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The Brachiopod *Antiquatonia coloradoensis* (Girty) from the Upper Morrowan and Atokan (Lower Middle Pennsylvanian) of the United States

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USGS

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By Thomas W. Henry

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Taxonomic and biostratigraphic analysis of a widespread and stratigraphically restricted, semireticulate productid brachiopod

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CONVERSION FACTORS

[Specimen measurements are in millimeters and centimeters, whereas other measurements are in feet and miles]

Multiply	By	To obtain
millimeter (mm)	0.0394	inch
centimeter (cm)	0.3937	inch
foot (ft)	0.3048	meter
mile (mi)	1.609	kilometer

The Brachiopod *Antiquatonia coloradoensis* (Girty) from the Upper Morrowan and Atokan (Lower Middle Pennsylvanian) of the United States

By Thomas W. Henry

ABSTRACT

Primary type specimens and topotypes of the large, semireticulate productid, *Productus inflatus* var. *coloradoensis* (Girty), collected near Leadville, Colo., form the basis for the redescription of this species. The type locality, for the first time, is firmly established stratigraphically in upper Morrowan (lower Middle Pennsylvanian) rocks of the lower part of the Belden Shale.

The identification and clarification of several previously poorly known physical features affirm assignment of Girty's species to the genus *Antiquatonia* Miloradovich, as currently restricted and understood. Detailed analysis of other collections of brachiopods assigned to *A. coloradoensis* and to related taxa confirms that the probable ancestor of *A. coloradoensis* is the lower and middle Morrowan *A. morrowensis* (Mather), which was described from the Ozarks region of northwestern Arkansas. One descendant of *A. coloradoensis* is *A. hermosana* (Girty), which is common in lower Desmoinesian strata of the southern Rocky Mountains and Paradox Basin. A descendant of *A. hermosana* may be *A. portlockiana* (Norwood and Pratten), which is common in uppermost middle and upper Desmoinesian strata in the Rocky Mountains and which is reported from Desmoinesian strata in the Midcontinent, Illinois Basin, and Appalachian Basin. However, the variability, taxonomy, and stratigraphic ranges of the species of *Antiquatonia* in the Desmoinesian of the eastern United States have not been resolved satisfactorily.

The stratigraphic range of *Antiquatonia coloradoensis* extends from the upper part of the Morrowan Series through the Atokan Series. The known geographic range of this species extends from the Eastern Great Basin, through the southern Rocky Mountains, the southern and central Midcontinent area, to the eastern and southern Appalachian Basin. It is a moderately common to rare component of open-bay, shelf-lagoon, and shelf-margin marine facies.

INTRODUCTION

Studies of the Mississippian and Pennsylvanian brachiopod faunas in the United States routinely deal with both taxonomic and stratigraphic problems. However, rarely are difficulties encountered that are as intricate as those confronted in the investigations of the large, semireticulate productids of the Lower to Middle Pennsylvanian Morrowan, Atokan, and Desmoinesian Series. Specifically, I am referring to the confusion in the literature about three things: (1) the exact geologic age and geographic site of the type locality of *Productus inflatus* var. *coloradoensis* Girty (1910), now referred to the genus *Antiquatonia* Miloradovich (1945) [emend. Sarycheva, 1949, and Sarycheva and Sokolskaya, 1952]; (2) the stratigraphic range and geographic distribution of this distinctive, biostratigraphically diagnostic productid; and (3) the proper taxonomic disposition and assignment of numerous collections from the United States of Morrowan, Atokan, and lower Desmoinesian specimens assigned to *Antiquatonia*. Like most productid brachiopods, *A. coloradoensis* is a highly variable taxon. A lack of understanding of its breadth of variability and lingering tendencies toward typologic application have contributed significantly to widespread misinterpretation of this species. This paper clarifies the situation.

REPOSITORIES AND LOCALITY REGISTER

All primary and secondary type specimens of *Antiquatonia coloradoensis* illustrated or measured in this paper are reposited at the U.S. National Museum of Natural History (Smithsonian) in Washington, D.C., and are identified with the prefix "USNM." All of the type specimens described as *Antiquatonia portlockiana* var. *quadratia* by Sturgeon and Hoare (1968) in their paper on the Pennsylvanian brachiopods of southeastern Ohio are included in the synonymy of *A. coloradoensis*, are reposited in the paleontologic

collections of the Orton Geological Museum at Ohio State University, and are identified by the prefix "OSU." Additional paratypes of the variety *quadratia* formerly reposited at Bowling Green State University now have been reposited at Ohio State University and given new specimen numbers (R.D. Hoare, oral commun., July 21, 1993) used in the current paper. Specimens of *Antiquatonia* from southwestern Missouri studied by me from the University of Missouri at Columbia are prefixed "UM."

The U.S. Geological Survey (USGS) collections studied for this report are cataloged in the so-called "Permo-Carboniferous" Fossil Locality Register. Collection numbers are suffixed by "–PC" and are prefixed by either "GR" (designating the green subregister) or "BL" (blue subregister).

ACKNOWLEDGMENTS

I am indebted to my colleague, Patrick K. Sutherland, University of Oklahoma, for providing additional data on the range of *Antiquatonia coloradoensis* in southern Oklahoma, Texas, and New Mexico and for enabling me to examine the collections of this and related species at the Oklahoma Museum of Natural History, University of Oklahoma, Norman. I also appreciate his thorough and constructive review of the manuscript. Robert B. Blodgett, USGS, also reviewed this manuscript.

Primary type specimens of *Productus inflatus* var. *coloradoensis* (Girty) were made available by Jann W.M. Thompson, Division of Paleobiology, Smithsonian Institution, for additional preparation and photography. Stig M. Bergstrom and Gale Gnidovec, Ohio State University, loaned me one set of Sturgeon and Hoare's (1968) type specimens of *Antiquatonia portlockiana* var. *quadratia* from southeastern Ohio. Richard D. Hoare, Bowling Green State University (BGSU), provided the additional paratypes of this named variety that were reposited previously at BGSU. Raymond L. Ethington, University of Missouri at Columbia, loaned additional specimens of *Antiquatonia* cataloged in the University of Missouri collections.

My appreciation is extended to Richard De Voto, formerly of the Colorado School of Mines, with whom I had several conversations about the stratigraphy and tectonic setting of the type area for Girty's species. Charles L. Rice, USGS, and Donald R. Chesnut, Jr., Kentucky Geological Survey, provided useful information on Appalachian Basin stratigraphy. T.L. Thompson, Missouri Geological Survey, discussed current information on the age of the Burgner Formation. C. Howard Brunton, British Museum (Natural History), provided an extensive written discussion of the genus *Antiquatonia* and its type species *Productus antiquatus* J. Sowerby. The late Mackenzie Gordon, Jr., USGS, encouraged my interest in pursuing this study and guided me through some of the intricacies of the taxonomic problems encountered. I also appreciate constructive comments by J. Thomas Dutro, Jr., USGS, Washington, D.C. Many of the photographs were made by Eric M. Fisher, USGS, and computer-graphic drawings were produced by Patricia Holroyd, USGS.

STRATIGRAPHY AND SETTING OF TYPE LOCALITY

TYPE LOCALITY AND COLLECTIONS

The type locality of *Antiquatonia coloradoensis* is in the high country of the southern Rocky Mountains between Leadville and Fairplay, Colo. (figs. 1 and 2). The site is above timberline in the Mosquito Range in the Alma mining district, a historic gold-producing area.

The primary type specimens of *Productus inflatus* var. *coloradoensis* Girty were collected in 1873 by A.C. Peale, who was the geologist in charge of the South Park Division of the Hayden Survey of parts of the Colorado Territory. When he collected this material, Peale was conducting a geologic reconnaissance of the mining districts and was accompanying the topographers who surveyed and compiled the first topographic maps of the region. His traverse section 18 (Peale, 1874, p. 229–233) was made on the ridge crest on the south side of the glaciated valley occupied by Fourmile Creek, extending on the east from just southwest of Sheep and Lamb Mountains to "the Horse Shoe" (the cirques east of Horseshoe Mountain) near the apex of the Mosquito Range on the west. Peale's panoramic sketch (1874, pl. IX) of this ridge was made looking southward from the north side of the broad valley (see fig. 2 of current report). This sketch identifies several features keyed to the traverse section, and the *approximate* geographic position of the collection can be plotted from these. The pertinent part of Peale's traverse section (in descending stratigraphic order) is quoted below:

37. Greenish-gray micaceous sandstones. Toward the top the beds become very coarse, 15 feet.
38. Limestones and bluish argillaceous shales with sandstones. The upper portion of the bed contains in blue shaly limestones fine specimens of *Productus semireticularis, P. nebrascensis, Spirifer opimus, Productus prattenanus*, and a *Pleurotomaria*, 57 feet.
39. Black shaly limestones, in the lower part of which we find the following fossils, *Productus, Spirifer,* and fragments of *Trilobites*, 34 feet.
40. Quartzitic sandstone laminated and micaceous, 15 feet.

According to this traverse section (Peale, 1874, p. 231–232), the top of unit 38 lies stratigraphically approximately 170 ft above a thick, light-colored "porphyritic volcanic rock."

S.F. Emmons conducted a detailed study of the Leadville-Fairplay area 9 years later in the summer of 1882 and produced the first geologic map of the area (1883). The following observations were made by Emmons (1886, p. 162) about the stratigraphic section on the ridge on the south side of Horseshoe Gulch:

> Directly above the White Porphyry is a bed of black carbonaceous shales; from one hundred to one hundred and fifty feet above it is an outcrop of dark, impure limestone, from which were obtained a large number of fossils, among which the following were recognized: *Chonetes granulifera, Productus cora, Productus nodosus* (variety of *Productus cora*), *Productus semireticulatus, Myalina perattanuata,* fragment of *Pinna* sp., fragment of *Aviculopecten, Phillipsia* sp., *Phillipsia major,* fragment of *Lingula* sp.

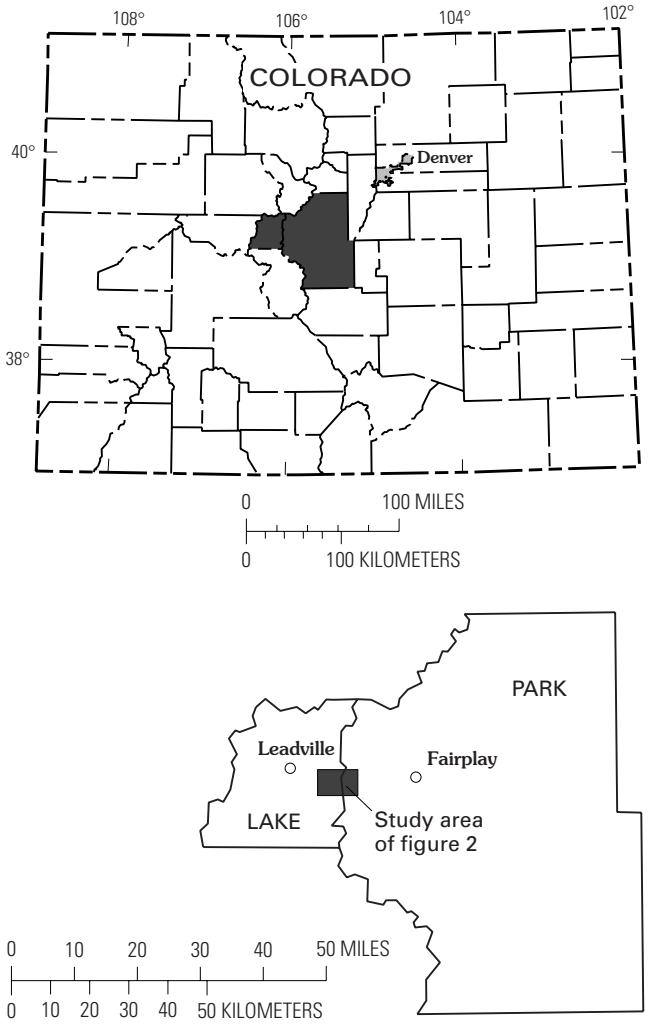


Figure 1. Location of Park and Lake Counties, Colo., communities of Fairplay and Leadville, and study area. Mosquito Range separates Park and Lake Counties. West and east parts of study area are Mount Sherman and Fairplay West 7.5-minute quadrangles, respectively.

The "White Porphyry" to which Emmons referred is the commonly applied, local name for the intrusive porphyry (mainly granodiorite and quartz monzonite) of Late Cretaceous-early Tertiary age that Chronic (1964) and Tweto (1974) mapped as a thick sill cropping out on the south side of the Horseshoe amphitheater (cirque) and extending to the ridge top west of the type locality of *P. inflatus* var. *coloradoensis*.

Girty's figured specimens (1903, pl. 3, figs. 1–3) of *Productus inflatus* McChesney (later designated the types of *P. inflatus* var. *coloradoensis*) were cited as from the "Weber formation (?): Leadville district (sta. 2281)" (Girty, 1903, p. 490). In his description of this station, Girty (1903, p. 525) conveyed the following information: "Leadville district; Weber shales, base of Weber formation (?). Near mouth of canyon of Fourmile Creek. The locality is bed 38 (and possibly 39) of section 18" of Peale (1874, p. 231). Essentially the same information was given by Girty (1903, p. 245) in his discussion of the faunas from the South Park area. However, the handwritten label accompanying lot USNM 8258 (from which Girty's primary types, USGS colln. GR2281–PC, were drawn) reads: "Carboniferous, Ridge E. of Horseshoe Mt., S. Park, Colo." Thus, Girty's original descriptions of this locality are misleading in that the collection was *not* taken from near the mouth of the canyon of Fourmile Creek but rather on the ridge crest south of the glacial valley occupied by Fourmile Creek (actually south of Horseshoe Gulch, a tributary of Fourmile Creek) and southeast of Horseshoe Mountain (see fig. 2).

Gordon (1975, p. D48) concluded that the type locality of *Antiquatonia coloradoensis* (USGS colln. GR2281–PC) probably was on "the crest of the ridge south of Four Mile (Horseshoe) Creek, about 2 miles east of Horseshoe Mountain and 8 miles west-southwest of Fairplay, Colo." He surmised that this locality would lie approximately in the $NE^1/_4$ sec. 18 (unsurveyed), T. 10 S., R. 78 W., at an altitude slightly greater than 12,400 ft and cautioned that this needed field verification.

Four collections of fossils from the ridge on the south side of Fourmile Creek were examined in addition to the type set for this study. I consider that all four of these (USGS collns. BL6852–PC, BL6852A–PC, BL12096–PC, and BL31394–PC) contain topotypes of *Antiquatonia coloradoensis*. The first two (BL6852–PC and BL6852A–PC) were made by J.H. Johnson in July 1930 from "near top of ridge south of Horseshoe cirques" (see fig. 2). Collection BL6852–PC was reported to occur "about 150 ft above porphyry," and BL6852A–PC was made about "50 ft stratigraphically higher" and slightly to the east of his first collection (Johnson, 1934, p. 33). Despite Johnson's USGS collns. BL6852–PC and BL6852A–PC being separated by about 50 ft of section in this immediate area, both are considered herein to contain topotypic material of *Antiquatonia coloradoensis*. This is justified because Girty's material (1903, p. 525) may have come from both beds 38 and 39 of Peale's traverse section 18 (1874, p. 231), representing a composite thickness of 91 ft. Both collections were correlated by Johnson (1934) with a section that he measured just north of the old townsite of Leavick (see B in fig. 2 and section below on "Measured Sections in Fourmile Creek Area"). The third collection that I examined (BL12096–PC) was made in 1953 by Ogden Tweto from the "Alma dist., Park Co., Colo.; ridge on south side Horseshoe Gulch." The fourth (BL31394–PC) was collected in 1991 by E.M. Fisher and me in an effort to locate the original site and obtain additional fossils from it. The locale of USGS collection BL31394–PC is plotted in figure 2, and its description follows:

Quadrangle.—Mount Sherman 7.5 minute.

Description.—Site on open swale on rounded, high alpine ridge south of Horseshoe Gulch, between Horseshoe Mountain and Lamb Mountain, at point 1.65 mi east-southeast of vertical angle elevation bench mark VABM

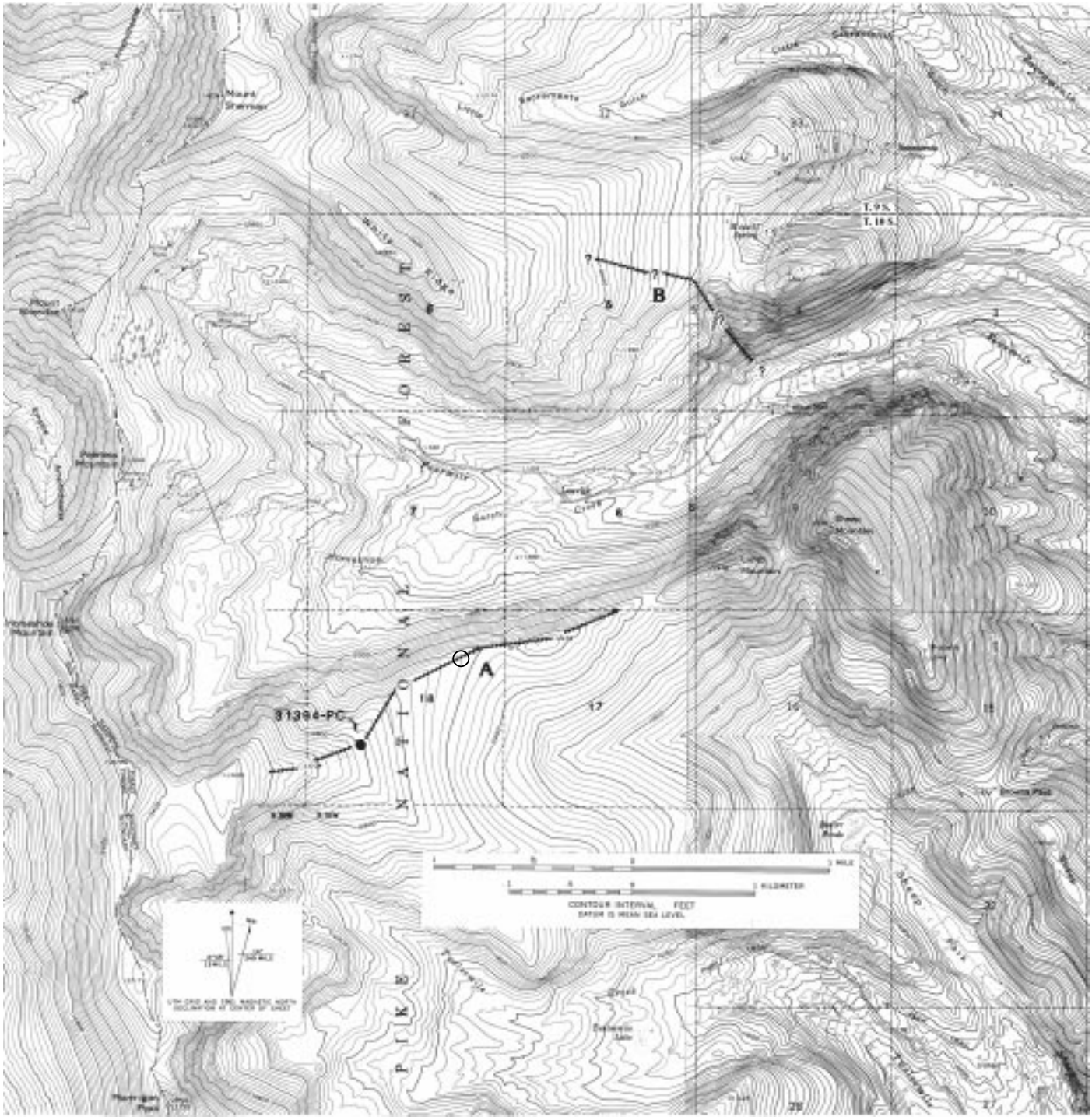


Figure 2. Composite map (scale 1:48,000) taken from adjacent parts of Mount Sherman and Fairplay West 7.5-minute-quadrangle topographic maps (U.S. Geological Survey, scale 1:24,000, 1961 and 1960, respectively), showing geographic features mentioned in text. Type locality of *Antiquatonia coloradoensis* (Girty) is depicted by filled circle, and approximate estimate of type locality by Gordon (1975, p. D48) is depicted by open circle. Zigzag lines indicate approximate traverses for measured sections: "A" indicates Kelly's (1983) Lamb Mountain section, and "B" indicates Johnson's (1934) Horseshoe Mountain section, which equals Kelly's (1983) White Ridge section. Approximate positions of land-survey section lines were added to pertinent parts of Mount Sherman sheet. Contour interval equals 20 ft on Fairplay West quadrangle and 40 ft on Mount Sherman quadrangle.

13,898 ft (on Horseshoe Mountain) and 1.5 mi southwest of abandoned ore mill at old Leavick townsite; site is 0.35 mi north-northeast of temporary bench mark TBM 13,128 ft (marked by three large cairns on small knoll held up by platy-weathering, coarse-grained quartzarenite).

Geographic coordinates.—Approx. C., SW$^1/_4$ sec. 18 (unsurveyed), T. 10 S., R. 78 W., Park County, Colo.; lat 39°10'35" N.; long 106°09'23" W.

Altitude.—12,805 ft, measured barometrically on highest fossiliferous bed on ridge crest.

Attitude.—Strike N. 40° W., dip 16° NE.

Stratigraphy.—Belden Shale (lower part); collected free-weathering and "crack-out" macrofossils from approximately 8 to 10 ft of alternating, nodular, micritic limestone and shale. Lower limestone: skeletal carbonate mudstone, medium-dark-gray to dark-gray, weathering medium light gray to yellowish gray. Shale: medium-dark- to dark-gray, slightly calcareous. Upper limestone (skeletal, brachiopodal, bryozoan wackestone to packstone): becoming more evenly bedded, slightly more skeletal, coarser grained, more sandy (containing quartz and feldspar grains), and thicker bedded upward, grading at top into fine-grained, pale-yellowish-brown-weathering, calcareous, skeletal, subarkosic sandstone; top beds make small ledges at ridge crest and on hillside.

Date collected.—Sept. 4, 1991.

The top of the beds from which USGS colln. BL31394–PC was obtained is approximately 160 ft stratigraphically (determined trigonometrically) above the top of the "White Porphyry" sill and probably is exactly equivalent to Johnson's (1934) colln. BL6852–PC. The site is about 400 ft higher on the ridge and about 0.75 mi southwest from where Gordon (1975, p. D48) inferred that Peale's original collection might have been made.

TECTONIC SETTING

Most of central and western Colorado, including Park and Lake Counties, was broken into a mosaic of fault blocks during the Pennsylvanian and Permian, when the ancestral Front Range and Sawatch and Uncompahgre Uplifts and the Central Colorado Trough were formed (De Voto and others, 1986). Syndepositional tectonism resulted in abrupt thickness and facies changes of alternating marine and nonmarine upper Paleozoic strata in the fault-bounded basins in many areas, including the Leadville-Fairplay area. There, the strata that are now referred to the Belden Shale and that contain the types of *Antiquatonia coloradoensis* were deposited in the South Park Subbasin of the Central Colorado Trough.

STRATIGRAPHY

The stratigraphic name Weber was applied initially in the Leadville-Fairplay area by Emmons (1883, 1886, p. 219) for the sequence of generally interbedded black shale, limestone, sandstone, and conglomeratic sandstone that now compose the Belden Shale, the Molas Formation, and tongues of the Minturn Formation (Middle Pennsylvanian). Emmons' application of the name Weber formation was based on the assumption that these beds correlated with the Weber quartzite of the Uinta Mountains of northeastern Utah. Girty (1903, p. 171) questioned this early correlation in his discussion of what became the type locality for *Antiquatonia coloradoensis*, as noted above, and utilized the name "Weber formation" with a query for these strata, a practice followed by many subsequent workers, including Johnson (1934) and Read (1934).

Brill (1942, p. 1385) proposed the name "Belden shale member of the Battle Mountain formation" for this sequence in central Colorado, later raised the Belden to formation rank (Brill, 1944, p. 624), and subsequently extended its use throughout the Central Colorado Trough (Brill, 1952, 1958). For a detailed discussion of the stratigraphic nomenclature in the Mosquito Range, see De Voto (1972, p. 142–145).

The Belden Shale (Morrowan and lower Atokan) in the Mosquito Range is normally underlain by the Molas Formation (Upper Mississippian? and Lower Pennsylvanian), a clastic red-bed sequence of silty, variegated shale and mudstone and other lithic types, interpreted in part as a residual soil blanketing the Leadville Dolostone (Lower Mississippian, Osagean), which was subaerially exposed and extensively karsted during the Late Mississippian and earliest Pennsylvanian (De Voto, 1972). In the Colorado Mineral Belt, of which the Mosquito Range is a part, the Leadville Limestone was originally deposited in intertidal to supratidal environments, extensively dolomitized during the Mississippian and (or) Pennsylvanian, and then recrystallized by mid-Cenozoic hydrothermal brines derived from an igneous source. Armstrong, Mamet, and Repetski (1992) proposed that the name Leadville Dolostone be applied to this formation in the current study area, and I follow that practice in this paper.

Tweto and Lovering (1977) described the Molas in the Mosquito Range as filling in caves and channelways in the Leadville and ranging in thickness there from a few inches to as much as about 40 ft. In the Fourmile Creek area, it is thin, extensively bleached by hydrothermal action (Tweto and Lovering, 1977; Armstrong, Mamet, and Repetski, 1992), and generally covered.

The Belden Shale on the south side of Fourmile Creek is about 670 ft thick (Kelly, 1983) and contains several wedges of coarse-grained, conglomeratic, terrigenous clastic deposits, interpreted as tongues of the overlying Minturn Formation (Chronic, 1964, p. 109; De Voto, 1972). These wedges pinch out to the south, and the Belden becomes thicker and more shaly. Farther northward in the Mosquito Range, many additional coarse terrigenous clastic deposits are present in the same correlative interval, and it is not feasible to differentiate the two formations.

Tweto (1974) mapped the ridge top south of Horseshoe Gulch as Minturn and Belden Formations undifferentiated for his geologic map of the area west of Fairplay. However, on notes with his field labels accompanying his USGS colln. BL12096–PC, Tweto indicated that it was from the Belden Shale and probably from its lower part. Unfortunately, no more light is shed by Tweto's notes regarding a more precise geographic locality for his collection other than that given in the preceding sentence.

MEASURED SECTIONS IN FOURMILE CREEK AREA

The invertebrate fossil collections studied came from the lower part of the Belden Shale slightly above the horizon where Read (1934) reported the "middle Pottsville" compression and impression flora from sections a short distance to the west of the current study area. It is possible to more precisely document the stratigraphic position of the invertebrate collections from two measured sections in the vicinity by Kelly (1983) and from one by Johnson (1934) on the north side of Fourmile Creek. Johnson's section on the north side of the glacial valley—his Horseshoe Mountain section—was remeasured by Kelly as his White Ridge section (plotted as sec. "B" in fig. 2). Kelly's other section, the Lamb Mountain section (sec. "A" in fig. 2), apparently follows the ridge crest on the south side of the glacial valley where the type locality of *Antiquatonia coloradoensis* is located.

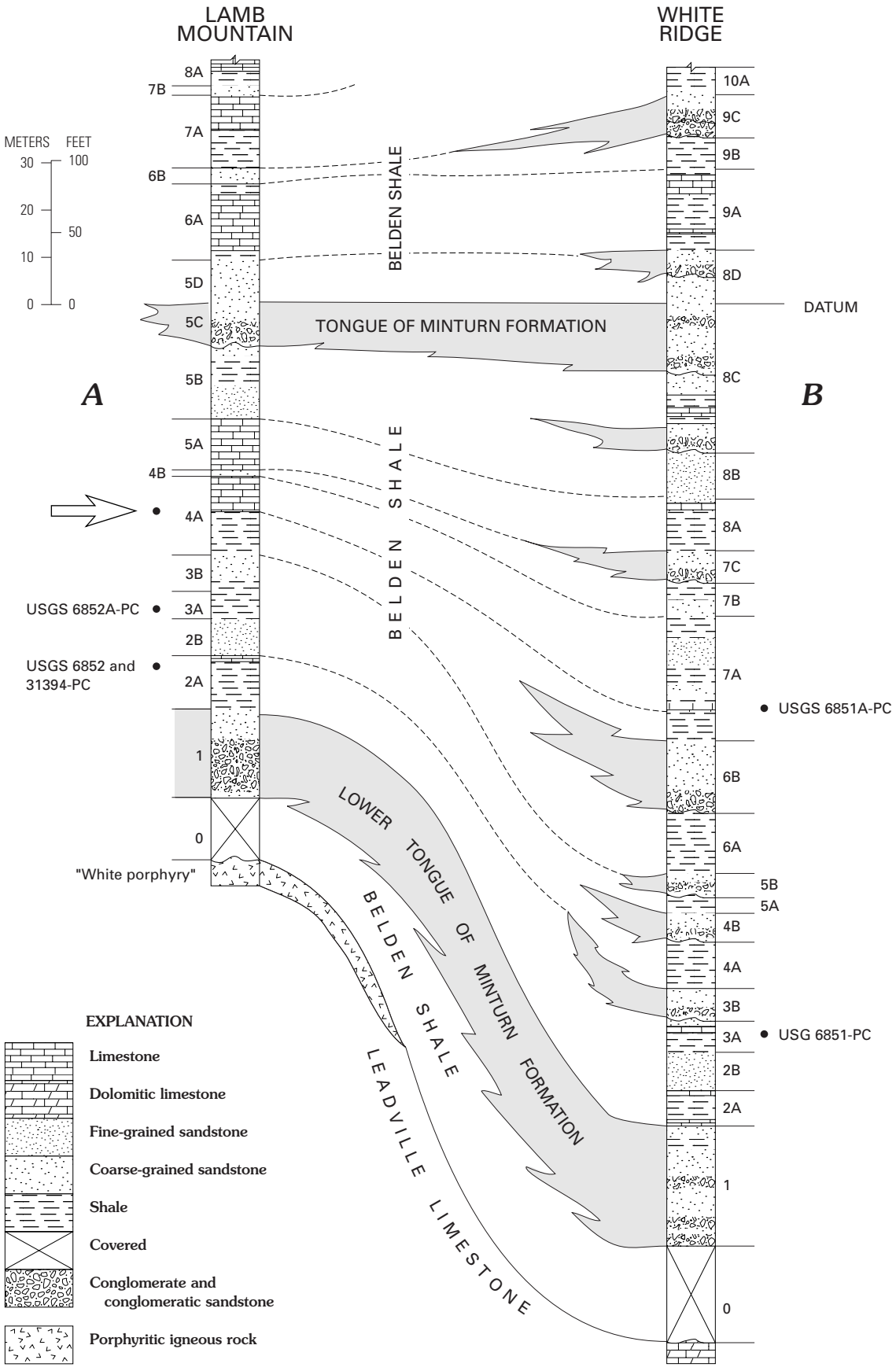
Kelly's (1983) Lamb Mountain section was measured above timberline mainly in "secs. 17 and 18, T. 10 S., R. 78 W." The lower part of the Lamb Mountain section and his correlation of it with his White Ridge section based on detailed petrographic and stratigraphic analysis and environmental interpretations are depicted in figure 3. The White Ridge and Lamb Mountain sections are separated by a major fault (south side upthrown) that Kelly (1983) interpreted as having been active during deposition of the Belden and Minturn sediments, thus partly explaining many of the major changes in interval thicknesses and lithofacies that occur in the short distance across the glacial valley occupied by Fourmile Creek.

Exactly where was the Lamb Mountain section measured? The ridge crest on the south side of Fourmile Creek (Horseshoe Gulch) affords the most accessible traverse and the best exposures of the Belden Shale, and the more resistant strata of the Belden, dipping gently eastward, also crop out on the north side of the ridge and extend eastward down the side of the glacial valley. The ridge top was also certainly the line of traverse made by Peale (1874). In this section, the Molas Formation is absent, and the Belden is underlain by a thick sill (the "White Porphyry" of local usage), intruded approximately along the contact between the Leadville and the Belden. TBM 13,474 ft in figure 2 is on the promontory formed by about the middle part of this sill. The Lamb Mountain section probably extends from just east of that point along the ridge crest east-northeastward to some point northeast of TBM 12,478 ft. The lower tongue of the Minturn Formation (fig. 3) forms the knob at TBM 13,128 ft in the line of the measured section, and the type locality of *Antiquatonia coloradoensis* occurs at the filled circle marking USGS colln. BL31394–PC.

Johnson (1934) collected and identified invertebrate fossils from several stratigraphic sections and localities throughout the Mosquito Range. Although J.H. Johnson identified most of the fossils himself, G.H. Girty corroborated and assisted in the identifications (Johnson, 1934, p. 16). Girty's distinctive handwriting appears on many of the collection labels, including those identifying specimens of *Productus coloradoensis* from collns. BL6852–PC and BL6852A–PC.

Johnson's (1934, p. 37–39) Horseshoe Mountain section was measured "uphill northward from old town of Leavick, following around hill and through first cirque." The approximate position of Johnson's Horseshoe Mountain section, plotted as "B" in figure 2, is compatible with Tweto's (1974) geologic map and Kelly's (1983) description. Johnson's (1934) designation of this measured section as the Horseshoe Mountain section is confusing. Horseshoe Mountain is on the crest of the Mosquito Range approximately 3 mi southeast of White Ridge (fig. 2).

Figure 3 (following page). Measured stratigraphic sections on both sides of Fourmile Creek in vicinity of type locality of *Antiquatonia coloradoensis* (Girty). Kelly's (1983) White Ridge section is same as Johnson's (1934, p. 37–39) Horseshoe Mountain section. Approximate locations of measured sections are shown by zigzag lines in figure 2. Data for Lamb Mountain and White Ridge sections, including correlation lines, are from Kelly (1983, pl. 1, meas. secs. 6 and 7); however, a different horizontal datum was used (Kelly's T–2 datum). Kelly's unit numbers are shown on sides of measured sections, and upper parts of both measured sections are not shown. Coarse-grained conglomeratic units (shown in gray on cross section) are interpreted as tongues of Minturn Formation that pinch out southward. See text for explanation of arrow on left of figure.


LAMB MOUNTAIN
WHITE RIDGE
METERS
FEET
30
20
10
0
100
50
0
A
B
8A
7B
7A
6B
6A
5D
5C
5B
5A
4B
4A
3B
3A
2B
2A
1
0
10A
9C
9B
9A
8D
8C
8B
8A
7C
7B
7A
6B
6A
5B
5A
4B
4A
3B
3A
2B
2A
1
0
DATUM
BELDEN SHALE
TONGUE OF MINTURN FORMATION
BELDEN SHALE
LOWER TONGUE OF MINTURN FORMATION
BELDEN SHALE
LEADVILLE LIMESTONE
USGS 6852A-PC
USGS 6852 and 31394-PC
"White porphyry"
USGS 6851A-PC
USG 6851-PC
EXPLANATION
Limestone
Dolomitic limestone
Fine-grained sandstone
Coarse-grained sandstone
Shale
Covered
Conglomerate and conglomeratic sandstone
Porphyritic igneous rock

This section includes several fossiliferous limestone and shale beds, the lower two of which are especially significant. Johnson's (1934, p. 39) lowest fossiliferous bed in the Horseshoe Mountain section, his unit 8, is described as an 11-ft-thick, dark-gray, sparsely fossiliferous, thin-bedded limestone from which he made colln. BL6851–PC. According to his measurements, the base of this unit is approximately 200 ft above the top of the Leadville Dolostone. It is this unit with which Johnson (1934, p. 33) correlated colln. BL6852–PC, which contains topotypes of *Productus inflatus* var. *coloradoensis* Girty. The next higher fossiliferous unit described in Johnson's (1934, p. 38) Horseshoe Mountain section, his unit 13, is a 13-ft-thick, highly fossiliferous, slightly calcareous, black shale, from which colln. BL6851A–PC was derived. The base of Johnson's unit 13 is roughly 440 ft above the top of the Leadville Dolostone. Johnson (1934, p. 33) correlated the strata from which he made colln. BL6852A–PC (the second topotypic collection of *coloradoensis*) with his unit 13. Thus, according to his measured section and correlation of collns. BL6852–PC and BL6852A–PC with it, these marine beds are separated by about 229 ft of unfossiliferous sandstone and cover on the north side of the broad glacial valley and by only about 50 ft of strata on the south side of the valley, where the types of *Antiquatonia coloradoensis* originated. A problem exists, however, with the upper of Johnson's two correlations.

As stated above, Kelly's (1983, pl. 1, meas. sec. 7) White Ridge section (fig. 3) is essentially the same as Johnson's Horseshoe Mountain section, just discussed. Kelly's section was measured in "secs. 4 and 5 (unsurv.), T. 10 S., R. 78 W.," just north and northeast of Leavick (fig. 2). By comparing interval (rock-unit) thicknesses and similarities of the two sets of lithic descriptions, Johnson's data can be interpreted quite reasonably in terms of Kelly's White Ridge section. Johnson's USGS collns. BL6851–PC and BL6851A–PC are plotted against Kelly's White Ridge section in figure 3.

From analysis of these sections and my personal observations in the field, I have made the following two conclusions. (1) Johnson's colln. BL6851–PC from the Horseshoe Mountain-White Ridge section correlates with the relatively thin, fossiliferous, alternating limestone and shale sequence in the top of Kelly's (1983) unit 2A of the Lamb Mountain section (fig. 3), which yielded Johnson's colln. BL6852–PC and my colln. BL31394–PC. Therefore, Johnson was correct in his correlation of the lower fossil-bearing unit in his Horseshoe Mountain section. (2) Johnson's BL6852A–PC probably came from Kelly's unit 3A, which he noted contains brachiopods but which I was unfortunately not able to recollect due to a sudden afternoon thunderstorm. Therefore, Johnson's colln. BL6851A–PC does *not* correlate with BL6852A–PC as he contended, but rather with the lower part of the limestone bed in unit 4A in the same section (see arrow in fig. 3).

MACROFAUNA

Table 1 lists the total macrofauna from USGS collns. GR2281–PC, BL6852–PC, BL6852A–PC, BL12096–PC, and BL31394–PC. Plates 1–3 show *Antiquatonia coloradoensis* from these and other collections. The other brachiopod taxa from this fauna are illustrated in plates 4 and 5.

Girty (1903, p. 243, table 12) identified the following brachiopods from USGS colln. GR2281–PC: *Productus inflatus* McChesney, *Productus cora* d'Orbigny, *Productus nebrascensis* Owen, and *Spirifer rockymontanus* Marcou. The eight specimens from this collection that he identified as *P. cora* (Girty, 1903, p. 364–367) are in the paleobiologic collections of the U.S. National Museum of Natural History (lot USNM 8259). His *P. cora* is the highly distinctive *Linoproductus nodosus* (Newberry). A slab containing several specimens of this species and two free-weathering specimens (one from GR2281–PC) are illustrated herein (pl. 4, figs. 13-17). The specimens from GR2281–PC that Girty referred to *Productus nebrascensis* and *Spirifer rockymontanus* could not be located in the USNM collections. From examination of the other related collections, I conclude that the small *Anthracospirifer* that Girty (1903, p. 364–367) identified as *Spirifer rockymontanus* is *A. tanoensis* Sutherland and Harlow (see pl. 4, figs. 18–20). Girty's (1903, p. 364–376) *Productus nebrascensis* is probably conspecific with the specimens that I tentatively identify as *Pulchratia*? *pustulosa* Sutherland and Harlow (see pl. 5, figs. 24–26). My additional identifications from four other collections from the type locality are shown in table 1, and several of these specimens are figured in plate 5.

Linoproductus nodosus is the most common brachiopod in the collections from the type locality of *Antiquatonia coloradoensis*, as can be seen in table 1 (130 specimens plus fragments). Although the shape is highly variable, *L. nodosus* is easily identified by a single row of large, almost recumbent body spines emerging from the pedicle valve exterior at or near the plane of symmetry of the valve. This is a common, geographically widespread linoproductid that has been identified from rocks of late Morrowan and early Atokan age from the Eastern Great Basin, Grand Canyon area of Arizona, northern Sonora (Mexico), southern Rocky Mountains, Ozarks, frontal Ouachitas, Ardmore Basin, Llano area of Texas, central and southern Appalachian Basin, and northern South America. Like most linoproductids, *L. nodosus* was gregarious, most commonly growing in closely packed clusters on and partially emersed in argillaceous- and carbonate-mud bottoms. The slab that is illustrated in plate 4, figure 15, contains a cluster of 10 specimens from USGS colln. BL31394–PC. Note that all but one of the specimens is oriented with brachial valve up (in growth position). The specimen identified by the "*x*" shows one of the body spines. The large specimen above the "*y*" on

Table 1. Invertebrate macrofauna from collections containing primary and secondary type specimens of *Antiquatonia coloradoensis* (Girty) from lower part of Belden Shale on ridge south of Fourmile Creek, near Fairplay, Colo.

[Presence denoted by "+" or by a number; specimens identified by Girty (1903, p. 243, table XII), interpreted in terms of modern taxonomy, that were not examined (or found) are identified by asterisk; absence denoted by dash]

Taxon	U.S. Geological Survey colln. no.				
	GR2281–PC	BL6852–PC	BL6852A–PC	BL12096–PC	BL31394–PC
ECHINODERMATA:					
Pelmatozoan columnals	*	+	+	+	+
Crinoid plates	–	+	–	+	+
Archaeocidaris	–	–	+	–	+
BRYOZOA:					
Rhombopora spp.	*	–	+	+	+
Fenestellid	–	–	+	+	+
Other bryozoans	–	–	+	+	+
COELENTERATA:					
Lophophyllid coral	–	4	–	–	1
Conularid	–	1	–	–	–
BRACHIOPODA:					
Neochonetes cf. *N. whitei*	–	3	18	1	6
Linoproductus nodosus	8	14	33	29	46
Antiquatonia coloradoensis	19	8	4	18	11
Sandia welleri	–	–	–	2	1?
Desmoinesia nambeensis	–	43	–	–	3
Pulchratia? *pustulosa*(?)	*	–	2	1	–
Productid, gen. & sp. indet.	–	–	–	–	1
Spirifer goreii	–	–	–	1	2
Anthracospirifer tanoensis	*	–	4	4	2
Composita ovata	–	1	3?	1	2
Composita gibbosa	–	1	1?	1	1?
PELECYPODA:					
Lima? sp. indet.	–	1	–	–	–
Myalinid	–	–	1	–	1
Pectenid (*Deltopecten*?)	–	–	1	–	–
GASTROPODA:					
Meekospira sp.	–	1	–	–	1
Sphaerodoma sp.	–	1	–	–	–
Euconospira taggarti	*	–	–	–	–
CEPHALOPODA:					
Orthoceratid sp. indet.	–	3	–	–	1
ARTHROPODA:					
Paladin? sp. (trilobite)	–	1	1	–	1

the same figure is an exfoliated interior of a brachial valve; the entire pedicle valve, the muscle fields and other interior features of the brachial-valve interior, and much of the cardinal area have been worn away. Note that the bumps forming a row along the midline of the brachial-valve interior correspond to the body spines on the pedicle-valve exterior.

I strongly suspect that Emmons' collection (1886, p. 162), cited above in the section "Type Locality and Collections," was from the same beds and locality as the type specimens of *Antiquatonia coloradoensis*, and I conclude that his *Chonetes granulifera* is *Neochonetes* cf. *N. whitei*, his *Productus semireticulatus* is *A. coloradoensis*, and his *P. cora* (together with his *P. nodosus*) is *Linoproductus nodosus*. However, the disposition of his collections is unknown, and, because of apparent differences in the faunal lists, it is not likely that specimens in Emmons' list were from Peale's 1873 collection (USGS colln. GR2281–PC) described in 1874.

CORRELATION AND AGE

The fauna documented from the lower part of the Belden Shale south of Fourmile Creek (table 1) is closely similar to faunas of the following four units: (1) the lower part of the La Pasada Formation (Lower and Middle Pennsylvanian) in the southern Sangre de Cristo Mountains of northern New Mexico (Sutherland and Harlow, 1973), (2) the basal 2.5 ft (upper Morrowan) of the type "Derryan" Series in southern New Mexico (Sutherland and Manger, 1984; Sutherland, 1991), (3) the middle slope unit of the Watahomigi Formation (Lower and Middle Pennsylvanian) of northern Arizona (Gordon, 1982), and (4) the upper part of the type Morrowan Series of the Ozark Mountains region (Henry, 1973; Sutherland and Henry, 1975, 1980; Henry and Sutherland, 1977). I would correlate the type beds of *Antiquatonia coloradoensis* with the *Zia novamexicana* Brachiopod Subzone (upper Morrowan equivalents) of the lower part of the La Pasada Formation, which is part of the *Linoproductus nodosus* Brachiopod Zone of the Midcontinent and the eastern United States.

The Belden Shale in this part of the Central Colorado Trough has been correlated with the upper Morrowan through most of the Atokan Series (lower and middle Middle Pennsylvanian) (De Voto, 1972, 1980; Mallory and others, 1972; Chronic, 1979). My data confirm that the lower part of the Belden Shale is indeed late Morrowan in age, although certainly some of the individual components of the *Linoproductus nodosus* Zone range upsection into generally accepted Atokan equivalents. The thin sections examined by me from colln. BL31394–PC contain only arenaceous foraminifers, and I do not have corroborative data from other faunal groups, particularly conodonts, because of the limited amount of matrix material packed out by us in 1991.

SYSTEMATIC PALEONTOLOGY

Characters measured on *Antiquatonia coloradoensis* and related taxa are shown in figure 4. In the succeeding text and tables, the following terms are used:

PV = pedicle (ventral) valve;
BV = brachial (dorsal) valve;
length of pedicle valve;
length of brachial valve (same as length from hinge to anterior margin, HAM);
hinge width = maximum width of hingeline of pedicle valve;
body width = maximum width of pedicle valve;
height = height of pedicle valve;
DBV = depth of brachial valve;
SL = surface length of pedicle valve from beak to anterior margin measured on surface of valve in plane of symmetry (also called "surface length," "surface measure," or "arc length" by some authors);
SLR = surface length to end of reticulation on pedicle valve; and
SLG = surface length to end of geniculation (beginning of trail) on brachial valve.

The standard statistical parameters (descriptive statistics) include the following: M=mode; $\bar{x}$=arithmetic mean; s=standard deviation; n=sample size. The statistical definitions and formulae are given in Miller and Kahn (1962) and Sokal and Rohlf (1969).

Phylum BRACHIOPODA Duméril, 1806
Class ARTICULATA Huxley, 1869
Order STROPHOMENIDA Öpik, 1934
Suborder PRODUCTINA Waagen, 1883
Superfamily PRODUCTACEA Gray, 1840
Family PRODUCTIDAE Gray, 1840
Subfamily RETARIINAE Muir-Wood and Cooper, 1960

Genus *ANTIQUATONIA* Miloradovich, 1945
[emend. Sarycheva, 1949, and Sarycheva and Sokolskaya, 1952]

DIAGNOSIS

Small to moderately large productids, subquadrate to subrectangular in outline, generally having large extended ears with maximum width at ears; flanks of pedicle valve steep, ears commonly set off from visceral area by curving, preauricular ridge bordered laterally by narrow sulcus; both valves generally geniculate, pedicle valve generally with trail, brachial valve with smaller trail; both valves costate, costellate, and rugose, strongly reticulate posteriorly; pedicle valve with three types of body spines: (1) generally large spines scattered on costae, (2) smaller spines on row set at low angle to hinge margin, and (3) row of large, stout halteroid spines generally set on curved preauricular ridge on lateral slopes overhanging ears; spines rare on brachial valve. Brachial-valve interior with small trilobate cardinal process, median lobe of process dorsally directed, spinelike lophidium; lateral ridges diverging from hinge, generally not extending down lateral margins. Interior of pedicle valve possessing transverse ridge across ears in some species, dendritic adductor muscles set on median ridge, finely grooved diductor muscle scars.

DISCUSSION

Antiquatonia was split off of the genus *Dictyoclostus* Muir-Wood (1930) by Miloradovich (1945), who chose as the type species *Productus antiquatus* J. Sowerby (1821, p. 15, pl. 317, figs. 1, 5, 6), from the Lower Carboniferous (Viséan) of Derbyshire, England. Sowerby's species was redescribed and refigured by Muir-Wood (1928, p. 114, pl. 6, fig. 7; pl. 7, figs. 1–4c; text-fig. 22), and a lectotype was selected but not figured. Most of the original type

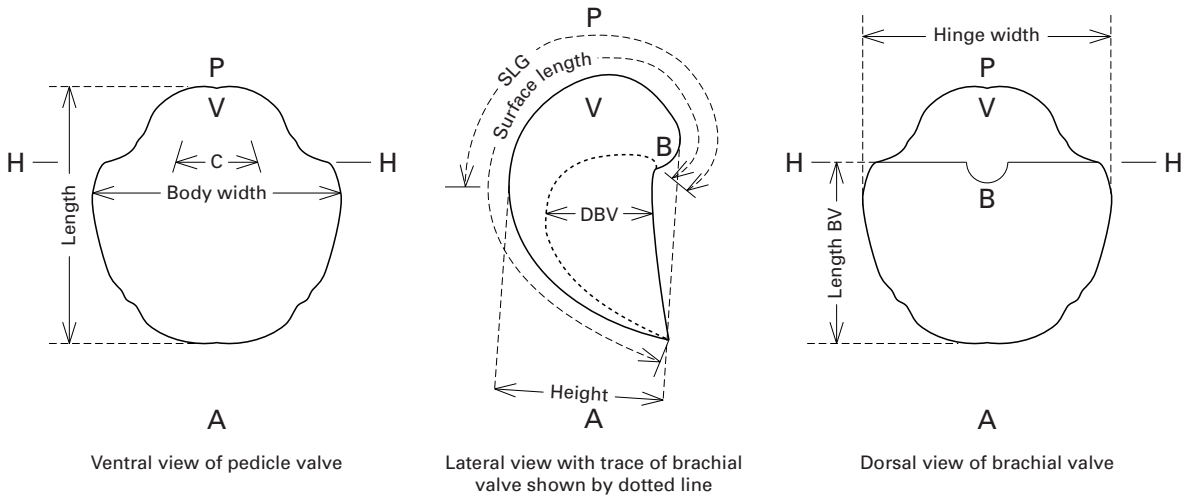


Figure 4. Characters measured on specimens of *Antiquatonia*. Abbreviations: A=anterior, B=beak, P=posterior, H=hingeline, V=venter. Measured characters in text and tables: **length** (maximum length of shell)=VA, **body width**=maximum width of pedicle valve (not hinge width), **hinge width**=maximum width of hingeline of pedicle valve, **surface length**=BVA=length along arch, measured on surface of pedicle valve in plane of symmetry (also called "surface measure" or "arc length from beak to anterior margin" by some authors), **DBV**=depth of brachial valve, **length BV**=length of brachial valve, **SLG**=surface length to end of geniculation (beginning of trail), **height**=height of pedicle valve, **c**=number of costae or costellae in 10 mm, measured at specified surface lengths.

specimens of *Productus antiquatus* figured by Sowerby are lost, and no interiors are available. For a more complete discussion of the type material, refer to Muir-Wood and Cooper (1960, p. 270–271).

Antiquatonia was not fully described by Miloradovich (1945) and was emended first by Sarycheva (1949, p. 167) and subsequently by Sarycheva and Sokolskaya (1952, p. 145). Lazarev (1990, p. 104, 125) assigned *Antiquatonia* to the Family Productidae Gray, 1840, and the Subfamily Retariinae Muir-Wood and Cooper, 1960, rather than to the Dictyoclostidae Stehli (1954) and Dictyoclostinae Stehli (1954), as proscribed by Muir-Wood and Cooper (1960) and Muir-Wood (1965).

As emended, *Antiquatonia* is a highly variable taxon in the development of most external features. This variability includes the size of the shell, extent of development of the trails, degree of development of a sulcus, coarseness of radial ornamentation, and size and density of body spines. To me and most workers who study North American upper Paleozoic brachiopods, one of the most salient characteristics of the species commonly referred to *Antiquatonia* is the conspicuous row of large spines that crosses the flanks of the pedicle valve; these spines are most commonly set on a ridge bordering a shallow sulcus that separates the flanks of the pedicle valve from the ears. Girty (1935, p. 7), in one of the last papers that he published, called these ridges "preaural ridges." Corresponding to the spine-bearing ridge on the exterior is a small groove on the interior of the pedicle valve and a corresponding ridge or flange on the interior of the brachial valve that fitted into the groove, thus separating the ears from the visceral area. These related features form weak points on the valves, and the ears of both valves commonly are broken off here. Girty (1935, p. 7) suggested that "the function of the ridge [on the brachial-valve interior] is not probably to shut off the auriculations from the interior of the shell but to serve as a hinging structure." Girty (1935, p. 9) also suggested separating *Productus hermosanus* Girty, *P. coloradoensis* Girty, *P. morrowensis* Mather, and other species of the "*hermosanus* Group" from the rest of the semireticulate productids on the basis of this feature. In Miloradovich's (1945) original description of *Antiquatonia* and in Sarycheva's (1949) and Sarycheva and Sokolskaya's (1952) emendment of that genus, references are made to Girty's preauricular ridges, and it is clear to me that this structure was intended as a major generic entity.

Sarycheva (1949) noted that a similar spine-bearing ridge on the pedicle valve and the related ridges on the brachical-valve interior that separate the auricular chambers from the visceral area are not present in the type species for *Antiquatonia*. Indeed, neither J. Sowerby's (1821, p. 15, pl. 317, figs. 1, 5, 6) original illustrations nor Muir-Wood's (1928, pl. 7, figs. 1, 3) photographs of *P. antiquatus* show these features, nor does Muir-Wood's description mention them. The absence of these features in *P. antiquatus* is confirmed by C. Howard Brunton (written commun., 1991). It is significant, however, that all of the species illustrated by Muir-Wood and Cooper (1960, pl. 94, figs. 1–11; pl. 95, figs. 4, 5) as examples of *Antiquatonia* do exhibit the preauricular ridge on the brachial-valve interior. My investigation of *A. coloradoensis* shows that the degree of development of

the preauricular ridges and related features is an intraspecific feature, at least in this species. Furthermore, the description for *A. coloradoensis* given herein of low internal flange around the anterior visceral margin of the pedicle valve (that rests in a groove on the brachial-valve interior) is a feature not reported previously in *Antiquatonia*, although it is developed in several other productid genera.

RANGE

Species currently assigned to the genus *Antiquatonia* are widely reported from the Lower Carboniferous (upper Tournaisian and Viséan) of Europe, Asia, Africa, and Australia and from the Upper Carboniferous (Namurian and higher strata) of Europe, Asia, and Australia. However, Lazarev (1990, p. 104) assigned the Tournaisian species to *Avonia* Thomas (1914), emend. Muir-Wood (1928). In North America, *Antiquatonia* is known from the lower part of the Upper Mississippian (Chesterian) presumably through the Lower Permian (Wolfcampian). However, Lazarev (1990, p. 104–106) would place the two species described as *Antiquatonia* by Cooper and Grant (1975) from the Lower Permian of Texas in a yet-unnamed genus more closely related to the genus *Reticulatia* Muir-Wood and Cooper (1960).

Antiquatonia coloradoensis (Girty)

Plates 1–3; plate 4, figures 1–12

Productus inflatus Girty (not McChesney, 1859, 1867), 1903, p. 359, pl. 3, figs. 1–3.

Productus inflatus? Girty (not McChesney, 1859, 1867), 1904, p. 52, pl. 11, figs. 5, 6; Boutwell (not McChesney, 1859, 1867), 1912, pl. 6, figs. 3, 4.

Productus inflatus var. *coloradoensis* Girty, 1910, p. 216 (part); Girty, 1915a, p. 65 (not pl. 8, figs. 1, 2); 1920, pl. 55, figs. 3, 4.

Productus inflatus coloradoensis Girty. Plummer and Moore, 1921, p. 48, 79, pl. 13, fig. 24.

Productus coloradoensis Girty. Girty, 1927, pl. 27, fig. 17 (not p. 73); 1935, p. 7–9, pl. 2, figs. 1–4.

Not *Productus coloradoensis* Girty. Snider, 1915, p. 80.

Not *Productus* cf. *coloradoensis* Arnold and Sadlick (not Girty, 1910), 1962, p. 248.

Productus morrowensis Morgan (not Mather, 1915), 1924, pl. 44, fig. 6.

Productus semireticulatus Smith and Siebenthal (not Martin, 1809), 1907, p. 7; Price (not Martin, 1809), 1916, p. 699 [part]; Morningstar (not Martin, 1809), 1922, p. 181 [part], pl. 8, fig. 6; Butts (not Martin, 1809), 1926, p. 213 (not pl. 67, fig. 12); Morse (not Martin, 1809), 1931, p. 311–312 [part], pl. 49, fig. 5(?), 6–8 (probably not).

Productus [*Dictyoclostus*] *semireticulatus* Chesnut (not Martin, 1809), 1981, p. 25; Chesnut (not Martin), 1991, p. 19.

Productus semireticulatus var. Morningstar (not Martin, 1809), 1922, p. 181–182 [part], pl. 8, figs. 4, 5.

Dictyoclostus coloradoensis (Girty). Ragan, 1959, p. 63–67, pl. 8, figs. 1–10.

Dictyoclostus inflatus var. *coloradoensis* (Girty). Plummer, 1950, pl. 12, fig. 9.

Dictyoclostus [*Antiquatonia*] *coloradoensis* (Girty). Smith and Ketner, 1975, p. 53.

Not *Dictyoclostus inflatus* var. *coloradoensis* (Girty). Gehrig, 1958, p. 7–8, 18–19, pl. 1, figs. 1–10; equals *Antiquatonia hermosanus* (Girty).

Dictyoclostus morrowensis (Girty). Gehrig, 1958, p. 7–8, 19, pl. 1, figs. 11–15.

Not *Dictyoclostus coloradoensis* (Girty). Sutton, 1938, p. 563.

Antiquatonia coloradoensis (Girty). Stehli, 1954, p. 317; Muir-Wood and Cooper, 1960, p. 272–273; Hoare, 1961, p. 57–58, pl. 7, figs. 6–9; Stevens, 1962 [at least part], p. 623, (?) pl. 95, figs. 2, 3, 5; Chronic, 1964, p. 109; Sutherland and Harlow, 1973, p. 51, pl. 11, figs. 1–5; Sutherland, 1991, p. 188; Sutherland and Grayson, 1992, p. 88–89, pl. 3, figs. 10–12; Rice and others, 1994, p. 92, table 2.

Not *Antiquatonia* cf. *A. coloradoensis* (Girty). Gordon, 1975, p. D48, pl. 5, figs. 1–9.

Dictyoclostus hermosanus Searight and Palmer (not Girty, 1903), 1957, p. 2131. Ragan (not Girty, 1903), 1959, p. 69–72, text figs. 1–6, pl. 9, figs. 1–6.

Antiquatonia hermosanus [sic] Hoare (not Girty, 1903), 1961, p. 56–57, pl. 6, figs. 1–3.

Part *Antiquatonia portlockiana* (Norwood and Pratten, 1855). Hoare, 1961, p. 53–54 [not pl. 5, figs. 1–7]. [Only material from Burgner Formation is included in *A. coloradoensis*.]

Antiquatonia portlockiana var. *quadratia* Sturgeon and Hoare, 1968, p. 47–48 [middle and upper Atokan but probably not Desmoinesian specimens], pl. 15, figs. 1–11.

Antiquatonia cf. *A. portlockiana quadratia* Sturgeon and Hoare. Chesnut, 1981, p. 25, 57–66, pl. 9, figs. 4–6.

Neospirifer cameratus Ragan (not Morton, 1836), 1959, pl. 3, fig. 10.

DESCRIPTION BASED ON TYPE SPECIMENS

Shell strongly concavo-convex, subcircular in ventral view, subtrapezoidal in anterior view; species medium to large for genus; maximum width generally at about midlength; largest relatively complete specimen (paratype USNM 121482) measures 73 mm SL, 44.7 mm length of pedicle valve, 41.5 mm maximum body width, 28.9 mm hinge width, 31.0 mm height.

Pedicle valve strongly convex near beak, becomes progressively, uniformly less convex anteriorly, without geniculation, almost planar on trail; trail variably developed, generally long, flaring slightly on some mature specimens, not distinctly set off from rest of valve; beak large, slightly overhanging, slightly incurved; umbo inflated, broad, prominent; steep lateral margins of umbo diverge at 100° to 110°, flare slightly anteriorly; very shallow, relatively narrow, rounded sulcus normally present on umbo, extends to anterior margin without deepening or broadening; single specimen with mere flattening across umbo; ears (generally broken off or chipped) moderately large, depressed, blunt (nonalate) posterolateral extremities; ears set off from venter by narrow, generally shallow groove developed just laterally to auricular ridges; auricular ridges subangular to subrounded, begin generally within about 12 mm of beak, enlarge slightly anteriorly, transect costellae, normally extend onto trail (where developed), becoming less conspicuous.

Surface ornamentation of pedicle valve consists of strong, fine, subrounded to subangular radial costellae on beak and umbo; costellae become slightly less elevated, broader anteriorly, increase irregularly by bifurcation; number of costellae varies considerably at given surface lengths across venter from specimen to specimen, ranges from 14 to 19 in 10 mm at 20 mm SL (*M*=15 and 16, $\bar{x}$=16.8, *n*=13), 13 to 17 (*M*= about 16) at 30 mm SL, 13 to 16 (*M*=14) at 40 mm SL, 13 to 16 at 50 mm SL; costellae tend to fuse anterior to base of large body spines, particularly on trail, and extend anteriorly from spine base as slightly raised ridges, imparting irregular, unequally costellate surface on trail; umbo has strong, concentric wrinkles, subequal in strength to radial costellae, imparting strong semireticulate pattern to umbonal area; surface length to end of reticulation ranges from 29 to 36 mm, with *M* around 30 or 31 mm; wrinkles extend onto ears, although not as prominently; ears ornamented with weaker radial costellae compared with umbo and trail; entire valve has fine, irregular concentric growth lamellae. Suberect body spines scattered across valve tend to be arranged in crude rows radiating from beak area; spines are small, spaced less than 5 mm apart on umbo, become larger, spaced as far as 10 mm apart on trail, have bases up to 1.1 mm in diameter. Single row of suberect halteroid spines initiates on either side of beak; spines are very small near beak, spaced as close as 1.5 mm apart, enlarge anteriorly, become more widely spaced, mounted on curved ridge located ventrally to groove demarcating ears, commonly not extending onto trail and to anterior margin of valve; largest spine base on anterior part of row measures around 2.1 mm on single specimen. Distinct row of fine hinge spines located on ears, extends laterally along hingeline or diverges from hingeline at about 5°; largest observed base of hinge spine 1.0 mm in diameter.

Brachial valve gently concave across visceral area, has slightly depressed, triangular area immediately anterior to beak of pedicle valve; valve geniculate anteriorly, anterolaterally, with short trail; angle of geniculation approximately 75° to 85°; line of geniculation somewhat rounded; visceral area generally has slight, broad fold, continuing anteriorly onto trail to anterior margin; ears slightly concave, set off from visceral region by slight fold. Valve reticulate across visceral area, has strong concentric rugae subequally prominent as radiating costellae; fine growth lamellae also present; only costellae and fine growth lines continuing anterior to geniculation; ears ornamented with fine growth lines; brachial valve aspinose, with dimples corresponding to body spines on opposite valve; row of dimples on slight fold defining inner margin of ears corresponds to row of spines on preauricular ridge on opposite valve.

Interior of pedicle valve has strongly elevated, elongate adductor-muscle platform, strongly impressed diductor scars, both posteriorly placed; adductor platforms slope posteriorly, have steep anterior margins, apparently smooth; diductor scars are well defined anteriorly, laterally, have deep, strong longitudinal striae; ears separated from visceral area by distinct, strong ridge that begins near posterior margin of valve, extends anteriorly to anterolateral extremity of visceral disc, becoming very weak, indistinct around anterior margin of visceral disc; ridge corresponding in position to preauricular groove on valve exterior; ridge slopes gradually posteriorly toward visceral area, has stronger, almost vertical anterior margin; ridge attains observed maximum width of 2.5 mm, height of about 3 mm near posterior extremity, ornamented with fine, rather widely spaced endospines, radial striae. Trail of valve with strong, anteriorly directed endospines, arranged in rough, concentric rows; remainder of valve interior with ornamentation reflecting ornamentation on valve exterior; auricular chamber smooth.

Visceral area of brachial-valve interior poorly known from type material. Cardinal process small, short, rounded, sessile, has small, medially grooved median lobe curving dorsally, flanked by two curved lateral lobes surrounding distinct pits; process supported by cardinal ridges, deflecting at low angle from hingeline; median septum, thin, low, extending to point just posterior of geniculation; adductor scars moderately deeply impressed; brachial ridges weak; weak flange apparently present as continuation of lateral ridges near posterolateral margin of valve on many specimens; where present or better developed, flange fits just posterior to ridge on opposite valve interior, continues anteriorly to about midlength, apparently generally disappears;

weak groove located just anterior to ridge (shelf or flange on pedicle-valve interior fits into this groove); trail ornamented with coarse, anteriorly directed endospines crudely arranged in concentric rows, bunched irregularly, producing slight, discontinuous ridge across anterior margin of visceral disc.

MEASUREMENTS

Measurements for the type material are given in table 2.

CATALOGED SPECIMENS

This paragraph lists reposited specimens of *Antiquatonia coloradoensis* (Girty) that are referenced in this paper. Specimens reposited in the U.S. National Museum of Natural History:

figured lectotype (USNM 35345)
figured paralectotypes (USNM 8258a–c, 11660a, 121482, 121483, 208827–208830)
unfigured measured paralectotypes (USNM 8258d, 11660b)
unfigured measured topotypes (USNM 476630–476634)
unmeasured topotypes (USNM 476635–476639; USNM 476661, 8 specimens)
figured hypotype (USNM 208805).

Measured specimens reposited at the University of Missouri (stars indicate specimens from the Burgner Formation, southwestern Missouri, originally identified by Ragan (1959) or Hoare (1961) as *Antiquatonia hermosana* (Girty):

UM	*13192	*13664a–h
	*13193	*13665a–j
	*13196	13671a–f
	*13197	13672a–g
	*13657a–e, g	13673a–f
	*13662a–g	14353
	*13663a–f, h	14354.

Specimens of *Antiquatonia portlockiana* var. *quadratia* Sturgeon and Hoare (now referred to *A. coloradoensis*) reposited at Ohio State University:

figured holotype (OSU 26020)
figured paratypes (OSU 26022–26026, 47102)
unfigured measured paratypes (OSU 26021, 26027, 47103–47109).

DISCUSSION OF TYPE MATERIAL

My redescription of *Antiquatonia coloradoensis* is based on 19 specimens from the original lot from USGS colln. GR2281–PC and an additional 41 specimens plus fragments from the four collections considered to contain topotypic material (USGS collns. BL6852–PC, BL6852A–PC, BL12096–PC, and BL31394–PC). The primary types originally were identified by Girty (1903, p. 359) as *Productus inflatus* McChesney (1859, 1867). Girty (1903, pl. 3, figs. 1–3) figured three of these specimens as engraved drawings (see table 5). Later, in a paper primarily dedicated to naming species from the Fayetteville Shale (Chesterian) of the Ozarks, Girty (1910, p. 216) made the following statement: "In 1903, I referred to McChesney's *P. inflatus* a group of shells from the Pennsylvanian of Colorado, expressing at the time a certain doubt whether they were actually identical with it [McChesney's taxon]. For this group I would now suggest the varietal name *coloradoensis*." To me, Girty clearly was designating the Colorado material the primary types of *Productus inflatus* var. *coloradoensis*, and, because the three figured specimens were from colln. GR2281–PC, it becomes the type collection. Gordon (1975, p. D48) selected as lectotype one of the specimens (USNM 35345) that Girty (1903, pl. 3, figs. 1–1b) initially illustrated and designated the remaining two specimens that Girty figured (USNM 121482 and 121483) and his 19 unfigured specimens (divided into lots USNM 8258 and 11660) as paralectotypes. In the current paper, I am illustrating photographically for the first time the lectotype (pl. 1, figs. 1–4) and the two previously figured paralectotypes (pl. 1, figs. 5–13) and an additional eight previously unfigured paralectotypes (pl. 1, figs. 14–19; pl. 2, figs. 1–15; pl. 3, figs. 1–15).

Most specimens in the five type collections are somewhat decorticated, cracked, and at least partially broken. The most complete specimens are the lectotype (refigured herein as pl. 1, figs. 1–4) and two of the paralectotypes (pl. 1, figs. 5–8; pl. 2, figs. 5–14). The ears are slightly broken on all three specimens, and the trail is broken on the right side of the first-cited paralectotype. The development of a trail in both valves seems to be a variable feature. The specimen figured as plate 1, figures 5–8, has most of the trail preserved, and the internal mold figured as plate 3, figures 5–7, has the complete pedicle-valve trail, showing the true shape of the slightly flaring trail, although the specimen is crushed posteriorly. In other specimens (for example, that shown in pl. 1, fig. 6), the trail seems to have been much shorter, although the trail, like the ears, is one of the most fragile portions of the shell and is easily broken.

The brachial-valve exterior is shown on four figured paralectotypes (pl. 1, figs. 13, 16; pl. 2, figs. 4, 10) and on eight unfigured paralectotypes, although the trails are broken on most of these. Portions of the interior of the brachial valve can be seen on several of the specimens where the exteriors are partially exfoliated (decorticated) or broken away or where the most of the shell was etched away by weathering. Plate 1, figure 13, reveals the obscure ridge or flange that, on some specimens, extended along the posterolateral extremity of the visceral disc, fitted into the groove

Table 2. Measurements (in millimeters) of figured and (or) measured primary type specimens and topotypes of *Antiquatonia coloradoensis* (Girty) from the upper Morrowan part of the Belden Shale, Park County, Colo., and of a hypotype from the upper Atokan Burgner Formation, Jasper County, Mo.

[Whole shells are figured and (or) measured primary type specimens and topotypes from the Belden Shale, Park County, Colo. The disarticulated brachial valve is a hypotype from the Burgner Formation, Jasper County, Mo. Specimens are reposited at the U.S. National Museum of Natural History (USNM), Washington, D.C. Asterisk indicates internal mold of pedicle valve; dash means data not available. Characters are defined in figure 4. *Abbreviations:* BV, brachial valve; HAM, hinge to anterior margin; PV, pedicle valve; SL, surface length along venter; SLG, surface length to geniculation (beginning of trail); SLR, surface length to end of reticulation. *Types:* h, hypotype; L, lectotype; P, figured paralectotype; p, measured paralectotype; t, measured topotype. *Designations for dimensions that could not be measured exactly:* a, approximate; e, estimated; m, minimum; t, estimated from twice half-width. Measurements by T.W. Henry]

USNM catalog number	Type	Length		SL	Width		Height	Depth	SLR (PV)	SLG (BV)	Trail length	Costellae in 10 mm at SL				
		PV	HAM (BV)		Hinge	Body						20 mm	30 mm	40 mm	50 mm	60 mm
Whole shells (articulated) from Belden Shale, Park County, Colo.																
208830 *.....	P	25 m	19 m	38 m	29.0 e	29.7 m	14.4 m	12 m	–	18 a	–	–	–	–	–	–
476630.....	t	27 m	20 m	40 m	–	–	–	8 m	–	–	–	–	–	–	–	–
476631.....	t	27 m	24 m	42 m	–	35 m	–	10 m	28 a	19	–	14 a	13 a	15	–	–
476632.....	t	27 m	–	45 m	22.0 a	31.1 a	–	14.7	28 a	20	–	–	–	–	–	–
8258c.....	P	28 m	–	45 m	25 m	33 m	–	14.5	29	20	–	16	17	14	–	–
208829.....	P	30 m	24 m	52 m	31.0 t	32.9 m	–	16.0	32	20	–	19	16	16	16	–
121483.....	P	35 m	25 m	63 m	33.4	39 m	21.5 m	16.9	32	20	–	15	–	–	–	–
11660b.....	p	35 m	27 m	65 m	30.0 e	39.6 a	21.8 m	–	32	–	–	16	14	13	16	16 a
476633.....	t	36.3 a	–	58	–	36.0 a	21.0 e	–	28	–	–	14	14	14 a	16 a	–
8258d.....	p	37 m	28 m	62 m	–	42.6 a	–	17.0	32	22	–	17 a	16	16 a	–	–
208827.....	P	37.7 a	28.4 a	68	32.8 t	39.7 a	22.7	15.8	32	21	–	15	14	14	–	–
8258b.....	P	38.1 a	30.3 a	68	25 m	38.6 a	21.9 a	–	29	–	–	16	15	15 a	–	13
208828.....	P	38.1	30.3 a	68	36.0 t	46.3 a	24.5 a	16.0	30	21	–	15	17	14	–	–
8258a.....	P	40 m	30.3 a	70 m	38.6 t	46 e	26 e	–	31	–	–	15 a	15	13 a	–	–
476634.....	t	40.5 a	–	80	–	48.8 a	26.6 a	–	30 a	–	–	–	–	–	–	–
35345.....	L	41.7 a	31.0 a	72	34.3	39.7	25.1 a	–	34	–	–	16	17	15	16 a	16 a
121482.....	P	44.7	–	73	28.9 a	41.5 a	31.0 a	–	33	–	–	14	13	13	13 a	–
11660a*.....	P	47.5 e	34.4 a	75 e	33.9 a	47.2 a	21 m	–	–	–	–	–	–	–	–	–
Brachial valve (disarticulated) from Burgner Formation, Jasper County, Mo.																
208805.....	h	–	[1]33.6	[1]57	42.4	–	–	–	–	[1]23	34	–	–	–	–	–

[1]Excluding cardinal process.

on the opposite valve, and helped seal off the auricular area from the body chamber or visceral cavity. The distinct lateral flange and groove also can be seen clearly in plate 2, figures 6, 8–10, which show a specimen that has a portion of the brachial valve broken away; the weak extension of this ridge or flange across the anterior part of the valve also is shown in plate 1, figure 19. The large internal mold (pl. 3, figs. 5–7) is of a complete pedicle valve, although the beak area is crushed, and the trail is long and slightly flaring at its extremities. This specimen had only a slight shelf extending around the anterior and anterolateral parts of the visceral cavity (see pl. 3, fig. 5). None of the specimens from the type locality reveal a strong flange or ridge extending from the auricular ridge distinctly and completely around the anterior portion of the visceral area of the brachial-valve interior, and, in some of the specimens, this ridge and groove apparently were not developed at all. The flange on the interior of the pedicle valve (pl. 2, fig. 9) resting in a groove in the interior of the brachial valve (pl. 2, figs. 6 and 11) is a distinctly different pattern from that developed in the genus *Tesuquea* Sutherland and Harlow (1973), in which a flange on the interior of the brachial valve (Sutherland and Harlow, 1973, pl. 6, figs. 9, 17, and 18) is opposite a thickened low ridge on the interior of the pedicle valve (their pl. 6, fig. 18).

The details of the musculature and cardinal process of the interior of the brachial valve are not preserved on any of the primary types, but some of the internal features can be seen on four of the unfigured topotypes from colln. BL12096–PC (USNM 476630–476632 and 476636), and on two uncataloged specimens from colln. BL31394–PC. The description of the musculature of the pedicle-valve interior is based on two internal molds (paralectotypes) figured herein (pl. 2, fig. 15; pl. 3, figs. 5–7), and eight unreposited topotypes.

The halteroid spines on the ridge on the pedicle-valve exterior were very large and long. Although not collectable, a specimen at the type locality, apparently in growth position, was observed by me that had slightly curving and tapering spines that on the anterior part of the valve attained a length of at least 4.5 cm.

INCLUSION OF *ANTIQUATONIA PORTLOCKIANA* VAR. *QUADRATIA* IN *A. COLORADOENSIS*

Sturgeon and Hoare (1968, p. 47–48, pl. 15, figs. 1–11) described *Antiquatonia portlockiana* var. *quadratia* from 16 specimens from strata that they called the "Lower Mercer limestone and shale" from southeastern Ohio. The holotype (OSU 26020) and 13 paratypes (OSU 26021–26025; OSU 47102–47109) are from a locality in Hocking County. The two remaining paratypes (OSU 26026–26027) are reportedly from the same stratigraphic units in nearby areas. These "Lower Mercer" strata correlate with the upper part of the Atokan Series (Zone of *Fusulinella*), according to Douglass (1987, p. 12, 13). Sturgeon and Hoare (1968, p. 48) stated that their variety is "rare to common in the Lowellville, Boggs, Upper Mercer, and Vanport units and rare to abundant in the Lower Mercer and Putnam Hill units." In other words, according to their identifications, the variety *quadratia* ranges from potentially upper Morrowan strata through upper Atokan equivalents of the Pottsville Formation and into the lower Desmoinesian equivalents of the Allegheny Formation. They included in their synonymy the material identified by Morningstar (1922) both as *Productus semireticulatus* Martin and *P. semireticulatus* var.

The "taxon" *Antiquatonia portlockiana* var. *quadratia* was essentially typologically defined. Little of the variability inherent in the type collections and discussed below was included in either the description or discussion in the original reference by Sturgeon and Hoare (1968, p. 47–48). I have examined the type specimens of this variety, and my measurements of the type material are presented in table 3. I include the upper Morrowan and Atokan specimens of *Antiquatonia portlockiana* var. *quadratia* Sturgeon and Hoare in the synonymy of *A. coloradoensis* (Girty) in spite of the minor differences discussed below. At best, *A. portlockiana* var. *quadratia* should be considered a named variety of Girty's *A. coloradoensis*.

Sturgeon and Hoare (1968, p. 48) contended that "*A. coloradoensis* (Girty) is less convex posteriorly than var. *quadratia*." The differences in external shape and ornamentation and in degree of development of internal features between the types of var. *quadratia* and the primary and secondary types of *A. coloradoensis* are insignificant. The range of variation in size and shape exhibited by the types of *quadratia* is encompassed by the observed external variation of *A. coloradoensis*. For example, Sturgeon and Hoare's holotype (OSU 26020, refigured herein as pl. 3, figs. 16–20) is almost identical in size and shape (including the degree of convexity of the posterior part of the pedicle valve) to the paralectotype that I figure as pl. 2, figs. 1–4 (USNM 208829). The newly figured paratype (OSU 47102, pl. 4, figs. 10–12) has its analog in the large, broad paralectotype (USNM 208828) figured as plate 2, figures 5–14. The only difference in these two specimens is that paralectotype USNM 208828 has no sulcus, an atypical but not unknown situation for the primary and secondary types of *A. coloradoensis*.

One observable difference between *Antiquatonia portlockiana* var. *quadratia* and *A. coloradoensis* (sensu stricto) is in the radial ornamentation, duly noted by Sturgeon and Hoare (1968, p. 48). However, both the types of *A. coloradoensis* and those of *quadratia* have about the same number of costellae, measured at comparable surface lengths on the exterior of the pedicle valve (see tables 2, 3). For *quadratia*, the number of costellae measured in 10 mm at 20 mm SL ranges from 15 to 17 (M=16, n=6), well within the range of *A. coloradoensis.* Both sets of types contain specimens on

Table 3. Measurements (in millimeters) of primary type specimens of *Antiquatonia portlockiana* var. *quadratia* Sturgeon and Hoare (referred herein to *A. coloradoensis* (Girty)) from upper Atokan strata of the "lower Mercer limestone and shale" of the Pottsville Formation, southeastern Ohio.

[Specimens are reposited in the Orton Geological Museum at Ohio State University (OSU). Asterisk indicates internal mold of pedicle valve; dash means data not available. Characters are defined in figure 4. *Abbreviations:* BV, brachial valve; HAM, hinge to anterior margin; PV, pedicle valve; SL, surface length along venter; SLG, surface length to geniculation (beginning of trail); SLR, surface length to end of reticulation. *Types:* H, holotype; P, figured paralectotype, p, measured paralectotype. *Designations for dimensions that could not be measured exactly:* a, approximate; e, estimated; m, minimum; t, estimated from twice half-width. Measurements by T.W. Henry]

OSU catalog number	Type	Length		SL	Width		Height	Depth	SLR (PV)	SLG (BV)	Trail length	Costellae in 10 mm at SL				
		PV	HAM (BV)		Hinge	Body						20 mm	30 mm	40 mm	50 mm	60 mm
Whole shells (articulated) or disarticulated pedicle valves																
26027*	p	25.5 e	–	45 e	35 e	34 e	21 e	–	–	–	–	–	–	–	–	–
26021	p	30.8 a	21.9 a	60	23.3 a	34.8	20.5	–	35	–	–	16	16	–	13 a	–
47102	P	32 m	24.5 m	50 m	42 t	46 e	18 m	–	25	–	–	17	16	13	12	–
26023	P	33.0	25 e	55 e	36 t	36.1 a	20 e	–	27	–	–	–	–	–	–	–
26026	P	33.2 a	22.3 a	62	32.4 a	22.3 a	20.2 a	–	27	–	–	16	15	–	–	–
26020	H	33.5	27.0 a	64	32.3	35.5	21.7	–	27	–	–	15 a	–	–	17 a	–
47105	p	34.1 a	26.5 a	65 a	28.7 a	36.7 a	20.9 a	–	25 a	–	–	16	15	14 a	13 a	–
47104	p	35 m	29 m	52 m	36.5 e	36.5 m	–	–	25 e	–	–	–	–	–	–	–
47103	p	40 e	32.5 e	65 e	38 t	44 e	21.6 a	–	32	–	–	16 a	–	–	–	–
Brachial valves (disarticulated)																
26024	P	–	[1]24.6	[1]30	31.8	33.8	–	–	–	[1]23	8	–	–	–	–	–
47107	p	–	[1]25.0	[1]27 a	28.3 a	34.8 a	–	–	–	[1]26	7 a	–	–	–	–	–
26022	P	–	[1]25.2 a	[1]28	21 e	36 e	–	–	–	[1]21	7	–	–	–	–	–
26025	P	–	[1]26.3	[1]30	32.7 a	37.3 a	–	–	–	[1]23	6	–	–	–	–	–
47106	p	[1]27e	[1]28 e	26.6 t	33.2	–	–	–	[1]23 e	–	–	–	–	–	–	
47108	p	–	[1]28.8 a	[1]29 e	26.4	36 e	–	–	–	[1]24 a	8 a	–	–	–	–	–
47109	p	–	[1]28.9 a	[1]28	34.7 a	40.8 a	–	–	–	[1]24	8 a	–	–	–	–	–

which the costellae fuse anteriorly to the bases of the large body spines and form "ribs," particularly on the anterior part of the pedicle valve over the body cavity and on the trail. These "ribs" extend anteriorly from the spine bases as a cluster of costellae on the slightly raised ridges, imparting an irregular, unequally costellate surface, similar to that of *A. portlockiana* (Norwood and Pratten, 1855). However, a few of the paratypes of *quadratia* do have only one large, raised costa extending anteriorly from the body spine bases rather than a cluster of "fasciculate" costellae (for example, OSU 26026, pl. 3, figs. 24, 25). Nonetheless, the right side of the anterior view of this specimen (pl. 3, fig. 25) shows the costa splitting into two costellae farther anteriorly on the trail. A small proportion of the types of *A. coloradoensis* have this single larger, higher costa anterior to the large body spines. This is considered a trivial difference.

One other characteristic of the radial ornamentation that Sturgeon and Hoare (1968, p. 47–48) did note was that the costellae tend to become "obsolete" anteriorly, particularly on the trail. However, all of the shells of the types of *A. coloradoensis* are at least slightly decorticated. The types of *quadratia* that show the costellation extending to the anterior extremities of the valve are also decorticated or worn. All of the shells that have the ornamentation becoming indistinct or subdued are well preserved and not decorticated at all. The strength of radial ornamentation is therefore a function of preservation and is not a valid taxonomic discriminator. This effect of preservation on the strength of the radial ornamentation has been observed by me with many different taxa of productid (and chonetid) brachiopods.

The primary types of *A. portlockiana* var. *quadratia* differ from the types of *A. coloradoensis* in having a generally relatively long trail and in having a generally weak flange and groove anteriorly and anterolaterally ringing the visceral area on the interiors. All of the disarticulated brachial-valve interiors from Sturgeon and Hoare's collection show *at least* a faint extension from the auricular ridges of a raised area or flange delimiting the visceral cavity anteriorly and anterolaterally. The disarticulated brachial valve figured as plate 4, figure 9 (OSU 26025), seems to have come from the same individual as the disarticulated pedicle valve figured as plate 3, figures 21 and 22 (OSU 26023). The ridge that continues anterolaterally from the cardinal ridges on the brachial-valve interior, separating the visceral chamber from the auricular area, fits neatly inside the ridge on the pedicle-valve interior that also separates the auricular area from the visceral chamber. This brachial-valve interior exhibits the weakest development of this ringing feature of the three refigured interiors and has the least amount of thickening of the valve at the point of geniculation. In fact, the shell material of this large valve is very thin. Three of the unfigured paratypes (OSU 47107–47109) have at best a weak extension and very thin valves also like OSU 26025.

In contrast to the situation just described, three of the relatively complete specimens (OSU 26020, 26021, and 26026) possess valves that are thickened at the demarcation of the trail anterior to the visceral area. The holotype (OSU 26020; see pl. 3, figs. 16–20) has a ragged, lamellose development of shelly material at this point. The dark area at the anterior margin of the specimen shown in plate 3, figure 17, is actually material from the pedicle valve. One of the other two articulated paratypes (OSU 26026, pl. 3, figs. 23–25) shows similar but less drastic lamellation of the shell at this point, as does the other paratype that I did not figure (OSU 26021). Two of the other figured disarticulated brachial valves (pl. 4, figs. 6–8 and figs. 1–5, OSU 26022 and 26024, respectively) and one of the unfigured interiors (OSU 47106) are also thickened near the anterior margin in a similar manner. The first of these disarticulated valves (OSU 26022) is strongly thickened and heavily lamellose. It can be inferred reasonably that the trails of all of these specimens developed and extended some distance above the substrate. They were repeatedly broken and regenerated. At any time, the trails were probably relatively short. To me, these thickened specimens are merely reflecting the variability inherent in this sample of a population in response to environmental conditions and do not have any taxonomic significance.

The paratype (OSU 26024) of *quadratia* illustrated as plate 4, figures 1–5, and discussed above has unusually coarsely developed internal features. At the point where the ridge delimiting the auricular chamber extends anterolaterally beyond the ears, it deflects somewhat abruptly; laterally at this point is a rather deep, concave "socket-like" structure that is not as clearly seen on any other specimen of *Antiquatonia* that I have examined. The muscle platforms and the brachial ridges are raised strongly on this specimen, and the anterior portion of the median septum, normally less than 1 mm high and less than 1 mm thick, is raised approximately 3.5 mm above the floor of the valve and is 3.0 mm thick at its lateral extremity where it bluntly terminates. The anterior surface of the septum is slightly sulcate at its terminus.

The large collections of *Antiquatonia* from the stratigraphically higher Putnam Hill Limestone Member of the Allegheny Formation that Sturgeon and Hoare (1968) included in this variety and that Morningstar (1922) identified from this member as *Productus semireticulatus* Martin or her undescribed variety should be examined carefully, because I believe that it is not likely that they are *A. coloradoensis*. Douglass (1987) reported the fusulinid *Beedina leei* (Skinner) in the Putnam Hill Limestone Member and correlated these strata with the basal part of the Desmoinesian Series.

Chesnut (1981, p. 25, 56–57, pl. 9, figs. 4–6) figured as *Antiquatonia* cf. *A. portlockiana quadratia* Sturgeon and Hoare three specimens from the Magoffin Member (Atokan) of the Breathitt Formation from Perry County, Ky. I also have large collections of this taxon from roadcuts along the Daniel Boone Parkway in the same area, and, without

reservation, I include the Magoffin species in Girty's *Antiquatonia coloradoensis*. The specimen figured by Chesnut (1981) as his plate 9, figure 6, is almost identical to the lectotype of Girty's species (see pl. 1, figs. 1–4, of current paper). I also include in *A. coloradoensis* specimens from my collections from the Winifrede Shale Member (formally named by Blake, Keiser, and Rice, 1994, p. 47–48) of the Kanawaha Formation in southern and central West Virginia. The Winifrede is the same marine band as the Magoffin Member of Kentucky and northern Tennessee.

DISCUSSION OF SUPPLEMENTAL BRACHIAL-VALVE INTERIORS

Well-preserved, complete interiors of *Antiquatonia coloradoensis* are rare. Among the best brachial-valve interiors available, at least in terms of the details of the visceral area and trail, are (1) the upper Atokan paratypes of var. *quadratia* discussed in detail in the preceding section, (2) several specimens from the Burgner Formation (upper Atokan; see discussion of age and notations about the specimens from the "E.J. Palmer collection" in the section below on "Comparison with *Antiquatonia hermosana*") of Missouri, and (3) several specimens from upper Morrowan and lower Atokan strata in the La Pasada Formation of the Sangre de Cristo Mountains in northern New Mexico.

Among the exceptionally well preserved specimens that I examined from USGS collns. BL8113–PC and BL25128–PC from the Burgner Formation are three relatively complete brachial-valve interiors, the best one of which is illustrated herein (USNM 208805, pl. 2, figs. 16–21). This specimen is an almost complete valve with relatively large, potentially pointed ears and a long trail. The maximum width of the shell for this specimen may have been at the hingeline rather than farther anteriorly. The lateral ridges supporting the cardinal process deflect anteriorly near the posterolateral extremities and form a ridge that separates the auricular chambers from the visceral disc (see pl. 2, fig. 17). However, these marginal ridges continue only a few millimeters anteriorly before disappearing and clearly do not continue across the anterior portion of the valve (see pl. 2, figs. 16–18). Rather than a flange delimiting the visceral chamber anteriorly and anterolaterally, at best, only a rough, weakly and irregularly developed thickening is present. The other two interiors are very similar in this respect, and this is also true for the fragmentary brachial-valve interior of *Antiquatonia coloradoensis* (UM 13193) that was figured by Hoare (1961, pl. 6, fig. 3) as *A. hermosana* (Girty) (see point 5 of "General Discussion" for amplification). Note on the hypotype that I am illustrating (USNM 208805, pl. 2, fig. 16) that the coarser endospines are confined to the auricular chambers and to a band about 10 mm wide around the anterior and anterolateral portions of the valve just anterior to the geniculation. The interior of the trail of the brachial valve is ornamented only with costellae, fine scattered endospines, and very fine growth lamellae. The pedicle valve corresponding to this interior would probably have been about the same size and shape as the paralectotype from Colorado illustrated in plate 2, figures 5–14 (USNM 208828), the maximum width of which is anterior to the hingeline.

Sutherland and Harlow's (1973) collection (item 3 above) has a few brachial-valve interiors, but neither of the two specimens that reveal the anterior margin and trail has any suggestion of the internal groove around the anterior margin of the visceral disc.

It would appear from the preceding analysis of the supplemental material that both the development of the length of the trails and the degree of development (if any) of the internal flange and groove in the anterior and anterolateral parts of the shell of *Antiquatonia coloradoensis* are variable characteristics within the species. Where developed, the structure of a flange on the interior of the pedicle valve (pl. 2, fig. 9) resting in a groove in the brachial valve (pl. 2, figs. 6, 11) is a distinctly different pattern from that found in *Tesuquea*, in which a flange on the interior of the brachial valve (Sutherland and Harlow, 1973, pl. 6, figs. 9, 17, 18) is opposite a thickened low ridge on the interior of the pedicle valve (1973, pl. 6, fig. 18).

INFERRED PHYLOGENY AND COMPARISON WITH OTHER SPECIES

INFERRED PHYLOGENY

Antiquatonia coloradoensis probably evolved from *A. morrowensis* (Mather, 1915), a robust form, the types of which are from a bioclastic, non-oolitic limestone bed in the basal part of the Prairie Grove Member of the Hale Formation (lower middle Morrowan) in northwestern Arkansas. There, *Antiquatonia morrowensis* ranges through the rest of the Hale Formation, through the Brentwood Limestone Member of the Bloyd Shale, and apparently into the basal part of the Dye Shale Member of the Bloyd (upper Morrowan). In turn, *A. coloradoensis* gave rise to *A. hermosana* (Girty), common in lower Desmoinesian strata of the southern Rocky Mountains and Paradox Basin. The latter species possibly gave rise to *Antiquatonia portlockiana* (Norwood and Pratten), which is common in uppermost middle and upper Desmoinesian strata in the Rocky Mountains and which is reported from throughout Desmoinesian strata in the Midcontinent, Illinois Basin, and Appalachian Basin. The trend in coarsening of the radial ornamentation of the lineage of *Antiquatonia* in North America from *A. morrowensis* through *A. coloradoensis*, through *A. hermosana*, and into *A. portlockiana* is striking and is shown in figure 5. Ages of *A. morrowensis* and its descendants are shown in figure 6.

COMPARISON WITH *ANTIQUATONIA MORROWENSIS*

The types of *Antiquatonia coloradoensis* (Girty) exhibit about the same size and shape as the types of *A. morrowensis* (Mather, 1915) and also possess a row of robust spines on the preauricular ridge along the flanks of the pedicle valve. *Antiquatonia coloradoensis* has a slightly deeper and more consistently developed sulcus, somewhat broader umbo, lower and more uniform convexity, a larger body cavity than Mather's species, and coarser radial ornamentation. The larger body cavity of *A. coloradoensis* is reflected by the greater distance to the end of reticulation on the pedicle valve (contrast a range from 28 to 34 mm SLR, $\bar{x}$ =32.4, to a range from 18 to 28 mm SLR, $\bar{x}$ =22.6). Perhaps the most conspicuous difference between the two species is in the relative coarseness of the radial ornamentation (see fig. 5). *Antiquatonia coloradoensis* is conspicuously more coarsely ornamented, the type collection having between 14 and 19 costellae ($\bar{x}$ =16.8, *M*=15 and 16, *n*=13) in 10 mm at 20 mm SL (fig. 5). Type specimens of *A. morrowensis* from the basal beds of the Prairie Grove Member of the Hale Formation range between 17 and 25 costellae in 10 mm at 20 mm SL ($\bar{x}$ =21.2, *M*=21 and 22, *n*=43). Collections of *A. morrowensis* from middle and basal upper Morrowan strata in the Ozarks (the Brentwood Limestone Member and the basal part of the Dye Shale Member of the Bloyd Shale, respectively, in northwestern Arkansas and equivalent strata in northeastern Oklahoma) do show a slight but statistically nonsignificant increase in the coarseness of radial ornamentation. The differences in this factor between the types of *A. morrowensis* and the type specimens of *A. coloradoensis*, in spite of the relatively small sample size of the latter species, are statistically highly significant.

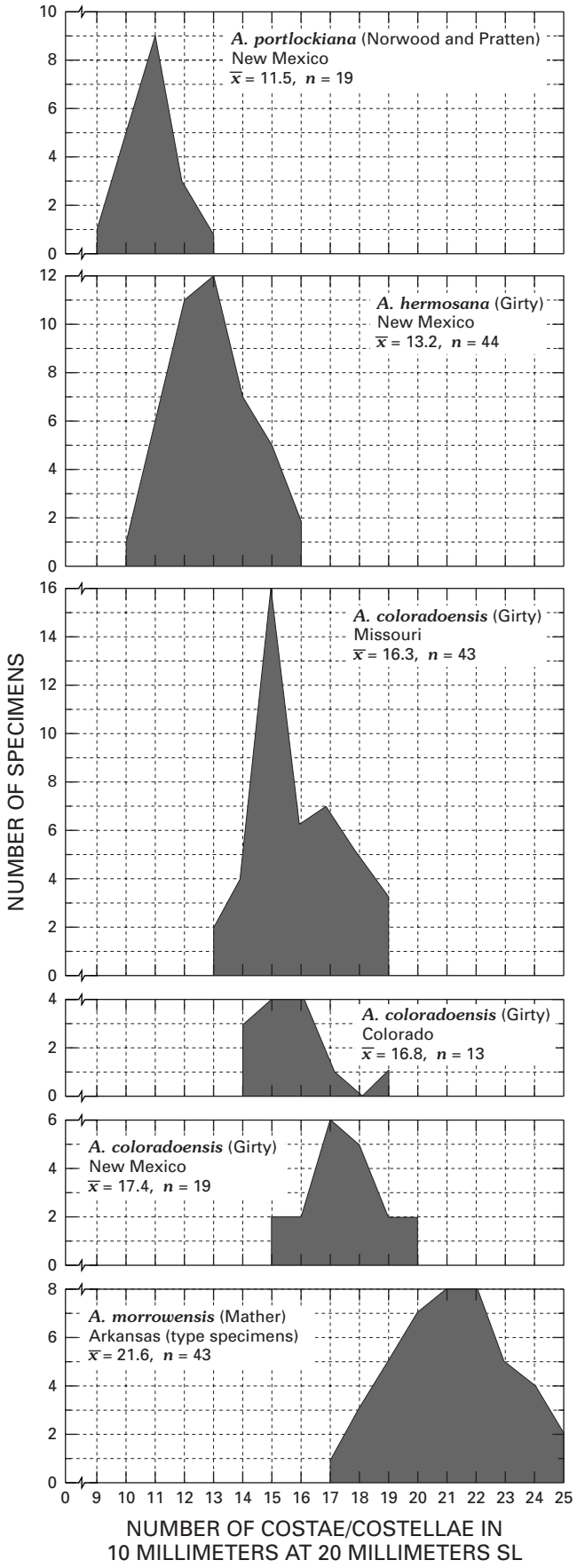


Figure 5. Number of costellae and costae in 10 mm across venter at 20 mm SL (surface length) for *Antiquatonia morrowensis* (Mather) and its probable descendants, listed from oldest to youngest: (1) *A. morrowensis* (Mather) from its type locality (early middle Morrowan) in Ozark Mountains, northwestern Arkansas; (2) *A. coloradoensis* (Girty) from upper Morrowan rocks of northern New Mexico, (3) *A. coloradoensis* (Girty) from its type locality (late Morrowan) in Colorado, (4) *A. coloradoensis* (Girty) from upper Atokan rocks of Missouri, (5) *A. hermonsana* (Girty) from lower Desmoinesian rocks of northern New Mexico, and (6) *A. portlockiana* (Norwood and Pratten) from lowest middle and lower upper Desmoinesian rocks of northern New Mexico. Note general progressive increase in coarseness of radial ornamentation (decrease in number of costellae and costae in 10 mm) in younger species. Differences between mean numbers of costae and costellae ($\bar{x}$) are statistically highly significant between all species. No significant differences exist between means of the samples of *A. coloradoensis* from the type locality in Colorado, from New Mexico, or from Missouri. Data for New Mexico material from Sutherland and Harlow (1973, fig. 24); other data from current study.

<table>
<tr><td rowspan="3">Desmoinesian</td><td>Upper</td><td rowspan="2">A. portlockiana</td></tr>
<tr><td>Middle</td></tr>
<tr><td>Lower</td><td>A. hermosana</td></tr>
<tr><td>Atokan</td><td></td><td rowspan="2">A. coloradoensis</td></tr>
<tr><td rowspan="3">Morrowan</td><td>Upper</td></tr>
<tr><td>Middle</td><td rowspan="2">A. morrowensis</td></tr>
<tr><td>Lower</td></tr>
</table>

Figure 6. Lineage of *Antiquatonia* in Lower and Middle Pennsylvanian strata in the United States.

COMPARISON WITH *ANTIQUATONIA HERMOSANA*

Antiquatonia hermosana also was described initially by Girty in his 1903 paper (p. 358, pl. 2, figs. 1–4) as a variety of *Productus semireticulatus* Martin (1809) from lower, middle, and upper Desmoinesian strata of the Hermosa Formation (Middle and Upper Pennsylvanian) in southwestern Colorado. Girty (1903, p. 358) noted considerable overlap in external features between these two taxa. Although the primary type material and other collections from these strata show considerable physical variation, *A. hermosana* differs from *A. coloradoensis* (Girty) in being generally larger and more robust and in having a broader and longer body cavity (thus continuing a trend from *A. morrowensis*), a flatter venter, a broader and shallower sulcus, slightly more enrolled ears, thus imparting a less angular appearance to the lateral extremities of the valves, and coarser radial ornamentation (see fig. 5). Sutherland and Harlow (1973, p. 51) made the following statement about the overlap and differences in radial ornamentation between *A. coloradoensis* and *A. hermosana* in their collections from the southern Sangre de Cristo Mountains, New Mexico:

> Our New Mexico specimens [identified as *A. coloradoensis*] from the [upper] Morrowan and lower Atokan intervals are closely similar to the Colorado specimens of *A. coloradoensis*, described by Girty, and are distinctly separable from our large collections of *A. hermosana* in the lower Desmoinesian. The lower Atokan specimens of *A. coloradoensis* have slightly coarser costae on the average than those in the [upper] Morrowan, and the lowest Desmoinesian specimens of *A. hermosana* have finer costae on the average than typical for that species. Although higher in the lower Desmoinesian a few specimens have finer costae approaching those of *A. coloradoensis*, the average specimen is much coarser.

Sutherland and Harlow (1973, p. 52) noted that the upper Atokan sequence in the southern Sangre de Cristo Mountains is sparsely fossiliferous but observed that their specimens of *Antiquatonia hermosana* from the lowermost Desmoinesian strata appear to be transitional forms from *A. coloradoensis*. Significantly, *A. portlockiana* occurs in northern New Mexico only in the highest middle Desmoinesian and lower upper Desmoinesian (Sutherland and Harlow, 1973, p. 52). I examined three well-preserved collections of specimens of *Antiquatonia* from sinkhole deposits constituting the Burgner Formation from (1) the E.J. Palmer collection, University of Missouri (UM) loc. 47; (2) USGS collections BL8113–PC and BL25128–PC (given to G.H. Girty from the Palmer collection); and (3) Hoare's (1961) Eldon collection from UM loc. 37. The Palmer collection (see Searight and Palmer, 1957, p. 2127–2128; Ragan, 1959) consists of material acquired from old coal mine dumps near the center of sec. 20, T. 28 N., R. 32 W., Jasper County, Mo. Hoare's (1961) collection (UM loc. 37) was from material exposed on the dump of an old coal mine on the Neville farm about 2.5 mi southwest of Eldon, in the $NW^1/_4$ $SE^1/_4$ sec. 6, T. 41 N., R. 16 W., Miller County, Mo. These sinkhole deposits are dated as Atokan on the basis of cephalopods (Unklesbay and Palmer, 1958) and middle and late Atokan on the basis of associated fusulinids and conodonts (see M.L. Thompson, 1953; T.L. Thompson, 1979). R.C. Douglass (written commun., January 1989) reported that the matrix from USGS colln. BL25128–PC contains the foraminifer *Bradyina* sp. and an advanced form of *Fusulinella*, indicating a definite late Atokan age. The first USGS lot (BL8113–PC) is part of Palmer's collection, from which Girty (1935, pl. 2, figs. 1–4) figured a superbly preserved pedicle-valve exterior as *Productus coloradoensis*. The repository was not mentioned in Girty's paper, and I could not find the specimen in the USNM or USGS collections, and R.L. Ethington (written commun., July 15, 1993) could not locate it in the University of Missouri collections. This specimen showed the acute and distinctly angular posterolateral extremities that characterize this species. Smith and Siebenthal (1907, p. 7) earlier had listed a collection of invertebrate fossils from this same mine dump on the Burgner mine property and identified the large *Antiquatonia* as *Productus semireticulatus* (Martin).

My measurements of the large collection of generally well preserved material from UM loc. 47 are presented in table 4. Searight and Palmer (1957) and Ragan (1959) reported both *Antiquatonia coloradoensis* and *A. hermosana* from this and other Burgner collections in southwestern Missouri, as did Hoare (1961) from other localities. Statistically, no significant difference exists (at 95 percent confidence limits) in the coarseness of radial ornamentation between the Burgner set that Ragan identified as *coloradoensis* and the set from this locality that he identified as *hermosanus* (the latter marked by two asterisks beside the catalog number in table 4). Furthermore, because continuous variation characterizes all of the other significant taxonomic characters noted between the two sets, I concluded that only one variable species (*A. coloradoensis*) is present in the Burgner collections.

Table 4. Measurements (in millimeters) of specimens identified as *Antiquatonia coloradoensis* (Girty) and *A. hermosana* (Girty) by Ragan (1959) from the Burgner Formation (upper Atokan), Jasper County, Mo., and referred herein to *A. coloradoensis* (Girty).

[Specimens are reposited at the University of Missouri (UM) at Columbia. Specimens are from the E.J. Palmer collection from mine dumps at UM locality 47 in SE$^1/_4$ sec. 20, T. 28 N., R. 32 W., 1.5 mi south of Carterville, Jasper County, Mo. Asterisk in first column indicates internal mold of pedicle valve; double asterisks after type identification indicate specimen identified by Ragan (1959) as *A. hermosana*; dash means data not available. Characters are defined in figure 4. *Abbreviations:* BV, brachial valve; HAM, hinge to anterior margin; PV, pedicle valve; SL, surface length along venter; SLG, surface length to geniculation (beginning of trail); SLR, surface length to end of reticulation. *Types:* R, specimen illustrated by Ragan (1959); r, specimen not illustrated by Ragan (1959). *Designations for dimensions that could not be measured exactly:* a, approximate; e, estimated; m, minimum; t, estimated from twice half-width. Measurements by T.W. Henry]

UM catalog number	Type	Length		SL	Width		Height	Depth	SLR (PV)	SLG (BV)	Trail length	Costellae in 10 mm at SL				
		PV	HAM (BV)		Hinge	Body						20 mm	30 mm	40 mm	50 mm	60 mm
Whole shells (articulated) or disarticulated pedicle valves																
13665g.....	r **	24.2 a	21.4	37	–	32.7 a	11.5	7.5	28	–	–	16	16	–	–	–
13664g.....	r **	27.7 a	26.0 a	50 a	–	35.5 a	18.9 a	–	30	–	–	13	–	–	–	–
13663a.....	r **	28.6 a	25.2 a	46	40 m	37.0 a	16.7 a	–	31	–	–	16	18	16	15	–
13671d.....	r	29 m	23 m	53 m	–	41 e	–	16.5 a	30	23	–	15	13	–	–	–
13664h.....	r **	29.2 m	–	50 m	–	39.0 a	–	–	32	–	–	15	16	16	15	15
13665j.....	r **	30 m	21 m	55 m	–	37.8 a	–	13.4	35	–	–	15	16	17	–	–
13672d.....	r	30 m	25 e	65 m	44.0 t	37.1 a	–	–	33	–	–	17	14	13	–	–
13664a.....	r **	31 m	25 m	55 m	–	34 m	–	15.0	33 a	–	–	15	16	14	–	–
13664c.....	r **	31 m	20 m	52 m	–	35.0 a	–	14.2	32	–	–	–	12	14	10	–
13665c.....	r **	31 m	26 m	45 m	40.0 e	38.6 e	–	–	28	–	–	19	15	14	–	–
13665a.....	r **	31 m	26 m	53 m	–	39 e	–	14.0	31	21	–	19	18	17	17 a	–
13662d.....	r **	31.4 m	22.5 m	58 m	–	38.5 m	21 m	16.9	30	18	–	–	13	–	–	–
13673d.....	r	31.4 a	25.3 a	52	–	39.6 a	25 e	–	32	–	–	14	14 a	–	–	–
13663c.....	r **	31.5 a	–	60	44.4 a	38.5 a	20.5 a	–	25	–	–	16	14	14	14	–
13665h.....	r **	32 m	22 m	58 m	–	39.2 a	–	16.6	29	–	–	18	18	17	–	–
13664d.....	r **	32 m	24 m	51 m	–	33.8 a	–	15.2	28	–	–	14	15	–	–	13
13664b.....	r **	32 m	–	53 m	42.4 t	42.0 t	–	–	32	–	–	14	14	–	–	–
13662e.....	r **	32.3 a	26.8 a	52	39.3 a	37.8 a	20.7 a	–	25	–	–	–	–	–	–	–
13665f	r **	32.5 a	22.4 a	60 a	43.6 a	40.7 a	23.9 a	–	34	–	–	15	14	15 a	–	–
13665b.....	r **	33.4 a	23.8 a	55	40.0 t	56.0 t[1]	23.2 a	–	33	–	–	19	19	17	–	–
13673c *.....	r	33.5 m	25.5 m	60 m	44.8 t	32.9	21.5 m	20.0	34	21	–	–	–	–	–	–
13672e.....	r	33.5 m	26 m	60 m	–	38.2 a	19 m	15.3	30	22	–	–	–	13	14	–
13665d.....	r **	34.0 a	24.4 a	55	–	41.4 e	–	–	28	–	–	15	14	13	14	–
13673e.....	r	34.0	27.0 a	59	42.1 a	40.1	21.6 a	–	33 a	–	–	–	–	–	17	–
13672f	r	34 m	28 m	58 m	–	35.0 a	19 m	13.2	29	22	–	–	–	–	–	–
14353.....	R	34 m	25 m	60 m	39.2 t	40.0 a	20 m	14.4	31	16	–	16	14	15	13	11
13663d.....	r **	34.2 a	26.2 a	58	–	37.9 a	–	–	29	–	–	15	14	–	12	–
13663b.....	r **	34.4 a	25.5 a	69	–	41.0 a	22.9 a	–	35	–	–	18	15	13 a	14	–
13665e.....	r **	34.8 a	26.5 a	60	53.8 t	40.8 e	–	–	35	–	–	15	14	14	–	–
13672c.....	r	35 m	24 m	62 m	–	38.5	20 m	15.0	38	23	–	18	14	14	11	12
14354.....	R	35 m	25 m	60 m	–	43.6	24 m	14.5	40	21	–	15 a	15 a	12	12 a	–

Table 4. Measurements (in millimeters) of specimens identified as *Antiquatonia coloradoensis* (Girty) and *A. hermosana* (Girty) by Ragan (1959) from the Burgner Formation (upper Atokan), Jasper County, Mo., and referred herein to *A. coloradoensis* (Girty)—Continued.

UM catalog number	Type	Length		SL	Width		Height	Depth	SLR (PV)	SLG (BV)	Trail length	Costellae in 10 mm at SL				
		PV	HAM (BV)		Hinge	Body						20 mm	30 mm	40 mm	50 mm	60 mm
Whole shells (articulated) or disarticulated pedicle valves																
13663f	r **	35.0 a	25.6 a	60	–	39.3 a	22.2 a	–	32	–	–	18	17	18	18	–
13663e	r **	35.2 a	24.9 a	70	48.4 t	38.5 t	22.7 a	–	32	–	–	16	15	14	12	–
13662a	r **	35.5	26.5 a	67	54.6 t	39.2 a	26.2 a	–	28 a	17 a	–	–	–	–	–	–
13672b	r	35.6 a	–	60 e	37.5 e	35.5	22.0 a	–	28	–	–	–	–	–	–	–
13673a	r	35.9	27.7 a	66	43 e	39.0	24.6 a	–	32	–	–	13	12	13	–	–
13671e	r	36.0 a	26.6 a	70	–	41.5 a	26.7 a	–	34	–	–	18	16	14	–	–
13662b	r **	36.0 a	27.1 a	66	–	40 e	21.7 e	–	29	19	–	17	15 a	–	–	–
13664f	r **	36.0 m	29.5 m	63 m	–	39.9 a	–	–	34	–	–	15	–	–	–	–
13671b	r	36.1 a	27 e	70	49.0 t	43.8	29 e	–	33	–	–	15	14	–	–	–
13662c	r **	36.2	28.8 a	68	–	39.2 a	26.3 a	–	31	–	–	15	15	13 a	12	–
13664e	r **	36.7	28.6 a	65	46.2 a	46.2 a[1]	23.6 a	–	32	–	–	17	17	15	12	–
13665i	r **	36.8 a	–	62	57.2 t	39.5 a	–	–	27	–	–	15	17	16	–	–
13662g	r **	37 m	24.4 m	55 m	–	35.0 a	23 m	13.7	32	–	–	17	–	–	–	–
13657a	r **	38.9	28.3 a	73	48.7	46.5	25.1 a	–	35	–	–	16 a	16	–	–	–
13671c	r	39.6 m	25.5 m	68 m	39.0 t	34.5 a	22.0 m	17.5	23	20	–	17	14	15	11	–
13657c	r **	39.7 a	–	60 a	47.7 e	45.0 e	–	–	32 a	–	–	15	14	14	16 a	–
13672a	r	39.9	28.5 a	78	48.8 a	43.1	28.1 a	–	34	–	–	17	16	14	–	–
13662f	r **	40.1 a	30.5 a	70	–	41.4 a	23.0 a	–	32 a	–	–	–	–	–	13	–
13673b	r	40.7 a	28.6 a	72	–	42.2 a	24.8 a	–	35	–	–	–	–	–	–	–
13657b	r **	42.5 a	33.5 a	80	51.5 a	48.8 a	28.3 a	–	25	–	–	15	16	17	–	–
13657d	r **	44.3 a	34.4 a	78 a	47.7 a	51.8 a[1]	26.6 a	–	29	–	–	15	–	–	–	–
13671a	r	47.0	27.5 a	78	52.0 t	43.0 a	28.0 a	–	31	–	–	17	16	17	13	–
13657e	r **	48 e	–	74 a	48.2	43.4 a	–	–	28	–	–	14	16	15	13	13
Brachial valves (disarticulated)																
13663h	r **	–	[2]22.8	[2]28	37.0 t	33.2	–	–	–	[2]20	8	–	–	–	–	–
13672g	r	–	[2]25.3	[2]37	38.3 a	36.3 a	–	–	–	[2]22	15	–	–	–	–	–
13671f	r	–	[2]26.7 a	[2]40	44.3 a	38.1 a	–	–	–	[2]20	20	–	–	–	–	–
13673f	r	–	[2]30.3	[2]51	48.6 t	47.2	–	–	–	[2]21	30	–	–	–	–	–
13657g	r **	–	[2]35 e	[2]50 e	53.4 t	67.8 t[1]	–	–	–	[2]21	29 e	–	–	–	–	–

[1]Specimen has flaring trail.
[2]Excluding cardinal process.

The number of costellae in 10 mm measured at 20 mm SL for the composite set from the Burgner ranges between 13 and 19 (M=15 and $\bar{x}$=16.3; see fig. 5). This range therefore overlaps heavily with that of the types of *A. coloradoensis* (fig. 5) from the Belden Shale, the range of which is from 14 to 19 (M=15 and 16 and $\bar{x}$=16.5). No statistically significant difference (99.5 percent confidence limits) exists for this feature between the Burgner sample and the types of *A. coloradoensis* from Colorado.

I also examined the University of Missouri's collection of specimens of *Antiquatonia*, including Hoare's figured specimens, from the Burgner Formation from Hoare's (1961, p. 18) UM loc. 37, mentioned above, from central Missouri. According to T.L. Thompson, Jr. (oral commun., November 15, 1991), UM loc. 37 near Eldon is about the same age (late Atokan) as the type Burgner in the southwestern part of the State. Hoare's Eldon collection consists of 11 relatively complete specimens or valves plus fragments. Hoare (1961, p. 56–58) typologically assigned specimens from this collection from the Burgner Formation to three *Antiquatonia* species: *A. hermosana*, *A. coloradoensis*, and *A. portlockiana*. He illustrated specimens as the former two species (UM 13192–13194 and UM 13195–13197, respectively), but his figured specimens assigned to *A. portlockiana* (Hoare, 1961, pl. 5, figs. 1–7) were from younger Pennsylvanian (middle and upper Desmoinesian) strata. The range of variation in the Burgner collection assigned by Hoare to these three discrete species is completely encompassed by the large collection of primary and secondary types of *A. coloradoensis* from the Mosquito Range. Size alone does not constitute a valid criterion on which to discriminate among these species.

COMPARISON WITH *ANTIQUATONIA PORTLOCKIANA*

Girty (1935, p. 9) suggested, with strong caveats, that *A. hermosana* might be a junior synonym of *A. portlockiana* (Norwood and Pratten). Sutherland and Harlow (1973, p. 32) concluded, however, that the two are discrete species and that *A. portlockiana* succeeds *A. hermosana* stratigraphically in the upper middle and upper Desmoinesian of northern New Mexico. I agree with their conclusion based on the New Mexico material. However, to fully resolve this question, large collections of topotypes of *A. portlockiana* need to be examined to determine more fully its characteristics and range of variation. Dunbar and Condra (1932, p. 216) noted that Norwood and Pratten (1855) had only two specimens when they described *A. portlockiana*, one from the St. Louis, Mo., area and the other from Illinois. The disposition of these two cotypes is not known. Dunbar and Condra also noted, however, that they had available large collections of topotypes from Charbonniere Bluffs, St. Louis County, Mo., from strata that they reported as "lower Fort Scott limestone" (middle Desmoinesian). They illustrated one of these topotypes (Dunbar and Condra, 1932, pl. 33, fig. 1a–c). In the absence of material with which to redescribe *A. portlockiana*, suffice it to say that it would appear that this species differs from *A. coloradoensis* in being slightly smaller, having a proportionally less inflated umbo, proportionally smaller ears, perhaps a more strongly incurved beak, and coarser radial ornamentation (see fig. 5).

GENERAL DISCUSSION

The confusion that exists in the literature about the nature and stratigraphic range (geologic age) of *Antiquatonia coloradoensis* (Girty) (see Carter and Carter, 1970, p. 218, 219) stems mainly from the following six factors.

1. When Girty (1910, p. 216) formally proposed the varietal name *Productus inflatus* var. *coloradoensis*, it was in a paper that was not illustrated and that was concerned primarily with naming the components of the invertebrate macrofauna of the Fayetteville Shale (Chesterian, Upper Mississippian) of the Ozark Mountains. In the 1910 paper, although it was clear that the primary types were from lower Middle Pennsylvanian strata of Colorado (see preceding section), he also *provisionally* referred to the newly named variety, *Productus inflatus* var. *coloradoensis*, a large, superficially similar, semireticulate productid from the basal part of the Fayetteville Shale. This material, also assignable to the genus *Antiquatonia* (as currently understood), differs from *A. coloradoensis* in a number of important ways. Specifically, the Fayetteville material is larger and proportionally broader, has a consistently deeper sulcus on the pedicle valve, and possesses both fewer and smaller body spines on the pedicle valve. It is *not* conspecific with *A. coloradoensis* and represents an unnamed, undescribed species that may have been ancestral to *A. morrowensis* (Mather).

2. Girty, in later publications, applied (again with reservation) the name *Productus inflatus* var. *coloradoensis* to other Mississippian collections as well. The first two of these publications (Girty, 1911, p. 42; 1915b, p. 46) were on the faunas of the Moorefield Formation (Meramecian and Chesterian) and Batesville Sandstone (Chesterian) of the Ozarks. To further complicate matters, in a subsequently published paper (1915c) primarily on the fauna from "the so-called Boone chert," from near Batesville, Ark., Girty (1915c, p. 27) referred material from the chert to the same variety, *P. inflatus* var. *coloradoensis*. Girty's fauna was mainly from Osagean-age beds of the Reeds Spring Chert Member of the Boone Formation (Kinderhookian through lower Meramecian). However, the fragmentary productids in question presumably were collected (USGS colln. GR1237B–PC) from the Spring Creek Member (Meramecian and lower Chesterian) of the Moorefield Formation and represent an unnamed species of semireticulate productid that is likely not an *Antiquatonia* at all. Girty (1915a, p. 65) later recognized that none of the Mississippian material was referable to *P. coloradoensis*. In all

fairness to Girty, who published over 40 major papers between 1900 and 1920, the order of publication of the papers was not the same as the order in which they were written. For example, the manuscript on the faunas from the Wewoka Formation (Girty, 1915a) was written after those on the Mississippian faunas of northern Arkansas (1915b, d).

Snider (1915, p. 80), in his study of the Chesterian faunas of northeastern Oklahoma, followed Girty's example and used the name *Productus coloradoensis* for Upper Mississippian forms, although he did not illustrate the species from the "Mayes limestone" (probably Moorefield Formation) thus referred. These Moorefield and Batesville forms, from strata slightly older than the Fayetteville Shale, probably belong to the unnamed *Antiquatonia* present in the Fayetteville. Many other authors (Croneis, 1930; Sutton, 1938; Nelson, 1961) also mistakenly assumed that *P. coloradoensis* is based on material from the basal part of the Fayetteville and used the name widely and indiscriminately for Mississippian antiquatonids. Carter and Carter (1970, p. 218–219) recognized that at least two taxa were involved.

3. Although Girty initially proposed the name for the Pennsylvanian specimens in the 1910 paper for the Colorado material, he later (1915a, p. 64, 65—the paper on the fauna from the Wewoka Formation) *again* presented the same name *Productus inflatus* var. *coloradoensis*, based on the same material, and treated it as though his earlier proposal (Girty, 1910) had not been made. I emphasize that Girty (1915a)—the Wewoka paper—is *not* the publication in which the name *coloradoensis* was first applied to the Pennsylvanian species, although it has been cited thusly by several workers. To quote Girty (1915a, p. 65):

> The best and most characteristic specimens referred to this variety [from the Wewoka Formation] resemble the form from Colorado identified by us as *P. inflatus* rather than the one described as *P. semireticulatus* var. *hermosanus*. Having studied what are probably characteristic specimens of *P. inflatus*, we have reached the conclusion that the shell from Colorado is a distinct form and propose for it the varietal name *coloradoensis*.

Contrary to Girty, I conclude that the material from the Wewoka Formation (upper Desmoinesian, Middle Pennsylvanian) that Girty (1915a, p. 64, 65, pl. 8, figs. 1, 2) referred to *P. coloradoensis* does not belong to this species at all. I examined both imperfect specimens (USNM 120914, 192095) that he figured from the lower part of the Wewoka Formation and sizable collections from throughout this formation. The Wewoka specimens are large and generally more coarsely costellate than *A. coloradoensis* and in many other respects are similar to specimens normally assigned to *A. hermosana* (Girty), which, however, are generally in lower and middle Desmoinesian strata.

4. The primary type specimens of *Productus inflatus* var. *coloradoensis* were reillustrated (as engraved figures) several times in publications for Carboniferous strata for other geographic areas (see table 5). Such reillustration was a widespread practice at the time, following the concept of "index fossils" and the convention of illustrating "typical fossils" for a given age, strata, and region. However, this practice created confusion in that the illustrated specimen(s) are indeed *Antiquatonia coloradoensis* (and therefore must be included in the synonymy of the species) but the material ostensibly referred to that species in a cited report may or may not be that taxon. Three examples follow. First, Boutwell (1912) reported *Productus inflatus* from the "Weber quartzite" (part of the Morgan Formation of current usage) of the Park City mining district of the Uinta Mountains, northern Utah. He illustrated several primary type specimens of Girty's *Productus inflatus* var. *coloradoensis* from the Fairplay-Leadville, Colo., area. Second, Girty (1920, pl. 55, figs. 4, 5) likewise reillustrated two of his primary types for Butler and others' "The Ore Deposits of Utah" (1920) as one of the "index fossils" for the Carboniferous of that region, but neither Girty (1920) nor Butler and others (1920) listed the species from any specific geographic or stratigraphic horizon in those papers. Third, Girty (1927) refigured one of his primary types as *P. coloradoensis* in Mansfield's (1927) monograph on the geology of southeastern Idaho. In this monograph, Mansfield (1927, p. 73) cited Girty's identification of this taxon in the "Wells formation." However, it is extremely doubtful that the large productid thus reported in the Utah or Idaho sequences is Girty's species at all.

5. The Burgner and Riverton Formations of southwestern and central Missouri consist of a series of dark shale and carbonate units deposited in sinkholes developed on the karsted Mississippian limestone surfaces and in other low regions on an irregular, undulating erosional surface on the flanks of the Ozark dome during the later Morrowan and early Atokan (see Seawright and Palmer, 1957; Hoare, 1961, p. 14; Thompson, 1979, p. N13–N16). As stated above in the section, "Comparison with *Antiquatonia hermosana*," R.C. Douglass concluded that the fusulinids from these sinkhole deposits indicate a late Atokan age for these strata. However, Girty (1935, p. 8) referred the upper Atokan Burgner strata at the Palmer locality (discussed above) to the "Cherokee formation," a stratigraphic term now reserved for the basal Desmoinesian (Middle Pennsylvanian) coal-bearing sequence overlying the Burgner Formation. Girty's reference of this Atokan material to the Cherokee undoubtedly has led to further uncertainty about the upper extent of the range of *Antiquatonia coloradoensis*. As indicated above, I concluded that a variable form more reasonably identified as *A. coloradoensis* is present in the Burgner collections, not both *A. coloradoensis* and *A. hermosana*.

6. *Antiquatonia coloradoensis* is present in the lower part of the Minturn Formation in the McCoy area of central Colorado. This taxon was reported by Stevens (1962) and is present in the USGS collections from this area. The Minturn strata in which this productid was reported by Stevens (1962, p. 618–620, unit 3) also contain *Fusulinella leyi* (Thompson), indicating equivalence with the upper part of the type "Derryan" Series (Atokan) in New Mexico and the

Table 5. Index to original (engraved) figures and replication of same in publications for lectotype and two paralectotypes of *Antiquatonia coloradoensis* (Girty) from the lower part of the Belden Shale (upper Morrowan equivalents), from U.S. Geological Survey colln. GR2281–PC, from near Fairplay, Park County, Colo.

Publication	Figured or identified as:	USNM 35345	USNM 121482	USNM 121483
Girty (1903)	*Productus inflatus* McCh.	Pl. 3, figs. 1–1b, figured specimen.	Pl. 3, figs. 2–2a, figured specimen.	Pl. 3, fig. 3, figured specimen.
Girty (1910)	*Productus inflatus* var. *coloradoensis* n. var.	Not illustrated, designated cotype.	Not illustrated, designated cotype.	Not illustrated, designated cotype.
Boutwell (1912)	*Productus inflatus*? McCh.	Pl. 6, figs. 3–3a, figured specimen.	–	Pl. 6, fig. 4, figured specimen.
Girty (1920)	*Productus inflatus* var. *coloradoensis* Girty.	Pl. 55, fig. 3, cotype	–	Pl. 55, fig. 4, cotype.
Girty (1927)	*Productus coloradoensis* Girty.	Pl. 27, fig. 17, cotype	–	–
Gordon (1975).....	*Antiquatonia coloradoensis* (Girty).	Not illustrated, designated lectotype.	Not illustrated, designated paralectotype.	Not illustrated, designated paralectotype.
This paper.....	*Antiquatonia coloradoensis* (Girty).	Pl. 1, figs. 1–4, lectotype	Pl. 1, figs. 5–8, paralectotype.	Pl. 1, figs. 9–13, paralectotype.

upper part of the Atokan Series of the Midcontinent. The three specimens that Stevens (1962, pl. 95, figs. 2, 3, and 5) illustrated as *A. coloradoensis* are captioned (1962, p. 628) as from Stevens' unit 9 of the Minturn Formation, reported to contain early Desmoinesian fusulinids and other brachiopods characteristic of that part of the Middle Pennsylvanian. He listed *A. coloradoensis* in his discussion of unit 3 (see Stevens, 1962, p. 623) but cited only *A. hermosana* in his discussion of the fauna of unit 9. Furthermore, the two large specimens that he illustrated as *A. hermosana* (1962, pl. 95, fig. 6; pl. 96, fig. 4) are also captioned as from unit 9. Without having looked at the Stevens collections from units 3 and 9, and assuming that the plate caption is correct, I suggest that the specimens that Stevens figured as *A. coloradoensis* in this paper are the rarer, smaller, more finely costellate variants of *A. hermosana* and should not be identified as *A. coloradoensis*. This question cannot be resolved by the USGS collections from the Minturn area, because most of these do not have corroborative biostratigraphic control from other faunal groups.

OCCURRENCES AND RANGES

Antiquatonia coloradoensis is reported from the southern Rocky Mountains, the Eastern Great Basin, the southern and central Midcontinent area, and both the eastern and southern parts of the Appalachian Basin. This productid is a component of the marine faunas interpreted to represent open-bay, shelf-lagoon, and shelf-margin facies.

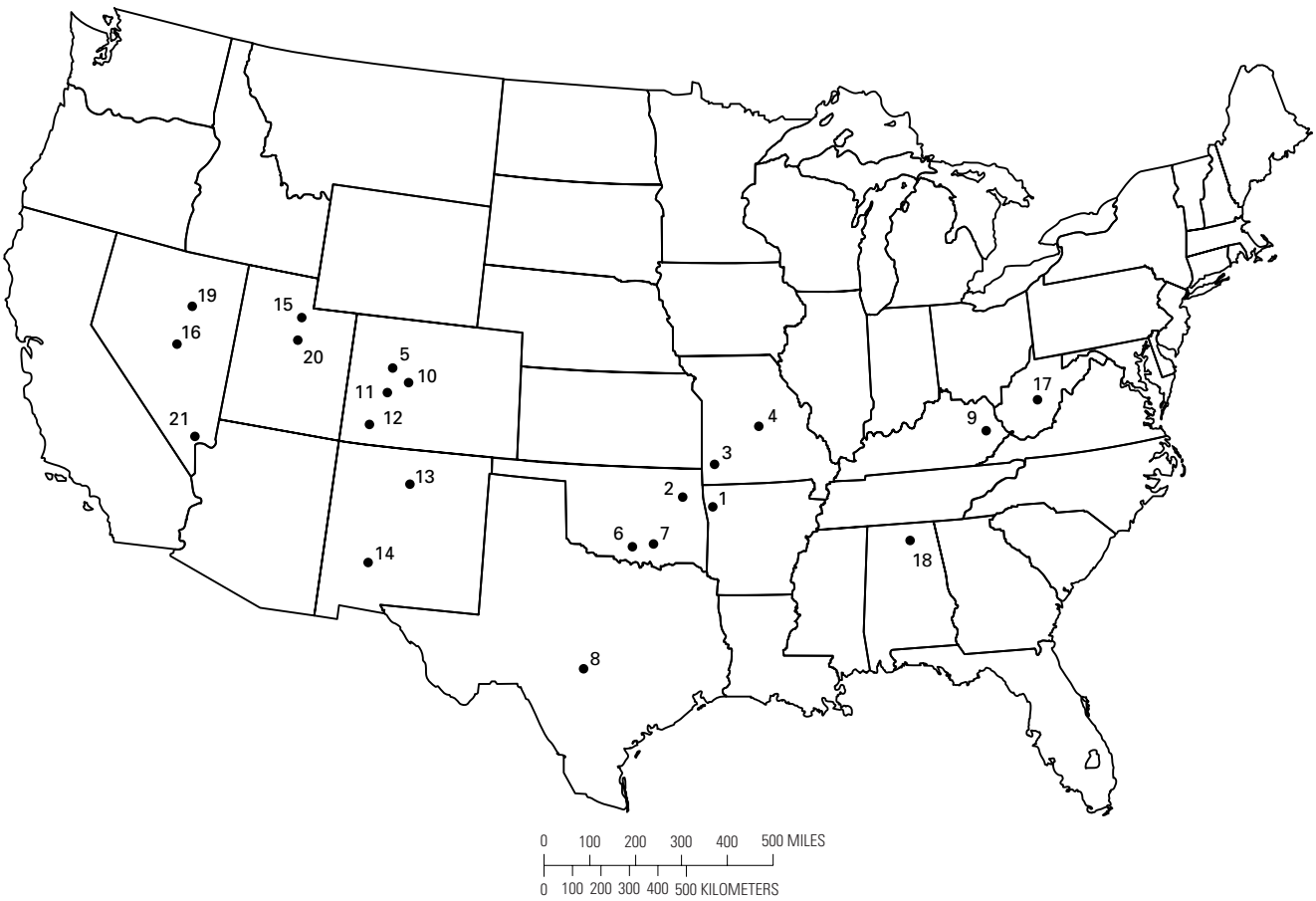
SOUTHERN ROCKY MOUNTAINS

Antiquatonia coloradoensis occurs in the northern part of the southern Rocky Mountains in the following strata and areas: (1) in the upper Morrowan strata of the lower part of the Belden Shale in the Fairplay, Colo., area (type locality; loc. 10 of fig. 7); (2) in the Belden Shale (upper Morrowan and Atokan equivalents) of the Eagle Basin near Crested Butte, Colo. (loc. 11 of fig. 7); (3) in the middle to upper Atokan parts of the Minturn Formation in central Colorado (loc. 5 of fig. 7); (4) in strata probably assignable to the Pinkerton Trail Formation (Atokan equivalents) in the lower part of the Hermosa Group in the San Juan region of southwestern Colorado (loc. 12 of fig. 7); and (5) in both the upper Morrowan and lower and middle Atokan equivalents of the La Pasada Formation in northern New Mexico (Sutherland and Harlow, 1973, p. 51) (loc. 13 of fig. 7).

In southern New Mexico, *Antiquatonia coloradoensis* is present in the upper Morrowan part of the type "Derryan" Series (Sutherland and Manger, 1984; Sutherland, 1991, p. 188) (loc. 14 of fig. 7) along with 11 species of "typical" late Morrowan brachiopods. Sutherland assigned these strata to his *Zia novamexicana* Brachiopod Subzone of the *Linoproductus nodosus* Zone. Gehrig (1958) also reported *Dictyoclostus inflatus* var. *coloradoensis* from *Fusulina*-bearing Desmoinesian strata of the Armendaris Group in southern New Mexico (Mud Springs Mountains, loc. 14 of fig. 7). However, Gehrig's specimens were examined by P.K. Sutherland (oral commun., Nov. 1, 1991), who reported that his Desmoinesian specimens identified as *D. inflatus* var. *coloradoensis* are, in fact, typical *A. hermosana* (Girty) and his Atokan specimens of *D. morrowensis* (Mather) are *A. coloradoensis*.

EASTERN GREAT BASIN

The material reported by Boutwell (1912) from the "Weber quartzite" (Weber? Formation) in the Park City district in northeastern Utah (loc. 15 of fig. 7) as *Productus inflatus*?, and later included in synonymy of *P. coloradoensis* by Girty, needs to be examined for possible assignment



LOCALITIES

EASTERN GREAT BASIN

15 Park City district, northeastern Utah
16 Northern Nye County, Nevada
19 Carlin, Nevada
20 Wasatch Mountains, near Provo, Utah
21 Arrow Canyon Range, Clark County, Nevada

SOUTHERN ROCKY MTNS.

5 Central Colorado
10 Fairplay, Colorado
11 Crested Butte, Colorado
12 San Juan region, southwestern Colorado
13 Northern New Mexico
14 Mud Springs Mountians, southern New Mexico

MIDCONTINENT

1 Northwestern Arkansas
2 Northeastern Oklahoma
3 Jasper County, Missouri
4 Miller County, Missouri
6 Ardmore Basin, southern Oklahoma
7 Northeastern flanks of the Arbuckle Mountains, southern Oklahoma
8 Llano area of Texas

APPALACHIAN BASIN

9 Floyd County, eastern Kentucky
17 Southern West Virginia in general vicinity of Boone County
18 Warrior coal field, southern Appalachians

Figure 7. Localities of verified or probable occurrences of *Antiquatonia coloradoensis* (Girty) in the United States. Numbers 1–21 correspond to areas identified in text.

to *Antiquatonia coloradoensis*. Just south of this area, I have identified *A. coloradoensis* from several collections from the Wasatch Mountains near Provo, Utah (loc. 20 of fig. 7), associated with Atokan *Profusulinella*-bearing rocks of the Bear Canyon Member of the Oquirrh Formation.

This species is known from three areas in Nevada. I have examined a small collection from the Ely Limestone (Upper Mississippian to Lower Permian) in northern Nye County (loc. 16 of fig. 7). These specimens are tentatively identified as *A. coloradoensis* and occur with a moderately diverse brachiopod fauna strongly suggesting an Atokan age for the strata. A second, recently obtained collection from the Bird Spring Formation (Pennsylvanian and Lower Permian) in the Arrow Canyon Range, Clark County (loc. 21 of fig. 7), also contains *A. coloradoensis* along with a moderately diverse late Morrowan or early Atokan brachiopod fauna. These brachiopods occur above the stratigraphically lowest *Eoschubertella* but below the lowest *Profusulinella* (Langenhein, Webster, and Weibel, 1984; Webster and Langenheim, 1984). Smith and Ketner (1975, p. 53) reported *A.*

coloradoensis from the upper Morrowan part of the Moleen Formation (Lower and Middle Pennsylvanian) near Carlin (loc. 19 of fig. 7).

MIDCONTINENT

Antiquatonia coloradoensis first appears in the Midcontinent in upper Morrowan strata and ranges apparently through the Atokan Series. The oldest confirmed appearance of *Antiquatonia coloradoensis* is in the Kessler Limestone Member of the Bloyd Shale in the upper part of the "type" Morrowan Series in northwestern Arkansas (loc. 1 of fig. 7) and in the physically correlative Greenleaf Lake Limestone Member of the McCully Formation in northeastern Oklahoma (loc 2. of fig. 7). Its youngest confirmed occurrence is in upper Atokan strata of the Burgner Formation of Jasper and Miller Counties, Mo. (locs. 3 and 4, respectively, of fig. 7).

Other Midcontinent occurrences of *Antiquatonia coloradoensis* follow. This species is rare in the Trace Creek Member of the Atoka Formation in northwestern Arkansas (loc. 1 of fig. 7). Sutherland and Grayson (1992, p. 84, 88–89) reported *A. coloradoensis* with other "typical" late Morrowan brachiopods in the Ardmore Basin of southern Oklahoma (loc. 6 of fig. 7) in the Golf Course Formation (upper Morrowan)—specifically in its Jolliff Member, in the lower parts of their unnamed units 1 and 2, and in the Otterville Member. They (Sutherland and Grayson, 1992, pl. 3, figs. 10–12) figured three well-preserved specimens from the lower part of the Bostwick Conglomerate Member of the overlying Lake Murray Formation. These strata contain *Fusulinella dakotaensis*, the lower of two zones of *Fusulinella* in the basin, and are correlated with the middle part of the Atokan Series. This species also occurs in the upper Morrowan part of the Wapanucka Limestone of southern Oklahoma on the northeastern flanks of the Arbuckle Mountains (loc. 7 of fig. 7) (P.K. Sutherland, oral commun., Nov. 1, 1991). The specimen that Morgan (1924, pl. 44, fig. 6) illustrated as *Productus morrowensis* Mather from the Wapanucka from this area belongs to Girty's species. *Antiquatonia coloradoensis* is in the lower Atokan part of the Marble Falls Limestone (Lower and Middle Pennsylvanian) of the Llano area of Texas, where it occurs abundantly with species of *Profusulinella* (P.K. Sutherland, oral commun., Nov. 1, 1991) (loc. 8 of fig. 7). It is most likely that the specimens figured by Plummer and Moore (1921, p. 79, pl. 13, fig. 24) and Plummer (1950, pl. 12, fig. 9) are from these lower Atokan strata. *Antiquatonia coloradoensis* does not occur in the *Fusulinella*-bearing beds in the upper part of the Marble Falls Limestone (P.K. Sutherland, oral commun., Nov. 1, 1991).

APPALACHIAN BASIN

Antiquatonia coloradoensis has been identified from three general areas in the Appalachian Basin, from Pennsylvanian strata that range in age from late Morrowan into the Atokan. The Morrowan and lower Atokan collections generally also contain *Linoproductus nodosus* (Newberry, 1861) and other faunal elements characteristic of the *L. nodosus* Brachiopod Zone. The stratigraphically highest collections (for example, those of the Winifrede Shale Member of the Kanawha Formation of West Virginia and the correlative Magoffin Member of the Breathitt Formation of Kentucky) contain *A. coloradoensis*, but the other brachiopods characteristic of the *L. nodosus* Zone are not present.

The first of these areas and the oldest known occurrence of *Antiquatonia coloradoensis* in the Appalachian Basin is in southern West Virginia (loc. 17 of fig. 7), where I have collected several specimens of this species from both the Eagle limestone of I.C. White (1891) and the Eagle shale of Hennen and Reger (1914) in the lower middle part of the Kanawha Formation. The strata of this marine band are now assigned to the Betsie Shale Member of the Kanawha Formation (Rice and others, 1987) and are upper Morrowan correlatives (Henry and Gordon, 1979, p. 101–102). *Antiquatonia coloradoensis* also occurs sparsely in this general vicinity in an overlying Kanawha marine unit in Boone County, W. Va., in what Price (1916) called the Seth limestone of Krebs (*in* Krebs and Teets, 1915). This marine band is the one that occurs just above the Cedar Grove coal bed in Kanawha and Fayette Counties, W. Va., and has been correlated more recently with the Campbell Creek Limestone of I.C. White (1885) by Blake, Keiser, and Rice (1994, fig. 2). I have collected both *L. nodosus* and *A. coloradoensis* from this marine unit in all three counties. Price (1916, p. 699) referred his Boone County collections from the Seth and from the stratigraphically higher Winifrede Shale Member to *Productus semireticulatus* (Martin, 1809). Both Price's Seth and Winifrede specimens are definitely Girty's species.

The second area where *Antiquatonia coloradoensis* is found is in eastern Kentucky (loc. 9 of fig. 7) in three stratigraphic units in the Breathitt Formation. The lowest occurrence is in the upper Morrowan Elkins Fork Shale Member in Floyd County. This species also was reported by Rice and others (1994, table 2) from the Kendrick Shale Member from strata that Rice (1980) identified as "open-bay" facies in Floyd and Pike Counties. On the basis of the distinctive goniatite faunas described by Furnish and Knapp (1966), the Kendrick beds correlate with the Trace Creek Shale Member, now considered the basal member of the Atoka Formation in northwestern Arkansas (see Rice and others, 1994, p. 91–93, for detailed discussion). All of the units just described also bear *L. nodosus* and other components of the *L. nodosus* Zone. The stratigraphically higher Magoffin Member contains a medium to large semireticulate

productid and a species of *Linoproductus* that is not Newberry's (1861) *L. nodosus.* Douglass (1987) placed the Magoffin Member of the Breathitt Formation in eastern Kentucky in the lower part of the Atokan Series, but this member is higher stratigraphically than the lowest strata correlated with the Atokan of northwestern Arkansas (see discussion of the Trace Creek Shale Member above). Morse (1931, p. 311–312, pl. 49, fig. 5, probably not figs. 6–8) identified the semireticulate productid as *Productus semireticulatus* (Martin, 1809) and probably also lumped specimens into Martin's taxon that I would identify as *Sandia* sp. Specimens of *Sandia* were identified as *Productus* [*Dictyoclostus*] *semireticulatus* by Chesnut (1981). As I mentioned above, in the section "Inclusion of *Antiquatonia portlockiana* var. *quadratia* in *A. coloradoensis*," Chesnut (1981, p. 25, pl. 9, figs. 4–6) referred specimens from the Magoffin to *Antiquatonia* cf. *A. portlockiana quadratia* Sturgeon and Hoare (1968). I would place this Atokan material from the Magoffin in *A. coloradoenis.* Probably, some of the middle and upper Atokan specimens from southeastern Ohio assigned to *A. portlockiana* var. *quadratia* by Sturgeon and Hoare (1968) are *A. coloradoensis* as well (see discussion in the section just cited).

The third area of occurrences of *Antiquatonia coloradoensis* is in the Warrior Coal Field of the southern Appalachians (loc. 18 of fig. 7); I have identified material from several cores from upper Morrowan strata of the Pottsville Formation from some of the collections made by Culbertson (1964). These cores also contain *Linoproductus nodosus*. *Antiquatonia coloradoensis* was identified by Butts (1926, p. 213) as *Productus semireticulatus* (Martin, 1809) from the Pottsville of the Warrior Coal Field. The specimen that he (Butts, 1926, pl. 67, fig. 12) figured as Martin's species, however, is from younger Pennsylvanian rocks of Illinois and is *not* assignable to Girty's species.

SUMMARY OF OCCURRENCES AND RANGES

It appears highly likely that *Antiquatonia coloradoensis* is restricted to the upper Morrowan and Atokan (lower Middle and middle Middle Pennsylvanian) strata in the Midcontinent, the southern Rocky Mountains, the Eastern Great Basin, and the Appalachian Basin. Its range in the Appalachian Basin is restricted to the marine bands of late Morrowan and Atokan age. Its highest known occurrence in the Appalachians is in the Magoffin Member of the Breathitt Formation and the Winifrede Shale Member of the Kanawha Formation in southern and central West Virginia. *Antiquatonia coloradoensis* does not appear to range upward into the Desmonesian Series and equivalent strata, although smaller, more finely costellate variants (morphotypes) form minor percentages in large collections of *A. hermosana*. Collections in which both *A. coloradoensis* and *A. hermosana* have been identified from other Atokan strata (for example, collections described by Brill, 1942, p. 1388; 1944, p. 626) and certainly from Desmoinesian rocks need to be re-examined in light of interspecific variation in populations of *Antiquatonia*. The Desmoinesian specimens of *Antiquatonia portlockiana* var. *quadratia* Sturgeon and Hoare from southeastern Ohio need to be carefully re-examined, because I believe that it is not likely that they are *A. coloradoensis*.

The Mississippian collections of *Antiquatonia* are not assignable to *A. coloradoensis*.

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PLATES 1–5

PLATE 1

Primary Type Specimens of *Antiquatonia coloradoensis* (Girty) from
Lower Part of Belden Shale, Park County, Colo. (USGS Colln. GR2281–PC)

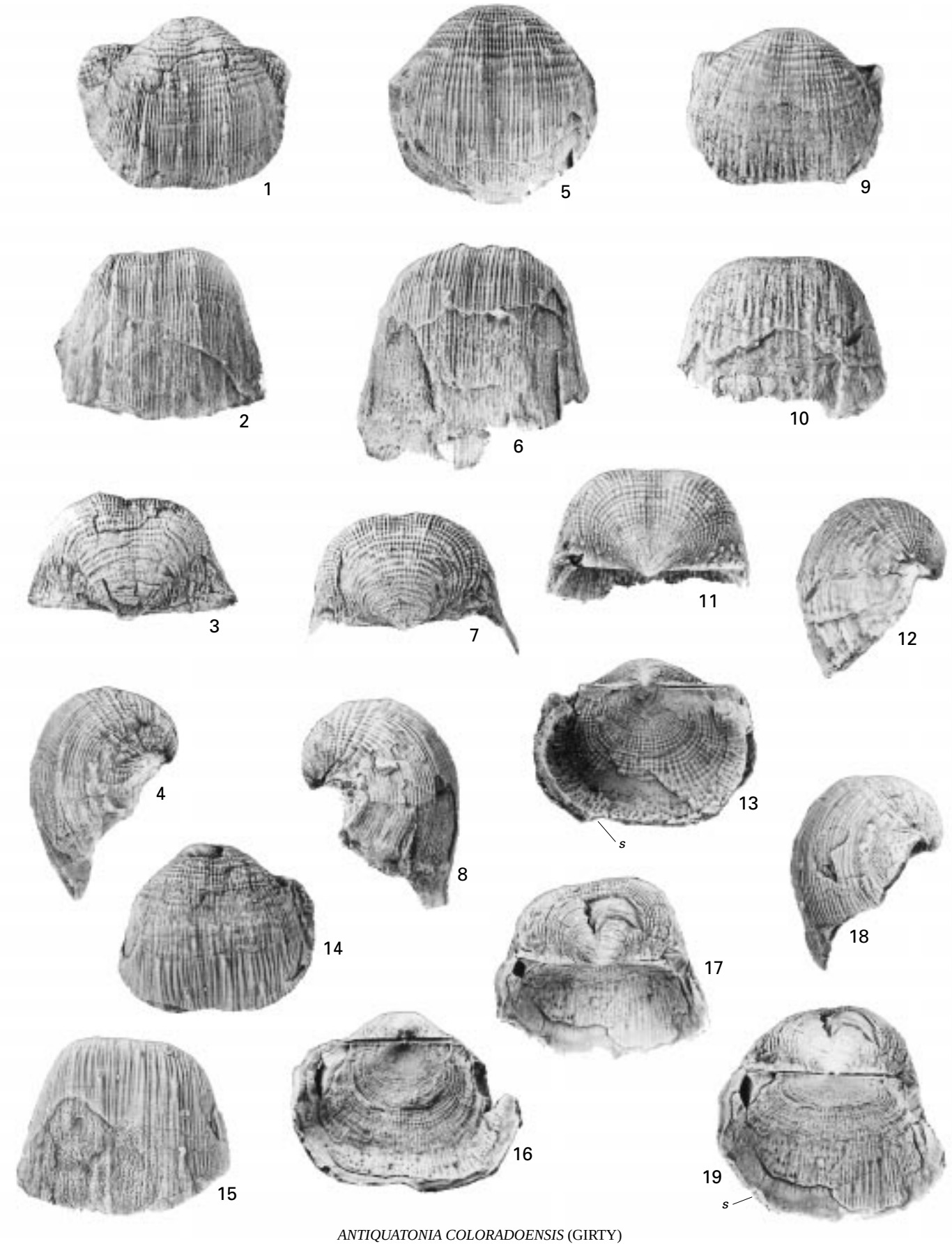
[All figures natural size]

Figures 1–4. Lectotype, USNM 35345; ventral, anterior, posterior, and lateral views of typical mature specimen; ears slightly broken; anterior portion of trail decorticated. Specimen was shown in Girty's (1903) plate 3, figures 1–1b, as *Productus inflatus* McChesney.

5–8. Paralectotype, USNM 121482; ventral, anterior, posterior, and lateral views of large specimen; ears broken, trail slightly broken; anterior view showing trail of brachial-valve interior; note trail partially broken, slightly flaring. Specimen was shown in Girty's (1903) plate 3, figures 2, 2a, as *Productus inflatus* McChesney.

9–13. Paralectotype, USNM 121483; ventral, anterior, posterior, lateral, and dorsal views of coarsely costellate specimen; trail broken, anterior portion of pedicle valve broken away, revealing part of trail of brachial-valve interior; note row of halteroid spines on arcuate ridge and row of smaller hinge spines on posterior view (fig. 11); flange on pedicle-valve interior (marked by "*s*") on dorsal view (fig. 13), continuing posteriorly and separating auricular chamber (ears broken away) from visceral chamber in dorsal view in area where brachial valve is missing. Specimen was shown in Girty's (1903) plate 3, figure 3, as *Productus inflatus* McChesney.

14–19. Paralectotype, USNM 208827; ventral, anterior, dorsal, posterior, lateral, and canted posterior views of typical specimen; note repaired injury to pedicle-valve beak area, shown particularly on posterior view (fig. 17); anterior part of trail decorticated; note weak flange (marked by "*s*") at edge of valve on canted posterior view (fig. 19) where brachial valve is broken away.



ANTIQUATONIA COLORADOENSIS (GIRTY)

PLATE 2

Primary Type Specimens of *Antiquatonia coloradoensis* (Girty) from Lower Part of Belden Shale, Park County, Colo. (USGS Colln. GR2281–PC), and Hypotype of *A. coloradoensis* from Burgner Formation, Jasper County, Mo. (USGS Colln. BL25128–PC)

[Figures natural size, unless otherwise indicated on plate]

Figures 1–4. Paralectotype, USNM 208829; ventral, anterior, posterior, and dorsal views of broken specimen; note hinge spines and row of large spines on arcuate ridge on posterior view (fig. 3).

5–14. Paralectotype, USNM 208828; nearly complete specimen with separable valves. Note lack of sulcus on pedicle valve (figs. 5, 6).

5–7. Ventral, anterior, and posterior views of large specimen with pedicle-valve trail partly broken off, revealing portion of interior of brachial-valve trail; note weak groove ("*g*") on figure 6, into which flange ("*s*") of figures 8, 9, and 10 fits when valve is closed.

8, 9. Views (×1 and ×2, respectively) of anterior portion of pedicle-valve interior showing flange ("*s*"), taken from portion of valve that was broken away just above arrow marked by "*g*" on figure 6.

10. Dorsal view of shell, showing flange ("*s*") around pedicle-valve interior where brachial valve is broken away; ear missing on specimen where ridge separates auricular area from visceral chamber.

11–13. Anterior, lateral, and ventral views of decorticated brachial-valve interior with pedicle valve removed; note groove ("*g*") in figure 11.

14. Lateral view of complete shell; pedicle-valve trail slightly broken.

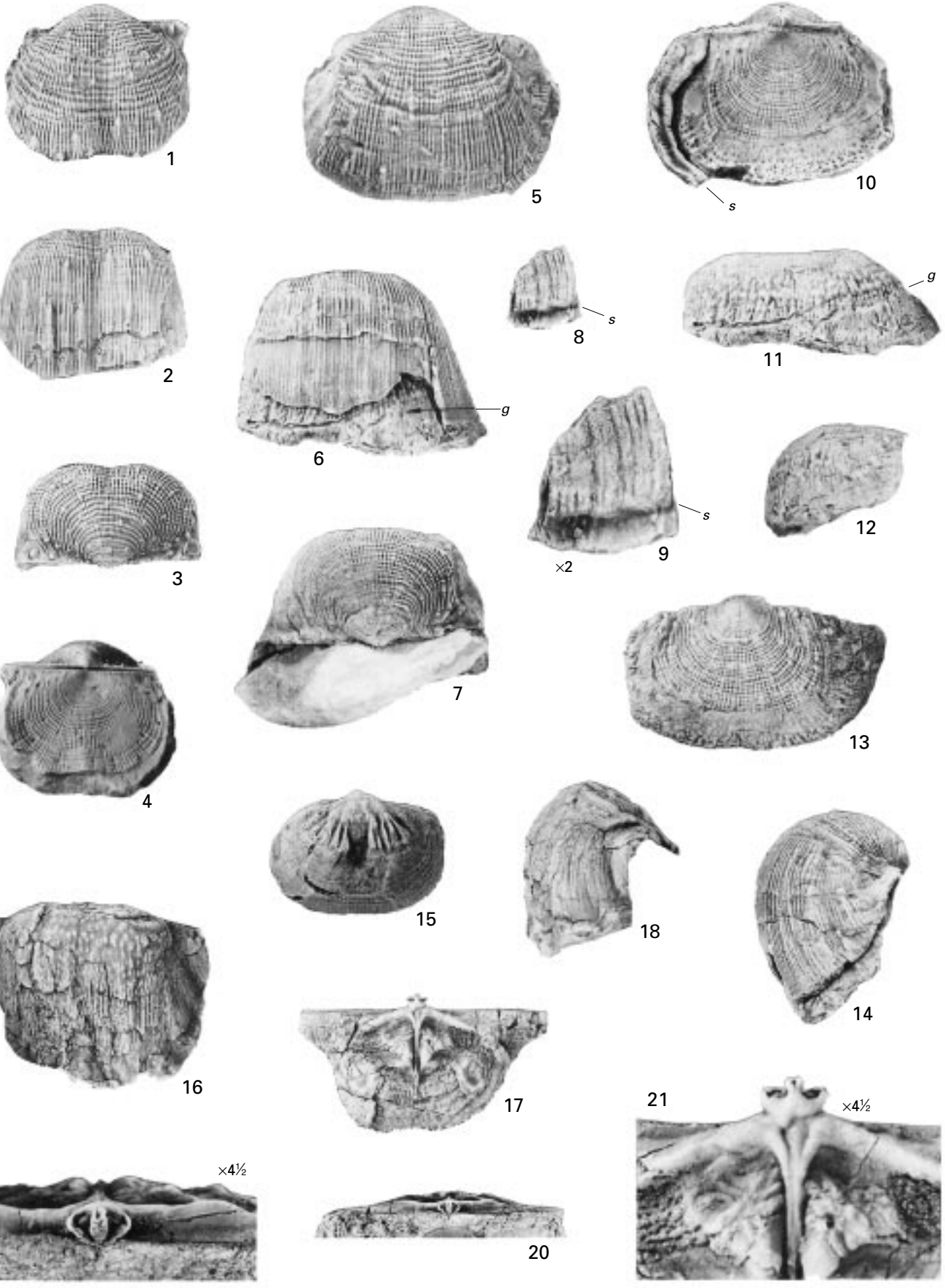
15. Paralectotype, USNM 208830; ventral view of internal mold of pedicle-valve interior.

16–21. Hypotype, USNM 208805; complete brachial-valve interior; note long trail, ridge attached to cardinal buttresses and separating auricular chambers from visceral area; ears slightly more extended than typical.

16–18. Anterior, ventral, and lateral views; compare lateral view of brachial-valve interior with lateral view of specimen shown in plate 2, figure 14, to get sense of size of body cavity.

19, 20. Posterior view (×4.5 and ×1, respectively) of cardinal area, showing cardinal process.

21. Ventral view (×4.5) of cardinal area, showing cardinal process, buttress plates, and median septum.



ANTIQUATONIA COLORADOENSIS (GIRTY)

PLATE 3

Primary Type Specimens of *Antiquatonia coloradoensis* (Girty) and
Primary Type Specimens of *A. portlockiana* var. *quadratia* Sturgeon and Hoare,
Herein Referred to *A. coloradoensis*

[All figures natural size]

Figures 1–15. Paralectotypes of *Antiquatonia coloradoensis* (Girty) from USGS colln. GR2281–PC, lower part of Belden Shale, Park County, Colo.

1–4. USNM 8258b; ventral, anterior, posterior, and lateral views of mature specimen having trail partly broken and ears missing.

5–7. USNM 11660a; canted ventral, anterior, and lateral views of internal mold of mature specimen; beak area crushed; note flaring margin of trail and very subdued flange, marked by "*x*."

8–11. USNM 8258a; ventral, anterior, lateral, and posterior views of large, broad specimen; note ears missing and anterior part of pedicle valve broken off showing part of interior of brachial valve and trail; note groove ("*g*") on brachial-valve interior into which flange (not preserved) of pedicle-valve interior fit; in lateral view (fig. 10), note row of spines sitting on external ridge ("*r*") of pedicle valve and aligning with groove ("*g*") in brachial-valve interior.

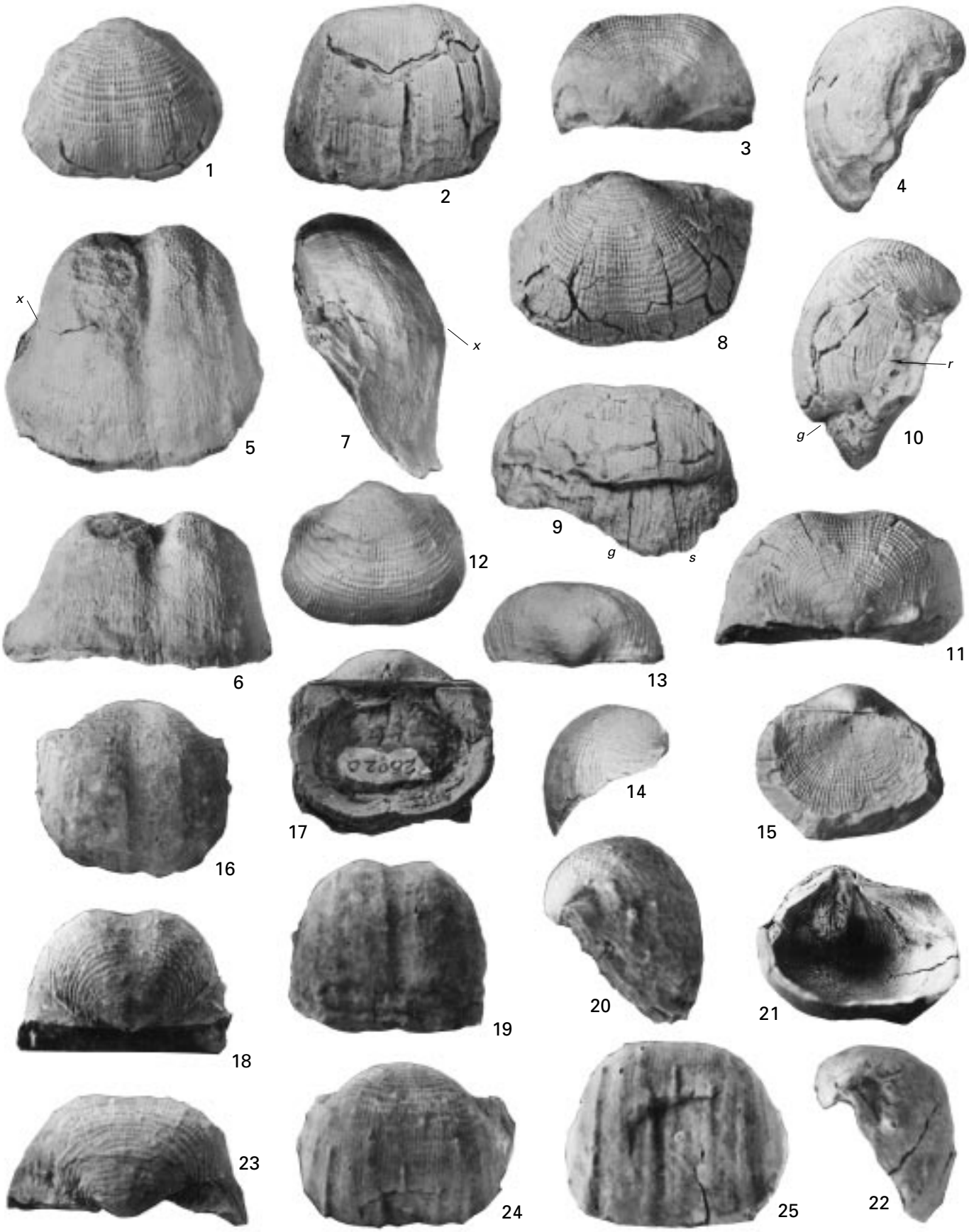
12–15. USNM 8258c; ventral, posterior, lateral, and dorsal views of small, broken specimen.

16–25. Primary type specimens of *Antiquatonia portlockiana* var. *quadratia* Sturgeon and Hoare, from "Lower Mercer limestone and shale," Pottsville Formation, Hocking County, Ohio.

16–20. Holotype, OSU 26020, loc. Hfg–5; ventral, dorsal, posterior, anterior, and lateral views of specimen with crushed brachial valve; note subdued ridges anterior to body spines, relatively short trail characterized by repeated breakage and thickening of both valves anteriorly, and pronounced, spine-bearing preauricular ridges on exterior of pedicle valve.

21, 22. Paratype, OSU 26023, loc. Hfg–5; slightly canted dorsal and lateral views of broken, disarticulated pedicle valve; note strong ridge separating ear from visceral chamber on interior, subdued ridge bearing row of body spines on exterior of valve; valve may be from same specimen as OSU 26025 (see pl. 4, fig. 9).

23–25. Paratype, OSU 26026, loc. Hs–3; posterior, ventral, and anterior views of slightly crushed articulated specimen with broken trail; note that exterior of pedicle valve has ridges extending anteriorly from bases of body spines.



ANTIQUATONIA COLORADOENSIS (GIRTY)

PLATE 4

Primary Type Specimens of *Antiquatonia portlockiana* var. *quadratia* Sturgeon and Hoare, Herein Referred to *A. coloradoensis* (Girty) [above line], and Representative Species of Brachiopods from Type Locality of *Antiquatonia coloradoensis* (Girty) [below line]

[Figures natural size, unless otherwise indicated on plate]

Figures 1–12. *Antiquatonia portlockiana* var. *quadratia* Sturgeon and Hoare, loc. Hfg–5, from "Lower Mercer limestone and shale," Pottsville Formation, Hocking County, Ohio.

1–5. Paratype, OSU 26024; complete, disarticulated brachial valve showing well-preserved interior; enlarged dorsal and posterior views (×3.5) of cardinal process; posterior, ventral, and lateral views (×1) of interior; note atypical, club-shaped boss at anterior end of median septum, pronounced ridges separating visceral chamber from auricular chamber.

6–8. Paratype, OSU 26022; anterior, ventral, and dorsal views (×1) of broken, disarticulated brachial valve; note flange around anterior of visceral area, thickening of anterior margin of shell at geniculation.

9. Paratype, OSU 26025; dorsal view (×1) of well-preserved brachial valve showing interior, ears slightly broken; note subdued flange around anterior margin; this valve may be from same specimen as OSU 26023 (see pl. 3, figs. 21, 22).

10–12. Paratype, OSU 47102; ventral, lateral, and posterior views of large, broken, disarticulated brachial valve; note row of hinge spines and row of large body spines on preauricular ridge.

13–17. *Linoproductus nodosus* (Newberry), from lower part of Belden Shale, Park County, Colo. Note single row of large body spines down venter of pedicle valves.

13, 14. Referred specimen, USNM 476640, USGS colln. BL12096–PC; lateral and ventral views of cracked, incomplete, mature pedicle valve.

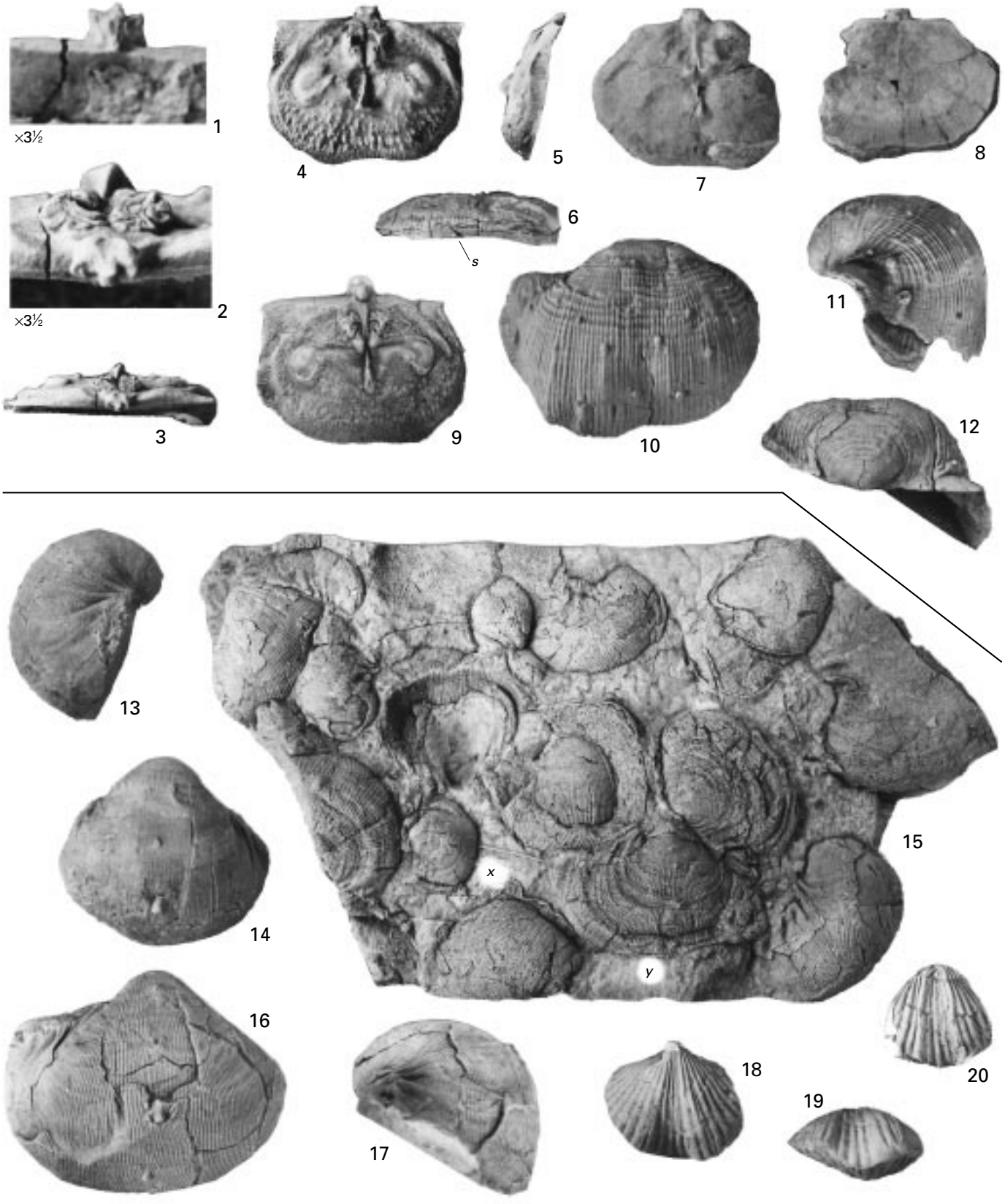
15. Referred specimens, USNM 476641, USGS colln. BL31394–PC; slab showing cluster of generally decorticated specimens mostly in growth position (pedicle valve down), viewed from bottom side of bed; note large body spine on venter on specimen marked by "*x*"; on specimen above "*y*," pedicle valve and most of brachial-valve muscle area have been worn away, revealing row of "bumps" corresponding to dimples on exterior of valve and spine row on opposite valve.

16, 17. Referred specimen USNM 476642, USGS colln. GR2281–PC; ventral and lateral views of broad, cracked, incomplete, mature pedicle valve.

18–20. *Anthracospirifer tanoensis* Sutherland and Harlow, from lower part of Belden Shale, Park County, Colo. Note three costae in sulcus of pedicle valve.

18, 19. Referred specimen USNM 476643, USGS colln. BL6852–PC; ventral and anterior views of uncrushed, articulated specimen with right ear missing.

20. Referred specimen USNM 476644, USGS colln. BL12096–PC; ventral view of crushed and broken articulated specimen; ears missing.



ANTIQUATONIA, LINOPRODUCTUS, AND *ANTHRACOSPIRIFER*

PLATE 5

Characteristic Elements of Brachiopod Fauna from Type Locality of *Antiquatonia coloradoensis* (Girty) from Lower Part of Belden Shale, Park County, Colo.

[All specimens are referred specimens. Figures natural size, unless otherwise indicated on plate]

Figures 1, 2. *Spirifer goreii* Mather.
- 1. USNM 476645, USGS colln. BL12096–PC; ventral view of crushed, complete young adult; note absence of fasciculation of costellae.
- 2. USNM 476646, USGS colln. BL31394–PC; ventral view of broken, slightly decorticated, disarticulated pedicle valve of a large specimen.

3–8. *Neochonetes* cf. *N. whitei* Sutherland and Harlow.
- 3–5. USNM 476647, USGS colln. BL31394–PC; ventral view ×1 and enlarged (×3) ventral and anterior views of articulated, slightly decorticated specimen; note extremely weak mesial fold in sulcus; gastropod(?) boring in pedicle valve.
- 6–8. USNM 476648, USGS colln. BL12096–PC; ventral view ×1 and enlarged (×3) ventral and anterior views of complete, slightly decorticated, articulated specimen; note absence of mesial fold in sulcus.

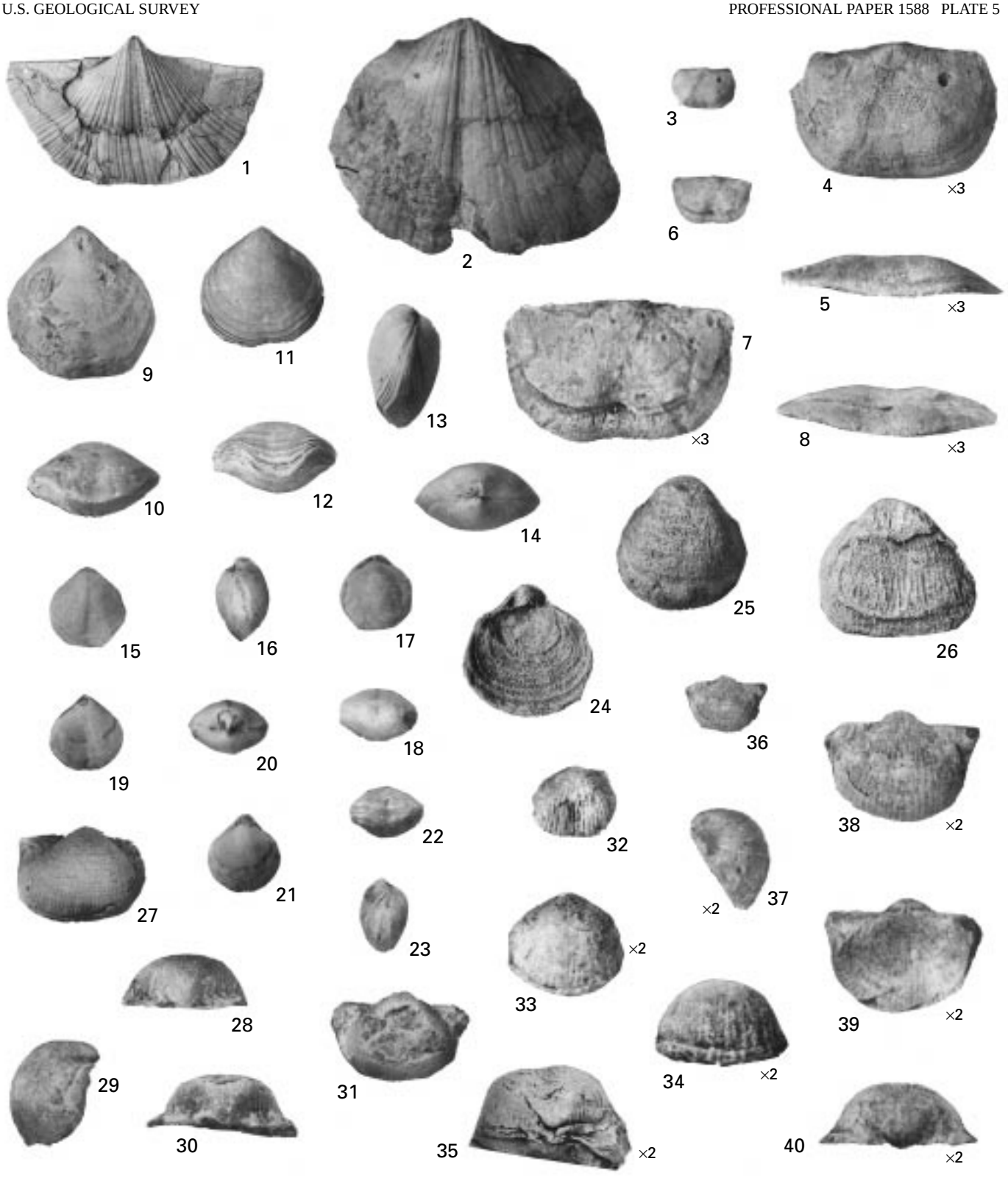
9–14. *Composita ovata* Mather.
- 9, 10. USNM 476649, USGS colln. BL12096-PC; ventral and anterior views of large, complete, articulated specimen.
- 11–14. USNM 476650, USGS colln. BL6852–PC; ventral, anterior, lateral, and posterior views of well-preserved articulated specimen with slightly broken beak.

15–23. *Composita gibbosa* Mather.
- 15–18. USNM 476651, USGS colln. BL6852–PC; ventral, lateral, dorsal, and anterior views of mature specimen.
- 19–23. USNM 476652, USGS colln. BL12096–PC; ventral, posterior, dorsal, anterior, and lateral views of mature specimen; beak slightly broken.

24–26. *Pulchratia*? *pustulosa* Sutherland and Harlow.
- 24, 25. USNM 476653, USGS colln. BL12096–PC; dorsal and ventral views of complete specimen, beak area slightly crushed.
- 26. USNM 476654, USGS colln. BL6852A–PC; dorsal view of complete, crushed specimen.

27–31. *Sandia welleri* (Mather).
- 27–29. USNM 476655, USGS colln. BL12096–PC; ventral, posterior, and lateral views of mature specimen; trail broken off.
- 30, 31. USNM 476656, USGS colln. BL12096–PC; posterior and ventral views of decorticated specimen; trail broken.

32–40. *Desmoinesia nambeensis* Sutherland and Harlow.
- 32. USNM 476657, USGS colln. BL6852–PC; dorsal view of incomplete specimen; ornamentation slightly coarser than typical.
- 33, 34. USNM 476658, USGS colln. BL6852–PC; enlarged (×2) dorsal and anterior views of internal mold of brachial valve; note prominent margin around edge of visceral disc.
- 35. USNM 476659, USGS colln. BL6852–PC; enlarged (×2) posterior view of internal mold of brachial valve.
- 36–40. USNM 476660, USGS colln. BL31394–PC; ventral view (×1) and enlarged (×2) lateral, ventral, dorsal, and posterior views of slightly broken, decorticated, articulated specimen.



SPERIFER, NEOCHONETES, COMPOSITA, PULCHRATIA?, *SANDIA,* AND *DESMOINESIA*

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