1990 Society of Vertebrate Paleontology

Niobrara Chalk Excursion Guidebook

Commemorating the 50th anniversary
of the Society of Vertebrate Paleontology
and 100 years of vertebrate paleontology
at the University of Kansas

Edited by S. Christopher Bennett

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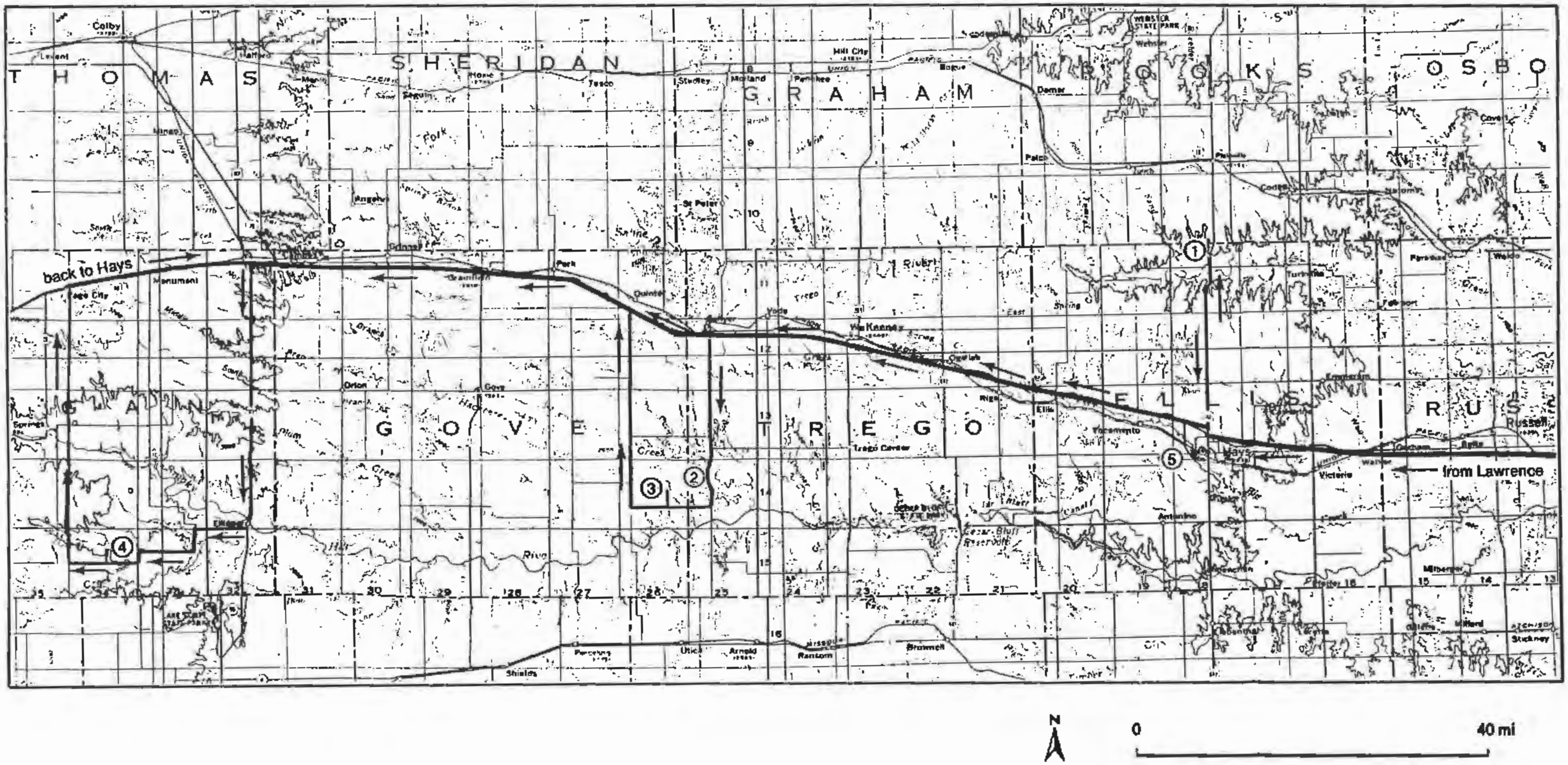

Map showing route of field trip.

Road log from Lawrence to the type area of the Niobrara Chalk October 9–10, 1990

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The Niobrara Chalk of western Kansas is known worldwide for the large numbers of excellently preserved fossil vertebrates.

The Niobrara Chalk crops out in a large area of western Kansas in a band running from northeast to southwest. It is divided into two members: the Fort Hays Limestone Member is the lower member, and the Smoky Hill Chalk Member the upper. The limestones and chalks of the Niobrara Chalk were deposited in moderately deep water with a very flat bottom. This resulted in largely undisturbed sedimentation over large areas. The possibility of correlating fine-scale lithostratigraphic features, as thin as 1 or 2 mm, over distances on the order of 150 km (90 mi) may be in marked contrast to the experiences of paleontologists working in other areas.

The Fort Hays Limestone Member ranges from 17 to 30 m (56–99 ft) thick in Kansas. Invertebrate fossils are common, but not diverse. Vertebrate fossils are quite rare. Frey (1972), however, suspected that teleost scales occur throughout the member. Vertebrate fossils most commonly occur near the base. These appear to be reworked from the underlying Codell Sandstone. However, *Ptychodus mortoni* was collected from the lower part of unit 16 of the measured section provided here. Scouring is more frequently observed in the Fort Hays Limestone Member than in the Smoky Hill Chalk Member. The age of the Fort Hays Limestone Member is lower Coniacian. The Fort Hays Limestone Member is a frequently used building stone in areas where it crops out, but it is rarely used for fence posts.

The Smoky Hill Chalk Member is considerably thicker than the Fort Hays Limestone Member. The composite stratigraphic section of the Smoky Hill as reported by Hattin (1982) is 180 m (594 ft). Invertebrate fossils are common and in many horizons are extremely numerous. Vertebrate fossils also are common. The age of the Smoky Hill Chalk Member is upper Coniacian through lower Campanian. The Sharon Springs Member of the Pierre Shale lies conformably on top of the Smoky Hill Chalk Member in western Kansas.

This road log will describe selected localities in order to examine the Niobrara Chalk in stratigraphic order. However, before concentrating on the Niobrara, the Cretaceous stratigraphy and fossil vertebrate record of western Kansas should be briefly reviewed in chronological order.

Kiowa Formation—The Kiowa Formation consists of dark-gray shales, tan mudstones, and sandstones deposited during the Kiowa–Skull Creek Cyclothem. The primary source work is that of Scott (1970). Fossil vertebrates include *Scapanorhynchus* sp., *Lamna* sp., *Scylorhinus* sp, *Leptostyrax macrorhiza* (Schultze et al., 1982), *Hybodus* sp., *Coelodus* sp., *Ceratodus frazeri* (Schultze, 1981), *Xiphactinus*? sp., chelonian, *Brachauchenius* sp., *Cimoliasaurus* sp., *Trinacromerum* sp., *Plesiosaurus*? sp., *Dakotasuchus kingi*, and dinosaur fragments.

Dakota Formation—The Dakota Formation consists of quartzose sandstones, siltstones, mudstones, and shales deposited as nonmarine and marginal marine sediments in the early part of the Greenhorn Cyclothem. Vertebrate fossils include *Dakotasuchus kingi* (Mehl, 1941), *Sylvisaurus condrayi* (Eaton, 1960), and a bird trackway (Snow, 1887).

Graneros Shale—The Graneros Shale consists of shales, sandstones, and skeletal limestones deposited as marine sediments in the early part of the Greenhorn Cyclothem. Hattin (1965) has published the most extensive account of this formation. Vertebrate fossils include *Ptychodus occidentalis* (Schultze et al., 1982).

Greenhorn Limestone—The Greenhorn Limestone consists of dark shaly chalks and chalky limestones deposited during the maximum transgression of the Greenhorn Cyclothem. The most extensive account of this formation is that of Hattin (1975a). Vertebrate fossils include *Protosphyraena bentoniana* and *Pachyrhizodus minimus* (Schultze et al., 1982).

Carlile Shale—The Carlile Shale consists of shales, shaly chalks, and chalky limestones deposited during the regressive phase of the Greenhorn Cyclothem. The most complete reference on the geology and paleontology is that of Hattin (1962). Vertebrate fossils include *Cretolamna appendiculata*, *Leptostyrax crassidens*, *Cretoxyrhina mantelli*, *Squalicorax falcatus*, *Coelodus streckeri* (Schultze et al., 1982), *Xiphactinus audax* (Schultze et al., 1982), *Ptychodus whipplei*, *Enchodus* sp., plethodid, "elopid" (Miller, 1958), *Desmatochelys lowi*, and a mosasaurid.

Niobrara Chalk—The Niobrara consists of chalky limestones and chalks deposited at the maximum transgression of the Niobrara Cyclothem.

Pierre Shale—The Pierre Shale consists of dark-gray shales deposited during the regressive phase of the Niobrara Cyclothem. The Sharon Springs Shale Member lies conformably on top of the Niobrara and is quite fossiliferous. Vertebrate fossils include *Protosphyraena gladius* (holotype of *P. gigas*), *Cimolichthys nepaholica* (holotype of *Empo lisbonensis*), *Toxochelys latiremis*, mosasaurs, and plesiosaurs.

Road log

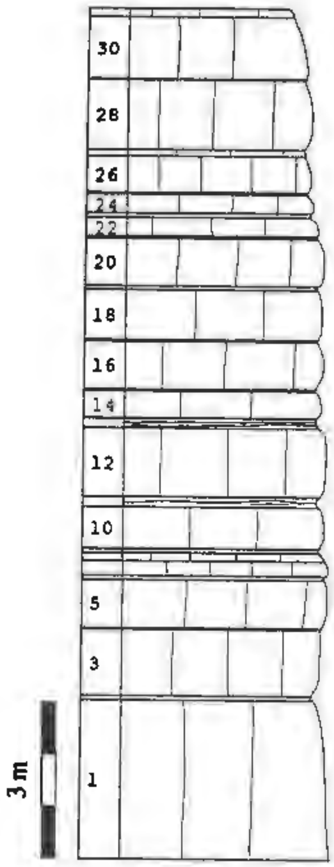
We leave Lawrence and drive 232 mi (371 km) west on I–70 to Hays. We take exit 159 and follow US–183 north 15 mi (24 km) to the roadcut just north of the Saline River.

STOP 1—Fort Hays Limestone Member.

The Carlile–Niobrara contact is the greatest hiatus in Upper Cretaceous sediments in the Great Plains. The Fort Hays Limestone Member of the Niobrara Chalk represents the initiation of the transgressive phase of the Niobrara cyclothem. Hattin (1975b) documented the fact that the Carlile–Niobrara contact is diachronous, and that the base of the Niobrara Chalk becomes increasingly younger as one progresses from the southwest to the northeast. The thickness of the Fort Hays Limestone Member at this exposure is considerably less than it is at sites in southern Trego County (see Frey, 1972; Hattin, 1982). The upper half of the Fort Hays Limestone Member exposures here are easily correlated through lithostratigraphy with units 28 through 51 of Frey (1972) and units 21 through 42 of Locality 1 of Hattin (1982). These same beds are nearly as thick at this locality as their counterparts in Trego County. The lower half of the Fort Hays Limestone Member at this locality is not easily correlated with any units in the Trego County sections. Furthermore, the remaining portion of the Trego County exposures is much thicker than the lower half of the exposure at stop 1. Therefore, our observations are in agreement with the conclusions of Hattin (1975b).

Invertebrates at this locality include *Pseudoperna congesta* and *Cremnoceramus browni*. If *Inoceramus deformis* and *Pycnodonte aucella* occur at this exposure, they would probably occur only in units 1 to 3. The diverse ichnofossils in the Fort Hays Limestone Member are described in Frey (1970).

Locality 1—East side of the roadcut on US–183 north of the Saline River in NE 1/4 sec. 3, T. 11 S., R. 18 W., Ellis County, Kansas. This is a nearly complete section from the Carlile–Niobrara contact to the base of the Smoky Hill Chalk Member. Unfortunately, the Fort Hays Limestone–Smoky Hill Chalk contact is not clearly delineated at this exposure. Fauna: *Pseudoperna congesta, Cremnoceramus browni, Ptychodus mortoni*, and *Gillicus arcuatus*.



Unit	Description	Thickness (cm)
31	A 10-mm blocky limestone above a 6-mm bentonite	17
30	Chalky limestone. Fossils: *Gillicus arcuatus*	119
29	Bentonite	2.5
28	Blocky limestone, upper 45 cm are softer	134
27	Cream- to buff-colored chalk forming reentrant	10
26	Blocky limestone	67
25	Gray shale forming reentrant, possibly a bentonite	4
24	Blocky limestone	35
23	Shale forming reentrant, with a 3-cm harder layer in the middle	8
22	Blocky limestone	34
21	Shale forming reentrant	2
20	Blocky limestone with a softer zone 16 cm above base	90
19	Shale forming reentrant	6
18	Blocky limestone	95
17	Bentonite	2
16	Blocky limestone with a heavily burrowed zone 39 cm above base. Fossils: *Ptychodus mortoni* found within first 39 cm	91
15	Shale forming reentrant	2.5
14	Blocky limestone	53
13	Shaly bioturbated chalk	19
12	Blocky limestone with a softer zone 78 cm above base	132
11	Shaly reentrant with a 5-cm harder layer 9 cm above the base. Fossils: burrows in harder zone	19
10	Limestone; upper 27 cm spalling and fragmented	81
9	Gray shaly parting	6
8	Chalk with a thin shaly parting at the base	16
7	Chalk	27
6	Gray shaly parting	8
5	Limestone. Fossils: burrows	92
4	Bentonite	4
3	Limestone. Fossils: *Cremnoceramus browni*, burrows	130
2	Shaly parting with a 7-mm bentonite	9
1	Limestone with a softer zone 1.88 m above base	305
	Total thickness of measured section	16.20 m

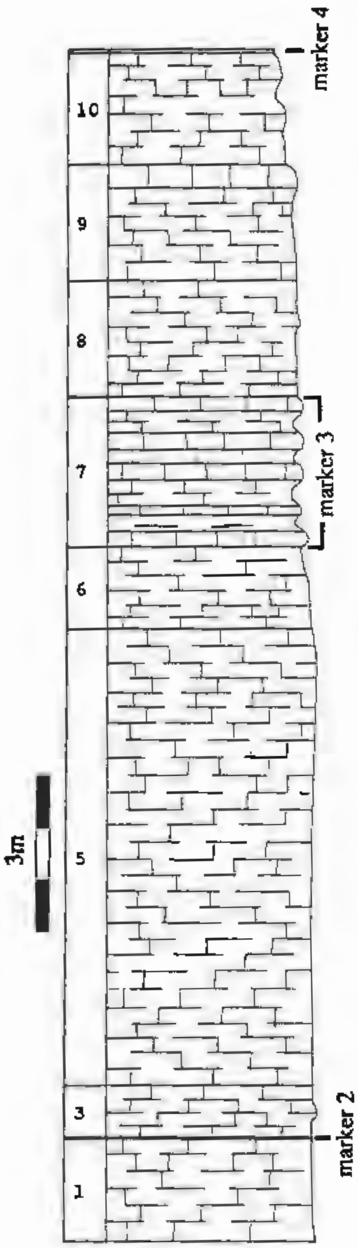
FIGURE 1—Measured section of Fort Hays Limestone Member at locality 1.

We go south on US–183 and return to I–70, then travel west 44 mi (70 km) to Collyer. We take exit 115 and turn south onto FAS–275. 10.5 mi (16.8 km) south of I–70, we cross Hackberry Creek, and 2.5 mi (4 km) further we stop on the west side of Wildcat Canyon.

STOP 2—Wildcat Canyon.

This locality was collected by personnel from the University of Kansas during the late 19th and early 20th centuries. It is also known as "Cat Hills" and "1 1/2 mi s. of Banner." The holotypes of *Martinichthys intermedius* and *M. alternatus* come from this locality (McClung, 1926). The sediments of this exposure are of the upper Coniacian age and include two biostratigraphic zones: the zones of *Protosphyraena pernicosa* and *Spinaptychus* n. sp.

Locality 2—Wildcat Canyon. Badlands on the south or west side of Hackberry Creek in SW 1/4 sec. 16, T. 14 S., R. 24 W., Trego County, Kansas. The exposure ranges from 2 m (6.6 ft) below Marker Unit 2 up to Marker Unit 4. Modified with some additions from the description of Locality 17 of Hattin (1982). Fauna: *Volviceramus grandis, Pseudoperna congesta, Durania maxima, Spinaptychus* n. sp., *Tusoteuthis longa, Zeugmatolepas* sp., *Ptychodus anonymous, Squalicorax falcatus, Cretoxyrhina mantelli, Paraliodesmus quadagnii, Protosphyraena nitida, P. pernicosa, P. tenuis* (documented in Stewart, 1988), *Pachyrhizodus minimus, Martinichthys intermedius, M. alternatus, M. ziphoides, Cimolichthys nepaholica,* and *Enchodus petrosus*.



Unit	Description	Thickness (cm)
12	Chalk. Hard, bioturbated and forms conspicuous ledge. With unit 11 below, it makes up Marker Unit 4. Fossils: *Platyceramus platinus, Pseudoperna congesta*	9.1
11	Bentonite	0.3
10	Chalk. Alternating harder and softer zones may erode to form ledges. Fossils: *Volviceramus grandis, Pseudoperna congesta, Enchodus petrosus*	216.5
9	Chalk. More resistant zones may produce ledges. Fossils: *Volviceramus grandis, Pseudoperna congesta*	222.6
8	Chalk. More resistant zones may produce ledges. We detected a 5-mm bentonite approximately 1.38 m above the base. Fossils: *Volviceramus grandis, Pseudoperna congesta*	228.7
7	Chalk and chalky limestone, yellow to orange. Alternating hard and soft zones erode to produce five subequally spaced ledges. This is Marker Unit 3. Fossils: *Volviceramus grandis, Pseudoperna congesta, Platyceramus platinus, Durania maxima, Zeugmatolepas* sp., *Xiphactinus audax, Ptychodus* sp.	289.6
6	Chalk, gray. Fossils: *Volviceramus grandis, Pseudoperna congesta, Platyceramus platinus, Stramentum haworthi, Durania maxima, Zeugmatolepas* sp., *Xiphactinus audax, Ptychodus* sp.	161.7
5	Chalk. A 60-cm-thick zone with numerous inoceramid fragments lies 6.08 m above base. Fossils: *Volviceramus grandis, Pseudoperna congesta, Platyceramus platinus, Protosphyraena pernicosa*	888.7
4	Bentonite	0.3
3	Chalk. Fossils: *Volviceramus grandis, Pseudoperna congesta, Platyceramus platinus*	100.8
2	Bentonite. Expanded by iron oxide and gypsum up to 4.9 cm. This is Marker Unit 2	2.5
1	Chalk. Fossils: *Volviceramus grandis, Pseudoperna congesta, Platyceramus platinus*	198.3
	Total thickness of measured section	23.19 m

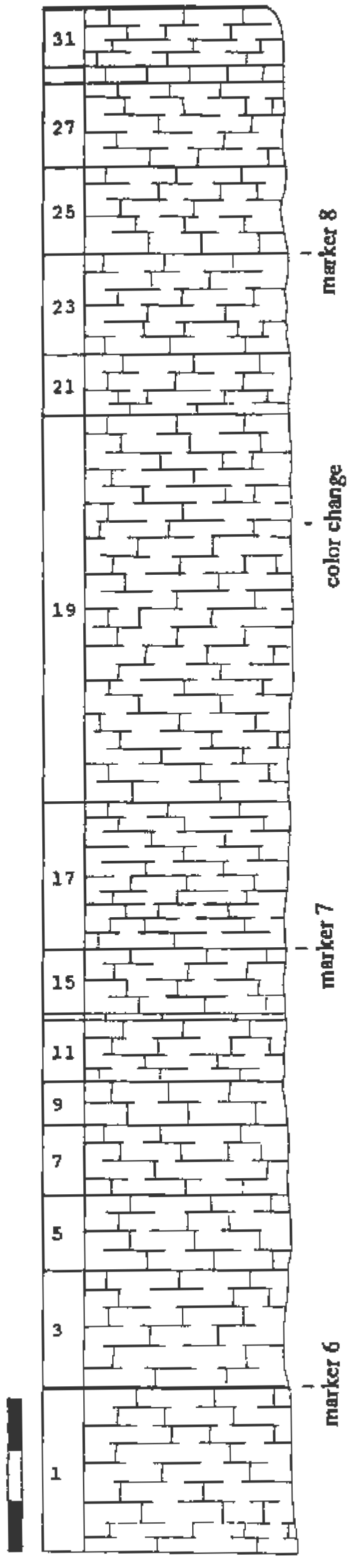
FIGURE 2—Measured section at Wildcat Canyon, locality 2.

We backtrack north 0.5 mi (0.8 km), turn west and travel 2.8 mi (4.5 km), and then travel north 1 mi (1.6 km) to the Castle Rock area. In order to see the exposures in stratigraphic order, we first stay to the left and go north of Castle Rock itself. After examining the northern outcrop area, go south past Castle Rock and continue south along the eastern edge of the bluffs.

STOP 3—Castle Rock.

Castle Rock was a well-known landmark on the Butterfield Overland Dispatch. It also has been the focus of studies on the weathering rate of the Smoky Hill Chalk Member (Williston, 1897; Smith, 1948). Exposures immediately to the north and south provide an overlapping section from the zone of *Cladoceramus undulatoplicatus* to above Marker Unit 12 (see localities 19 and 18, respectively, in Hattin, 1982). The zone of *Cladoceramus undulatoplicatus* is of lower Santonian age. The upper part of the section, particularly that above unit 19 of Locality 4, is of upper Santonian age. The correlation we offer of the lower strata north of Castle Rock with the higher strata south of Castle Rock differs somewhat from the treatment of Hattin (1982). Our measurements of the strata of this locality differ from those of Hattin (1982) above unit 21. Unit 24 at Locality 3 corresponds to unit 5 of Locality 4 (Locality 18 of Hattin, 1982) and is Marker Unit 8. The uppermost bentonite at Locality 3 (unit 32) is the lower bentonite of Marker Unit 9. The massive caprock that forms the top of Castle Rock and other pinnacles in this area is Marker Unit 10 of Hattin (1982). It performs the same function at some other well-known Smoky Hill Chalk Member exposures such as Monument Rocks in western Gove County and Castle City in eastern Logan County.

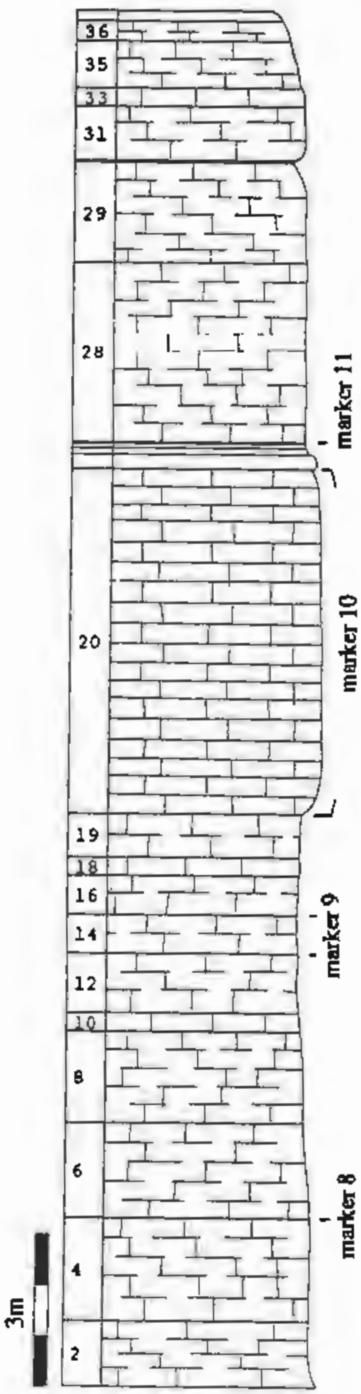
Locality 3—Exposures on the south or west side of Hackberry Creek and north of Castle Rock in NE 1/4 sec. 2, T. 14 S., R. 26 W., Gove County, Kansas. The exposure ranges from 3 m (10 ft) below Marker Unit 6 up to Marker Unit 9. Modified with some additions from the description of Locality 19 of Hattin (1982). Fauna: *Durania maxima*, *Cladoceramus undulatoplicatus*, *Platyceramus platinus*, *Pseudoperna congesta*, *Baculites* sp., *Tusoteuthis longa*, *Clioscaphites* sp., *Zeugmatolepas* sp., *Ptychodus mortoni* (described in Stewart, 1980), *Squalicorax* sp., *Cretoxyrhina mantelli*, *Protosphyraena tenuis* (Stewart, 1988), *Ichthyodectes ctenodon*, *Pachyrhizodus minimus*, holocentrid alpha, *Caproberyx* sp., *Toxochelys latiremus*, *Pteranodon* sp., *Nyctosaurus* sp., *Ichthyornis* sp.



Unit	Description	Thickness (cm)
33	Chalk. With unit 32 below, forms part of Marker Unit 9	5
32	Bentonite	1
31	Chalk	110
30	Ferruginous seam	0.1
29	Chalk	33
28	Ferruginous seam	0.1
27	Chalk	165
26	Bentonite	0.7
25	Chalk	168
24	Bentonite, waxy	1
23	Chalk. Fossils: *Squalicorax falcatus*, holocentrid alpha	196
22	Bentonite, rather indurate where weathered	0.5
21	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*, *Squalicorax falcatus*, holocentrid alpha	117
20	Bentonite	0.3
19	Chalk. Flaky where weathered. The color change from predominately gray to a lighter color takes place in this unit approximately 1.5 to 3 m below the top. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*, *Toxochelys latiremus*	750
18	Bentonite	0.6
17	Chalk. Flaky where weathered. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*, *Durania maxima*, *Tusoteuthis longa*, *Cretoxyrhina mantelli*	286.5
16	Bentonite, greenish-gray. This is Marker Unit 7	1.5
15	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	125.5
14	Bentonite	0.3
13	Chalk, rather soft	12.5
12	Bentonite	0.6
11	Chalk. Fossils: *Platyceramus platinus*, *Cladoceramus undulatoplicatus*, *Pseudoperna congesta*	120.5
10	Bentonite	0.9
9	Chalk. Fossils: *Cladoceramus undulatoplicatus*, *Pseudoperna congesta*	83.7
8	Ferruginous seam	0.1
7	Chalk. Fossils: *Pseudoperna congesta*	134.2
6	Bentonite	0.6
5	Chalk. Fossils: *Platyceramus platinus*	149.5
4	Bentonite	0.6
3	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	228.6
2	Bentonite. This is Marker Unit 6	2.5
1	Chalk. Fossils: *Cladoceramus undulatoplicatus*, *Pseudoperna congesta*	330.8
	Total thickness of measured section	30.27 m

FIGURE 3—Measured section at locality 3 north of Castle Rock.

Locality 4—Exposures south of Castle Rock in SW 1/4 sec. 1 and NW 1/4 sec. 12, T. 14 S., R. 26 W., Gove County, Kansas. The exposure ranges from 1 m (3.3 ft) below Marker Unit 8 up to 3 m (10 ft) above Marker Unit 12. Modified with some additions from the description of Locality 18 of Hattin (1982). Fauna: *Platyceramus platinus*, *Pseudoperna congesta*, *Baculites* sp., *Zeugmatolepas* sp., *Enchodus shumardi*, holocentrid alpha, *Caproberyx* sp., *Kansius sternbergi* (the syntypic series was collected at this locality [Hussakof, 1929], and so were all other inoceramid commensal fishes collected by G. Sternberg).



Unit	Description	Thickness (cm)
38	Chalk	21.4
37	Bentonite	0.3
36	Chalk	39.6
35	Chalk. Fossils: *Pseudoperna congesta*	91.4
34	Bentonite	0.2
33	Chalk, forms rounded ledge. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	35
32	Bentonite	0.3
31	Chalk, resistant. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	102.3
30	Bentonite	2.1
29	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	195.2
28	Chalk. Upper 27.5 cm darker, organic rich. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	347.6
27	Bentonite	4.6
26	Chalk. Fossils: *Pseudoperna congesta*	9.2
25	Bentonite	0.9
24	Chalk. Fossils: *Pseudoperna congesta*	10.7
23	Bentonite	0.9
22	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	29
21	Bentonite	0.6
20	Chalk, very resistant, bioturbated. Forms a caprock on outcrops. This is Marker Unit 10. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*, *Baculites* sp., *Stramentum haworthi*, *Zeugmatolepas* sp.	669.2
19	Chalk with five subequally spaced bentonites. Fossils: *Platyceramus platinus*, *Inoceramus balticus*, *Pseudoperna congesta*, *Baculites* sp., *Clioscaphites choteauensis*	82.3
18	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	35.1
17	Bentonite	0.2
16	Chalk. Fossils: *Platyceramus platinus*, *Inoceramus balticus*, *Pseudoperna congesta*, *Baculites* sp., *Clioscaphites choteauensis*	76.2
15	Bentonite. With units 13 and 14 below forms Marker Unit 9	1.8
14	Chalk. A lighter bioturbated zone 9.2 cm thick is in the middle. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*, *Zeugmatolepas* sp., holocentrid alpha	77.7
13	Bentonite	0.7
12	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	117.5
11	Bentonite	1.2
10	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	36.6
9	Bentonite	0.3
8	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	177
7	Bentonite	0.9
6	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	186.1
5	Bentonite. This is Marker Unit 8	1.2
4	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	201.2
3	Bentonite	0.3
2	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	128.2
1	Bentonite	1.2
	Total thickness of measured section	26.86 m

FIGURE 4—Measured section at locality 4 south of Castle Rock.

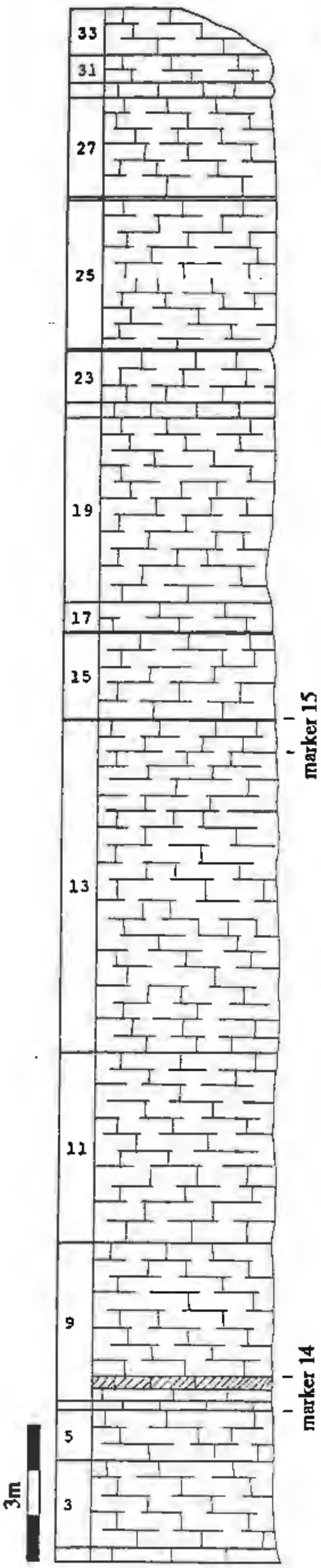
Leaving Locality 4, we follow the road up to the top of the bluffs and go 0.5 mi (0.8 km) south, turn west and drive 4 mi (6.4 km) west, then turn north and follow FAS–278 and 272 15 mi (24 km) to Quinter and I–70. We take I–70 33 mi (53 km) west to Oakley where we spend the night. If we were not pressed for time, we would visit the Fick Fossil Museum in Oakley that has interesting displays of Niobrara fossils, artwork made from fossils, and historical items.

We leave Oakley and take US–83 south. Beginning about 16 mi (25.6 km) south of Oakley, small outcrops of yellow chalk can be seen on either side of the highway. The light-gray rock cropping out further north is the Tertiary Ogallala Sandstone. Six miles (9.6 km) further (22 mi [35 km] south of Oakley), a bridge crosses the Smoky Hill River. The small number of abandoned buildings in the grove of trees just south of the river is Elkader. Five miles (8 km) east of Elkader are Monument Rocks which we will not visit for lack of time. One-half mile (0.8 km) south of Elkader we turn west onto County 474. We travel 4.6 mi (7.4 km) west, 2 mi (3.2 km) south, and then turn left. Here the road passes between the Little Pyramids. Like Castle Rock to the east, the Little Pyramids have the caprock (Marker Unit 10) at the top. We continue 5 mi (8 km) west, 1 mi (1.6 km) south, and 3.8 mi (6.1 km) west. We stop just south of a large bluff on the south side of Twin Butte Creek.

STOP 4—Twin Butte Creek.

This locality and others like it along the south side of Twin Butte Creek (or just Butte Creek) were extensively collected in the 1870's by field parties led by B. F. Mudge and S. W. Williston for the Yale Peabody Museum, and by E. D. Cope and C. H. Sternberg (collections now in the American Museum). It is representative of the upper half of the Smoky Hill Chalk Member. The upper half of the Smoky Hill Chalk Member is rather uninteresting as regards macroinvertebrate and vertebrate biostratigraphy; it is all within the zones of *Platyceramus platinus* and *Protosphyraena gladius* and *P. tenuis*. However, it has produced large numbers of vertebrates.

Locality 5—Bluff and exposures on the south side of Twin Butte Creek in W 1/2, sec. 16, T. 15 S., R. 34 W., Logan County, Kansas. The exposure ranges from Marker Unit 14 up to just below Marker Unit 16. Modified with some additions from the description of Locality 18 of Hattin (1982). A prominent fault runs roughly east to west along the line between the NW 1/4 and SW 1/4. Fauna (from this locality or adjacent ones along Twin Butte Creek): *Platyceramus platinus, Inoceramus (Endocostea) balticus, Pseudoperna congesta, Baculites* sp., *Xiphactinus audax, Clidastes, Platecarpus, Tylosaurus, Toxochelys, Ctenochelys stenopora, Protostega*, pelomedusid, *Pteranodon, Nyctosaurus, Hesperornis, Ichthyornis.*



Unit	Description	Thickness (cm)
39	Weathered chalk to top of outcrop	~
38	Seam	1
37	Chalk	61
36	Bentonite	1.5
35	Chalk	30.5
34	Bentonite	1
33	Chalk	213
32	Selenite seam	8
31	Chalk	327
24	Bentonite, very pale orange clay, greatly expanded by iron oxide and gypsum. The latter crops out as selenite ledges	3.7
23	Chalk, grayish-yellow	111.4
22	Gypsiferous seam	0.6
21	Chalk	32.1
20	Bentonite	0.6
19	Chalk	400.0
18	Ferruginous/gypsiferous seam	0.6
17	Chalk	64.4
16	Bentonite	2.9
15	Chalk, the bottom 30 cm is paler and the 31 cm above that is poorly laminated and resistant	183
14	Bentonite	2.5
13	Chalk, gray, with numerous pyritized inoceramids and limonitic inclusions. Upper 52 cm is well laminated, and a 3-cm bed of light granular chalk lies just below it. Forms smooth slope. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	722.5
12	Bentonite	0.6
11	Chalk. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*	414.5
10	Bentonite	1.2
9	Chalk. Darker, organic rich zone 27.4 cm thick is 30.5 cm above base; it and units 6–8 are Marker Unit 14. Fossils: *Platyceramus platinus*, *Pseudoperna congesta*, *Baculites* sp.	347.5
8	Bentonite	0.6
7	Chalk. Fossils: *Pseudoperna congesta*	21.3
6	Bentonite	0.6
5	Chalk. Fossils: *Inoceramus balticus*, *Platyceramus platinus*, *Pseudoperna congesta*	109.0
4	Bentonite	0.9
3	Chalk. Fossils: *Inoceramus balticus*, *Pseudoperna congesta*, *Baculites* sp.	192.2
2	Bentonite	0.6
1	Chalk	33.5
	Total thickness of measured section	33.9 m

FIGURE 5—Measured section at locality 5 along Twin Butte Creek.

Leaving Locality 5 we drive 3.2 mi (5.1 km) west, turn north and continue 10.5 mi (16.8 km) to the Smoky Hill River and 1 more mile (1.6 km) to Russell Springs. The exposures along the Smoky Hill River to the east and west of Russell Springs are those which were collected by O. C. Marsh and his field parties in 1870 through 1872. These exposures are somewhat higher in the Smoky Hill Chalk than those at Locality 5, but are smaller in area and vertical extent.

We go west through the middle of Russell Springs and then turn north onto K–25. We drive 12 mi (19 km) north, and then take US–40 east 20 mi (32 km) to I–70. We continue 81 mi (129.6 km) east to Hays. We take exit 157 south and follow signs to Sternberg Museum on the campus of Fort Hays State University.

STOP 5—Sternberg Memorial Museum.

The Sternberg Memorial Museum has one of the very best collections of Smoky Hill Chalk fossils. The collection contains the finest specimens collected by G. F. Sternberg and other through many years of work in the Smoky Hill Chalk Member. The exhibits include a complete specimen of *Platyceramus platinus* measuring 90 x 86 cm, skeletons of *Cretoxyrhina mantelli, Xiphactinus audax* (containing a whole *Gillicus arcuatus* skeleton), *Ectenosaurus clidastoides*, and *Trinacromerum*, type skulls of *Pteranodon sternbergi* and *P. walkeri*, and the holotype skeleton of *Nyctosaurus bonneri*. In addition, there are exhibits about regional history and the Sternberg family.

Calcareous nannofossils from the Niobrara of western Kansas

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Abstract

The calcareous nannofossils are the fossil representatives of the dominant phytoplankton in the Niobrara Sea. Their incalculable abundance in the Niobrara Chalk attests to their role as the base of the food chain which supported the more famous vertebrates of the Niobrara. The fossils from this group of rapidly evolving, environmentally sensitive algae provide a relatively high-resolution biostratigraphy that can be globally-correlated as well as a wealth of paleoecological information on the state of the surface waters during Niobrara deposition.

The nannofossil biostratigraphy we have developed recognizes at least 15 distinct zones and subzones in the Niobrara (Coniacian–Lower Campanian) with an average duration of <700 ky. The addition of intra-basinal biohorizons increases this resolution significantly.

Various aspects of the Niobrara nannofossil assemblages indicate that the surface waters of the Niobrara Sea were similar to, but distinctly different from, "normal" oceanic surface waters of the Upper Cretaceous. The presence of significant braarudosphaerids, "bloom" events of *Marthasterities furcatus*, sporadic occurrences of the calyptrosphaeraceans, and unusually low abundances of arkhangelskiellids indicate surface-water instability with the strong suggestion of some small degree of hyposalinity. Higher abundances of the zeugrhabdotids in the Smoky Hill Chalk Member indicate higher surface-water fertility than in the Fort Hays Limestone Member and correlative oceanic chalks. The presence of several taxa indicate a stronger boreal tie during the later (Campanian) part of Niobrara deposition.

Introduction

The calcareous nannofossils are a group of low-magnesium calcite fossils varying in size from approximately 1 to 20 mm. The majority of these objects contain the diagnostic skeletal features (i.e. proximal and distal shields) which allow them to be easily classified with the planktonic Coccolithophyceae, an extant class of the algal Division Haptophyta. The individual circular to oval skeletal elements (coccoliths) articulate by means of a tongue and groove arrangement to form a complete hollow sphere (coccosphere). Modern coccolithophyceaens make up a significant portion of the oceanic phytoplankton assemblage, especially in oligotrophic areas such as gyre centers. There are other calcareous nannofossils, however, which are of unknown biological affinity or are known to be other types of algae (i.e. some *Thoracosphaera* are calcareous dinoflagellates). Thus, the calcareous nannofossils are really an operational group rather than a truly biological one.

Because of their small size, it was only after microscopes of suitable resolution became available (the late nineteenth century) that these tiny objects were recognized to be the major volumetric constituent of chalk. Since then, it has been established that calcareous nannofossils comprise the most important sedimentary constituent of oceanic pelagic sediments. Using material from the voyages of H.M.S. Challenger, Thomas Huxley (1868) named these forms "coccospheres" based upon their spherical shape when fully articulated. The Upper Cretaceous sediments of the North American Western Interior Basin were some of the first sedimentary deposits recognized to contain calcareous nannofossils. Dawson (1874) reported their presence in the Boyne Formation of the Manitoba Escarpment. Subsequent reports of calcareous nannofossils from the chalks of Kansas (Williston, 1893; McClung, 1898) and Minnesota (Woodward and Thomas, 1895) indicated their widespread distribution in the chalk facies in the eastern part of the basin. The presence of calcareous nannofossils in the shaly facies of the western part of the basin was documented by Goodman (1951), who identified them from the specks in the speckled shales of Alberta and Montana. Rezak and Burkholder (1958) commented on the presence of calcareous nannofossils from the Niobrara Chalk and Pierre Shale of the Western Interior of the United States.

The first biostratigraphic study was by Trexler (1967) on nannofossils from the Greenhorn and Niobrara cyclothems of central Colorado and the Black Hills (Wyoming and South Dakota). However, the taxonomy utilized cannot be reconciled with modern concepts. Many of the names used are now restricted to taxa found only in the Cenozoic. In addition, his small, generalized line drawings prevent reassignment to fit the modern taxonomic base. Despite these shortcomings, Trexler's work did demonstrate the general stratigraphic distribution of nannofossils in the Niobrara. A few samples of the Niobrara were included in the taxonomic study of the Upper Cretaceous of Bukry (1969), although the stratigraphic placement of these samples is impossible to ascertain. Covington (1985, 1986) used extensive SEM observation in his investigation of the nannofossils from the area of the Smoky Hill type section (western Kansas). Although Covington (1985) deals briefly with the Niobrara nannofossil biostratigraphy, the spacing of his reported samples is widely variable (1 to > 14 m [3.3 to > 46 ft]) and is useful only to indicate the general biostratigraphic succession.

We have undertaken to further exploit the rich fossil beds of the Niobrara by a basinwide taxonomic, biostratigraphic, and paleoecologic analysis. Our major reference section is the western Kansas section so well documented by Hattin (1982). The results discussed below are the result of examination of samples with <1-m (3.3-ft) spacing throughout the Niobrara of the Smoky Hill type area. For the purposes of this field trip guide, we will concentrate on this area.

Biostratigraphy

The Niobrara Chalk in the type area of the Smoky Hill Chalk Member includes strata of the lower Coniacian through lower Campanian. This interval is divisible into the seven nannofossil zones of Sissingh (1977). In addition, several of the subzonal indicators proposed by Perch–Nielsen (1979, 1985) are useful in the sequence. For the purposes of this field guide, we have restricted ourselves to use of the published zonation as it appears in Perch–Nielsen (1985) with those modifications useful for subdividing the Niobrara of the type area. Using this scheme, the pertinent Cretaceous zones are designated CC13–CC19 (with "CC" meaning Cretaceous Coccolith Zone). Some of these zones can be subdivided using subzonal indicators: these are designated by letters with a being stratigraphically lowest within a zone. All seven of these zones can be recognized in the Niobrara of the type area, although the zonal boundaries are uncertain, in some cases, due to the rarity of the zonal taxa. The stratigraphic distribution of these zones and subzones is illustrated in fig. 1.

The lower 18.3 m (60.4 ft) of the Fort Hays Limestone Member in the type section is within the *Marthasterites furcatus* Zone (CC13) of the uppermost Turonian through lower Coniacian. The nominate taxon *M. furcatus* is present throughout the Fort Hays but is not common. This may explain why it is not reported in the two Fort Hays samples of Covington (1985). The presence of *Lithastrinus septenarius* throughout this interval indicates the upper (lower Coniacian) subzone CC13b. Forchheimer (1972) defined *L. septenarius* as having seven rays ". . . proximally and distally surrounded by triangular rays" (p. 54). She compared this form to *Lithastrinus grillii*, a six-rayed form, but not to *Lithastrinus moratus*, another seven-rayed form. Perch–Nielsen (1979, 1985) explained that the rays of *L. moratus* are short and blunt compared to the long, slightly curving rays of *L. septenarius*. We have found, however, that the rays of *L. septenarius* are often broken and resemble the rays of *L. moratus*. In addition, there are numerous transitional forms between the ancestral *L. moratus* and the descendent *L. septenarius* in the lower Fort Hays. It is clear that the base of the *Marthasterites furcatus* Zone (i.e CC13a) is missing in the Fort Hays and is probably included in the hiatus at the base of the Fort Hays documented by Hattin (1975).

The presence of *Micula decussata* and the absence of *L. grillii* places the rest of the Fort Hays (18.3–21.5 m [60.4–70.9 ft]) in the *Micula decussata* Zone (CC14). The first 18.3 m (60.4 ft) of the Fort Hays contain common transitional forms between *Quadrum gartnerii* (which arose in the early Turonian) and *M. decussata*. Our placement of the first *M. decussata* is significantly below that of Covington (1986), who reported this datum at approximately 10 m (33 ft) above the base of the Smoky Hill Chalk Member (near top of bed 58, Locality 1, of Hattin, 1982) in the type area (Covington, 1986). Because of this (erroneous) placement, the resultant *M. furcatus* Zone was abnormally thin (approximately 10 m [33 ft]). This perceived anomoly prompted Covington (1986) to speculate that part of the zone was represented by a disconformity. However, our re-examination indicates that *M. decussata* occurs well into the Fort Hays, so that Covington's disconformity is unnecessary.

Hattin (1975, 1982) documented the succession of inoceramids from the Fort Hays at Hackberry Ranch (Trego County, Kansas) including *Inoceramus deformis* Meek (1.1–8.6 m [3.6–28.4 ft] above the base of the Fort Hays), *Inoceramus (Cremnoceramus) inconstans* Woods (7.9–14.9 m [26–49 ft] above base), *Inoceramus (Cremnoceramus) browni* Cragin (9.6–14.9 m [31.7–49.2 ft] above base), and *Inoceramus (Volviceramus) koeneni* Mueller (uppermost Fort Hays). This sequence indicates that the Fort Hays in Trego County spans most of the lower to mid-Coniacian and is in full agreement with the nannofossil data.

The next nannofossil zone (the Reinhardtites anthophorus Zone; CC15) spans the interval from 28.8 to 57.2 m (95–188.8 ft) in the Smoky Hill type area. This zone is based on the FAD of *Reinhardtites anthophorus*, which has been correlated to the late early Santonian (Sissingh, 1977; Perch-Nielsen, 1985). Perch-Nielsen (1979, 1985) noted that the FAD of *R. anthophorus*, *Lithastrinus grillii*, and *Micula concava* were synchronous in her sections and suggested the latter two datums as alternate zonal events for the first *R. anthophorus*. In our study area, however, these are three distinct biostratigraphic events. The FAD of *R. anthophorus* (at 28.8 m [95 ft]) and *L. grillii* (at 31.8 m [104.9 ft]) are similar and occur significantly before the FAD *M. concava* (39.5 m [130.4 ft]). In the Canadian Atlantic margin, Doeven (1983) also found that *M. concava* occurs after *R. anthophorus*. We have therefore divided CC15, using *R. anthophorus* to mark the first subzone, CC15a (upper Lower Santonian). We use the FAD *M. concava* to mark the base of CC15b, which is in the Upper Santonian.

The FAD of *Lucianorhabdus cayeuxii* marks the top of the *Reinhardtites anthophorus* Zone and the base of the overlying *L. cayeuxii* Zone (CC16). This zone, which is dated as late Santonian by Sissingh (1977), comprises the interval from 57.2 to 128.2 m (188.8–423 ft) in the western Kansas section. In our study, *L. cayeuxii* first occurs at 57.2 m (188.8 ft), and is common in some samples. Covington (1986) reported that this fossil was too sporadic in its occurrence to be useful as a stratigraphic marker. Perch-Nielsen (1979, 1985) suggests that the FAD *L. cayeuxii* coincides with the last occurrence of *L. septenarius* (at the base of the *L. cayeuxii* Zone). In our study area, *L. septenarius* is present up to 93.3 m (307.9 ft), approximately 36 m (118.8 ft) above the base of the *L. cayeuxii* Zone. We have designated the stratigraphic interval between these two events as an informal subzone CC16a. This nannofossil LAD occurs approximately 13 m (42.9 ft) below reported occurrences of the ammonite *Clioscaphites vermiformis* (Meek & Hayden) of late middle Santonian age. Subzone CC16b is informally designated as that interval from the last *L. septenarius* to the first *Calculites obscurus* (base of CC17).

The next younger biohorizon of Sissingh (1977) is the FAD of *Calculites obscurus*. Sissingh (1977) correlates this biohorizon with the earliest Campanian, although later work by Perch-Nielsen (1979, 1985) placed it in the late Santonian. This biohorizon occurs at 128.2 m (423 ft) at location 18 in the study area. It is very rare and smaller in size than typical in the first few meters. It becomes a common constituent in CC18. Covington (1986) rejected the use of this biohorizon for the Smoky Hill because its occurrence is somewhat sporadic. While it is true that it does not occur commonly in all samples above its first stratigraphic appearance, it is present in sufficient abundance so as to be used for biostratigraphic zonation.

Perch-Nielsen (1979, 1985) also reports the last occurrence of *Eprolithus floralis* as a substitute marker event for the end of the *L. cayeuxii* Zone. We found, however, that the last occurrence of *E. floralis* is at 49.5 m (163 ft; within the *R. anthophorus* Zone; CC15) in the

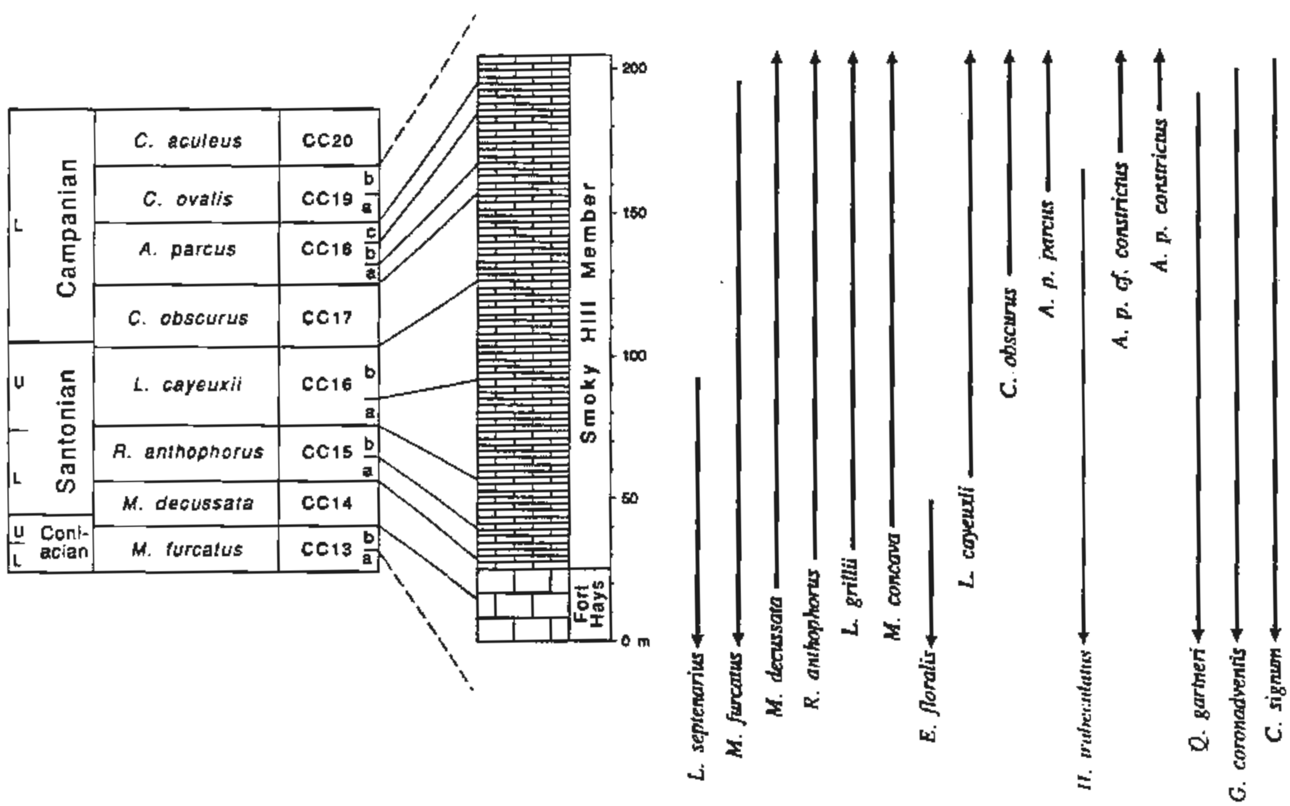

FIGURE 1—Distribution of calcareous nannofossil zones, subzones, and diagnostic species in the Niobrara of the Smoky Hill type area, western Kansas.

western Kansas section. The reason for this abnormally old local extinction in the Smoky Hill is enigmatic at present.

The base of the Campanian in the Smoky Hill of the type area is marked by the FAD of *Aspidolithus parcus parcus* at 157 m (518 ft). This bed, and those in immediate stratigraphic proximity to it, lack age-diagnostic macrofossils. The *A. p. parcus* Zone persists from 157 to 196.9 m (518–649.8 ft) in the western Kansas section. The evolution of *A. parcus constrictus* from *A. parcus parcus*, by progressive diminution of the central area, is preserved in the upper Smoky Hill Chalk Member. This evolutionary transition, as outlined by Wise (1983) has been used by Perch–Nielsen (1985) as a basis for subzonal division of the *A. parcus* Zone (CC18). Because all three subspecies are common in western Kansas, we use Perch–Nielsen's three subzones for CC18.

Subzone CC18a spans from 157 m to 167 m (518–551 ft) at location 20. Another possibly useful event in this subzone is the last occurrence of *Helicolithus trabeculatus* at 165 m (544.5 ft). Perch–Nielsen (1979) used the first occurrences of *Aspidolithus parcus* ssp. cf. *A. p. constrictus* and *Bukryaster hayi* as co-markers for the base of CC18b. *Bukryaster hayi* does not occur in western Kansas, although it is known from correlative Niobrara in eastern South Dakota. *Aspidolithus parcus* ssp. cf. *A. p. constrictus* is common beginning at approximately 170 m (561 ft) in location 24 in western Kansas. This subzone spans from 167 m to 184.9 m (551–610.2 ft). The FAD of *Aspidolithus parcus constrictus* is used as one of the co-markers for the base of CC18c by Perch–Nielsen (1979; 1985). This subzone spans from 184.9 m to 196.9 m (610.2–649.8 ft) within location 21 in western Kansas. The last appearance of *Quadrum gartnerii* is at 190.9 m (630 ft). This last occurrence is much later than generally reported. *Ceratolithoides verbeekii*, one of Perch–Nielsen's subzonal markers for CC18b, is not present in western Kansas, although it is also known from the Niobrara of eastern South Dakota.

In the Smoky Hill of the type area, the LAD of *Marthasterites furcatus* occurs within 10 m (33 ft) of the top of the member, in bed 32, locality 21, of Hattin (1982). This event also has been used as a zone marker by several authors although it may not be a reliable marker in northern latitudes (Perch–Nielsen, 1985). This zone spans from 196.9 m (649.8 ft) to the top of the Smoky Hill Member. Doeven (1983) reported the successive disappearance of *Corollithion signum* and *Gephyrorhabdus coronadventis* within CC19. These two species disappear after 203.9 m (672.9 ft) and 200.9 m (663 ft), respectively, in western Kansas. This also indicates that the deposition of the Smoky Hill Chalk Member ended within zone CC19 (Early Campanian). Because *B. hayi* does not occur, it is difficult to tell whether deposition ends during CC19a or CC19b.

Paleoecology

Covington (1985) documented the unusually good preservation that is typical of several horizons within the Smoky Hill Chalk Member of the type area (western Kansas). Examination of samples from central Kansas, southern and northeastern Nebraska, and southeastern and southwestern South Dakota indicate that such preservational characteristics are widespread within the Smoky Hill. Scanning electron microscopic examinations of fracture sections along bedding planes reveal a large number of intact or only moderately disturbed coccospheres or monospecific clusters of nannofossils. Their pristine preservation is indicative of the minimal post-depositional disturbance, by either bioturbation or bottom currents, that was typical during Smoky Hill deposition. Included within the intact coccospheres of the Smoky Hill are numerous examples of the cylindrical skeletons of *Biscutum* n. sp. These unusual structures prompted Covington (1985) to coin the term "coccocylinders" to describe their uncommon morphology.

The nannofossil assemblages within the Niobrara exhibit several notable features which indicate that, despite the pelagic nature of the sedimentary environment, the surface waters differed in character from those in the open oceans. One of the most notable features is the relative paucity of holococcoliths (members of the family Calyptrosphaeraceae, whose coccoliths are composed of loosely packed, minute (<1 µm), rhombic crystallites). These forms, including the biostratigraphically important genera *Lucianorhabdus* and *Calculites*, are generally associated with deposition in marginal settings (Thierstein, 1976) and/or shallow settings with water depths up to a few hundred meters (Perch–Nielsen, 1985). Although the Niobrara paleoenvironment would seem to fit this description, holococcoliths are rarer and more sporadic in occurrence than one would expect. An argument could be made that the dissolution-susceptible holococcoliths were removed by diagenesis (which is often the case in deeper, open oceanic sites), but the pristine preservation in many Smoky Hill horizons refutes this hypothesis. It is more likely that some ecological factor limited the distribution of these forms, although the nature of that factor is presently unknown.

Other nannofossils are present in the Niobrara assemblages, which suggests that marginal oceanic conditions of some type existed in the basin. Braarudosphaerids are fairly common in the Smoky Hill of the type area, including well-preserved dodecahedral coccospheres (Covington, 1985, Fig. 1B). Thierstein (1976) has indicated the preference of these forms for marginal conditions during the Cretaceous. Unusually high abundances of other taxa in certain horizons also indicate abnormal surface-water conditions during Niobrara deposition. The most striking of these are "blooms" of *Marthasterites furcatus*. Two distinct bloom events have been observed from the Smoky Hill Chalk Member of north-central Kansas and south-central Nebraska. A strongly developed abundance event (*M. furcatus* >35% of the total assemblage) has been observed from the lower Smoky Hill of central Colorado. Although the high abundances of *M. furcatus* from central Colorado may be the result of preferential preservation during diagenesis, the pristine preservation in the Kansas and Nebraska assemblages indicates that these "blooms" cannot be explained by diagenetic processes. At present, the biostratigraphic framework for the Smoky Hill is too poorly documented to ascertain whether these bloom events are isochronous between localities, although their gross stratigraphic positions indicate approximate synchroneity.

The occurrence of *Seribiscutum primitivum* within the Smoky Hill Chalk Member suggests that the Niobrara Seaway had a true oceanic link with the boreal seas. The restriction of this species to boreal and austral realms has been noted by several authors including Thierstein (1976), Roth and Bowdler (1981) and Wise (1983). Its distribution within the Smoky Hill is not fully documented although it appears to be restricted to the upper Smoky Hill in the type area.

Studies suggest that there is relatively little endemism among the calcareous nannofossils of the Niobrara. Covington (1986) identified and described two new genera, three new species, and two new subspecies from the Smoky Hill, although they have not yet been validly published. Two additional taxa unique to the upper Smoky Hill have been identified (Watkins, unpublished data). The small degree of endemism in the Western Interior nannofossil assemblages is in stark contrast to the high degree of endemism recognized in the invertebrate macrofossil assemblages.

Conclusions

Biostratigraphic investigation of the Niobrara in western Kansas indicates the presence of seven standard zones. Use of auxiliary marker taxa allow a greater degree of stratigraphic resolution. Some of the marker species are rarer than usual and the reported range of at least one marker species (*Eprolithus floralis*) is significantly shorter than observed elsewhere. These difficulties do not seem to arise from preservational bias, as many horizons within the Niobrara exhibit pristine nannofossils. On the contrary, the peculiar nature of some Niobrara assemblages seems to be controlled by paleoecologic factors. It appears that the surface-water mass in the Niobrara Sea was atypical for the "normal" Late Cretaceous ocean. These conditions may be the same which excluded ammonites in central Kansas through most of the Niobrara deposition. There are suggestions of oceanic communication with the boreal realm during deposition of the upper Smoky Hill. In addition, there are some indications of minor floral endemism during the latter part of the Niobrara cycle.

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Niobrara Formation vertebrate stratigraphy

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Abstract

After more than a century of exploration, the only definitive statements concerning the distribution of vertebrate species in the Niobrara Formation pertain to perhaps six mosasaur species, four species of *Protosphyraena*, and the shark genus *Ptychodus*. The Smoky Hill Chalk Member accumulated over an interval of five million years and can be separated into at least six distinct vertebrate faunal zones of unequal duration. Some vertebrate taxa are represented only in single zones. At least 30 fish species are restricted to only a part of the Smoky Hill Chalk, as are many tetrapod species. Some distributional changes appear to be the result of deepening water, some from cooling, some from apparent anagenetic evolution, and some apparently are due to extinction. Many vertebrate species show no detectable change throughout Smoky Hill Chalk deposition.

Introduction

The history of the stratigraphic nomenclature of the Niobrara Formation in Kansas has been adequately reviewed by Hattin (1982). One of the earliest approaches to internal stratigraphy of the Smoky Hill Chalk Member was to recognize a yellow chalk above and blue shale below. Williston (1893, 1897) explained that this is a weathering phenomenon and is therefore an invalid stratigraphic division. However, it is still adhered to by newcomers to the Niobrara Chalk. It was Williston (1893) who first recorded that *Volviceramus* ("Haploscapha") is abundant in the lower Niobrara, but that *Platyceramus* ("the large, thin-shelled, four-foot inoceramid") is the only obvious inoceramid in some of the higher horizons. He also noted here (1893) that two mosasaur genera (presumably *Tylosaurus* and *Platecarpus*) are found throughout the member, but that *Clidastes* is only found in the upper chalk. Furthermore, he believed that *Uintacrinus* was found in only one horizon near the middle of the member (Williston, 1893). Five years later, he said, "Several species of Inoceramus are apparently found in all horizons, but the Haploscaphas are abundant only in the lower horizons, and I never have found *H. grandis* or those allied to that species in the upper horizons. On the Smoky Hill River near the mouth of the Hackberry there are places where these shells can be gathered by the wagon load, often distorted, but not rarely in extraordinary perfection. A very thin shelled Inoceramid measuring in the largest specimens forty four by forty six or eight inches is not rare over a large part of the exposures" (Williston, 1897, p. 241). Logan (1897) clearly used the term "Pteranodon beds" to mean the Smoky Hill Chalk Member. Williston (1897) recognized the same usage of *Pteranodon* beds and subdivided them into the *Rudistes* and the *Hesperornis* beds. He also stated that the boundary between *Rudistes* and *Hesperornis* beds can be traced from east of Monument Rocks to the Saline River north of Wakeeney to the south fork of the Solomon River near Lenora. He was apparently referring to the sequence including and immediately below the middle caprock, Marker Unit 10 of Hattin (1982).

Lamenting the typically poor stratigraphic data that accompanied Niobrara vertebrate fossils, Williston (1897) said, "I need not call the attention of future collectors to the importance of locating the horizon of specimens more accurately than has been before." It is unfortunate that this plea has gone largely unheeded until recently.

Bass (1926) utilized bentonite sequences and resistant ledges for correlations within a limited section near the base of the Smoky Hill Chalk in Ellis County. Russell (1929) detailed a sequence of 86 bentonites throughout much of the Smoky Hill Chalk Member, but excluded three sections comprising about 250 ft (75 m). He also proposed a four-part lithostratigraphic division of the Smoky Hill Chalk Member. Elias (1931) examined the stratigraphic schemes of Williston (1897) and Russell (1929), and concluded that the *Rudistes* beds of the former correspond to subdivisions I and II of the latter, and that the *Hesperornis* beds correspond to subdivisons III and IV.

The next paleontologist to take up the question of Niobrara vertebrate biostratigraphy added the observation that *Protosphyraena* is more common in, or restricted to, the lower Smoky Hill Chalk (Bardack, 1965).

Russell (1967b) proposed that the mosasaur species in the Smoky Hill Chalk Member provide a two-fold division with *Clidastes propython*, *Platecarpus ictericus*, and *Tylosaurus proriger* in the upper chalk, and *Clidastes* *liodontus*, *Platecarpus coryphaeus*, and *Tylosaurus nepaeolica* in the lower chalk. Miller (1968) discussed earlier uses of lithology and bentonite sequences for correlating exposures of the Smoky Hill Chalk and concluded that this method of correlation would be of little use in the upper part of the member. He also conceived a division of the Smoky Hill Chalk into six biostratigraphic zones (Miller, 1968). These were based on invertebrate species.

Russell (1970) noted that, because the mosasaur fauna of the contemporaneous Mooreville Member of the Selma Chalk was dominated by *Clidastes*, the relative rarity of *Clidastes* in the Niobrara Chalk was because of more boreal influences there. Russell (1975) stated that most of the vertebrate fossils from the Niobrara Chalk were from the upper horizons and considered those fossils to be of early Campanian age. Stewart (1979) proposed that there are different stratigraphic ranges of the four species of *Protosphyraena* within the Smoky Hill Chalk.

The first real attempt at a thorough lithostratigraphy and invertebrate biostratigraphy of the Smoky Hill Chalk was that of Hattin (1982). In this work he generated a composite measured section for the entire member, designated 23 lithologic marker units in that member, and gave stratigraphic ranges for invertebrate species.

Stewart (1988) documented the distribution of four *Protosphyraena* species proposed earlier (Stewart, 1979), and compared those with ranges of those species in Mississippi and Alabama sediments. This was the first mapping of vertebrate-fossil occurrences in the Smoky Hill Chalk. The last 15 years have seen a resurgence of interest in Niobrara stratigraphy, and probably as many or more advances have been made in that period as in the previous century. This framework is submitted in the hopes that other researchers will test it and improve upon it. It is unfortunate that newly curated material from the Yale Peabody Museum collection of Niobrara vertebrates is not incorporated into this work. It is apparent that Marsh's collectors kept fairly accurate field notes, at least in the early years.

Invalid records

Cope (1875, p. 297) listed *Lamna macrorhiza* sp. nov. from "Ellis County, Niobrara Epoch." However, the caption of figures 9 and 10 of his Pl. 42 indicate the locality is Rooks County. Ellis and Rooks counties are adjacent. These specimens could be reworked from the Codell Sandstone Member into the basal Fort Hays Limestone Member, since a similar species occurs there, and that unit is exposed in both of those counties. In fact, the type section is on the common border of those two counties. Meyer (1974) considered the taxon represented in Cope's figures 9 and 10 of Pl. 42 as being synonymous with *Leptostyrax macrorhiza* (Pictet and Campiche, 1858). If this is the case, it would be from strata of Albian age, and the Codell Sandstone Member is of Turonian age. There is a *Leptostyrax* species (referred to *Plicatolamna* by some authors) in the Codell Sandstone Member. This is *Leptostyrax crassidens*. Its teeth are not so laterally compressed as those illustrated by Marsh. Herman (1975) recognized Cope's material as the type series of *Plicatolamna macrorhiza* (Cope, 1875), but considered *Lamna macrorhiza* Pictet and Campiche, 1958 to be a separate species which he assigned to the genus *Paraisurus*. Whatever the correct assignment of Cope's material, the specimens are almost certainly not from the Niobrara Chalk Formation.

Herman (1975, p. 64) indicated that *Ptychodus whipplei* occurs in the Niobrara Formation of Kansas. This conception probably stems from the claim of Cope (1875) that it is found in the Niobrara Formation along the Arkansas River. Williston (1900a, 1900b) was correct to conclude that any Kansas *Ptychodus whipplei* records from the Arkansas River area in Kansas must be from the "Benton Formation" (now the Graneros Shale, Greenhorn Limestone, and Carlile Shale formations). *Ptychodus whipplei* does occur in the Fairport Chalk Member of the Carlile Shale Formation (Martin and Stewart, 1977) and the Codell Sandstone Member of the same formation. It is possible that specimens from the Codell Sandstone Member may be reworked into the basal Fort Hays Limestone Member. Russell (1988) listed *P. occidentalis* from the Niobrara Formation. The only Kansas specimens of this species listed by Williston (1900a, 1900b) came from the Graneros Shale (Cenomanian).

Applegate (1970) and Russell (1988) mention *Pseudocorax affinis* from the Smoky Hill Chalk. Both records are somewhat in error. As Meyer (1974) noted, the Coniacian through lower Maestrichtian specimens of *Pseudocorax* in the Gulf area are of teeth lacking serrations. Teeth of *Pseudocorax affinis* (Agassiz, 1843), the type species of the genus, are consistently serrated. *Pseudocorax laevis* Leriche, 1906 is the name that should be applied to the earlier, smaller, and unserrated teeth (Herman, 1975) such as those from the Smoky Hill Chalk Member.

Valid records

Fort Hays Limestone Member

Vertebrate fossils are rare in the Fort Hays Limestone Member. Williston (1897, p. 237) mentioned a Jewell County plesiosaur. This is the holotype of an elasmosaurid, *Thalassonomosaurus nobilis* (originally *Elasmosaurus nobilis*), number 1640 in the Yale Peabody Museum collection (Williston, 1906). I witnessed Richard Zakrzewski collect a tooth of *Ptychodus mortoni* near the middle of the member. I have noted a shark vertebra in the lower part. Frey (1972) mentioned that shark teeth are rare in the Fort Hays Limestone Member, except in the basal bed. The scouring of the Carlile Shale at the Niobrara/ Carlile contact (Frey, 1972) suggests that the teeth in the basal bed may be reworked from the Codell Sandstone Member. Frey (1972) illustrated *Squalicorax*, *Cretoxyrhina*, and *Cretolamna* teeth from the Fort Hays Limestone. He also stated that *Squalicorax* is the most common shark tooth in the member. Frey (1972) indicated that, unlike the shark teeth, isolated teleost scales occur in all parts of the Fort Hays Limestone Member. The type description of *Micropycnodon kansasensis* lists the holotype as coming from 1 mi (1.6 km) west of the town of Webster in Rooks County (Hibbard and Grafham, 1941). That town site is now beneath Webster Reservoir. If the type locality is truly due west of that site, it also is underwater. Assuming the accuracy of this description, we may conclude that the specimen is from the Fort Hays Limestone Member. However, exposures of the Smoky Hill Chalk Member also occur nearby.

Smoky Hill Chalk Member

There is a long-standing misconception that few vertebrate fossils are found in the lower parts of the Smoky Hill Chalk Member (Williston, 1893; Russell, 1975). The articulated skeletons of Niobrara vertebrates typically come from the upper part of the member, but vertebrate fossils occur from the base of the Smoky Hill Chalk Member upwards, and almost any substantial exposure will yield some identifiable vertebrate remains (Stewart, 1988).

Zone of *Protosphyraena pernicosa*—The zone of *Protosphyraena pernicosa* includes Marker Units 1, 2, and probably 3 of Hattin (1982). *Volviceramus grandis* is the dominant inoceramid in this zone and extends into the overlying zone of *Spinaptychus* n. sp. *Tusoteuthis longa* is a common fossil in the zone of *P. pernicosa* and can be found throughout the Smoky Hill Chalk Member. This zone is of late Coniacian age.

Many vertebrate genera and some species that occur in the lowest part of the Smoky Hill Chalk Member also have a record in older Kansas rocks. Among the sharks, *Ptychodus anonymous* and *Ptychodus martini* are known from the Greenhorn and Carlile formations, but *Ptychodus mortoni* has no pre-Niobrara record in the Western Interior. *Squalicorax falcatus* and *Scapanorhynchus rhaphiodon* likewise occur in those two formations. Teeth of *Cretoxyrhina mantelli* show a rather gradual size increase from the Graneros Shale to the Smoky Hill Chalk Member. By early Smoky Hill Chalk Member deposition, some specimens of this shark attained a length of 6.7 m (20 ft). *Cretolamna appendiculata* likewise has a stratigraphic range at least as far back as the Graneros Shale in Kansas. Most Niobrara records of *Pseudocorax laevis* with adequate locality data known to me are from the zone of *Protosphyraena pernicosa*. Several actinopterygians of "holostean" grade occur in the lower parts of the Smoky Hill Chalk Member. *Micropycnodon kansasensis* (Hibbard and Grafham, 1941) has no pre-Niobrara record and may be limited to this horizon, but also may be found in the Fort Hays Limestone Member (see above). *Protosphyraena* is known from pre-Niobrara horizons, but there is no record of *P. pernicosa* or *P. nitida*. Much North American *Protosphyraena* taxonomy is based on pectoral fin morphology, but there are no pre-Niobrara fin records in North America. Stewart (1979, 1988) suggested that *Protosphyraena nitida* does not occur as low as *Protosphyraena pernicosa* in the lower part of the Smoky Hill Chalk Member. However, consultation and field observations with Mike and Pam Everhart convince me that *Protosphyraena nitida* is a rare member of the lowest Smoky Hill Chalk Member fauna. It does, however, continue into the zone of *Spinaptychus* n. sp., whereas *P. pernicosa* does not. *Belonostomus* specimens are known only from the zone of *Volviceramus grandis*, which encompasses the zones of *P. pernicosa* and *Spinaptychus* n. sp. (Schultze and Stewart, ms).

Paraliodesmus guadagnii occurs in shells of *Volviceramus grandis* and perhaps *Platyceramus platinus* s.l. in this zone (see Stewart, this volume). The only *Lepisosteus* specimen from the Smoky Hill Chalk Member is the oldest North American record of a lepisosteid (Wiley and Stewart, 1977). Lepisosteids apparently continued in near-shore and freshwater environments up to the present, but this is the only known record of this primitive and unnamed species.

Xiphactinus audax, *Ichthyodectes ctenodon*, *Gillicus arcuatus*, *Apsopelix anglicus*, *Pachyrhizodus caninus*, and *P. minimus* have earlier records in Kansas and continue beyond the Niobrara Chalk. I cannot detect any definite morphological changes in these taxa throughout their stratigraphic ranges. They are known from all following faunal units unless otherwise indicated; *Saurodon leanus* first appears in Kansas in this horizon and apparently persists throughout Smoky Hill Chalk Member deposition. All known records of *Bananogmius zitteli* in Kansas seem to be from this zone. *Martinichthys* occurs here, but seems to terminate just below the zone of *Spinaptychus* n. sp.

Cimolichthys nepaholica is well known from this horizon, and there are no documented earlier records in North America. This species continues into the Pierre Shale. *Enchodus gladiolus* is the most common *Enchodus* species in this horizon, but *E. petrosus* also is present. Both continue into the Pierre Shale. Two specimens of an unnamed holocentrid (one was described by Bardack, 1976) have been found in inoceramids in this faunal unit.

This horizon produces the oldest records of *Chelosphargis advena*. Likewise, the first records of *Toxochelys latiremis* occur here, but continue through the Sharon Springs Shale Member of the Pierre Shale. The specimens from the two formations have often been referred to different species, but they are conspecific according to Nicholls (1988).

Platecarpus occurs very early in the zone of *Protosphyraena pernicosa*. I find the distinction between *Platecarpus ictericus* and *P. coryphaeus* questionable. *Platecarpus ictericus* is the older name. *Platecarpus ictericus* continues through Niobrara deposition into the Pierre Shale. Two tylosaurine mosasaurs have been found in this horizon, *Tylosaurus nepaeolicus* and *Tylosaurus* n. sp. Russell (1967b) stated that he believed that *T. nepaeolicus* was limited to the lower horizon of the Smoky Hill Chalk Member, but that *T. proriger* was found in the upper part. Stewart (1988) implied that some evidence contradicted this hypothesis. It now appears that the supposedly contradictory specimens of *T. proriger* are actually an undescribed species.

The only plesiosaur remains I have seen from the zone of *Protosphyraena pernicosa* are very rare propodials of juveniles. There are no pre-Niobrara pterosaurs in Kansas, and I know of no definite records in the lower part of the zone of *Volviceramus grandis*. The first definite records of which I am aware are in the upper part of *V. grandis* not far below the zone of *Spinaptychus* n. sp. No hesperornithiforms occur in the Smoky Hill below Marker Unit 11 of Hattin (1982). Contrary to several sources, there are no Coniacian hesperornithids yet known in North America. *Ichthyornis* makes its first known appearance in Kansas at the Greenhorn/Carlile contact (Walker, 1967; Martin and Stewart, 1982). It was probably a rare member of the Smoky Hill Chalk Member fauna from the start. At least one specimen (KUVP 21502) is known from the zone of *Volviceramus grandis*.

ZONE OF *SPINAPTYCHUS* N. SP.—This zone includes Marker Units 4 and 5 of Hattin (1982). This zone produces many specimens of *Durania maxima* and *Tusoteuthis longa*. *Volviceramus grandis* is the dominant inoceramid. The zone is of late Coniacian age.

Spiral coprolites, argued to be enterospirae by Stewart (1978), occur in this horizon. McAllister (1985) has conclusively demonstrated that such structures can be found in the colon of dissected *Scyliorhinus canicula*. Presumably, they can also be expelled intact from the rectum. Their presence in this horizon and absence in other horizons of the Smoky Hill Chalk Member implies the presence of some heretofore undetected shark taxon in this zone. Other types of coprolites occur in all horizons of the Smoky Hill Chalk Member. The last appearance of *Ptychodus anonymous* may be in this zone, although locality data are not sufficient to prove that they did not become extinct in the zone of *Protosphyraena pernicosa*. *Pseudocorax laevis*, although rare, is present in this zone. *Protosphyraena nitida* makes its last appearance in the Western Interior in this zone (Stewart, 1988). This zone produces the lowest records of *Protosphyraena tenuis* and *P. gladius*.

Inexact locality data prevent us from knowing for certain whether the holotypes of *Niobrara encarsia* and *Luxilites striolatus* come from this zone or the zone of *Protosphyraena pernicosa*.

Enchodus dirus is a relatively rare species in the Smoky Hill Chalk, and the earliest demonstrable records are from this unit. It apparently continues to the top of the formation. *Stratodus apicalis* occurs in this horizon and might be found in earlier horizons. It continues into the Pierre Shale.

Pteranodon is abundant in this horizon, but the lack of well-preserved skulls from this zone prevent us from telling what species is present. *Ichthyornis* cf. *I. anceps* occurs in this zone, as does a smaller species of *Ichthyornis*.

ZONE OF *CLADOCERAMUS UNDULATOPLICATUS*—*Cladoceramus undulatoplicatus* is the dominant inoceramid in this zone. This zone is of early Santonian age. Hattin (1982, p. 22) indicated that the uppermost occurrence of *C. undulatoplicatus* was unit 11 of his measured section of his locality 19. I have collected a very large specimen of *C. undulatoplicatus* somewhat higher in that section in unit 17. A phenomenon I have not seen noted in the literature of the Kansas Niobrara Chalk is the upward trend toward thicker (and presumably larger) shells in *C. undulatoplicatus*. Scott and Cobban (1964) mentioned that a specimen of *C. undulatoplicatus* from the top of its range in the Smoky Hill Shale near Pueblo, Colorado, was unusually large and rather smooth. *Cladoceramus undulatoplicatus* is particularly useful for inter-regional and intercontinental correlations. It occurs in the middle shale unit of the Smoky Hill Shale Member of the Niobrara Formation of the Pueblo Basin in Colorado (Scott and Cobban, 1964), the Vinson Chalk of the Austin Group of Texas (Young, 1985); and the English Chalk (Cleevely and Morris, 1987).

The zone of *C. undulatoplicatus* is not well collected for vertebrates. One assumes continuity of species found below and above (*Pseudocorax laevis, Paraliodesmus guadagnii, Protosphyraena gladius, Enchodus petrosus*). Applegate (1970) regarded *Pachyrhizodus leptopsis* as a synonym of *P. caninus*. *Pachyrhizodus leptopsis*, however, is a valid species (Hay, 1903; Stewart and Bell, 1989). Its lowest documented occurrence in the Western Interior is in this zone.

Zone of *Clioscaphites vermiformis* and *C. choteauensis*—This zone contains Marker Units 8 through 10 of Hattin (1982). It is of Upper Santonian age. One thick and easily located lithologic unit, unit 17 of locality 19, of Hattin (1982) does not fit conveniently into either the zone of *Cladoceramus undulatoplicatus* or the zone of *Clioscaphites vermiformis* and *C. choteauensis*. Neither *Cladoceramus* nor *Clioscaphites* has been recorded there. Since it produces very little in the way of vertebrate or invertebrate macrofossils, this is not a major problem. Williston (1897) apparently used the caprock (Marker Unit 10, of Hattin, 1982) to mark the boundary between his *Rudistes* and *Hesperornis* beds. It is not clear to which of these Williston intended to assign this caprock. As used here, the caprock lies at the top of the zone of *C. vermiformis* and *C. choteauensis*. Unit 20 of locality 19 of Hattin (1982) lies at the bottom. *Uintacrinus socialis* occurs in this zone (as low as Marker Unit 9 of Hattin, 1982; Hattin, personal communication, 1987).

This zone contains the last records of *Ptychodus mortoni* in the midcontinent (Stewart, 1988) and the last records of *Pseudocorax laevis* in the midcontinent. *Squalicorax* specimens from this zone are already distinguishable from samples of *Squalicorax falcatus* from low in the Smoky Hill Chalk.

There is a small pycnodont in this zone. It is not *Micropycnodon* and is probably not *Hadrodus*. *Paraliodesmus guadagnii* makes its last known appearance in this zone.

Contrary to Wiley and Stewart (1981), there are no definite records of *Bananogmius evolutus* known from below the caprock. There is, however, some other plethodid species in this zone. *Laminospondylus* occurs in this zone. It has an earlier record in Texas, but not in Kansas. The earliest occurrence of *Apateodus* in the Niobrara Chalk is from this horizon, based on the recollection of Mike Everhart (personal communication, 1990). Numerous *Enchodus shumardi* specimens have been found in this zone. It is unknown from earlier horizons.

All *Urenchelys abditus*, *Caproberyx*, *Trachichthyoides*, and holocentrid alpha have been found only within specimens of *Platyceramus platinus* within a 12-m (40-ft) stratum near the base of this zone (Stewart, this volume).

Omosoma garretti and the sole occurrence of *Kansius sternbergi* are reported from exposures that contain this zone, but they probably come from the zone *Spinaptychus sternbergi* which is exposed in the upper parts of that locality.

Zone of *Spinaptychus sternbergi*—All records of *Spinaptychus sternbergi* come from above Marker Unit 10 (Stewart, ms.). One site in this horizon produced a rather ornate type of *Zeugmatolepas*. The range of *Zeugmatolepas* as noted by Hattin (1982) did not extend above Marker Unit 10. Most Niobrara specimens *Uintacrinus socialis* seem to come from this zone. *Uintacrinus socialis* of considerable importance for correlations. It is also recorded in Uinta basin of Utah, England, Westphalia, and Australia. This zone produced the last record of *Laminospondylus* in the Smoky Hill Chalk Member. The earliest occurrence of *Bananogmius evolutus* seems to be in this zone, but it continues into the Pierre Shale. It appears that all known *Leptecodon rectus* and *Omosoma garretti* occur within *Platyceramus platinus* valves in this zone (Stewart, this volume). The syntypic and only known series of *Kansius sternbergi* seems to come from this zone. It is also possible that it came from the zone below this. The earliest record of *Tylosaurus proriger* I can document is from this horizon. It may occur earlier in the Niobrara Chalk. *Parahesperonis alexi* seems to be limited to this zone. These represent the earliest hesperornithiforms in sediments of the Niobrara Cyclothem.

Uppermost Smoky Hill Chalk Member—Zone of *Hesperornis*—I have examined the holotype of *Calantica* (*Titanolepas*) *martini*; the matrix is hard and red. The specimen is attached to a mold of a *Baculites*. A specimen of *Stramentum haworthi* is attached to the same *Baculites* mold. It may be from Marker Unit 21, which Hattin (1982) described as containing a reddish-weathering portion and producing a smooth species of *Baculites*. However, examination of the holotype leads me to believe that *Calantica martini* is a species of *Zeugmatolepas*.

Rhinobatos incertus is known from a horizon that appears to be near the Niobrara/Pierre contact, but faulting in that region complicates the problem. This zone produces the last records of *Cretoxyrhina mantelli* in the midcontinent. It is not known to occur in approximately the upper 40 ft (12 m) of the Smoky Hill Chalk Member (J. Bussen, personal communication, 1990). *Squalicorax* cf. *S. kaupi* from this zone is distinguishable from *Squalicorax* in zone of *Clioscaphites*. The only known specimen of *Hadrodus marshi* is probably from this zone. *Protosphyraena tenuis* makes its last appearance in this zone. The earliest definite records of *Saurocephalus* in Kansas are from this zone. "*Saurodon*" *pygmaeus* certainly occurs in this zone, as does *Bananogmius favirostris*. It may be that any or all of these three first occur in the zone of *Spinaptychus sternbergi*, but locality data are inexact. All three continue into the Pierre Shale.

Protostega is present in this zone but cannot definitely be ruled out from being in the underlying zone. Probably all Niobrara Chalk specimens of *Hesperornis*, *Baptornis*, and *Apatornis* come from this zone.

Taxonomic review

PTYCHODONTIDS—*Ptychodus anonymous* has a pre-Niobrara record and exists in the Smoky Hill Chalk Member through the zone of *Protosphyraena pernicosa*, and possibly into the zone of *Spinaptychus* n. sp. *Ptychodus martini* is only known from the zone of *Protosphyraena pernicosa*. *Ptychodus mortoni* has no pre-Niobrara record in Kansas and survives nearly up to Marker Unit 10 in the zone of *Clioscaphites choteauensis*. It survives later in the southern United States (Stewart, 1988).

ODONTASPIDS—There are a few published accounts of pre-Niobrara *Scapanorhynchus* teeth in Kansas. Within the Smoky Hill Chalk Member, it appears to be relegated to the zone of *Protosphyraena pernicosa*. An undetermined species of *Odontaspis* also occurs within this zone.

ANACORACIDS—*Squalicorax falcatus* has a well-substantiated pre-Niobrara record in Kansas and is found in all lower horizons of the lower Smoky Hill Chalk Member. It grades upward through the overlying Smoky Hill Chalk into *Squalicorax kaupi*. The differences between the various temporal morphs are particularly evident in larger teeth from each horizon. *Pseudocorax laevis* has not been published from any pre-Niobrara sediment in Kansas. It ranges from the zone of *Volviceramus grandis* to the zone of *Clioscaphites vermiformis* and *C. choteauensis* in the Smoky Hill Chalk Member.

CRETOXYRHINIDS—*Cretolamna appendiculata* has a substantial pre-Niobrara record in Kansas. It apparently continues throughout the Smoky Hill Chalk Member and into the Pierre Shale. *Cretoxyrhina mantelli* likewise is well known in pre-Niobrara rocks in Kansas and continues throughout most of the Smoky Hill Chalk Member. However, it may be absent from the upper few feet of the Smoky Hill Chalk Member, and has never been found in the Pierre Shale. It survived somewhat longer along the Gulf Coast.

RHINOBATIDS—*Rhinobatos* has only a limited known Niobrara occurrence high in the zone of *Hesperornis*.

LEPISOSTEIDS—There is a single known occurrence of *Lepisosteus* in the Niobrara Formation, specifically from the zone of *Protosphyraena pernicosa* (Wiley and Stewart, 1977). This is the oldest substantiated record of a ginglymode in North America.

PYCNODONTIDS—All Smoky Hill Chalk Member specimens of *Micropycnodon* known to me are from the zone of *Protosphyraena pernicosa*. The single published record of *Hadrodus marshi* is probably from the zone of *Hesperornis*. Within the zone of *Clioscaphites vermiformis* and *C. choteauensis* is an undetermined pycnodont that is not *Micropycnodon* and is probably not *Hadrodus*.

AMIOIDS—*Paraliodesmus* is well known from the zone of *Protosphyraena pernicosa* and the zone of *Clioscaphites vermiformis* and *C. choteauensis*. Whether it was continuously present in Kansas during the intervening interval is not known.

PACHYCORMIDS—*Protosphyraena nitida* and *Protosphyraena pernicosa* are the only pachycormids known from the zone of *P. pernicosa*. *Protosphyraena tenuis*, *P. gladius*, and *P. nitida* coexisted during the zone of *Spinaptychus* n. sp. *Protosphyraena tenuis* is the only pachycormid known from the zone of *Cladoceramus undulatoplicatus*. It is likely that *P. gladius* will be found there in the future, because both species occur below and co-occur from the zones of *Clioscaphites vermiformis* and *C. choteauensis* to the top of the Smoky Hill Chalk Member. Only *P. gladius* is known from the Pierre Shale.

ASPIDORHYNCHIDS—*Belonostomus* certainly occurs within the zone of *Protosphyraena pernicosa*, and perhaps somewhat later during Niobrara deposition.

ICHTHYODECTIDS—*Xiphactinus*, *Ichthyodectes*, and *Gillicus* have pre-Niobrara records and are present from the beginning of Smoky Hill Chalk Member deposition into the Sharon Springs Shale Member (Martin and Stewart, 1982).

SAUROCEPHALIDS—There are no pre-Niobrara records of saurocephalids in North America, but *Saurodon* is present throughout Smoky Hill Chalk Member deposition and into the Pierre Shale. The first definite records of *Saurocephalus* in the Smoky Hill Chalk Member are from the zone of *Hesperornis*, as is the first record of an unnamed genus represented by "*Saurodon*" *pygmaeus*. Both of these occur in the Sharon Springs Shale Member.

PLETHODIDS—Of the three recognized species of *Bananogmius* in the Smoky Hill Chalk Member, *B. zitteli* seems to be present in the zone of *Protosphyraena pernicosa* but may not occur any higher. *Bananogmius evolutus* is unknown below the zone of *Spinaptychus sternbergi*, but continues into the Sharon Springs Shale Member. The earliest definite records of *B. favirostris* is from the zone of *Hesperornis*. Very little can be said of the ranges of *Luxilites striolatus* and *Niobrara encarsia*, each known from a single specimen. However, it is probable that they come from either the upper part of the zone of *Protosphyraena pernicosa*, or else from the zone of *Spinapytchus* n. sp. I cannot assign the holotype of *Zanclites xenurus* to any definite stratigraphic interval. There is no consensus on how many species of *Martinichthys* are valid, and there is little stratigraphic data for many of the primary types. However, *M. ziphoides*, *M. intermedius*, and *M. alternatus* seem to come from the uppermost levels of the zone of *Protosphyraena pernicosa*. It is probable that all species of *Martinichthys* come from this interval, although it is possible that some may extend into the zone of *Spinaptychus* n. sp.

Pachyrhizodontids—Of the three pachyrhizodontid species in the Niobrara Chalk, *P. minimus* and *P. caninus* have both pre- and post-Niobrara records. "*Pachyrhizodus*" *leptopsis* is known from the zone of *Cladoceramus undulatoplicatus* and the zone of *Clioscaphites vermiformis* and *C. choteauensis*. It continues into the Mooreville Chalk (Campanian) of the Gulf Coast (Stewart and Bell, 1989).

Urenchelyids—All known specimens of *Urenchelys abditus* are from the zone of *Clioscaphites vermiformis* and *C. choteauensis*. Other species have earlier records in the Old World, but none occurs later.

Cimolichthyids—*Cimolichthys nepaholica* is the only cimolichthyid from the Smoky Hill Chalk Member; it has no pre-Niobrara record but extends from the base of the Smoky Hill Chalk Member into the Sharon Springs Shale Member.

Enchodontids—*Enchodus petrosus* and *Enchodus gladiolus* apparently extend from the base of the Smoky Hill Chalk Member into the Sharon Springs Shale Member (Goody, 1976). *Enchodus dirus* extends from the zone of *Cladoceramus undulatoplicatus* to the top of the Smoky Hill Chalk Member. I cannot verify the presence of *Enchodus shumardi* below the zone of *Clioscaphites vermiformis* and *C. choteauensis*, and it appears to continue to the top of the Smoky Hill Chalk Member.

Dercetids—*Stratodus apicalis* apparently occurs from the zone of *Spinaptychus* n. sp. into the Pierre Shale. It is possible that records from earlier horizons will be found. *Leptecodon rectus*, which may not be a dercetid, occurs within the valves of *Platyceramus platinus* in the zone of *Spinaptychus sternbergi*.

Apateodus—The earliest reliable record of *Apateodus* in North America is in the zone of *Clioscaphites vermiformis* and *C. choteauensis*. It continues into the Pierre Shale. This genus is generally regarded as incertae sedis within the aleposauroids.

Ferrifrons—The holotype of *Ferrifrons rugosus* is a composite specimen (Chorn, 1979; Schultze et al., 1982). There is no available family to contain this genus.

Polymixiids—The only Niobrara polymixiid is *Omosoma garretti*. It is found within valves of *Platyceramus platinus* in the zone of *Spinaptychus sternbergi*.

Holocentrids—An unnamed genus of holocentrid occurs within the zone of *Protosphyraena pernicosa*. *Trachichthyoides*, *Caproberyx*, and two unnamed genera occur within valves of *Platyceramus platinus* in the zones of *Clioscaphites vermiformis* and *C. choteauensis*. *Kansius sternbergi* may come from that zone, but more probably comes from the zone of *Spinaptychus sternbergi*.

Toxochelyids—*Toxochelys latiremis* is present from virtually the beginning of Smoky Hill Chalk Member deposition. It continues into the Pierre Shale. The holotype of *Lophochelys natatrix* apparently comes from either the zone of *Spinaptychus sternbergi* or that of *Hesperornis*. The locality data are insufficient for certainty at this time. I cannot shed any light on the ranges of other Niobrara toxochelyids.

Protostegids—Some species of *Protostega* is present in the zone of *Hesperornis*, but I cannot tell which.

Mosasaurids—*Platecarpus ictericus* ranges throughout the Smoky Hill Chalk Member and into the Pierre Shale. *Tylosaurus* n. sp. is limited to the zone of *Protosphyraena pernicosa*.

Elasmosaurids—I can shed no light on the stratigraphic distribution of Smoky Hill Chalk Member elasmosaurids.

Polycotylids—Several skeletons assigned to the genus *Trinacromerum* have been found in the zone of *Hesperornis*. Fragmentary material from lower in the Smoky Hill Chalk Member are inadequate for closer identification. It is curious that Williston (1893, 1897) found plesiosaurs to be more common in the lower beds than in the upper. I am aware of a few juvenile propodials found in the lowest zones of the Smoky Hill Chalk Member, but otherwise know of no lower chalk specimens. Certainly nearly all the partial skeletons of Niobrara polycotylids have been collected from the upper horizons of the Smoky Hill Chalk Member (O. Bonner, personal communication, 1982). All locality data for published KU Niobrara plesiosaur specimens giving at least county information list Logan or Wallace counties except for one listed only as Gove County (Schultze et al., 1985).

Pteranodontids—*Pteranodon* does not seem to be present at the beginning of Smoky Hill Chalk Member deposition, but it is clearly present in the upper levels of the zone of *Protosphyraena pernicosa*. It continues throughout the remainder of Smoky Hill Chalk Member deposition. The earliest occurrence of *Nyctosaurus* that I can document is in the zone of *Clioscaphites vermiformis* and *C. choteauensis*. It apparently continues into the zone of *Hesperornis*.

Ichthyornithids—Some species of *Ichthyornis* is present in the zone of *Protosphyraena pernicosa*, and at least two species occur in the zone of *Spinaptychus* n. sp. The alpha taxonomy of *Ichthyornis* is in need of revision. It appears that every interval of the Smoky Hill Chalk Member contains some species of *Ichthyornis*.

Baptornithids—What little locality data are available for *Baptornis advenus* indicate that it is from the zone of *Hesperornis*.

Hesperornithids—*Parahesperornis alexi* seems to be limited to the zone of *Spinaptychus sternbergi*. *Hesperornis* is apparently restricted to the levels above that zone in the Smoky Hill Chalk Member and in later sediment in the Western Interior.

Discussion

I suggest that the reasons for these distributions are threefold: climatic change or deepening water, extinction, and evolution of new forms.

Hattin (1982) proposed that the distribution of *Durania* and *Texanites* (*Spinaptychus*) in the Smoky Hill Chalk Member are related to warm climatic intervals. This hypothesis has merit and suggests an explanation of temporal and geographic distribution of some vertebrate taxa. It is true that *Durania* seems to be more common in the upper part of the zone of *Protosphyraena pernicosa* and in the zone of *Spinaptychus* n. sp. than in any other Smoky Hill Chalk Member interval. This suggests that *Martinichthys* and *Bananogmius zitteli* may be warm indicators, since they coincide with the upper part of the zone of *P. pernicosa*. Indeed, *Bananogmius zitteli* or *B. auratus* occurs in Cenomanian horizons in Texas. Other plethodids known from southern localities are *Enrischorhinchus* in Texas, and *Moorevillia* and *Bananogmius crileyi* in the Mooreville Formation. If *Protosphyraena pernicosa* is a warm-water taxon, then the reason for its extinction is not clear. It is unknown outside of Kansas. In general, the pattern may be one of cooling throughout post-Turonian times, with periodic slightly warmer intervals. If *Cimolichthys* came by way of cooling, we might expect to see pre-Coniacian *Cimolichthys* further north. Next would come the slight warming in latest Coniacian times with the appearance of *Bananogmius zitteli*, *Martinichthys*, and *Spinaptychus* n. sp. (*Spinaptychus* is thought to be the aptychus of *Texanites*, an ammonite of Tethyan affinities.) However, this general period coincides with the last appearance of *Scapanorhynchus*, *Ptychodus anonymous*, and *P. martini* in Kansas. *Scapanorhynchus* persists in New Mexico, Texas, Alabama, and North Carolina. However, it does occur in the Mesa Verde Formation, north of Kansas. If these were extirpated by climatic cooling, why did they not reappear with the latest Coniacian warming?

The late Santonian extirpation of *Ptychodus mortoni*, *Pseudocorax laevis*, and *Pachyrhizodus leptopsis* from the Western Interior is almost certainly related to temperature. All three continue in Texas and/or Alabama. *Ptychodus mortoni* continues in the Mooreville Formation of Alabama (Applegate, 1970) and *Pseudocorax* persists in the base of the Taylor Group (Campanian) and the Wolf City Formation (Campanian) of Texas, the Brownstone Marl (Campanian) of Alabama, the Coffee Sand (Campanian) of Mississippi, and the base of the Mooreville Formation (Santonian) of Alabama (Meyer, 1974). *Pachyrhizodus leptopsis* is probably a Tethyan form. It occurs in older Texas rocks and in the Mooreville Formation (Campanian) of Alabama. An indicator of cooling at that time is the appearance of *Apateodus* in the Smoky Hill Chalk Member.

Continued cooling later in the Santonian apparently brought in northern plethodids (*Bananogmius evolutus* and *B. favirostris*) and *Parahesperornis*. Both species of *Bananogmius* continue into the Pierre Shale. Neither occurs in Texas or Alabama. The last appearance of *Laminospondylus* in Kansas is in this horizon; cooling also could be the cause of this. Likewise, the first appearance of *Hesperornis* in the Niobrara Chalk could be related to cooling. It continues into the Pierre Shale. It is fairly well established that the hesperornithiforms had a generally boreal distribution (Russell, 1967a, 1988; Bardack, 1968; Martin and Stewart, 1982; Bryant, 1983). "*Saurodon*" *pygmaeus* also appears in Kansas at that time and is otherwise known only from the Pierre Shale of South Dakota and Wyoming. The appearance of *Saurocephalus leanus*, certainly present by the zone of *Hesperornis*, cannot be attributed to temperature changes. It is present in post-Niobrara rocks from Canada to the East Texas and Mississippi embayments. The last appearance of *Cretoxyrhina mantelli* in the zone of *Hesperornis* also is the last appearance in the midcontinent. It persists later in Alabama (Mooreville, Eutaw formations, Russell, 1988) and Mississippi (Eutaw Formation, Russell, 1988), contrary to statement by Cappetta (1987, p. 99) that the taxon never attained the Campanian. Therefore, I conclude that its extirpation in Kansas stems from cooling.

Published accounts may cause some to question that *Cimolichthys* could be an indicator of cooling temperatures. It first occurs in Cenomanian horizons of the English Chalk (Woodward, 1902). The southernmost North American record is in Texas (Bardack, 1965). The record of *Cimolichthys* in the Mooreville Chalk (Applegate, 1970) is unfounded, and none has been found since 1970 (G. Bell, personal communication, 1988).

If the scenario of continued cooling is generally accurate for post-Turonian times in Kansas, the mosasaur fauna does not seem to reflect it. The concept of *Clidastes* as a warm-water mosasaur (Russell, 1970) seems well founded. *Clidastes* is probably more common in the upper Smoky Hill Chalk Member than in the lower (Williston, 1897), and it certainly continues in the Pierre Shale of Kansas, Wyoming, and South Dakota. An alternative reason for the disappearance of some species, including *Pseudocorax laevis*, from Kansas could be deepening water. Evolution of new forms is responsible for the succession of *Clioscaphites*, *Spinaptychus*, and *Squalicorax* species in the Western Interior.

The "*Rudistes*" and "*Hesperornis*" beds are not very useful names. *Durania* is found throughout much of the Smoky Hill Chalk Member (Hattin, 1988). *Hesperornis* is apparently not found in the beds immediately above Marker Unit 10 of Hattin (1982) and certainly is not at all even a moderately common taxon where it does occur higher in the Smoky Hill Chalk Member. Part of the confusion is that *Parahesperornis* would have been known to Williston as *Hesperornis* (Martin, 1984). Perhaps "Hesperornithid beds" would be more accurate.

Future collecting will probably alter some of the stratigraphic range data given here. A likely area for change will be in the ranges of some of the smaller sharks. The small teeth are almost never noticed by casual searching and must be collected intentionally. Many of the very small osteichthyans remain to be named and studied. I have made very little mention of the ranges of the rarer mosasaur and turtle species. The taxonomy of the polycotylid plesiosaurs is not stable, and the elasmosaurids have been treated as though each specimen is a new species.

The Smoky Hill Chalk Member ichthyofauna is unusual in its paucity of small, non-lamniform sharks. Many beds of this age throughout the world have horizons where teeth are concentrated, and from which small teeth may be screened or otherwise extracted. The Smoky Hill Chalk Member is an exception in two respects. First, there are very few horizons where bones or teeth are concentrated. The few exceptions are lenses of inoceramid and ostreid debris that occur at irregular intervals. Dissolution of these lenses in acetic acid often yields a residue of small bones and teeth, but these are almost entirely those of actinopterygians. At one locality I have recovered a few teeth of *Rhinobatos*, and the teeth of *Pseudocorax* in another. Nonetheless, my limited investigations of these lenses lead me to conclude that the chondrichthyan fauna was quite limited and numerically overwhelmed by the abundance of actinopterygians. This is certainly in contrast to the ratios of absolute numbers of chondrichthyan to actinopterygian teeth in sands and conglomerates in earlier Upper Cretaceous strata in Kansas. There also is a definite difference in the taxonomic diversity of these two groups in Smoky Hill shell lenses compared to sands and conglomerates in earlier Kansas horizons. I attribute these differences in large part to the deep water and apparently reduced oxygen levels near the sea floor.

The composition of the Smoky Hill Chalk Member chondrichthyan fauna is similar to that termed the *Ptychodus–Cretoxyrhina* association in the usage of Meyer (1974). He defined that association thus: "Faunas with low diversity but large numbers of individual teeth. Dominated by *Squalicorax*, *Cretoxyrhina*, and *Ptychodus* with very little else present. Found in thin-bedded silty calcarenites with thick dark olive gray shale interbeds and chalk-limestone facies (Niobrara Group)." Meyer (1974) characterized the *Ptychodus–Cretoxyrhina* association as differing from most other Upper Cretaceous shark associations by having more anacoracids than *Odontaspis*. The Smoky Hill Chalk Member is even more extreme in this respect than most of his Texas examples of the *Ptychodus–Cretoxyrhina* association in having very nearly no *Odontaspis* at all. Meyer (1974) explained the abundance of pelagic sharks in this association and absence of other types as being the result of deposition in deeper water.

Within the Niobrara Chalk, there is a general upward trend of continuing reduction of chondrichthyan diversity. First, *Scapanorhynchus* and two species of *Ptychodus* are lost. Next, *Ptychodus mortoni* and *Pseudocorax laevis* disappear. Eventually, even *Cretoxyrhina mantelli* is lost. The apparently brief appearance of *Rhinobatos* near the top of the member may be due to improved oxygenation and/or shallower water.

Except for brief intervals, the Smoky Hill Chalk Member ichthyofauna seems to be devoid of acanthomorph teleosts. Upper Cretaceous faunas from Lebanon apparently produce a higher percentage. This may be, in part, a result of a generally negative preservational bias in the case of the Kansas chalk acanthomorphs. Some of the inoceramid-ostreid calcarenites yield elements of acanthomorphs that appear to be different from those preserved within inoceramids (Stewart, this volume). This could have to do with proximity to shore. The only acanthomorphs in the Smoky Hill Chalk Member seem to be tied to areas with topographic relief (particular bivalves). Even though only sporadically present, the diversity and abundance of Smoky Hill Chalk Member acanthomorphs appears to be greater than in earlier Upper Cretaceous horizons in the Western Interior.

Conclusions

Even in the last two decades, most collecting of vertebrate fossils in the Smoky Hill Chalk Member have been performed without proper stratigraphic data. Our understanding of the vertebrate biostratigraphy of the Smoky Hill Chalk Member is rapidly increasing. The "Niobrara vertebrate fauna" is, in reality, composed of several faunas. Many of the faunal changes within the Niobrara Chalk seem to be due to climatic change or change in water depth. Others are due to extinction, and yet others are due to evolution. There are still species and genera of invertebrates, fish, and reptiles to be described. Although some of these organisms are rather large (on the order of meters), others are quite small. One of the undescribed teleosts is the most numerous vertebrate species known in collections from the Niobrara Formation.

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Taxonomic listing by zone

Zone of *Protosphyraena pernicosa*

Volviceramus grandis *Actinocamax* sp.
Durania maxima
Pseudoperna congesta
Tusoteuthis longa
Zeugmatolepas sp.

Squalicorax falcatus
Scapanorhynchus rhaphiodon
Pseudocorax laevis
Cretoxyrhina mantelli
Ptychodus mortoni
Ptychodus martini
Ptychodus anonymous

Belonostomus sp.
Micropycnodon kansasensis
Lepisosteus sp.
Protosphyraena pernicosa
Protosphyraena nitida
Paraliodesmus guadagnii

Xiphactinus audax
Ichthyodectes ctenodon
Gillicus arcuatus
Saurodon leanus
Apsopelix anglicus
Pachyrhizodus minimus
Pachyrhizodus caninus
Albulidae
Cimolichthys nepaholica

Enchodus gladiolus
?*Laminospondylus transversus*
Bananogmius zitteli
Martinichthys ziphoides
other plethodids
holocentrid

Toxochelys latiremis
Chelosphargis advena

Platecarpus ictericus
Tylosaurus nepaeolica
undesc. tylosaurid
Ichthyornis sp.

Zone of *Spinaptychus* n. sp.

Durania maxima
Pseudoperna congesta
Volviceramus grandis
Tusoteuthis longa
Spinaptychus n. sp.
Zeugmatolepas sp.
last *Ptychodus anonymus*
last *Ptychodus martini*
Ptychodus mortoni
Pseudocorax laevis
Squalicorax falcatus

spiral coprolites—imply presence of some rare shark
Cretoxyrhina mantelli
? *Cretolamna appendiculata*

? *Paraliodesmus guadagnii*
Protosphyraena nitida
Protosphyraena tenuis
Protosphyraena gladius
Xiphactinus audax
Ichthyodectes ctenodon

Gillicus arcuatus
? *Saurodon leanus*
? *Pachyrhizodus minimus*
? *Pachyrhizodus caninus*
Laminospondylus transversus
Cimolichthys nepaholica
Enchodus dirus
Enchodus petrosus
Stratodus apicalis

Zone of *Cladoceramus undulatoplicatus*

Cladoceramus undulatoplicatus
Platycermus platinus s.l.
Durania maxima
Pseudoperna congesta
Tusoteuthis longa
Zeugmatolepas sp.

Ptychodus mortoni
Squalicorax falcatus
Cretolamna appendiculata
Cretoxyrhina mantelli

Protosphyraena tenuis

?Xiphactinus audax
? Ichthyodectes ctenodon
Saurodon leanus
Gillicus arcuatus
Pachyrhizodus caninus
Pachyrhizodus minimus
Pachyrhizodus leptopsis

Cimolichthys nepaholica
Enchodus dirus
Enchodus gladiolus

? Platecarpus ictericus

small *Ichthyornis*

Zone of *Clioscaphites vermiformis* and *C. choteauensis*

Pseudoperna congesta
Platyceramus platinus s.s.
Inoceramus balticus
Durania maxima
Lucina sp.
Philopteria sp.
Tusoteuthis longa
Clioscaphites vermiformis
Clioscaphites choteauensis
Baculites sp.
Zeugmatolepas sp.
Uintacrinus socialis

Ptychodus mortoni
Squalicorax cf. *S. falcatus*
Pseudocorax laevis
Cretoxyrhina mantelli
? *Cretolamna appendiculata*

pycnodont
Paraliodesmus guadagnii
Protosphyraena tenuis
Protosphyraena gladius

Xiphactinus audax
Ichthyodectes ctenodon
Gillicus arcuatus
? Saurodon leanus
Apsopelix anglicus
Urenchelys abditus
Pachyrhizodus caninus
Pachyrhizodus minimus
"*Pachyrhizodus*" *leptopsis*
Plethodidae undet.
Cimolichthys nepaholica
Laminospondylus transversus
Enchodus shumardi
Enchodus gladiolus

Enchodus petrosus
Apateodus sp.
Stratodus apicalis
Caproberyx sp.
Trachichthyoides sp.
holocentrid alpha
holocentrid beta

plesiosaur, cf. polycotylid

Toxochelys latiremis

? Platecarpus ictericus

Pteranodon sp.
Nyctosaurus sp.
Hierosaurus sp.

Ichthyornis sp.

Zone of *Spinaptychus sternbergi*

Pseudoperna congesta
Platyceramus platinus
? Inoceramus balticus
Pseudoperna congesta
Tusoteuthis longa
Spinaptychus sternbergi
Zeugmatolepas sp.

Xiphoctinus audax
Ichthyodectes ctenodon
Gillicus arcuatus
Saurodon leanus

Apsopelix anglicus
Pachyrhizodus caninus
Pachyrhizodus minimus
Bananogmius evolutus
Cimolichthys nepaholica
Laminospondylus transversus
Enchodus shumardi
Stratodus apicalis
Leptecodon rectus
Apateodus sp.
Omosoma garretti
?Kansius sternbergi
?Prosaurodon pygmaeus

Ectenosaurus clidastoides
Tylosaurus proriger
? Platecarpus ictericus

Nyctosaurus sp.
Pteranodon

Parahesperornis alexi

Zone of *Hesperornis*

Ostrea rugosa
Ostrea falcata
Durania maxima
Tusoteuthis longa
Baculites sp.
Rugaptychus sp.
Zeugmatolepas martini

Squalicorax sp. aff. *S. kaupi*
Cretoxyrhina mantelli
? Cretolamna appendiculata
Platecarpus ictericus
Clidastes propython
Tylosaurus proriger

Trinacromerum osborni

Hesperornis
Baptornis
Apatornis

Niobrara Formation symbiotic fish in inoceramid bivalves

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Abstract

At the end of the first century of paleontological exploration of the Niobrara Chalk of Kansas, its fish fauna seemed archaic relative to contemporaneous fish faunas in having very few acanthomorphs. That perception must now be significantly altered to accommodate at least four undescribed holocentrid species, as well as a polymixiid, *Omosoma garretti* Bardack, 1976. All known specimens of these five species come from within inoceramid bivalves, as do all known specimens of *Leptecodon rectus* Williston, 1899, *Kansius sternbergi* Hussakof 1929 and *Urenchelys abditus* Wiley and Stewart, 1981, and most specimens of an amioid, *Paraliodesmus guadagnii* Dunkle, 1969. More than 100 individual inoceramids from the Smoky Hill Chalk Member have been found to contain fish, and more than 1,000 individual fish, mostly acanthomorphs, come from within inoceramids. From data provided by Russell (1988), it appears that more than 28% of all Niobrara fish in museum collections are inoceramid commensal acanthomorphs. Three temporally and taxonomically distinct inoceramid-fish communities existed during deposition of the Smoky Hill Chalk Member in the zones of *Volviceramus grandis* (late Coniacian), *Clioscaphites choteauensis* (late Santonian), and *Spinaptychus sternbergi* (late Santonian).

Introduction

Many types of fish symbiosis have been documented with various coelenterates, mollusks, and echinoderms. Inquilinism is traditionally used in ichthyological literature in a broader sense than in sociobiological literature. In the ichthyological context, it simply denotes an animal which frequents the interior of another animal without detriment to the host. One of the most familiar examples is the pearlfish (Carapidae), which are known to be commensals of pearl oysters, sea cucumbers, and starfish. At least two species of the apogonid *Apogonichthys* inhabit the conch *Strombus bituberculatus* (Gudger, 1927). Two related examples of present-day fish-bivalve commensalism are particularly relevant to the topic at hand. Able (1974) demonstrated that the nocturnal cyclopterid *Liparis inquilinus* occupies *Placopecten magellanicus* (Gmelin) during most or all of the post-larval and pre-reproductive part of its life cycle. He also concluded that probably no other species of the genus *Liparis* does so (Able, 1973). This fish probably occasionally occupies *Aequipecten irradians*. The pectens are not entirely willing hosts, but show no apparent benefit or detriment (Able, 1974). Juvenile red hake, *Urophycis chuss* (Walbaum), also occupy *P. magellanicus*, especially by day. Laboratory experiments show that hake prefer non-living shells to living pectens and often excavate a chamber beneath the shells (Steiner et al., 1982). It appears that most fish that are inquilines of mollusks are nocturnal. The inquilines of pectens (juvenile *Urophychus chuss* and *Liparis inquilinus*) are more frequently found within pectens diurnally than nocturnally (Able, 1974; Steiner et al., 1982). Likewise, two species of cardinal-fish (*Apogonichthys*, an inquiline of the gastropod *Strombus*), are nocturnal (Gudger, 1927).

History of inoceramid inquiline research

Within the first decade or so of scientific fossil collecting in the Niobrara Formation of Kansas, collectors recovered several small fish preserved upon pieces of inoceramid bivalves. Several species of the Inoceramidae, some quite large, occur in the Smoky Hill Chalk Member. *Volviceramus grandis* is an almost spherical inoceramid occurring in the lower horizons of the Smoky Hill Chalk Member. Its lower (left) valve is bowl-shaped and its upper (right) valve is caplike. Also within the zone of *Volviceramus grandis* is a platter-shaped inoceramid generally identified as *Platyceramus platinus* sensu lato. Above the zone of *V. grandis* is the zone of *Cladoceramus undulatoplicatus*. This fairly flat inoceramid is remarkable because of the undulating plications that radiate from the umbonal area. Above that zone is the zone of *Platyceramus platinus* sensu stricto. This is a fairly compressed, nearly quadrate inoceramid measuring over 1 m (3.3 ft) on a side. The axial length can exceed 2 m (6.6 ft). Some of the shells, of which only the prismatic (calcitic) layer is preserved, attain a thickness of more than 4 cm (1.6 inches) along some edges.

The earliest discovery of Niobrara fish preserved upon inoceramid shells is from an 1874 collection made by Benjamin Mudge for O. C. Marsh. It was not until 1899, however, that S. W. Williston described the first fish, *Leptecodon rectus*, preserved on a fragment of *Platyceramus platinus*. Williston (1899, 1900) also mentioned that several specimens of a smaller, undetermined teleost were preserved on the same fragment. Hussakof (1929) described three small acanthomorph skeletons from the Smoky Hill Chalk Member as holocentrids and assigned them to the new genus and species *Kansius sternbergi*. Perhaps it was his unfamiliarity with the Niobrara Chalk fauna and preservation that precluded his recognizing that these skeletons bore the undulating impression of an inner surface of a *Platyceramus platinus* valve, and that the interstitial calcite crystals among the bones demonstrated that the skeletons had been pressed against some flat object. It was Dunkle (1969) who first stated that fish could be found within Niobrara Chalk inoceramid shells; in this work he described an amioid halecostome, *Paraliodesmus guadagnii*, that he had found by intentionally searching within inoceramids.

Bardack's (1976) description of a new polymixiid species, *Omosoma garretti*, preserved with a second specimen of *Leptecodon rectus* on an inner surface of a *Platyceramus platinus* valve, prompted him to discuss the cause of such associations. His explanation was that inoceramid valves would open upon death, exposing the inner surfaces of both valves. He reasoned that since all the inoceramid fragments bearing these fish had epizoa (primarily ostreids) on the outer surface, these must represent upper (right) valves. He believed that the fish found on a given inoceramid specimen (he reported as many as 50 *Kansius* on one specimen) must have been swept together by current action and buried rapidly. He believed that only rarely were these fish species preserved in chalk matrix, and then only in unusually hard chalk. In short, he believed that these associations were entirely coincidental and due to fortuitous substrates.

Wiley and Stewart (1981) described the first Mesozoic eel from North America (*Urenchelys abditus*) from within a specimen of *Platyceramus platinus*. They stated that the specimen shared the interior of that bivalve with several specimens of an undescribed holocentrid, but did not offer an interpretation of this unusual context.

Recent research

I have indicated elsewhere (Stewart, 1982, 1987, 1990) an interpretation that several Late Cretaceous halecostome fish provide paleontologic evidence of inquilinism. My investigations confirm the findings of Dunkle (1969) that fish do indeed occur within articulated valves of inoceramids in the Smoky Hill Chalk Member, and not merely on open valves as was suggested by Bardack (1976). Three faunal zones within the Smoky Hill Chalk Member contain fish-inoceramid associations. The first lies within the zone of *Volviceramus grandis*. Here, specimens of *Paraliodesmus guadagnii* and an undescribed holocentrid may be found on or within specimens of *Volviceramus grandis*, and the undescribed holocentrid also occurs within articulated valves of *Platyceramus platinus* s.l. In the *Clioscaphites choteauensis* zone, *Paraliodesmus guadagnii*, *Urenchelys abditus*, and four undescribed holocentrid species are found within valves of *Platyceramus platinus* s.s. I have assigned one of the undescribed species to the genus *Trachichthyoides* and a large one to *Caproberyx* sp. The geologically youngest fish-inoceramid association comes from the zone of *Spinaptychus sternbergi*. Here, *Omosoma garretti* and *Leptecodon rectus* are preserved within valves of *Platyceramus platinus* s.s. The only occurrence of *Kansius sternbergi* may have come from the zone of *Clioscaphites choteauensis*, but might also be from the zone of *Spinaptychus sternbergi*.

The first problem with Bardack's interpretation (1976) is the taxonomic distinction between those fish species found on or within inoceramids and those distributed elsewhere in the chalk matrix. There are several small fish species, some of them quite common, that are only found at large in the chalk matrix. Among these are *Enchodus gladiolus*, *Enchodus shumardi*, *Apsopelix anglicus*, and an albulid. These species have never been found within inoceramids. Conversely, of the at least nine species of fish found within inoceramids, only two specimens of one species have ever been found outside of inoceramids in the chalk. The only technical exception is that fragments of disarticulated fish may be found on the exteriors of some *Platyceramus platinus* that contain other individuals of those species. In such cases one can usually see compressional ruptures in the inoceramid valves and follow a trail of fish skeletal elements through those ruptures onto the outer (usually lower) surface of the inoceramid. If the chances of landing on an inoceramid were the same for all small dead fish, it would be extremely improbable for over 1,200 specimens of one set of small fish species to be found on (or within) inoceramid valves and for several hundred individuals of another set never to be so preserved.

Another problem with Bardack's interpretation (1976) is that *Platyceramus platinus* is usually preserved with both valves in approximate articulation and occluded. According to the study of Schafer (1972), bivalves do not open widely after death unless the ligament dries out or currents or other agents disrupt the valves. Therefore, fish preserved on the inner surface of a weathered inoceramid valve does not necessarily mean the fish came to rest against an open inoceramid. The same situation would result from fish within an occluded pair of valves being exposed after the upper valve had largely weathered away. It is true, however, that many specimens of *Volviceramus grandis* are preserved with the cap valve open.

The orientation of epizoa growing on an inoceramid can give some insight into the life position of the host. The fact that epizoans encrust the outer side of an inoceramid valve does not guarantee that this valve is a right (upper) valve. Hattin (1982) and Stewart (1990) state that epizoa are often found on the exteriors of both the upper and lower valves of Smoky Hill Chalk Member inoceramids. This phenomenon is difficult to explain if the filter-feeding epizoa (ostreids and cirripeds) were living simultaneously on upper and lower valves of a large, recumbent bivalve. One would intuitively expect filter-feeders to be fouled by sediment if situated between the bottom valve and a very soft and fine-grained substrate. Nonetheless, Hattin (1982) proposed that the substrate was so watery as to permit this.

I object to that interpretation for a number of reasons. Hattin (1982, 1984) mentions Smoky Hill rudists (*Durania maxima*) that show encrusting ostreids restricted by the water-sediment boundary. If they were restricted by this boundary on a rudist, why not on an inoceramid? Indeed, I have noted a water-sediment boundary on lower valves of fish-containing *Platyceramus platinus* as indicated by presence or absence of the left (lower) valves of the encrusting ostreids and the presence or absence of articulated lepadomorph thoracican cirripeds (*Zeugmatolepas* sp.). However, logic dictates that the preserved position of the lower *Platyceramus platinus* valve was not the position while the epizoa were living. One consistently observes that the size and distribution of ostreids is the same on the upper and lower valves of a given *P. platinus* in the Smoky Hill Chalk Member, but that the size and distribution of ostreids varies greatly among individual *P. platinus*. It would seem more parsimonious to hypothesize an upright, presumably byssate, life orientation for *P. platinus* than to suggest that the supporting sediment would not significantly inhibit the settlement and growth of ostreids on the lower valve. The free (right) valves of the ostreids are often preserved on the upper valve of a *P. platinus*, but not on the rim area of the lower valve (fig. 1b). One would predict that if a toppled inoceramid stayed somewhat above the sediment-water interface for some period of time, unsupported ostreids on its lower valve would lose their free (right) valves as they decayed, the lower (left) valve being cemented to the host (fig. 1b). I assume that during the life of the *P. platinus*, the number and distribution of *Zeugmatolepas* on one valve generally conformed to that of the opposite valve. As preserved, however, only isolated *Zeugmatolepas* plates may be found on upper valves, whereas none are found around the rim of the bottom valve (within an area generally corresponding to that where the ostreids lack the free valve),

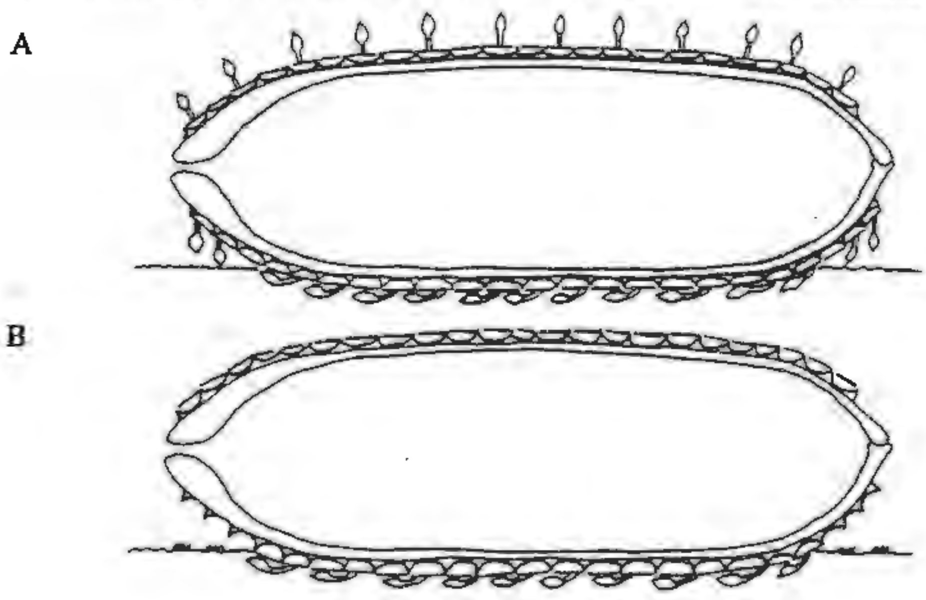

FIGURE 1—Diagrammatic cross sections of *Platyceramus platinus* and its epifauna in the axial plane. A) *Platyceramus* immediately after toppling. All epizoa are intact and *Zeugmatolepas* beneath the lower valve are oriented away from the umbo. B) *Platyceramus* after death of epizoa, but before burial. The *Zeugmatolepas* that formerly covered the upper (right) valve are gone as are those that were on the exposed portion of the lower (left) valve. The right valves of *Pseudoperna* on the exposed portion of the lower *Platyceramus* valve have also fallen away.

and well-articulated *Zeugmatolepas* are found in the central part of the lower *P. platinus* valve. *Zeugmatolepas* are disarticulated on the upper valve and absent from the rim of the lower valve because the plates of the cirripeds would disassociate once the animal decayed. They are articulated and well preserved in the central area of the lower valve because the sudden toppling of the host pressed them against the sediment (fig. 1). The *Zeugmatolepas* had not been projecting into the sediment prior to compaction, because there is no sediment between them and the ostreids to which they are attached. If the sediment had not been coherent enough to choke out the filter-feeders on the underside of an inoceramid, it would not have been coherent enough to ensure the preservation of articulated ostreids and cirripeds beneath the inoceramid. A well-defined boundary between articulated and disarticulated epizoa beneath a *P. platinus* implies a well-defined water-sediment boundary.

The orientation of the articulated *Zeugmatolepas* beneath the *Platyceramus platinus* provides useful information. In numerous specimens of *Platyceramus* examined, the *Zeugmatolepas* are oriented such that their free ends are directed away from the umbo and generally perpendicular to the growth lines of the *P. platinus* (fig. 2). I interpret this to be the result of water rushing out from beneath the *P. platinus* as it fell over. The pattern is, of course, preserved only where the *Zeugmatolepas* were pressed against the substrate. Alternatively, the pattern could be explained as the life position of the *Zeugmatolepas*. However, the stalks seem too elongate to be held in such a fixed position.

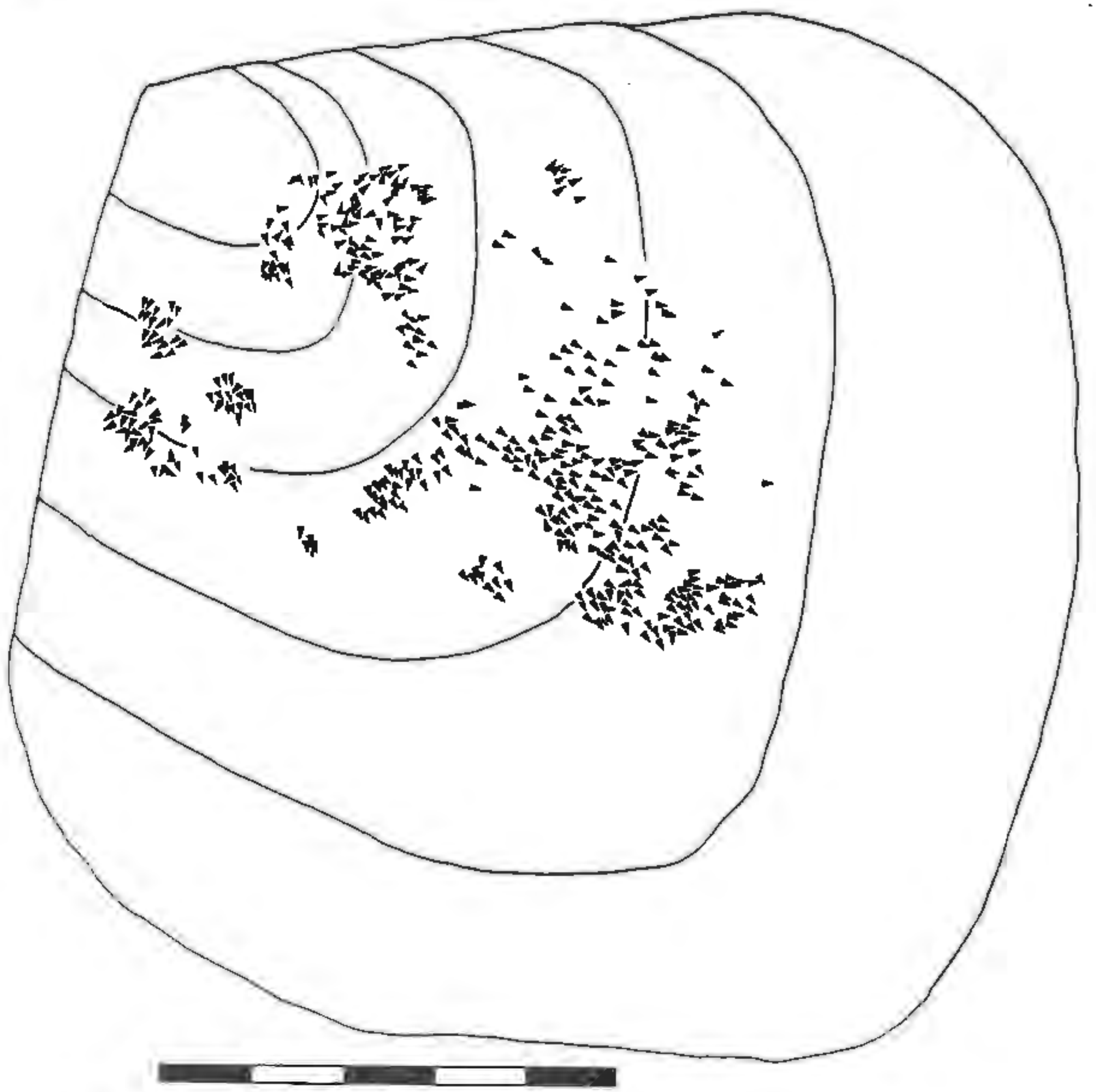

FIGURE 2—View from above a *Platyceramus platinus* as preserved, looking through the left valve. Arrows show the orientations of individual lepadomorph cirripeds (*Zeugmatolepas* sp.) beneath specimen hosting many disarticulated individuals of inoceramid alpha. University of Kansas Vertebrate Paleontology (KUVP) 60682. Scale equals 50 cm (20 inches).

Hattin (1982) objected to a hypothetical upright orientation of *Platyceramus* because none has been found in that position, and because Erle Kauffman (personal communication to Hattin) has seen no evidence of byssal attachment. The second statement is difficult to evaluate, but it is not surprising that no *Platyceramus* have been found preserved in an upright position in the Smoky Hill Chalk Member, because the average deposition rate was, according to Hattin (1982), approximately 0.036 mm/year. I have observed many *Platyceramus platinus* specimens that have a crushed anterior margin, part preserved vertically and part horizontally, indicating a rather steep angle here relative to the generally flat surface of the majority of the shell. This surface on the anterior margin is essentially a rudimentary lunule. However, I cannot state that this surface is entirely devoid of ostreids. Seitz (1962) argued that a close relative of *Platyceramus platinus*, *Platyceramus mantelli mantelli*, could have had a byssus.

Some soft anatomy of the inoceramids is preserved. In many specimens of *P. platinus* from the zone of *Clioscaphites choteauensis*, and in a few from the zones of both *Volviceramus grandis* and *Spinaptychus sternbergi*, gills are visible. In many instances, fish preserved within those *P. platinus* specimens are found between or beneath the gills (fig. 3). This implies that those inoceramids were alive or only very recently deceased when the fish died (Stewart, 1982, 1987, 1990).

These findings are the basis for the hypothesis that the fish found within the Smoky Hill Chalk Member inoceramids were inquilines of the inoceramids, that *Platyceramus platinus* lived in an upright rather than recumbent position, and that the toppling of a *P. platinus* containing fish led to the death of both the host and the inquilines. A ligament strong enough to open such a large bivalve in an erect position may not be strong enough to open it in a recumbent position.

Implications

The conclusion that these entombed fish were inquilines of inoceramids leads to several additional hypotheses. The first is that many species of inquiline fish interacted with one another as well as with their hosts. In the zone of *Volviceramus grandis*, both *Paraliodesmus* and an undescribed holocentrid have been found in the same inoceramid specimen. Numerous multi-species occurrences are known from the zone of *Clioscaphites*

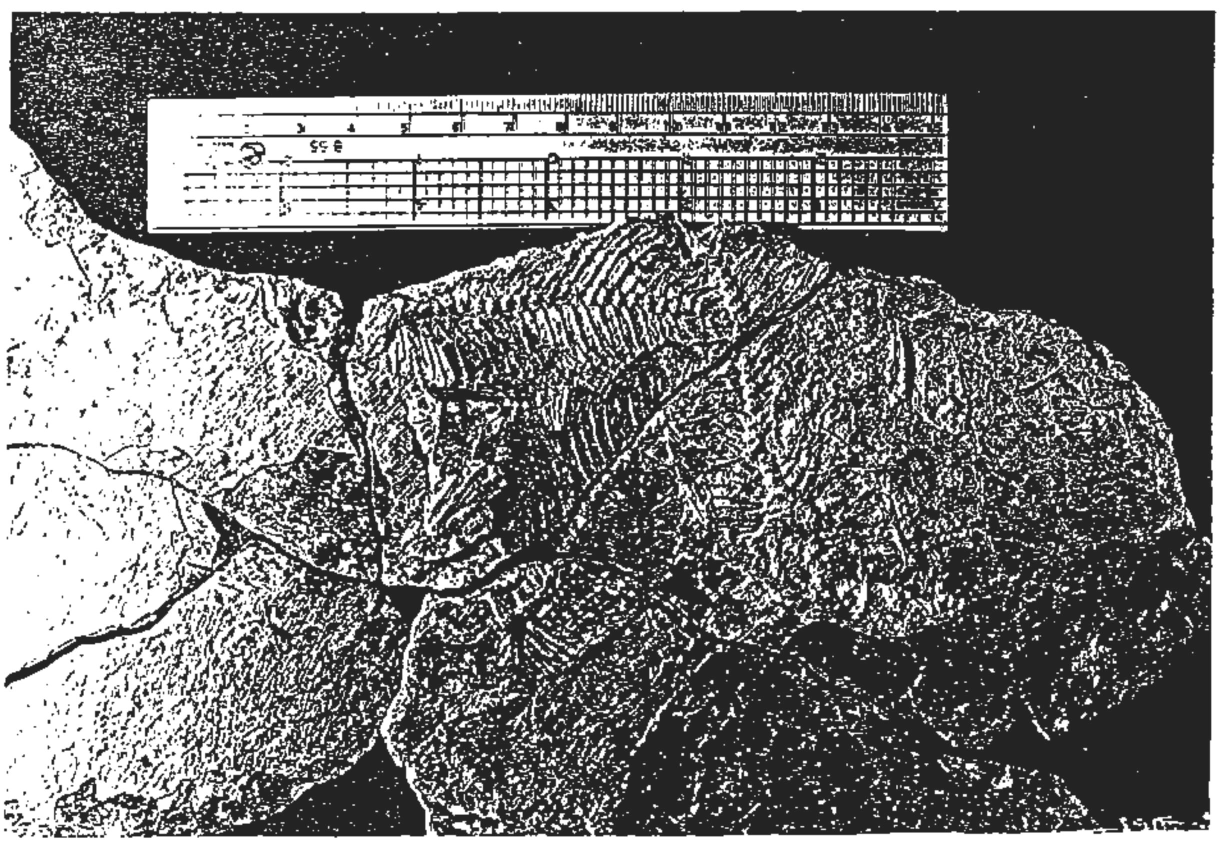

FIGURE 3—Photograph of three holocentrid alpha, KUVP 69479–69481, preserved within *Platyceramus platinus*, showing gills of the host overlapping the fish skeletons. The gills are the thin, finely striated layer. Scale equals 15 cm.

choteauensis. One specimen of *Platyceramus platinus* hosts both *Paraliodesmus* and an undescribed holocentrid I will here refer to as holocentrid alpha. Two contain *Urenchelys abditus* and holocentrid alpha. Three specimens of *Platyceramus platinus* host holocentrid alpha and *Trachichthyoides*. Four more contain holocentrid alpha and *Caproberyx*. Up to three fish species may have cohabitated. *Paraliodesmus*, *Trachichthyoides*, and holocentrid alpha are preserved in one *Platyceramus platinus*. Among these species, only *Paraliodesmus* is known to have preserved stomach contents. Although it was clearly carnivorous, there is no indication that it preyed on any other inquiline fish species.

In the zone of *Spinaptychus sternbergi*, only two inquiline fish species are known: *Omosoma garretti* and *Leptecodon rectus*. As many as 36 *Omosoma* have been found in an individual *Platyceramus platinus*. Only two *Leptecodon* specimens are known. Each was found in a *P. platinus* with several specimens of *Omosoma*. In one *Leptecodon*, the stomach definitely contains a small teleost, possibly *Omosoma* (fig. 5). The other *Leptecodon* may have an *Omosoma* in its alimentary cavity, but it is unclear because of the nature of its preservation. It is possible that this fish within a fish within an inoceramid is evidence that predators had penetrated the defenses of the inquiline fish species. The fact that this is the geologically

TABLE 1—One-way analysis of variance of the first 10 caudal centra of holocentrid alpha.

Specimen no.	KUVP 49403	KUVP 65700	KUVP 49403	KUVP 57251	KUVP 47247	KUVP 69467, 69469, 69470, 69472, 69473	KUVP 49403	KUVP 65697	AMNH 9840	USNM 336382–336386
Measurement in mm	28.7	20.6	22.4	24.3	19.3	23.9	22.4	27.6	21.7	26.8
	25.7	23.8	22.9	21.3	23.1	26.5	21.6	27.8	21.6	23.0
	26.8	20.9	19.1	23.9	20.4	26.5	21.7	28.5	21.2	21.2
	27.3	26.1	20.2	24.7	24.2	26.8	20.8	27.5	21.2	21.7
	24.9	21.6	21.0	25.5	22.8	28.7	21.7	26.9	21.7	24.5
	28.0	25.5	22.7	23.4						
	28.5	26.1	26.5							
	29.2	24.6								
	27.9									

Analysis of variance

DUE TO	DF	SS	MS = SS/DF	F-RATIO
Factor	9	312.91	34.77	11.54***
Error	50	150.59	3.01	
Total	59	463.50		

LEVEL	N	MEAN	ST. DEV.
C1	9	27.47	1.45
C2	8	23.65	2.31
C3	7	22.11	2.39
C4	6	23.85	1.44
C5	5	21.96	2.03
C6	5	26.48	1.71
C7	5	21.64	0.57
C8	5	27.66	0.58
C9	5	21.48	0.26
C10	5	23.44	2.7

Pooled St. Dev. = 1.74

*** = $P < 0.001$

youngest of the known inoceramid-fish communities adds appeal to this idea.

A second hypothesis is that the individual fish of a given species within a particular inoceramid specimen could be members of a school. Among most schooling fish, the individuals of a particular school are of similar length. This is, in part, a product of the fact that swimming speed is related to size (Bond, 1979). To test the idea that these could represent schools, I measured the first 10 caudal vertebrae in 10 groups of holocentrid alpha, the most common holocentrid in the zone of *Clioscaphites choteauensis*. These measurements were analyzed through a one-way analysis of variance. The variance of size among the groups is significantly greater than variance within groups at the 0.001 level of significance (table 1). The same test was applied to six groups of *Omosoma garretti* from the zone of *Spinaptychus sternbergi*. Again, the size variance among the groups is significantly greater than that within groups at the same level of significance (table 2). Thus, it seems probable that at least the groups of holocentrid alpha and *Omosoma garretti*, the two most numerous inoceramid inquilines, represent schools. Both are typically found in fairly large groups. For holocentrid alpha, the group may be as large as 104 individuals

TABLE 2—One-way analysis of variance of the first 10 caudal centra of *Omosoma garretti*.

Specimen no.	KUVP 32398	FMNH PF43040	KUVP 65738	FHSM VP-5115	AMNH 9837–9838	KUVP 59016–59017
Measurement in mm	12.8	13.4	16.5	13.9	17.6	10.6
	16.4	12.3	14.1	13.6	17.2	11.2
	14.7	13.5	15.5	14.0		
	15.4	11.2	17.7			
	16.7	11.6	18.3			
	14.3	10.8	16.8			
	14.8	11.3				
	15.6	12.8				
	14.9	12.0				
	14.0	13.6				
	14.9	12.8				
	17.2					
	17.2					
	17.4					
	11.1					
	15.4					
	16.8					

Analysis of variance

DUE TO	DF	SS	MS = SS/DF	F-RATIO
Factor	5	130.84	26.17	3.79***
Error	35	66.41	1.90	
Total	40	197.26		

LEVEL	N	MEAN	ST. DEV.
C1	17	15.27	1.67
C2	11	12.3	0.99
C3	6	16.48	1.52
C4	3	13.83	0.21
C5	2	17.4	0.28
C6	2	10.9	0.42

Pooled St. Dev. = 1.38

*** = $P < 0.001$

(KUVP 49403), and as many as 47 for *Omosoma garretti* (KUVP 32398).

Some extant holocentrids, the most diverse and abundant family among the inoceramid inquilines, seem to return to the same cave or crevice daily. Longley and Hildebrand (1941) provided an account of an individual of *Holocentrus ascensionis* that inhabited the same hole every day for a month. In another instance, 13 *Sargocentron vexillarius* were forced by poison from a hole in cay rock, and later hopped a 6-inch (15-cm) barrier to re-enter that pool at lower tide (McKenny, 1959). In this light, it is conceivable that each school of inoceramid inquilines had its own inoceramid and did not indiscriminately occupy appropriate specimens. No living holocentrid or polymixiid is known to participate in a commensal or mutualistic relationship, but many eels and all holocentrids utilize crevices, caves, or overhangs for shelter.

All extant holocentrids are nocturnal feeders and spend daylight hours in or near overhangs, crevices, etc. in coral or rocks. Many extant inquiline teleost species are also nocturnal. Two species of *Apogonichthys* are inquilines of *Strombus* and are nocturnal. Two excellent examples are *Urophycus chuss* and *Liparis inquilinus*, which are inquilines of pectens. Diurnal trawls of these pectens produce many more of these two species than do nocturnal trawls (Able, 1974; Steiner et al., 1982). Consequently, I posit that these Cretaceous inquilines were nocturnal. It is not difficult to understand why these fish would find it advantageous to enter inoceramids. It is well

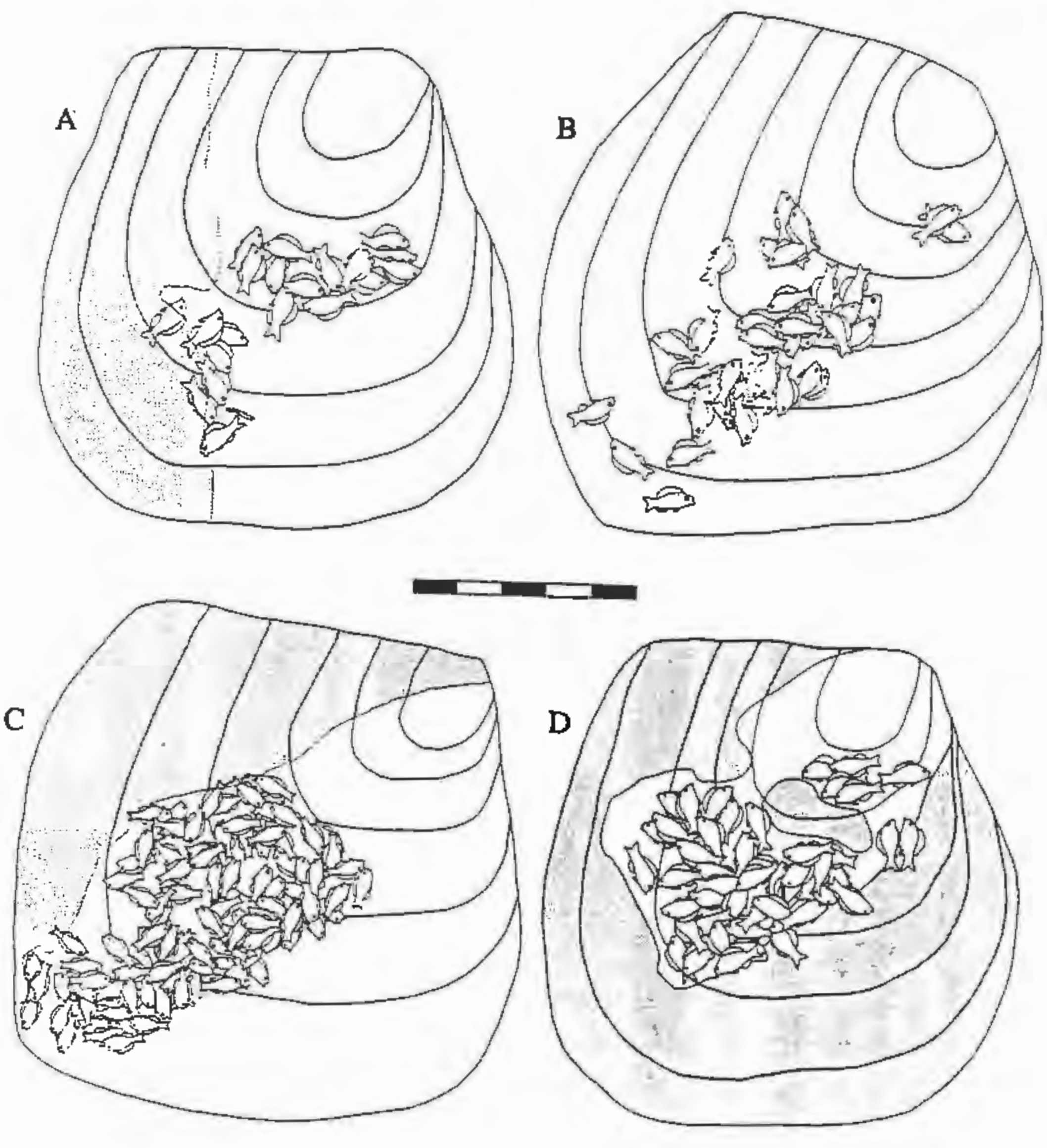

FIGURE 4—Diagrammatic representation of orientation of holocentrid alpha in four partial *Platyceramus platinus*. Shaded areas are areas of shell not preserved due to erosion or concretions A) KUVP 47241 and 69467–69483; B) KUVP 47245; C) KUVP 49403; D) KUVP 65697. The single elongate fish on A is the holotype of *Urenchelys abditus*, KUVP 47241. Scale equals 50 cm (20 inches).

known that numerous types of predatory vertebrates occur in the Smoky Hill Chalk Member. The floor of the Niobrara sea was essentially monotonous and flat except for the occasional bivalves and their epizoans, which formed small islands of life. Any tactic that could produce a sheltered place for resting would be useful. Likewise, nocturnal activity might be less hazardous than diurnal.

Although the benefits of inquilinism to the fish are clear, it is not immediately obvious whether the inoceramids benefited from this relationship. Perhaps fish defecation within the host would be beneficial.

A question arising from the concept of Cretaceous inquiline fish is whether their inquilinism was obligate. Species of *Trachichthyoides, Caproberyx, Omosoma*, and *Urenchelys* occur in European Upper Cretaceous rocks, and *Omosoma* and *Urenchelys* also are known from Lebanon, as are numerous holocentrid genera. One species of *Omosoma* comes from Africa. In none of these deposits is there indication of inoceramid-halecostome associations. It is therefore unlikely that any of these genera were obligate inquilines of inoceramids. It is curious that Kansas is the only area from which Cretaceous inquiline fish have been reported. The only non-Niobrara record is from the Fairport Chalk Member of the Carlile Formation (Stewart, 1982, 1987, 1990). As Kauffman (1990) has noted, the viscera of large deep-water inoceramids such as *P. platinus* may have occupied from one-half to one-third the internal shell area. In such an arrangement, considerable space in the mantle cavity would have been available to the inquiline fish. If the position of the fish in fig. 4 is indicative of the position of the mantle cavity, the viscera were extremely confined.

Significance to the Niobrara ichthyofauna

At the end of the first century of investigation of the Niobrara Chalk vertebrates, only one acanthomorph had been described from these deposits (Patterson, 1964), and that species was known from only three specimens. This single acanthomorph species contrasted markedly with fish faunas from contemporaneous deposits such as at Sahel Alma in Lebanon and at Westphalia in Germany. Patterson (1964) listed 13 acanthomorph species from the former and eight from the latter. In fact, most small fish are rare in the Smoky Hill Chalk Member. Exceptions are *Apsopelix anglicus* and small species of *Enchodus*, particularly *E. shumardi*.

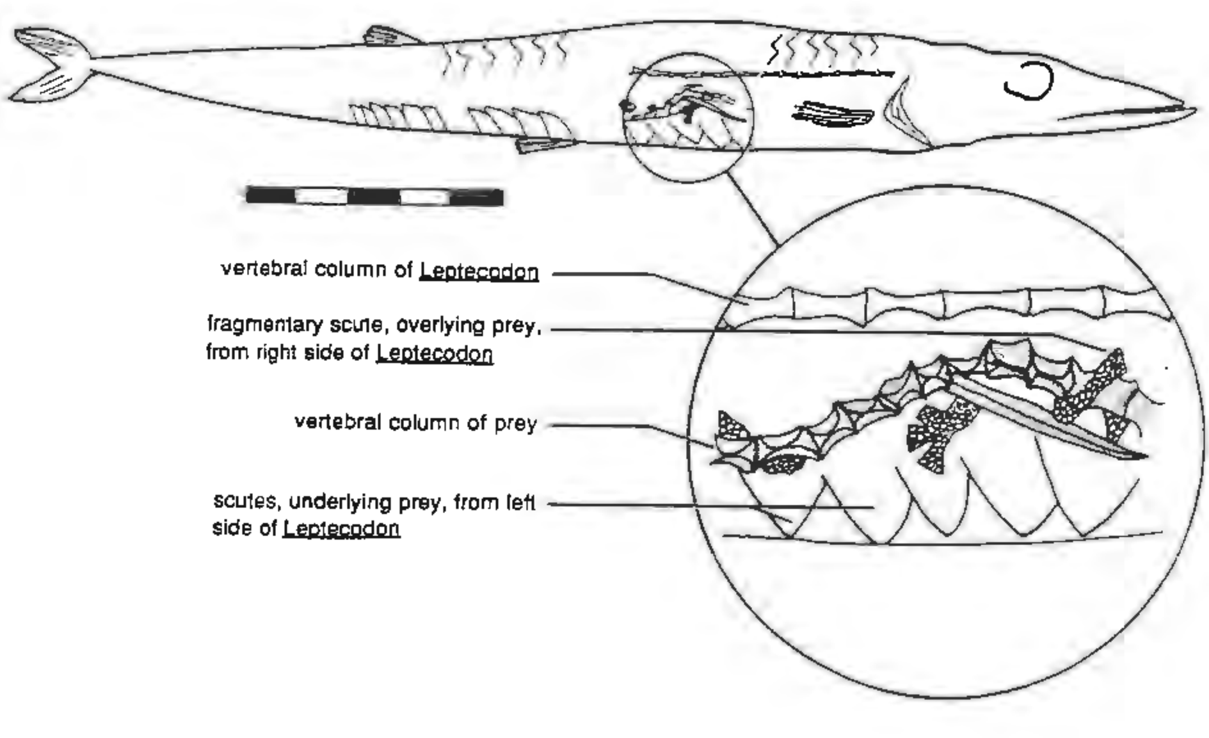

FIGURE 5—Drawing of holotype of *Leptecodon rectus*, KUVP 35, showing enlargement of a smaller ingested fish above the left scutes and beneath the right scutes of the gastric region. Scale equals 5 cm (2 inches).

By 1988, Russell could cite several more species of Niobrara acanthomorphs. He also noted (1988) that he had located 4,222 fish specimens in Niobrara vertebrate collections, and that they constituted 58% of the vertebrate fossils in Niobrara collections. This is probably an underestimate, if one takes into account that some early collectors (or their minions, in the case of O. C. Marsh) preferred to concentrate on Niobrara tetrapods. To date, I have noted a minimum of 1,230 individual fish preserved within inoceramids in the Niobrara Chalk formation of Kansas. If none of these was included in Russell's figures, then these represent over 29% of the known Niobrara fish fossils. Acanthomorphs (1,210) constitute nearly 29% of the total; holocentrids (1,069) are 25% of the total; and one species, holocentrid alpha (1,033), is 24%. If any of the 4,222 fish specimens Russell (1988) documented from the Niobrara Formation included any of these inoceramid commensals, then the percentages are higher.

These figures must produce a radical change in the way we view the Niobrara fish fauna, particularly in relation to contemporaneous fish faunas. One of the greatest ironies of this shift in perspective is that the most common vertebrate species in Niobrara collections is now an undescribed holocentrid. This is even more remarkable when one considers that all known specimens of this and the other inquilines from the zone of *Clioscaphites choteauensis* come from a 9.3-m (30.7-ft) stratum that probably represents only slightly more than 5% of Smoky Hill Chalk Member deposition in Kansas (Hattin, 1982).

Bardack (1976) argued that that the dead bodies of the fish species found on inoceramid shells were initially more widespread than we now perceive, but that those resting on a soft chalk substrate were not preserved. There may truly be a preservational bias in this regard; however, it seems to be a bias against or for certain taxa. It seems that the inquiline taxa experience a positive preservational bias. As noted above, there are over 1,200 individual fish of at least nine species found within inoceramids, and possibly two or three individuals of one of those species preserved away from inoceramids. It is very possibly true that acanthomorphs not lying within inoceramids tended to be generally lost in soft chalk sediments. Acid residues from inoceramid prism-lag deposits within the zone of *Clioscaphites choteauensis* have produced fin spines and other elements of acanthomorphs. However, these fossils appear to be either from juveniles of the inquiline taxa or from non-inquiline taxa.

Until recently, most vertebrate paleontologists collecting in the Smoky Hill Chalk Member focused much more attention on the larger fish of that deposit, thus introducing some collecting bias. The last 15 years have witnessed something of a reversal of that bias, with increased emphasis on the small fish species, particularly the inoceramid inquilines.

Conclusions

At least nine species of halecomorph actinopterygians have been found within inoceramid shells in the Smoky Hill Chalk Member of the Niobrara Formation of Kansas. These occur in three horizons. The majority of these fish, in both absolute numbers and systematic diversity, are acanthomorph fish. These acanthomorphs account for approximately 25% of all catalogued Niobrara fish. The fish are believed to be inquilines of the inoceramids and, in many cases, inhabited living inoceramids and died within the inoceramids. The fish were probably nocturnal, as are extant fish inquilines of mollusks, and some species appear to be preserved as schools.

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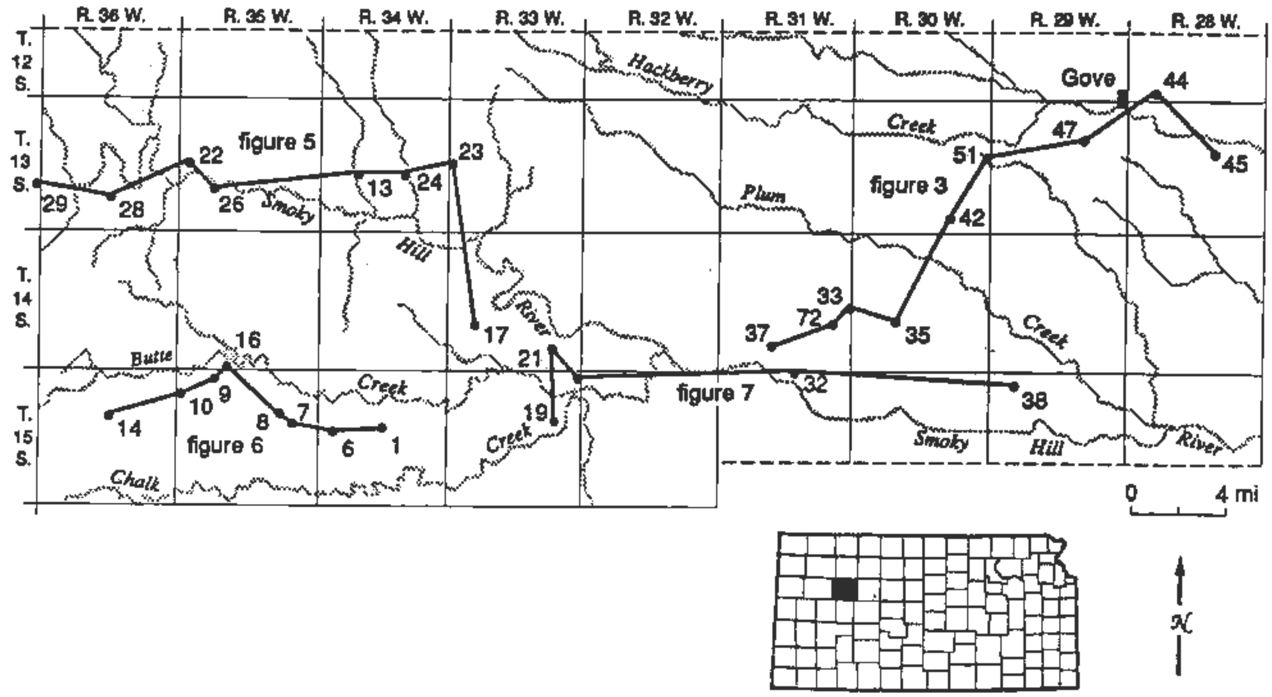

FIGURE 1—Map of localities in Gove and Logan counties. Dashed lines between localities show their order in figs. 3 and 5–7.

Inferring stratigraphic position of fossil vertebrates from the Niobrara Chalk of western Kansas

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Abstract

The stratigraphy of the Smoky Hill Chalk Member of the Niobrara Chalk in western Kansas is well understood thanks to the work of Hattin (1982) and Stewart (1988). Marker units identified by Hattin (1982) allow quick determination of the stratigraphic position of a specific outcrop, in turn making it possible to use locality data to infer stratigraphic position of specimens collected long ago. This technique is particularly useful in the upper half of the Smoky Hill Chalk Member where biostratigraphy is not informative and which has produced the majority of the fossil vertebrates. The stratigraphic distribution of the type skulls of the pterosaur *Pteranodon* is examined as an example of the procedure. This technique may be useful in further studies of the large collections of fossil vertebrates from the Smoky Hill Chalk Member.

Introduction

The Smoky Hill Chalk Member of western Kansas is famous for the very large number of specimens of fossil vertebrates it has produced. The collection of fossil vertebrates from the Smoky Hill Chalk Member was begun in earnest by O. C. Marsh and the Yale College Scientific Expedition in 1870. That and subsequent expeditions by Marsh and colleagues in 1871 and 1872 were so successful in the discovery of abundant remains of fish, turtles, mosasaurs, plesiosaurs, pterosaurs, and birds that Marsh hired professional collectors, including B. F. Mudge and S. W. Williston, to work the Niobrara Formation for him each year through 1879. During this 10-year period, Marsh amassed the largest and one of the most important collections of Niobrara vertebrates. Since the 1870's collecting of Niobrara vertebrates has been almost continuous. H. T. Martin of the University of Kansas collected a great deal of material, providing the core of the large collection at the University of Kansas and selling specimens to many other museums. George F. Sternberg collected for many years and like H. T. Martin sold specimens widely, but saved much of the best material for the Sternberg Memorial Museum in Hays, Kansas. In addition many other individuals have made small but good collections of specimens.

The majority of fossil vertebrates were collected before the stratigraphy of the Niobrara Formation was adequately understood, and their stratigraphic positions are unknown. The most that the collectors recorded was whether the specimen was from gray (or blue) shale or yellow chalk. The gray/yellow dichotomy is not particularly useful because it is largely a weathering phenomenon (Williston, 1897; Miller, 1968), and often the color change is found at different levels in the same outcrop.

Most studies of fossil vertebrates from the Smoky Hill Chalk Member have suffered from a lack of stratigraphic information, and authors have often had to rely on the fact that exposures of the eastern end of the outcrop area in Ellis County are low in the Smoky Hill Chalk Member while those of the western end in Logan County are higher. Bardack (1965) located many of the old localities, but at the time the stratigraphy was not sufficiently well known to determine stratigraphic positions of those localities with any precision. The purpose of this report is to show that it is now possible to determine the stratigraphic positions of specimens from locality data. Although precise locality data are best, often even rather vague locality data are sufficient to determine the stratigraphic position of a specimen.

It is important to note that almost all of the Yale Peabody Museum (YPM) collection was collected before 1881 when the old Wallace County was separated into Wallace and St. John counties. The latter was changed to

Logan County in 1885 (Elias, 1931). Bardack (1965) noted that the present Logan County was formerly called St. John County but did not mention that it was formerly a part of Wallace County. The Niobrara Formation is not widely exposed in the modern Wallace County. Many specimens in the YPM and other collections are listed as being collected in Wallace County, but almost all of them are from what is now Logan County.

Stratigraphy

The stratigraphy of the Smoky Hill Chalk Member of the Niobrara Chalk Formation in western Kansas is now well understood. Hattin (1982) described the stratigraphy of the Smoky Hill Chalk Member and identified 23 marker units. Hattin's marker units are the completion and perfection of the pioneering work of Russell (1929), and they allow quick determination of the stratigraphic position of an outcrop in the field. The invertebrate biostratigraphy of the Smoky Hill Chalk Member was examined by Miller (1968) and Hattin (1982), and Stewart (1988) showed that vertebrates can also be useful for biostratigraphy in the Smoky Hill Chalk Member. Biostratigraphic zonations based on inoceramids and species of the fish *Protosphyraena* divide the Smoky Hill Chalk Member into four zones.

Biostratigraphic zonations do not subdivide the upper half of the Smoky Hill Chalk Member. This is unfortunate because the upper half of the Smoky Hill Chalk Member has produced the vast majority of fossil vertebrates. Stewart (1988) noted that this is not because the lower half is unfossiliferous (fossils may actually be more common in the lower parts), but rather because the upper parts were more intensively collected. Letters sent to O. C. Marsh by his collectors S. W. Williston and E. W. Guild (alias E. S. Field) indicate that they concentrated on the upper part because they believed the hunting better, particularly in regard to the birds and pterosaurs for which O. C. Marsh paid the most money. Whatever the reason, most fossil vertebrates have been collected from the upper part of the Smoky Hill Chalk Member and biostratigraphy is of no use in determining the relative stratigraphic position of these specimens. Therefore it is necessary to rely on the stratigraphic marker units.

Hattin (1982) and Russell (1929) both designated marker units which allow quick determination of stratigraphic position, and in many cases both authors used the same markers. Marker units identified by Russell (1929) are based almost entirely on bentonite sequences and are lettered, while those identified by Hattin (1982) also may include units of unusual lithology and are numbered. In addition to the marker units, many other bentonites are readily recognizable and traceable in the field. These are particularly useful in correlating small outcrop areas with larger outcrops nearby. In this paper Hattin's marker units are used when possible, but Russell's Marker Unit H between Marker Units 17 and 18 also is used because it is readily identified and widely exposed.

If the exact locality of a specimen is known, one only needs to compare the exposure at the locality with the composite stratigraphic column of Hattin (1982). When the exact locality is not known or the exposure at the particular locality is of limited vertical extent and between marker units, a number of nearby outcrops are examined. Despite some regional variations it is remarkable how uniform the bentonite sequences are across the outcrop area in western Kansas. The uniformity makes precise correlations of outcrops possible.

Pteranodon

The utility of this method for inferring stratigraphic position from locality data was examined with the pterosaur *Pteranodon*. The postcranial skeleton is of no taxonomic value at the species level, and although *Pteranodon* occurs in two size classes, this is sexual dimorphism in size (Bennett, 1987). The skull appears to be taxonomically useful at the species level. Five nominal species of *Pteranodon* are based on skulls, and they differ in the size and shape of the cranial crest and the angle between the occiput and the palate. The type skulls of *Pteranodon longiceps*, *P. marshi*, and *P. eatoni* have a reclined occiput that is plesiomorphic for pterodactyloids, while those of *P. sternbergi* and *P. walkeri* have a more upright occiput. In the absence of stratigraphic information, it was hypothesized that the cranial morphology evolved from a reclined occiput to an upright occiput, and that a single species or lineage of *Pteranodon* was present in the Smoky Hill Chalk Member. If this were the case, one would not expect the two morphologies to co-occur.

In order to test the hypothesis, finding the stratigraphic positions of the pertinent specimens was necessary. The localities of the type skulls of *Pteranodon* as well as nearby outcrops were visited and stratigraphic columns measured. Localities are shown in fig. 1 and the stratigraphic columns are listed in appendix 1. The columns were compared to the composite stratigraphic column of Hattin (1988), and stratigraphic positions of the outcrops were determined. Finally a stratigraphic position or range from which the specimen came was determined from the columns and any other available information about the position or locality of the specimen.

Pteranodon walkeri—FHSM VP 221—This skull was collected by G. F. Sternberg from 2 mi (3.2 km) northeast of Penokee, sec. 13, T. 8S., R. 24 W., Graham County, Kansas (Bardack, 1965). Locality 55 in sec. 13, T. 8 S., R. 24 W. has Marker Unit 18 in the middle of a 10-m (33-ft) exposure, and Localities 54 and 60 to the southwest and northeast, respectively, are both a little lower (fig. 2). In this case the exact locality is known and although the exact horizon is not known, the type skull must have came from within 5 m (16.5 ft) above or below Marker Unit 18.

Pteranodon sternbergi—FHSM VP 339—This skull was collected by G. F. Sternberg from sec. 12, T. 8 S., R. 22 W., Graham County, Kansas, about 1 mi (1.6 km) west of Bogue and between Highway 24 and the south fork of the Solomon River (Bardack, 1965). An outcrop in the NE 1/4 of sec. 12, T. 8 S., R. 22 W. has abundant remains of *Inoceramus (Volviceramus) grandis*. The presence of *I. grandis* indicates that the specimen is from Stewart's (1987) Biostratigraphic Zone A or B and quite low in the Smoky Hill Chalk Member. Marker Unit 4 is visible near the top of the approximately 8 m (26.4 km) of exposure and also is exposed in other nearby outcrops. Although the exact horizon of the type skull is unknown, it must have come from approximately Marker Unit 4 or a short distance below.

Pteranodon longiceps—YPM 1177—This skull was collected May 2, 1876, by S. W. Williston. Williston's 1876 field notebook lists the locality as "3 mi. NE of Monument Rocks in fine yellow chalk," and a map in the YPM archives shows that the specimen was collected on the west side of the first drainage east of Monument Rocks and about 3 mi (4.8 km) north of the Smoky Hill River. This is approximately Locality 72. Comparison of this locality with Locality 37 to the southwest and Localities 33 and 35 to the northeast shows that Locality 72 ranges from 4 m (13.2 ft) below Marker Unit 15 up almost to Marker Unit 16 (fig. 3). At Locality 72, the chalk is gray from 1.5 m (5 ft) above Marker Unit 15. The fact the the skull was collected in yellow chalk while the chalk in the lower parts of the exposure is gray suggests that it came from at least 2 m (6.6 ft) above Marker Unit 15 and below Marker Unit 16.

Pteranodon eatoni—YPM 1179—This skull was collected in 1875 by E. W. Guild (alias E. S. Field) from the "Smoky Hill River, near Castle Rock." If near Castle Rock can be taken to mean within a couple of miles, this is adequate to bracket the stratigraphic position. Hattin's (1982) Localities 18 and 19 are just south of and just north of Castle Rock, respectively. These two exposures range from approximately 3 m (10 ft) below Marker Unit 6 to 3 m (10 ft) above Marker Unit 12. However, the chalk more than 5 m (16.5 ft) below Marker Unit 8 is dark gray, and the type skull is in pale-yellow chalk. Therefore, the skull was probably collected between 5 m (16.5 ft) below Marker Unit 8 and 3 m (10 ft) above Marker Unit 12.

Pteranodon marshi—YPM 2594—This skull was collected July 20, 1877, by S. W. Williston from "near Smoky Hill River, Wallace Co." A chronological listing of all specimens collected by the field party shows that they had been moving east from Russell Springs for a

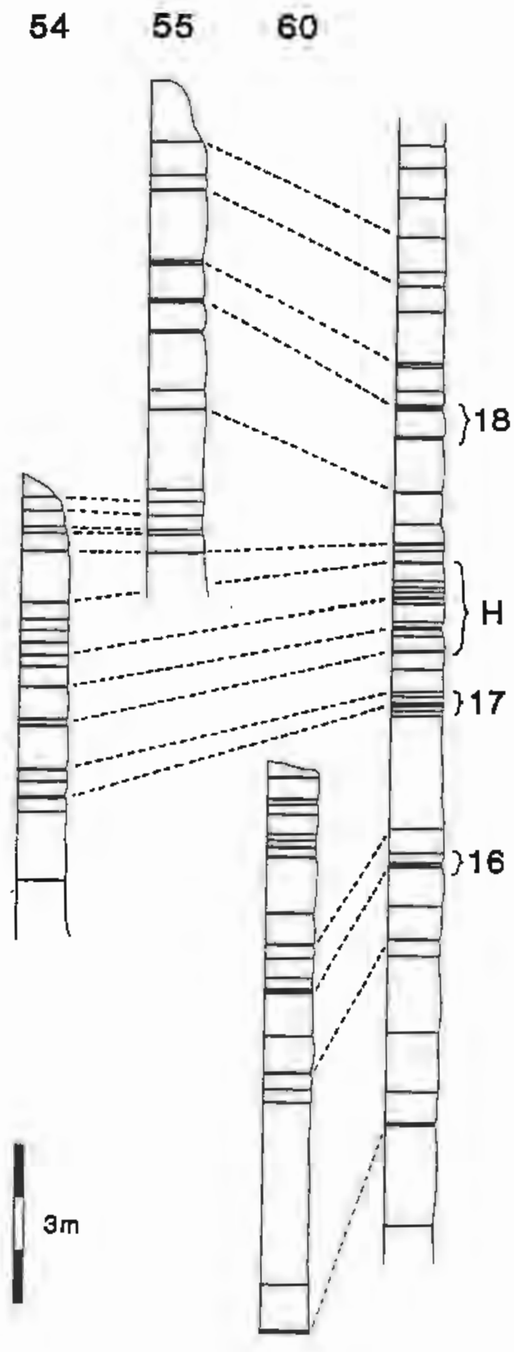

FIGURE 2—Correlation of stratigraphic columns of localities in Graham County. Black bands indicate bentonites, seams, and in a few instances a change in lithology, white indicates chalk. Localities are numbered across the top and arranged in order from west to east. The unnumbered column at right is the composite stratigraphic column from Hattin (1982). Numbers (and letter) at right identify marker units. Vertical position in the figure is not significant.

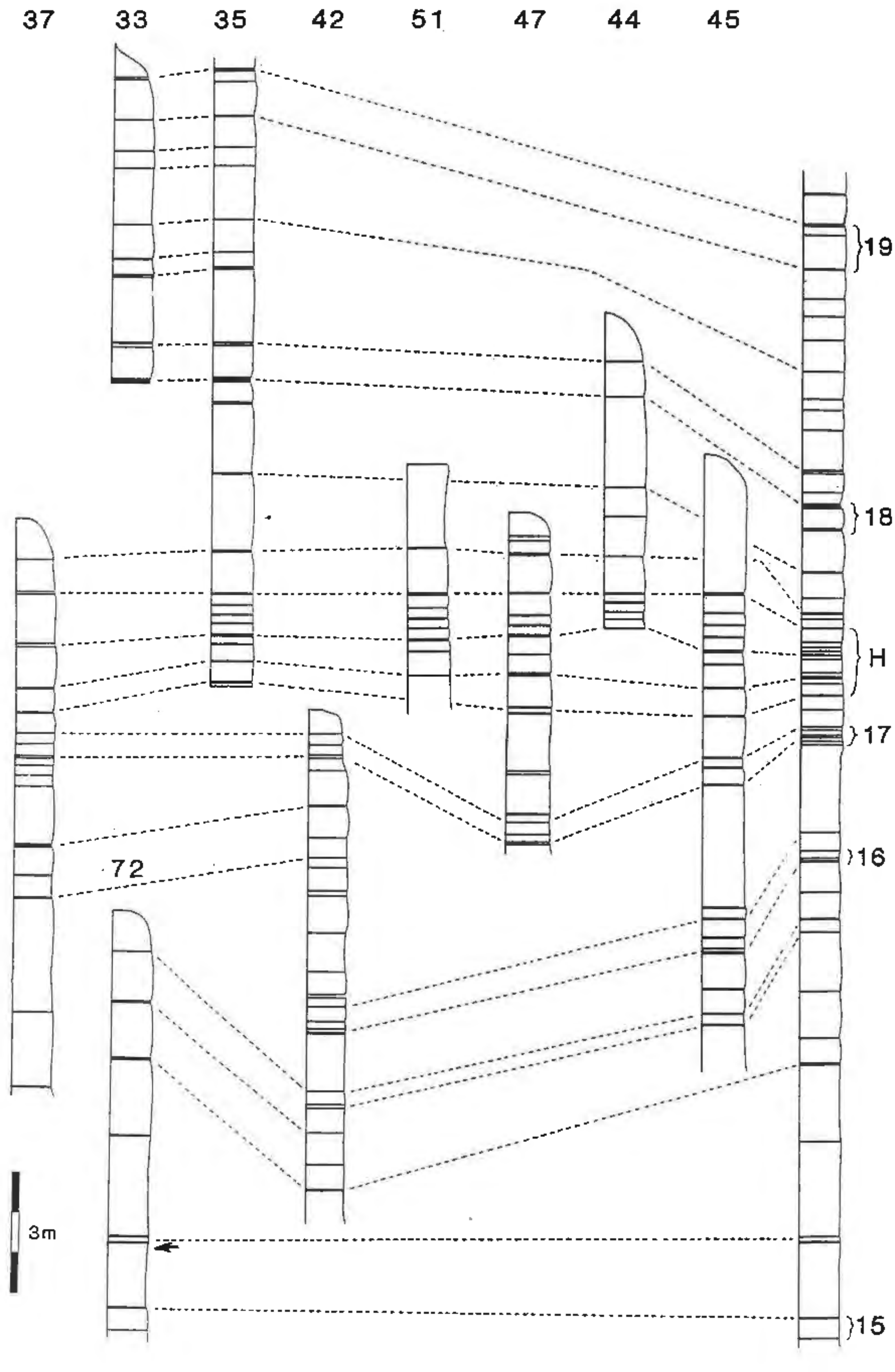

FIGURE 3—Correlation of stratigraphic columns of localities in western Gove County. Format as in fig. 2. Arrow by Locality 72 indicates change from gray to yellow chalk.

number of weeks and collected a mosasaur on Plum Creek in western Gove County also on July 20. The skull was presumably collected somewhere near there. Localities 33, 35, and 42 are on either side of Plum Creek and indicate that exposures on Plum Creek are between Marker Units 16 and 19 (fig. 3). Therefore, the skull was probably collected between those marker units.

A plot of the stratigraphic positions of the type skulls (fig. 4) shows that skulls with upright occiputs are found throughout the Smoky Hill Chalk Member from Marker Unit 4 up to Marker Unit 18, while skulls with reclined occiputs occur between Marker Units 8 and 19. Therefore, the two morphologies co-occur.

Discussion

The stratigraphic distribution shows that skulls with upright occiputs occurred throughout the Smoky Hill Chalk Member, and that skulls with reclined occiputs occurred with them in the upper part of the Smoky Hill Chalk Member. Because the two morphs co-occur they cannot be early and late forms of a single evolving species or lineage and the hypothesis is falsified. The two morphs are probably separate species of *Pteranodon* that coexisted throughout at least part of the time of deposition of the Smoky Hill Chalk Member.

This study shows that it is possible to determine the stratigraphic positions of specimens from the Smoky Hill Chalk Member from locality data even if they were collected over 100 years ago. When applied to even a small number of specimens, the procedure can have the power to reject theories.

While determining the stratigraphic positions of other specimens not discussed in this paper, many other localities were visited and measured. Additional measured sections covering much of Logan County and part of Gove County are included in figs. 3 and 5–7. The pattern of the exposures is interesting. In the northwestern part of the exposures in Gove County (fig. 3) and much of Logan County (figs. 5 and 6) as well as in western Graham County (fig. 2), the zone between Marker Units 15 and 20 is almost exclusively exposed. The zone between Marker Units 10 and 15 is exposed in places in eastern Logan and western Gove counties (Locality 18, Hattin's localities 22 and 23), but the caprock (Marker Unit 10) and the chalk below appear to be more widely exposed in those areas (fig. 7). This may be a result of a bias toward outcrops that are larger and easier to measure; other parts of the Smoky Hill Chalk Member may be extensively exposed but in outcrops that are small and difficult to measure. On the other hand it is possible that the chalk between Marker Units 10 and 15 and above Marker Unit 20 erodes more easily and is not widely exposed. More study of this problem is needed. The apparently biased distribution suggests that a majority of the fossil vertebrates collected from the Smoky Hill Chalk Member came from a rather restricted zone between Marker Units 15 and 20. This may have important implications for future studies of fossil vertebrates from the Smoky Hill Chalk Member.

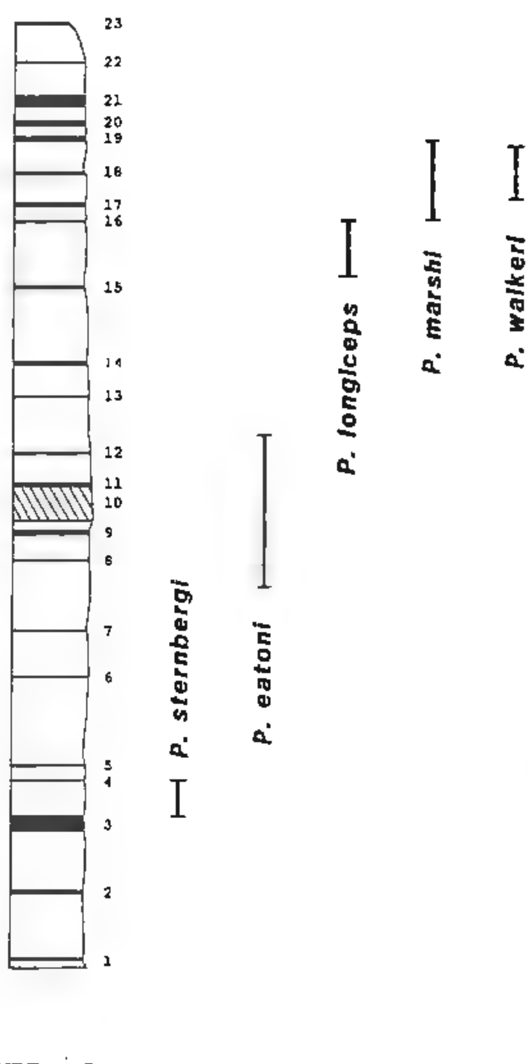

FIGURE 4—Inferred stratigraphic positions or ranges of type skulls of *Pteranodon* plotted against the composite stratigraphic column from Hattin (1982).

Conclusions

Hattin (1982) stated that the composite column and marker units made it possible to precisely determine the stratigraphic positions of Smoky Hill Chalk Member outcrops. This paper shows that it is possible to determine the stratigraphic positions of specimens collected long ago. This technique should prove useful in studies of other taxa from the Smoky Hill Chalk Member. In addition, this study demonstrates that the marker units of Hattin (1982) do make it possible for collectors to determine the stratigraphic position of specimens. Ninety years ago, Williston (1897, p. 245) wrote, "I need not call the attention of future collectors to the importance of locating the horizon of specimens more accurately than has been done heretofore." For many years after that statement was made, the stratigraphy of the Smoky Hill Chalk Member was only poorly understood. We now have the means to do as Williston suggested, and all future collectors should record horizon and locality as accurately as possible.

Acknowledgments—J. D. Stewart and O. W. Bonner shared their extensive knowledge of the Smoky Hill Chalk Member. This work would not have been possible without the generous funding of NSF Dissertation Improvement Grant BSR–8700547.

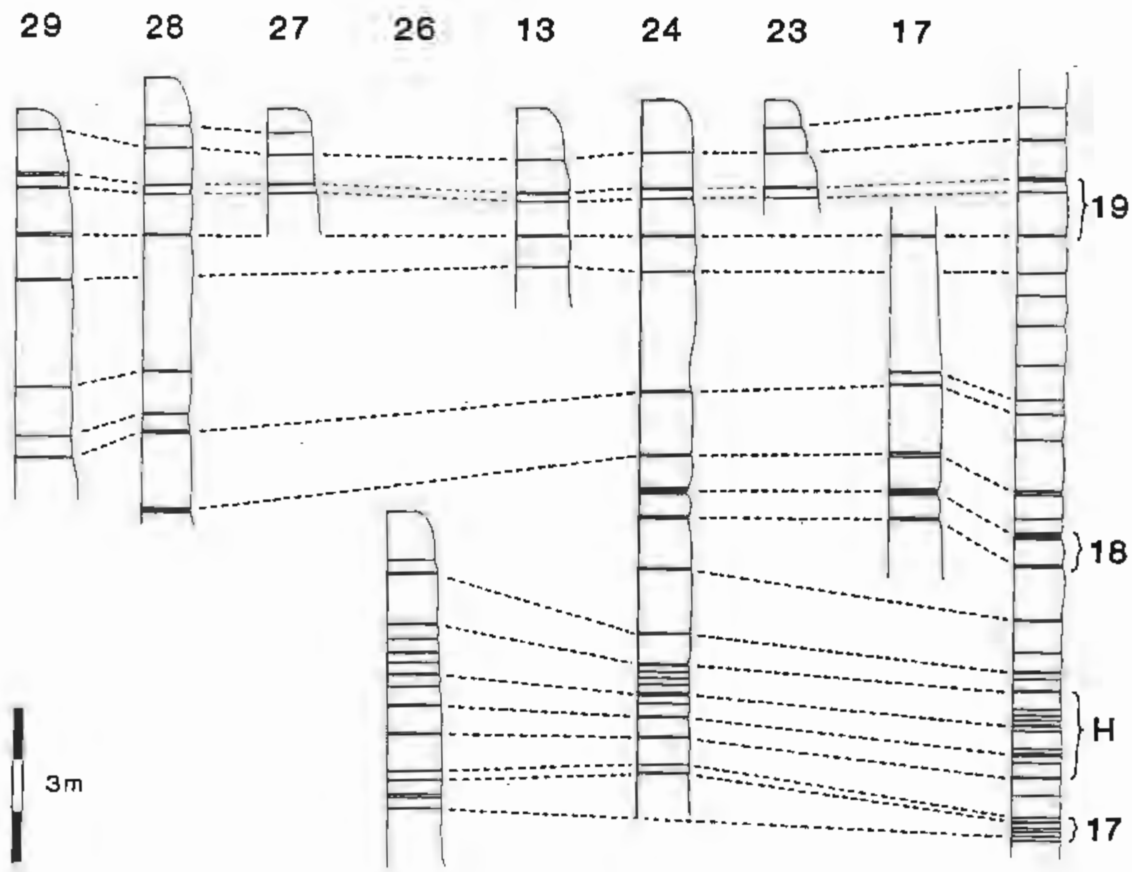

FIGURE 5—Correlation of stratigraphic columns of localities along the Smoky Hill River in Logan County. Format as in fig. 2.

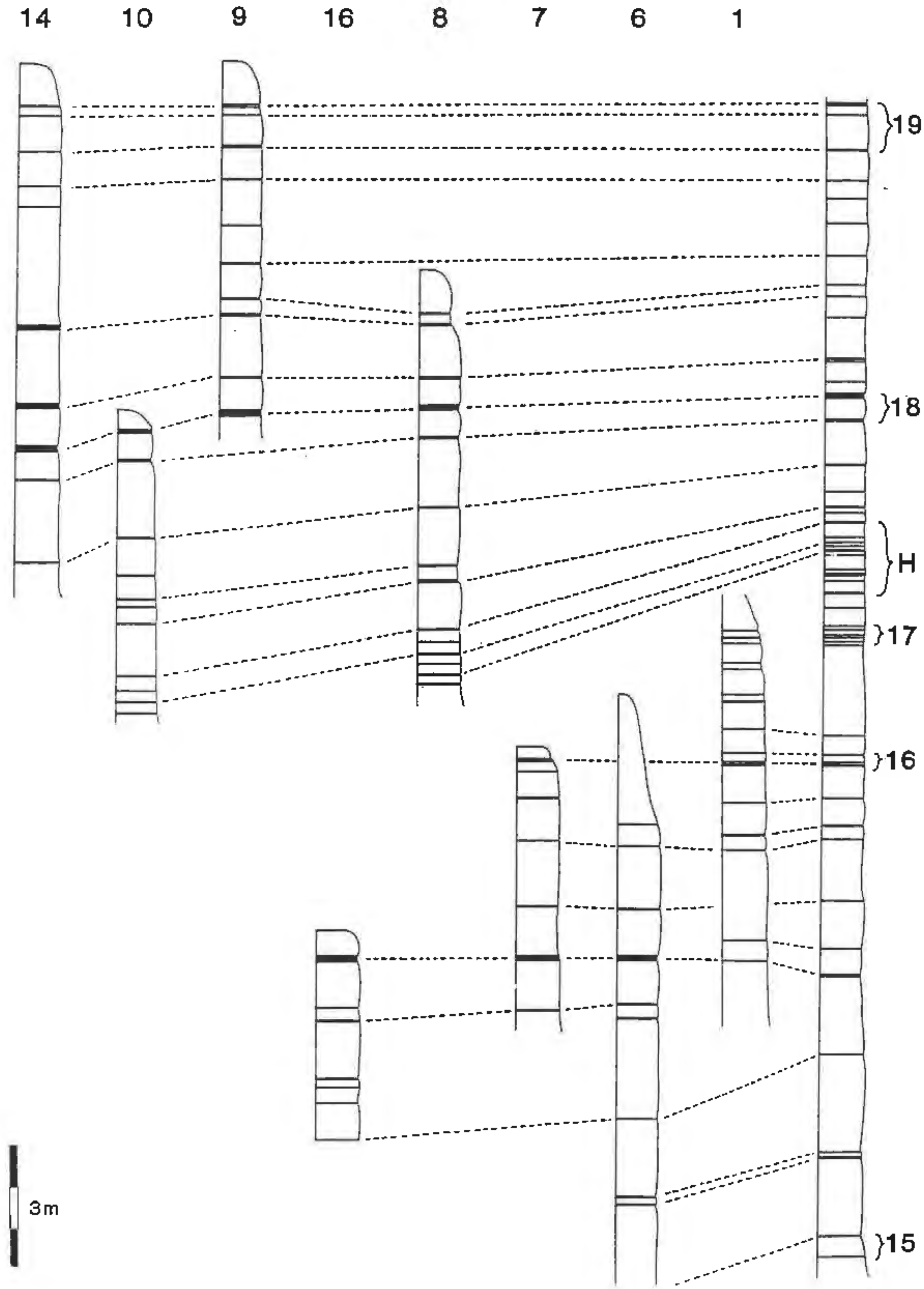

FIGURE 6—Correlation of stratigraphic columns of localities along Twin Butte Creek in Logan County. Format as in fig. 2.

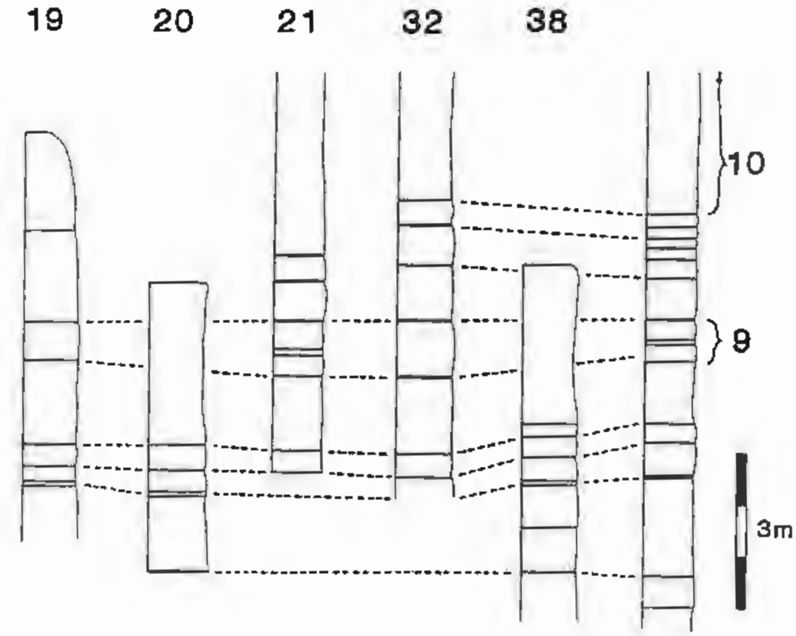

FIGURE 7—Correlation of stratigraphic columns of localities in southeastern Logan and southwestern Gove Counties. Format as in fig. 2.

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Appendix 1

MEASURED STRATIGRAPHIC SECTIONS AT LOCALITIES IN FIGS. 2, 3, AND 5–7. ALL MEASUREMENTS IN CM.

LOCALITY 1—W 1/2 of SW 1/4, sec. 15, T. 15 S., R. 34 S., Logan County, Kansas Base at 3,020 ft (906 m). Units 12–16 are Marker Unit 16.

Unit	Description	Thickness (cm)
33	Yellow chalk to top of the outcrop	~100
32	Ferruginous seam	0.2
31	Yellow chalk	15
30	Ferruginous seam	0.2
29	Pale chalk	3.8
28	Ferruginous seam	0.3
27	Yellow chalk	12
26	Ferruginous seam	0.2
25	Yellow chalk	46
24	Massive white chalk—forms resistant ledge	15
23	Yellow chalk	56
22	Massive white chalk—forms slight ledge	16
21	Tan silty chalk seam	0.8
20	Massive white chalk	2
19	Yellow chalk	63.5
18	Ferruginous seam	0.8
17	Yellow chalk	56
16	Ferruginous seam	0.3
15	Yellow chalk	21.5
14	Ferruginous seam	0.2
13	Yellow chalk	7
12	Ferruginous seam	1.5
11	Yellow chalk	86
10	Ferruginous seam	0.3
9	Yellow chalk	76
8	Ferruginous seam—forms prominent reentrant	1.5
7	Yellow chalk	34
6	Ferruginous seam	0.2
5	Yellow chalk	213
4	Ferruginous seam	0.3
3	Yellow chalk	48
2	Ferruginous/gypsiferous seam	0.8
1	Massive yellow chalk	167
Total thickness of measured section		1,045.4 cm

LOCALITY 6—S 1/2 of line between sec. 17 and 18, T. 15 S., R. 34 W., Logan County, Kansas. Base at 3,010 ft (903 m). Units 1–2 are Marker Unit 15.

Unit	Description	Thickness (cm)
21	Yellow chalk to top of outcrop	305
20	Bentonite	0.6
19	Massive chalk	51
18	Ferruginous seam—locally expanded to 2.5 cm by selenite	0.6

17	Yellow chalk	147
16	Gypsiferous seam—locally altered to selenite and may have local limonitic inclusions	3
15	Chalk	109
14	Bentonite unit—2.5 cm of orange to red-brown clay expanded by gypsum and iron oxide	12.7
13	Chalk	102
12	Bentonite	3.8
11	Chalk	29
10	Bentonite	3
9	Gray chalk	235
8	Ferruginous seam—locally expanded to 1 cm by selenite	0.1
7	Tan chalk	185
6	Gypsiferous seam	2
5	Tan chalk	14
4	Bentonite—locally expanded by selenite	2.5
3	Gray chalk	201
2	Bentonite unit—1 cm of white clay surrounded by iron oxide	3
1	Light gray chalk	46

Total thickness of measured section 1,455.3 cm

Locality 7—NW1/4, sec. 13, T. 15 S., R. 35 W., Logan County, Kansas. Base at 3,050 ft (915 m). Units 13–14 are part of Marker Unit 16.

Unit	Description	Thickness (cm)
15	Yellow chalk to top of outcrop	30.5
14	Pale-cream-colored chalk—in fresh chalk it is an indistinct 2.5-cm seam of powdery gypsum	6.4
13	Yellow chalk	23
12	Unit—two ferruginous/gypsiferous seams separated by 0.8-cm gray chalk	1.4
11	Gray chalk	60
10	Ferruginous seam—locally produces large limonitic inclusions up to 6.5 cm thick	1.5
9	Gray chalk	100
8	Ferruginous/gypsiferous seam	0.8
7	Gray chalk	153
6	Bentonite	2.5
5	Gray chalk	114
4	Bentonite unit—6 cm of gray, yellow, and orange clay expanded by iron oxide and gypsum	12.7
3	Gray chalk	117
2	Ferruginous/gypsiferous seam	1.8
1	Gray chalk	61

Total thickness of measured section 685.6 cm

Locality 8—Butte in NE 1/4 of SE 1/4, sec. 11, T. 15 S., R. 35 W., Logan County, Kansas. On the north or upside of a fault. Base at 3,100 ft (930 m). Units 20–22 are Marker Unit 18.

Unit	Description	Thickness (cm)
31	Yellow chalk to the top of the outcrop	–
30	Ferruginous/gypsiferous seam	3.2
29	Yellow chalk	21

28	Bentonite	6.4
27	Massive yellow chalk	119
26	Ferruginous/gypsiferous seam	2.5
25	Tan chalk	2.9
24	Seam	0.6
23	Yellow chalk	61
22	Bentonite unit—8.5 cm of silty chalk expanded by gypsum and iron oxide, forms a major reentrant	11.4
21	Chalk	61
20	Bentonite	6.4
19	Tan chalk	160
18	Ferruginous/gypsiferous seam	2.5
17	Massive gray chalk	132
16	Ferruginous/gypsiferous seam—crops out as selenite	2.5
15	Gray chalk	32
14	Bentonite	6.7
13	Gray chalk—forms a rounded cap on outcrop	109
12	Bentonite	4.4
11	Pale-tan chalk	28
10	Seam	0.6
9	Gray chalk	26
8	Ferruginous/gypsiferous seam	1.8
7	Gray chalk	21
6	Ferruginous seam	1.4
5	Gray chalk	23
4	Bentonite	4.4
3	Gray chalk	18
2	Ferruginous seam	2
1	Gray chalk	61
Total thickness of measured section		931.7 cm

Locality 9—Small butte in NE 1/4 of NE 1/4, sec. 5, T. 15 S., R. 35 W., Logan County, Kansas. Base at 3,090 ft (927 m). Units 1–2 are part of Marker Unit 18 and units 18–22 are Marker Unit 19.

Unit	Description	Thickness (cm)
23	Yellow chalk to top of bluff	–
22	Bentonite	7
21	Yellow chalk	16.5
20	Ferruginous seam	0.6
19	Yellow chalk—a seam cropping out as selenite lies 44 cm above bottom	70
18	Ferruginous/gypsiferous seam	4.4
17	Tan chalk	2.5
16	Gypsiferous seam—with iron oxide film at bottom	1
15	Massive yellow chalk	71
14	Bentonite—crops out as a selenite	3.8
13	Massive yellow chalk	105
12	Ferruginous seam	0.5
11	Yellow chalk—a seam lies 21 cm above bottom	86
10	Ferruginous/gypsiferous seam—crops out as a selenite ledge	2.5
9	Yellow chalk	79
8	Ferruginous/gypsiferous seam	2.5
7	Yellow chalk	32
6	Bentonite unit—1.1 cm of waxy gray clay expanded by gypsum and iron oxide	5.1

5	Yellow chalk	142
4	Bentonite unit—1.2 cm of gray clay expanded by gypsum and iron oxide.	2.5
3	Yellow chalk	76
2	Bentonite unit—gray, olive, and tan clays, expanded by iron oxide	14
1	Chalk	91
Total thickness of measured section		841.9 cm

LOCALITY 10—West 1/2 of line between secs. 6 and 7, T. 15 S., R. 35 W., Logan County, Kansas. Base at 3,150 ft (945 m). Units 20–22 are Marker Unit 18.

Unit	Description	Thickness (cm)
23	Chalk to top of the outcrop	–
22	Bentonite unit—7.5 cm of gray clay, expanded by iron oxide and gypsum	10
21	Chalk	61
20	Bentonite unit—4.3 cm of red-brown clay between powdery gypsum	5.7
19	Gray chalk	178
18	Ferruginous/gypsiferous seam	3.2
17	Massive yellow chalk	85
16	Seam—crops out as selenite	2
15	Massive yellow chalk	55
14	Seam—crops out as selenite	2
13	Massive yellow chalk	14
12	Seam—crops out as selenite	2
11	Massive yellow chalk	36
10	Ferruginous/gypsiferous seam	3.8
9	Yellow chalk—a 1-cm gypsiferous seam lies 25 cm above the bottom	117
8	Ferruginous/gypsiferous seam	3.8
7	Gray chalk	32
6	Ferruginous/gypsiferous seam	1.4
5	Gray chalk	25
4	Ferruginous/gypsiferous seam	2
3	Gray chalk	23
2	Ferruginous seam	2
1	Gray chalk	30
Total thickness of measured section		693.9

LOCALITY 13—North end of line between secs. 20 and 21, T. 13 S., R. 34 W., Logan County, Kansas. Base at 2,920 ft (876 m). Units 4–8 are Marker Unit 19.

Unit	Description	Thickness (cm)
11	Yellow chalk to top of the outcrop	–
10	Seam	0.3
9	Yellow chalk	60
8	Bentonite	3.4
7	Yellow chalk	14
6	Seam	0.5
5	Yellow chalk	63.5
4	Unit—two ferruginous seams, the lower 0.2 cm and upper 0.5 cm thick, separated by chalk	2.2

3	Yellow chalk	58
2	Ferruginous seam	0.3
1	Yellow chalk	89

Total thickness of measured section 291.2

Locality 14—SE 1/4 of SW 1/4, sec. 10, T. 15 S., R. 36 W., Logan County, Kansas. Base at 3,210 ft (963 m). Units 18–24 are Marker Unit 19 and units 4–6 are Marker Unit 18.

Unit	Description	Thickness (cm)
25	Yellow chalk to top of the outcrop	~
24	Ferruginous seam	1
23	Yellow chalk	3.8
22	Ferruginous seam	1
21	Yellow chalk	20
20	Ferruginous seam	0.8
19	Yellow chalk	84
18	Ferruginous seam	0.5
17	Yellow chalk	81
16	Ferruginous seam	0.5
15	Yellow chalk	48
14	Ferruginous seam	0.5
13	Yellow chalk	277
12	Bentonite unit—4.4 cm of dark-gray to brown silty chalk that weathers shaly, expanded by gypsum and iron oxide, forms a reentrant	13
11	Gray chalk	170
10	Bentonite unit—1.7 cm of gray clay and flaky, waxy gray material, expanded by gypsum, forms a reentrant	11
9	Gray chalk	86
8	Dark-gray seam	0.6
7	Chalk	3.8
6	Bentonite unit—10.2 cm of dark-gray to red-brown clay, expanded by gypsum, produces a major reentrant	11.4
5	Gray chalk	63.5
4	Ferruginous/gypsiferous seam	3.2
3	Gray chalk—a 10-cm-thick band of darker gray chalk lies 94 cm above bottom	190
2	Bentonite	2
1	Gray chalk	91

Total thickness of measured section 1,163.6 cm

Locality 16—Small exposure just south of Twin Butte Creek on line between SE 1/4 and SW 1/4, sec. 33, T. 14 S., R. 35 W., Logan County, Kansas Base at 3,040 ft (912 m).

Unit	Description	Thickness (cm)
11	Yellow chalk to top of the outcrop	61
10	Bentonite unit—2-cm gray clay, expanded by iron oxide and gypsum	14
9	Yellow chalk	109
8	Seam—crops out as a selenite seam with occasional limonitic inclusions	1
7	Yellow chalk	31
6	Ferruginous/gypsiferous seam—crops out as limonitic ledges	2

5	Yellow chalk	132
4	Ferruginous/gypsiferous seam	1.7
3	Yellow chalk	16.5
2	Darker gray chalk—weathers slightly shaly	37
1	Gray chalk	91

Total thickness of measured section 496.2 cm

LOCALITY 17—SW 1/4, sec. 20, T. 14 S., R. 33 W., Logan County, Kansas. Base at 2,880 ft (864 m). Units 2–4 are Marker Unit 18.

Unit	Description	Thickness (cm)
17	Chalk to top of the outcrop	–
16	Gypsiferous seam—with gray inclusions, crops out as selenite ledge	2.5
15	Yellow chalk	256
12	Gypsiferous seam—crops out as selenite ledge	3.8
11	Yellow chalk	22
10	Gypsiferous seam—crops out as selenite ledge	3.8
9	Yellow chalk	125
8	Bentonite	3.2
7	Chalk	5.1
6	Seam—produces a minor reentrant	0.2
5	Yellow chalk	61
4	Bentonite unit—8.9 cm of pale-gray clay expanded by iron oxide and gypsum	11.4
3	Yellow chalk	41
2	Bentonite unit—gray clay expanded by gypsum and iron oxide	6.7
1	Yellow chalk	122

Total thickness of measured section 663.7 cm

LOCALITY 18—Small outcrop south of Twin Butte Creek in E 1/2 of SW 1/4, sec. 13, T. 15 S., R. 34 W., Logan County, Kansas. Base at 2,950 ft (885 m). Unit 8 are Marker Unit 13. (Not illustrated.)

Unit	Description	Thickness (cm)
11	Yellow chalk to top of the outcrop	–
10	Seam—with occasional limonitic inclusions	0.2
9	Yellow chalk—with occasional limonitic inclusions, commonly around inoceramids	103
8	Unit—two ferruginous seams, the upper 0.4 cm and the lower 0.7 cm separated by chalk, produces a reentrant	5
7	Yellow chalk	184
6	Ferruginous seam—locally thickens to 1 cm or includes selenite, produces small limonitic inclusions	0.3
5	Yellow chalk—with numerous *Inoceramus balticus* shells	109
4	Ferruginous seam—produces many small limonitic inclusions	2
3	Yellow chalk	30.5
2	Seam—invisible in fresh chalk, but produces limonitic inclusions where weathered	0.0
1	Yellow chalk	152

Total thickness of measured section 585.9 cm

LOCALITY 19—Little Pyramids, at east end of line between secs. 11 and 14, T. 15 S., R. 33 W., Logan County, Kansas. Base at 2,780 ft (834 m). Units 8–9 are probably Marker Unit 9.

Unit	Description	Thickness (cm)
12	Yellow chalk to the top of the outcrop	183
11	Seam—visible as a fine line on outcrop	0.0
10	Yellow chalk	170
9	Seam—crops out as a selenite seam with occasional limonitic inclusions	0.4
8	Yellow chalk	71
7	Gray chalk	158
6	Ferruginous/gypsiferous seam	1
5	Gray chalk	43
4	Bentonite	1
3	Gray chalk	31
2	Paler, less laminated band	10
1	Gray chalk	120
Total thickness of measured section		788.4 cm

LOCALITY 20—SE 1/4 of NE 1/4, sec. 1, T. 15 S., R. 33 W., Logan County, Kansas. Base at 2,730 ft (819 m).

Unit	Description	Thickness (cm)
8	Gray chalk to top of the outcrop	305
7	Ferruginous/gypsiferous seam—produces limonitic inclusions	1
6	Gray chalk	47
5	Bentonite unit—0.4 cm of gray clay expanded by iron oxide and gypsum	1.3
4	Gray chalk	41
3	Harder, pale-gray band	7.6
2	Gray chalk	141
1	Ferruginous seam	1.5
Total thickness of measured section		545.4 cm

LOCALITY 21—East end of line between secs. 26 and 35, T. 14 S., R. 33 W., Logan County, Kansas. Base at 2,750 ft (825 m). Units 5–9 are Marker Unit 9.

Unit	Description	Thickness (cm)
14	Yellow chalk to top of outcrop	610
13	Ferruginous/gypsiferous seam	2
12	Yellow chalk	46
11	Gypsiferous seam	2
10	Gray to yellow chalk	71
9	Selenite seam—between thin films of iron oxide	1.5
8	Gray chalk	51
7	Paler, less laminated chalk	13
6	Gray chalk	38
5	Bentonite unit—pale-gray clay expanded by iron oxide	1.3
4	Gray chalk	140

3	Bentonite	0.3
2	Gray chalk	41
1	Ferruginous/gypsiferous seam—produces limonitic inclusions	0.3
Total thickness of measured section		1,018.4 cm

LOCALITY 23—Tiny outcrop just north of road on W 1/2 of line between secs. 18 and 19, T. 13 S., R. 33 W., Logan County, Kansas. Base at 2,900 ft (870 m). Units 1–4 are part of Marker Unit 19.

Unit	Description	Thickness (cm)
9	Massive yellow chalk to top of the outcrop	51
8	Ferruginous seam	0.5
7	Massive yellow chalk	48
6	Ferruginous seam	0.5
5	Massive yellow chalk	62
4	Unit—two 0.5-cm ferruginous seams separated by chalk	3.5
3	Massive yellow chalk	18
2	Seam	0.0
1	Massive yellow chalk	38
Total thickness of measured section		221.5 cm

LOCALITY 24—Six-Mile Creek just north of two small buttes in W 1/2 of NW 1/4, sec. 23, T. 13 S., R. 34 W., Logan County, Kansas. Base at 2,940 ft (882 m). Units 1–4 are part of Marker Unit 17, units 26–28 are Marker Unit 18, and units 36–40 are Marker Unit 19.

Unit	Description	Thickness (cm)
43	Yellow chalk to top of the outcrop	–
42	Ferruginous seam	0.5
41	Massive yellow chalk	66
40	Unit—two 0.5-cm iron oxide seams separated by chalk	3.8
39	Yellow massive chalk	18
38	Seam	0.4
37	Yellow massive chalk	68
36	Unit—two ferruginous seams, the upper 0.5 cm and the lower 0.3 cm, separated by chalk	2.5
35	Massive yellow chalk—seams lie at 79, 140, and 185 cm above the bottom	66
34	Seam	0.4
33	Massive yellow chalk	224
32	Ferruginous seam—produces a sharp reentrant	3.2
31	Yellow chalk	117
30	Seam	2
29	Yellow chalk	61
28	Bentonite unit—4 cm of tan clay and silty chalk, expanded by gypsum and iron oxide	12
27	Gray chalk	41
26	Ferruginous/gypsiferous seam	5.2
25	Gray chalk	94
24	Bentonite	2.9
23	Gray chalk	119
22	Ferruginous/gypsiferous seam	4.4

21	Gray chalk	58
20	Bentonite unit—crops out as two closely spaced limonitic ledges	4.1
19	Gray chalk	13
18	Seam	0.2
17	Gray chalk	13
16	Seam	0.2
15	Gray chalk	13
14	Seam	0.2
13	Gray chalk	14
12	Bentonite unit—4.2 cm of orange material, expanded by iron oxide	5.2
11	Gray chalk	15
10	Ferruginous seam	1
9	Gray chalk	25
8	Bentonite unit—3.5 cm of mixed yellow and gray clay, expanded by iron oxide	4.4
7	Gray chalk	36
6	Bentonite	2.5
5	Gray chalk	52
4	Ferruginous seam	0.5
3	Gray chalk	14
2	Bentonite	1.5
1	Gray chalk	91

Total thickness of measured section 1,275.1 cm

LOCALITY 26—Small area just west of road in NE 1/4 of SE 1/4, sec. 20, T. 13 S., R. 35 W., Logan County, Kansas. Base at 2,930 ft (879 m). Units 2–10 are Marker Unit 17 and units 12–28 are Marker Unit H.

Unit	Description	Thickness (cm)
31	Gray chalk	92
30	Tan clay seam—crops out as a 1.5-cm selenite ledge	0.5
29	Gray chalk	25
28	Bentonite	3.2
27	Gray chalk	93
26	Bentonite unit—0.9 cm of gray clay expanded by iron oxide	3.5
25	Gray chalk	28
24	Ferruginous seam	0.6
23	Gray chalk	23
22	Ferruginous/gypsiferous seam	1.5
21	Gray chalk	19
20	Ferruginous seam	0.6
19	Gray chalk	20
18	Bentonite unit—2.8 cm of orange clay expanded by iron oxide	4.4
17	Gray chalk	20
16	Bentonite	1.3
15	Gray chalk	37
14	Bentonite	3.8
13	Gray chalk	52
12	Bentonite	2
11	Gray chalk	69
10	Gypsiferous seam—locally may contain iron oxide	0.5
9	Gray chalk	19
8	Ferruginous seam—with a few limonitic inclusions	0.5
7	Gray chalk	27

6	Ferruginous seam—with limonitic inclusions	0.8
5	Gray chalk	6.4
4	Ferruginous seam—with limonitic inclusions	0.5
3	Gray chalk	22
2	Ferruginous seam	0.5
1	Gray chalk	122
Total thickness of measured section		698.6 cm

LOCALITY 27—W 1/2 of NW 1/4, sec. 19, T. 13 S., R. 35 W., Logan County, Kansas. Base at 2,980 ft (894 m). Units 1–4 are part of Marker Unit 19.

Unit	Description	Thickness (cm)
9	Yellow chalk to top of the outcrop	46
8	Seam	0.5
7	Massive yellow chalk	41
6	Seam	0.5
5	Massive yellow chalk	53
4	Unit—two ferruginous seams, the upper 0.5 cm and the lower 0.3 cm thick, separated by chalk	3.3
3	Yellow chalk	15
2	Seam—crops out as a 1-cm-thick selenite ledge	0.5
1	Yellow chalk	91
Total thickness of measured section		250.8 cm

LOCALITY 28—Just south of Hwy. 25 on line between secs. 27 and 28, T. 13 S., R. 36 W., Logan County, Kansas. Base at 3,070 ft (921 m). Units 14—18 are Marker Unit 19.

Unit	Description	Thickness (cm)
23	Yellow chalk to top of the outcrop	91
22	Tan seam—crops out as selenite ledge 5 cm thick	1
21	Massive yellow chalk	43
20	Tan clay seam—crops out as selenite ledge	1
19	Yellow chalk	69
18	Dark-tan silty seam - crops out as selenite ledge 2.5 cm thick	1
17	Yellow chalk	16.5
16	Gypsiferous seam—crops out as selenite ledge 2.5 cm thick	0.8
15	Yellow chalk	75
14	Ferruginous/gypsiferous seam—crops out as thick selenite ledge	3.8
13	Yellow chalk	254
12	Selenite seam	2.5
11	Yellow chalk	79
10	Selenite seam	2.5
9	Chalk—bottom half gray and top half yellow	29
8	Bentonite unit—2.1 cm of pale-gray silty clay, expanded by iron oxide and gypsum	7
7	Yellow and gray chalk 142	

6	Gypsiferous seam	2.5
5	Chalk	4
4	Seam	0.5
3	Chalk	1.2
2	Seam	2
1	Gray and yellow chalk	31
Total thickness of measured section		859.3 cm

LOCALITY 29—Small outcrop on S side of the Smoky Hill River in N 1/2 of SE 1/4, sec. 24, T. 13 S., R. 3 7W., Logan County, Kansas. Base at 3,050 ft (915 m). Units 10–14 are Marker Unit 19.

Unit	Description	Thickness (cm)
17	Yellow chalk to top of the outcrop	39
16	Ferruginous seam—crops out as selenite	1
15	Yellow chalk	80
14	Unit—two 2-cm ferruginous seams separated by chalk	7
13	Gray chalk	22
12	Bentonite	2.9
11	Gray chalk	84
10	Unit—two 1.5-cm ferruginous seams separated by chalk	5.1
9	Gray chalk	81
8	Ferruginous/gypsiferous seam—crops out as a selenite ledge	2.5
7	Gray chalk	201
6	Seam—crops out as a 2-cm selenite ledge	0.5
5	Gray chalk	94
4	Ferruginous seam	0.8
3	Gray chalk	38
2	Bentonite unit—2.8 cm of orange clay expanded by iron oxide	3.8
1	Gray chalk	91
Total thickness of measured section		753.6 cm

LOCALITY 32—Monument Rocks. NW 1/4 of SW 1/4, sec. 34, T. 14 S., R. 31 W., Gove County, Kansas. Base at 2,650 ft (795 m). Units 6–8 are Marker Unit 9.

Unit	Description	Thickness (cm)
16	Chalk to top	–
15	Gray and tan chalk—with occasional bands of paler, less laminated chalk	510
14	Ferruginous/gypsiferous seam	0.5
13	Gray chalk	46
12	Ferruginous/gypsiferous seam	2
11	Gray chalk—a paler band 10 cm thick lies 29 cm above bottom	72
10	Ferruginous/gypsiferous seam	0.4
9	Gray chalk	102
8	Bentonite unit—1.2 cm of gray clay, expanded by gypsum and iron oxide	2.6
7	Gray chalk—a paler, less laminated chalk band 13 cm thick lies 40 cm above the bottom	105
6	Ferruginous/gypsiferous seam	2.5

5	Gray chalk	144
4	Ferruginous/gypsiferous seam	0.7
3	Gray chalk	45
2	Gypsiferous seam—with 0.1 cm iron oxide in the middle	0.5
1	Gray chalk	52
Total thickness of measured section		1,185.2 cm

LOCALITY 33—Middle of NE 1/4, sec. 24, T. 14 S., R. 31 W., Gove County, Kansas. Base at 2,820 ft (846 m). Unit 1 is part of Marker Unit 18 and units 17–19 are Marker Unit 19.

Unit	Description	Thickness (cm)
20	Chalk to top of the outcrop	–
19	Unit—two ferruginous seams, the upper 0.8 cm and the lower 0.2 cm thick, separated by chalk, forms a reentrant	4.5
18	Yellow chalk	97
17	Ferruginous seam	0.5
16	Yellow chalk	75
15	Ferruginous seam	0.5
14	Yellow chalk	42
13	Ferruginous seam	0.5
12	Yellow chalk	135
11	Hard white chalk seam	0.5
10	Yellow chalk	81
9	Selenite seam	3
8	Yellow chalk	36
7	Bentonite	5.1
6	Yellow chalk	157
5	Seam—crops out as selenite	1.5
4	Yellow chalk	9
3	Seam—crops out as selenite	0.4
2	Yellow chalk	76
1	Bentonite unit—12 cm of mixed tan, gray, and very pale gray clays, expanded by iron oxide	13
Total thickness of measured section		737.5 cm

LOCALITY 35—Steep south-facing cliff in SW 1/4 of SE 1/4, sec. 20, T. 14 S., R. 30 W., Gove County, Kansas. Base at 2,810 ft (843 m). Units 3–19 are Marker Unit H, units 23–25 are Marker Unit 18, and units 42–45 are Marker Unit 19.

Unit	Description	Thickness (cm)
52	Yellow chalk to top of the outcrop	–
51	Unit—two ferruginous seams, the upper 2.5 cm and the lower 0.5 cm, separated by chalk	5.6
50	Massive yellow chalk	71
49	Seam	0.1
48	Massive yellow chalk	53
47	Seam	0.1
46	Massive yellow chalk	71
45	Unit—two seams, the upper tan clay 0.7 cm and the lower 0.3 thick, separated by chalk, produces a reentrant	4.8
44	Yellow chalk	24

43	Seam	0.0
42	Yellow chalk	80
41	White chalk seam	2
40	Yellow chalk	72
39	Seam	0.1
38	Yellow chalk	46
37	Gypsiferous seam	0.2
36	Yellow chalk—a seam lies 76 cm above the bottom	130
35	Seam	0.1
34	Massive yellow chalk	78
33	Ferruginous seam	0.5
32	Massive yellow chalk	37
31	Dark-brown clay seam—produces a reentrant	5.1
30	Massive yellow chalk	173
29	Ferruginous seam	2
28	Massive yellow chalk	7
27	Seam	0.1
26	Massive yellow chalk	75
25	Tan clay seam—produces a reentrant	11
24	Yellow chalk	49
23	Tan clay seam	6.4
22	Yellow chalk—weathers orange	165
21	Bentonite unit—2 cm of gray clay, expanded by iron oxide and gypsum	3.6
20	Massive yellow chalk—a 0.8-cm ferruginous seam lies 108 cm above the bottom	182
19	Ferruginous/gypsiferous seam	4.9
18	Yellow chalk	98
17	Bentonite unit—1.5 cm of gray clay expanded by iron oxide and gypsum	4.2
16	Yellow chalk	24
15	Bentonite unit—0.5 cm of gray clay expanded by gypsum	3.5
14	Yellow chalk	20
13	Ferruginous/gypsiferous seam	3.2
12	Yellow chalk	19
11	Ferruginous/gypsiferous seam	2
10	Yellow chalk	25
9	Bentonite unit—2 cm of pale gray clay, expanded by iron oxide and gypsum	6
8	Yellow chalk	18
7	Ferruginous/gypsiferous seam	3
6	Yellow chalk	38
5	Bentonite	2.8
4	Yellow chalk	47
3	Ferruginous/gypsiferous seam	2.5
2	Yellow chalk	10
1	Ferruginous seam	0.6
Total thickness of measured section		1,686.4 cm

LOCALITY 37—Outcrop north of and higher than Monument Rocks in NW 1/4 of SE 1/4, sec. 28, T. 14 S., R. 31 W., Gove County, Kansas. Base at 2,710 ft 9813 m). Units 13–23 are Marker Unit 17.

Unit	Description	Thickness (cm)
34	Massive yellow chalk to top of the outcrop	~100
33	Seam	0.5
32	Massive yellow chalk—seams lie at 10, 36, and 52 cm above the bottom	78
31	Unit—two 1-cm ferruginous/gypsiferous seams separated by chalk, forms a reentrant	6
30	Massive yellow chalk	119
29	Unit—two 2.5-cm brown silty seams separated by soft dark tan chalk, produces a reentrant	7.5
28	Massive yellow chalk	100
27	Selenite seam	2.9
26	Massive yellow chalk	57
25	Selenite seam	2.9
24	Massive yellow chalk	47
23	Seam	0.4
22	Massive yellow chalk	25
21	Seam	0.4
20	Massive yellow chalk	37
19	Seam	0.4
18	Massive yellow chalk	6
17	Seam	0.4
16	Massive yellow chalk	18
15	Seam	0.4
14	Massive yellow chalk	23
13	Gypsiferous seam—with iron oxide films at top and bottom	0.5
12	Massive yellow chalk	28
11	Seam—invisible in fresh chalk, crops out as a selenite ledge	0.0
10	Massive yellow chalk—a 0.5-cm seam lies 41 cm above the bottom	140
9	Bentonite unit—4.9 cm of brown clay expanded by selenite	10
8	Yellow chalk	66
7	Bentonite	1.8
6	Yellow chalk	52
5	Bentonite	3
4	Yellow chalk	275
3	Gray chalk	180
2	Selenite seam	2
1	Gray chalk	25

Total thickness of measured section 1,315.1 cm

LOCALITY 38—Small bluff in W 1/2 of NW 1/4, sec. 6, T. 15 S., R. 29 W., Gove County, Kansas. Base at 2,660 ft (798 m).

Unit	Description	Thickness (cm)
13	Yellow chalk to top of the outcrop	~300
12	Seam	0.1
11	Massive yellow chalk	23
10	Seam	0.1

9	Massive yellow chalk	38
8	Seam	0.4
7	Yellow chalk—unit has lots of *Pseudoperna*	46
6	Soft reddish band - forms a reentrant	7.6
5	Yellow chalk—unit has lots of *Pseudoperna*	81
4	Ferruginous seam	1
3	Yellow chalk—unit has lots of *Pseudoperna*	83
2	Ferruginous seam	0.5
1	Yellow chalk	108
Total thickness of measured section		688.7 cm

Locality 42—Small butte in SW 1/4 of NW 1/4, sec. 35, T. 14 S., R. 30 W., Gove County, Kansas. Base at 2,770 ft (831 m). Units 15–21 are Marker Unit 16 and units 42–49 are Marker Unit 17.

Unit	Description	Thickness (cm)
50	Yellow chalk to top of the outcrop	~
49	Seam	0.4
48	Yellow chalk	28
47	Seam	0.4
46	Yellow chalk	25
45	Seam	0.4
44	Yellow chalk	10
43	Seam	0.4
42	Yellow chalk	31
41	Seam	0.4
40	Yellow chalk	85
39	Ferruginous seam—produces an 8.9-cm reentrant	2.5
38	Yellow chalk	78
37	Seam	0.5
36	Yellow chalk	47
35	Seam	0.4
34	Yellow chalk	25
33	Seam	0.4
32	Yellow chalk	57
31	Unit—two 0.3-cm ferruginous seams separated by 11.4 cm of chalk. 4 cm above the lower seam is a faint ferruginous seam	12
30	Yellow chalk—the upper part is tinged with red	90
29	Ferruginous seam	0.1
28	Yellow chalk	97
27	Ferruginous/selenitic seam—produces a reentrant	0.3
26	Yellow chalk	55
25	Ferruginous seam—produces a reentrant	0.7
24	Yellow chalk	7.6
23	Seam	0.4

22	Yellow chalk	20
21	Seam	0.4
20	Yellow chalk	35
19	Seam	0.4
18	Yellow chalk	17
17	Seam	0.4
16	Yellow chalk	9
15	Ferruginous clay seam	2
14	Yellow chalk	141
13	Ferruginous clay seam—produces a reentrant	1
12	Yellow chalk	32
11	Ferruginous seam	0.5
10	Yellow chalk	9.5
9	Ferruginous seam	0.1
8	Yellow chalk	60
7	Ferruginous seam	0.1
6	Yellow chalk	77
5	Ferruginous seam	0.1
4	Yellow chalk	61
3	Clay seam	1.5
2	Yellow chalk	86
1	Ferruginous seam	0.2
Total thickness of measured section		1,209.1 cm

Locality 44—Small outcrop in NW 1/4 of SW 1/4, sec. 32, T. 12 S., R. 28 W., Gove County, Kansas. Base at 2,640 ft (792 m). Units 1–11 are part of Marker Unit H.

Unit	Description	Thickness (cm)
18	Massive yellow chalk to the top of the outcrop	240
17	Clay seam	1.5
16	Massive yellow chalk	85
15	Soft orange chalk	219
14	Massive yellow chalk—forms ledge	69
13	Ferruginous seam	0.1
12	Yellow massive chalk	97
11	Seam—locally selenitic	0.3
10	Yellow chalk	89
9	Clay seam—crops out as ferruginous ledge	4.4
8	Yellow chalk	17
7	Bentonite	3.7
6	Yellow chalk	22
5	Ferruginous seam	0.5
4	Yellow chalk	18
3	Ferruginous seam	0.5
2	Yellow chalk	20
1	Bentonite unit—0.6 cm of gray clay, expanded by iron oxide	4.1
Total thickness of measured section		891.1 cm

Locality 45—West side of small butte at the end of long bluff, in S 1/2 of SE 1/4, sec. 15, T. 13 S., R. 28 W., Gove County, Kansas. Base at 2,600 ft (780 m). Units 8–12 are Marker Unit 16, units 18–22 are Marker Unit 17, and units 24–38 are Marker Unit H.

Unit	Description	Thickness (cm)
39	Massive yellow chalk to the top of the outcrop	668
38	Bentonite unit—1.4 cm of gray clay, expanded by gypsum and iron oxide, crops out as two selenitic seams in a reentrant	5.1
37	Yellow chalk	41
36	Gypsiferous seam	2
35	Yellow chalk	26
34	Bentonite	3.5
33	Yellow chalk	27
32	Bentonite unit—1.4 cm of brownish-tan clay, expanded by gypsum and iron oxide	2.5
31	Yellow chalk	30
30	Bentonite	6
29	Yellow chalk—the top 6 cm are silty and soft	28
28	Ferruginous/gypsiferous seam	2.5
27	Yellow chalk—the bottom half is granular, paler, and forms a rounded resistant ledge	53
26	Bentonite unit—2.6 cm of pale-gray clay, expanded by iron oxide and gypsum	3.5
25	Gray and yellow chalk	66
24	Bentonite	3.8
23	Gray chalk	100
22	Ferruginous/gypsiferous seam	2
21	Gray chalk	20
20	Ferruginous/gypsiferous seam	2
19	Gray chalk	38
18	Bentonite	2.5
17	Gray chalk	296
16	Ferruginous/gypsiferous seam	2
15	Chalk	24
14	Gypsiferous seam—crops out as a selenite ledge	1.5
13	Yellow chalk	41
12	Ferruginous/gypsiferous seam	3.5
11	Tan chalk	23
10	Bentonite	2.5
9	Chalk	7
8	Bentonite unit—1 cm of gray-green clay, expanded by iron oxide and gypsum	5.1
7	Gray chalk	83
6	Gypsiferous seam	2

5	Gray chalk	57
4	Bentonite	4.4
3	Gray chalk	23
2	Gypsiferous seam	2
1	Gray chalk	122
Total thickness of measured section		1,831.4 cm

LOCALITY 47—Outcrop near bottom of draw in NE 1/4 of SW 1/4, sec. 11, T. 13 S., R. 29 W., Gove County, Kansas. Base at 2,660 ft (798 m). Units 1—8 are Marker Unit 17 and units 18—30 are Marker Unit H.

Unit	Description	Thickness (cm)
40	Massive yellow chalk to top of the outcrop	–
39	Seam	0.1
38	Yellow chalk	56
37	Seam	0.1
36	Yellow chalk	11
35	Seam	0.1
34	Yellow chalk	31
33	Soft tan chalk—forms a reentrant	5.1
32	Ferruginous seam	0.5
31	Yellow chalk	91
30	Ferruginous/gypsiferous seam	2.5
29	Yellow chalk	50
28	Seam	2.5
27	Yellow chalk	21
26	Seam	2.5
25	Yellow chalk	20
24	Ferruginous/gypsiferous seam	7
23	Yellow chalk	41
22	Ferruginous seam—locally expanded to 3.8 cm	0.5
21	Yellow chalk—a 1-cm gypsiferous seam lies 12.7 cm down from the top	44.5
20	Ferruginous/gypsiferous seam	8.9
19	Gray and yellow chalk	75
18	Ferruginous/gypsiferous seam	3
17	Yellow chalk	13
16	Ferruginous/gypsiferous seam	3
15	Gray to yellow chalk	137
14	Gypsiferous seam	0.6
13	Gray chalk	9

12	Gypsiferous seam	0.6
11	Gray chalk	97
10	Ferruginous/gypsiferous seam	2.5
9	Yellow chalk	16.5
8	Ferruginous/selenitic seam	1.2
7	Yellow chalk	29
6	Ferruginous/selenitic seam	1.2
5	Chalk	18
4	Gypsiferous seam	0.6
3	Chalk	7
2	Ferruginous seam	0.5
1	Gray chalk	30.5.
Total thickness of measured section		1,115 cm

LOCALITY 51—N 1/2 of SE 1/4, sec. 13, T. 13 S., R. 30 W., Gove County, Kansas. Base at 2,740 ft (822 m). Units 2–14 are Marker Unit H.

Unit	Description	Thickness (cm)
17	Yellow chalk to top of the outcrop	~200
16	Reddish-tan clay seam	1.9
15	Yellow chalk 107	
14	Ferruginous/gypsiferous seam	5
13	Yellow chalk	30
12	Ferruginous/gypsiferous seam	1
11	Yellow chalk	24
10	Ferruginous/gypsiferous seam	2.5
9	Yellow chalk	22
8	Ferruginous/gypsiferous seam	2.2
7	Yellow chalk	25
6	Bentonite unit—4.4 cm of orange clay expanded by gypsum, produces a major reentrant	7
5	Chalk	24
4	Ferruginous/gypsiferous seam	1.9
3	Chalk	56
2	Gypsiferous seam	1
1	Gray chalk	~
Total thickness of measured section		510.5 cm

LOCALITY 54—Small exposure just south of the road in NE 1/4 of SW 1/4, sec. 22, T. 8 S., R. 24 W., Graham County, Kansas. Base at 2,250 ft (675 m). Units 4–10 are Marker Unit 17 and units 14–28 are Marker Unit H.

Unit	Description	Thickness (cm)
39	Massive yellow chalk to top of the outcrop	51
38	Ferruginous seam	0.3
37	Massive yellow chalk	27

36	Ferruginous seam	0.1
35	Massive yellow chalk	29
34	Ferruginous seam	0.1
33	Massive yellow chalk	11
32	Ferruginous seam	0.1
31	Yellow chalk	32
30	Bentonite	2.9
29	Yellow chalk—a 0.1-cm ferruginous seam lies 41 cm above the bottom	92
28	Ferruginous/gypsiferous seam	3.4
27	Yellow chalk—bottom 10 cm is softer and produces a reentrant	31
26	Ferruginous/gypsiferous seam	1
25	Yellow chalk	22
24	Tan ferruginous seam	0.6
23	Yellow chalk	22
22	Grayish-tan clay seam	1.5
21	Yellow chalk	22
20	Bentonite	3.9
19	Yellow chalk	18
18	Reddish-tan clay seam	2
17	Yellow chalk	36
16	Reddish-tan clay seam	2.5
15	Yellow chalk	56
14	Bentonite	2.9
13	Yellow chalk	10
12	Bentonite	1.5
11	Gray chalk	77
10	Ferruginous/gypsiferous seam	2
9	Gray chalk	18
8	Ferruginous/gypsiferous seam	2
7	Gray chalk	24
6	Unit—two ferruginous/gypsiferous seams, the upper 1 cm and the lower 1.6 cm thick, separated by chalk	4.6
5	Gray chalk	24
4	Ferruginous/gypsiferous seam	0.6
3	Gray chalk	128
2	Ferruginous/gypsiferous seam	0.5
1	Gray chalk	122

Total thickness of measured section 884.5 cm

LOCALITY 55—Small outcrop on east side of small draw in N 1/2 of SW 1/4, sec. 13, T. 8 S., R. 24 W., Graham County, Kansas. Base at 2,240 ft (672 m). Units 17–19 are Marker Unit 18.

Unit	Description	Thickness (cm)
30	Yellow chalk	114
29	Seam	0.4
28	Yellow chalk	62
27	Ferruginous seam	0.4
26	Massive yellow chalk	28
25	Ferruginous seam	1.5
24	Massive yellow chalk	132
23	Pale-gray clay seam	2
22	Yellow chalk	5.6
21	Ferruginous seam	0.2

20	Yellow chalk	63
19	Bentonite	10
18	Yellow chalk	52
17	Bentonite	5.7
16	Yellow chalk—a 0.2-cm ferruginous seam lies in the middle	109
15	White chalk seam	0.2
14	Yellow chalk	36
13	Dark-tan clay seam	2
12	Soft yellow chalk	150
11	Massive yellow chalk—forms a resistant ledge	23
10	Ferruginous seam	0.2
9	Massive yellow chalk	28
8	Seam	0.1
7	Massive yellow chalk	26
6	Seam	0.1
5	Massive yellow chalk	10
4	Seam	0.1
3	Massive yellow chalk	33
2	Ferruginous seam	2
1	Yellow chalk	91
Total thickness of measured section		935.5 cm

Locality 60—Just north of road and west of oil well in E-W middle of line between secs. 6 and 7, T. 8 S., R. 23 W., Graham County, Kansas. Base at 2,250 ft (675 m). Units 13–17 are Marker Unit 16.

Unit	Description	Thickness (cm)
45	Indistinct ferruginous seam	1
44	Yellow chalk	34
43	Bentonite	1.9
42	Yellow chalk	35
41	Bentonite	2
40	Yellow chalk	9.5
39	Soft tan clay seam	0.3
38	Yellow chalk	16.5
37	Seam	0.0
36	Yellow chalk	36
35	Ferruginous seam	0.3
34	Yellow chalk	13.3
33	Ferruginous seam	0.4
32	Yellow chalk	11.4
31	Bentonite	2.2
30	Yellow chalk	14
29	Ferruginous seam	0.1
28	Yellow chalk	4.4
27	Ferruginous seam	0.5
26	Yellow chalk	104
25	Ferruginous seam	0.1
24	Pale-yellow chalk	3.5
23	Ferruginous seam	0.3
22	Yellow chalk	56
21	Bentonite	2.5
20	Yellow chalk	23

19	Red-tan clay seam	0.7
18	Yellow chalk	37
17	Ferruginous seam	0.6
16	Yellow chalk	20
15	Ferruginous seam	0.5
14	Yellow chalk	6.7
13	Bentonite	2
12	Yellow chalk	81
11	Seam	0.1
10	Yellow chalk	69
9	Bentonite	2.9
8	Yellow chalk	31
7	Ferruginous seam	0.2
6	Yellow chalk	24
5	Ferruginous seam	0.1
4	Gray chalk	342
3	Ferruginous/gypsiferous seam	1.2
2	Gray chalk	84
1	Bentonite	5.1
Total thickness of measured section		1,080.3 cm

LOCALITY 72—West side of drainage in NW 1/4 of SW 1/4, sec. 24, T. 14 S., R. 31 W., Gove County, Kansas. Base at 2,740 ft (822 m). Units 4–5 are Marker Unit 15.

Unit	Description	Thickness (cm)
18	Resistant yellow chalk—forms a cap on outcrop	100
17	Ferruginous seam—in 25 cm reentrant	0.2
16	Massive yellow chalk	120
15	Soft yellow chalk—forms a reentrant	6.5
14	Massive yellow chalk—a 0.2-cm ferruginous seam lies 90 cm above the bottom	132
13	Bentonite unit—2.5 cm of gray clay expanded by iron oxide	6
12	Yellow chalk—a seam lies 89 cm above the bottom	183
11	Bentonite	2.5
10	Yellow chalk	242
9	Ferruginous/gypsiferous seam	1.8
8	Yellow chalk	12.5
7	Ferruginous/gypsiferous seam	2.5
6	Gray chalk	155
5	Bentonite	2.5
4	Paler granular chalk—a seam lies 34 cm above the bottom	54
3	Gray chalk	500
2	Ferruginous/gypsiferous seam	2.5
1	Gray chalk	100
Total thickness of measured section		1,623.0 cm

Upward continuity of the Niobrara fauna with the Pierre Shale fauna

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Abstract

Similarities between the vertebrate faunas of the Sharon Springs Member of the Pierre Shale (lower Campanian) and the Smoky Hill Chalk Member of the Niobrara Formation (upper Santonian-lower Campanian) are best explained as the descent of the younger fauna from the older. The differences, however, appear to be due to several factors, of which the combination of more than one vertebrate biostratigraphic horizon in the Smoky Hill fauna may be the most crucial. The impact of the black shale depositional environment, represented by the Sharon Springs Member, is not well understood because the vertebrate component of the topmost portion of the Smoky Hill (*Scaphites hippocrepis* I, II, III zones) is poorly known.

Introduction

The Upper Cretaceous (Campanian) Pierre Shale and its lateral equivalents occur throughout much of the Western Interior of North America. These deposits mark the last major advance of the epeiric sea across North America (fig. 1). The Pierre Shale is divisible into several members, of which the Sharon Springs Member marks the seaway during maximum transgression (fig. 2).

At the type locality in western Kansas (fig. 1, locality 5), the Sharon Springs Member consists of a 35-m (116-ft)-thick lower unit of "dark-gray soft flaky shale having a few concretions of yellow chalky limestone . . . ," a middle unit 27 m (89 ft) thick of "hard buttress-weathering shale...rich in organic material and in varied limestone concretions, and has yielded abundant vertebrate and a few invertebrate fossils," and a 3-m (10-ft)-thick upper unit of "hard-platy-weathering slightly phosphatic shale that contains numerous layers of soft highly weathered phosphate nodules..." (Gill, Cobban, and Schultz, 1972, p. 11). Elsewhere, however, the shale is not so readily divisible.

History of collecting

The first reported fossil vertebrate from the Sharon Springs was the long-necked plesiosaur *Elasmosaurus platyurus* (Cope, 1868). The specimen, a partial skeleton, came from near McAllister, Kansas (fig. 1, locality 5). Cope later described other specimens from the area, including several species of mosasaurs (Cope, 1871), and the turtle *Toxochelys latiremis* (Cope, 1873).

Samuel Williston, from the University of Kansas, led several expeditions to McAllister beginning in 1873. He also explored exposures of the Sharon Springs along the Cheyenne River in South Dakota (fig. 1, locality 2). Some of the specimens collected were described in a series of papers on reptiles (Williston, 1897, 1898, 1903, 1906; Williston and Case, 1892; Case, 1898) and fishes (Stewart, 1899, 1900).

In 1903 and 1904, a small party from the American Museum of Natural History collected from the Sharon Springs near Edgemont, South Dakota, and from Redbird, Wyoming (fig. 1, localities 3 and 4). Some of the fishes were later described (Bardack, 1965; Bardack and Sprinkle, 1969; Goody, 1970, 1976), as were the turtles (Hay, 1905; Zangerl, 1953), mosasaurs (Russell, 1967), and a plesiosaur (Welles, 1952).

Fredrick Loomis, from Amherst College, also collected near Redbird, Wyoming, in 1903, and later described a new species of mosasaur, *Platecarpus brachycephalus*, from there (Loomis, 1915). In 1948, David Dunkle, from the National Museum of Natural History, made a small collection at Redbird cited by Gill and Cobban (1966). He returned again in 1973 on behalf of the Cleveland Museum of Natural History and made another small collection. The University of Nebraska State Museum collected in northwestern Nebraska in 1966, and discovered the toothed bird *Hesperornis* sp. there (Martin and Tate, 1967).

In 1967, the Field Museum of Natural History collected a nearly complete skull of the aberrant mosasaur *Globidens* (Russell, 1975) near Fairburn, South Dakota (fig. 1, locality 1). The South Dakota School of Mines has collected sporadically for many years from near Fairburn,

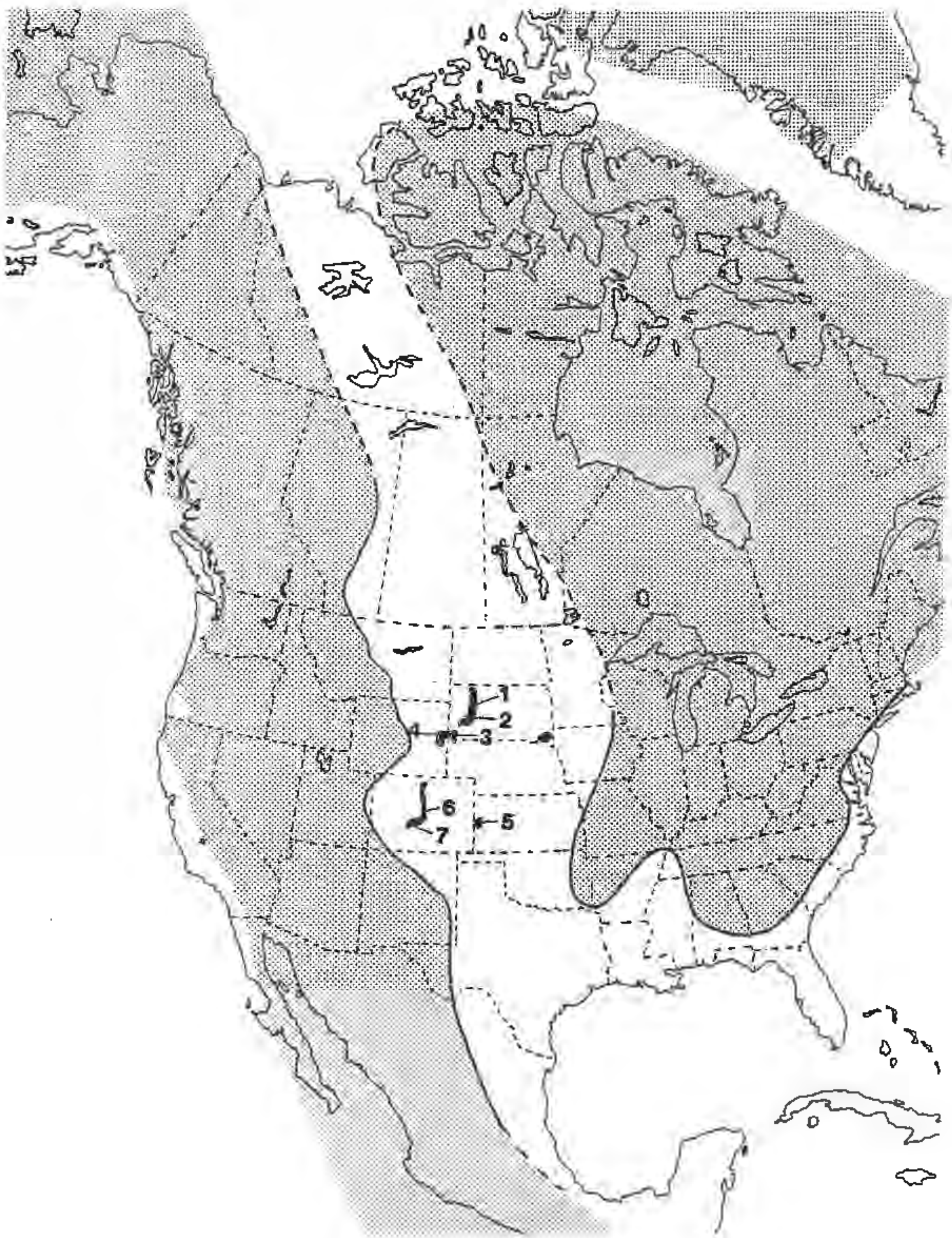

FIGURE 1—Surface distribution of the Sharon Springs Member of the Pierre Shale (black) and vertebrate localities superimposed on a map of the epeiric seaway during the deposition of the Sharon Springs. Localities: 1—Fairburn and surrounding areas, SD; 2—Buffalo Gap, SD; 3—Edgemont, SD; 4—Redbird, WY; 5—McAllister, KS; 6—Ft. Carson, CO; 7—Canon City, CO (seaway map adapted from Gill and Cobban, 1966).

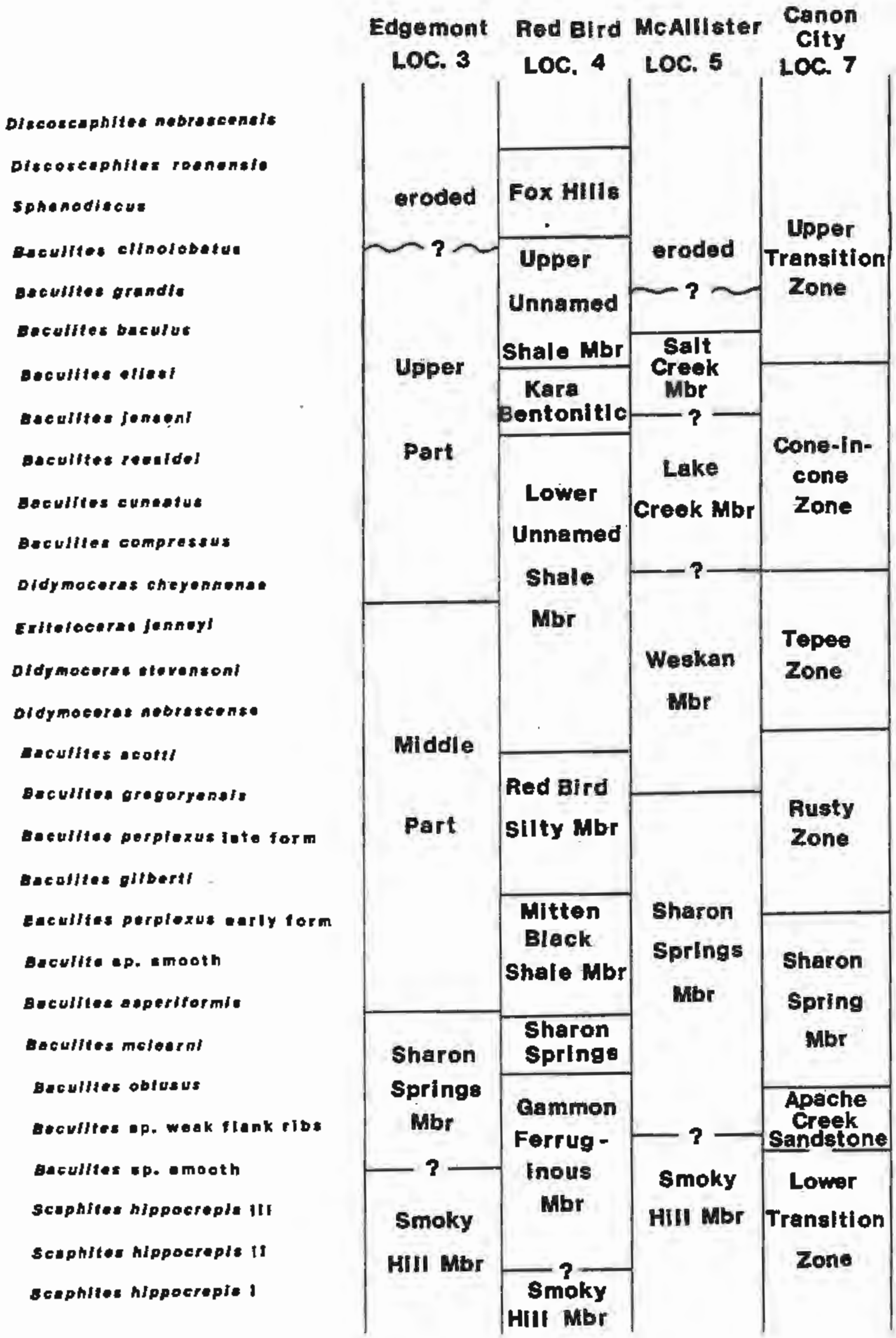

FIGURE 2—Stratigraphy of the Pierre Shale (data from Gill, Cobban, and Schultz, 1972; Scott and Cobban, 1975).

Buffalo Gap, and several other localities in Pennington County, South Dakota (Welles and Bump, 1949; J. Martin, personal communications).

The University of Colorado Museum began collecting at Redbird, Wyoming, in 1973 as a result of obtaining two large collections of vertebrates from amateur paleontologists Asa Maxson and James Mellinger. I continued this work on behalf of the CU Museum between 1975 and 1980 and made a field census of specimens to provide a data base for interpreting the taphonomy and paleoecology of the Sharon Springs (Carpenter, 1988).

Comparison of the faunas

The number of vertebrate specimens recovered per square kilometer of outcrop in the Sharon Springs equals or exceeds that for the Smoky Hill Chalk Member in western Kansas. However, these specimens have not attracted as much attention as those from the chalk due, in large part, to encrustment and damage by selenite crystals. These crystals are a byproduct of deep weathering of the shales. Sulfur liberated by the break-down of pyrite combines with calcium in the shale to form this morph of gypsum (Schultz, 1964). Only bones recovered from concretions are undamaged by selenite growth.

Data gathered from field and museum collection inventories indicate that the early Campanian Sharon Springs vertebrate fauna is a continuation of the older Smoky Hill fauna (late Santonian-earliest Campanian). This is demonstrated by the presence of the fish *Saurocephalus*, the turtle *Toxochelys latiremis*, and the mosasaurs *Clidastes propython*, *Platecarpus ictericus*, and *Tylosaurus proriger* (table 1).

Notably absent, however, are the fishes *Martinichthys brevis* and *Omosoma garretti*, and the turtle *Protostega gigas*. How much this difference is due to the Smoky Hill faunal list combining more than one biostratigraphic level is not known. As Williston (1897) and Russell (1967) have noted, there is a marked change in the vertebrate fauna of the Smoky Hill from the lower, or *Rudistes* beds to the upper, or *Hesperornis* beds.

The Smoky Hill Chalk Member spans several invertebrate zones according to Hattin (1982), thus changes in the vertebrate fauna are not unexpected. Stewart (1988) has shown that the four species of *Protosphyraena* in the Smoky Hill Chalk Member are stratigraphically restricted. Stewart (this volume) and Bennett (this volume) are attempting to place the vertebrate species of the Smoky Hill in their correct stratigraphic context. Most previous collections have lumped Smoky Hill vertebrate specimens together without regard to stratigraphic occurrence. In order to more adequately determine the evolution of the Sharon Springs vertebrate fauna from the upper Smoky Hill vertebrate fauna, it will be necessary to better know the vertebrate content of the *Scaphites hippocrepis* I, II, and III zones.

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TABLE 1—Comparison of the vertebrate faunas of the Smoky Hill Chalk Member of the Niobrara Formation and the Sharon Springs Member of the Pierre Shale. Compiled with the assistance of J. D. Stewart.

	Smoky Hills	Sharon Springs
Class Chondichthyes		
Subclass Elasmobranchii		
Order Euselachii		
Superfamily Galeomorphii		
Family Cretoxyrhinidae		
Cretoxyhina mantelli	X	
Pseudocorax laevis	X	
Cretolamna appendiculata	X	X
Family Anacoracidae		
Squalicorax falcatus	X	
S. kaupi	X	
S. cf. *S. kaupi*	X	
Family Ptychodontidae		
Ptychodus martini	X	
P. anonymous	X	
P. mortoni	X	
P. polygyrus	X	
P. enterospira	X	
Class Osteichthyes		
Subclass Actinopterygii		
Superorder Neopterygii		
Division Pycodontiformes		
Family Pycnodontidae		
Hadrodus marshi	X	
Micropycnodon kansasensis	X	
Division Ginglymodi		
Family Lepisosteidae		
Lepisosteus sp.	X	
Division Halecostomi		
Subdivision Halecomorphi		
Order Amiiformes		
Family ?Caturidae		
Paraliodesmus guadagnii	X	
Order Pachycormiformes		
Family Protosphyraenidae		
Protosphyraena sp.	X	
P. nitida	X	
P. pernicosa	X	
P. recurvirostris	X	
P. gladius	X	X
P. tenuis	X	
Order Aspidorhynchiformes		
Family Aspidorhynchidae		
Belonostomus sp.	X	
Order Asarotiformes		
Family Asarotidae		
Asarotus arcanus	X	
undescribed holostean		X

	Smoky Hills	Sharon Springs
Subdivision Teleostei		
Order Ichthyodectiformes		
Family Ichthyodectidae		
Gillicus arcuatus	X	X
Ichthyodectes ctenodon	X	X
Xiphactinus audax	X	X
undescribed ichthyodectid	X	
Family Saurocephalidae		
Saurocephalus lanciformis	X	X
Saurodon leanus	X	X
"S." pygmaeus	X	X
Order Osteoglossiformes		
Family Plethodidae		
Banogmius evolutus	X	X
B. zitteli	X	
B. favirostris	X	
Luxilites striolatus	X	
Martinichthys brevis	X	
M. ziphoides	X	
M. acutus	X	
M. alternatus	X	
M. gracilis	X	
M. latus	X	
Niobrara encarsia	X	
Zanclites xenurus	X	
Order Elopiformes		
Family Pachyrhizodontidae		
Pachyrhizodus caninus	X	X
P. minimus	X	X
"P." eptopsis	X	
Order Anguilliformes		
Family Urenchelidae		
Urenchelys abditus	X	
Order Beryciformes		
Family Holocentridae		
Kansius sternbergi	X	
Order incertae sedis		
Family Crossognathidae		
Apsopelix anglicus	X	
Suborder Neoteleostei		
Family Cimolichthyidae		
Cimolichthys nepaholica	X	X
Family Enchodontidae		
Enchodus petrosus	X	X
E. gladiolus	X	X
E. shumardi	X	
E. dirus	X	
Family Dercetidae		
Stratodus apicalis	X	X
Leptecodon rectus	X	
"Anguillavus" hackberryensis	X	
Suborder Paracanthopterygii		
Family Polymixiidae		
Omosoma garretti	X	
Teleostei incertae sedis		
Ferrifrons rugosus	X	

	Smoky Hills	Sharon Springs
Subclass Sarcopterygii		
Order Coelacanthida		
Family Coelacanthidae		
Macropoma? sp.	X	
Class Reptilia		
Order Chelonia		
Family Pelomedusidae		
Bothremys barberi	X	
Family Toxochelyidae		
Toxochelys latiremis	X	X
Lophochelys natatrix	X	
L. niobrarse	X	
Ctenochelys stenopora	X	
C. procax	X	
Prionochelys glaeotergum	X	
Cynocercus incisivius	X	
Porthochelys laticeps	X	
Family Protostegidae		
Protostega gigas	X	
P. potens	X	
Chelosphargis advena	X	
Calcarichelys cf. *C. gemma*	X	
Archelon copei	X	
Order Plesiosauria		
Family Polycotylidae		
Polycotylus sp.	X	
P. latipinnis	X	
Dolichorhynchops osborni	X	
Family Elasmosauridae		
Elasmosaurus platyurus		X
Styxosaurus browni		X
S. snowii	X	
Alzadasaurus pembertoni		X
A. kansasensis	X	
Thalassonomosaurus marshii	X	
Thalassiosaurus ischiadicus	X	
Order Squamata		
Family Mosasauridae		
Platecarpus tympaniticus	X	X
P. somenensis	X	
P. cf. *P. somenensis*		X
Mosasaurus ivoensis	X	
Clidastes propython	X	X
C. liodontus	X	
Globidens dakotensis		X
Ectenosaurus clidastoides	X	
Halisaurus sternbergi	X	
T. proriger	X	X
T. nepaeolicus	X	
Order Pterosauria		
Family Pteranodonidae		
Nyctosaurus gracilis	X	
Pteranodon sp.		X
P. longiceps	X	
P. sternbergi	X	

		Smoky Hills	Sharon Springs
	Order Ornithopoda		
	Family Hadrosauridae		
	Claosaurus agilis	X	
	unidentified hadrosaurine	X	
	Order Ankylosauria		
	Family Nodosauridae		
	Heirosaurus sternbergi	X	
Class Aves			
	Order Hesperornithiiformes		
	Family Hesperornithidae		
	Hesperornis regalis	X	X
	H. crassipes	X	
	H. gracilis	X	
	H. altus	X	
	Parahesperornis alexi	X	
	undescribed hesperornithiforms		X
	Family Baptornithidae		
	Baptornis advenus	X	
	Order Ichthyornithiformes		
	Family Ichthyornithidae		
	Ichthyornis dispar	X	
	I. victor	X	
	I. agilis	X	
	I. validus	X	
	I. tener	X	