Texigryphaea in the Glencarin Formation near Two Buttes, Colorado, with notes on an assemblage of Texigryphaea from the Kiowa Formation of southern Kansas

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TEXIGRYPHAEA IN THE GLENCAIRN FORMATION NEAR TWO BUTTES, COLORADO, WITH NOTES ON AN ASSEMBLAGE OF *TEXIGRYPHAEA* FROM THE KIOWA FORMATION OF SOUTHERN KANSAS

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Abstract—An assemblage of *Texigryphaea* from the Glencairn Formation near Two Buttes, Colorado includes about equal numbers of *T. tucumcarii* and *T.* aff. *T. pitcheri,* in contrast to Glencairn assemblages in the Dry Cimarron area, in which *T.* aff. *T. pitcheri* is very uncommon. The Two Buttes fauna as a whole is much less diverse than in the Dry Cimarron area, and includes some elements, such as *Ostrea larimerensis,* that are characteristic of the northern part of the southern Western Interior province. The Lower Cretaceous fauna at Two Buttes, Colorado represents a transition between the diverse, normal-marine late Albian faunas to the south and the depauperate, probably brackish faunas to the north and west. An approximately contemporaneous *Texigryphaea* assemblage from a coquinoid limestone in the upper Kiowa Formation at Avilla Hill, south-central Kansas, consists mainly of *T. pitcheri*. Individuals in this assemblage display a high degree of variation in shell form and nearly all have medium to large attachment scars, probably reflecting life in a relatively turbulent, high-density environment, on a substrate consisting mostly of shells and shell fragments. The *Texigryphaea* morphology in the upper Kiowa is moderately similar to that of the Two Buttes assemblage, whereas the Dry Cimarron texigryphaeas are very different from both.

INTRODUCTION

A small exposure of the Glencairn Formation along the south side of Two Butte Creek, about 8 km northeast of Two Buttes Mountain, Prowers County, Colorado, contains a late Albian marine fauna dominated by *Texigryphaea*. This locality (UNM locality 1329; SE¼, sec. 23, T27S, R45W; Figs. 1, 2) marks the northernmost occurrence of *Texigryphaea,* which also ranges through Texas, northern Mexico, eastern New Mexico, Oklahoma and south-central Kansas. A collection of texigryphaeas was made from this locality in order to compare their morphology with that of Glencairn texigryphaeas in the Dry Cimarron area about 80 km to the south (see Kues and Lucas, 1987). In addition, an approximately contemporaneous assemblage of texigryphaeas from the upper Kiowa Formation at Avilla Hill, Comanche County, Kansas, is described and its relationships to the Glencairn assemblages discussed. All specimens illustrated in this paper are reposited in the University of New Mexico (UNM) Department of Geology paleontology collection.

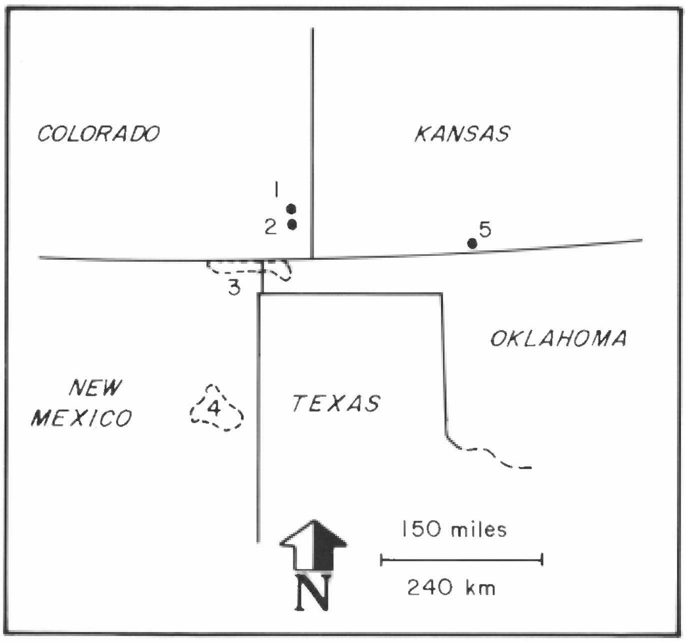

FIGURE 1. Location of late Albian *Texigryphaea*-bearing units mentioned in text. 1, Glencairn, Two Buttes locality; 2, Glencairn, Horse Creek locality of Cobban (1987); 3, Glencairn, Dry Cimarron localities of Kues and Lucas (1987); 4, Tucumcari Shale localities of Kues et al. (1985); 5, Kiowa, Avilla Hill locality.

TWO BUTTES FAUNA

Previous studies

Darton (1905a, b, 1906) first reported Lower Cretaceous marine fossils from this locality, and Stanton (1905) also briefly described the locality and its fauna. Both workers assigned the texigryphaeas to *Gryphaea corrugata* Say, a species which at that time was believed to include several varieties (Hill and Vaughan, 1898) now generally treated

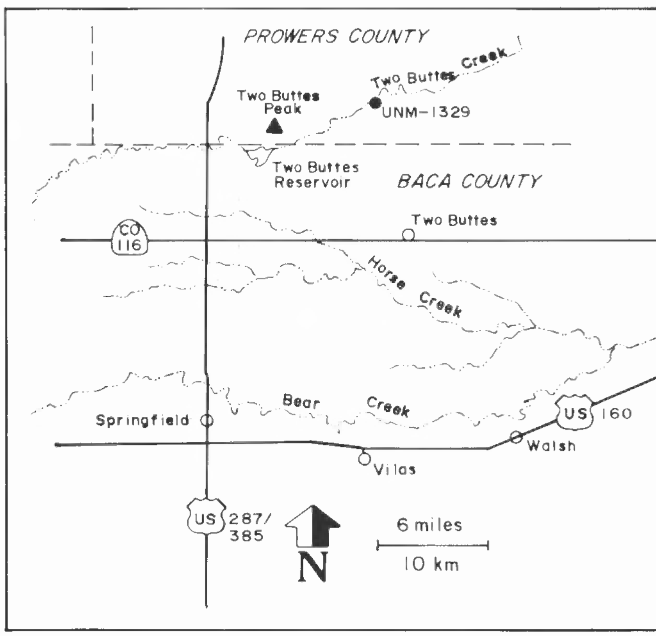

FIGURE 2. Location of the Two Buttes Glencairn exposure (UNM-1329) in southeastern Colorado.

TABLE 1. Mean left valve proportions of texigryphaeas from the Two Buttes, Colorado locality. N, number of specimens measured; L, length; H, height; P, periphery of left valve surface; BL, beak length; BE, beak elevation; SW, sulcus width; DA, length from anterior margin to sulcus; HW, hinge width; A, angle of umbo inclination; NNM, number of specimens not measured; T, total specimens. See Kues and Lucas (1987) for illustration of these valve parameters.

	N	L/H	W/H	P/H	BL/H	BE/H	SW/L	DA/L	HW/L	A	NNM	T	%
T. tucumcarii (typical)	4	.80	.44	1.67	.22	.12	.25	.81	.24	82°	7	11	22
T. tucumcarii (broad)	–	–	–	–	–	–	–	–	–	–	12	12	24
T. aff. *T. pitcheri*	11	.99	.39	1.54	.17	.12	.22	.69	.23	68°	8	19	38
T. tucumcarii transitional to *T.* aff. *T. pitcheri*	7	.91	.42	1.64	.22	.15	.24	.74	.23	70°	1	8	16

as distinct species (e.g., *T. tucumcarii*). The name *G. corrugata* was suppressed as a *nomen nudum* by Fay (1975); *T. pitcheri* (Morton) is used instead. Later workers (e.g., Sanders, 1934; McLaughlin, 1954; Voegeli and Hershey, 1965) considered the texigryphaea-bearing unit in this area to be the Kiowa Shale Member of the Purgatoire Formation (of Stose, 1912), but added no new information about its paleontology. Long (1966) measured a stratigraphic section near the locality discussed here and reported *G. corrugata* and the ammonoid *Eopachydiscus brazoensis* from this unit. He transferred the unit to the Glencairn Shale, an assignment followed by subsequent authors. Scott (1970a) noted the co-occurrence of *Inoceramus comancheanus* and *I. bellvuensis* at the locality and was the first to consider the texigryphaeas to be *T. tucumcarii* rather than *T. corrugata*. Cobban (1987) studied the Glencairn fauna at a locality along Horse Creek, about 20 km south of the locality discussed here, and noted the abundant occurrence of *T. tucumcarii*, together with several other species of bivalves and at least four species of ammonoids.

Texigryphaea

About 100 specimens of *Texigryphaea* from the Two Buttes locality were collected from shale slopes about 2 to 4 m above the top of the basal sandstone bed of the Glencairn. The source of the specimens was one or more fine- to medium-grained sandstone beds a little higher in the section. Scott (1970a) noted that the *T. tucumcarii* interval here is about 14 m below the top of the Glencairn. Most of the specimens were fragmented; only 22 mature left valves were complete enough to allow measurements (Table 1) of all or some of the features necessary to document adequately morphological variation (Kues and Lucas, 1987). Twenty-one percent of the left valves were collected in a state of articulation with their right valves.

Variation among Two Buttes texigryphaeas is similar to that observed in Dry Cimarron Glencairn assemblages, except that *T.* cf. *T. washitaensis* (Hill and Vaughan) was not observed at the Two Buttes locality. A major difference between the two faunas, however, is the relative proportion of different forms. In the Dry Cimarron Glencairn, 90% of the identifiable mature left valves represent the continuum of variation characteristic of *T. tucumcarii*. The left valves of this species have an oval to round commissure, relatively small beaks and an angle of umbonal inclination that is nearly perpendicular (85°) to the plane of the commissure, imparting a deep, straight, oval-to-round shape to the valve. The typical (narrower) and broad forms of *T. tucumcarii* are also present in the Two Buttes Glencairn (Fig. 3A–C), but together represent 46% of the total specimens examined.

A third form identified in the Dry Cimarron Glencairn (about 7% of the mature left valves) is characterized by an umbonal plane that is more inclined away from vertical (mean = 76°) than is the case in most specimens of *T. tucumcarii*. This produces a lower, more arcuate valve with a straight to distinctly concave postero-dorsal margin and often a well-developed posterior flange. This form, called *T.* aff. *T. pitcheri* (Kues and Lucas, 1987), is much more abundant in the Two Buttes Glencairn (Figs. 3D-M) than in the Dry Cimarron area, representing about 38% of the identifiable mature left valves at the first-mentioned locality. An additional 16% of the Two Buttes specimens appear to be transitional between *T. tucumcarii* and *T.* aff. *T. pitcheri*.

A summary of the left valve proportions of *Texigryphaea* forms identified at Two Buttes appears in Table 1, and can be compared with similar measurements of these forms in the Dry Cimarron Glencairn (table 2 in Kues and Lucas, 1987). The relatively few measured specimens in the collections from Two Buttes (about one-tenth as many as from the Dry Cimarron) accounts for at least part of the minor variations among the characteristics of the same form at the two localities.

Epizoans are rare on Two Buttes texigryphaea valves. Of left valves having one-half or more of their surface uncovered by matrix, about 60% lacked traces of boring or attached organisms, and the remainder displayed only rare oysters or borings. No serpulid tubes or bryozoans were observed. Dry Cimarron texigryphaeas likewise experienced relatively light infestation by epizoans, but were colonized to a greater degree than the Two Buttes assemblage. About 48% of the Dry Cimarron valves lacked epizoans. Of the 52% that displayed traces of epizoans, about one-third were significantly affected, a few to the point of having become thoroughly riddled with sponge and barnacle excavations. My overall impression is that the environment in which the Two Buttes texigryphaeas lived was less conducive to survival and settling of epizoan organisms than was the case in the Dry Cimarron area to the south. As there were no obvious differences in *Texigryphaea* abundance or density from the Dry Cimarron localities to Two Buttes, the decline in epizoan abundance northward must be attributed to other factors.

The frequency of an attachment scar is also different between the Two Buttes and Dry Cimarron areas. The Dry Cimarron texigryphaeas generally remained attached to the substrate for only a very short time after they settled. Ninety-five percent of the left valves examined either lack discernible attachment scars or display very small (less than 3 mm)

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FIGURE 3. Molluscs of the Glencairn Formation, near Two Buttes, Colorado; all × 1. A–C, *Texigryphaea tucumcarii* (Marcou), external, internal and umbonal views of left valve, UNM 9565. D–F, *Texigryphaea* aff. *T. pitcheri* (Morton), ventral, dorsal and umbonal views of articulated specimen, UNM 9566. G–I, *T.* aff. *T. pitcheri* (Morton), ventral, dorsal and umbonal views of articulated specimen with well-developed posterior flange, UNM 9567. J, K, *T.* aff. *T. pitcheri* (Morton), external and internal views of left valve with strongly developed attachment scar across umbo, UNM 9568. L, M, *T.* aff. *T. pitcheri* (Morton), external and internal views of a distorted, strongly flanged left valve, UNM 9569. N, O, *Ostrea larimerensis* Reeside, external and internal views of right (?) valve, UNM 9570. P, *Inoceramus* cf. *I. comancheanus* Cragin, part of mold of left valve, UNM 9571.

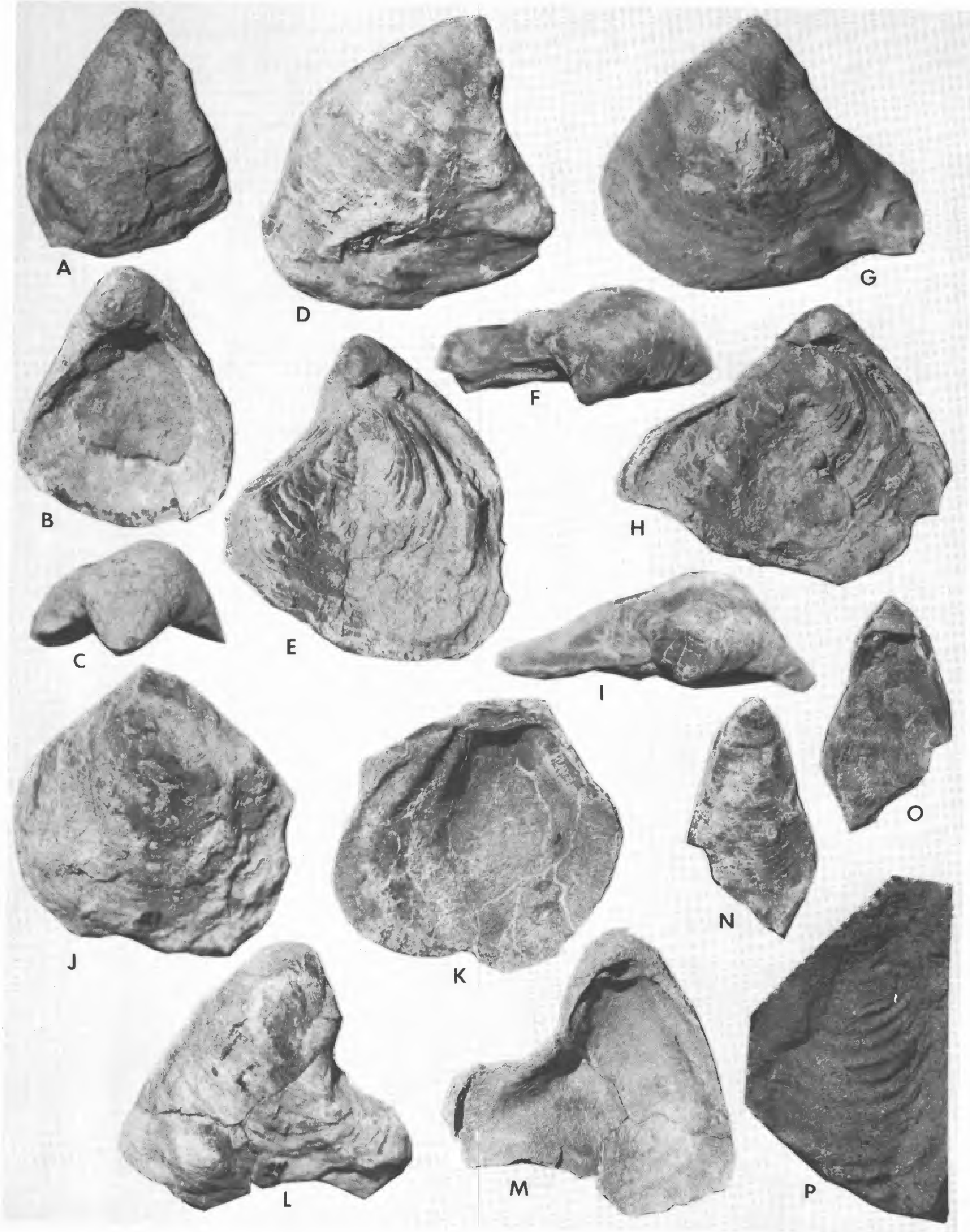
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TABLE 2. Comparison of size of attachment scars on texigryphaeas from the Glencairn Formation of the Two Buttes and Dry Cimarron areas, and the Kiowa Formation of Avilla Hill, Kansas.

ATTACHMENT SCARS	DRY CIMARRON GLENCAIRN	TWO BUTTES GLENCAIRN	AVILLA HILL UPPER KIOWA
Absent	63%	38%	2%
Small (0-3 mm)	31	36	1
Medium (3-10 mm)	5	16	33
Large (10 + mm)	1	10	64

scars (Table 2). Specimens with medium or large (greater than 10 mm) attachment scars are rare. This pattern fits the model proposed by Stenzel (1971), in which larvae utilize small shell fragments resting on a soft, muddy substrate as initial attachment sites, but soon become free living, maintaining a suitable position on the substrate by a series of orientation adjustments with subsequent growth.

Some Two Buttes texigryphaeas, on the other hand, tended to remain attached for a longer period of time. Seventy-four percent of the Two Buttes left valves have no more than a small attachment scar, but 16% possessed medium-sized and 10% large scars (Table 2). In several extreme cases, the attachment site was a large, shallow pit some 15 to 25 mm in diameter, representing 20 to 30% of the total beak-to-venter periphery of the valve. The long period of attachment represented by scars of this magnitude resulted in distortion of the beak and umbo and affected subsequent growth of the valve as well, sometimes producing atypically low, circular valves (e.g., Fig. 3J–K). The epitome of this trend of young texigryphaeas remaining cemented to a hard substrate for a long period of time is displayed by the Kiowa assemblage from Comanche County, Kansas, discussed below.

Associated fauna and environment

No attempt was made during this study to sample intensively the fauna associated with *Texigryphaea* at the Two Buttes locality, but a few general observations are made here. The large, elongate, thin-shelled, free-living oyster *Ostrea larimerensis* (Fig. 3N–O), together with possible representatives of a closely related species, *O. noctuensis*, rank second in abundance to *Texigryphaea* at Two Buttes. Both species were described by Reeside (1923) from Albian units in northern Colorado and southern Wyoming, and the Two Buttes area is the extreme southeastern limit of their geographic range. Cobban (1987) reported both species in the Glencairn at Horse Creek, but they are not present in the Dry Cimarron Glencairn or in the Kiowa Formation of Kansas.

Inoceramids are moderately abundant, but are represented mainly by small shell fragments. Only *I.* cf. *I. comancheanus* (Fig. 3P) was observed, but Cobban (1987) reported *I. bellvuensis* at Horse Creek, and Scott (1970a) reported both species at the Two Buttes locality. Among the ammonoids, *Eopachydiscus marcianus* (=*E. bravoensis*) is the only species known from the Two Buttes locality; Cobban (1987) reported that species and at least three others from Horse Creek, which indicates that the Two Buttes and Horse Creek Glencairn exposures are coeval with the Glencairn of the Dry Cimarron area (Kues and Lucas, 1987).

According to the paleogeographic reconstructions of Scott (1977, 1986) and Kauffman (1984) for the Albian Western Interior seaway, Glencairn deposition in the Two Buttes area may have occurred somewhat farther off the western shoreline than did deposition of the Dry Cimarron Glencairn, which includes a significant thickness of upper shoreface and even fluvial sandstones at some localities. However, the lithofacies of the Glencairn, and the stratigraphic/sedimentological occurrence of the *Texigryphaea* assemblage near Two Buttes, is not significantly different from that observed in the Dry Cimarron Glencairn. Substrate, turbulence and depth were apparently approximately similar in the two areas.

The diversity of the Two Buttes Glencairn fauna appears to be much lower than that of the Dry Cimarron. In part this is probably due to such factors as less study and much smaller exposure area, but may also reflect the beginning of changes in the marine environment, such as lowered salinity, that dramatically reduced diversity in the Glencairn and equivalent units to the north and west (Long, 1966; Kues and Lucas, 1987). *Texigryphaea* had little tolerance of lowered salinity (Stenzel, 1971), as did the ammonoids that are well-represented at Horse Creek (Cobban, 1987). Thus, normal or near-normal marine salinity prevailed in the Two Buttes area during the time the fossiliferous Glencairn sediments were being deposited there. *Ostrea larimerensis* and *O. noctuensis* are species primarily of the northwestern part of the southern Western Interior province of Scott (1977, 1986) and the southern part of the "boreal" realm (or central interior subprovince of Kauffman, 1984). As such, their occurrence in the Two Buttes fauna, but absence farther south and east marks about the southernmost influence of northern species on the predominantly Tethyan-derived faunas that inhabited the southern part of the Albian seaway. If these oysters were salinity-tolerant, as their distribution farther north and west and the ecology of other Cretaceous as well as modern *Ostrea* species would suggest, their appearance in the Two Buttes Glencairn may indicate transitory or perhaps slowly pervasive declines in salinity, possibly coupled with lowered temperatures. In any case, the composition and lessened diversity of the Two Buttes fauna suggests that it is transitional between the diverse, normal-marine faunas to the south and the depauperate faunas to the northwest along the western edge of the late Albian Western Interior seaway.

AVILLA HILL, KANSAS

Introduction

In an effort to compare western late Albian texigryphaea assemblages (Tucumcari Shale, Glencairn Formation: Kues et al., 1985; Kues and Lucas, 1987) with contemporaneous assemblages on the eastern side of the seaway, a collection of more than 100 *Texigryphaea* specimens was made from a thin limestone unit in the Kiowa Formation in Comanche County, south-central Kansas. This locality (UNM 1328) is on the northwest side of Avilla Hill, in the NE1/4 NW1/4 SW1/4, sec. 36, T34S, R19W, about 1.2 km due west of Kansas State Highway 1, and 4.6 km north of the Kansas-Oklahoma border (Fig. 4).

This locality and its abundant *Texigryphaea* fauna was briefly described by Prosser (1897), Vaughan (1897), Bullard (1928) and most recently by Fay (1965), who measured a detailed stratigraphic section there. A thick (42 m) section of the Kiowa is exposed along the dissected slopes of Avilla Hill, consisting mainly of dark gray shale intervals with several thin ledges of sandstone and limestone. Several of these units are abundantly fossiliferous, but the collection described here is from a thin (0.5–0.75 m), white to light yellow-brown bed of limestone

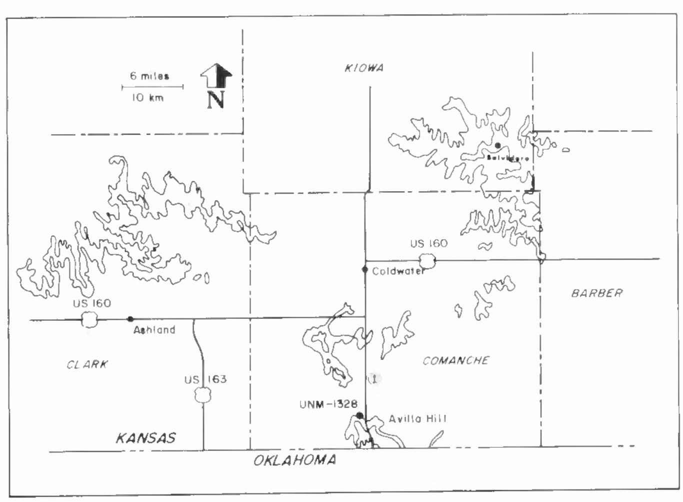


FIGURE 4. Location of UNM locality 1328, Avilla Hill, Kiowa Formation, Comanche County, Kansas.

composed primarily of shells and fragments of *Texigryphaea* near the top of the section, just below the summit of the hill. Details of sections measured in this area by Bullard (1928) and Fay (1965) differ, but both workers noted coquinoid or shell breccia limestones near the top of the Kiowa, which are without doubt the interval from which the collection described here was made. Lower in the Kiowa, an estimated 12 m below the upper limestone, is another interval from which abundant, purple-stained texigryphaeas erode. These are predominantly typical specimens of *T. navia,* a species that occurs sparingly if at all in the uppermost Kiowa at this locality.

Texigryphaea

The assemblage described here provides an opportunity to examine variability within texigryphaeas from a thin, lithologically homogeneous unit that is approximately contemporaneous with Glencairn texigryphaea assemblages in the Two Buttes and Dry Cimarron areas. Furthermore, both the Glencairn and Avilla Hill upper Kiowa faunas lived at about the same latitude, near the northernmost range of *Texigryphaea,* but on opposite sides of the late Albian seaway. The occurrence of the Avilla Hill texigryphaeas, in a bioclastic limestone composed mainly of their shells, is quite different from that of the Glencairn texigryphaeas, which lived in relatively quiet conditions on a muddy sand substrate. Thus the effect of different environmental conditions on the morphology of these contemporaneous eastern and western assemblages may also be studied.

The sample from the upper Kiowa limestone consisted of 127 specimens of *Texigryphaea,* of which 110 were measured. Articulated specimens comprise 8.7% of the specimens. Seven features of the left valve known from previous studies to be important in assessing *Texigryphaea* morphology (height, length, width, length of convex surface (P), beak length, angle of umbo inclination and length of attachment scar: Kues and Lucas, 1987) were measured (Table 3). Every specimen displayed evidence of cemented and boring epizoans, and many had been extensively colonized. Cemented epizoans were chiefly small texigryphaeas and ostreines; clionid sponges and acrothoracic barnacles accounted for most of the borings.

Nearly all left valves in this assemblage (Fig. 5) are characterized by an inclined umbo (mean angle of inclination = 72°), very small beak (mean beak length/valve height = 0.09), weak to obscure sulcus and a medium to large attachment scar that strongly distorted the beak and umbo and averaged about 17% of the entire beak-to-venter periphery of the valve. In relatively undistorted specimens the beak is deflected strongly posteriorly, and its tip overhangs the posterior edge of the hingeline bourrelet. The valves on average are smaller than texigryphaeas in the Glencairn and Tucumcari formations, reaching a maximum height of about 70 mm. Most specimens are between 50 and 65 mm high. The inclination of the umbo displaces the area of maximum valve convexity (or valve midline) to near the anterior margin, and produces a relatively low, shallow valve having an average width/height ratio of 0.37 and an average periphery/height ratio of 1.43, both less than is typical of the deeper, more strongly curved valves of *T. tucumcarii* in the Glencairn (Kues and Lucas, 1987). A few left valves are extremely shallow (W/H = 0.22; Fig. 5P, Q). Variation in valve shape is considerable, ranging from slightly arcuate/elongate to broadly arcuate to broadly triangular. The posterior lobe is moderately to greatly extended posteriorly, and the postero-dorsal margin is straight to moderately concave. Despite this variation in valve shape, the more conservative, less variable features of these valves mentioned above suggest assignment of nearly all specimens to a single species. This might also be expected from their occurrence within a thin bed at a single restricted locality.

Previous reports of the texigryphaeas in the upper Kiowa of Avilla Hill have been equivocal about their specific identity, referring them to *T. pitcheri* and *T. navia* (Prosser, 1897; Bullard, 1928), forms intermediate between *T. navia* and *T. tucumcarii* (Vaughan, 1897) or leaving them specifically indeterminate (Twenhofel, 1924; Fay, 1965). Scott (1970b) did not include the Avilla Hill locality in his Kiowa monograph, but referred (1970a) to a section about a km south of the locality discussed in this paper, and noted *T. corrugata* (= *T. pitcheri*) as the only texigryphaea near the top. Scott (1970a) considered the upper part of the Kiowa at his Avilla Hill locality to be within the *Inoceramus comancheanus* zone and slightly older than the Glencairn in the Dry Cimarron area and at Two Buttes.

Despite some existing uncertainties in the exact characteristics and variability of mature valves of *T. pitcheri,* related to the fact that the holotype is a small, immature individual, the great majority of specimens considered here seem best placed in that species. Some small specimens in this assemblage are morphologically similar to the holotype of *T. pitcheri* (figured by Stanton, 1947, pl. 10, figs. 4, 5 and Fay, 1975, figs. 19, 20), when allowance is made for the ecological plasticity of shell form and distortion by large attachment scars that are widespread in the assemblage. Further, some mature specimens are similar to what previous authors called *T. pitcheri* or *T. corrugata sensu stricto* from the Kiowa (e.g., Hill and Vaughan, 1898, pl. 12, pl. 18, figs. 1, 2; pl. 19; Twenhofel, 1924, pl. 23, fig. 1). Further study of texigryphaeas in other Kiowa exposures, and in Texas and Oklahoma, is required to judge whether the concept of *T. pitcheri* employed here adequately encompasses the numerous assemblages in those areas to which the name *T. pitcheri* or *T. corrugata* has been applied.

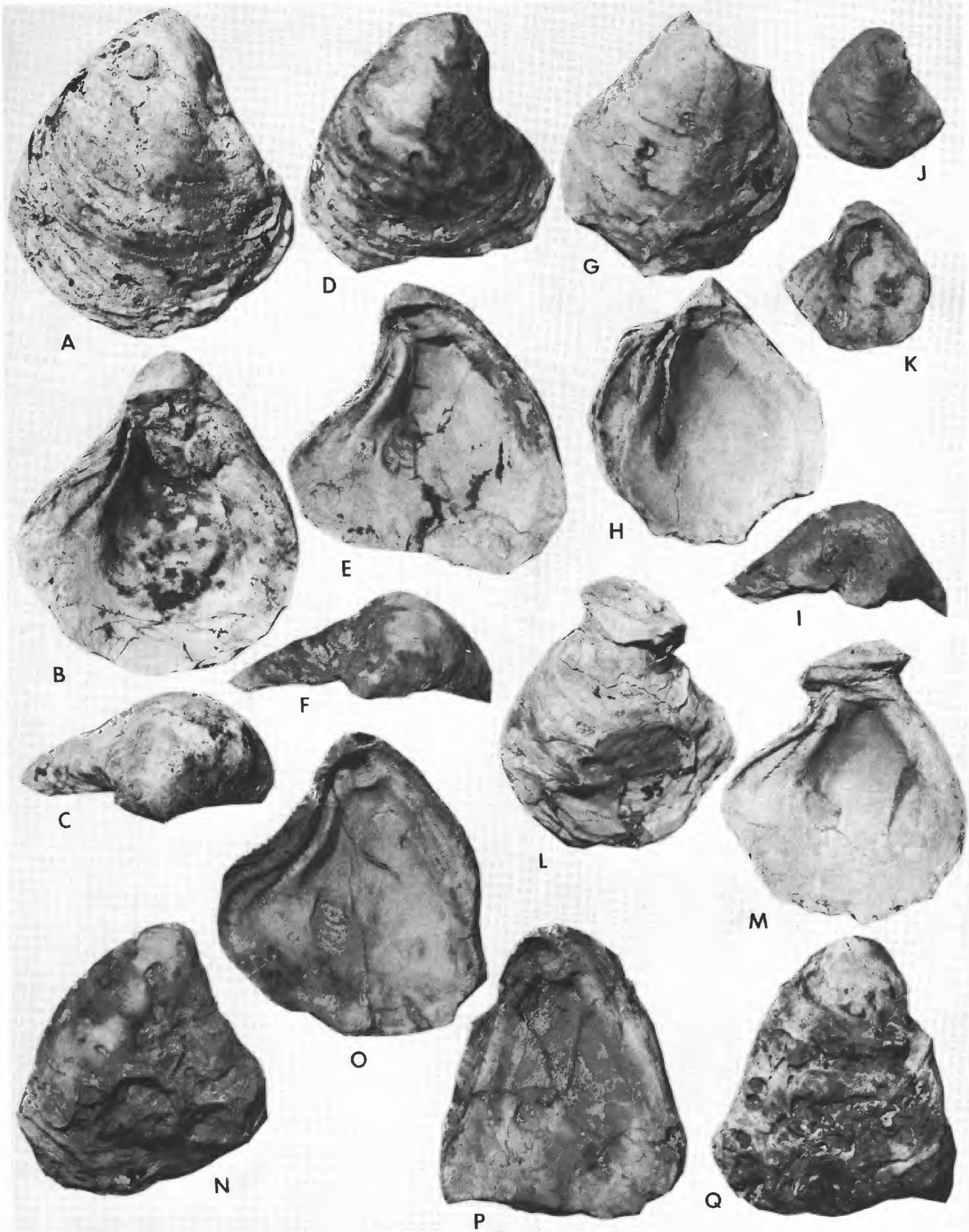
The subspecies *Texigryphaea corrugata belviderensis* was established by Hill and Vaughan (1898) for large specimens in the Kiowa having a more triangular outline and flatter form (Stanton, 1947) than typical representatives of *T. pitcheri*. Twenhofel (1924) reported that average specimens of *T. p. belvidernesis* were 75–85 mm high; one of the cotypes (Hill and Vaughan, 1898, pl. 10; Stanton, 1947, pl. 13) has a height of approximately 100 mm. Scott (1970b) included in this subspecies forms having a narrowly rounded keel that graded into both *T. pitcheri* and *T. navia,* but did not report the subspecies from Avilla Hill (Scott, 1970a). No specimens attaining even the average size of *T. p. belviderensis* are present in the Avilla Hill assemblage discussed here. However, smaller specimens having the relatively flat, triangular shape of this subspecies are present. The subspecies has never been adequately described, and the very general characterization of its shell shape seems well within the range of variation of *T. pitcheri* in the Kiowa Formation. Whether very large specimens at other localities are sufficiently distinct from *T. pitcheri sensu stricto* to warrant subspecific status remains to be seen.

Some specimens included here in *T. pitcheri* are nearly identical to the form referred to as *T.* aff. *T. pitcheri* in the Glencairn of the Two Buttes and Dry Cimarron areas (compare, for example, Fig. 3D, E and Fig. 5N, O). Within the Avilla Hill assemblage, specimens having the *T.* aff. *T. pitcheri* form intergrade so completely with "typical" specimens of *T. pitcheri* that separation was neither possible nor desirable. In general, the *T.* aff. *T. pitcheri* form possesses a somewhat deeper left valve and slightly less inclined umbo. Ninety-five percent of the specimens in the collection from the Avilla Hill locality belong to *T. pitcheri,* as that name is used here.

A few valves display similarity to other species of *Texigryphaea.* About 5% of the specimens are relatively massive, thick, elongate valves with a strongly inclined umbonal angle of inclination (Fig. 6A, B) that appear to be more closely related to *T. navia* than to *T. pitcheri.* Unlike typical examples of *T. navia,* however, these specimens lack the distinctive keel or carina along the valve midline, and are here considered *T.* aff. *T. navia*. Abundant typical specimens of *T. navia* occur lower in the Kiowa at this locality. Apparently, with time and/or

TABLE 3. Mean left valve proportions of texigryphaeas from the Kiowa Formation, Avilla Hill, Kansas. Abbreviations as in Table 2, plus AS, length of attachment scar.

	N	L/H	W/H	P/H	BL/H	AS/P	A
T. pitcheri	95	.87	.37	1.43	.09	.17	72°
T. aff. T. navia	4	.73	.36	1.53	.18	.12	64°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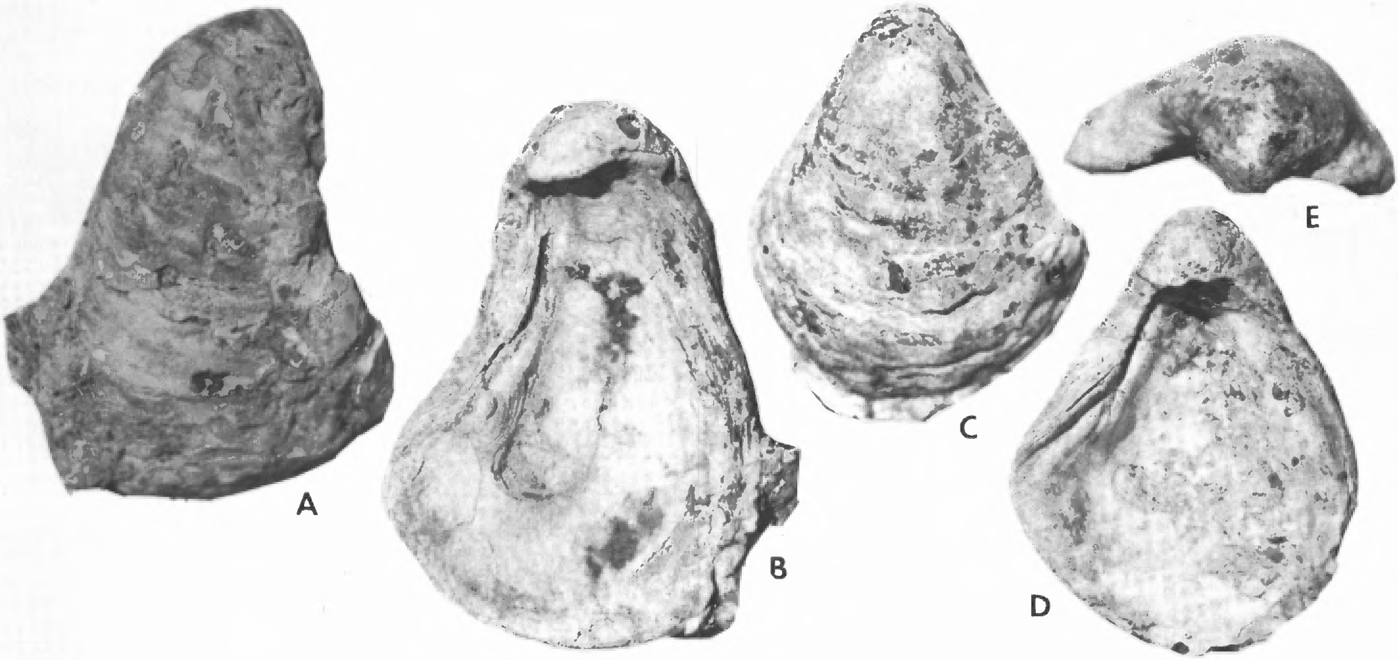

FIGURE 6. *Texigryphaea* from the upper Kiowa Formation at Avilla Hill, Comanche County, Kansas, all ×1. A, B, *T.* aff. *T. navia* (Hall), external and internal views of a left valve, UNM 9563. C–E, *T. pitcheri* (Morton), external, internal and umbonal views of a left valve showing convergence toward *T. tucumcarii* (Marcou), UNM 9564.

change in environment, the *T. navia* shell morphology became uncommon and converged toward that of *T. pitcheri* in some respects.

A second form (Fig. 6C–E) that diverges from the norm of *T. pitcheri* is characterized by rather oval, non-arcuate left valves superficially similar to the typical form of *T. tucumcarii* present in the Glencairn Formation. The umbonal angle of inclination is closer to perpendicular (mean angle = 79°) than is usual in the *T. pitcheri* specimens in this assemblage, and the posterior lobe is less extended and curved. These valves are, however, relatively shallow (L/H = 0.34; P/H = 1.52), as is the case with *T. pitcheri*. This form represents about 5% of the total valves and is completely gradational with typical examples of *T. pitcheri*. It represents moderate morphological convergence toward the shell form of *T. tucumcarii*, but its affinities with *T. pitcheri* are clear.

Environment

The thin limestone unit from which the Avilla Hill Kiowa texigryphaeas were collected is composed of a dense accumulation of shells in a matrix of light brown, silty, argillaceous limestone. *Texigryphaea* shells comprise the greatest part of the volume of this limestone; associated epizoan organisms were the only other fossils observed. Although small to medium-sized shell fragments are abundant, so too are complete, generally disarticulated valves of *Texigryphaea*. Similar beds occur elsewhere in the Kiowa, forming a shell conglomerate lithofacies containing mixed-transported and disturbed-neighborhood assemblages that may consist entirely of *Texigryphaea* (Scott, 1970b).

The high concentration of *Texigryphaea* shells suggests that this area of seafloor was densely covered with shells and shell fragments, probably in conditions of relatively high turbulence. Little fine-grained sediment was exposed or available for habitation by other benthonic organisms. If this view is correct, the texigryphaeas were preserved in or near the area where they lived—the coquinoid limestone representing a gradual buildup of their shells through a short period of time. An alternative hypothesis, that this shelly facies resulted from current or storm concentration of shells derived from other areas, is not favored. Many of the texigryphaea specimens are complete and unabraded, and about 10% have both valves articulated. Moreover, all sizes of shells are well represented in the assemblage. Epizoan colonization, which on many valves is extreme, is limited primarily to the external surfaces of both left and right valves, suggesting that many of the texigryphaeas were living when colonization occurred. All of these observations are more consistent with the idea that this assemblage represents a disturbed but essentially *in situ* buildup rather than a severely transported, storm or current-controlled deposit.

A substrate covered with a high density of living texigryphaeas together with the shells of dead individuals would be highly favorable to the proliferation of boring and cementing epizoans—a distinctive feature of this assemblage. In addition, such a substrate might account for the almost ubiquitous presence of medium-sized to large attachment scars on individual specimens (Table 2). According to Stenzel (1971), the spat of soft-sediment-dwelling texigryphaeas settled on whatever small shell fragments they could find but soon became free-living as they grew far larger than their attachment object. In an area of seafloor covered primarily by large shells or shell fragments, with little fine-grained sediment exposed, most of the attachment sites for larval texigryphaeas would be large. A free-living existence would be passively attained late in growth rather than early. Several mature left valves in this assemblage were preserved still attached to the 10-to-25-mm-wide shells on which they had begun their growth (Fig. 5L, M).

In a high-energy, hard-substrate environment, remaining cemented to the substrate for a longer time might also have been advantageous to a young texigryphaea. Becoming free-living too early would subject a small shell to damage as it was tossed across neighboring larger, more stable shells. In contrast, in a quiet, muddy environment, a small free-living texigryphaea would soon become partially embedded in the sub-

FIGURE 5. *Texigryphaea pitcheri* (Morton) from the upper Kiowa Formation at Avilla Hill, Comanche County, Kansas, all ×1. A–C, External, internal and umbonal views of a relatively non-arcuate left valve, UNM 9556. D–F, External, internal and umbonal views of a typical left valve, UNM 9557. G–I, External, internal and umbonal views of a left valve distorted by large attachment scar across umbo, UNM 9558. J, K, External and internal views of an immature left valve, UNM 9559. L, M, External and internal views of a left valve cemented to its initial attachment site, a right valve of a small texigryphaea, UNM 9560. N, O, External and internal views of a left valve, UNM 9561. P, Q, Internal and external views of an unusually flat left valve, UNM 9562.

strate and maintain an optimum orientation by the steps outlined by Stenzel (1971).

The generally low, shallow, arcuate shape of most of the Avilla Hill texigryphaeas probably also reflects life on a relatively firm substrate, in conditions of moderate to perhaps relatively high water agitation (Scott, 1970b; Kues and Lucas, 1987). A broad but shallow, flattened shell would be less likely to be moved or flipped over than a deeper, more convex shell, which would be highly unstable on a firm substrate in turbulent water. The wide variation in the shape of the left valves observed in this *Texigryphaea pitcheri* assemblage most likely resulted from a complex of factors related to the microhabitat in which each individual lived. Slight variations in water agitation and available substrate, together with variable but generally prolonged time of attachment and perhaps crowding of some individuals during their growth may all have influenced the final shapes of the mature valves.

DISCUSSION

The morphologic relationships between texigryphaeas of the Glencairn Formation in the Dry Cimarron (Kues and Lucas, 1987) and Two Buttes areas, and in the upper Kiowa Formation at Avilla Hill are suggested in Figure 7. Each taxon represents a fairly variable array of specimens characterized by specific and distinctive morphological features of the left valve. Overlap between the Glencairn and Kiowa assemblages occurs only in the presence in both assemblages of *Texigryphaea* aff. *T. pitcheri,* a form that is gradational with the broad form of *T. tucumcarii* in the Glencairn and with *T. pitcheri* in the upper Kiowa. *Texigryphaea tucumcarii* and *T.* cf. *T. washitaensis* are not present in this Kiowa assemblage. A form probably derived from *T. navia* is rare in the upper Kiowa; typical representatives of this species are abundant lower in the formation. *Texigryphaea navia* is not present in either the Glencairn or Tucumcari formations, but existed in east-central New Mexico and west-central Texas prior to the deposition of these formations (Brand, 1953; Kues, 1986).

The Two Buttes Glencairn *Texigryphaea* assemblage is in general similar to that of the Dry Cimarron, although it has fewer different forms and a smaller relative abundance of *T. tucumcarii*. It differs also in having a much greater proportion of the form called here *T.* aff. *T. pitcheri,* and a larger percentage of individuals having medium to large attachment scars. In these features this component of the Two Buttes assemblage resembles to a moderate degree the upper Kiowa Avilla Hill assemblage. Firm conclusions about the significance of these relationships must await study of other *Texigryphaea* assemblages in the Kiowa of south-central Kansas.

The results reported here indicate some questions about the paleobiology of *Texigryphaea* that deserve further investigation. For example, it is unclear to what degree shell morphology reflects ecophenotypic as opposed to genetic controls. In this and previous papers (e.g., Kues, 1986; Kues and Lucas, 1987) I have grouped shells of similar morphology into "forms" without being overly concerned about whether they fit comfortably into established species. It appears to me that some forms correspond fairly closely to species established by previous workers, whereas other, equally distinct forms represent ecological variants or transitional morphologies between two species. It also seems possible that similar forms may have arisen independently in different areas in response to the onset of similar environments. Separating ecological from genetic variations among contemporaneous assemblages, tracking evolutionary change in forms through time and identifying groups that probably represent biospecies will require (if it can be done at all) study of many more *Texigryphaea* assemblages through the entire geographic and stratigraphic range of the genus.

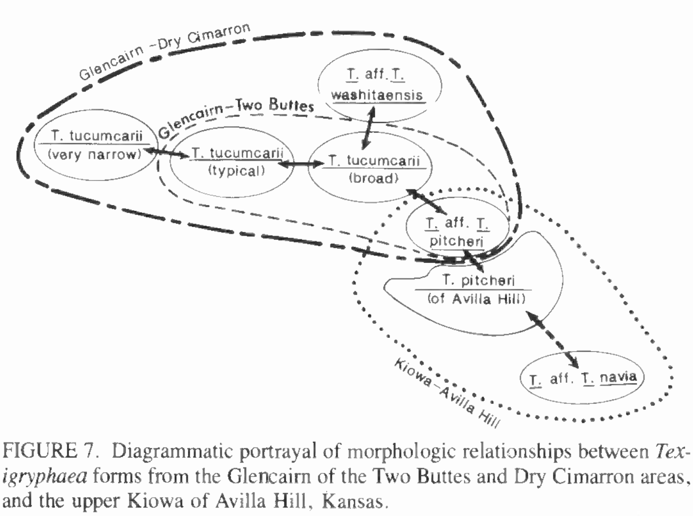

FIGURE 7. Diagrammatic portrayal of morphologic relationships between *Texigryphaea* forms from the Glencairn of the Two Buttes and Dry Cimarron areas, and the upper Kiowa of Avilla Hill, Kansas.

The assemblages discussed in this paper illustrate some of these complexities. For example, the similarities between the *T.* aff. *T. pitcheri* component of the Two Buttes fauna and *T. pitcheri* from the upper Kiowa of Avilla Hill could be interpreted strictly as ecological convergence—an ecophenotypic response to similar environmental conditions that were only marginally present within the habitat of *Texigryphaea* to the south, in the Dry Cimarron area. This seems unlikely, as the occurrence of *Texigryphaea* in the Glencairn of the Two Buttes and Dry Cimarron areas is more similar than either is to the coquinoid limestone assemblage at Avilla Hill. Alternatively, and perhaps more likely, the Two Buttes *Texigryphaea* assemblage could have been affected by a moderate influx of Kiowa elments that only rarely reached areas farther south. Migration of faunal elements westward across the southern Western Interior seaway was more significant than eastward migration (Scott, 1986). If partial barriers (e.g., islands, peninsulas, shoals) existed in southeastern Colorado and southwestern Kansas, as Long (1966) suggested, influx of Kiowa elements westward may have left their imprint on the Two Buttes *Texigryphaea* fauna without being able to migrate significantly southward past the barrier into the Dry Cimarron Glencairn. Larval dispersal patterns, controlled by currents, would have been important in this regard.

Another way of explaining the observed relationships between the texigryphaeas at Avilla Hill and the Two Buttes and Dry Cimarron areas is to suppose that *Texigryphaea* populations extended more or less continuously across the seaway from south-central Kansas to the Two Buttes area, and from there south along the western shoreline to the Dry Cimarron and Tucumcari areas. The northward extent of *Texigryphaea* (along an east-west line from south-central Kansas to the Two Buttes area) was apparently mainly controlled by a decrease in the salinity of the seaway at that latitude (Kues et al., 1987). The change from the arcuate-shallow-inclined umbo morphology of *T. pitcheri* to the east to the mixed *T.* aff. *T. pitcheri*-*T. tucumcarii* forms at Two Buttes, to the *T. tucumcarii*-dominated assemblages of the Dry Cimarron and Tucumcari areas could be interpreted as clinal variation. The absence of Albian exposures between south-central Kansas and the Two Buttes area of southeastern Colorado makes this idea difficult to test.

The distribution of the various forms of *Texigryphaea* discussed in this paper suggests the following tentative hypothesis. *Texigryphaea pitcheri* and *T. tucumcarii* probably normally represented genetically isolated populations on the eastern and western sides of the Albian seaway, respectively. Adjustments during growth to local ecological conditions superimposed a considerable ecophenotypic imprint on the genetically determined morphologies of each population, in some cases producing a limited degree of convergence between the two species. In areas such as Two Buttes, larval influx from the east and/or other factors resulted in a significant mixing of the two species and interbreeding between them, producing forms with shell features intermediate between the typical morphologies of the two species. The absence of *T. tucumcarii* in Kiowa faunas, and the very low proportion of *T. pitcheri*-like individuals in the Dry Cimarron Glencairn and Tucumcari faunas, suggest that areas of overlap and genetic interchange between significant numbers of both species were restricted and had little effect on the morphology of either species throughout most of their geographic ranges.

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Trinidad Sandstone above Pierre Shale at Raton, Colfax County, New Mexico. Photograph by W. T. Lee circa 1900–1910, courtesy of the U.S. Geological Survey and R. Eveleth, NMBMMR.