

# The late Cenomanian oyster *Lopha staufferi* (Bergquist, 1944) – the oldest ribbed oyster in the Upper Cretaceous of the Western Interior of the United States

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“The life of man is of no greater importance to the universe than that of an oyster.”  
David Hume (1711-1776), Scottish Philosopher

## ABSTRACT:

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*Lopha staufferi* (Bergquist, 1944) is a medium-sized, ribbed, Late Cretaceous oyster with a slightly curved axis and a zigzag commissure; it appears suddenly and conspicuously in upper Cenomanian rocks in the Western Interior Basin of the United States. At maturity, the ribs on both valves thicken into steep flanks that allow the oyster to increase interior volume without increasing its exterior footprint on the seafloor. *Lopha staufferi* is the first (earliest) ribbed oyster in the Late Cretaceous of the Western Interior, but has no ancestor in the basin. It disappears from the rock record as suddenly as it appeared, leaving no direct descendent in the basin. In the southern part of the basin where it is well constrained, *L. staufferi* is restricted stratigraphically to the upper Cenomanian *Metoicoceras mosbyense* Zone (= *Dunveganceras conditum* Zone in the north). *Lopha staufferi* has an unusual paleogeographic distribution, occurring in only two, widely scattered areas in the basin. It has been found at several localities near the western shoreline of the Late Cretaceous Seaway in west-central New Mexico and adjacent Arizona, and in localities 1,900 km (1,200 mi) to the northeast near the eastern shoreline in northeastern Minnesota, but nowhere in between. In west-central New Mexico and adjacent Arizona, *L. staufferi* is a guide fossil to the Twowells Tongue of the Dakota Sandstone.

**Key words:** Cenomanian; Oysters; U. S. Western Interior; Taxonomy; Paleogeography; Biostratigraphy; Sweepstake Routes; Zigzag Commissure; Twowells Tongue; Dakota Sandstone.

## INTRODUCTION

Fossil oyster species in the Upper Cretaceous of the Western Interior can make excellent guide fossils: they occur in great numbers; are preserved as original shells rather than as less detailed internal molds because

they have calcitic (not aragonitic) shells; are generally geographically widespread (although often to a specific environment); can evolve quickly (limiting their stratigraphic range); and can be morphologically distinct making them easy to identify in the field. Over the past six years we have examined the middle and late Turon-

ian ribbed oysters *Cameleolopha bellaplicata* and *C. lugubris* (Hook and Cobban 2011, 2012) and the early Coniacian smooth oyster *Flemingostrea elegans* (Hook 2010) in morphological and stratigraphic detail. Each of these species is an important guide fossil that has proven valuable in deciphering the geology of New Mexico and elsewhere in the Western Interior.

Hook and Cobban (2012) have shown that ribbed oysters of the *Cameleolopha bellaplicata* – *lugubris* lineage could have originated in central New Mexico during the middle Turonian in the warm, aerated, nutrient-rich, near-shore waters of the Late Cretaceous Seaway. However, there is an older ribbed oyster preserved in upper Cenomanian rocks in west-central New Mexico and adjacent Arizona that appeared suddenly and then disappeared. This oyster, *Lopha staufferi* (Text-fig. 1) is not a simple ribbed oyster built on a generalized plan that could be the ancestor of the smaller, younger, inequivalved species of *Cameleolopha* mentioned above. Instead, it is a larger, subequivalved species with a slightly curved axis and a very pronounced zigzag commissure. It appears suddenly in rocks of early late Cenomanian age in central

New Mexico and adjacent Arizona in the Twowells Tongue of the Dakota Sandstone; then, it disappears just as suddenly as it appeared.

Cobban (1977, p. 20) suggested that *Lopha staufferi* could have migrated from Europe or Africa, where ribbed oysters are common in the upper Cenomanian. However, *L. staufferi* has an unusual geographic distribution. It occurs in two widely separated areas and only in these two areas: (1) western New Mexico and adjacent eastern Arizona and (2) 1,900 km (1,200 mi) to the northeast in northeastern Minnesota (Text-fig. 2). In the former area, it occurs near the western shoreline of Late Cretaceous Seaway; in the latter, near the eastern shoreline of the seaway (Text-fig. 2). In both localities, *L. staufferi* has been collected from lower upper Cenomanian rocks.

Described originally as the new species *Ostrea (Alectryonia) staufferi* by Bergquist (1944, p. 15), *Lopha staufferi* (Text-fig. 1) is a medium sized (up to 85 mm in height), subequivalved, biconvex oyster with a slightly curved axis that is ornamented with 10–12 pronounced, angular plications generally only on the outer portion of the shell. At maturity, these plications thicken into prongs that form the steep flanks of the shell. These prongs create an interlocking, zigzag commissure. Attachment scars on left valves are variable in size, but are generally large. Left valves are often attached to right valves of other individuals of the species. Therefore, the plications are usually more conspicuous on right valves. The adductor muscle scar is large, broad below and narrow and indented above, and is located closer to the ventral margin of the shell than to the hinge line.



Text-fig. 1. A well-preserved specimen of the late Cenomanian (Late Cretaceous) ribbed oyster *Lopha staufferi* (USNM 619375) from the Twowells Tongue of the Dakota Sandstone at USGS Mesozoic locality D7091, Navajo County, Arizona. This left valve has a height of 59.5 mm, a length estimated at 34.5 mm, a small attachment area, and a slightly curved axis. Eight sharp-crested plicae are present on the unbroken portion of the shell; the total rib count is estimated at 12 at the valve margin. Primary plicae originate near the umbo; secondary plicae are formed by bifurcation of existing ribs. Ribs have not yet thickened into steep flanks at the valve margin. See Text-fig. 8 for stratigraphic position

## STRATIGRAPHY/BIOSTRATIGRAPHY

*Lopha staufferi* has been found in only two widely scattered areas in the Western Interior: northeastern Minnesota and west-central New Mexico and adjacent eastern Arizona. In both areas, it occurs in rocks of early late Cenomanian age.

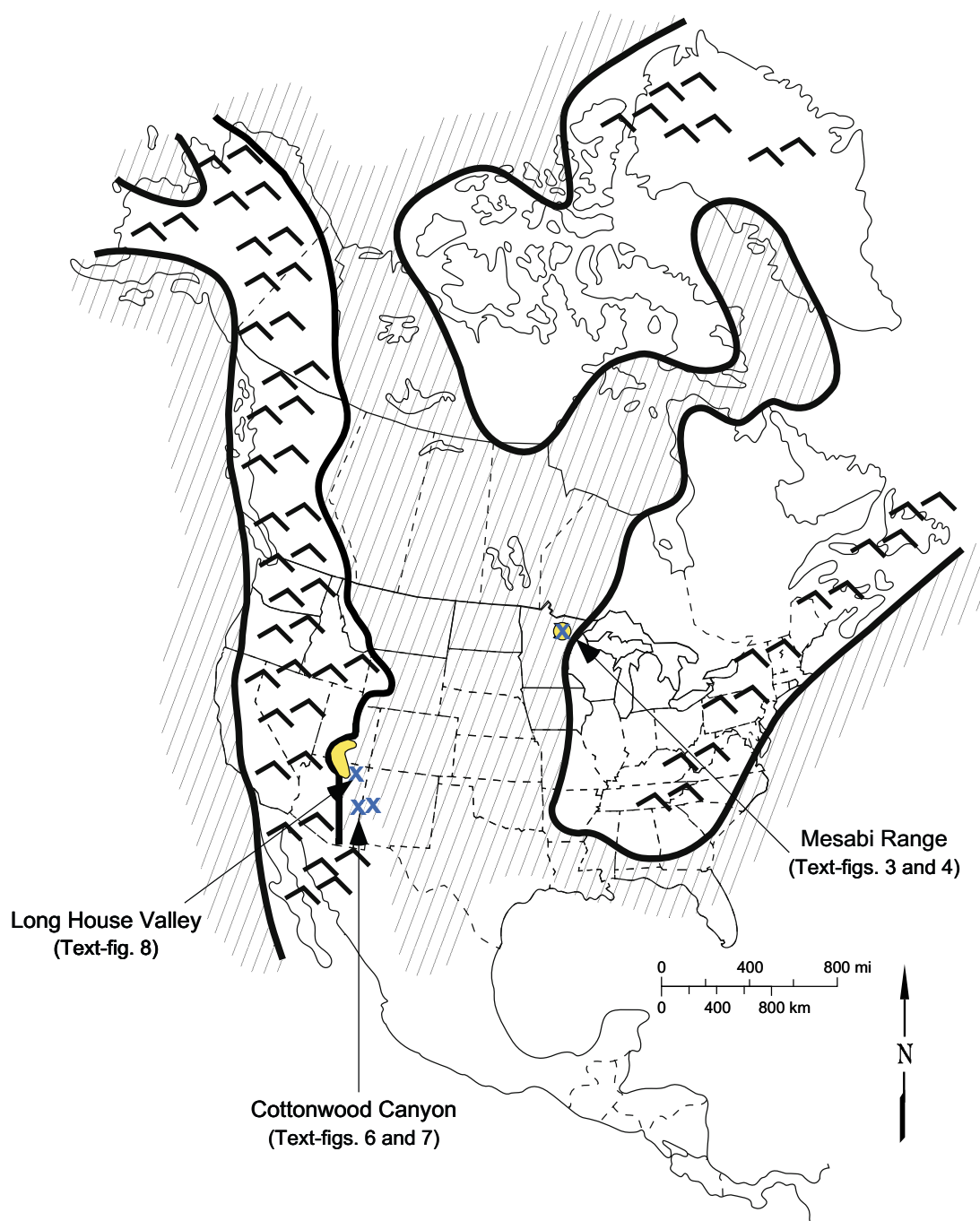
### Minnesota

The type specimens of *Lopha staufferi* came from shales and conglomerates in the Upper Cretaceous Coleraine Formation at the Arcturus Mine, Marble, Itasca County, Minnesota (Text-fig. 3). The Arcturus mine is located in the Mesabi Range of northeastern Minnesota (Text-fig. 2). Bergquist (1944, p. 1) stated that “[g]ood fossil specimens were difficult to find during the field season of 1937 when [I] visited the region.” According to Merewether (1983, p. 34), most of the Coleraine

Formation exposed in mines in northeastern Minnesota has been extracted, so that the outcrops no longer exist.

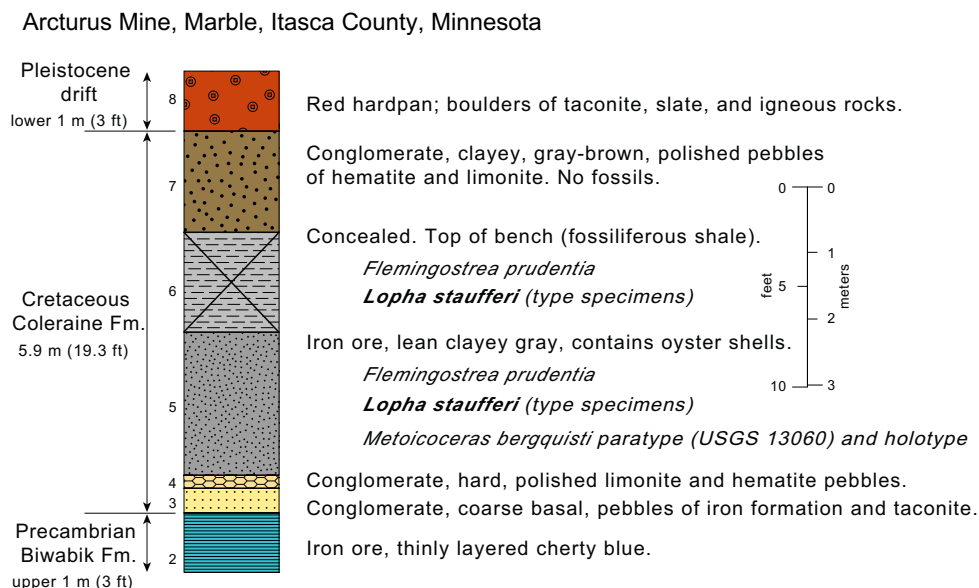
Bergquist (1944, pp. 2, 3) reported that the Cretaceous sediments of the Mesabi mining district were "...spread as a mantle over an uneven surface of tilted Huronian [Precambrian] iron ore formations. They are exposed beneath the drift in mines.... A prevailing basal

conglomerate composed of fragments of heavy ferruginous chert and iron ore, paint rock, and porphyry pebbles indicate[s] it was derived from the underlying iron formations and other pre-Cambrian rocks....The coarse conglomerate grades vertically into fine pebble conglomerate or grit, ...the fine conglomerate bears marine fossils and grades upwards into a ferruginous grit and



Text-fig. 2. Paleogeographic map of North America showing the approximate extent of the Late Cretaceous Seaway during the late Cenomanian. The western shoreline in Utah and Arizona is adapted from Cobban and Hook (1984, fig. 4); the remaining shoreline configurations are from Williams and Stelck (1975, fig. 5).

Localities where *Lopha staufferi* has been collected are shown by the symbol x; areas where *Flemingostrea prudentia* has been collected are shown in yellow



Text-fig. 3. Graphic section of the Cretaceous Coleraine Formation in the Arcturus Mine, Marble, Itasca County, Minnesota, where all the type specimens of *Lopha staufferi* (Bergquist) and the paratype (USGS 13060) and holotype specimens of *Metoicoceras bergquisti* Cobban were collected. Measured by C.R. Stauffer and R.E. Gile on August 8, 1928 (Bergquist 1944, pp. 6, 7). All lithologies have been altered and are shown schematically

sandstone containing an abundant molluscan fauna .... In the northeast corner of the Arcturus mine ... [t]en to 18 feet of coarse basal conglomerate is overlain by 12 to 20 feet of fossiliferous gritty lean ore. In the upper part of the grit are erosion channels filled with green shales making patches 4 to 5 feet thick and containing abundant oyster shells....”

Bergquist’s (1944) systematic study of the fauna of the Coleraine Formation was based on the 1928 (and earlier) field work of Dr. C. R. Stauffer and R. E. Gile (Minnesota Geological Survey). Bergquist reproduced nine of their descriptive measured sections and identified a large marine fauna from the Coleraine Formation in the Mesabi Range. The invertebrate portion of the fauna included 11 species of oysters, 30 species of clams, and 4 species of ammonites.

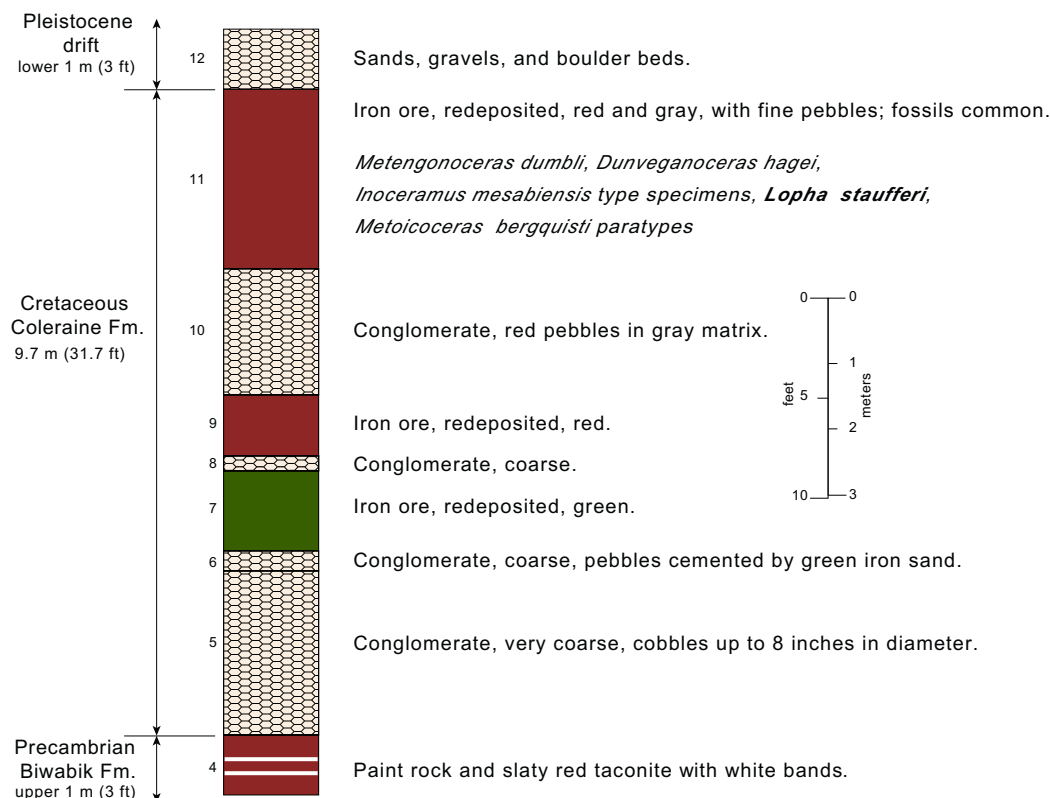
Bergquist (1944) augmented the earlier fossil collections with some new material. However, neither Bergquist nor the earlier collectors, Stauffer and Gile, tied their collections to specific units in the measured sections. Therefore, the positions of key taxa shown on Text-figures 3 and 4 represent our best guesses as to their stratigraphic positions. This “casual” collecting was probably the result of a similar fauna occurring in each fossiliferous stratum in the extremely thin Upper Cretaceous deposits in the Mesabi Range: 5.9 m (19.3 ft) at the Arcturus Mine (Text-fig. 3) and 9.7 m (31.7 ft) at the Hill Annex Mine (Text-fig. 4).

In his systematic description of *Lopha staufferi*,

Bergquist (1944, p. 16) indicated that the specimens came from the conglomerate and shale of the Coleraine Formation at the Arcturus mine (Text-fig. 3), the Hill Annex mine (Text-fig. 4), and the mines at Coleraine and Bovey, Minnesota. The eight type specimens of *L. staufferi* (Bergquist 1944, pl. 9, figs 1–8, 10) came from the Coleraine Formation at the Arcturus mine (Text-fig. 3). The excellent preservation of the type specimens of *L. staufferi* suggests that most came from the lower energy shales rather than the higher energy conglomerates.

Bergquist (1944, p. 15) recorded and described, but did not illustrate, the oyster *Ostrea* [now *Flemingostrea*] *prudentia* White, 1876 from the same horizons and localities as *Lopha staufferi*. If this determination is correct – there is nothing in the description to indicate it is not – then *Flemingostrea prudentia* and *Lopha staufferi* share very similar geographic and stratigraphic distributions. Cobban and Hook (1984, p. 263, fig. 4), using USGS Mesozoic (Denver) locality data, showed the distribution of *F. prudentia*, which is confined to the upper Cenomanian *Metoicoceras mosbyense* Zone in Arizona and Utah, in an arcuate belt that is parallel to the western shoreline of the seaway (Text-fig. 2). Kirkland (1996, p. 41, pl. 4, figs A–C) recorded *F. prudentia* from Black Mesa, northeastern Arizona, also in the *M. mosbyense* Zone. An unpublished USGS fauna (D9012) from 3.4 m (11 ft) below the top of the Dakota Sandstone from Coconino County, Arizona, contains *F. prudentia* along with undiagnostic bivalves and gastropods. A collection

## Hill Annex Mine, Calumet, Itasca County, Minnesota



Text-fig. 4. Graphic section of the Cretaceous Coleraine Formation in the Hill Annex Mine, Calumet, Itasca County, Minnesota, where the type specimens of *Inoceramus mesabiensis* Bergquist were collected. Measured by C. R. Stauffer and G. A. Thiel on July 13, 1928 (Bergquist 1944, p. 7). All lithologies have been altered and are shown schematically

3 m (9 ft) higher in the Dakota (D9013) contains the oyster *Pycnodonte newberryi*, which has its first occurrence in the overlying *Vascoceras diartianum* Zone (Text-fig. 5). There are no other records of *F. prudentia*.

In his paper on the fossil molluscan record from the northeastern part of the Late Cretaceous Seaway, Cobban (1983) studied some of the more important species that Bergquist (1944) described. In particular, Cobban looked at the ammonites and an inoceramid in an attempt to place the Coleraine fauna into the standard Western Interior ammonite zonation. For the most part, the Coleraine taxa are species found nowhere else in the Western Interior. However, some are closely related to species that are used as zonal indices for the upper Cenomanian (Text-fig. 5) or are restricted to these zones. For example, *Inoceramus mesabiensis* Bergquist (1944, p. 12, pl. 5, figs 3–6, 8) is closely related to a smaller and less convex species that occurs in the upper Cenomanian *Dunveganoceras albertense* Zone in Wyoming (Cobban 1983, p. 5). Specimens described by Bergquist (1944, p. 29) as *Metacalycoceras?* sp. and

*Acanthoceras?* sp. are *Dunveganoceras hagei* Warren and Stelck (Cobban 1983, p. 13), also of early late Cenomanian age. Haas (1951, p. 2, fig. 1) described a nearly complete specimen of *Dunveganoceras* from the Coleraine Formation as *Dunveganoceras* cf. *D. pondi*. *Metoicoceras bergquisti* Cobban (1983, pp. 14, 15) – based on specimens described as *M. aff. M. swallowi* by Bergquist (1944, p. 30, pl. 10, figs 10–12) – resembles *M. geslinianum* (d’Orbigny) that occurs in the *Euomphaloceras septemseriatum* Zone. Bergquist’s (1944, p. 8, 30) *Metengonoceras* cf. *M. dumblei* (sic) is indeed *M. dumbli* (Cobban 1983, p. 11), which is known to range as high as the lower upper Cenomanian *Dunveganoceras pondi* Zone. The ammonite and inoceramid evidence places the Coleraine Formation in the lower part of the upper Cenomanian, between the *Dunveganoceras pondi* and the *Euomphaloceras septemseriatum* zones. The oyster *Flemingostrea prudentia* places it in the middle of this range, in the *Metoicoceras mosbyense* Zone (Text-fig. 5). Kauffman *et al.* (1993, p. 429, fig. 3) placed *Lopha staufferi* and *Inoceramus*

*mesabiensis* in their biozone CE-7B along with the ammonites *Dunveganoceras conditum* and *Metoicoceras mosbyense*. This assignment places *L. staufferi* in the upper Cenomanian *Dunveganoceras conditum* (= *Metoicoceras mosbyense*) Zone in Minnesota (Text-fig. 5).

### New Mexico/Arizona

The biostratigraphic evidence for the placement of *Lopha staufferi* in the upper Cenomanian *Metoicoceras mosbyense* Zone is compelling along the Arizona/New Mexico state line. At Cottonwood Canyon (Text-figs 6, 7), Apache County, Arizona, and Catron County, New Mexico, the index ammonite *M. mosbyense* occurs below (D6171), with (D6173), and above (D6174) *L. staufferi* in the upper 10 m (33 ft) of the Twowells Tongue of the Dakota Sandstone. Cobban and Kennedy (1990) illustrated several specimens of the ammonite *Calycoceras obrieni* Young, 1957, which co-occurs with *M. mosbyense*, from the D6173 level at Cottonwood Canyon. They also presented a graphic measured section of the upper part of the Twowells Tongue (Cobban and Kennedy 1990, fig. 1).

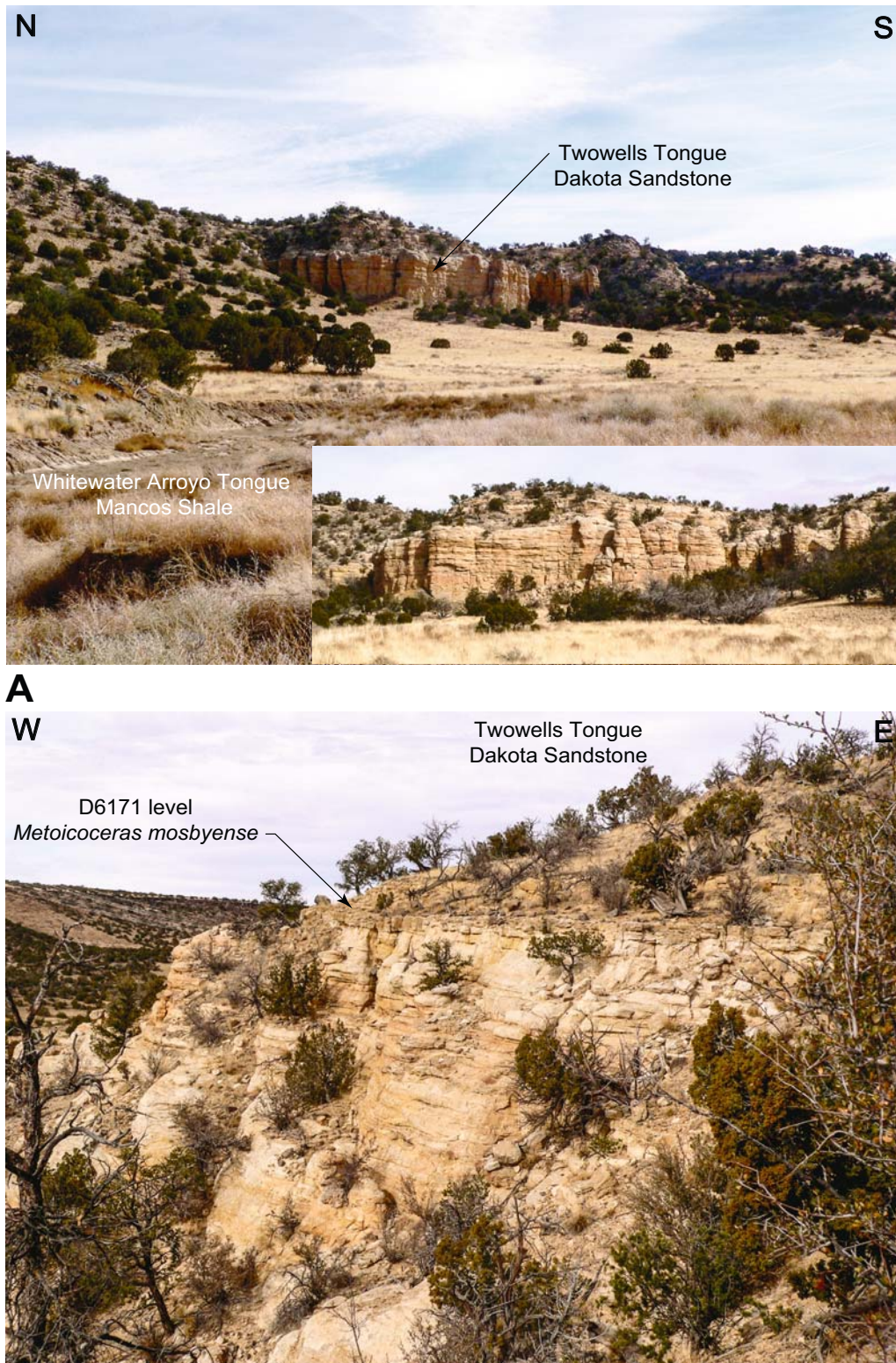
The bivalve fauna co-occurring with *Lopha staufferi* at Cottonwood Canyon (Text-fig. 7, D6173 level) is exceptionally rich, in both the number of species and the number of individuals within each species. Unit 8, a 23 cm- (9 inch-) thick bed of highly fossiliferous sandstone referred to as the “ammonite bed”, has yielded at least 12 species of clams, 2 species of oysters, 2 species of ammonites, and several species of gastropods. The oysters are preserved primarily as original shells, but in-

ternal molds are common. The clams and ammonites are generally preserved as internal molds that occasionally have some altered shell material clinging to them. The oyster, *Rhynchostreon levis* Stephenson, 1953, is exceptionally large there and occurs in vast numbers.

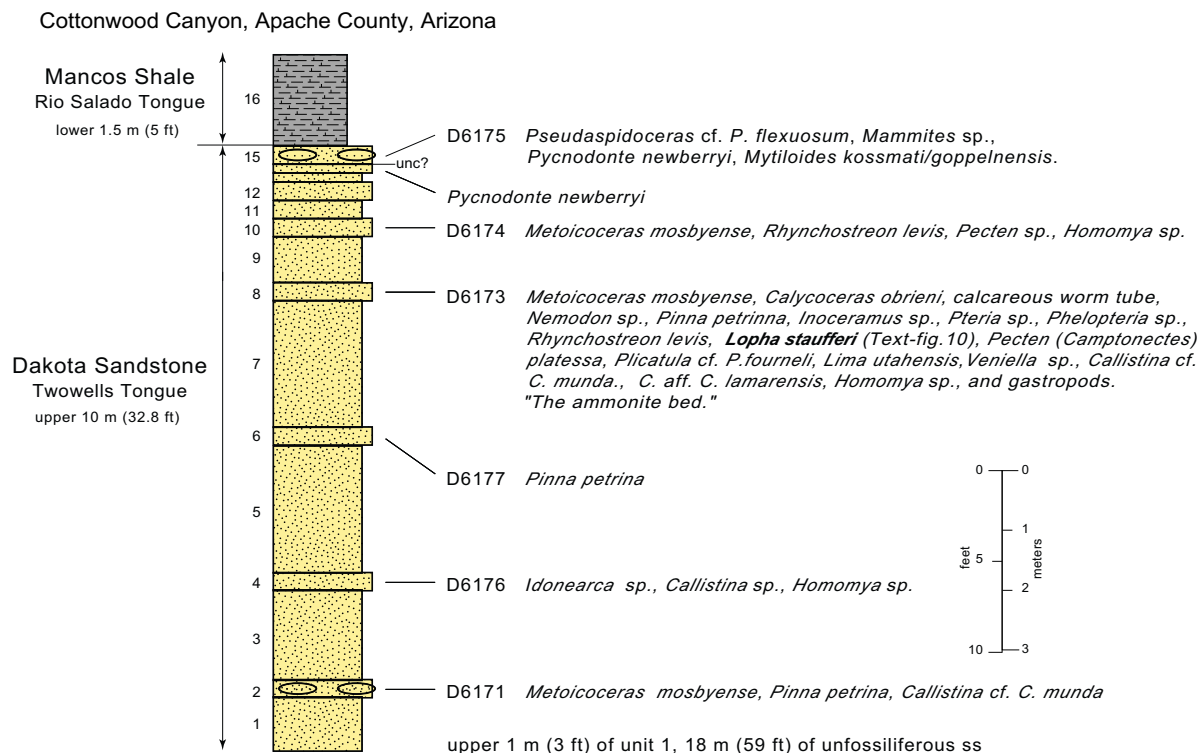
A left valve of *Rhynchostreon levis* (USNM 619381, D6178) collected from the ammonite bed in Cottonwood Canyon about a kilometer south of the measured section (Text-fig. 7) displays radial color-bands. This specimen (see Text-fig. 10F) is a moderate-sized individual (for this area), having a height of 35.2 mm and a length of 31.4 mm. Preserved color bands in Late Cretaceous oysters are rare in the Western Interior. Kirkland (1996, pl. 5I) illustrated a left valve of *R. levis* that preserves radial color bands from Howell Mesa, Arizona, from the late Cenomanian *Euomphaloceras septemseriatum* Zone near the base of the Mancos Shale. Cobban (1977, pl. 15, figs 17, 18) illustrated two right valves of the oyster *Pycnodonte* aff. *P. kellumi* displaying radial color bands, but noted (p. 17) that the color bands occur on both valves. Both of his specimens are from the middle Cenomanian Paguate Tongue of the Dakota Sandstone, Catron County, New Mexico. Cobban (1977, pl. 19, fig. 5) also illustrated two specimens of *Plicatula* cf. *P. ferryi* from the upper Cenomanian Twowells Sandstone Tongue of the Dakota Sandstone of Cibola County, New Mexico, with color bands. Hook and Cobban (2012, fig. 8K, L) illustrated an articulated specimen of *Cameleolopha bellaplicata* from the middle Turonian Fite Ranch Sandstone Member of the Tres Hermanos Formation, Lincoln County, New Mexico, that appears to have concentric color bands. Both concentric

Stage	SW Shoreline Ammonite Zone	NE Shoreline Ammonite Zone
C E N O M A N I A N	<i>Nigericeras scotti</i>	<i>Nigericeras scotti</i>
	<i>Neocardioceras juddii</i>	<i>Neocardioceras juddii</i>
	<i>Burroceras clydense</i>	<i>Burroceras clydense</i>
	<i>Euomphaloceras septemseriatum</i>	<i>Euomphaloceras septemseriatum</i>
	<i>Vascoceras diartianum</i>	<i>Vascoceras diartianum</i>
	<i>Metoicoceras mosbyense</i>	<i>Dunveganoceras conditum</i>
	? (= <i>Dunveganoceras</i> spp.)	<i>Dunveganoceras albertense</i> <i>Dunveganoceras problematicum</i>
	<i>Calycoceras canitaurinum</i>	<i>Dunveganoceras pondi</i>

Text-fig. 5. Upper Cenomanian Ammonite Zonation used in the Western Interior of the United States. Chronologic species of the genus *Dunveganoceras* are common in the northern part of the Western Interior, but do not occur in New Mexico. Four species of *Dunveganoceras* are used to define the lower part of the upper Cenomanian in the north (Minnesota); whereas species of *Calycoceras* and *Metoicoceras* are used in the south (Arizona and New Mexico)



Text-fig. 6. Outcrop photographs of the Twowells Tongue of the Dakota Sandstone exposed in Cottonwood Canyon in SE 1/4 sec. 3, T. 10 N., R. 31 E., The Rincon, AZ-NM, 7.5-minute quadrangle, Apache County, Arizona. **A** – Distant view of the almost vertical cliff formed by the lower, unfossiliferous portion of the Twowells with exposures of the Whitewater Arroyo Tongue of the Mancos Shale in the foreground. Note white bentonite bed at lower left. Inset photograph shows a closer view of the Twowells cliff. **B** – Still closer view of the Twowells showing the resistant ledge of concretionary sandstone (D6171 level) that marks the first appearance of the zonal index ammonite *Metoicoceras mosbyense*. *Lopha staufferi* is found about 7 m (22 ft) higher in the section at the D6173 level (see Text-fig. 7)



Text-fig. 7. Graphic section of the upper part of the Twowells Tongue of the Dakota Sandstone and lower portion of the Rio Salado Tongue of the Mancos Shale exposed on the eastern side of Cottonwood Canyon in the NE 1/4 NE 1/4 section 3, T. 10 N., R. 31 E, The Rincon AZ-NM, 7.5-minute quadrangle, Apache County, Arizona. Section measured by E. R. Landis and W. A. Cobban on September 9, 1969. An unconformity is inferred between the late Cenomanian *Metoicoceras mosbyense* fauna (D6174) and the early Turonian *Pseudaspidoceras* cf. *P. flexuosum* fauna (D6175) because (1) the stratigraphic interval between the two collections is 1 m (3 ft) and (2) the ubiquitous *Euomphaloceras septemseriatum* fauna is not present between the two. This thin interval has to represent six ammonite zones: the five uppermost Cenomanian zones (see Text-fig. 5) and the lowermost Turonian zone. Compare this section with that at Long House Valley (Text-fig. 8), where the *Euomphaloceras septemseriatum* Zone is at least 3.2 m (10.7 ft) thick. Rock symbols are self-explanatory. Collections and fauna updated from Cobban and Kennedy (1990, fig. 1)

and radial color bands are visible on the specimens of the Recent *Lopha cristagalli* (see Text-fig. 9).

At the Long House Valley measured section (Text-fig. 8), Navajo County, Arizona, 240 km (150 mi) to the northwest of Cottonwood Canyon, *Lopha staufferi* (D7091) occurs in a 15 cm- (6 inch-) thick, ledge-forming sandstone that marks the top of the Twowells Tongue. The specimen of *L. staufferi* (USNM 619375) shown as Text-fig. 1 came from this collection. An earlier collection (D4514) from this level yielded the ammonite *Metoicoceras mosbyense*. The Twowells is only 2 m (6.5 ft) thick here. A 5 cm- (2 inch-) thick crumbly limestone about 30 cm (1 ft) above the base of the overlying main body of the Mancos Shale contains the ammonites *Sciponoceras gracile* (Shumard, 1860) and *Moremanoceras scotti* (Moreman, 1942), and the oyster *Pycnodonte newberryi* (Stanton, 1894) from USGS Mesozoic locality D7092, together indicative of the upper Cenomanian *Euomphaloceras septemseriatum* Zone (Text-fig. 5). This limestone forms the base of the 3.2 m- (10.7 ft-) thick Bridge Creek Limestone Beds, which lie

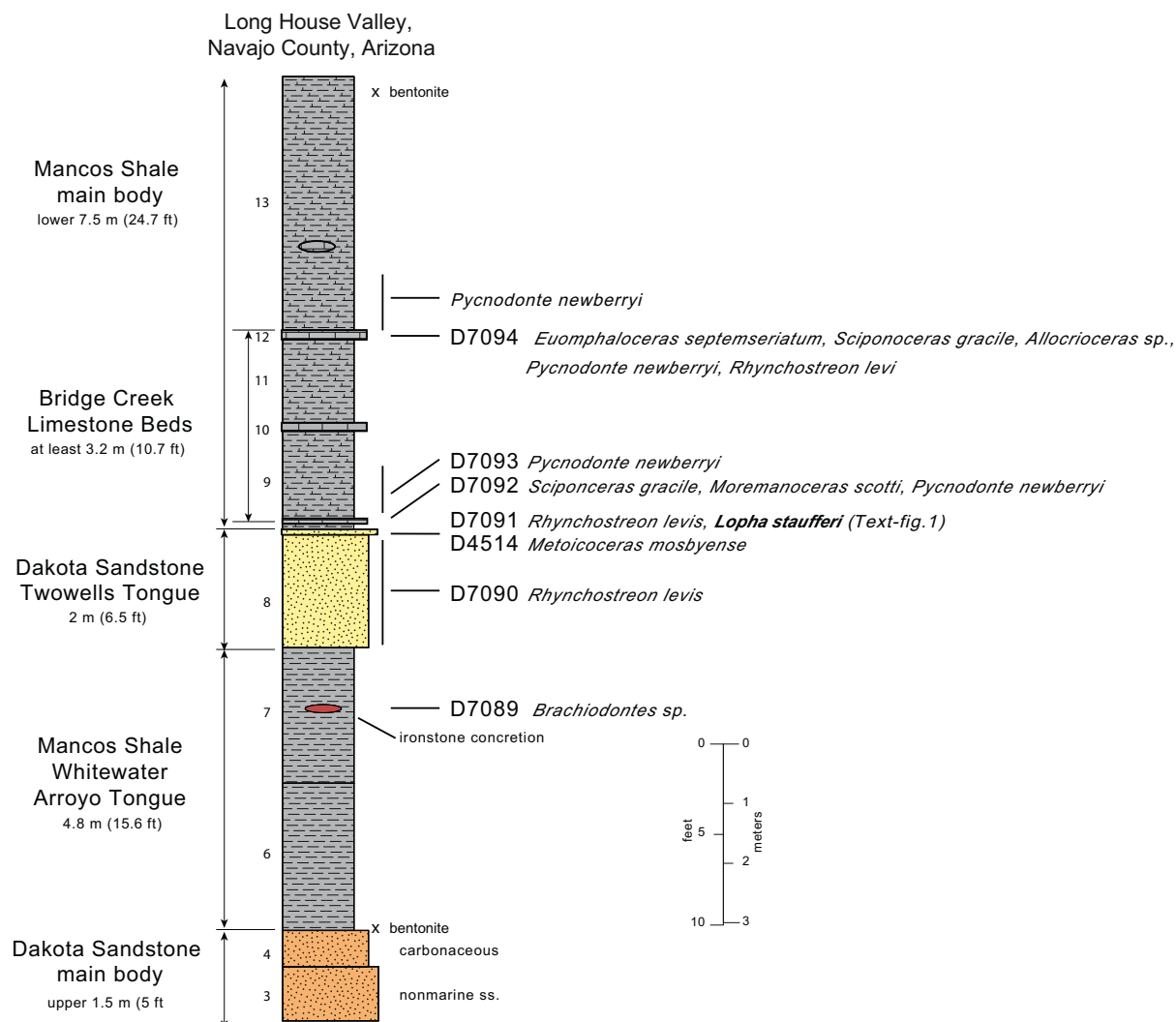
entirely within the *Euomphaloceras septemseriatum* Zone.

Collections containing *Lopha staufferi* from the lower part of the Twowells Tongue in west-central New Mexico (Cobban 1977, table 3 and p. 20) include *Calycoceras obrieni*, which co-occurs with *L. staufferi* in Cottonwood Canyon (Text-fig. 7, D6173). Interestingly, an inoceramid identified as *Inoceramus* cf. *I. mesabiensis* by Cobban (1977, table 3) occurs in the upper part of the underlying Whitewater Arroyo Tongue of the Mancos Shale in west-central New Mexico. Kirkland (1996, p. 42 and pl. 5, figs B, C) records *Lopha staufferi* from Black Mesa, northeastern Arizona, in the Dakota Formation in the *Metoicoceras mosbyense* Zone.

#### SYSTEMATIC PALEONTOLOGY

Family Ostreidae Rafinesque-Smaltz 1815  
 Subfamily Lophinae Vyalov [Vialov] 1936, p. 19  
 Genus *Lopha* Röding 1798, p. 168





Text-fig. 8. Graphic section of the upper part of the main body of the Dakota Sandstone, the Whitewater Arroyo Tongue of the Mancos Shale, the Twowells Tongue of the Dakota Sandstone, and lower portion of main body of the Mancos Shale in Long House Valley, northwestern side of Black Mesa 21.3 km (13.2 mi) south and 20.9 km (13.0 mi) west of the northeast corner of the Kayenta 15-minute quadrangle, Navajo County, Arizona. Section measured by E. R. Landis and W. A. Cobban on October 9, 1969. The D7092 fauna from the base of the Bridge Creek Limestone Beds represents the *Euomphaloceras septemseriatum* Zone. Rock symbols are self-explanatory

TYPE SPECIES: *Lopha cristagalli* (Linnaeus 1758, p. 704.)

DESCRIPTION: Stenzel (1971, p. N1157) characterized this medium sized (up to 11 cm long), biconvex genus with a medium to large sized attachment area as being subequivalved with 6 to more than 50 sharp radial plicae, which produce a zigzag valve commissure. He noted that the subgenus *Lopha* has two ecomorphs. The first based on *L. cristagalli* (Text-fig. 9) is equivalved and has a roughly globular shape with up to 12 deep, sharp, radial plicae, whose apex angles decrease from near the axial hinge to the point farthest from it. The surfaces of both valves are roughened by numer-

ous small, low, rounded, equisized protuberances; there are no imbricating squamae. Intermittent spines on left valves are recurved as claspers for support on the substrate. The second ecomorph based on *Dendostrea folium* (Linnaeus, 1758) has a lancelet to ovate shape with many radial plicae. The surfaces of its valves have many closely set growth squamae, but no protuberances.

DISTRIBUTION: Triassic to Recent; mostly tropical; worldwide.

DISCUSSION: Placement of the fossil species *staufferi* in the genus *Lopha* is based on pragmatic con-

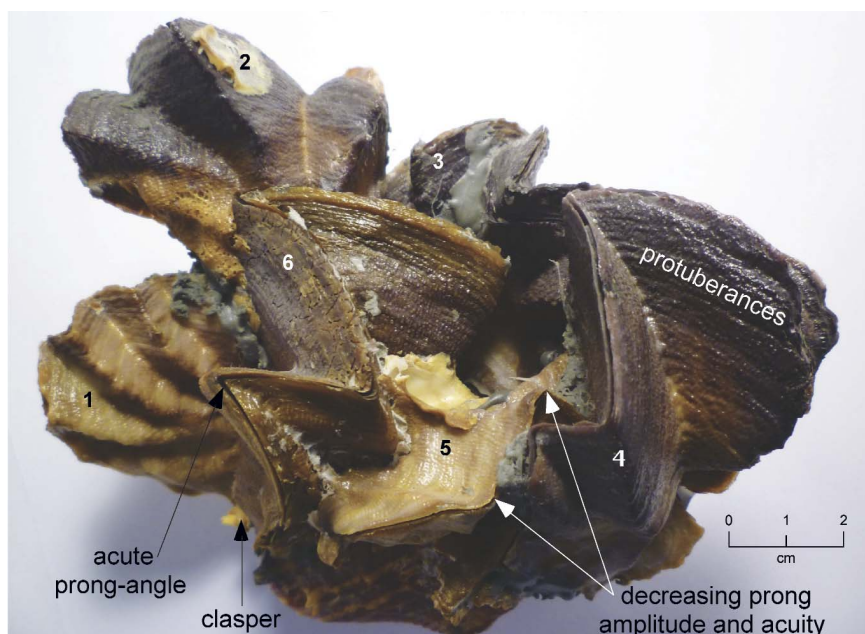
siderations. The 10–12 angular, radial plicae creating a zigzag commissure fit nicely with the first ecomorph; the imbricating squamae fit better with the second ecomorph. The slightly curved axis and the lack of spines and claspers do not fit with either. The large attachment scar and attachment to other valves of the same species indicate that *staufferi* lived horizontally on the seafloor. Both of the Recent ecomorphs live in nearly vertical positions with ecomorph 1 attached to mangroves or other bivalves (see Text-fig. 9); ecomorph 2 grows on stems of Gorgonacea or sea fans and develops long, cylindrical xenomorphs on its right valves. In addition, *L. staufferi* embraces at least one characteristic of the subgenus *Abruptolopha*: at maturity, both valves of *L. staufferi* abruptly stop growing in height but continue to accumulate wall thickness, creating steep flanks that increase the interior volume of the shell. However, *Abruptolopha* has more than 50 narrow crested plications that are interrupted three to five times by abrupt increases in slope of the shell profile.

*Lopha staufferi* (Bergquist, 1944)  
(Text-fig. 10A–E)

1944. *Ostrea (Alectryonia) staufferi* n. sp.; Bergquist, pp. 15, 16, pl. 9, figs 1–10.  
1977. *Lopha staufferi* (Bergquist); Cobban, p. 20, pl. 19, figs 8, 9.  
1996. *Lopha staufferi* Bergquist (*sic*), 1944; Kirkland, p. 42, pl. 5, figs B, C.

DESCRIPTION: The best description of *Lopha staufferi* is that of Bergquist (1944, p. 15, pl. 9, figs 1–10), which is based on numerous original shell specimens, often fully articulated and weathered free of matrix that were collected from at least four localities in the Mesabi Range of northeastern Minnesota. Bergquist's (1944, pl. 9, figs 1–8, 10) types consist of eight specimens. The holotype (Bergquist 1944, pl. 9, figs 4, 5) is an articulated individual that has a height of 55 mm, a length of 28 mm, a maximum convexity of 32 mm at the anterior margin and 20 mm at the posterior margin, and at least 8 angular plicae. Bergquist's (1944, p. 15) detailed description is reproduced below, then supplemented by illustrations, observations, and measurements of specimens from Cottonwood Canyon (Text-figs 7, 10) and Long House Valley (Text-figs 1, 8).

“Shells somewhat variable in thickness, outline, and in degree of ornamentation. Small to medium size. Typical forms curve toward rear. Both valves about equally inflated; left valve may be deeper. Anterior margin of left valve of holotype rises abruptly to meet down-curved anterior margin of right valve; surfaces then slope to flattened posterior region. This relationship is true of all shells but not as pronounced on most. Scar of attachment on left valve varies in size, that on the holotype covers almost one-third of shell; some show smaller areas, while some are attached along entire under surface or along the posterior part of the shell. Many left valves are attached to right valves of other individuals so that posterior and ventral margins are flattened to down-curved. Some shells have a posterodorsal winglike extension, but this is lacking on the



Text-fig. 9. A cluster of six individuals of the oyster *Lopha cristagalli* (Linnaeus) that grew on a spiny clamshell (Recent, from the Indo-Pacific realm, in the authors' collection). These six show considerable morphologic variation, which is caused in part by crowding. Individual #1 has eight slightly curved, low amplitude, plicae; claspers (modified hyote spines) on the left valve are firmly wrapped around the spines on the clamshell. Individual #2 has four, higher amplitude, broader wavelength plicae on a shell with essentially the same height. Individuals #4 and #6 have the highest amplitude plicae: #4 has four plicae and #6 has three. Individual #5, the smallest, which has to fit in the space between #4 and #6, has three plicae and is misshapen due to crowding. The zigzag commissure is well developed on all six individuals. *Lopha cristagalli* received its specific name (*crista* [L.] = comb + *gallus* [L.] = cock) because of its resemblance to a rooster's comb and is often called the cockscomb oyster

holotype. Beaks not prominent, curved on some specimens. Area of hinge on holotype is wedge-shaped, 32 mm at base, 11 mm on anterior margin, and narrowed to 6 mm on posterior margin; on others the area is roughly triangular; all show considerable curvature. Resilifer curved, broad and pronounced on left valve, may occupy about one-third of hinge area; closer to anterior margin than posterior. Adductor scar large, broad below, narrowest and indented above, situated close to posteroventral area.

Anterior margin of shell exhibits a series of deeply indented, geometrically V-shaped notches, giving sharply interlocking edges where valves meet. Anterior surface of right valve generally ornamented by 10 to 12 prominent costae, immature forms show smaller number. Costae are V-shaped in cross section and continuous to interlocked edges. These are not clearly defined on dorsal third or posterior portion of valve but are radiate and broadly curved from the frontal region, new ones added by bifurcation or intercalation. Costae tend to irregularity along crests. Because of large attachment area, the lower valve does not always clearly show the costae, but generally 10 to 12 are indicated along the anterior and ventral margins, where the edges become sharply V-shaped. Some shells lack ribbing except along anterior marginal area, remainder of surface then being irregular and roughened only by growth lines.”

**PALEOECOLOGY:** *Lopha staufferi* was an attached, epifaunal, suspension-feeding oyster. Its paleogeographic and stratigraphic positions in New Mexico and Arizona indicate that it lived in nearshore, relatively high energy, warm water, sandy environments. In northeastern Minnesota, *L. staufferi* is found in nearshore deposits, but in water temperatures that were probably much cooler than those to the southwest.

**OCCURRENCE:** *Lopha staufferi* is known from only two widely scattered areas in the Western Interior: near the eastern shoreline of the Late Cretaceous Seaway in northeastern Minnesota and near the western shoreline in western New Mexico and adjacent Arizona (Text-fig. 2). In New Mexico and Arizona *L. staufferi* occurs in the main body and the Twowells Tongue of the Dakota Sandstone (Text-figs 7, 8) where it is associated with the late Cenomanian ammonites *Metoicoceras mosbyense* and *Calycoceras obrieni*, placing it in the upper Cenomanian *M. mosbyense* Zone (Text-fig. 5). It appears to be approximately the same age in Minnesota, where it is not as well constrained due to the absence of index ammonites in the Coleraine Formation (Text-figs 3, 4).

The unusual geographic distribution of *Lopha stauf-*

*feri* (as well as that of *Flemingostrea prudentia*) along the western shoreline of the Late Cretaceous Seaway in New Mexico and Arizona and along the eastern shoreline in northeastern Minnesota – but nowhere in between – requires comment. Recent oyster species disperse by planktonic larvae, which can have a free-swimming period of up to six days (Stenzel 1971, p. N1035). With no continuous coastline linking the two widely separated areas, it seems unlikely that *L. staufferi* spread gradually along one coastline then to the other, especially with no known intermediate localities. Island-hopping does not appear to be a viable option, because no islands are known in the seaway at this time and there are no localities in the central part of the seaway between the two areas where *L. staufferi* has been found, even though there are outcrops of the same age rocks.

The 1,900 km (1,200 mi) separating the two occurrences (Text-fig. 2) suggest that oceanic currents could have been responsible for this dispersal pattern. If so, then at least two end-member options are possible: larval dispersement or attachment of oysters to floating objects such as driftwood. Current velocities of 200 to 250 cm/sec (173 to 216 km/day) have been recorded for the present-day Gulf Stream (Stenzel 1971, p. N1035). With a six-day, free-swimming period, larvae could conceivably travel up to 1,300 km if caught in the Gulf Stream today. If *L. staufferi* had a slightly longer free-swimming larvae (9 days), the distance between New Mexico and Minnesota could be covered, assuming a current with the Gulf Stream velocity linked the two areas. If such a current existed, the driftwood oysters could have made it from one shoreline to the other as well. However, these arguments and assumptions are conjecture. Perhaps there were other coastal areas on the eastern margin of the seaway that contained these oyster species, but were removed by erosion. At this time, all that is known is that two oyster species, *L. staufferi* and *Flemingostrea prudentia*, have similar stratigraphic and geographic distributions.

Seventy-six years ago George Gaylord Simpson (1940) proposed the term “sweepstakes routes” to explain the present-day distribution of mammals that were thought to have crossed large bodies of water by floating on natural rafts. He illustrated this concept with a whimsical diagram showing a sweepstakes route between Africa and Madagascar, which he entitled “The African-Malagasy Sweepstakes” (Simpson 1940, fig. 6). Lemurs in the Eocene, mice in the Miocene, and hipopotami in Pleistocene held winning tickets; whereas, small cats, small monkeys, shrews, and rodents were disappointed ticket holders. Simpson (1940, p. 156) noted that “...a ‘sweepstake route’ is...indeterministic. Its use depends purely on chance and is therefore un-

predictable.... It is not to be supposed that ...rafts are the sole means of transport involved.” The known distributions of both *Lopha staufferi* and *Flemingostrea prudentia* suggest they held winning sweepstake tickets in the late Cenomanian.

A modern disaster indicates that sweepstakes routes still exist, albeit using man-made objects as rafts. Barnacle-encrusted debris from the tsunami that struck Japan on March 11, 2011 washed ashore in California two years later in April 2013 (<http://www.dailymail.co.uk/news/article-3033123/Boat-chunk-Oregon-coast-thought-tsunami-debris.html>). Other debris, including a portion of a dock, 21m- (70 ft-) long, harboring living organisms has shown up off the coast of Oregon. The distance between Japan and Oregon is roughly 8,000 km (5,000 mi). “John Chapman, a research scientist at Oregon State University’s Hatfield Marine Science Center, said hundreds of millions of other organisms also hitchhiked across on the dock – some of which are invasive species never before seen on this part of the west coast”(www.huffingtonpost.com/2012/06/06/Japan-tsunami-debris-oregon-dock\_n\_1574558.html.)

Whether such an event occurred during the late Cenomanian that could have uprooted and transported trees out to sea is unknown, but would still require a current or sustained winds between the two widely separated areas to establish the known distributions of *Lopha staufferi* and *Flemingostrea prudentia*. Elder (1988), studied the geometry of volcanic ash distribution in the Western Interior Seaway and found patterns suggesting high altitude westerly winds during the latest Cenomanian. This suggests that if the dispersal of these two oysters were related to currents, then movement could have been from west to east. Occasional fragments of wood bored by *Teredolithus* sp. (ship worms) occur in marine rocks in the Western Interior Upper Cretaceous, indicating that wood entered the sea and floated at least moderate distances out to sea before sinking to the seafloor. For example, Hook and Cobban (2012, p. 79,

figs 2, 4) reported bored wood in the marine Fite Ranch Sandstone Member of the Tres Hermanos Formation at Bull Gap Canyon, Lincoln County, New Mexico, more than 90 km (50 mi) seaward of their inferred middle Turonian shoreline. However, no oyster-encrusted wood was collected from this area. Kirkland (1996, p. 53) reported widely scattered occurrences of shipworm tubes (*Teredolithus* sp.) all across Black Mesa, northeastern Arizona, from the Dakota Formation, Mancos Shale, and Toreva Formation, including rocks from the *Metoicoceras mosbyense* Zone.

DISCUSSION: Cobban (1977, p. 20) stated that *Lopha staufferi* resembles several of the plicate oysters of the same age that are common in the Upper Cretaceous of Europe and Africa, particularly *Lopha* [*Rastellum*] *diluviana* (Linnaeus, 1767). A specimen from the Upper Cretaceous of Bell County, Texas, identified and illustrated as *Ostrea diluviana* by White (1884, p. 295, pls 40, fig. 1 and 41, figs 1, 2) indicates that White’s *O. diluviana* and *L. staufferi* are distinct species. Among other differences, White’s (1884) specimen is larger (height = 115 mm, length = 79 mm), has more ribs (22), and a large, comma-shaped muscle scar (height = 35 mm, length = 20 mm) located closer to the hinge line. The specimen illustrated by Coquand (1869, pl. 40, figs 1–4) as *O. diluviana* is also too large and has 20 ribs and a large, kidney-shaped muscle scar located too close to the hinge line. In addition, Ayyasami (2006, p. 238) in a well-dated Cretaceous sequence in southern India, places *Lopha* (*Actinostreon*) *diluviana* in the (much younger) middle Turonian *Lewesiceras anapadense* Zone.

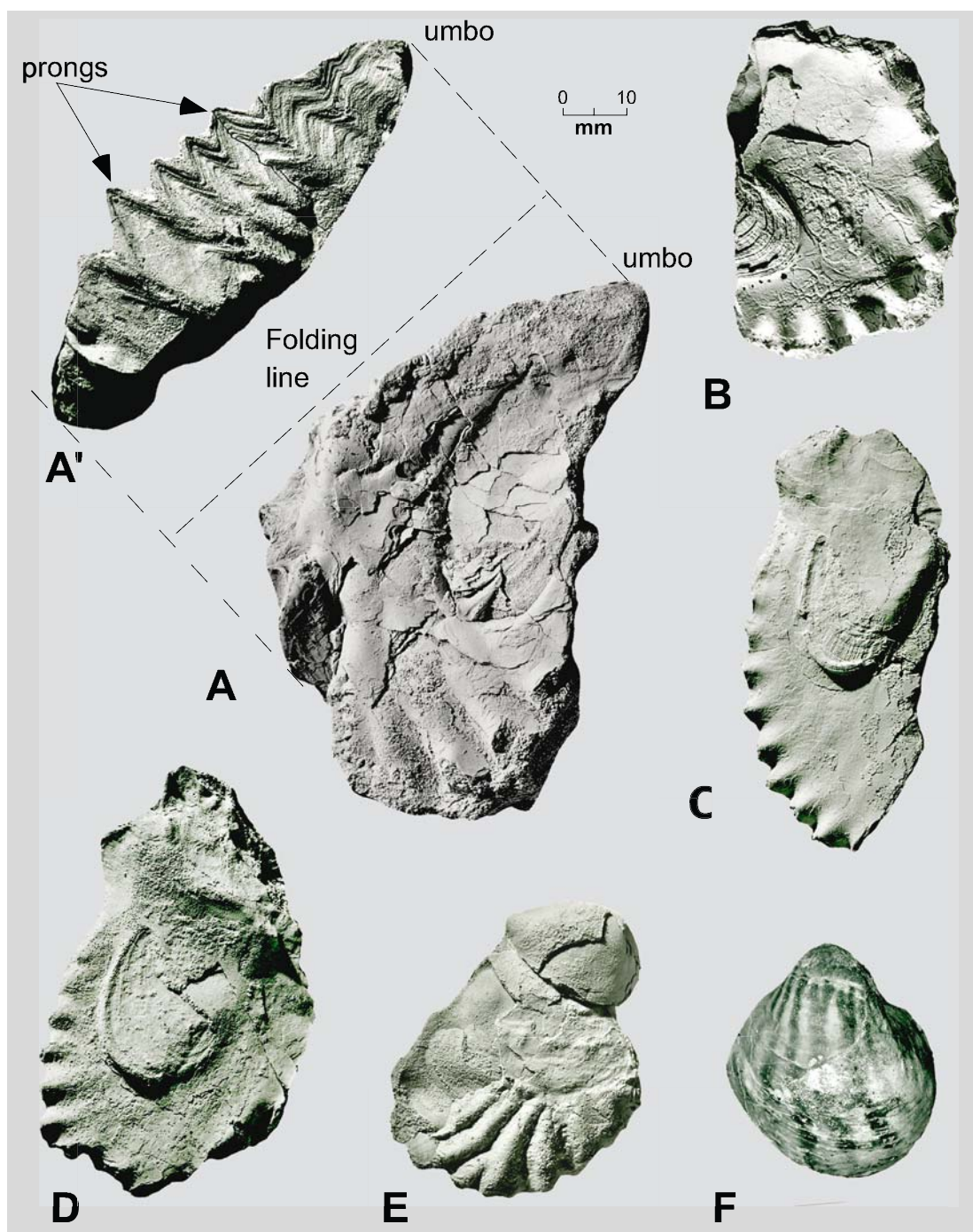
The collection of *Lopha staufferi* from Cottonwood Canyon (Text-fig. 7, D6173 level) consists of 23 specimens and at least 38 individuals because 15 specimens consist of a left valve attached to a right valve. Most of the specimens are preserved as original shells (Text-fig. 10A–E), although the valves are generally incomplete and not articulated; a few are internal molds. Most of the

Text-fig. 10. Fossil oysters from the ammonite bed, USGS Mesozoic localities D6173 (A–E) and D6178 (F), Twowells Tongue of the Dakota Sandstone exposed in Cottonwood Canyon in SE 1/4 sec. 3, T. 10 N., R. 31 E. and NE 1/4 sec. 3, T. 10 N., R. 31 E., respectively, The Rincon Ariz. – N. Mex. 7.5-minute quadrangle, Apache County, Arizona. **A** – External and oblique side (posterior) view of a left valve of *Lopha staufferi* (USNM 619376). Note the curved axis, large attachment scar, and four rounded ribs in A. The oblique view (A') shows the posterior flank, an abrupt, 90° change in curvature of the shell that occurs at maturity(?) and seven high amplitude, narrow, crested ribs that do not show in the top view. These thickened plications form a zigzag commissure with the right valve. The prong angle becomes more acute with increasing distance from the umbo as the amplitude of the prong increases. **B** – Internal view of an incomplete left valve of *L. staufferi* (USNM 619377) with nine ribs preserved around the periphery of the shell. The large, raised, muscle-attachment platform is composed of concentric lamellae. The smooth portion of this valve corresponds to the external attachment area of the valve, which is attached to the right valve of another individual of the same species. **C** – Internal view of an incomplete left valve of *L. staufferi* (USNM 619378) with eight ribs preserved around the periphery of the shell. The large muscle attachment area is again a raised platform, composed of concentric lamellae. The smooth inner portion of this valve corresponds to the attachment area, where externally the valve is attached to the right valve of another individual of the same species. **D** – Internal view of an incomplete left valve of *L. staufferi* (USNM 619379) with 14 ribs preserved around the periphery of the shell. The large muscle attachment area is again a raised platform composed of concentric lamellae. The smooth portion of this valve corresponds to the attachment area of the valve, which is attached to the right valve of another individual of the species. **E** – External view of a right valve of *L. staufferi* (USNM 619380) with nine ribs preserved around the outer half of the shell. Ribs arise by both intercalation and bifurcation. The bulge at the umbo is an internal mold of a left valve of *Rhynchostreon levis* partially covered by shell. **F** – External view of a left valve of *R. levis* (USNM 619381) that preserves dark, radial color bands. The dark color bands are approximately the same width as the lighter interbands. Two sets of two color bands close to the umbo merge ventrally to form two wider color bands

internal molds were probably covered originally by shells that broke off during weathering on the outcrop or collecting, as shown by the partially shell-covered internal mold of *Rhynchostreon levis* (USNM 619381) in Text-figure 10E. Usually, the prongs – thickened extensions of the plicae on the valve flanks where the shell convexity changed abruptly (geniculated) from slightly to greatly convex – on the outer portion of the shell were broken (Text-figs 10B–D).

The largest, most complete, illustrated specimen (USNM 619376, Text-fig. 10A–A') is a left valve with a slightly curved axis, five plications visible on the ventral portion of the shell, a height of 81 mm, a length of 47 mm, and a thickness of 27 mm. Its prongs (Text-fig. 10A'), prong angles, and zigzag commissure are discussed in detail in the next section of the paper.

The largest specimen in the D6173 collection (not illustrated) is a right valve, free of matrix internally, that has



a straight axis, 12 plications on the outer portion of the shell (two still elongated into prongs), a height of 86 mm, a length of 47 mm, and a minimum thickness of 24 mm.

Adductor muscle attachment areas are large, raised platforms on many of the specimens in this collection. For example, the muscle attachment pad on USNM 619379 (Text-fig. 10D) has a height of 25 mm, a length of 20 mm and is raised above the interior surface of the shell by approximately 1 mm. These muscle pads are composed of aragonite that is deposited on the calcitic outer portion of the shell (Stenzel 1971, p. N963). In many, perhaps most, fossil oysters, this aragonitic pad has been dissolved, leaving a cavity filled with secondary calcite or sediment.

### THE ZIGZAG COMMISSURE

The function of zigzag deflections of the commissures of brachiopods and oysters has been a subject of investigation for more than 100 years. Cummins (1903, p. 131) appears to have been the first researcher to interpret the zigzag deflection as a protective device in the Paleozoic brachiopod genus *Platystrophia*: “The greatly increased length of the mantle border of a plicated shell as compared with a smooth shell of the same size, is obvious. Such a plicated shell could admit the respiratory and food-bearing currents of water, and at the same time keep out foreign particles and disagreeable visitors, because the greatly lengthened slit between mantle margins would not necessitate so wide a gaping of the valves of the shell.”

Schmidt (1937, p. 27–30) also interpreted the zigzag deflection of the Paleozoic brachiopod *Sphaerirhynchia* (= *Wilsonia*) as a protective device, arguing that relative to an undeflected commissure, it either increases the area of the slit without increasing the risk of harmful particles entering, or reduces that risk without reducing the area of the opening. Schmidt (1937) quantified her interpretation by treating harmful particles as idealized spheres and analyzing the degree of protection afforded by the zigzag commissure at three different amounts of opening.

Rudwick (1964) – in his now classic paper on the function of zigzag deflections in the commissures primarily of brachiopods and secondarily of oysters – explores these ideas even further using the paradigm approach that he pioneered. Stenzel (1971, p. N1025–N1026, fig. J48) offers a simplified version of Rudwick’s (1964) highly technical, quantitative analysis. Text-fig. 11, redrawn from Stenzel (1971, fig. J48), shows a schematic view of a generalized plication on the margin of an oyster shell with a prong angle of  $2\alpha$ . The bisectrix of the prong angle on oyster shells is assumed to

be perpendicular to the commissural plane of the shell.

Two points ( $P_1, P_2$ ) on opposite valves are in contact when the valves are closed. When the oyster opens its valves, these two points separate by a distance  $b$ . However, the width of the slit ( $w$ ) that opens perpendicular to the sides of the plication is narrower than  $b$ , because  $w = \sin(\alpha) \times b$ . The prong angle  $2\alpha$  is always less than  $180^\circ$ ; therefore,  $\alpha$  is always less than  $90^\circ$  and  $\sin(\alpha)$  is always less than 1. As a result,  $w [= \sin(\alpha) \times b]$  is always less than  $b$ . In other words, the diameter of the largest spherical particle that can enter the mantle cavity through the plication slit is  $w$ , which is less than the point-separation distance  $b$ . When  $2\alpha = 180^\circ$ , the commissure is a straight line. Therefore,  $\sin(\alpha) = 1$ ,  $\sin(\alpha) \times b = b$ , and the largest spherical particle that can enter the mantle cavity through the (straight) commissure slit has a diameter of  $b$ , the point-separation distance  $P_1P_2$ .

Rudwick (1964) showed that the plication angles of successive prongs on a valve are unequal and form a progressively decreasing series with the most acute angle ( $2\alpha$ ) on the prong farthest away from the hinge axis (umbo) and the least acute, the one nearest. Rudwick (1964, p. 138) also showed that the relative amplitude of the prongs must decrease in a graded way toward the hinge axis.

The specimen of *Lopha staufferi* (USNM 619376) shown as Text-fig. 10A’ demonstrates these prong relationships quite strikingly. In Text-fig. 12A’ its plication prongs have been traced in blue along a white growth band. This tracing is shown directly above the shell in Text-fig. 12B. The measured prong angles on this lower valve make a series of six angles that decrease progressively from  $111^\circ$  to  $43^\circ$  proceeding from the dorsum (umbo or hinge line) toward the ventral margin of the shell. The amplitude of the prongs decreases in the opposite direction toward the umbo, where the amplitudes of the prongs are suppressed completely. According to Rudwick (1964, p. 138), “[g]rading ensures that the slit... is as wide as possible, without detracting from the degree of protection given. This would minimize the extra resistance to the flow of water through the gape, caused by drag against the lengthened edges of the valves. Any zigzag must be a compromise between protection and rate of flow.”

This graded series of prong angles and prong amplitudes is well shown on specimens of *Lopha staufferi* illustrated by Bergquist (1944, pl. 9, figs 4, 5) and Kirkland (1996, pl. 5B). Another species of Late Cretaceous oyster in which this graded series of prong angles is well expressed is *Ostrea diluviana* illustrated by Coquand (1869, pl. 40, fig. 2) and White (1884, pl. 40, fig. 1). The Recent oyster *L. cristagalli* (Text-fig. 9) also displays graded prong angles and prong amplitudes, although the

ventral margins of the valves are not thickened into steep flanks as they are in *L. staufferi*.

Zigzag commissures provide protection by acting as straining devices while the valves are open. The zigzag slit allows particles below a critical size (diameter) to enter the mantle cavity, but rejects particles greater than that critical diameter. Stenzel (1971, p. N1000) stated that the "...extent to which [Recent] oysters open their mantle/shell while feeding is astoundingly small. The opened gap is 2–3.5 mm wide at the ventral valve margins of full-grown individuals (shells 80–110 mm high) of *Crassostrea virginica*...", which has a straight, non-plicate valve commissure. While feeding, the oyster establishes a water current into the mantle cavity by beating cilia located on its gills. An inhalant current takes water toward its mouth; whereas the exhalant current removes it from the mantle cavity. Thus, the gills perform two functions, respiration and food (primarily nannoplankton) straining. Stenzel (1971, p. N1000) noted further that individuals of *C. virginica* "...pump and strain for brief periods (5–15 minutes) at a rate of 41 liters per hours (*sic*) at the best and attain a sustained rate of 37.4 liters per hour...."

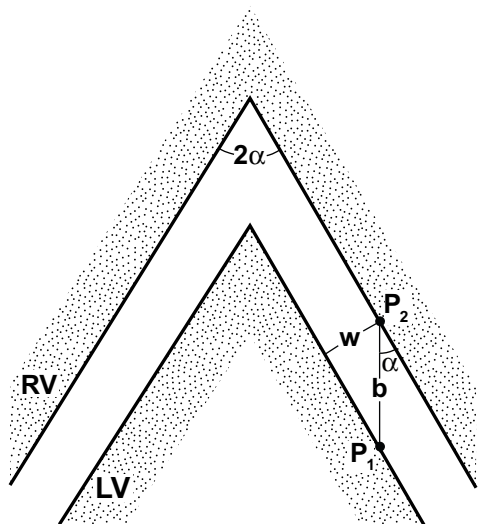
In discussing the Recent oysters *Lopha cristagalli* (see Text-fig. 9) and *Pycnodontes hyotis*, Rudwick (1964, p. 159) concluded that the "...zigzag slit is not a passive straining device, but protects the animal with an active and highly sensitive warning device." This is particularly true of *P. hyotis*, which is the more accessible of the two species, occurring along the Great Barrier Reef where it is easier to study. In *P. hyotis*, "...the

mantle edges lining the slit are sensitive.... If a swimming animal or other object touches the side of the slit, the valves immediately snap shut, by a rapid contraction of the 'quick' portion of the adductor muscle."

In addition to its protective function on *Lopha staufferi*, the onset of the zigzag commissure, which does not appear until late in the growth cycle of the oyster, allows the oyster to grow larger by increasing the interior volume of the shell. The inner portion of the shell is smooth (Text-fig. 10B–D), indicating that the commissure is straight for much of the growth of the species. This is especially evident on left valves, which are generally attached to the substrate over a large percentage of the valve (Text-fig. 10A–D). Then, at maturity the curvature of both valves increases abruptly as the valve flanks form; both slightly convex valves diverge toward the commissure at almost 90° angles, instantaneously increasing the volume of the mantle cavity substantially, while not altering significantly the footprint (area) of the shell (Text-fig. 10A–A'). This abrupt change in curvature of the valves creates flanks that are almost perpendicular to the commissural plane. This ability to grow up, rather than out, should have given *L. staufferi* an advantage on the very crowded, late Cenomanian seafloor in the Cottonwood Canyon area. Crowding may have been as big a trigger for flank growth as maturity. The corrugation of the oyster flanks that resulted from thickening the costae (ribs) into prongs may have increased the strength of the shell as well (as first suggested by Cooper 1937, p. 40, for brachiopods).

The specimens from Cottonwood Canyon illustrated in Text-fig. 10 offer a contrast between an oyster species that has a zigzag commissure, *Lopha staufferi* (Text-fig. 10A–E), and one that has a straight commissure, *Rhynchostreon levis* (Text-fig. 10F). Both oyster species occur in abundance and attain large size in Cottonwood Canyon (Text-fig. 7), where they occur together in the same bed (unit 8) and, thus, occur in the same paleoenvironment. Of the two species, *R. levis* appears to have been the more successful evolutionarily. Stratigraphically, it ranges from the middle Cenomanian *Acanthoceras amphibolum* Zone, at least four zones below the *Metoicoceras mosbyense* Zone, through at least the upper Cenomanian *Euomphaloceras septemseriatum* Zone (see Text-fig. 5; Cobban 1977, pp. 18, 19, tables 1 and 3; and Cobban *et al.* 1989, p. 63), two zones above. Geographically, *R. levis* is common in New Mexico, Arizona, Utah, and Montana.

*Lopha staufferi*, on the other hand, is definitely confined to the upper Cenomanian *Metoicoceras mosbyense* Zone in west-central New Mexico and adjacent Arizona, and is probably in the same zone in northeastern Minnesota, where it is not as well constrained. Both



Text-fig. 11. Schematic geometry of a prong (plication) on the zigzag commissure of an oyster. LV = left valve; RV = right valve;  $P_1$ ,  $P_2$  = two points in contact when the valves are closed;  $b$  = separation distance between  $P_1$  and  $P_2$  when the valves are open;  $w$  = width of slit perpendicular to sides of plication; and  $2\alpha$  = prong angle. Redrawn from Stenzel (1971, fig. J48). See text for discussion

*L. staufferi* and *Rhynchostreon levis* should have been subjected to dangers from the same harmful particles/predators at Cottonwood Canyon; yet, neither the quantitatively more efficient particle strainer, nor the ability to grow up rather than out appears to have conferred a long-term competitive advantage to *L. staufferi*.

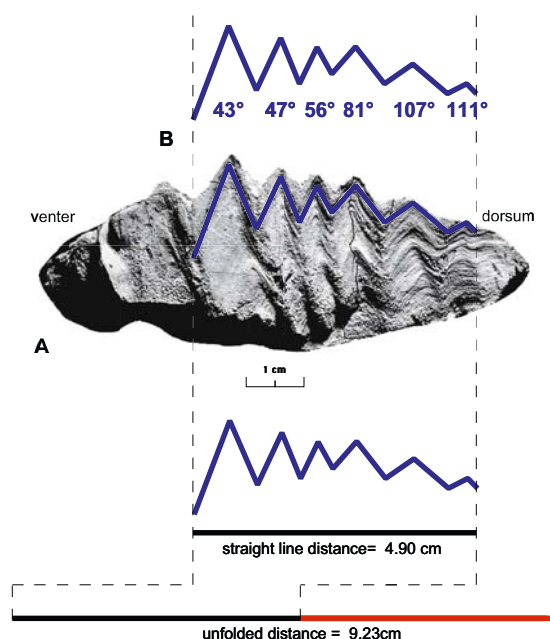
## SUMMARY

*Lopha staufferi* is the earliest ribbed oyster to appear in strata deposited in the Late Cretaceous Seaway in the Western Interior of the United States. In New Mexico and Arizona, where it is well dated, it is associated with the late Cenomanian ammonites *Metoicoceras mosbyense* and *Calycoceras obrieni*, placing it in the upper Cenomanian *M. mosbyense* Zone. The next well-defined, ribbed oyster to appear in this sequence in the Western Interior is the small, plano-convex species, *Cameleolopha* aff. *C. bellaplicata*, which occurs in the middle Turonian *Prionocyclus hyatti* Zone, more than three million years later (Hook and Cobban 2012, fig. 3). Rather than being a small, simple, ribbed oyster built on generalized plan that could have given rise to

the younger *Cameleolopha* lineage, *L. staufferi* is a larger, subequivalved species with a slightly curved axis and a very pronounced zigzag commissure. It appears suddenly in rocks of early late Cenomanian age in northeastern Minnesota and west-central New Mexico and adjacent Arizona, then, disappears just as suddenly as it appeared.

The steep flanks that appear at maturity in the growth of the shell are formed of angular prongs created by thickening of the ribs. The 10–12 prongs on each valve interlock to create a zigzag commissure composed of a graded series of increasingly more acute angles and greater amplitude ventrally away from the umbo. The zigzag slit that forms when the valves are opened acts as a protective sieve that increases the area of the valve gap and filters out particles that are greater than a critical diameter, keeping the filter-feeding oyster from clogging its system. These prongs, which grow at  $\sim 90^\circ$  to both valves, increase the convexity of both valves and expand the interior volume of the shell, without increasing the footprint of the individual on the seafloor. This latter feature may have been an adaptation to cope with crowding on the seafloor.

*Lopha staufferi* is a good guide to the Twowells Tongue of the Dakota Sandstone in west-central New Mexico and adjacent Arizona where it occurs abundantly in the Upper Cenomanian *Metoicoceras mosbyense* Zone (Text-fig. 5). It also occurs in rocks of approximately the same age in the Coleraine Formation of northeastern Minnesota, but nowhere in between.



Text-fig. 12. Posterior flank of USNM 619376 (Text-fig. 10A) showing the zigzag plications of a left valve of *Lopha staufferi* from US Geological Survey Locality D6173, Cottonwood Canyon, Arizona. The plication prongs have been traced along a white band in A and reproduced in B with measured prong angles that show a decreasing graded series away from the dorsum. As the prong angle becomes increasingly more acute ventrally, the prong amplitude increases. The zigzag commissure of this specimen, which is incomplete, has increased the effective line-length opening of the shell by a minimum of 88% (percent increase =  $[(9.2 \text{ cm} - 4.9 \text{ cm})/4.9 \text{ cm}] * 100\% = 88\%$ )

## Acknowledgments

We owe a debt of gratitude to K. C. McKinney, US Geological Survey, Denver, Colorado. He not only provided us with help in accessing collections, but also (along with the late Robert Burkholder) photographed the specimens shown in Text-figures 1 and 10. All of these photographed fossils have been assigned United States National Museum (USNM) numbers and are deposited in the US National Museum in Washington, D.C. USGS fossil collections shown with a number that begins with the prefix D are housed in the Federal Center in Denver, Colorado; otherwise, they are stored in the US National Museum in Washington, D.C. We thank Drs. R.M. Leckie (Professor of Geology, University of Massachusetts) and J.I. Kirkland (Utah State Geologist) for reviewing the paper for us. Their constructive suggestions and criticisms are greatly appreciated. Dr. Ireneusz Walaszczyk, University of Warsaw, kindly identified the inoceramids from the D6175 collection shown in Text-fig. 7, as *Mytiloides kossmati/goppelnensis*. Final drafting of all text-figures is by Little Hawk Studios, Magdalena, New Mexico.



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## EPILOGUE

In early 2010 when Bill and I started thinking about a paper on the Turonian oyster, *Cameleolopha bellaplicata*, he knew we had to discuss older ribbed oysters in the Western Interior Upper Cretaceous. Bill, in a handwritten letter to me dated 10/4/2010, initiated the research that led to this paper. In his precise, almost microscopic cursive, he wrote:

“Steve,

*I believe you have a copy of Harlan Bergquist’s paper on the Cretaceous of the Mesabi Iron Range in Minnesota in which he describes the new species *Ostrea staufferi*, a plicate oyster of late Cenomanian age. The oyster occurs also in Apache County, Arizona, close to the New Mexico boundary. We probably should deal with this in the bellaplicata manuscript. The upper part of the Twowells Sandstone in Cottonwood Canyon in Apache County contains a large molluscan assemblage including staufferi. See the enclosed Survey Bulletin 1881 and other papers on the ammonite fauna. Also photographs of some of the Cottonwood oysters taken by the late Bob Burkholder. If you want more data, I can send you the total assemblage from Cottonwood Canyon.*

*Cheers,  
Bill”*

Shortly after Bill wrote the letter, he sent me the entire collection of *Lopha staufferi* fossils from Cottonwood Canyon along with the photographs he mentioned. In our paper on the evolution of the oyster genus *Cameleolopha* (Hook and Cobban 2012), we only mentioned (p. 89) that *L. staufferi* was the oldest ribbed oyster known from the Late Cretaceous Seaway in the Western Interior Basin and gave a very general description of it:

“Plicate (ribbed) oysters are unusual elements of middle Cenomanian to early Coniacian (early Late Cretaceous) faunas in the Western Interior. This is especially true of members of the Family Ostreidae.

The oldest ribbed member of the Ostreidae in the Western Interior is *Lopha staufferi* Berquist (*sic*) from the late Cenomanian *Metoicoceras mosbyense* Zone in Minnesota (Berquist (*sic*) 1944), western New Mexico (Cobban 1977, p. 20; and Cobban and Kennedy 1990), and eastern Arizona (Kirkland 1996, p. 42). *Lopha staufferi* is a medium sized oyster (up to ~8 cm) with subequal valves and 8–12 angular plications on the outer half of both valves that give the shell a distinctive zigzag commissure (line of closure). Paleogeographically, *L. staufferi* has been found on the eastern shoreline (Minnesota) of the Late Cretaceous Western Interior Seaway and the western shoreline (Arizona and New Mexico), but nowhere in between.”

Unfortunately, the wheels of progress roll slowly, especially when doing the careful, painstakingly meticulous research that Bill required. Other projects were farther along, such as the paper on the Juana Lopez Member of the Mancos Shale (Hook and Cobban 2013) and the Tokay Tongue of the Mancos Shale (Hook and Cobban 2015), and required our attention. Then, Bill’s health declined and he went into an assisted living facility, gradually needing full time care. Regardless of his deteriorating health, his mind was very sharp when it came to geology.

This paper reflects Bill’s thoughts as well as my own and is as true to Bill’s spirit as I can make it. However, he and I did not discuss sweepstakes routes. That section of the paper was added in early July 2015.

Stephen C. Hook  
July 10, 2015