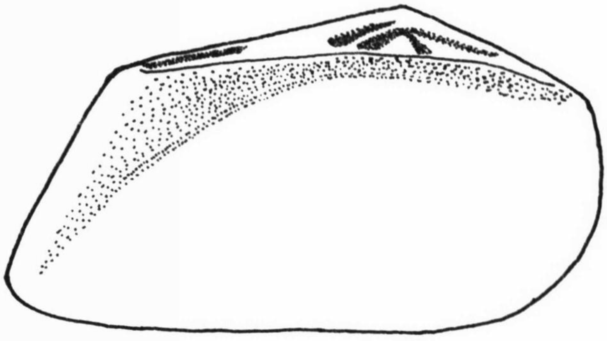

FIG. 18. Sketch of *Crassatellina oblonga* MEEK, 1871, about ×5.

DESCRIPTION.—Shell moderate size, elongate, subquadrate, inequilateral, equivalved. Beak inflated, slightly opisthogyrate. Dorsal margin about three-fourths the shell length, sloping anteriorly and posteriorly, posterior portion longer than anterior segment, each segment straight. Anterior margin smoothly curved; ventral margin nearly straight, slightly concave in mid-part, posteroventral corner sharp; posterior margin straight, inclined anteriorly. Umbonal ridge sharply arched, extending from beak to posteroventral corner, posterior umbonal surface very slightly concave. Impression of smooth growth lines variable, closely spaced.

Description of cardinal area based on latex casts of MEEK's original specimens (USNM 12414), which are LVs; structure of RV inferred from the LV. LV with one triangular cardinal tooth, centrally located on hinge plate. Two cardinal sockets: anterior socket subparallel to anterior hinge margin, deep, expanded anteriorly; deep posterior socket oblique to hinge line, slightly expanded posteriorly; both sockets connected dorsally by shallow groove, anterior lateral tooth extending into cardinal area as dorsal ridge of anterior socket; lateral socket deep and dorsal to lateral tooth. Posterior lateral tooth extending from posterodorsal corner to mid-point on posterior hinge margin; ventral to deep lateral socket as long as tooth. Ligament (?) groove shallow, slightly oblique to hinge line, separated from posterior cardinal socket by thin, straight partition extending the width of the hinge plate and oblique to hinge line. Partition not as high as cardinal tooth. Cardinal platform between ligament groove and posterior lateral tooth smooth and gently convex.

Right valve with two diverging cardinal teeth connected by a low ridge; cardinal socket deep, triangular. Both cardinal teeth expanded ventrally. Anterior and posterior lateral teeth narrow and dorsal to lateral sockets.

Anterior and posterior muscle scars shallowly impressed, anterior scar an elongate oval directly ventral to anterodorsal corner and elongated in a ventral-dorsal direction. Posterior scar located on posterior umbonal surface and opposite posterodorsal corner, oval shaped and slightly extending onto umbonal ridge.

Pallial line straight and lightly impressed; pallial muscle scars shallow, narrow grooves normal to pallial line and extending dorsally about one-fourth the shell height; scars more deeply impressed on anterior half of shell.

DISCUSSION.—The preceding interpretation of fragmentary molds is significantly different from MEEK'S (1871), who described two cardinal teeth in each valve and a posterior socket divided by a thin lamina. Apparently MEEK interpreted the convex surface of the hinge plate as a posterior cardinal tooth. His own sketch (Fig. B, p. 301) shows the surface to be only slightly raised. The groove posterior to the thin lamina is interpreted as a ligament attachment area because of its great length and shallow, narrow, unexpanded shape. It is quite different from the deep and rounded cardinal sockets. The thin lamina probably was more useful in ligament attachment than in articulation because of its great length, low height, and fragile narrow shape. Thus, the genus *Crassatellina* is characterized by one cardinal tooth and two sockets on the LV, and two cardinal teeth and one socket on the RV, by an internal ligament, and by one anterior and one posterior lateral tooth on each valve.

The familial rank of this genus was doubted by MEEK (1871, p. 300) and by STEPHENSON (1923, p. 264). MEEK hesitatingly placed *Crassatellina* in the Crassatellidae because of its "external aspect of a *Crassatella,* from which, however, it is widely removed generically by its hinge characters . . ." (MEEK, 1871, p. 300). STEPHENSON (1923) compared the genus to *Etea,* but followed MEEK (1876) in separating it because hinge features were so poorly known. Clarification of this problem must await systematic revision of the Crassatellidae and more complete material of *C. oblonga.* However, tentatively the species is retained in the family.

TYPES.—Holotype: USNM 12414 (height 8.5 mm., length 15.6 mm.); representative specimens: KU 500196, 500198-500202.

OCCURRENCE AND MATERIAL.—MEEK (1871) and TWENHOFEL (1924) found the species in "Mentor beds" near Smolan and at Natural Corral. Internal and external molds and casts were found at Locs. M5 and K1 in sandstone and in siliceous concretions in dark-gray shale. It ranges from the lower part to the uppermost Kiowa in southern and central Kansas.

PALEOECOLOGY.—This species may have been a shallow burrowing filter-feeder as are modern species of *Crassatella.*

Genus CRASSINELLA Guppy, 1874

CRASSINELLA SEMICOSTATA Scott, n. sp.

Plate 5, figures 3-6

DESCRIPTION.—Shell small to moderate, triangular, subequilateral, equivalved. Beak pointed, opisthogyrate, incurved. Umbo slightly inflated, surface smoothly convex. Posterior dorsal margin very slightly concave, anterior dorsal margin straight; angle around beak 95°. Anteroventral margin semicircular; posterior margin more sharply curved. Ornamented by low, rounded, concentric ribs with rounded interspaces about as wide as ribs; prominent on ventral half of valve, faint or absent on umbo; very thin, closely spaced growth lines superimposed.

Cardinal area of LV consisting of a shallow, anterior cardinal socket; a narrow cardinal tooth diverging anteriorly; a deep resilifer bounded posteriorly by a narrow platform distinct from outer edge of valve; posterior lateral groove long and narrow. Cardinal area of RV consisting of small anterior cardinal tooth formed by expansion of anterior shell margin; deep, narrow cardinal socket diverging anteriorly; posterior cardinal tooth large, expanded ventrally, surface slightly indented; triangular resilifer deep, posterior to cardinal teeth; anterior lateral groove long and narrow. Muscle scars oval and slightly impressed.

Measurements of RV KU 500268; length 4.6 mm., height 4.1 mm., width 1.3 mm.

DISCUSSION.—Material here assigned to *Crassinella semicostata* was initially identified as *Corbulamella? crassicostata* (CRAGIN, 1894) by SCOTT (1967a,b). A comparison of these specimens with illustrations in OLSSON (1961) has resulted in reevaluation of their systematic position. The absence of a chondrophore, rostrum, and inflation clearly indicate that these specimens are not corbulids. Their overall shape, ornamentation, and dentition are characteristic of the genus *Crassinella* as described by OLSSON (1961, p. 181).

The exterior features of this species are similar to those of *Corbula crassicostata* CRAGIN, 1894b, but it differs in important aspects. *Crassinella semicostata* is not as inflated as most corbulids, nor is it rostrate or gaping, which are important characters of *C. crassicostata.* These specimens are somewhat similar to TWENHOFEL'S figured specimen (1924, pl. 15, fig. 10) which he identified as *C. crassicostata;* however, the specimen is lost. TWENHOFEL stated that the valve has one concentric rib per mm.; and his specimen has a higher beak and straighter dorsal margins than *C. semicostata.* A specimen in the University of Kansas Museum of Invertebrate Paleontology (KU 500261, pl. 5, fig. 8) labeled *Corbula crassicostata* and collected in the early 1960's by the museum staff is much larger and has a higher beak than *C. semicostata;* however, it is not distinctly rostrate or gaping. Concentric ribbing is distributed across most of the shell surface. Without CRAGIN'S types, which have been destroyed, and without new material, the validity of CRAGIN'S description cannot be assessed.

TYPES.—Holotype: KU 500268; paratypes: KU 500262, 500263a-b, 500264a-b, 500265-500267, 500269-500280.

Occurrence and Material.—Calcareous shells and external molds and casts are sparse to abundant in shale, mudstone, and sandstone. Ranges throughout the Kiowa in central and southern Kansas.

Superfamily CARDIACEA Goldfuss, 1820—Family CARDIIDAE Goldfuss, 1820

Genus TRACHYCARDIUM Mörch, 1853

TRACHYCARDIUM KANSASENSE (Meek, 1871)

Plate 4, figures 2, 3

Cardium kansasense Meek, 1871, p. 307.——Cragin, 1895b, p. 377.——Twenhofel, 1924, p. 63, pl. 15, fig. 1-8. Provides prior synonymy.

Cardium? mudgei Cragin, 1894a, p. 6.——Twenhofel, 1924, p. 63.

Description.—Shell moderate-sized, subovate, slightly higher than long, moderately inflated; beaks projecting beyond hinge line, very slightly prosogyrate. Dorsal margins sloping gently away from beak; anterior and ventral margins gently curved; posteroventral corner sharply curved; posterior margin nearly straight to slightly convex, sloping to meet posterodorsal margin. Umbonal surface broadly arched, anterior valve surface gently sloping and smoothly convex; umbonal ridge highest part of valve, abruptly flexed to form steep posterior surface.

Valve surface ornamented by radial costae and concentric growth lines. Costae rounded ridges about as wide as interspaces; costae surmounted by nodes between adjacent growth lines; nodes taper upwards to spinelike projections; nodes strongest on margins of valve, weakest on umbones; nodes on early part of valve elongate parallel to shell length, nodes on later part of valve subquadrate to elongate parallel to shell height. Growth lines marked by shallow concentric grooves; on later growth stages a thin ridge between and parallel to adjacent growth lines connects nodes on adjacent costae, ridge inconsistently developed on various parts of valve. ventral valve margin crenulated by costae.

Hinge line arched, conforming to shape of dorsal margin; two cardinal and lateral teeth on each valve. On RV anterior cardinal tooth narrow and subparallel to anterodorsal margin; posterior cardinal tooth large, triangular, hook-shaped, diverging posteriorly below beak; anterior cardinal socket between the two cardinal teeth deep and triangular; posterior cardinal socket behind posterior cardinal tooth, narrow, slightly expanded ventrally, diverging slightly from posterodorsal margin; lateral teeth tab-shaped, ventral to lateral sockets on valve margin. Ligament groove narrow, extending between posterior cardinal and lateral sockets, bounded ventrally and separated from cardinal socket by a thin lamina. Dentition of LV matching that of RV, but large triangular cardinal tooth anterior and smaller cardinal tooth posterior.

Other interior features as described by Meek (1871, 1876).

Discussion.—Meek (1876) questioned without explanation the inclusion of this species in *Cardium*. Following Keen's (1958) classification this species is assigned to *Trachycardium* because: (1) shell quadrate or suboval, 2) no posterior gape, 3) hinge line arched and about parallel to ventral margin, 4) anterior lateral teeth present, 5) many closely spaced, rounded, noded costae with interspaces only slightly wider, 6) posterior slope with costae, and 7) shell margin crenulate. It differs from other species of the genus by 1) having nodes centrally located on costae, not on edge, and 2) by a more nearly equilateral shell.

Meek (1876) stated that the species did not have nodes, but Twenhofel (1924) observed them. The nodes are about as high as costae, tapering to a pointed termination and triangular. Specimens in most sandstones and shell conglomerates are abraded, nodes near margins being reduced to low rounded beads. Features of the shell that vary are 1) degree of convexity, and 2) ratio of costae width to interspace width.

Cragin (1894a) erected *Cardium? mudgei* on the basis of narrower interspaces and concentric lamellae that form "strong hood-like imbrications" where they cross costae. Cragin's species is placed in synonymy with *T. kansasense* because several of my specimens (KU 500428, 500203) show lamellar crenulations across parts of some costae, which would correspond to Cragin's description.

Types.—Holotype: USNM 7905. Four specimens are cataloged under this number, three internal molds and one external mold. A note in the tray by Stanton states that these specimens are of two species, the other being *Protocardia salinaensis?*. The two larger internal molds have strongly prosogyrate, large beaks that project well beyond the shell margin and are definitely protocardiids. The smallest internal mold is closer to the form of *Cardium* but it is too incomplete to assign confidently to a species. The fourth specimen is also incomplete and shows external ornamentation, which consists of low, rounded radial costae and radial grooves, possibly two growth lines are visible and where they cross the costae small swellings develop on the costae. Toward most of the ventral margin the number of costae is reduced by alternate costae terminating above the margin, but in one lateral area the costae continue to the margin; from the termination point, which approximately marks one growth line, each continuing costa is bounded on both sides by very faint parallel grooves, interspaces are flat. This very different ornamentation is here interpreted to be the result of some combination of abrasion and partial preservation (see also Cragin, 1895b, p. 377). The variability in development of ornamentation supports this view in contrast to the possibility that this specimen is of a different species. Ornamentation of several new worn shells have ornamentation that approaches the above-described features. Therefore, only this latter specimen can stand as holotype. The following specimens show all of the features described for the species: KU 500203, 500204a,b, 500205, 500428a-c.

Occurrence and Material.—Calcitic shells are found in shell conglomerates, internal and external casts and molds are in sandstones and shales. The species is found at most localities and ranges from the base to the top of the Kiowa.

Reeside & Cobban (1960, p. 29) reported *Trachycardium kansasense* from the Upper Albian Mowry and Aspen shales in Wyoming and Montana associated with *Neogastroplites*. Cobban & Reeside (1952b, p. 1929) recorded *Cardium (Nemocardium)* n. sp. aff. *C. kansasense* from the top of the Aspen Shale in southwestern Wyoming.

Paleoecology.—Recent *Trachycardium* is a shallow-burrowing filter-feeder common in sand substrates. It is the dominant member of a shallow water community that ranges in depth from 0 to 63 m. (Thorson, 1957). On the Gulf Coast it is an indicator of the inlet assemblage (Parker, 1956), and other firm, sandy substrate areas.

Genus PROTOCARDIA Beyrich, 1845

PROTOCARDIA TEXANA (Conrad, 1857)

Cardium (Protocardium) texanum Conrad, 1857, p. 150, pl. 6, fig. 6a-c.

Protocardium texanum (Conrad). Cragin, 1895b, p. 377.

Protocardia texana (Conrad). Adkins & Winton, 1920, p. 75, pl. 18, fig. 7.——Twenhofel, 1924, p. 80, pl. 20, fig. 1-6. Provides prior synonymy.——Adkins, 1928, p. 159, pl. 2, fig. 5

Discussion.—Twenhofel (1924) placed *Protocardia salinaensis* in synonymy with *P. texana* by interpreting the former as an immature form. All small specimens, less than about 17-20 mm. high, are equilateral; but larger specimens apparently have a produced beak that becomes higher as the shell becomes larger. Ornamentation is the same. This suggests that growth is nonallometric, or alternately, that internal molds may not reflect the shape accurately.

A variation in ornamentation is the development of a narrow groove on some concentric ribs on a few specimens. It is not a constant feature and probably not of taxonomic importance.

Types.—Original material lost. Representative specimens: KU 500206, 500208, 500209.

Occurrence and Material.—Cragin (1895a,b), Gould (1900), and Twenhofel (1924) reported external and internal molds and casts of the species from sandstone, siltstone, and shell conglomerates in central and southern Kansas. New material ranges throughout the Kiowa. Range in Texas is Fredricksburg to Washita groups.

Paleoecology.—*Protocardia* probably functioned in the same manner as *Trachycardium kansasense,* and preferred a similar environment.

Superfamily SOLENACEA Gray, 1823—Family SOLENIDAE Gray, 1823

Genus LEPTOSOLEN Conrad, 1865

LEPTOSOLEN OTTERENSIS Cragin, 1894

Leptosolen otterensis Cragin, 1894a, p. 8, pl. 1, fig. 2.——Twenhofel, 1924, p. 73, pl. 19, fig. 9.

Leptosolen conradi Meek (in part). Twenhofel, 1924, p. 73, pl. 14, fig. 4; not fig. 2, 3.

Discussion.—This species differs from *Leptosolen conradi* Meek (1871) by the anterior fold in shell, by its somewhat shorter length, and by more angular growth lines around anterior and posterior margins. Meek's figure of the type specimen (1876, pl. 2, fig. 12a,b) shows that the shell surface anterior to the beak is smoothly curved, whereas Twenhofel's specimen (1924, pl. 14, fig. 4) clearly shows that a low fold interrupts the shell surface anterior to the beak.

Types.—Type specimen unknown. Representative specimens: KU 500210-500212.

Occurrence and Material.—Cragin's only specimen was from dark-gray shale west of Belvidere, about 30-40 ft. above the Kiowa base. Twenhofel collected the specimen figured in Pl. 14, fig. 4 from the uppermost sandstone at Natural Corral. New specimens are casts from dark-gray shale in central Kansas. Ranges throughout the Kiowa.

Paleoecology.—Recent species of Solenidae are active, deep-burrowing filter-feeders in mud substrate. *Ensis* is most common in the shallow shelf Gulf Coast assemblage (Parker, 1956).

EXPLANATION OF PLATE 3

Figure

1,2,5,7. *Ostrea rugosa* Scott, n. sp.——*1*. Internal latex cast of LV, ×2, Loc. S4, KU 500097a.——*2*. External latex cast of RV, ×2, Loc. S4, KU 500098b.——*5*. Internal latex cast of LV, ×2, unit 15, Loc. M4, KU 500103b.——*7*. External latex cast of LV, ×2, Loc. S4, KU 500426b (p. 66).

3. *Anomia* sp. indet.; incomplete LV, ×2, unit 12, Loc. C1, KU 500076 (p. 65).

4. *Pteria salinensis* (White); internal latex cast of RV, ×2, unit 9, Loc. S8, KU 500072b (p. 63).

6. *Gervillia mudgeana* (White); internal sandstone cast of RV of articulated specimen, ×2, Loc. S6, KU 500071a (p. 63).


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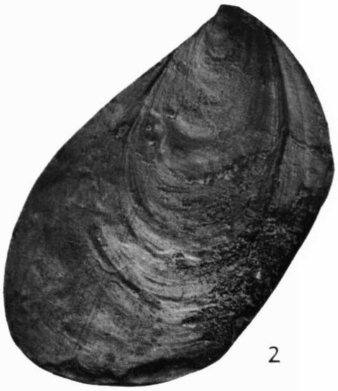
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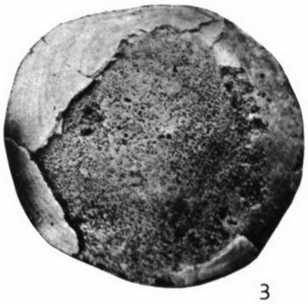
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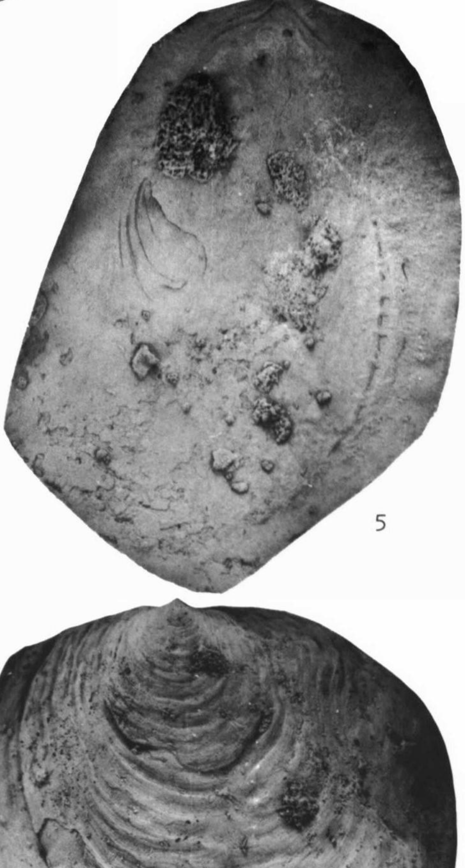
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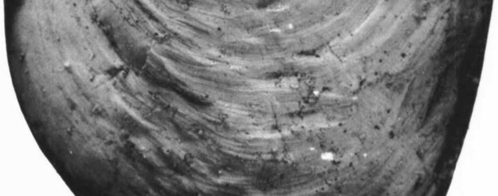
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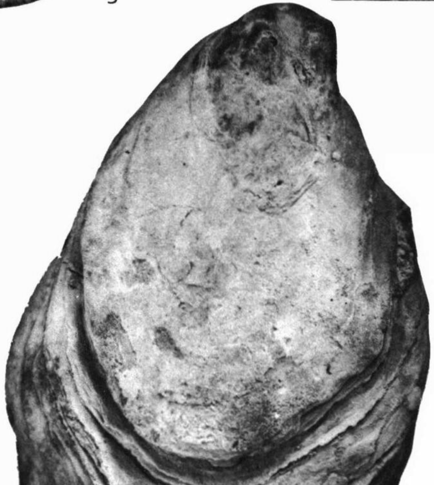

6

Superfamily TELLINACEA Latreille, 1825— Family TELLINIDAE Latreille, 1825

Genus TELLINA Linné, 1758

TELLINA? sp. indet.

Discussion.—Molds of small, elliptical, nearly equilateral shells with thin growth lines are tentatively assigned to *Tellina.* The subcentral beaks are not prominent. No other features are recognized. The specimens cannot be placed in *Tellina subscitula* Meek (1871) which has a narrower, elongate outline with a concave anterior dorsal margin.

Occurrence and Material.—Molds are more common in dark-gray shale, rare in sandstone, in the lower part of the Kiowa in central and southern Kansas. Representative specimens: KU 500214-500217.

Paleoecology.—Recent Tellinas are active, burrowing detritus-feeders. *Tellina* communities thrive in a clean, hard sand substrate from the intertidal zone to a depth of 9 meters (Thorson, 1957) but different species live on different substrates from muddy to gravelly. *Tellina* is rare in the upper sound and inlet Gulf Coast assemblages, and abundant in the shallow shelf and deeper shelf assemblages (Parker, 1956).

Genus LINEARIA Conrad, 1860

LINEARIA KANSASENSIS Twenhofel, 1924

Linearia kansasensis Twenhofel, 1924, p. 74, pl. 12, fig. 9, 10.

Description.—Shell thin, moderate size, elongate, elliptical, slightly convex, nearly equilateral, equivalved. Beak small, slightly anterior to mid-line. Dorsal margins moderately sloping, very slightly convex; anterior and posterior margins evenly rounded; ventral margin shallowly convex. Ornamented by thin, concentric growth lines; anterior one-fifth and posterior one-tenth of surface with narrow radial striae. Dorsal-anterior rib at margin of radial ornamentation most prominent, sloping anteriorly from beak, ornamentation lightly impressed on interior.

Cardinal area small; anterior cardinal socket on left valve dorsal and in front of anterior tooth, moderately deep, bottom narrowly rounded, expanding ventrally, diverging dorsally only slightly from tooth; anterior cardinal tooth long, expanding interiorly directed anteriorly; posterior cardinal socket behind tooth, shallow and shorter than tooth; posterior cardinal tooth degenerate, very slight swelling on cardinal plate. Lateral teeth narrow, moderately long; lateral teeth on left valve dorsal to socket, on right valve teeth ventral to socket. Anterior muscle scar elongate-oval, more prominent than posterior scar. Pallial line unknown.

Discussion.—This species is assigned to *Linearia* as redescribed by Stephenson (1941), because of the anteriorly sloping cardinal teeth, and the radial sculpture.

Types.—Twenhofel designated a "cotype" series of specimens to represent the species but no holotype. Therefore, I here designate as lectotype specimen KU 500218, figured by Twenhofel (1924, pl. 12, fig. 9). The external mold of this wax cast as well as the other figured specimen are lost. Paralectotypes are KU 500219-500230.

Occurrence and Material.—Twenhofel (1924) reported the species from "Mentor beds" west of Smolan. Additional material cames from other sandstone localities in Saline County. Range of species is approximately through the middle Kiowa.

Paleoecology.—Habits and requirements of this species probably were similar to those of *Tellina* rather than of *Macoma* or *Abra,* because the form of *Linearia* is more like *Tellina* and because its articulated valves are common in thin-bedded sandstone. The abundance of this species in sandstone suggests that it formed a dominant community on a sand substrate.

Genus ARCOPAGELLA Meek, 1871

ARCOPAGELLA MACTROIDES Meek, 1871?

?*Arcopagella mactroides* Meek, 1871, p. 309, fig. A, B.——Twenhofel, 1924, p. 61, pl. 12, fig. 4-8.

Discussion.—Internal casts are referred to this species because their outline and form are similar. Dentition is not completely shown. Muscle scars are relatively deeply impressed on one specimen in contrast to the "faintly marked" impressions described by Meek (1871).

Types.—Holotype: USNM 12411; representative specimens: KU 500231, 500232.

Occurrence and Material.—Meek (1871) and Twenhofel (1924) found the species common in "Mentor beds" west of Smolan. New specimens came from Loc. R3, more than 50 ft. above the base of the Kiowa, and unit 4, Loc. K1, central and southern Kansas.

Paleoecology.—Habits and requirements of this species probably were similar to *Tellina* and *Linearia.*

EXPLANATION OF PLATE 4

Figure

1. Inoceramus bellvuensis Reeside, external latex cast of RV, ×1, unit 10, Loc. C2, KU 500380b (p. 64).

2,3. Trachycardium kansasense (Meek).——*2.* Close-up view of ornamentation, external latex cast, ×4.5, pits on end of spines due to air bubbles trapped in latex, unit 3, Loc. S9, KU 500428b. ——*3.* Exterior of left valve, ×2.7, Loc. M7, KU 500203 (p. 73).

4. Scolicia sp. indet.; trail, ×1, in sandstone, unit 12, Loc. C1, KU 500415 (p. 87).

5,6. Crassostrea kiowana (Twenhofel); internal and external views of LV, ×2, unit 7, Loc. K3, KU 500077 (p. 67).

Suborder ARCTICINA Newell, 1965—Superfamily VENERACEA Rafinesque, 1815—Family VENERIDAE Rafinesque, 1815

Genus CYPRIMERIA Conrad, 1864

CYPRIMERIA KIOWANA Cragin, 1895

Cyprimeria texana var. *kiowana* CRAGIN, 1895b, p. 378.

Cyprimeria kiowana CRAGIN. TWENHOFEL, 1924, p. 67, pl. 10, fig. 1; pl. 13, fig. 13. Provides prior synonymy.——ADKINS, 1928, p. 163.

DISCUSSION.—CRAGIN (1895b) did not describe the species, but distinguished it from *Cyprimeria texana* by size and convexity. TWENHOFEL (1924) raised the variety to the rank of species, and separated it from *C. texana* and *C. crassa* by its greater thickness and larger size. A statistical analysis might demonstrate the validity or synonymy of this species.

TYPES.—Original specimens lost; representative specimens: KU 500236, 500237.

OCCURRENCE AND MATERIAL.—Calcareous shells are common in shell conglomerates in central and southern Kansas; molds are rare in sandstone; ranges throughout the Kiowa. *Cyprimeria texana* and *C. crassa* are Fredericksburg species, but PERKINS (1960) also reports *C. texana* from the Grayson.

PALEOECOLOGY.—*Venus,* the most abundant modern representative of the family, is a shallow-burrowing filter-feeder forming open-sea communities on moderately firm, clean, sandy substrates at depths from 7 to 40 m. (THORSON, 1957). *Cyprimeria* is abundant in some sandy conglomerates suggesting that it too, may have been gregarious on a sandy substrate.

Genus FLAVENTIA Jukes-Browne, 1909

FLAVENTIA BELVIDERENSIS (Cragin, 1894)

Tapes belviderensis CRAGIN, 1894a, p. 7, pl. 1, fig. 12, 13.

Mactra siouxensis smolanensis TWENHOFEL, 1924, p. 75, pl. 8, fig. 10.——ADKINS, 1928, p. 167.

DISCUSSION.—CRAGIN'S (1894a) figures of *Tapes belviderensis* show hinge features that characterize *Flaventia* as redescribed by STEPHENSON (1952). Two of TWENHOFEL'S paratypes of *"Mactra siouxensis somalenensis,"* which are in hand, also have these features. STANTON (1925, p. 340) suggested that TWENHOFEL'S variety might be a venerid. The species is similar to *F. ludana* STEPHENSON (1952) from the Woodbine in Texas, but it differs from the latter by more broadly curved anterior and posterior margins, by the anteriorly directed anterior cardinal tooth of the left valve and by the less strongly bifid posterior cardinal tooth of the right valve.

TYPES.—Original specimens lost; representative specimens: KU 500238a-b, 500239, 500240a-b, 500241-500260.

OCCURRENCE AND MATERIAL.—Calcareous shells are common in shell conglomerates in southern Kansas, and molds are common to abundant in sandstone in central Kansas; ranges throughout the Kiowa.

PALEOECOLOGY.—*Flaventia* may have been a nearshore analogue of *Venus.*

Order MYOIDA Stoliczka, 1870—Superfamily MYACEA Goldfuss, 1820—Family CORBULIDAE Gray, 1823

PALEOECOLOGY.—Many Recent species of this family are shallow burrowing filter-feeders on a firm substrate. *Corbula contracta* is common in the upper sound Gulf Coast assemblage, and *C. swiftiana* is common in the deeper continental shelf environment (PARKER, 1956). In the Black Sea and the Sea of Azov the *Venus-Corbula* biocoenosis forms the shallow shore community on a clean, fine-grained sand substrate (CASPERS, 1957). Salinity ranges from 9 to 20‰; temperature ranges from 1.7° to 12° C. *Corbula* occurs with *Cardium* but is more abundant above 4 m.

In the Kiowa the presence of corbulid species in sandstones, less commonly in tan silty clays, and rarely in dark-gray shale suggests that they were part of a nearshore, sand substrate community.

Genus CORBULA Lamarck, 1799

CORBULA? SMOLANENSIS (Twenhofel & Tester, 1926)

Plate 5, figures 7, 9, 10

Leda acuminata TWENHOFEL, 1924, p. 72, pl. 21, fig. 4.——ADKINS, 1928, p. 87.

Leda smolanense TWENHOFEL & TESTER, 1926, p. 561.

DESCRIPTION.—Shell, small, ovate, rostrate, inequilateral, subequivalved, greatly inflated. Beak rounded, erect. Valves with long, compressed rostrum; RV slightly more inflated and more rostrate than LV. Posterior keel on RV slightly developed. Ornamented by narrow, rounded concentric ribs and narrow, v-shaped interspaces, fainter on rostrum and umbo.

On RV cardinal socket shallow, laterally elongate, ventral and anterior to small cardinal tooth; resilifer elongate, concave trough bounded on posterior ventral end by a low, laterally elongate swelling; anterior hinge margin expanded into a flat plate dying out ventrally. Anterior muscle scar circular, shallowly impressed, placed at ventral anterior corner; posterior muscle scar a circular, raised platform ventral to rostral constriction. Ventral margin, dorsal anterior, and dorsal posterior margins of RV grooved for receiving margins of LV.

Measurements of RV, KU 500281a; length 9.3 mm., height 6.0 mm., width 2.4 mm.; LV, KU 5000282: length 8.6 mm., height 5.5 mm., width 2.3 mm.

DISCUSSION.—The species undoubtedly belongs in this family but is tentatively assigned to the genus *Corbula* until the characteristic hinge features of LV are known. The species is similar in form and ornamentation to

Corbula wenoensis Adkins (1920) and may be synonymous.

Types.—Original specimen lost; syntype, internal latex cast of RV: KU 500281a; syntype, internal mold of LV: KU 500282; external mold of LV, KU 500303a-b; external latex cast of RV, KU 500281b.

Occurrence and Material.—Twenhofel (1924) found the species common in "Mentor beds" west of Smolan, at Mentor, and at Natural Corral. Internal and external molds and casts are common in sandstone and shell conglomerate, and rare in shale in central and southern Kansas ranging throughout the Kiowa.

CORBULA? FENTI Scott, n. sp.

Plate 5, figures 1, 2

Description.—Shell, small, elongate oval, moderately inflated, inequilateral, subequivalved. Beak small, incurved, erect. Umbo inflated, broadly arched. Right valve slightly more rostrate than LV; rostrum an upturned posterior extension of valve. Ornamented by broad, concentric wrinkles separated by narrow, deep interspaces; fine growth lines superimposed.

Hinge line of RV with large, anterior cardinal tooth and narrow posterior tooth formed by thickened shell edge; anterior pit narrow, elongate, oblique to hinge line; resilifer very deep and oval. Other interior features unknown.

Measurements of LV, KU 500284: length 5.5 mm., height 3.3 mm., width about 2 mm.

Discussion.—A variant form (KU 500285) at Loc. S4 has a longer, more constricted rostrum; but not enough specimens are available on which to define a distinct species. A larger form (KU 500299) at Loc. S2 has similar ornamentation and is tentatively included with this species. This form is represented by specimens KU 500283a-b (Loc. S4); KU 500284-500298, 500300-500302. The species is named in honor of Nick Fent, consulting geologist in Salina, Kansas, who made available an excellent new fossil locality and whose enthusiasm for geology was inspiring.

Types.—Holotype: KU 500284; paratypes: KU 500285, 500283a,b, 500284-500298; 500300-500302.

Occurrence and Material.—Internal and external casts are common to very abundant in sandstone and some shell conglomerates throughout the Kiowa in central and southern Kansas.

Subclass ANOMALODESMATA Dall, 1889—Order PHOLADOMYOIDA Newell, 1965—Suborder PHOLADOMYINA Newell, 1965—Superfamily PHOLADOMYACEA Fleming, 1828—Family PHOLADOMYIDAE Fleming, 1828

Genus PHOLADOMYA Sowerby, 1823

PHOLADOMYA? BELVIDERENSIS Twenhofel, 1924

Pholadomya? belviderensis Twenhofel, 1924, p. 79, pl. 20, fig. 7
——Adkins, 1928, p. 139.

Discussion.—Although dentition is unknown, the species has other features suggestive of the genus: cancellate ornamentation, prosogyrate beaks, and the posterior elongation. At least 17 radial costae are present, although no complete specimens have been seen.

Types.—Original specimens lost. Representative specimens: KU 500305, 500314.

Occurrence and Material.—Twenhofel (1924) found the species in the "Champion shell bed" and in a sandstone-shale unit 54 to 92 ft. above the base at Belvidere, and in "Mentor beds" west of Smolan and at Natural Corral. Additional specimens come from dark-gray shale, shell conglomerate, and sandstone in central and southern Kansas. Ranges from the base to the top of the Kiowa.

Paleoecology.—The posteriorly drawn-out, gaping shell-form with moderately sinuate pallial line, characteristics of the genus, suggest a moderately deep-burrowing, filter-feeder habit. No whole specimens were found in place, so preferred substrate type is unknown, but most likely it was sandy mud or muddy sand.

Genus HOMOMYA Agassiz, 1843

Paleoecology.—*Homomya* probably was a shallow-burrowing filter-feeder most common in firm, sandy substrates.

HOMOMYA sp. A

Plate 5, figures 11, 12

Description.—Shell moderate size, elongate oval, inequilateral, equivalved, moderately inflated, posterior greatly produced. Beak pointed, incurved, erect, about one-third the length from anterior end; umbonal area broadly arched. Dorsal anterior margin sloping steeply, anterior margin moderately curved, ventral margin slightly convex, posterior sharply curved, dorsal posterior margin sloping moderately towards beak, slightly concave. Lunule and escutcheon elongate, the latter longer. Ornamented by concentric, broad, flat ridges, and narrow interspaces.

Hinge line short; dentition and ligament type unknown. Adductor muscle scars oval, near anterior and posterior margins about at mid-height.

Measurement of articulated specimen KU 500306; length 29.3 mm., height 20.0 mm., width (LV partially preserved) 15.0 mm.

Discussion.—The species is similar to *Homomya tarrantensis* Perkins (1960), but is smaller, beaks are not as close to the front, the posterior dorsal slope is concave, and no gape is seen. It differs from *Homomya alta* Roemer (1849) by its more elongate form. The latter species was reported by Cragin (1895b) from the Kiowa in southern Kansas.

Occurrence and Material.—Internal casts are common in thin, iron oxide-cemented siltstone bands at Loc. S2, about 30 ft. above the Kiowa base. The form is represented by a cast of articulated valves: KU 500306 (unit 2, Loc. S2); KU 500307-500309.

HOMOMYA sp. B

Plate 5, figures 13, 14

Description.—Shell large, trigonal oval, inequilateral, equivalved, strongly inflated, posterior margin moderately produced. Beak rounded, incurved, erect, about one-third the length from anterior end. Umbonal area broadly arched and inflated. Dorsal anterior margin short, sloping steeply; anterior end asymmetrically curved, narrow; dorsal posterior margin steeply sloping, nearly straight. Lunule poorly defined, escutcheon oval, short. Ornamented by low, rounded concentric ridges. Interior features unknown.

Measurements of articulated external cast (KU 500310): length 55.0 mm., height 40.5 mm., width about 36 mm.

Discussion.—This species is similar to *H. alta* but it is longer and more produced posteriorly.

Occurrence and Material.—The single articulated specimen is from the uppermost surface of sandstone unit 3, Loc. S9. The specimen was in life position with the anterior two-thirds buried in sandstone, and the posterior one-third projecting upwards. The commissure line was oriented approximately N. 50 E. Range is lower Kiowa, central Kansas.

Class SCAPHOPODA Bronn, 1862—Family SIPHONODENTALIIDAE Simroth, 1894

Genus CADULUS Philippi, 1844

Subgenus CADULUS (GADILA) Gray, 1847

CADULUS (GADILA) PRAETENUIS Stephenson, 1952

Cadulus praetenuis Stephenson, 1952, p. 143, pl. 34, fig. 7-9.

Discussion.—This unornamented species is assigned to the subgenus *Gadila* as redescribed by Emerson (1962), because the apical orifice is not contracted by callus ring as it is in the subgenus *Cadulus,* and the apertural orifice is oval in outline.

Types.—Holotype: USNM 105615; paratypes: USNM 105616a-b, 105617, 105618. Representative specimens: KU 500311, 500312a-c.

Occurrence and Material.—Cragin (1895b) and Twenhofel (1924) noted *Dentalium* sp. from Kiowa sandstones and shell conglomerates. New calcareous shells come from shell conglomerate and cone-in-cone layers, and casts were found in sandstones in the lower Kiowa of central and southern Kansas. In Texas the species is found in the Woodbine Formation.

Paleoecology.—Recent scaphopods burrow into sandy to muddy substrates from depths of low tide level to more than 200 m. They capture Foraminifera or other benthonic microorganisms. On the Gulf Coast *Cadulus* is common in the shallow and deep shelf assemblages (Parker, 1956).

Class GASTROPODA Cuvier, 1797—Subclass STREPTONEURA Spengel, 1881 — Order ARCHAEOGASTROPODA Thiele, 1925 — Superfamily PATELLACEA Rafinesque, 1815—Family ACMAEIDAE Carpenter, 1857

Genus ACMAEA Escholtz, 1830

ACMAEA SOHLI Scott, n. sp.

Plate 6, figure 7

Description.—Shell small, subconical, elliptical; rounded apex slightly anterior of center; anterior slope slightly steeper and shorter than posterior slope, both greatly convex; muscle scar horseshoe-shaped, open end offset to right of anterior, joined by pallial line. Exterior features unknown.

Discussion.—This species differs from *Acmaea galea* Sohl (1960) and *A.? occidentalis* (Hall & Meek, 1856) and by its much smaller size, by the convexity of the anterior and posterior slopes and by the elliptical apertural outline.

Occurrence and Material.—The holotype and only specimen is an internal mold (KU 500315, 3.2 mm. long, 3.0 mm. wide, 1.5 mm. high) on a chip of sandstone

EXPLANATION OF PLATE 5

Figure

1,2. *Corbula? fenti* Scott, n. sp.——*1*. Latex cast of LV, =6, Loc. S4, KU 500284.——*2*. Latex cast of RV, ×4, Loc. S4, KU 500283b (p. 77).

3-6. *Crassinella semicostata* Scott, n. sp., ×4.——*3*. Internal view of RV, unit 3, Loc. M3, KU 500268.——*4*. External view of valve in Fig. 3.——*5*. External view of LV, same locality, KU 500267.——*6*. Internal view of valve in Fig. 5 (p. 72).

8. *?Corbula crassicostata* Cragin; external view of RV, ×4, Loc. K1, KU 500261.

7,9,10. *Corbula? smolanensis* (Twenhofel & Tester).——*7*. External latex cast of RV, ×2.7, specimens in Fig. *7,10* collected by W. H. Twenhofel, locality unknown, KU 500281b.——*9*. External latex cast of LV, ×6, articulated specimen, unit 9, Loc. S8, KU 500303b.——*10*. Internal latex cast of RV, ×2.7, locality unknown as for Fig. 7, KU 500281a (p. 76).

11,12. *Homomya* sp. A; internal sandstone molds of RV & LV, ×2, unit 2, Loc. S2, KU 500306, KU 500307 (p. 77).

13,14. *Homomya* sp. B; sandstone cast of external mold of articulated specimen, ×1, LV and dorsal view of specimen, unit 3, Loc. S9, KU 500310 (p. 78).


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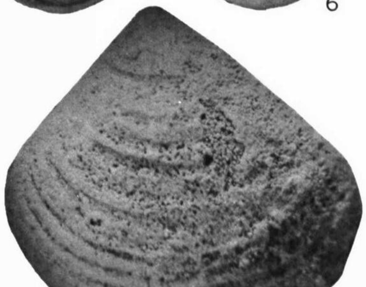
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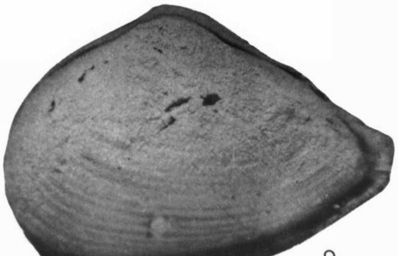
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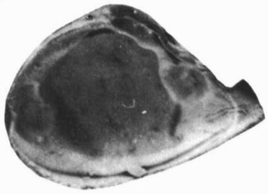
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containing a specimen of *"Anisomyon cragini."* The locality given by Twenhofel (1924, p. 54) is "Mentor bed, 5 miles west of Smolan," which is about in the middle of the Kiowa.

Paleoecology.—Patellids live on a firm substrate such as rocks, from the intertidal zone to about 92 m. They feed on sea weed or algae.

TROCHID GASTROPOD INDET.

Plate 6, figure 5

Discussion.—A single incomplete calcareous trochid shell (KU 500316) was found in a lower Kiowa shell conglomerate at Loc. K1. The body whorl (width 6.4 mm.) and part of the penultimate whorl are preserved. The nonumbilicate shell has abutting sutures and flat-sided whorls with a small shelf on the shoulder. Thin, closely spaced, prosocline growth lines are crossed by many very thin spiral striae resulting in a faint cancellate pattern. The shell has ornamentation very similar to that of *Atira,* but the Kiowa specimen differs by the closed umbilicus and by the flat-sided whorls.

Superfamily NERITACEA Rafinesque, 1815—Family NERITIDAE Rafinesque, 1815

Genus OTOSTOMA d'Archiac, 1859

OTOSTOMA MARCOUANA (Cragin, 1894)

Neritoma marcouana Cragin, 1894b, p. 62.——Stanton, 1947, p. 61, pl. 47, fig. 5-8. Provides prior synonymy.

Discussion.—Stanton's (1947) thorough description is based on several nearly complete specimens including some of Cragin's original material. The species is placed in *Otostoma* because the inner lip septum bears five or six small denticles as seen on the holotype (and in pl. 47, fig. 7, 8, Stanton, 1947).

Types.—Holotype: USNM 32674; plesiotype: USNM 103084; representative specimens: KU 500317, 500318a-b, 500319, 500320.

Occurrence.—The species is reported from lower Kiowa shell conglomerate in Kiowa County and from sandstone and shell conglomerate ranging to the top of the Kiowa in Saline and McPherson counties. Two additional external molds of the spire are from sandstone. The larger specimen is about 8 mm. high and 7 mm. wide. Occurs in the Kiamichi in Texas.

Paleoecology.—All known marine Cretaceous neritids are associated with shallow-water species (Sohl, oral communication, 1966).

Superfamily AMBERLEYACEA Wenz, 1938—Family AMBERLEYIDAE Wenz, 1938

Genus AMBERLEYA Morris & Lycett, 1851

AMBERLEYA MUDGEANA (Meek, 1871)

Turbo mudgeana Meek, 1871, p. 313.——Stephenson, 1952, p. 145.

Amberleya mudgeana (Meek). Stanton, 1947, p. 57, pl. 49, fig. 14, 15. Provides prior synonymy.

Discussion.—Stephenson (1952) placed *Amberleya mudgeana* in the genus *Turbo* because *Amberleya* has "a strongly noded shell with a much higher spire." However, the peristome of this species is not continuous and in one plane as it is in *Turbo,* and therefore, the species is better assigned to *Amberleya.*

Cragin (1894a) defined *Margarita marcouana* on the basis of two specimens; Twenhofel (1924) identified one additional specimen, all from the Kiowa at Loc. K1. Stanton (1947) followed an unpublished suggestion by Cragin and placed *M. marcouana* in synonymy with *A. mudgeana.*

Types.—Holotype: USNM 7903; plesiotype: USNM 77640; representative specimens: KU 500321, 500322.

Occurrence and Material.—Meek's (1871) specimens came from sandstone about 12 miles southwest of Salina. Cragin's and Twenhofel's material came from the Champion Draw section at Belvidere, probably from shell conglomerates in the lower Kiowa. I collected one external mold from sandstone (unit 3, Loc. S7), and a slightly crushed calcareous shell from shell conglomerate

EXPLANATION OF PLATE 6

Figure

1. Neogastropod indet.; front view, ×4, unit 8, Loc. K1, KU 500373 (p. 82).

2,3. *Mathilda* sp. indet.; latex casts of spire and base, ×2.5, unit 1, Loc. S5, KU 500350b, KU 500351b (p. 80).

4. *Gegania* sp. indet.; front view, ×4, reconstruction of spire based on observations of complete shell, unit 3B, Loc. E6, KU 500392 (p. 80).

5. Trochid indet.; oblique apical view, ×2.5, unit 10, Loc. K1, KU 500316 (p. 79).

6. *Pirsila?* sp. indet.; latex cast of external mold, ×6, front view, Loc. S4, KU 500378b (p. 82).

7. *Acmaea sohli* n. sp. Scott; dorsal view of internal mold, ×4, collected by W. H. Twenhofel from "Mentor bed," 5 miles west of Smolan, KU 500315 (p. 78).

8. Pyramidellid indet.; internal casts of several specimens in concretion, ×4, unit 2, Loc. S2, KU 500375 (p. 82).

9. Streptoneuran indet.; latex cast of external mold, ×2.5, unit 3, Loc. S7, KU 500374 (p. 82).

10. Aporrhaid indet.; latex cast of external mold, ×2, unit 15, Loc. M4, KU 500358 (p. 81).

11. Cerithiopsid indet.; incomplete shell indicated by arrows ×5.5, associated with *Turritella belviderei* and *Crassinella semicostata,* unit 3B, Loc. E6, KU 500430 (p. 81).

12. *Turritella belviderei* Cragin; spire with strong ribs but nodes not developed, ×2.5, unit 2, Loc. E3, KU 500323 (p. 80).

13. *Turritella kansasensis* Meek; latex cast of external mold, ×2.5, unit 9, Loc. S8, KU 500349 (p. 80).

at Loc. M7. Occurs in lower to middle Kiowa in central and southern Kansas. In Texas the species is found in the Kiamichi Formation.

Paleoecology.—The occurrence of *Amberleya* suggests a nearshore, shallow-water environment.

Order MESOGASTROPODA Thiele, 1925—Superfamily CERITHIACEA Fleming, 1822—Family TURRITELLIDAE Woodward, 1851

Genus TURRITELLA Lamarck, 1799

Paleoecology.—Recent *Turritella* forms communities of a large number of individuals in shallow marine waters (0-92 m.), on sandy mud or muddy sand bottoms (Thorson, 1957). They are filter-feeders that burrow just beneath the sediment-water interface.

TURRITELLA BELVIDEREI Craign, 1897

Plate 6, figure 12

Turritella belviderei Cragin, 1897, p. 134.——Stanton, 1947, p. 71, pl. 56, fig. 8-10. Provides prior synonymy.

Discussion.—A variation from Stanton's (1947) description is the presence on a few shells of very thin spiral striae between the longer and flat spiral ridges. A specimen from Kiowa County (unit 10, Loc. K1) bears a thin stria below the second ridge on the adapical side of the whorl. The early whorls of *Turritella belviderei* may have very thin spiral striae alternating with slightly broader and higher ridges; the later whorls have six or seven flat ridges with very slight nodes, and the troughs may retain the thin striae. Fragments of this variant may be confused with *T. kansasensis,* which differs by a near absence of spiral ornamentation.

Types.—Plesiotypes: USNM 103139a-c; representative specimens: KU 500323-500348.

Occurrence and Material.—*Turritella belviderei* is found in shale, shell conglomerate, and sandstone in central and southern Kansas. It ranges throughout the Kiowa. In Texas the species occurs in the Kiamichi.

TURRITELLA KANSASENSIS Meek, 1871

Plate 6, figure 13

Turritella kansasensis Meek, 1871, p. 312.——Twenhofel, 1924, p. 57, pl. 18, fig. 3-5. Provides prior synonymy.

Discussion.—Twenhofel (1924) states that "the essential difference between this species and *Turritella belviderei* appears to be in the presence of nodes on the spirals of the latter." A more apparent difference is the absence or faint and inconsistent development of very thin spiral striae compared with the six or seven broad spiral ridges on *T. belviderei.*

Types.—Holotype: USNM 7899; representative specimen: KU 500349.

Occurrence and Material.—Twenhofel reported this species from most "Mentor bed" localities in central Kansas. Studied material consists of incomplete external molds in sandstone from Locs. S7 and S8, from the uppermost sandstone at Loc. M4, and one specimen from sandstone at Loc. R2.

Family MATHILDIDAE Cossmann, 1912

Paleoecology.—*Mathilda* and *Gegania* may have been shallow burrowing or epifaunal filter-feeders.

Genus MATHILDA Semper, 1865

MATHILDA sp. indet.

Plate 6, figures 2, 3

Description.—Shell medium size, turriculate; more than eight whorls, slightly convex, suture impressed; apical angle about 24°; many spiral striae of different widths crossed by moderately strong growth lines slightly convex towards aperture; third carina above suture widest and highest; aperture oval, incompletely known, base rounded, non-umbilicate; inner lip thickened.

Occurrence and Material.—Two incomplete external molds KU 500350a-b (10 mm. high, 4 mm. wide) and KU 500351a-b, in sandstone, Loc. S5, about middle Kiowa.

Genus GEGANIA Jeffereys, 1884

GEGANIA sp. indet.

Plate 6, figure 4

Description.—Shell globose, turriculate, medium size; whorls rounded; suture impressed; spiral striae few, strength variable, crossed by thinner axial ribbing that form nodes on striae; aperture subovate, short siphonal notch at base of inner lip; apical angle 48° to 50°; height 15 mm., width 3 mm.

Discussion.—The species is similar to *Gegania parabella* (Wade) figured in Sohl (1960, p. 134, pl. 18, fig. 25, 43).

Occurrence and Material.—A single calcareous shell (KU 500392) was found in shell conglomerate (unit 3B, Loc. E6), middle Kiowa. The spire was broken during preparation.

Family CERITHIIDAE Fleming, 1828

Genus CASSIOPE Coquand, 1865

CASSIOPE sp. cf. C. LAEVICULA (Stainbrook, 1940)

Cerithium laeviculum Stainbrook, 1940, p. 713, pl. 33, fig. 23.

Description.—Shell large, turriculate, elongate ovate in outline, seven whorls; whorl sides gently convex, body whorl higher but slightly narrower than preceding whorl. Aperture unknown; ornamentation weak, not well known.

Types.—Holotype and paratypes in collection of Bureau of Economic Geology, the University of Texas, Austin. Representative specimen: KU 500379a-c.

Occurrence and Material.—An external mold, partly coated by secondary iron sulfide, was found in sandstone in the lower Kiowa (unit 3, Loc. S9). The species was originally found in the Kiamichi in the southern part of the Texas Panhandle (Stainbrook, 1940).

Paleoecology.—*Cassiope* is common in very near-shore, marine to brackish environments.

CERITHIOPSID GASTROPOD INDET.

Plate 6, figure 11

Description.—Shell turriculate, seven whorls, whorl sides nearly flat, suture impressed; apical angle very small, about 10°; very faint spiral ornamentation.

Occurrence and Material.—A single incomplete calcareous shell is imbedded in a large block of shell conglomerate, middle Kiowa (unit 3B, Loc. E6, KU 500430).

Superfamily STROMBACEA—Family APORRHAIDAE Philippi, 1836

Paleoecology.—Recent aporrhaids are marine, shallow water detritus-feeders living at or just below the sediment-water interface.

Genus DREPANOCHILUS Meek, 1864

DREPANOCHILUS KIOWANUS (Cragin, 1894)

Anchura kiowana Cragin, 1894b, p. 66.

Anchura (Drepanochilus) kiowana Cragin. Stanton, p. 102, pl. 65, fig. 6-10.

Anchura (Drepanochilus) kiowana var. *marquettensis* Stanton, 1947, p. 103, pl. 65, fig. 5, 11.

Discussion.—This species as described by Cragin (1894b), Stainbrook (1940), and Stanton (1947) belongs in the genus *Drepanochilus,* which differs from *Anchura* by having a short canal and spiral striae on body whorl (Sohl, 1960, p. 99). *Drepanochilus* ranges from Lower Cretaceous to Eocene; and *Anchura s.s.* is generally restricted to the Upper Cretaceous.

The validity of the var. *marquettensis* is questionable and should be tested by statistical analyses. Ten incomplete specimens collected at Brookville (unit 3, Loc. S9) do not seem to differ greatly from specimens elsewhere. The single specimen discussed below from southwest of Marquette (unit 15, Loc. M4) is a different species. The significance of differences in spiral striae on the body whorl is difficult to assess with the limited material in hand.

Types.—Syntypes: USNM 32673; figured plesiotypes: USNM 77562, 77563a-b; syntypes of var. *marquettensis*: USNM 77654a-b; representative specimens: KU 500352a-c, 500353a-b, 500354, 500355, 500356a-b, 500357.

Occurrence and Material.—*Drepanochilus kiowanus* is reported from shell conglomerates and sandstone ranging from the base to the middle of the Kiowa in Kiowa and Clark Counties and from the middle to the top of the Kiowa in Saline and McPherson Counties. Additional specimens have been found in shale and siltstone in Clark County, and in middle and uppermost sandstone in Ellsworth, McPherson, and Saline Counties. Most of the specimens are incompletely preserved; those in sandstone are external molds, external casts and molds are found in shale, and weathered calcareous shells occur in shell conglomerates. An incomplete internal mold that has a body-whorl shape approaching that of aporrhaids was found in unit 3, Loc. M3. The species occurs in the Kiamichi of Texas.

APORRHAID GASTROPOD INDET.

Plate 6, figure 10

Discussion.—One external mold differs from *Drepanochilus kiowanus* by having whorl ribs that are higher, broader, more concave, and more widely spaced. The shell form is larger and more robust than is common in *D. kiowanus.* A generic assignment can not be made because the wing is not preserved. Height 27 mm., width 12 mm.

Occurrence.—An external mold was found in uppermost sandstone (unit 15, Loc. M4); latex cast: KU 500358.

Superfamily NATICACEA Gray, 1834—Family NATICIDAE GRAY, 1834

Genus EUSPIRA Agassiz, 1838

EUSPIRA SMOLANENSIS (Twenhofel, 1924)

Natica? smolanense Twenhofel, 1924, p. 56, pl. 7, fig. 6.

Natica smolanense Twenhofel. Stainbrook, 1940, p. 709, pl. 33, fig. 12, 13.

Discussion.—This species is placed in the genus *Euspira* as diagnosed by Sohl (1960) because the suture between whorls is impressed and the umbilicus is open. The specimens described by Stainbrook (1940) seem to have the same characters.

Types.—Original specimens lost; Twenhofel's paratypes: KU 500359-500361. Plesiotypes in collection of Bureau of Economic Geology, University of Texas, Austin. Representative specimens: KU 500362a-b, 500364-500370.

Occurrence and Material.—Twenhofel found this species in "Mentor beds" about middle Kiowa in Saline County. My specimens came from sandstone and shale at several localities and range from the middle to the top of the Kiowa in central Kansas. Several poorly preserved specimens of naticid form came from unit 3, Loc. M3. One specimen shows that the umbilicus is open. Growth striae are preserved on several specimens. Generally these specimens are smaller than those described by Twenhofel and Stainbrook, although the incomplete preservation may be misleading.

Paleoecology.—In Cretaceous rocks *Euspira* is found associated with shallow, warm water, marine species. Although it is related to *Natica,* a carnivore, *Euspira* may not have been carnivorous on bivalves because it is not associated with bored shells.

Family AMPULLINIDAE Cossmann, 1907

Genus "AMPULLINA" Bowdich, 1882

"AMPULLINA" sp. indet.

Tylostoma elevata (Shumard), in part. Twenhofel, 1924, p. 59, pl. 22, fig. 3; not pl. 16, fig. 5.

Description.—Shell medium size, turbiniform, four or five rapidly expanding convex whorls, suture abutting, spire less than half as high as body whorl, apical angle about 75 degrees; aperture unknown, cross sectional outline of body whorl egg-shaped; umbilicus narrow; ornamented by very thin, prosocline growth lines. Height of KU 500371, 27.5 mm., width 22.0 mm.

Discussion.—These specimens differ from *Tylostoma elevata* (Shumard, 1854) by having a body whorl larger than the spire and by the smaller size. Twenhofel (1924) collected one shell that is as large as *T. elevata* (pl. 16, fig. 5), but most specimens are smaller and interpreted by him to be immature individuals. Stanton (1947) applies *T. elevata* to specimens with varices, but with a body whorl larger than the spire.

The new specimens are similar in form to *"Ampullina" potens* Wade (1926), which differs by having a well defined shoulder and an impressed suture. History of the name *"Ampullina"* was reviewed by Sohl (1960), who concludes that it is a *nomen nudum;* but no valid name has been proposed in place of it.

Occurrence and Material.—Twenhofel collected his figured specimen (KU 500371, unit 12, Loc. K1) and other smaller forms from shell conglomerates in the Kiowa at Belvidere. He reported smaller specimens from "Mentor beds" in Saline and McPherson Counties. My material comes from a middle Kiowa shale and cone-in-cone layer, Loc. M3, and from the uppermost sandstone at Loc. M4 (KU 500372a-b).

NEOGASTROPOD INDET.

Plate 6, figure 1

Description.—Shell turriculate, five slightly convex whorls, abutting suture. Base not completely known, columella long and may lead into a long canal. Apical angle 45°, height about 9.2 mm. Ornamentation lacking or faint. This specimen is considered a neogastropod because of the suggestion of a long canal.

Occurrence and Material.—The single, partial, abraded, calcareous shell is from unit 8A, Loc. K1, shell conglomerate (KU 500373).

STREPTONEURAN GASTROPOD INDET.

Plate 6, figure 9

Description.—Shell turriculate, four whorls preserved; shoulders gently convex on earlier whorls, shoulder sloping outward on the third whorl, no shoulder on fourth whorl, suture abutting. Ornamented by one, flat-topped spiral ridge on the adapical side of whorl; the ridge on the two intermediate whorls with a narrow groove on the adapical half of the ridge. Apical angle about 50°; partial height 20 mm., width of fourth whorl about 16 mm.

Discussion.—Although the specimen cannot now be identified, it is included because it is distinct and easily recognizable. Perhaps future work will find additional specimens that can be classified.

Occurrence and Material.—A single external mold is from sandstone unit 3, Loc. S7, middle Kiowa: KU 500374.

Subclass EUTHYNEURA Spengel, 1881—Order ENTOMOTAENIATA Ehrenberg, 1831—Superfamily PYRAMIDELLACEA d'Orbigny, 1840

PYRAMIDELLID GASTROPOD INDET.

Plate 6, figure 8

Description.—Shell, very small, turriculate, five whorls or more; whorls flat-sided; suture impressed; base of body whorl rounded; apical angle small, about 15°; whorls smooth, base of last whorl with single spiral stria disappearing about one-half whorl before aperture; aperture oval, inner lip appearing to have two broad denticles. Incomplete height 5.7 mm., width 2.4 mm.

Discussion.—The species seems to have most of the diagnostic features of this family and is similar to species of *Tiberia* (*in* Wenz, 1940, p. 843; p. 876, fig. 2571, 2572, 2573), which is a Tertiary genus.

Occurrence and Material.—The species is abundant in siltstone at Loc. S2, about 30 ft. above the Kiowa base. Specimens are iron oxide casts of external molds and internal gypsum molds, all from concretions. KU 500375-500377.

Paleoecology.—Recent relatives of this family are parasites on echinoderms. This Cretaceous form probably had a different host or even mode of life, because echinoderms are rare in the Kiowa.

Order CEPHALASPIDAE Fischer, 1883—Superfamily ACTEONACEA d'Orbigny, 1842—Family ACTEONIDAE d'Orbigny, 1842

Genus PIRSILA Stephenson, 1952

PIRSILA? sp. indet.

Plate 6, figure 6

DESCRIPTION.—Shell, very small, fusiform, three gently convex whorls, gradually enlarging, body whorl higher (height 1.1 mm.) than spire; suture impressed; cross sectional outline of body whorl oval; shell smooth; height 1.9 mm., width 1.2 mm.

DISCUSSION.—This specimen is similar in form and lack of ornamentation to *Pirsila* (STEPHENSON, 1952). However, because of incomplete preservation, the base of the columella cannot be seen, on which a twisted fold characterizes the genus.

OCCURRENCE AND MATERIAL.—A single external mold (KU 500378a-d) was found in sandstone, middle Kiowa, Loc. S4.

PALEOECOLOGY.—Most opisthobranchs are carnivores preying on Foraminifera and ostracodes directly below the sediment-water interface.

Class CEPHALOPODA Cuvier, 1797—Subclass AMMONOIDEA Zittel, 1884—Order AMMONITIDA Zittel, 1884—Suborder AMMONITINA Hyatt, 1889

PALEOECOLOGY.—SCOTT (1940) suggested that both *Oxytropidoceras* (including species now assigned to *Adkinsites*) and *Engonoceras* were good swimmers in a shallow (13-17 m.), marine habitat, periodically subjected to tides or storm-generated currents.

Superfamily HOPLITACEAE H. Douvillé, 1890 —Family ENGONOCERATIDAE Hyatt, 1900

Genus ENGONOCERAS Neumayr & Uhlig, 1887

ENGONOCERAS BELVIDERENSE (Cragin, 1894)

Ammonites belviderensis CRAGIN, 1894a, pl. 1, fig. 3-5.

Engonoceras belviderense (CRAGIN). HYATT, 1903, p. 158, pl. 18, fig. 4, 5.——TWENHOFEL, 1924, p. 87, pl. 11, fig. 1-4.

Buchiceras (Sphenodiscus) belviderensis var. *mons-comancheanus* CRAGIN, 1900, p. 27, pl. 1, fig. 1-6.

Engonoceras belviderense var. *mons-comancheanum* (CRAGIN). ADKINS, 1928, p. 262.

Buchiceras (Sphenodiscus) belviderensis var. *uddeni* CRAGIN, 1900, p. 30, pl. 1, fig. 3, 4.

Engonoceras uddeni (CRAGIN). HYATT, 1903, p. 159, pl. 18, fig. 1-6.

Buchiceras (Sphenodiscus) belviderensis var. *mentorianus* CRAGIN, 1900, p. 31, pl. 1, fig. 6, 7.

DISCUSSION.—CRAGIN (1900) separated *Engonoceras* ***belviderense*** var. ***mons-comancheanum*** [sic], which has the typical characters of the species, from var. ***uddeni*** by differences in the suture patterns. Var. ***monscomancheana*** has saddles 1 to 8 rounded (counting each individual saddle beginning with the first saddle adjacent to the external lobe on the venter) and saddles 9, 10 bilobed, and lobes regularly digitate; var. ***uddeni*** has saddles 7, 11 to 13 bilobed, the others rounded, and some lobes irregularly digitate. HYATT (1903) raised var. ***uddeni*** to the rank of species and distinguished it from *E.* ***belviderense*** by the latter's more compressed whorl profile with straight flanks and flatter venter. Also *E.* ***uddeni*** has "only one line of nodes" above umbilicus.

Because the specimens were poor, TWENHOFEL (1924) doubted the validity of CRAGIN's varieties, and, if he knew of HYATT's monograph, certainly did not recognize the differences as the basis for defining species. The profile of the whorl flanks of specimens from Bavaria (Loc. S6) vary from straight to slightly convex; venter profile varies among specimens, most having a slightly convex venter, few having a flat venter. The number of rows of nodes varies from three in the early whorls to one or two in the body chamber. The extreme variability in position of bilobed saddles relative to the external lobe is indicated by HYATT (1903, p. 161). He describes one specimen that has saddles 6 to 10 on one side bilobed and on the other side saddles 8 and 9 only are bilobed. Therefore, *E. uddeni* cannot be distinguished from *E. belviderense*.

One specimen from near Brookville (Loc. S9) differs slightly from a Bavaria specimen by having sutures so closely spaced that lobes invade preceding lobes, and by having less expanded and less digitate lobes. (Compare CRAGIN, 1900, pl. 1, fig. 5,6.) CRAGIN named the Brookville variant var. *mentorianus* [sic]. The significance of this variation cannot be evaluated because not enough specimens with preserved sutures are available from the two localities.

TYPES.—Original specimens lost. HYATT (1903, p. 159) states that the specimen illustrated on his pl. 18, fig. 4, 5 is CRAGIN's type for *E.* ***belviderense*** and was in CRAGIN's collection at Colorado College. On p. 160 HYATT states that the specimen illustrated on pl. 19, fig. 1-3 is the type for var. ***uddeni***, but its disposition is unknown. The specimen on pl. 19, fig. 4, 5 is USNM 23147. Representative specimens: KU 500381-500385, 500424a-b.

OCCURRENCE AND MATERIAL.—CRAGIN reported the species ranging from the basal shell conglomerate upward about 30 ft. in shales near Belvidere (Loc. K1); it was found also in Saline County near Brookville and in McPherson County west of Lindsborg. HYATT (1903) reports the latter specimen from northeast of Little River, Rice County. TWENHOFEL found the species only in "Mentor beds" 5 miles west of Smolan in Saline County. O. S. FENT (oral communication, November, 1966) has specimens from about the middle of the Kiowa (about 5 ft. above lake level, Loc. R3) west of Little River.

Six partial internal and external casts were collected from sandstone at Locs. S9 and S6. Thus, the species ranges from the base to the middle of the Kiowa. In Texas it occurs in the Comanche Peak Formation.

Superfamily ACANTHOCERATACEA Hyatt, 1900—Family BRANCOCERATIDAE Spath, 1933

Genus ADKINSITES Spath, 1931, emend. Young, 1966

ADKINSITES BRAVOENSIS (Böse, 1910)

Schloenbachia bravoensis Böse, 1910, pl. 3, fig. 6; pl. 4, fig. 1-5.
Adkinsites bravoensis (Böse), Young, 1966, p. 119-124, fig. 7a, 16h, 17e, f, 19c, e, 21a, c, f; pl. 9, fig. 1-4; pl. 22, fig. 4; pl. 27, fig. 4; pl. 28, fig. 3, 4; pl. 31, fig. 1; pl. 35, fig. 2. Provides prior synonymy.

Discussion.—According to Young (1966) *Adkinsites bravoensis* is characterized by 1) moderately densely spaced ribs that are sharply geniculate and asymmetric with steeper side adoral; 2) large umbilical bullae on juvenile whorls; and 3) intercalated and bifurcated ribs on juvenile stage only. One whorl fragment (KU 500386) and two immature specimens (15 mm. and 30 mm. whorl diameter; KU 500387; unit 8, Loc. C3) possess these features. An additional whorl fragment (KU 500389) does not show any distinctive features and is not assigned to a species. The two juvenile shells are compressed, sharply keeled with geniculate, narrowly rounded ribs, of which every third extends to umbilicus and and has a small bulla, the intervening two ribs extend across two-thirds of the whorl.

Types.—Young (1966) designated one of Böse's figured specimen (1910, pl. 4, fig. 4, 5) as lectotype, because Böse did not choose a holotype. The lectotype is at Instituto de Geología de Mexico, Mexico City. Representative specimens: KU 500386, 500387.

Occurrence and Material.—Shell fragments and casts in sandstone were found in Clark County from 0 to 60 ft. above the base of the Kiowa. Young (1966, p. 13) reports the species from the Kiowa above the "Champion shell bed" in southern Kansas. The species is widely distributed in Texas where it characterizes a fossil zone in the Kiamichi Shale (Young, 1966). In southern Kansas the *A. bravoensis* range zone includes the lower 50 to 60 ft. of the Kiowa above the *Manuaniceras powelli* zone (Scott, in press).

?ADKINSITES IMLAYI Young, 1966

Adkinsites imlayi Young, 1966, fig. 15h, 16a, c, e, 19d, 20e, f; pl. 24, fig. 2; pl. 25, fig. 4; pl. 27, fig. 2; pl. 29, fig. 1-3; pl. 31, fig. 6. Provides prior synonymy.

Discussion.—This species differs from other species of *Adkinsites* by the wider rib interspaces, and by the higher and narrower ribs. Two of my specimens are tentatively assigned to this species because ribs are narrowly rounded and interspaces are about twice as wide as the ribs. The specimen described and figured by Twenhofel (1924, p. 89, pl. 11, fig. 5) has "large coarse ribs" and was placed in this species by Young (1966).

Types.—Holotype: Bureau of Economic Geology, The University of Texas, Austin, no. 35425. Representative specimens: KU 500388, 500390.

Occurrence and Material.—Specimens are internal molds in sandy shell conglomerate (unit 10, Loc. K1). Twenhofel (1924) reported fragments from shell conglomerate about 53 ft. above the Kiowa base at Belvidere. The species is restricted to the Kiamichi of Texas and is common in the *Adkinsites bravoensis* Zone (Young, 1966).

AMMONITIDA INDET.

Discussion.—Imprints of two ammonoid shells cannot be confidently placed in any genus. The better preserved specimen is 14 by 19 mm. in diameter; umbilicate, and has an evolute, non-keeled, narrow shell; body chamber is large; ribs are faint and simple.

Occurrence and Material.—The two partial imprints in claystone (KU 500391a-b) were found 40 ft. above the Kiowa base at Loc. C4.

Phylum ARTHROPODA Siebold & Stannius, 1845—Class CRUSTACEA Pennant, 1777—Subclass OSTRACODA Latreille, 1806—Order PODOCOPIDA Müller, 1894—Suborder PODOCOPINA Sars, 1866—Superfamily CYTHERIACEA Baird, 1850—Family CYTHERIDAE, Baird, 1850

Genus CYTHERIDEA Bosquet, 1852

CYTHERIDEA? AMYGDALOIDES (Cornuel, 1846)

Figure 19, *A, B*

Cythere amygdaloides Cornuel, 1846, p. 197, pl. 7, fig. 1-9.
Cytheridea amygdaloides (Cornuel). Alexander, 1929, p. 69, pl. 4, fig. 16, 17.

Description.—Carapace heavily calcified, medium size; lateral view elongate subtriangular, cardinal angles obtuse, greatest height slightly anterior to middle, greatest length slightly below middle, dorsal outline asymmetrically arched, ventral outline flatly convex, ends dissimilar, anterior outline broadly rounded asymmetrically, posterior outline narrowly rounded; in dorsal view anterior end slightly narrower than posterior, greatest width about at middle, sides convex; inequivalved, left valve larger than right valve, overlap greatest dorsally and ventrally; surface punctate, though poorly preserved; length 0.92 mm., height 0.56 mm., width 0.44 mm.

Discussion.—This carapace is very similar to, though larger than any of those illustrated by Alexander (1929). Inner surface could not be observed in these articulated specimens. The taxonomic assignment made by Alexander can be accepted tentatively, although this genus apparently has been redefined because it is restricted to

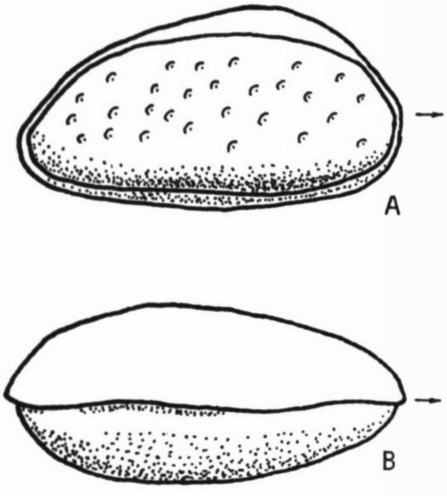

Fig. 19. Sketches of *Cytheridea? amygdaloides* (about ×55); *A*, lateral view of RV; *B*, dorsal view.

post-Eocene time (Benson and others, 1961; van Morkhoven, 1962). When internal features of the species are described, its generic status will be clarified.

R. S. Taylor identified the specimens and reviewed the description, which follows his suggested format (Taylor, 1965).

Types.—Holotype is in the collection of the Bureau of Economic Geology, The University of Texas, Austin. Representative specimens: KU 500393, 500394a-b, 500395.

Occurrence and Material.—The figured specimen is from sandstone in the middle of the Kiowa, unit 12, Loc. C1; two disarticulated carapaces, from the same horizon, were too delicate to clean and probably are in this taxon. One carapace found in shale (unit 2, Loc. M3) was broken before identified. It was similar to these Clark County specimens. A mold in shale (unit 2L, Loc. E6) appears to be of an ostracode, but the outline is incompletely exposed and indeterminant. These specimens were found during binocular examination of rock samples and no special effort was made to study Kiowa microfossils. R. L. Kaesler reported (oral comm., 1966) that some samples contain an abundant ostracode fauna.

This species ranges from upper Kiamichi to lower Duck Creek in Texas (Lozo, 1943).

Paleoecology.—Cytherideidae contain many marine to brackish water and only few fresh water species. The poor preservation of punctae in this Clark County specimen suggests that the carapace was abraded by the sand in which it was deposited.

Subclass MALACOSTRACA Latreille, 1802—Superorder HOPLOCARIDA Calman, 1904—Order STOMATOPODA Latreille, 1817—Family SQUILLIDAE Latreille, 1803

Genus SQUILLA Fabricius, 1787

SQUILLA? KIOWANA Scott, n. sp.

Plate 7, figure 5

Description.—Body of moderate size, cephalothorax partly covered by carapace, longer than wide, slightly tapered anteriorly; dorsal surface punctate; second pair of thoracopods very large, four posterior thoracic somites free; abdomen incompletely known, four to five segments; telson unknown; thorax and abdomen apparently smooth.

Cephalon with two free somites; antennular somite bearing a pair of antennules incompletely known; acron bearing a pair of blister-shaped eyes; both somites with an apparent median carina continuous across each; antennae with two-segmented peduncle, exopod unknown, endopod with many-jointed flagellum. Rostrum unknown.

Other cephalon appendages and first pair of thoracopods unknown. Second pair of thoracopods very much larger than others, presumably forming raptorial claws; dactylus unknown. Third through fifth pairs of thoracopods with narrower and shorter segments bearing short, triangular spines on margin. Sixth through eighth thoracopods with long, narrow segments, incompletely known. Abdominal appendages unknown.

Length of cephalothorax (KU 500396; unit 4, Loc. S9) 21 mm., width of cephalon about 4.5 mm. Partial abdomen and thorax (KU 500397a-b; unit 2L, Loc. E6), five segments, length 14 mm., width 6.7 mm.

Discussion.—Although the telson is unknown, this species is tentatively assigned to the genus *Squilla* because the cephalon appears to be narrower than in the genus *Sculda*, the length to width ratio of the free thoracic segments and abdominal segments appears to be more like that of *Squilla*, and the abdomen surface apparently lacks spines. For a complete description of *Squilla* and *Sculda* see Holthuis & Manning (1968).

Because of the incomplete preservation of certain features, *Squilla? kiowana* cannot be compared completely with *Paleosquilla brevicoxa* Schram, 1968. The carapace of *S.? kiowana* appears to narrow slightly anteriorly and the anteriolateral corners appear to possess small projections that may be spines. The dorsal side of the carapace cast is punctate, which probably reflects the presence of spines. The median carina is very short in contrast with the long carina of *Paleosquilla.* The thoracic and abdominal somites are smooth and bear rounded anterior margin. *S.? kiowana* is unique among fossil stomatopods in having a spined carapace and in having triangular spines on the thoracopods.

Types.—Holotype: KU 500396; paratype: KU 500397a-b.

Occurrence and Material.—Molds and casts of segments and fragments, partly coated with a thin chitinous film, are scattered in dark-gray shale of the middle Kiowa in central Kansas.

Paleoecology.—Most modern species of Stomatopoda inhabit marine, shallow waters (0-145 m., rarely to 950 m.) and are predators in tropical to subtropical seas; some species inhabit temperate waters. In mud substrates of bays and inlets *Squilla* makes U-shaped burrows 2-5 cm. in diameter having openings 45 to 75 cm. apart (Bigelow, 1931). Other species dwell on sandy bottoms or in crevices in reefs. On the Gulf Coast *Squilla empusa* is characteristic of the lower sound assemblage and is also common in inlets and shallow shelf assemblages (Parker, 1956).

The occurrence in dark-gray shales of the Kiowa suggests that the mode of life of this species was similar to modern mud-dwelling species.

Phylum ECHINODERMATA Laske, 1778—Subphylum ASTEROZOA Zittel, 1895—Class STELLEROIDEA Lamarck, 1816—Subclass OPHIUROIDEA Gray, 1840—Order OPHIURIDA Miller & Troschel, 1840—Suborder CHILOPHIURINA Matsumoto, 1915—Family OPHIURIDAE Lyman, 1865

Genus OPHIURA Lamarck, 1801

OPHIURA sp. indet.

Figure 20

Discussion.—A single internal cast of the aboral side of a specimen was found. The external mold of the aboral side was inadvertently damaged in preparation. No shield sutures can be seen in the external mold of the arms. The vertebral ossicles of the arms are well preserved. Arms are incompletely exposed and the exposed portion is 7.5 mm. long. The central disc is incompletely preserved, and the diameter between the first ossicles of an opposite pair of arms is about 1.9 mm.

Occurrence and Material.—This single specimen, KU 500398a-d, is from sandstone unit 9, middle Kiowa, Loc. S8. Berry (1941) described species from the Denison Formation near Ft. Worth.

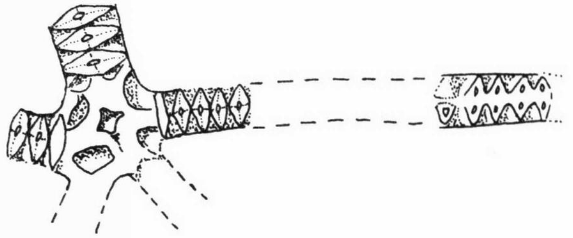

Fig. 20. Sketch of *Ophiura* sp. (about ×7), aboral view of internal mold.

Paleoecology.—Many living ophiuroids are carnivores in shallow marine to slightly brackish waters. On the Gulf Coast ophiuroids are characteristic of the upper sound and inlet assemblages (Parker, 1956).

TRACE FOSSILS

DOMICHNIA

Genus ARENICOLITES Salter, 1857

Description.—Burrows are vertical and oblique to stratification, cross section is circular to elliptical, 1-4 mm. diameter; openings are generally paired, 7-10 mm. apart, suggesting connection in a U-shaped burrow.

Occurrence and Material.—Burrows in sandstone were collected at Loc. O1 (KU 500399) and seen at Loc. S1.

MISCELLANEOUS FORMS

Plate 7, figures 1, 2

Description.—The following trace fossils probably were formed by filter-feeders and predators. A sandstone burrow cast (pl. 7, fig. 2) in dark-gray shale was parallel to stratification, branched at both ends, and curved upwards to connect with the overlying sandstone. Diameter is about 35 mm., collected portion is 150 mm. long. The cast consisted of very fine-grained quartz sand, clay, and a few phosphatic pebbles and fish scales. The irregular, lumpy surface is similar to that of *Ophiomorpha,* and perhaps it was made by a crab. Unit 1, Loc. E1, KU 500400.

EXPLANATION OF PLATE 7

Figure

1. Domichnia; vertical burrow in sandstone, ×0.8, with a ring of sand detritus around opening; note associated *Chondrites;* unit 11, Loc. C1, KU 500409 (p. 86).
2. Domichnia; probable crab burrow, ×0.6; note slightly pebbly surface; unit 1, Loc. E1, KU 500400 (p. 86).
3. *Rhizocorallium* sp. indet.; trail in sandstone parallel to stratification, ×0.8, middle Kiowa, N½, SW, sec. 25, T. 30 S., R. 23 W., Clark County, KU 500414 (p. 87).
4. Repichnia; burrow casts on underside of siltstone, ×0.8; note burrows penetrating upwards into the unit across stratification; unit 4, Loc. C1, KU 500416 (p. 87).
5. *Squilla? kiowana* Scott, n. sp.; chitinous imprint in shale, ×3.5, unit 4, Loc. S9, KU 500222 (p. 85).
6. Decapod chela in shell conglomerate, ×1, associated with *Crassinella semicostata* and *Turritella belviderei,* unit 3B, Loc. E6, KU 500429.
7. *Chondrites* sp. indet.; burrows in sandstone filled with dark-gray shale, ×2.5, unit 11, Loc. C1, KU 500410 (p. 87).

1

2

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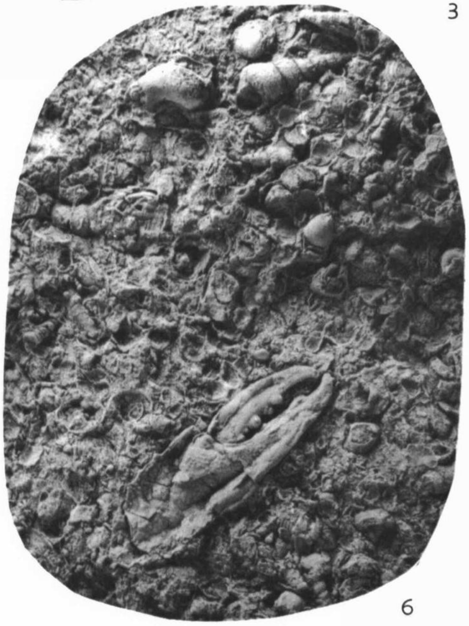

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7

A unique long, slender vertical dwelling burrow in sandstone is 3 mm. in diameter with a circular cross section and is more than 45 mm. long. Unit 6, Loc. S1, KU 500401. A similar type burrow, tapering distally, elliptical cross section, 4 mm. in diameter, is found in claystone unit 12, Loc. M5.

A larger circular dwelling burrow, 10-12 mm. in diameter, is vertical or slightly oblique to stratification in sandstone unit 20, Loc. S9, KU 500402, 500403; and unit 6, Loc. R3.

The largest vertical dwelling burrows are elliptical in cross section, 20-40 mm. greatest diameter; the largest one collected is 150 mm. long. The burrow walls are stratified and the burrow filling is homogeneous sand. Occurs in thin-laminated, yellow-brown sandstone (unit 13, Loc. E1, KU 500404, 500405; and CSE, sec. 23, T. 16 S. R. 1 E., Dickinson County, KU 500230).

A small, vertical to oblique dwelling burrow (pl. 7, fig. 1) consists of an inner tube, 4 mm. in diameter, filled with shale, and an outer tube, 10-15 mm. in diameter, filled with sandstone. On the uppermost stratification plane the outer tube forms a mound-shaped ring, unit 11, Loc. C1, KU 500409. A similar type burrow, lined with limonite, is from unit 11, Loc. M4.

FODINICHNIA

Genus CHONDRITES Sternberg, 1833

Plate 7, figure 7

Description.—These short, straight, burrows are about 0.5 mm. in diameter, and branch sharply at a 40-55° angle. A series of branches parallel stratification, and the main stem abruptly cross cuts stratification. Commonly the tubes are filled with dark-gray shale.

Occurrence and Material.—*Chondrites* are common to rare in thin-laminated sandstones and in micrite fillings in some *Gryphaea* valves in southern Kansas. Representative specimens: KU 500410, 500411a-b.

REPICHNIA

Genus RHIZOCORALLIUM Zenker, 1836

Plate 7, figure 3

Description.—This elongate furrow consists of a horseshoe-shaped, shallow groove parallel to stratification that partly encircles a series of concentric arched ridges. The arched ridges are the terminations of scoop-shaped laminae that are very slightly oblique to stratification. The entire furrow disturbs a thickness of strata no greater than 5-10 mm. Some furrows cross cut the simple type of Repichnia. The larger specimen is 110 mm. long, 75 mm. wide; the smaller is 80 mm. long (incompletely preserved) and 55 mm. wide.

Occurrence and Material.—Two specimens in very thin-laminated sandstone were collected from unit 8, Loc. C3 (KU 500413), and from an unmeasured section, about 100-120 ft. above the base of the Kiowa on the west cliff of Clark County State Lake, N½ SW, Sec. 27, T. 30 S., R. 23 W. (KU 500414). Other specimens were seen in sandstone at Loc. R6.

Genus SCOLICIA DeQuatrefages, 1849

Plate 4, figure 4

Description.—This flat, relatively straight trail with parallel sides is 5 mm. wide and 37 mm. long, and has straight, transverse ridges about 1 mm. wide that appear to be thin, short laminae oblique to stratification. No longitudinal furrows seen.

Occurrence and Material.—A single trail in calcareous sandstone, unit 12, Loc. C1, KU 500415.

MISCELLANEOUS FORMS

Plate 7, figure 4

Description.—This group includes straight to sinuate to irregular burrow casts that are circular to elliptical in cross section, and that parallel stratification or cut it at a very low angle for part of the burrow length. Some casts are on the underside of strata representing surface benthos, and many cross cut strata and connect with the upper surface. These groups can be distinguished by diameter size: 1-2 mm., 4-5 mm., and 8-12 mm. No morphologic differences are apparent, and the limits are not without overlaps in a few specimens. No attempt was made to determine the distribution and associations of these size groups, except that any two or even three may occur together.

Occurrence and Material.—These burrows and casts are most common in siltstone and very fine-grained sandstone; well-developed burrows are less common in dark-gray shale, although well-developed silt mottles may be present. Repichnia are found throughout the Kiowa in central and southern Kansas. Representative specimens: KU 500416-500418, unit 4, Loc. C1.

APPENDIX A—METHODS OF STUDY

FIELD METHODS

Field work was conducted during parts of three summers, 1964, 1965, and 1966. Forty-three localities were visited and stratigraphic sections were measured where available. The sections were divided into homogeneous lithologic units or units of regularly alternating rock types. Contacts between gradational units were picked where the succeeding lithology became dominant. Because the Kiowa has no consistent stratigraphic marker beds, the base or the top was included wherever possible. If one or the other of these contacts was not exposed, its approximate position was determined from geologic maps prepared by P. C. Franks on aerial photographs, generally at the scale of 1:20,000, or on topographic maps, scales 1:24,000 or 1:250,000; changes in topography and vegetation were also considered. Errors in thicknesses thus determined probably do not exceed 10-15 feet.

Fossils were collected from about 100 units, and bulk samples from about 80 of these units. Shale and mudstone intervals were trenched, and bedding planes were carefully examined for fossils. A large sample bag was filled with shale from several levels to represent the entire unit. The position and arrangement of fossils in sandstone and shell conglomerate units were described; and generally bulk samples consisting of large slabs or many smaller blocks were collected from a large area. The blocks and slabs were selected because of the number and well-preserved condition of fossils in them. No attempt was made to collect a given area, volume, or weight because the variable condition of the exposures, the variation in dispersion of fossils, and the differences in density of the several lithologies made such a procedure impractical and inconsistent. A randomized sampling procedure would have been fruitless at many localities, and much good material would have been overlooked. Although the selected specimen in the block was not chosen randomly, all the other specimens within the block were, assuming that fossils are distributed randomly in the rock and are independent of one another.

Where *Turritella* sp. was exposed on extensive bedding plane surfaces its azimuthal orientation was measured. Nearly complete specimens generally not in contact with others were chosen. Some blocks were oriented to North and brought to the laboratory for measurement. In poorly stratified sandstone the measurements were made on specimens within a thickness of less than 10 cm.; circular histograms (Fig. 4a, b, d) were prepared from these data.

LABORATORY METHODS

The samples were cleaned and all identifiable specimens counted. The samples were split along as many bedding planes as practical to find a large number of specimens. Each valve of articulated specimens was counted as one. Identifiable bivalve fragments largers than 2-4 mm. were counted, and gastropod shells with two or more whorls were counted. More than 7100 specimens were counted. Identification and counting were carried out as objectively as possible; however, several factors caused some bias. Fragments of a few species were more readily identified, and thus these species tended to be more abundant. Large specimens tended to be recognized more readily than small specimens. Very plain and simple species that were not well known could be easily overlooked. In spite of these inconsistencies, the relative abundance data in Table 3 are semiquantitative descriptions of what I saw in the samples.

Because of the variable quality of exposures, no attempt was made to determine the absolute abundance or density of fossils. Most quantitative studies of relative abundance are based upon sample weight or volume (Imbrie, 1955; Ferguson, 1962) to insure random collecting of specimens. However, because this approach was impractical in treating the many different Kiowa lithologies, the method of counting a certain minimum number of randomly selected specimens, which is used by botanists (Cottam, Curtis, & Hale, 1953), was tried. This method of relative abundance studies seems superior to collecting a specified sample weight or area, because the objective of the study is the number of specimens of each species relative to the total fauna, not to the volume of rock. Absolute abundance studies may have interpretive value in describing in-place assemblages, but they are of little value in describing geographic and stratigraphic variations of mega-invertebrates.

The principle underlying the counting of a specified number of specimens is given by Cottam, Curtis, & Hale (1953, p. 748):

> The main factor affecting such accuracy of relative proportions of each species in a population is the number of individuals that appear in the total sample. If a given species predominates in the population, the proportions may be determined accurately by a small sample. For species representing lesser and lesser fractions of the total, more or larger sampling units are needed to assess their correct proportions. As a general statement, it appears that about 30 individuals of a particular species should be encountered in the total sample before confidence may be placed in statements about its relative density.

Commonly it is impossible to collect 30 specimens of one fossil species. However, one corollary to this empirical rule is that the total number of specimens in the sample should equal the number of species times 30 to have a standard error in relative abundance less than 22 percent (percentage calculated by Cottam, Curtis, & Hale, 1953). If this guideline is not achieved in collecting, one sample can be compared with another by the following corollary. The number of species that can be safely compared regarding relative abundance is the total number of specimens divided by 30. These two corollaries plus verification of the required minimum sample size facilitates relative abundance studies of paleontologic material. Cumulative curves of specimens plotted against increasing relative abundance as suggested by Ager (1963, p. 188) verify this minimum number, which is determined by the point at which the curve becomes asymptotic.

This empirical rule was tested with multiple samples from several localities. Results of the two or three more abundant species are plotted on Figure 21, *C-J*. Blocks of sandstone and shell conglomerate from each unit were separated into subsamples and specimens were counted separately. Because fossils were sparse in shale and mudstone, two samples were taken from only one locality (unit 6, Loc. C3). It is important to note that different collecting methods were used in taking these two samples. The smaller sample was collected by taking random, grab samples from a trench. Specimens of the larger sample were deliberately picked from the outcrop by Dr. Teichert and myself.

These samples show that between 30 and 40 specimens of each species give a relatively accurate measure of relative abundance. Anomalous and abrupt increases, as in Figure 21, graph *C*, occur in very small subsamples of less than 25 specimens.

The effect of sample size on diversity of species was tested in the same way (Fig. 21, *A*, *B*). The number of new species were plotted versus the cumulative number of specimens beginning with the largest number of species and proceeding to the sample with

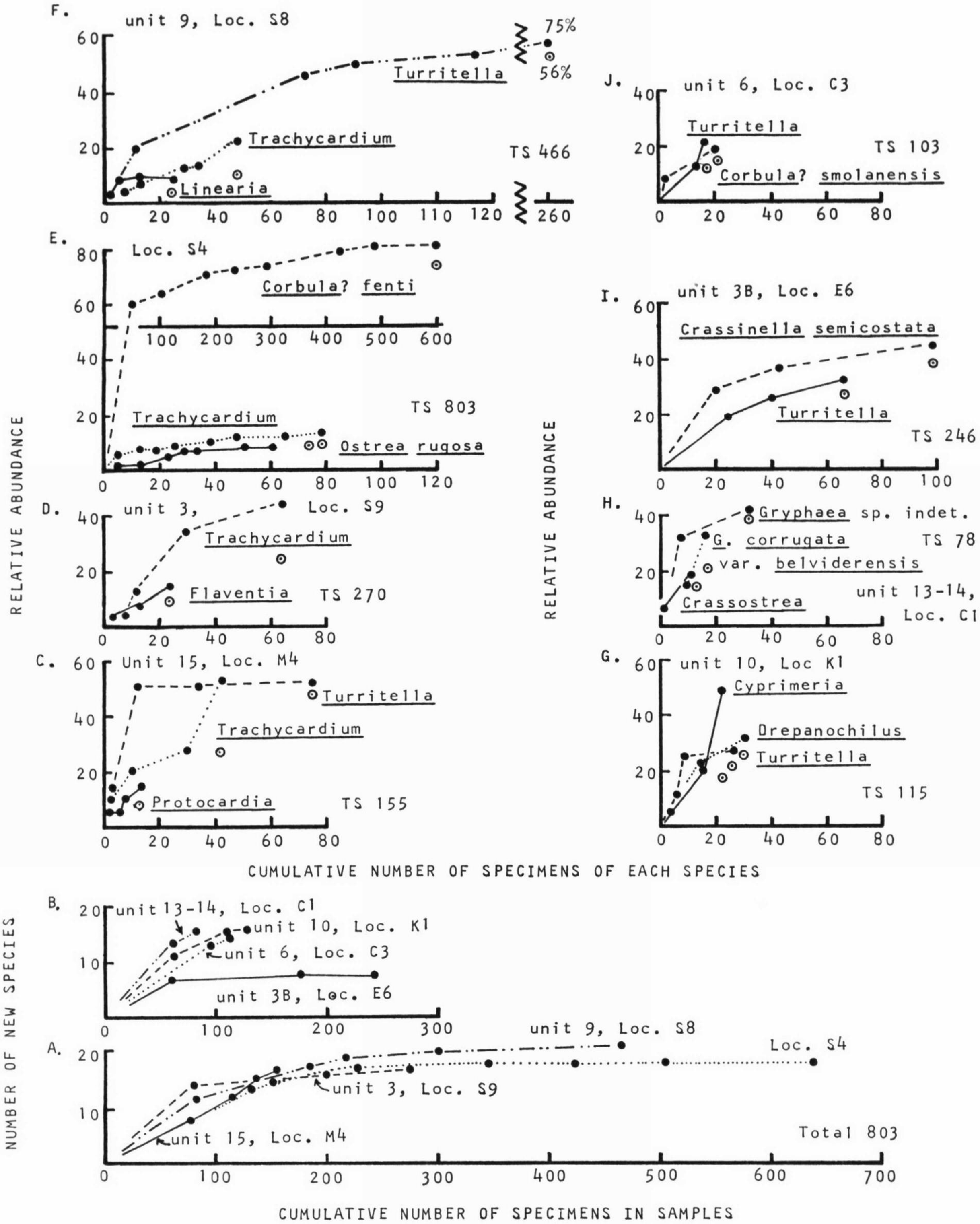

FIG. 21. Graphs showing variation in relative abundance of taxa and in number of new species as the number of specimens increases. Cumulative curves *A* and *B* show the variation in number of taxa as a function of the number of specimens. Cumulative curves *C-J* show the variation in relative abundance of taxa as a function of the number of specimens of the species. *TS* refers to total number of specimens of all species in the sample. Circled dot represents the average relative abundance of each species in the combined sample. Note change in horizontal scale in upper part of graph *E*.

smallest number of new species. Generally more than 150 specimens per total sample were necessary to have most of the species represented. Samples from nine localities qualify and 20 samples contain 100 or more specimens. Fossils were so sparse in some units that 20 specimens was a large, although inadequate sample.

In summary, a sample from the Kiowa Formation consisting of 30 to 40 specimens of each species or a sample of 30 specimens times the number of species should be adequate for relative abundance studies; and a sample of 150 to 200 total specimens from the Kiowa should provide reliable species diversity data.

SIMPSON'S DIVERSITY COEFFICIENT

Of the many techniques to measure species diversity, Simpson's coefficient (Simpson, 1949) was used because it takes into consideration the relative abundance of the species. The equation is:

$$\frac{N(N-1)}{\Sigma n(n-1)}$$

where *N* is the total number of specimens in the sample and *n* is the number of individuals of each species. The equation shows the average number of pairs of specimens to be selected from a sample "to obtain a pair of the same species" (Ager, 1963, p. 241). If the sample contained one species, only one pair would need to be selected and the diversity coefficient would equal one. But if every individual represented a different species, the coefficient would be infinity. Large samples are needed to give good results; in Ager's (1963) example, samples contained from 248 to 752 specimens. The variation in size of samples from the Kiowa probably explains why trends in the coefficient are not distinct. Some samples of a few specimens and a few species had very high coefficients, whereas very large samples of many species had low coefficients because a few species were very abundant. Therefore, differences in the coefficient probably are significant only for samples of 100 or more specimens. No major interpretations are based upon variations in this coefficient because most samples were too small.

JACCARD COEFFICIENT OF ASSOCIATION

This coefficient recently was applied to paleoecologic studies by Kaesler (1966). The equation is based upon presence-absence data of species and is stated as follows:

$$S_J = \frac{a}{a+b+c}$$

where *a* is the number of samples containing the two items being compared, *b* is the number in which one item is present alone, *c* is the number in which only the second item is present. This coefficient is based only on positive matches and is therefore suitable for grouping together species that are preserved together and may have lived together (Kaesler, 1966).

Not all species were used in calculation of the Jaccard coefficient. Only those species or groups of species (indicated by brackets in Fig. 5, 6) found at four or more localities were used. All trace fossils were included in one group. Localities with less than four taxa were excluded. Even then several less common species (*Cardita?, Pecten,* and *Cucullaea)* did not fit into any association. In general, however, this coefficient of association arranged the species and other items into categories very similar to those derived empirically.

APPENDIX B—DESCRIPTIONS OF LOCALITIES

Localities are shown on Figure 1, measured sections are plotted on Figures 10-13.

CLARK COUNTY

C1. CNL sec. 30, T 31 S, R 22 W. Units 1-7 measured on east-facing hill east of road; units 7-17 measured on east-facing road cut, about 9 miles north of Ashland on county road.
C2. SW SW sec. 34, T 31 S, R 23 W. Up west and north slopes of south trending canyon on south side of county road, 6½ miles north, northwest of Ashland on county road.
C3. NE NW½ NE sec. 12, 2 32 S, R 22 W. West face of isolated hill north and east of northernmost ridge leading from gravel pit, about 7 miles north of Sitka.
C4. NW SW sec. 35, T 32 S, R 24 W. East sloping draw east of trail road and directly north of fence line (Mt. Nebo locality of Prosser, 1897); 6 miles west of Ashland on U.S. Highway 160, 1 mile north, ½ mile west on trail road, ¼ mile north to fence.
C5. NE Cor sec. 25, T 32 S, R 25 W. On west side of Jacob's Well directly east of trail road, 1 mile east of U.S. Highway 283-160.

ELLSWORTH COUNTY

E1. CS½ sec. 33, T 15 S, R 7 W. North cut bank on Smoky Hill River, 2 miles east of Kanopolis on county road, 1 mile south on trail road.
E2. SE NW NW sec. 20, T 16 S, R 6 W. Easternmost shore bluff at Yankee Run.
E3. SW SE NW sec. 28, T 16 S, R 7 W. Northwest-facing cut bank on south side of Thompson Creek, about ¼ mile northeast of county road.
E4. WL NW SW and NW NW SW sec. 1, T 17 S, R 6 W. Cut bank on south side of stream and slope above terrace on south side of stream, about 2 miles southeast of Kanopolis Dam.
E5. NE sec. 3, T 17 S, R 6 W. Shore bluff next to control tower of Kanopolis Dam. Not measured, section similar to locality E6.
E6. CNE sec. 4, T 17 S, R 6 W. West-facing beach bluff on east bank of second bay west of State camping ground.
E7. CEL sec. 22, T 17 S, R 6 W. East-facing bluff in pasture directly west of road, ½ mile south of Kansas Highway 4. Not measured, found no fossils, 15 feet of section in lower half of Kiowa.
E8. Two-tenths mile W of CNL sec. 29, T 17 S, R 6 W. Bank and barrow ditch on south side of road, about 1½ miles west of Kansas Highway 4.
E9. N½ sec. 32, T 17 S, R 6 W. Railroad cut 0.1 mile east of center N½, directly east of Kansas Highway 4. Not measured, sandstone float; found no fossils.
E10. CEL SE NE sec. 36, T 17 S, R 6 W, and NW NW sec. 31, T 17 S, R 5 W, McPherson County. Knolls capped by fossiliferous sandstone, upper part of Kiowa, in each of the two pastures, 2 miles east of Langley on county road, 1 mile south on trail road in pasture.

KIOWA COUNTY

K1. CN½ sec. 16, T 30 S, R 16 W. Section measured at head of north-trending draw ("Champion Draw") and up hill to east, ½ mile south of Belvidere.
K2. CE½ W½ sec. 36, T 30 S, R 16 W. Up east of slope of north-trending draw, about 4 miles southeast of Belvidere on tertiary road, and 1 mile east on trail road in pasture. (Probably "Stokes" or "Black Hill" locality in old literature.)
K3. CNE sec. 16, T 30 S, R 17 W. North face of south bluff

on Medicine Lodge River, 2 miles west of Belvidere on secondary road, about 4 miles west on tertiary road.

K4. CSL SE sec. 2, T 30 S, R 18 W. Southwest corner of road junction, about 4 miles directly east of State Highway 1. Near "Greenleaf Ranch" locality.

McPHERSON COUNTY

M1. CS½ NE sec. 13, T 17 S, R 1 W. North-trending gully about ¼ mile west of county road, 2 miles north of county road to Roxbury. Good section of lower Kiowa, not measured, no invertebrate fossils found.

M2. CS½ sec. 19, T 17 S, R 2 W. West-trending gully in pasture; basal Kiowa, not measured, no fossils found; 4½ miles east of U.S. Highway 81, 1½ miles south of Lindsborg.

M3. NE SE sec. 1, T 17 S, R 5 W. Southwest end of Buildex's pit 2 miles north of Kansas Highway 4.

M4. E½ E½ SE sec. 32, T 17 S, R 5 W (units 1-7), CW½ NE sec. 5, T 18 S, R 5 W. 4 miles south of Marquette, 4 miles west on county road, one mile north on secondary road, about 1 mile into pasture from secondary road ("Natural Corral" area).

M5. CS½ NW SE sec. 23, T 18 S, R 2 W. West creek bank, 1½ miles west of Game Preserve.

M6. N½ SW sec. 29, T 18 S, R 5 W. Northwest-facing cutbank directly east of county road, 5 miles north of Windom.

M7. S½ EL sec. 5, T 19 S, R 5 W. Hilltop 0.1 mile and hilltop 0.2 mile north of SE Cor. sec. 5. Go 1½ miles north of Windom, 1 mile east, 1 mile north. Type area of "Windom Member."

M8. NW sec. 19, T 19 S, R 5 W. Float in pasture directly north of railroad, ½ mile west of Windom.

OTTAWA COUNTY

O1. CW½ SW sec. 28, T 12 S, R 2 W. In hills southwest of farm, 3 miles east of U.S. Highway 81. No section measured.

RICE COUNTY

R1. CS½ NW sec. 3, T 18 S, R 6 W. West slope of north-trending draw in pasture west of county road, south of Langley.

R2. CN½ NE NE sec. 9, T 19 S, R 6 W. North-facing cutbank in pasture southwest of section corner, 2 miles northeast of Little River.

R3. CNW sec. 13, T 19 S, R 7 W. East slope above spillway of Hawthorne's Lake, 2 miles west of Little River.

R4. N½ SW sec. 16, T 20 S, R 6 W. Collecting locality for *Crassostrea* coquina, along south bank of drained stock pond in pasture; no measured section.

R5. CNL NW sec. 17, T 20 S, R 6 W. Collecting locality for *Crassostrea* coquina, in barrow ditch along road; no measured section.

R6. SW NE sec. 27, T 20 S, R 10 W. Collecting locality in pasture directly east of road, ½ mile north of Raymond.

SALINE COUNTY

S1. SW sec. 18, T 13 S, R 2 W. Along northwest-southeast gully; base exposed in SE¼ in west-trending gully. No invertebrate fossils found.

S2. SE NW sec. 29, T 13 S, R 2 W. In pasture ¼ mile south of O. S. Fent's house.

S3. SW Cor sec. 36, T 13 S, R 4 W. Road cut on south side of Interstate Highway 70, about 6 miles west of Salina junction, lower part of Kiowa, no invertebrate fossils found.

S4. SL SW SW sec. 15 and NL NW NW sec. 22, T 15 S, R 2 W. Float from small knolls on either road side, 3 miles east of Mentor; type locality of "Mentor Member."

S5. WL W½ sec. 27 and SE SE SE sec. 28, T 15 S, R 2 W. Hill slopes on both sides of road, directly north of Kansas Highway 4, 4 miles east of U.S. Highway 81.

S6. CSW sec. 10, T 15 S, R 4 W. Float from west shoulder of ridge on north side of draw; 3 miles south of Bavaria.

S7. WL SW sec. 15, T 15 S, R 4 W. Section measured along section line road; collections made at section corner and in E½ SE SE sec. 16, in small draw; 4 miles south of Bavaria (Smolan locality).

S8. CSE SE sec. 17, T 15 S, R 4 W. Section measured along east-trending gully on bombing range, Smoky Hill Air Force Base; 4 miles south, 1 mile west of Bavaria (locality 5 miles west of Smolan).

S9. NW Cor sec. 10, T 15 S, R 5 W. Section measured from stream level under bridge to hilltop ¼ mile south; collections made from under bridge and in gully west of bridge; ¼ mile south of Brookville.

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