

Early Triassic Terebratulid Brachiopods from the Western Interior of the United States

GEOLOGICAL SURVEY PROFESSIONAL PAPER 1057



Early Triassic Terebratulid Brachiopods from the Western Interior of the United States

By PETER R. HOOVER

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*Description and illustration of five species of
terebratulid brachiopods, and discussion of their
distribution and developmental and evolutionary history*



UNITED STATES DEPARTMENT OF THE INTERIOR

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GEOLOGICAL SURVEY

H. William Menard, *Director*

Library of Congress Cataloging in Publication Data

Hoover, Peter R.

Early Triassic Terebratulid Brachiopods from the Western Interior of the United States
(Geological Survey Professional Paper 1057)

Bibliography: p. 19

Includes index

Supt. of Docs. No.: I 19:16:1057

1. Terebratulida, Fossil. 2. Paleontology--Triassic. 3. Paleontology--The West.

I. Title. II. Series: United States Geological Survey Professional Paper 1057

QE797.T29H66

564'.8

77-608314

For sale by the Superintendent of Documents, U.S. Government Printing Office

Washington, D.C. 20402

Stock Number 024-001-03182-5

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EARLY TRIASSIC TEREBRATULID BRACHIOPODS FROM THE WESTERN INTERIOR OF THE UNITED STATES

By PETER R. HOOVER¹

ABSTRACT

This study of five species of terebratulid brachiopods from Lower Triassic marine rocks of the western interior of the United States is based entirely on existing museum collections. New genera and species described in this paper are: *Portneufia episulcata*, n. gen. and n. sp. (Dielasmatidae); *Rhaetina incurvirostra*, n. sp. (Dielasmatidae); *Vex*, n. gen. (type species: *Terebratula semisimplex* White) (Terebratulidae); *Obnixia*, n. gen. (type species: *Terebratula thaynesiana* Girty) (Cryptonellidae); and *Periallus woodsidensis*, n. gen. and n. sp. (Zeilleriidae). The developmental history of the cryptacanthiine *Obnixia thaynesiana* is discussed in detail on the basis of studies of exceptionally well preserved silicified material. The terebratulids here described are endemic elements of the poorly known Early Triassic shelly fauna. Although they clarify evolutionary changes across the eral boundary, their closest associations are with Mesozoic, rather than Paleozoic faunas. Although knowledge of the associated fauna is meager, the brachiopods themselves can be used as the basis of a crude biostratigraphic zonation suitable for correlation.

Автореферат

Описано и обсуждено пять видов теребратулидных брахиопод из морских нижнетриасовых отложений западных районов внутренней части Соединенных Штатов. К этим таксонам относятся *Portneufia episulcata*, новый род и вид (Dielasmatidae), *Rhaetina incurvirostra*, новый вид (Dielasmatidae), *Vex*, новый род (типовой вид: *Terebratula semisimplex* White) (Terebratulidae), *Obnixia*, новый род (типовой вид: *Terebratula thaynesiana* Girty) (Cryptonellidae), *Periallus woodsidensis*, новый род и вид (Zeilleriidae). На основании изучения исключительно хорошо сохранившегося кремневого материала детально обсуждается история развития криптакантин *Obnixia thaynesiana*. Описанные теребратулиды представляют собой эндемичные элементы плохо известной нижнетриасовой раковинной фауны. Хотя они разъясняют эволюционные изменения на границе эр, они более близки к мезозойским, чем к палеозойским формам. Изучение основано только на коллекциях, имеющихся в музеях. Хотя знания о сопутствующих фаунах недостаточны, сами брахиоподы могут быть применены для обоснования грубого биостратиграфического расчленения, годного для корреляции.

INTRODUCTION

This study was designed to enhance the meager biostratigraphic data base for the Triassic of the Western United States. Marine strata are uncommon in the Lower Triassic of the western interior of the United States, and well-preserved fossils are rare. This situation has led to a basically lithostratigraphic approach in most previous geologic reconnaissance studies. Ammonites were recognized early as potential biostratigraphic indices (White, 1880), and the distributions of other relatively common mollusks, particularly the pelecypods, were later brought to bear on the problem. Even the ammonites, biostratigraphically the most useful Early Triassic faunal elements, are quite provincial (Dagys, 1974), and correlations across the great distances separating their rare occurrences commonly have been quite subjective (Silberling and Tozer, 1968). During the last 20 years, our knowledge of the stratigraphic range of the conodonts has been extended across the Permian-Triassic boundary, and conodonts now show great potential for Triassic biostratigraphic zonation. The contribution of this report to the knowledge of Early Triassic terebratulid brachiopods not only adds to our understanding of the organisms themselves, but also increases their usefulness in the Lower Triassic.

PREVIOUS WORK

Early Triassic terebratulid brachiopods, rare in the western interior of the United States, usually occur monospecifically in bands or zones. Thus, published descriptions rarely cover a diverse terebratulid assemblage. The first descriptions (White, 1880), from a section in southeastern Idaho (fig. 1, loc. 44), included no illustrations, but were repeated later with figures (White, 1883). Of the two forms discussed, only *Terebratula semisimplex* was illustrated. The other, cited as *Terebratula augusta* Hall and Whitfield, was neither described nor illustrated, and White was dubious about his identification. His specimens of *T. augusta* (USNM 8191) are preserved at the USNM (U.S. National Museum of Natural History, of the Smithsonian Institution) in Washington, D.C. Although they are too fragmentary and poorly preserved to identify with any terebratulids de-

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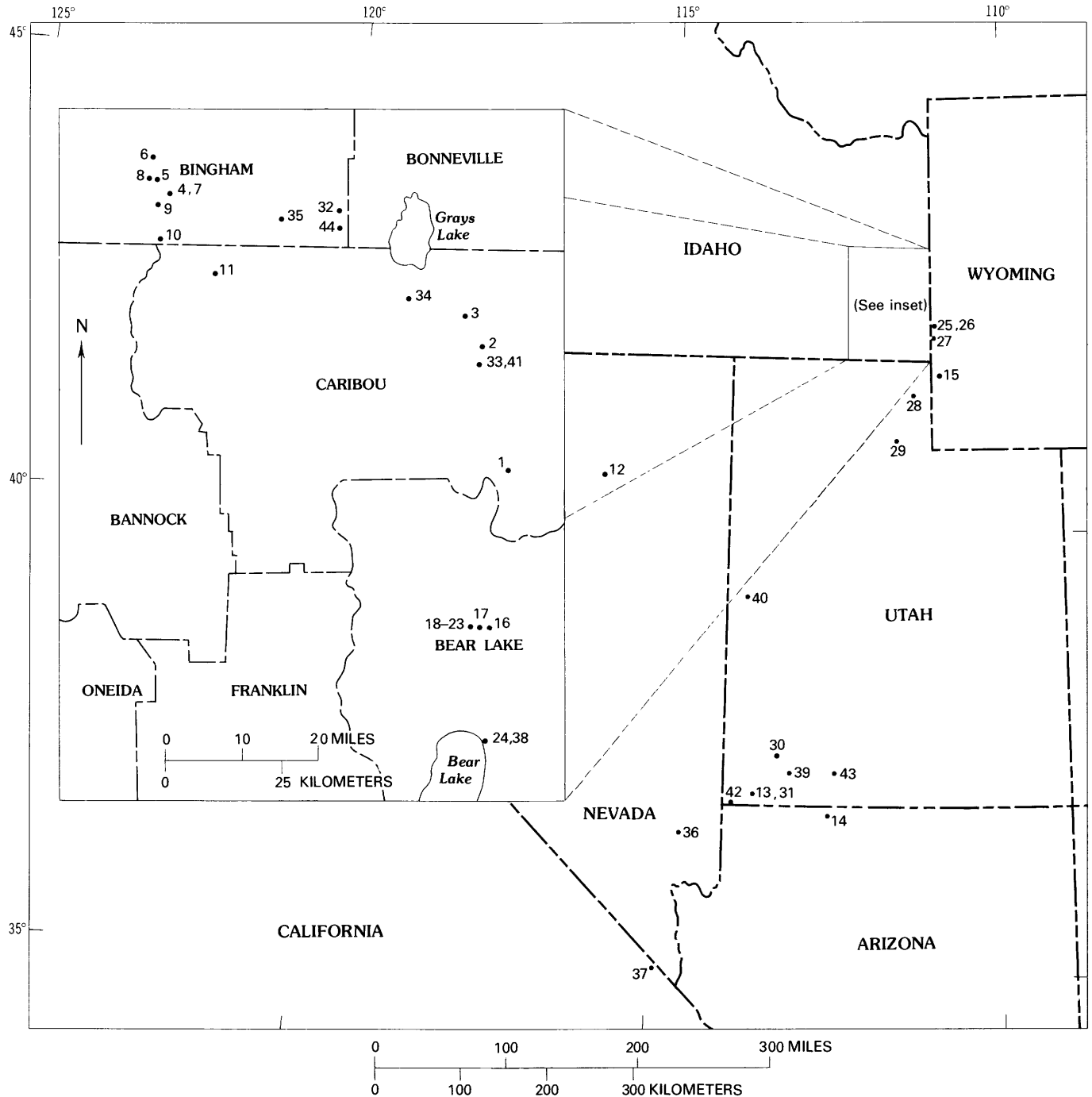


FIGURE 1. — Index map showing locations of collections cited in this report.

scribed here, they may easily be distinguished from types of *T. augusta* Hall and Whitfield (USNM 12548a,b) by their weaker beak ridges, larger size, and lack of a prominent median septum. Nearly 50 years elapsed before publication of the next report describing Early Triassic terebratulids. Girty (1927) described a rhynchonellacean, two spiriferinaceans, and *Terebratula thaynesiana*. Types of *T. thaynesiana* also come from southeastern Idaho (fig. 1,

loc. 21). Newell and Kummell (1942) included brief descriptions and illustrations of a form, referred to *Terebratula margaritowi* Bittner, from the Dinwoody Formation at several localities in southeastern Idaho and southwestern Montana. Closely spaced serial sections of forms used by Newell in making this identification suggest they are identical with *Periallus woodsidensis*, n. gen., n. sp., and are not dielasmatids as heretofore supposed (Dagys, 1965, p. 137).

PRESENT STUDY

Collections of Triassic marine fossils housed at several institutions were examined, and all identifiable North American Early Triassic brachiopods were brought to the USNM for more intensive examination. Previous paleontological investigators did not examine the comparatively conservative terebratulids in detail, and internal characters now thought to be of primary taxonomic importance were rarely documented.

Most Early Triassic terebratulids are small (less than 10 millimeters (mm) in maximum dimension) and are preserved as calcium carbonate. The only feasible accurate method of studying the internal details of such forms, other than laborious preparation with a needle, is to make three-dimensional reconstructions based on closely spaced serial sections. The making of such sections is extremely time consuming and, unless considerable care is exercised in the maintenance of parallel sections, the results may be misleading. (See Westbroek, 1969, and Singeisen-Schneider, 1976.) Though this technique permits the use of calcareous specimens to document ontogenetic development and population variability of internal structures (for examples, see Baker, 1972), it is not practical on a large scale when other methods can be used.

Many of the collections surveyed in this study include silicified specimens, which commonly may be removed from the calcitic matrix by etching with dilute acids. In the process, structures of extreme delicacy may be revealed, as shown in the specimens of *Obnixia thaynesiana* (Girty) from locality 37 (pl. 3, figs. 1-13).

Through the combined use of several preparation techniques, topotypic material of previously described North American Early Triassic terebratulids has been studied in detail. Both ontogenetic development and population variation have been documented for *Obnixia thaynesiana* (Girty). The study shows that, rather than two very generalized terebratulids in the North American Lower Triassic, there are at least five endemic species that have taxonomically and functionally distinctive internal skeletal elements. These fossils are not only diagnostic of the strata in which they occur, but they also illustrate, in a single organic group, the nature of evolutionary links across an era boundary of prime importance.

ACKNOWLEDGMENTS

The studies leading to this report were made during tenure of a National Research Council Postdoctoral Fellowship, held at the U.S.G.S. (U.S. Geological Survey) in Washington, D.C. The writer and this report have materially benefitted from discussions with and critical review by J. M. Berdan, G. A. Cooper, J. T. Dutro, Jr., R. E. Grant, N. J. Silberling, F. G. Stehli, and B. R. Wardlaw. Illustrations were in part drafted by Elinor Stromberg, of the U.S.G.S. Photographic services were provided by R. H. McKinney, H. E. Mochizuki, and Kenji Sakamoto of the U.S.G.S. and by G. A. Cooper of the Smithsonian Institution, Washing-

ton, D.C. Russian translation of the author's abstract was kindly provided by Dr. M. A. Semikhatov, of the Geological Institute of the Academy of Sciences, Moscow, U.S.S.R.

FOSSIL LOCALITIES CITED IN THIS REPORT

The material studied for this report comes from several different sources. Most specimens were collected by U.S.G.S. geologists during investigations of the phosphate reserves of the western interior of the United States, around the turn of the century. (See fig. 1 and the list of fossil localities below.) Because those phosphate deposits are of late Paleozoic age, many of the fossil collections bear that designation, despite their derivation from rocks now known to be of Triassic age.

Locality numbers having the suffix "PC" are from the U.S. Geological Survey's upper Paleozoic catalog, kept in Washington, D.C. Those having the suffix "(Green)" belong to G. H. Girty's old upper Paleozoic catalog at the U.S.G.S. in Washington, D.C. Numbers without prefix or suffix are from the Survey's Mesozoic catalog, also in Washington, D.C. Those having the prefix "M" come from a similar Mesozoic catalog at U.S.G.S. offices in Menlo Park, Calif. Those having the prefix "USNM" are held by the U.S. National Museum of Natural History, which also houses the Washington, D.C., collections of the U.S.G.S. All type, figured, and measured specimens from this report have been assigned USNM catalog numbers and are in the USNM Paleobiology Collections in Washington, D.C.

Locality information on specimen labels has been supplemented by information on original register file cards, field labels, maps and notebooks, and more recent geologic and topographic maps. Such additions appear in brackets.

Map index number (see fig. 1)	Original locality number	Description of locality, stratigraphic assignment, collector, and year of collection
1	76 PC	Idaho, Caribou County, Snowdrift 1:24,000 quad., SE corner of NE $\frac{1}{4}$ SE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 27, T. 9 S., R. 45 E. [Peak at alt. 8,640-8,660 ft.] Woodside Formation. [G. R.] Mansfield and [G. H.] Girty, Aug. 31, 1911
2	823-PC	Idaho [Caribou County, Lane's Creek 15-min quad.]; sec. 1, T. 7 S., R. 44 E. [Probably] Thaynes Formation. [G. R.] Mansfield, 1912.
3	826-PC	Idaho [Caribou County, Lane's Creek 15-min quad.]; section unknown T. 6 S., R. 44 E. [Probably] Thaynes Formation. [R. W.] Richards, 1912.
4	1271-PC	Idaho [Bingham County, Yandell Springs 15-min quad.]; NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 31, T. 3 S., R. 38 E.]. Portneuf Limestone [Member] of Thaynes Formation [G. R.] Mansfield and [G. H.] Girty, Aug. 27, 1913.
5	1274-PC	Idaho [Bingham County, Higham Peak 7 $\frac{1}{2}$ -min quad., SW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 25, T. 3 S., R. 37 E.]. Portneuf Limestone [Member of Thaynes Formation]. [G. R.] Mansfield and [G. H.] Girty, Aug. 28, 1913.
6	1284 PC	Idaho [Bingham County, Higham Peak 7 $\frac{1}{2}$ -min quad.]; low spur, east scarp [SW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 2, T. 3 S., R. 37 E.]. Portneuf Limestone [Member of Thaynes Formation]. [G. R.] Mansfield and [G. H.] Girty, Sept. 5, 1913.
7	1289 PC	Idaho [Bingham County, Yandell Springs 15-min quad., NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 31, T. 3 S., R. 38 E.]. Portneuf Limestone [Member of Thaynes Formation]. [?] Merritt and [G. H.] Girty, Sept. 1913.
8	1291 PC	Idaho, Bingham County, Higham Peak 7 $\frac{1}{2}$ -min quad., SE $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 24, T. 3 S., R. 37 E.]. Portneuf Limestone [Member of Thaynes Formation]. [G. R.] Mansfield and [G. H.] Girty, Aug. 29, 1913.
9	1304a-PC	Idaho [Bingham County, Yandell Springs 15-min quad.]; 775 ft southwest of top of hill, [SW $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 1, T. 4 S., R. 37 E.]. Probably Thaynes Formation. [G. R.] Mansfield and [G. H.] Girty, Sept. 6, 1913.

Map index number (see fig. 1)	Original locality number	Description of locality, stratigraphic assignment, collector, and year of collection	Map index number (see fig. 1)	Original locality number	Description of locality, stratigraphic assignment, collector, and year of collection
10	1315-PC	Idaho, Bingham County, Yandell Springs 15-min quad.; SE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 36, T. 4 S., R. 37 E. [Probably Thaynes Formation.] [G. R.] Mansfield and [G. H.] Girty, Aug. 25, 1918.	36	7885 (Green)	Nevada [Clark County, probably in the Moapa 15-min quad.]; "Valley of Fire," Muddy Mtns., $\frac{1}{4}$ mi east of White Basin fault, $\frac{1}{4}$ mi south of Old Arrowhead Road. Moenkopi Formation in fault block. C. R. Longwell, July 8, 1924.
11	1336-PC	Idaho [Caribou County, Jeff Cabin Creek 7 $\frac{1}{2}$ -min quad.]; sec. 24, T. 5 S., R. 37 E. "Ross Fork [Limestone Member]" of Thaynes Formation. G. R. Mansfield, July 26, 1913.	37	7897 (Green)	[California, San Bernardino County, Ivanpah and Mescal Range 15-min quads., near center, sec. 32, T. 15 $\frac{1}{2}$ N., R. 14 E.]; 1 mi northwest of Kokoweef Peak. [Probably Moenkopi Formation.] D. F. Hewett, Oct. 28, 1926.
12	18017-PC	Nevada, Elko County, Carlin [15-min] quad.; NE $\frac{1}{4}$ sec. 16, T. 31 N., R. 52 E. [Railroad District]. Permian of J. F. Smith and K. B. Ketner. [J. F.] Smith and [K. B.] Ketner, 1958.	38	5013	Idaho [Bear Lake County, Montpelier 7 $\frac{1}{2}$ -min quad.]; approx. sec. 13, T. 15 S., R. 44 E.; from slide on east side of gulch east of Hot Springs. [Probably Thaynes Formation.] F. B. Weeks, Sept. 27, 1907.
13	614a (Green)	Utah [Washington County, probably La Verkin No. 4 NW 7 $\frac{1}{2}$ -min quad.], canyon east of Toquerville on road to Virgin City. [Probably Moenkopi Formation.] J. E. Whitfield, Oct. 3, 1885.	39	18595	Utah, Washington County, [probably in the Zion National Park 30-min quad.]; Kolob Section S.; Dry Creek Section. Virgin Limestone [Member of Moenkopi Formation]. H. E. Gregory, Sept. 22, 1940.
14	961 (Green)	Arizona [Mohave or Coconino County, Fredonia NE 7 $\frac{1}{2}$ -min quad.], 10 mi south-southwest of Kanab, Utah. [Probably Moenkopi Formation]; thin limestones interbedded in reddish-brown arenaceous shales. C. D. Walcott and party, Sept. 6, 1882.	40	M-108	Utah [Millard County, Cowboy Pass 15-min quad.]; secs. 18 and 19, [T. 16 S., R. 16 W.]; Confusion Range. Measured section, about 870 ft above base of Triassic section [probably Moenkopi Formation]. [C. A.] Repenning and [R. K.] Hose, Oct. 19, 1955.
15	3769 (Green)	Wyoming [Lincoln County, Cokeville 30-min quad.]; center of sec. 32, T. 23 N., R. 118 W. Fork of Rock Creek, 7 $\frac{1}{2}$ mi north of Nugget. Thaynes Formation. A. C. Veatch, July 27, 1905.	41	M-853	Idaho, Caribou County, Upper Valley 7 $\frac{1}{2}$ -min quad.; NE $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 13, T. 7 S., R. 44 E.; on east side of drain between Bacon and Timothy Creeks. Upper [part of] Portneuf Limestone Member of Thaynes Formation, about 100 ft above the top of the Lanes Tongue [of Ankareh Formation] redbeds. R. Rioux and J. Dyni, 1959.
16	7313 (Green)	Idaho [Bear Lake County, Montpelier Canyon 7 $\frac{1}{2}$ -min quad., SW $\frac{1}{4}$ NE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 6, T. 13 S., R. 45 E., Waterloo Mountain. Questionable basal [part of] Woodside Formation, but structurally very complex. C. L. Breger, June 16, 1909.	42	USNM 9342	Utah [Washington County], 9 mi southwest of St. George. Virgin Limestone Member of Moenkopi Formation. A. A. Graffam, [Date unknown.]
17	7376 (Green)	Idaho [Bear Lake County, Montpelier 7 $\frac{1}{2}$ -min quad.]; sec. 1, T. 13 S., R. 44 E.; [measured section in] Montpelier Canyon [just east of town of Montpelier]; Thaynes Formation [about 717 ft above the base and 1,565 ft below the top of the unit there exposed]. [C. L.] Breger, June 9, 1909.	43	USNM 9343	Utah, Kane County, Moenkopi Formation (?). [Probably collected by] Fawcett. [Date unknown.]
18	7390 (Green)	Idaho [Bear Lake County, Montpelier 7 $\frac{1}{2}$ -min quad.]; sec. 2, T. 13 S., R. 44 E.; [measured section in] Montpelier Canyon [just east of town of Montpelier]. Thaynes Formation [about 1,849 ft above the base and 433 ft below the top of the unit there exposed]. [C. L.] Breger and [G. H.] Girty, June 11, 1909.	44	USNM 9344	Idaho, [Bingham County]; about 65 mi north of the Utah line, 18 mi west of the Wyoming line, and 5 mi west of Gray's Lake. [Probably Portneuf Limestone Member of Thaynes Formation.] A. C. Peale, 1877.
19	7395 (Green)	[Same as 7390 (Green)]; about 3 mi east of the town of Montpelier, on the north side of the road. [About 418 ft above the base and 1,864 ft below the top of the unit there exposed]. G. H. Girty, June 11, 1909.			
20	7397 (Green)	[Same as 7390 (Green). Same horizon as 7376 (Green).] C. L. Breger and G. H. Girty, June 11, 1909.			
21	7406 (Green)	[Same as 7390 (Green). About 2072 ft above the base and 210 ft below the top of the unit there exposed; probably equivalent of Portneuf Limestone Member of Thaynes Formation.] C. L. Breger, June 5, 1909.			
22	7409 (Green)	[Same as 7390 (Green).] C. L. Breger, June 7, 1909.			
23	7431 (Green)	[Probably same as 7390 (Green).] Near base of Thaynes Formation. [C. L.] Breger and [G. H.] Girty, June 10, 1909.			
24	7435 (Green)	Idaho [Bear Lake County, Montpelier 7 $\frac{1}{2}$ -min quad.]; approx. sec. 13, T. 15 S., R. 44 E.; Thaynes Formation, [equivalent stratigraphically to 7397 (Green)]. C. L. Breger, Sept. 1909.			
25	7444 (Green)	Wyoming [Lincoln County, Montpelier, Idaho-Wyoming 30-min quad.]; NE $\frac{1}{4}$ SW $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 30, T. 27 N., R. 119 W.; Thaynes Formation. G. H. Girty, July 6, 1909.			
26	7466 (Green)	Wyoming [Lincoln County, Montpelier, Idaho-Wyoming 30-min quad.]; SE $\frac{1}{4}$ SW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 30, T. 27 N., R. 119 W.; west face of Sublette Range, north of Raymond Canyon. Thaynes Formation. G. H. Girty, June 7, 1909.			
27	7470 (Green)	Wyoming [Lincoln County, Montpelier, Idaho-Wyoming 30-min quad.]; NE corner of SE $\frac{1}{4}$ NE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 6, T. 26 N., R. 119 W.; Thaynes Formation. G. H. Girty, July 2, 1909.			
28	7478 (Green)	Utah [Rich County, Woodruff 7 $\frac{1}{2}$ -min quad.]; Woodruff, branch hollow of Twelve Mile Creek south of Road Hollow. Thaynes Formation. C. L. Breger, Aug. 24, 1907.			
29	7717 (Green)	Utah [Morgan County, Devil's Slide 7 $\frac{1}{2}$ -min quad.]; north side of Weber Canyon, 1 mi west of Devil's Slide. [Probably Moenkopi Formation.] G. H. Girty, Sept. 15, 1911.			
30	7758 (Green)	Utah [Iron County, Kanarraville 7 $\frac{1}{2}$ -min quad.]; $\frac{1}{2}$ mi east of Kanatra. [Probably Moenkopi Formation.] [H.] Graff, July 18, 1907.			
31	7787 (Green)	Utah [Washington County, La Verkin No. 4 NW 7 $\frac{1}{2}$ -min quad.], near center, sec. 18, T. 42 S., R. 12 W.; about 6 mi southwest of Virgin City. Lower limestone [part] of Moenkopi Formation, 300 ft above base of unit. [J. B.] Reeside, Oct. 3, 1919.			
32	7813 (Green)	Idaho [Bingham County, Crane's Flat 15-min quad.]; near SE $\frac{1}{4}$ corner [?], sec. 2, T. 4 S., R. 41 E.; about 13 mi north and 5 $\frac{1}{2}$ mi west of Henry, Idaho. Thaynes Formation. [P. V.] Roundy and [G. R.] Mansfield, Aug. 1916.			
33	7825 (Green)	Idaho [Caribou County, Upper Valley 7 $\frac{1}{2}$ -min quad.]; SE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 13, T. 7 S., R. 44 E. [Probably Thaynes Formation.] R. W. Richards, 1912.			
34	7835 (Green)	Idaho [Caribou County, Lane's Creek 15-min quad.]; near SE corner, sec. 5, T. 6 S., R. 43 E.; about 5 mi east and a little north of Henry, on a little knob at base of the 7037 ft peak. Upper [part of the] Thaynes Formation. [G. R.] Mansfield and [P. V.] Roundy, July 10, 1915.			
35	7879 (Green)	Idaho [Bingham County, Crane's Flat 15-min quad.]; SE $\frac{1}{4}$ sec. 9, T. 4 S., R. 40 E. "Ross Fork Limestone [Member]" of Thaynes Formation. G. R. Mansfield, 1923.			

STRATIGRAPHIC SETTING OF THE BRACHIOPODS

An inherent disadvantage in a study of museum collections is that the investigator must rely almost entirely upon the judgement of previous field workers for the geographic, stratigraphic, and temporal annotations of the collections. In an area of rapid lateral facies change and rare diagnostic Early Triassic fossil horizons, such as the North American western interior, the approach to stratigraphy is lithic. Facies and (or) formation boundaries are commonly diachronous in such a situation, so that it is not surprising that formation names have proliferated or that the formal applicability of these names is regionally restricted.

The brachiopods discussed here were collected from the Woodside, Dinwoody, Thaynes, and Moenkopi Formations and commonly occur in thin, monospecific bands or zones, isolated from one another and from most other diagnostic fossils. The age of these units and their regional interrelationships are unclear. McKee and others (1959) produced a generalized correlation chart for Triassic stratigraphic units in the United States. Pertinent parts of that chart appear here as figure 2. The Woodside Formation, originally defined (Boutwell, 1907) in the Park City district, northeastern Utah, was later extended to northern Utah, western Wyoming, and southwestern Montana (Kummel, 1954). Beds in the Confusion Range in west-central Utah, originally referred to the Woodside (Newell, 1948), were reassigned to the Thaynes Formation (Hose and Repenning, 1959). The so-called "Mackentire Tongue" of the Woodside Formation, defined in Duchesne County, Utah, is of demonstrable

IDAHO		WYOMING	MONTANA	UTAH		NEVADA	ARIZONA	CALIFORNIA								
Central-eastern	Southeastern-most	Central-western	Southwestern	Northwestern	SW	South	Middle-northern	SE (San Bernardino County)								
Portneuf Limestone Member of Thaynes Formation	Portneuf Limestone Member of Thaynes Formation	Thaynes Limestone	Thaynes Formation	Ankareh Formation (lower part)	Moenkopi Formation (lower part)	Moenkopi Formation (lower part)	Moenkopi Formation (lower part)	Moenkopi Formation (lower part) and unnamed formations								
Portneuf Limestone	Lanes Tongue of Ankareh Formation			Thaynes Limestone	Thaynes Formation	Thaynes Limestone	Moenkopi Formation (lower part)	Moenkopi Formation (lower part)	Moenkopi Formation (lower part)	Moenkopi Formation (lower part) and unnamed formations						
Unit E ¹ Sandstone and limestone																
Unit D ² Black limestone																
Unit C ² Tan silty limestone																
Unit B ² Black limestone																
Unit A ² Lower limestone																
Dinwoody Formation	Woodside Formation	Woodside Formation	Woodside Formation	Woodside Formation												
	Dinwoody Formation	Dinwoody Formation	Dinwoody Formation													

¹Fort Hall Member¹ of Thaynes Formation.

²Ross Fork Limestone Member² of Thaynes Formation.

FIGURE 2. — Generalized correlation chart of Lower Triassic (Scythian) stratigraphic units in parts of the western interior of the United States.

Permian age (McKelvey and others, 1956; 1959), so that in places, the Permian-Triassic boundary is within the Woodside. The Woodside commonly overlies Permian units referable to the Phosphoria and Park City Formations and underlies the Triassic Thaynes Formation (or Limestone or Group). It tongues out westward in southeastern Idaho and southwestern Montana into the Dinwoody Formation (Kummel, 1954).

The Dinwoody Formation, originally defined (Condit, 1917) in the Wind River Mountains, Wyo., commonly overlies various members of the Park City, Shedhorn, and Phosphoria Formations (Permian) and may be overlain by Woodside, Thaynes, or younger units. The Dinwoody generally appears to be a lateral equivalent of the Woodside in southeastern Idaho, southwestern Montana, and western Wyoming (Kummel, 1954).

The Thaynes Formation was originally defined in the Park City district, Uinta Mountains, Utah (Boutwell, 1907), where it overlies the Woodside and underlies the Ankareh Formation. In southeastern Idaho, the Thaynes was divided into three units (Mansfield, 1916; 1920), now recognized as members (Kummel, 1954): the basal "Ross Fork Limestone Member,"² the middle "Fort Hall Member,"³ and the upper Portneuf Limestone Member. The Thaynes is recognized in southeastern Idaho, northeastern Utah, and western Wyoming and is apparently equivalent to a part of the Moenkopi Formation in parts of southern Utah, Arizona, Nevada, and California.

The Moenkopi Formation, defined in the Grand Canyon region, Arizona (Ward, 1901), is a unit of Early and Middle(?) Triassic age in Arizona, Colorado, California, Nevada, and southern Utah. It appears to be equivalent in age to all of the Thaynes and parts of the Woodside in Idaho, Wyoming, and Utah.

FAUNAL RELATIONSHIPS

Early Triassic brachiopods are rare worldwide. In North America, described terebratulids of Early Triassic age have been limited to the genus *Terebratula* [sensu lato], and have been formally assigned to but three species: *T. margaritowi* Bittner, *T. semisimplex* White, and *T. thaynesiana* Girty. Specimens assigned to *T. augusta* Hall and Whitfield (White, 1880; 1883) (USNM 8191)—but never described or figured—are too fragmentary to permit any taxonomic assignment other than "not *T. augusta* Hall and Whitfield." In the 35 years since the last of these descriptions was published, it has become better understood that the taxonomic position of such forms must be based on characteristics other than external form and size. Dagys (1974), in a summary of his extensive studies of the world distribution of Triassic brachiopods, cited only a few genera of Early Triassic brachiopods, among which are three terebratulids: ?*Sulcatinella* Dagys, *Fletcherithyris* Campbell, and *Plectoconcha* Cooper, the last typically a Late Triassic genus. His generic identifications of North American forms

suggest he has had no opportunity to study pertinent material firsthand but has had to rely heavily on the small body of extant literature.

In several Early Triassic brachiopod assemblages, which include rhynchonellaceans, spiriferinaceans, and athyridaceans, Dagys (1974, p. 292) identified the terebratulid *Fletcherithyris margaritowi* Bittner as a globally cosmopolitan element. He recognized it in collections from the upper Induan (Dienerian) of Idaho and the Olenekian (Smithian and most of the Spathian) of North America, from Primor'ye of the northeast U.S.S.R. just north of Vladivostok, from Japan, from Mangyshlak of the eastern shore of the Caspian Sea, Kazakhstan, U.S.S.R., and from the Balkans. Although comparative material from many of these areas was not available to me, Dagys' identifications of North American material, at least, are suspect. Specimens in the present study externally similar to *Fletcherithyris* Campbell may be assigned confidently either to *Rhaetina* Waagen, which lacks the characteristic dental plates of *Fletcherithyris*, or to *Periallus*, new genus, a zeilleriid, having the distinctive loop of that family. Similarly, internal characters of a form assigned by Dagys to *Plectoconcha* Cooper [*T. semisimplex* White] require erection of a new, albeit plectoconchiine, genus. A superficial cosmopolitanism may exist in Early Triassic terebratulids, in that morphologically similar, but not genetically identical forms, evolved in geographically separated areas. Our knowledge of the range of variation in suprageneric groups of terebratulids in the Early Triassic is so poor that I cannot state with confidence that homeomorphic pairs such as *Fletcherithyris-Rhaetina*, or *Fletcherithyris-Periallus* are not more closely related than at the generic level. Forms able to survive the mysterious rigors of the Permian-Triassic transition must have been generalized, so that they could exploit marginally favorable environments. The broad genetic base that made possible such extensive external homeomorphy may also have been responsible for the variety of internal skeletal arrangements that are considered of taxonomic significance at the generic level.

North American Early Triassic terebratulids occupy pivotal positions in several phyletic lineages. They include the oldest known representatives of the Family Zeilleriidae, the Subfamilies Zugmayeriinae and Plectoconchiinae, and the genus *Rhaetina*, and the youngest reported representatives of the Cryptacanthiinae. Paleozoic antecedents of most of the forms are difficult to determine, and the overall aspect of the brachiopod fauna is Mesozoic.

BIOSTRATIGRAPHIC IMPLICATIONS

Only a small number of the fossil localities covered by this report are well-defined stratigraphically—most collections were made more than 50 years ago when the regional stratigraphy was neither so well known nor so finely subdivided as it is today. Little matrix was collected with the macrofossils. Most commonly, only that rock adherent to individual fossil specimens was retained. Because of time limitations, no field investigations were possible in the

²Units A, B, C, and D of fig. 2.

³Unit E of fig. 2.

present study. Some conclusions of a biostratigraphic nature, however, are possible, on the basis of the distributions of the terebratulids themselves.

Three of the terebratulid species, *Portneufia episulcata*, n. gen., n. sp., *Rhaetina incurvirostra*, n. sp., and *Periallus woodsidensis*, n. gen., n. sp., are quite rare. The first two were recovered from the Portneuf Limestone Member of the Thaynes Formation, but each is so uncommon, and our knowledge of the stratigraphic position of the collecting localities is so poor, that it is difficult to determine whether they are limited to that unit. *Periallus woodsidensis* has not been recognized in any of the collections from the upper part of the Thaynes Formation. It is probably limited to the Woodside and Dinwoody Formations and the "Ross Fork Limestone Member"⁴ of the Thaynes Formation. *Obnixia thaynesiana* (Girty), the most widespread form here described, has been recovered from the Thaynes and Moenkopi Formations from southeastern Idaho to southeastern California (fig. 1), but, with one possible exception, it has not been recovered stratigraphically below the *Meekoceras* ammonite zone which defines the base of the Thaynes Formation. At locality 16, a form questionably referred to *O. thaynesiana* is associated with *P. woodsidensis*. This locality is in a structurally complex region, and the formation assignment made in the field (basal(?) part of the Woodside Formation) may be in error. On the basis of all other occurrences in this study, the only unit in which these terebratulids could occur is the "Ross Fork Limestone Member" of the Thaynes Formation. Girty (in Mansfield, 1916, p. 39; in Mansfield, 1920, p. 50) recognized *Terebratula semisimplex* White as an index of the Portneuf Limestone Member of the Thaynes Formation. The distribution of *Vex semisimplex* (White) revealed in this study bears out his conclusions.

SYSTEMATIC PALEONTOLOGY

The use of descriptive terms such as anterior, posterior, ventral, dorsal, mesial, distal, length, width, height, and thickness, follows that of Williams and Rowell (1965). Several other terms are introduced to denote morphologic features of potential taxonomic value.

Anterior separation is the horizontal distance between the anterior extremities of the loop, whether it be terebratuliform ("short") or terebratelliform ("long"). This measure has little application in early developmental stages. *Loop length* is measured from the most posterior point on the dorsal umbo to the most anterior point of the loop. *Loop width* and *loop thickness* are maxima and are measured in a plane normal to the longitudinal axis of the loop. *Length of the ascending lamellae* or *length of the transverse band* is measured from the most posterior part of the ascending lamellae or transverse band to the anterior extremities of the loop. *Distance to crural processes* is measured along the longitudinal axis of the loop, from the most posterior point on the dorsal umbo to an imaginary line connecting the two crural points.

Several subscripts are used to qualify measurements. The subscript "e" indicates that the measurement was estimated and is probably correct only to the nearest millimeter. The subscript "c" indicates that the specimen was crushed in such a way as to render the measurement less than representative; if "e" is also present, the measurement was estimated, to correct this deficiency. The subscript "b" indicates that the specimen in question is broken, and it indicates that a part of the specimen necessary for the measurement is missing; this too may be accompanied by the subscript "e," indicating that the measurement was estimated. A measure across any structure having bilateral symmetry (for example, a measure of brachiopod hinge width), may be estimated by doubling the half measure, which equals the distance from the symmetry plane to the distal extremity. Use of this procedure is indicated by the subscript "h."

Order TEREBRATULIDA Waagen, 1883

Superfamily DIELASMATACEA Schuchert, 1913

Family DIELASMATIDAE Schuchert, 1913

Subfamily ZUGMAYERIINAE Dagys, 1963

Genus PORTNEUFIA, n. gen.

Etymology of name.—F. *Portneuf* = name of rock unit + L. *-ia* = feminine suffix.

Diagnosis.—Dielasmatidae with falsifer crura and long loops, with inner hinge plates and convoluted anterior commissure.

Description.—Dielasmatids having subequally biconvex valves and suberect to erect ventral beak. Surface commonly smooth.

Ventral valve hinge area expanded in lateral view. Pedicle foramen medium sized, mesothyridid to permesothyridid. Subtriangular delthyrium closed apically by small, short, disjunct deltidial plates. Beak ridges faint; interarea curved, poorly defined.

Dorsal valve hinge region resected in lateral view, accommodating expanded part of opposite valve. Beak in lateral view thin, obtusely pointed in dorsal view.

Ventral interior has distinct pedicle collar and short dental plates. Hinge teeth short, tabular.

Dorsal interior with or without distinct cardinal process. Outer socket ridges very low; sockets shallow, roofed mesially by wide triangular outer hinge plates, which join ventral extremities of short inner socket ridges. Crura falsifer (*sensu* Dagys, 1974), with deep crural bases rising anteromesially of hinge plates as crural processes, descending anterodistally as keels, which may be supported apically by crural plates. Inner hinge plates present, variable. Low median myophragm developed. Loop with long descending and ascending lamellae, but anterior parts unknown.

Type species.—*Portneufia episulcata*, n. sp.

Occurrence.—Same as for species.

Comparison.—*Portneufia* is distinguished from both *Adygelloides* Dagys and *Zugmayeria* Waagen by the relatively complex convolution of its anterior commissure and its

⁴Units A, B, C, and D of fig. 2.

apparent terebratelliform loop and from *Adygelloides*, in particular, by its distinct inner hinge plates.

Discussion.—*Portneufia* represents the oldest known zugmayerine dielasmatid; the other two genera referable to the subfamily are known only from the Upper Triassic. The Paleozoic antecedents of *Portneufia* may have been forms like *Dielasma* King (s. s.), which are quite similar, but which bear septalial plates reaching the floor of the valve. A single specimen (USNM 242053; pl. 1, figs. 9, 10) best shows loop detail. It appears terebratelliform, but because the anterior parts are not preserved and because some forms (for example, *Aulacothyroides* Dagys and *Anadyrella* Dagys) that bear a glossothyropsiform mature loop are developmentally dielasmoid, it seems premature here to alter the above suprageneric designations.

***Portneufia episulcata*, n. sp.**

Plate 1, figures 1-10

Etymology of name.—*L. episulcata* = episulcate.

Diagnosis.—Small episulcate *Portneufia*.

Description.—Medium-sized subequally biconvex shells, elongate oval to subtriangular in outline, having suberect to erect ventral beak. Anterior commissure episulcate to sulciphate. Surface smooth, anteriorly marked by faint concentric growth lines.

Ventral valve symmetrically domed, posteriorly expanded in lateral view; steeply domed in anterior view. Medium-sized mesothyridid to permesothyridid pedicle foramen. Subtriangular delthyrium closed apically by small short disjunct deltidial plates. Beak ridges faint; interarea curved, poorly defined.

Dorsal valve in lateral view more steeply sloping anteriorly; having crescentic posteriorly resected hinge margins, accommodating expanded posterior part of opposite valve. Anteromesial slope faceted, only incipiently sulcate, produced anteroventrally as short curved tongue. Beak in lateral view thin, obtusely pointed in ventral view.

Ventral interior having distinct pedicle collar and short dental plates. Hinge teeth short, tabular, long axes oriented posteromesially, rounded points directed anteromesially; not markedly hooked. Muscle scars indistinct.

Dorsal interior has distinct bilobate cardinal process or simple apical pit. Outer socket ridges very low; sockets shallow, widely divergent anteriorly, roofed mesially by wide triangular outer hinge plates which join ventral extremities of short inner socket ridges; outer hinge plates sloping slightly dorsomesially. Crura falsifer (*sensu* Dagys, 1974): deep crural bases joined medially to outer hinge plates; crural bases rising anteromesially of hinge plates as high crural processes at about one-fourth valve length anterior to beak, descending anterodistally as keels, supported only apically by short crural plates. Narrow inner hinge plates present, variably oriented, separated mesially by thin gap. Long very low median myophragm extending anteriorly about one-half valve length. Loop apparently about two-fifths width of

valve. Descending and ascending lamellae of loop slender; loop probably terebratelliform, but anterior parts not preserved.

	Length (mm)	Width (mm)	Thickness (mm)	Dorsal valve length (mm)	Distance to crural processes (mm)	Loop width (mm)
Locality 4:						
USNM 242049	7.9	7.6	4.6	6.5
USNM 242050	11.4	11.8	3.0
USNM 242051 (holotype)	15.1	10.9	8.5	13.2	3.3	4.7 _{be}
USNM 242052	14.4 _h	16.0 _e	3.4	5.6 _h

Types.—Holotype: USNM 242051; figured paratypes: USNM 242049, 242053; measured paratypes: USNM 242049, 242050, 242052.

Occurrence.—*Portneufia episulcata* has been recovered only from locality 4, in the Portneuf Limestone Member of the Thaynes Formation, on the Fort Hall Indian Reservation, Bingham County, Idaho (fig. 1). The horizon from which this sample was collected was originally assigned to the basal part of the Ankareh Formation, a name now restricted to a sandstone overlying the Thaynes Formation.

Comparison.—*Portneufia episulcata* is monotypic. It may be distinguished from other North American Early Triassic terebratulids by its episulcate anterior commissure and its distinctive dorsal cardinalia.

Subfamily DIELASMATINAE Schuchert, 1913

Genus RHAETINA Waagen, 1883

Diagnosis.—Small to large dielasmatids with sulciphate to rectimarginate anterior commissure, suberect to incurved ventral beak and epithyridid pedicle foramen. Septalial plates present; dental plates absent; crura infulifer; dorsal median septum low or absent.

Type species.—*Terebratula gregaria* Suess, 1854, Akad. Wiss. Wien, Math.-naturwiss. Kl. Denkschrift, v. 7, p. 42, pl. 2, figs. 13-15.

Occurrence.—*Rhaetina* was first described (as *T. gregaria* Suess) from the Kössenschichten (Rhaetian) of the Eastern Alps. Since then, specimens have been reported from rocks ranging in age from Permian (Gemmellaro, 1899) to Jurassic (Moisseiev, 1938), in Western and Central Europe: the Permian form has since been shown to belong to a distinct dielasmatacean family. *R. incurvirostra*, n. sp., is the first reported occurrence of the genus in North America.

Comparison.—*Rhaetina* may be distinguished from *Adygella* Dagys, *Adygelloides* Dagys, *Aspidothyris* Diener, *Dinarella* Bittner, *Fletcherithyris* Campbell, and *Sulcatinella* Dagys by its lack of dental plates, and from *Coenothyris* Douvillé, *Cruratula* Bittner, and *Dinarella* Bittner by its epithyridid pedicle foramen. *Propygope* Bittner has a broadly sulcate dorsal valve and markedly triangular outline.

Discussion.—Although *Rhaetina* is unknown in the Permian of North America, closely homeomorphic species

of *Dielasma* King and *Fletcherithyris* Campbell are reported from the Permian and Triassic, respectively (Cooper and Grant, 1976; Dagys, 1974). Specimens originally reported as *Rhaetina lepton* Gemmellaro (1899), have been shown (Stehli, 1962; Cooper and Grant, 1976) to be more properly assigned to the Family Heterelasminidae, as they lack outer hinge plates connecting the inner socket ridges and crural bases.

***Rhaetina incurvirostra*, n. sp.**

Plate 1, figures 11-24

Etymology of name.—L. *incurvo* = incurved + L. *rostrum* = beak.

Diagnosis.—Rectimarginate to incipiently uniplicate *Rhaetina* having an extremely incurved ventral beak.

Description.—Medium- to large-sized terebratulids having subequally biconvex valves; elongate oval in outline, with long incurved ventral beak and apparent rectimarginate anterior commissure. Surface smooth or marked by faint growth lines.

Ventral valve having large long extremely incurved beak; beak commonly extending over dorsal umbo for distance of several millimeters. Large epithyridid, anteriorly labiate pedicle foramen. Disjunct deltidial plates apically filling delthyrium; deltidial plates not visible externally, but lying between pedicle collar and exterior of dorsal umbo. Long dorsal pedicle collar extension, semicircular in cross section, visible in dorsal and posterior views. Beak ridges poorly developed.

Dorsal valve has sharp beak covered by incurved ventral beak. Evenly domed in lateral and anterior views.

Ventral interior has anteriorly elongate pedicle collar pressed tightly against deltidial plates, acting as peduncular trough or channel; posterior and lateral parts of collar relatively normally proportioned. Dental plates and dental ridges not developed. Muscle scars indistinct. Hinge teeth small, short, tabular, arising anteromesially, hooked dorsomesially.

Dorsal interior has small transverse bilobate cardinal process. Hinge sockets long, narrow, shallow. Thin outer socket ridges differentiated from valve wall, forming narrow secondary articulatory furrow distally; thin low inner socket ridges not appreciably overhanging sockets. Elongate triangular, mesially convex, anterodistally concave outer hinge plates arising at dorsal margins of inner socket ridges; ventromesially directed crura arising at junction of outer and inner hinge plates, extending only ventrally therefrom. Inner hinge plates ventromesially convex, anterodistally concave, joining dorsal margins of crura to valve floor. Median ridge very low, extending about one-half valve length. Crura infulifer to lobothyroid; crural processes long, broad; points acute, located anterior to anterior ends of hinge plates, closely appressed mesially. Loop terebratuliform: short, extending less than one-half valve length; narrow, about one-fourth valve width at anterior extremities. Transverse band closely appressed and almost parallel to descending lamellae.

	Total length (mm)	Total width (mm)	Total thickness (mm)	Dorsal valve length (mm)	
Locality 8:					
USNM 242054 (holotype)	22	18.5 _b	12.0 _c	20	
USNM 242055	28	21	13.0 _c	25	
	Loop length (mm)	Loop width (mm)	Loop depth (mm)	Distance to crural processes (mm)	Length of transverse band (mm)
Locality 8:					
USNM 242731	9.8	6.2	3 _e	5	3.3 _e

Types.—Holotype: USNM 242054; figured specimens: USNM 242054, 242060, 242731; measured specimens: USNM 242054, 242055, 242731.

Occurrence.—*R. incurvirostra* has been recovered from localities 2 and 8, in eastern Idaho (fig. 1). The sampled horizon probably is within the Thaynes Formation.

Comparison.—*R. incurvirostra* is the oldest species of the genus. It may be distinguished from most species of *Rhaetina* by its rectimarginate to incipiently uniplicate anterior commissure. From those species having such a commissure, which include the Norian-Rhaetian *R. taurica* Moisseiev and the Carnian-Norian *R. pyriformis* (Suess), it may be distinguished by its extremely incurved ventral beak. Of these two, it is probably more closely related to *R. pyriformis*. It may readily be distinguished from other North American Early Triassic terebratulids by its larger size and strongly incurved ventral beak.

Superfamily TEREBRATULACEA Gray, 1840

Family TEREBRATULIDAE Gray, 1840

Subfamily PLECTOCONCHIINAE Dagys, 1974

Genus VEX, n. gen.

Etymology of name.—L. *vexo* = vexation.

Diagnosis.—Incipiently uniplicate, secondarily multicostate terebratulaceans with narrow loop and long delicate descending lamellae, no inner hinge plates or dental plates, keeled crural bases, and crural process points anterior to hinge plates.

Type species.—*Terebratula semisimplex* White, 1879, U.S. Geol. and Geog. Survey Terr. (Hayden), Bull., v. 5, no. 1, p. 108.

Occurrence.—Specimens referable to *Vex* have been recovered from the Thaynes Formation in Bingham and Caribou Counties, southeastern Idaho.

Comparison.—*Vex* is easily distinguished from most other terebratulids by its incipiently uniplicate and secondarily multicostate anterior commissure. Its dorsal valve is rarely geniculate as are those in the Paleozoic dielasmataceans *Hemiptychina* Waagen and *Dielasmata* Waagen, and it lacks the septalial plates characteristic of those forms. The Paleozoic Notothyrididae, although similar externally, are long-looped forms having entire hinge plates. Of the de-

scribed Mesozoic genera, *Vex* is most similar to *Plectoconcha* Cooper. The loops of both forms are not well known; and, although the latter genus is commonly larger than *Vex*, they are otherwise similar externally. Serial sections parallel to the commissural plane of a topotypic specimen of *Vex semisimplex* (White) (USNM 8190b) show a relatively long and narrow loop, compared to the short broad structure observed in specimens of *Plectoconcha aequiplicata* (Gabb) (USNM 242083; pl. 2, figs. 6, 7). In *Plectoconcha* the points of the crural processes are at or posterior to the ends of the hinge plates. In *Vex* they are anterior of that position.

Vex semisimplex (White)

Plate 1, figures 25-42; Plate 2, figures 1-5

Terebratula semisimplex White, 1879, U.S. Geol. and Geog. Survey Terr. (Hayden), Bull., v. 5, no. 1, p. 108; White, 1880, U.S. Geol. and Geog. Survey Terr., Ann. Rept. 12 (1878), p. 108, pl. 31, figs. 3a-c; Girty, 1927, U.S. Geol. Survey Prof. Paper 152, pl. 30, figs. 5-7.

Diagnosis.—Small variably costate *Vex*.

Description.—Small- to medium-sized terebratulids; ventral fold and dorsal sulcus incipient to weakly developed. Shells subtriangular to subpentagonal in dorsal outline; widest anterior to midlength; deepest at or slightly posterior to midlength. Anterior commissure rectimarginate to incipiently uniplicate, complicated by costal traces of variable height and amplitude. Costae distinct, originating at variable distances from umbo.

Ventral valve more convex, has erect to incurved beak and small- to medium-sized round pedicle foramen. Beak ridges poorly developed. Deltoidal plates disjunct. Surface distally irregularly costate, mesially smooth or marked by faint growth lines.

Dorsal valve having slightly pointed beak produced to fill open delthyrium of opposite valve. Profile evenly domed in anterior and lateral views. Surface ornament as for opposite valve.

Ventral interior having distinct pedicle collar, but lacking dental plates. Teeth large, tabular, recurved.

Dorsal interior having well-developed bilobate cardinal process with raised rim. Sockets broad, deep, roofed by massive recurved socket ridges. Outer hinge plates broad, planar, arising from ventral margin of inner socket ridges; inner hinge plates absent. Small triangular fossae bounded in anterior view by inner socket ridges, outer hinge plates, and dorsal keels of crura. Crural processes at anterior ends of outer hinge plates; crura somewhat keeled dorsally, but keels never extending to valve floor as septalial plates. Median septum absent; low myophragm separating paired elongate-oval anteriorly expanded adductor muscle scars which extend one-half valve length. Loop dielasmoid, delicate, with comparatively large crural processes, slender descending lamellae, and broad transverse band. Loop about two-fifths as wide as dorsal valve; from one-half to two-thirds as long. In serially sectioned paralectotype specimen (USNM 8190b), loop length = 7.0 mm, loop width = 3.5 mm, length of transverse band = 1.0 mm, distance to crural processes = 2.7 mm.

	Length (mm)	Maximum width (mm)	Maximum thickness (mm)	Dorsal valve length (mm)
Locality 3:				
USNM 242061	11.4	10.5	6.2	10.0
USNM 242062	12.7 _b	12.6	6.9 _c	10.6 _b
USNM 242063	12.9	12.6	7.5	11.4
Locality 6:				
USNM 242069	14.9	13.4	10.2	13.2
Locality 7:				
USNM 242070	6.2	5.4 _c	3.5	5.4
USNM 242071	7.0	6.2	4.3	6.0
USNM 242072	8.6	7.7	5.0	7.2
USNM 242073	10.7	9.5	6.1	9.1
USNM 242074	11.7	10.6	6.6	10.2
Locality 32:				
USNM 242075	16.0 _{bc}	13.3	10.0 _c	13.8
Locality 33:				
USNM 242076	11.4	9.4	7.0	9.6
USNM 242077	12.0	12.4	7.5	10.3
USNM 242078	12.5 _b	12.2 _b	7.5	11.0 _c
USNM 242079	13.0	12.0	7.9	11.2
USNM 242080	14.3	13.4	10.0	12.7
Locality 41:				
USNM 242064	7.4	7.5	3.7	6.4
USNM 242065	9.2	8.1	6.0	7.8
USNM 242066	10.8	9.5	6.5	9.5
USNM 242067	13.6	11.1	8.5 _c	11.1
USNM 242068	16.9	14.0 _b	9.7	15.4
Locality 44:				
USNM 8190a (lectotype)	13.9	11.2	8.4	12.0
USNM 8190b (sectioned paralectotype)	14.0	10.5 _c	8.1 _c	12.1

Types.—Lectotype: USNM 8190a; measured specimens: USNM 8190a, 8190b, 242061-242080; figured specimens: USNM 8190a, 8190b, 242063, 242065, 242069, 242071-242075, 242081, 242082.

Occurrence.—The type locality of *V. semisimplex* (White) is only approximately known. The syntype specimens collected by A. C. Peale of the Hayden Territorial Survey in 1877 were later described by White (1880). The section from which the specimens were collected probably is within the Crane's Flat 15-min quadrangle, in southeastern Idaho (fig. 1, loc. 44). White (1883, p. 106) placed the collecting horizon about 500 m stratigraphically above a bluish-gray limestone unit containing *Meekoceras gracilitatis*. Because the *M. gracilitatis* zone defines the base of the Thaynes Formation, barring structural complications within the section, the *V. semisimplex* horizon may be placed within the upper part of the Thaynes, probably in the Portneuf Limestone Member. Indeed, Girty (in Mansfield, 1916, p. 39; in Mansfield, 1920, p. 50) reported that the horizon of *T. semisimplex* was within that unit. Only five specimens collected by Peale could be located in the National Collections. One (USNM 8190b) has been serially sectioned (pl. 2, figs. 1-5) to show the internal details of the species, which have not been previously described. In the present study, *V. semisimplex* is recognized at localities 3, 5-7, 9, 32-34, 41, and 44.

Comparison.—*Vex* is monotypic. Its differentiation from other similar costate or plicate terebratulid genera is discussed under the genus. It is easily distinguished from the other North American Early Triassic terebratulids by its incipiently uniplicate and secondarily multicostate anterior commissure.

Discussion.—The simulated ontogenetic series (pl. 1, figs. 25–32) shows the great variability in radial ornament. This variability led Girty to describe an additional (unpublished) subspecies, best represented here by plate 1, figure 30. He correctly recognized that this form was a manifestation of infraspecific variability.

Superfamily CRYPTONELLACEA Thomson, 1926

Family CRYPTONELLIDAE Stehli, 1965

Subfamily CRYPTACANTHIINAE Stehli, 1965

Discussion.—Stehli (1965) placed this subfamily within the Family Mutationellidae Cloud and included within it the genera *Cryptacanthia* White and St. John, *Gacina* Stehli, and *Glossothyropsis* Girty. Since that time several authors (Dagys, 1968, 1974; Cooper and Grant, 1976) have recognized that the subfamily more properly belongs within the Cryptonellidae, on the basis of similarity of loop development in the cryptacanthiine and cryptonellid genera. The range of the subfamily is here extended upward into the Norian and is expanded to include *Obnixia*, n. gen., and *Anadyrella* Dagys.

Dagys (1974) placed the Ladinian and Norian genus *Anadyrella* with *Aulacothyroides* Dagys in the Aulacothyroideidae. Of the two, only the loop development of *Aulacothyroides* has been documented (Dagys, 1972). It has strong inner hinge plates and dorsal median septum, and in its loop development shows additional important differences from *Obnixia*. Although *Obnixia* reaches the glossothyropsiform stage very early in its development (dorsal valve length approximately 2.5 mm), this stage is attained much later in *Aulacothyroides* (dorsal valve length approximately 5.6 mm). In addition, the ascending lamellae of *Aulacothyroides* derive from a median vertical plate in the centronelliform stage, whereas those of *Obnixia* grow directly from the echmidium. In contrast, *Anadyrella* lacks a median septum, and its septalial plates, only questionably homologous with the inner hinge plates of *Aulacothyroides*, are much reduced. *Anadyrella* has been associated with *Aulacothyroides* solely on the basis of its cardinalia and the character of its mature loop. But the progression of loop development in *Anadyrella* is unknown, and the genus at present is represented by only three individuals referred to one species. Although *Anadyrella* (Dagys, 1974, p. 186, fig. 129) clearly possesses more robust septalial plates than does *Obnixia*, the similarities between the two, and the differences between *Aulacothyroides* and *Obnixia*, are sufficiently compelling, in my opinion, to justify placing *Anadyrella* and *Obnixia* in the same subfamily; thus, *Anadyrella* is reassigned from the Aulacothyroideidae to the Cryptacanthiinae.

Genus *OBNIXIA*, n. gen.

Etymology of name.—L. *obnixus* = resolute.

Diagnosis.—Sulcate cryptacanthine terebratulids having no inner hinge plates; loop development entirely from primary elements, proceeding through precentronelliform, centronelliform, cryptacanthiform, and glossothyropsiform stages.

Description.—Cryptacanthine terebratulids having unequally biconvex valves bearing a variably developed dorsal sulcus and ventral fold. Surface smooth or with rare concentric lamellae. Radial ornament wanting.

Ventral valve more convex. Beak suberect to erect in lateral view. Beak ridges sharp, defining palintrope. Pedicle foramen small, mesothyridid. Deltidial plates thin, conjunct.

Dorsal valve less convex. Faint median sulcation evident early in ontogeny, more pronounced in mature specimens.

Interiors as for species.

Type species.—*Terebratula thaynesiana* Girty, 1927, U.S. Geol. Survey Prof. Paper 152, p. 435, pl. 30, figs. 5–7.

Occurrence.—Same as for species. If *Anadyrella infrequens* Dagys proves congeneric with *Obnixia*, the stratigraphic range of the combined genera will extend into the Upper Triassic (Norian) and the geographic range, into the northeastern part of the U.S.S.R. (approximately long 165° E., lat 60° N.).

Comparison.—*Obnixia* is easily distinguished from the late Paleozoic genus *Cryptacanthia* by its distinctive loop development and by its lack of inner hinge plates. The Devonian and early Carboniferous genus *Gacina* bears an entire, but perforate inner hinge plate, and in loop development attains only a modified centronelliform stage. The Permian genus *Glossothyropsis* bears a strong median septum and commonly is more markedly sulcate. *Glossothyropsis juvenis* Cooper and Grant, from the Upper Permian Hegler and Rader Limestone Members of the Bell Canyon Formation of west Texas, may be related to *Obnixia* more closely than at the generic level. It differs in bearing a distinct apical dorsal median septum and small, but disjunct, inner hinge plates.

Discussion.—Dagys (1974, fig. 163) suggested that the Aulacothyroideidae—represented by the genera *Aulacothyroides* and *Anadyrella*, of Ladinian through Norian age—arose from a basic dielasmatacean stock early in the Triassic; whereas the Cryptonellacea, including such forms as *Cryptacanthia* and *Glossothyropsis*, came to a suitably cryptic end in the Upper Permian. Examination of ontogenetic series of *Obnixia thaynesiana* suggests a rather different evolutionary scheme. The ontogenetic development of the loop of *Obnixia* closely parallels that of *Glossothyropsis*, from which it differs only in its reduced median septum, lack of inner hinge plates, and less markedly crenulate anterior commissure. Because the two best known late Paleozoic cryptacanthine genera (*Cryptacanthia*, *Glossothyropsis*) already show phenotypes combining these characters, it is plausible that cryptacanthines surviving into the Triassic might resemble *O. thaynesiana*. From *O. thaynesiana* it is a short morphologic step to *Anadyrella*, requiring only the

total loss of an already vestigial median septum and the somewhat more distinctive development of apical (septalial) plates, which structures already appear in some specimens of *O. thaynesiana*. (See pl. 2, fig. 26.) The phylogenetic scheme that such a relationship implies warrants reconsideration of the evolutionary development within the Terebratulida as outlined by Dagys (1974).

***Obnixia thaynesiana* (Girty)**

Plate 2, figures 8-27; plate 3, figures 1-13

Terebratula thaynesiana Girty, 1927, U.S. Geol. Survey Prof. Paper 152, p. 435, pl. 30, figs. 5-7.

Diagnosis.—Small sulcate cryptacanthine terebratulids having no inner hinge plates; loop development entirely primary, proceeding through precentronelliform, centronelliform, very brief cryptacanthiform, and relatively long glossothyropsiform stages.

Description.—Small shells having unequally biconvex valves, subtrigonal to subpentagonal in outline, bearing variably developed dorsal sulcus and ventral fold. Length and width subequal; thickness commonly about one-half of either (fig. 3). Surface smooth or bearing rare concentric growth lamellae; lamellae more conspicuous anteriorly. Radial ornament wanting.

Ventral valve more convex, domed in anterior view, maximum convexity in lateral view posterior to midvalve. Beak broadly rounded in dorsal view, suberect to erect in lateral view. Beak ridges sharp, defining palintrope. Pedicle foramen small, mesothyridid. Deltidial plates thin, conjunct.

Dorsal valve less convex, has greatest convexity in lateral view at or posterior to midvalve. Faint sulcation initiated early in ontogenetic development, at a length of about 4 mm, becoming angular and pronounced in mature individuals.

Ventral interior having blunt anteriorly divergent dorso-posteriorly recurved hinge teeth, supported by short dental plates of quite variable expression. Pedicle collar distinct, short, thin.

Dorsal interior lacking median septum; low myophragm developed in later stages of ontogeny. Socket ridges reflexed somewhat distally (laterally), fitting into insets of mesially recurved ventral valve hinge teeth. Outer hinge plates narrow, in mature ontogenetic stages surmounted by a slight swelling of shell material. Crural bases distinct, attached to hinge plates by their ventral edges, bearing no inner hinge plates on their mesial margins. Crural bases unsupported dorsally by crural plates, but tiny divergent axial plates preserved in some mature specimens. Low myophragm separating faint striate adductor muscle scars may be present: never a striking feature of shell interior and never entering into development of loop during ontogeny. Loop long, anteriorly

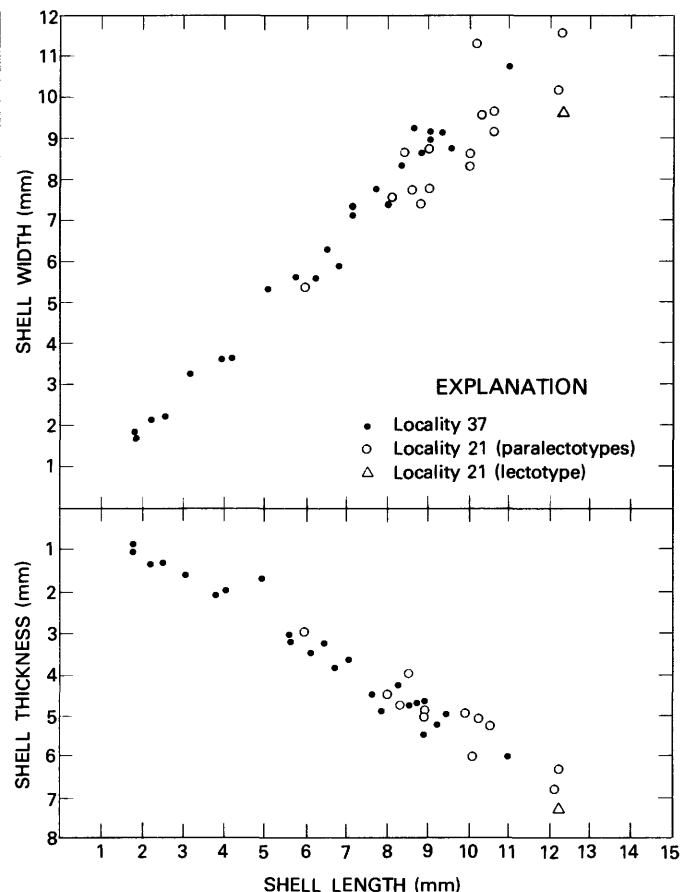


FIGURE 3.—Scattergram of dimensions of *Obnixia thaynesiana* (Girty) from southeastern Idaho (loc. 21) and southeastern California (loc. 37).

and laterally variably spinose, spines directed distally. Spine bases appearing as conical cavities on proximal faces of descending branches of loop. Crural processes low, mesially curved. Spines most commonly directed anteriorly at junction of descending and ascending lamellae. Ascending branches of mature specimens meeting in smoothly curved posteromesially notched junction just anterior to crural processes. Loop development proceeding through precentronelliform, centronelliform, very brief cryptacanthiform, and relatively long glossothyropsiform stages (table 1). Loop length varying from about one-half that of dorsal valve in centronelliform stage to about two-thirds that of dorsal valve in mature glossothyropsiform stages (fig. 4). Loop width about one-half dorsal valve width in valves less than 2.5 mm wide; this ratio about two-fifths in wider valves (fig. 5). Length of ascending lamellae varying from about one-third loop length in smallest cryptacanthiform specimens to about three-fifths in mature glossothyropsiform loop (fig. 6). Distance to crural processes about one-half loop length until end of cryptacanthiform stage; approximates one-third loop length in glossothyropsiform stage (fig. 7).

TABLE 1. — Measurements (in mm) of dorsal valve and loop parameters for a simulated ontogenetic series of *Obnixia thaynesiana* (Girty), from southeastern California (loc. 37)

[n/a = not applicable. The loop is not resected anteriorly until about midway through the cryptacanthiform developmental stage]

Catalogue No. USNM-	Developmental stage	Anterior separation	Valve length	Valve width	Loop length	Loop width	Loop depth	Ascending lamellae length	Distance to crural processes
242119	Precentronelliform	n/a	1.45	1.6 _{be}	0.6	0.45	0.15	n/a	0.35
242120	Precentronelliform	n/a	1.9	2.0 _{be}	0.9	0.55	0.2	n/a	0.45
242121	Precentronelliform	n/a	1.1	1.2 _e	0.7	0.45	0.2	n/a	0.3
242122	Centronelliform	n/a	1.5	1.6	0.9	0.5	0.3	n/a	0.3
242123	Cryptacanthiform	n/a	2.0 _e	1.5	0.6	0.4	n/a	0.4 _e
242124	Cryptacanthiform	0.1	2.0	2.25 _f	1.2	0.55	0.5	0.3	0.45
242125	Cryptacanthiform	0.15	2.15	2.4 _h	1.4	0.6	0.5	0.5	0.6
242126	Glossothyropsiform	0.25 _{ce}	1.15	0.7 _e	0.4	0.4	0.5
242127	Glossothyropsiform	0.3 _{ce}	3.0 _e	2.2	0.85	0.55	0.8	0.7
242128	Glossothyropsiform	0.45 _{ce}	3.35	4.1	2.2	1.2	0.7	1.1	0.85
242129	Glossothyropsiform	0.9	4.5 _e	4.4 _h	3.0	1.5	0.8	1.35	1.3
242130	Glossothyropsiform	0.6 _e	3.0	2.0 _e	1.3	1.5	1.1
242131	Glossothyropsiform	1.0 _{be}	4.5 _{be}	2.9 _b	1.9	1.2	1.3 _b	1.5 _{be}
242132	Glossothyropsiform	0.5	5.1	5.4	3.7	1.7	1.1	1.5	1.2
242133	Glossothyropsiform	1.4	5.8	6.7 _{be}	4.0	2.5	1.2	2.2	1.4
242134	Glossothyropsiform	0.6 _e	6.6	7.2	4.9	2.7	1.5	2.9	1.5

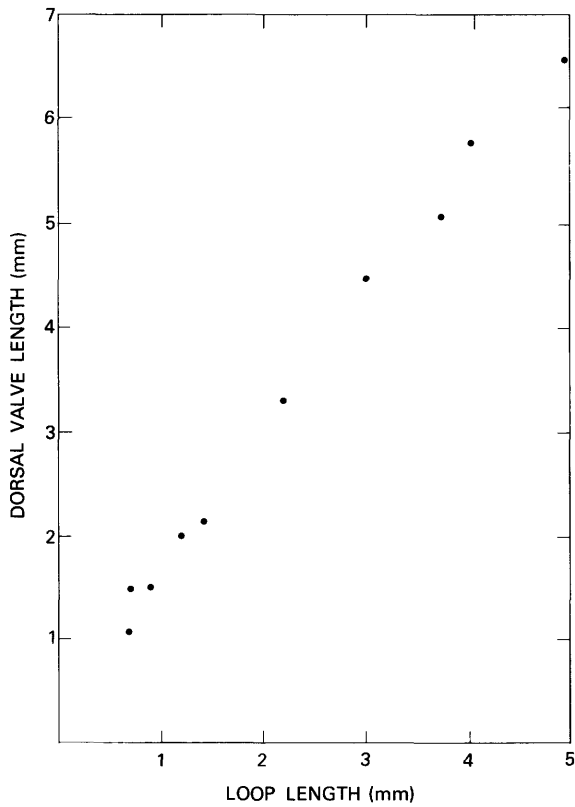


FIGURE 4. — Scattergram of dorsal valve length and loop length of *Obnixia thaynesiana* (Girty) from southeastern California (loc. 37).

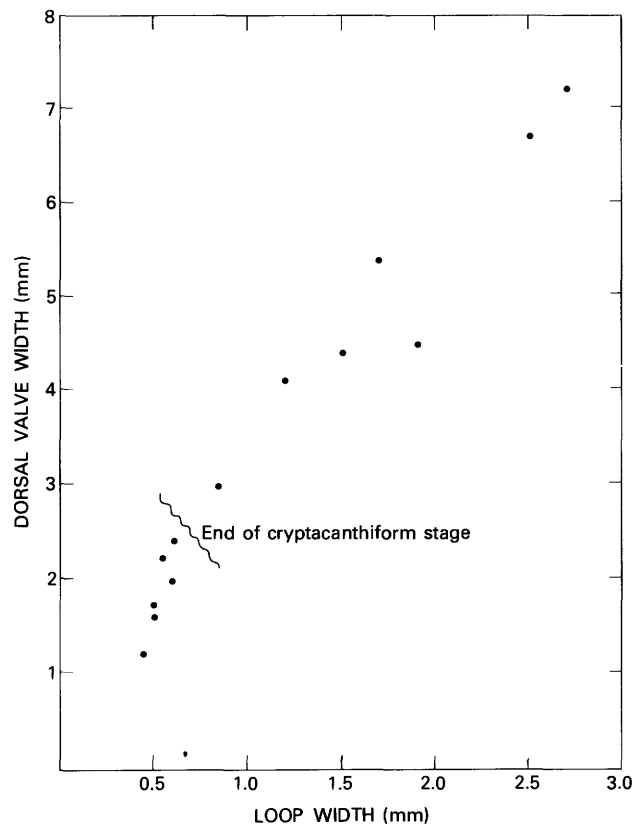


FIGURE 5. — Scattergram of dorsal valve width and loop width of *Obnixia thaynesiana* (Girty) from southeastern California (loc. 37).

	Total length (mm)	Total width (mm)	Total thickness (mm)	Dorsal valve length (mm)
Locality 21:				
USNM 121558 (lectotype)	12.3	9.7	7.3	10.8
USNM 121559a	8.8	7.5	4.7	7.8
USNM 121559b	10.6	9.7	5.3	9.2
USNM 121559c	12.2	10.3	6.8	10.5 _e
USNM 121559d	12.3	11.7	6.3	11.8
USNM 242084	6.0	5.4	3.0	5.2
USNM 242085	8.6	7.8	4.0	7.7
USNM 242086	8.1	7.6 _e	4.5 _e	7.2 _e
USNM 242087	9.0	7.8 _e	5.0	7.9
USNM 242088	8.4	8.7	4.8	7.1
USNM 242089	9.0	8.8	4.9	7.5
USNM 242090	10.0	8.4 _e	5.0 _e	8.9
USNM 242091	10.3 _e	9.6 _e	5.1 _e	9.1 _e
USNM 242092	10.6 _e	9.2	5.3 _e	9.3
USNM 242093	10.2	11.4	6.0 _e	9.0
Locality 37:				
USNM 242094	1.8	1.7	0.9	1.5
USNM 242095	1.8	1.8	1.0	1.4
USNM 242096	2.2	2.1	1.3	1.9
USNM 242097	2.5	2.2	1.3	2.0
USNM 242098	3.1	3.2	1.6	2.7
USNM 242099	3.9	3.6	3.1	3.2
USNM 242100	4.1	3.6	2.0	3.5
USNM 242101	5.0	5.3	1.7	4.3
USNM 242102	5.7	5.6	3.1	4.9
USNM 242103	5.7	5.6	3.2	4.8
USNM 242104	6.2	5.6	3.5	5.3
USNM 242105	6.5	6.3	3.3	5.7
USNM 242106	6.8	5.9	3.9	6.0
USNM 242107	7.1	7.1	3.7	6.4
USNM 242108	7.1	7.2	3.7	6.2
USNM 242109	7.7	7.8	4.5	6.9
USNM 242110	8.0	7.5	4.9	6.9
USNM 242111	8.3	8.4	4.3	7.4
USNM 242112	8.6	9.3	4.8	7.8
USNM 242113	8.8	8.7	4.8	7.7
USNM 242114	9.0	9.0	5.5	8.2
USNM 242115	9.0	9.2	4.7	8.2
USNM 242116	9.3	9.2	5.3	8.4
USNM 242117	9.5	8.8	5.0	8.6
USNM 242118	11.0	10.8	6.1	9.8

Types.—Lectotype: USNM 121558; figured specimens: USNM 121558, 242095, 242098, 242100, 242101, 242104, 242105, 242108, 242111, 242115, 242116, 242119-242125, 242128, 242129, 242131-242139; measured specimens: USNM 121558, 121559a-d, 242084-242134.

Occurrence.—*O. thaynesiana* has been confidently identified from the Thaynes Formation and from its stratigraphic equivalents from southeastern Idaho to southeastern California (locs. 10, 12-31, 36-40, 42, 43). (See fig. 1 and "Fossil Localities Cited in this Report.") Its morphology changes very little over this broad geographic range, though more southern examples are somewhat more transverse.

Comparison.—The genus *Obnixia* is monotypic. *O. thaynesiana* may be distinguished from its most similar apparent relative, *Anadyrella infrequens* Dagys, by its smaller size, less robust septalial plates, and distinctive loop development scheme. It may easily be distinguished from other

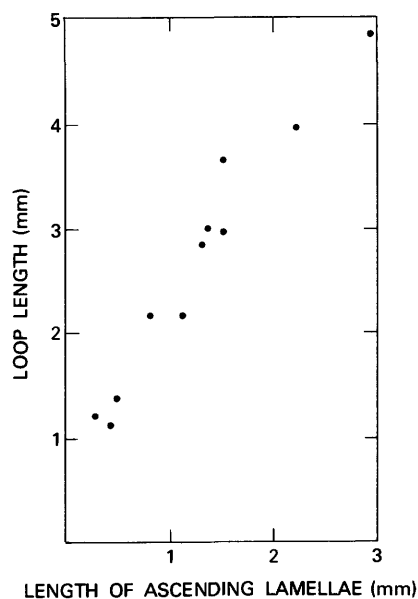


FIGURE 6.—Scattergram of loop length and length of ascending lamellae of *Obnixia thaynesiana* (Girty) from southeastern California (loc. 37).

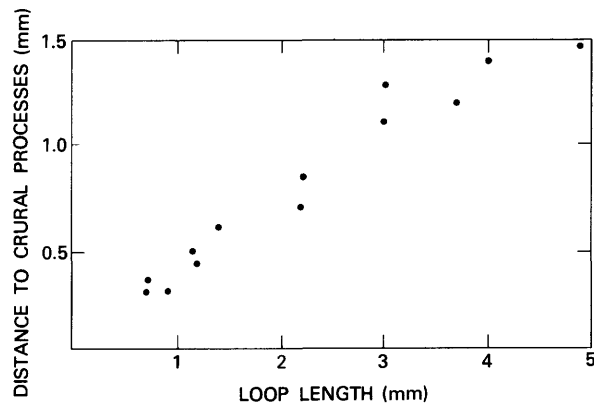


FIGURE 7.—Scattergram of loop length and distance to crural processes of *Obnixia thaynesiana* (Girty) from southeastern California (loc. 37).

North American Early Triassic terebratulid brachiopods by its sulcate anterior commissure.

Loop development in Obnixia thaynesiana (Girty).—Terebratulid classification is made difficult by extensive homeomorphy. Shell form and outline not only may vary considerably within a single small genetic unit, but also they may appear similar in genetically distantly related forms. Until recently, however, it was less well understood that such presumably conservative structures as the terebratulid loop might also be subject to the vagaries of homeomorphy (Dagys, 1974; Cooper and Grant, 1976). Recent studies of loop development in late Paleozoic and Mesozoic terebratulids (Cooper, 1957; Dagys, 1968, 1972, 1974; Baker, 1972) have shown that many different genetic stocks may achieve

similar mature brachial support (loop) structures and that the previous simplistic terebratulid classification on the basis of "short" or "long" loops needs reevaluation. The difference between forms having similar mature loop designs often can only be discerned, for many species, if a relatively complete developmental series is available for study.

In calcareous specimens, loop detail can rarely be observed directly and commonly is reconstructed on the basis of serial sections or acetate peels. Pearson (1977) has reviewed serial grinding as applied to brachiopods. This technique has the advantage in that it reveals the successive laminae, laid down during the growth of an individual, that are preserved in many calcareous specimens. These laminar traces may then be used to reconstruct ontogenetic stages. Cooper (1959) was justifiably critical of serial grinding techniques as used at that time. His main criticisms were the difficulty of maintaining parallel sections and the difficulty in making the intervals between successive sections sufficiently small that minute structures of taxonomic significance could be seen.

Silicified specimens, such as those used by Cooper (1957) in his study of loop development in *Cryptacanthia*, are much more easily prepared, as one need only remove the surrounding calcareous matrix and shell infilling by etching in a weak acid. However, disadvantages are inherent in the use of silicified specimens. Silicification is a poorly understood phenomenon, but we do know that structures so preserved need not be replaced in their entirety. In addition, detail of ontogenetic significance within the shell is commonly lost during silicification. As time was short during this study and as the equipment available was not specifically designed for serial grinding, I have used that technique only where necessary to show the internal structures of unsilicified type specimens of taxonomic importance (for example, *Obnixia thaynesiana* (Girty) and *Vex semisimplex* (White)).

Calcified paralectotype specimens of *Obnixia thaynesiana* from southeastern Idaho were serially sectioned at intervals of 0.15 mm, and acetate peel impressions were taken at each interval. Selected diagnostic sections normal to the longitudinal axis of one such specimen (USNM 242139) are shown in figure 8. Sections of another paralectotype specimen (USNM 242135), oriented in the commissural plane, were projected onto plexiglass sheets and stacked to form a three-dimensional replica of the valve interiors. A stereo-pair photograph of this reconstruction appears on plate 2, figure 24. These figures illustrate the characteristic lack of inner hinge plates, the weak dorsal median myophragm, and the long anteriorly spinose glossothyropsiform loop of the mature *Obnixia thaynesiana*. Unfortunately, topotypic specimens were not silicified, and serial sectioning of a representative sample to document loop development would not have been feasible.

Finely preserved specimens from locality 37 (San Bernardino County, Calif.) were, however, judged conspecific with the syntypic suite. Etched from the surrounding limy matrix, these silicified specimens provide a good sampling of representative postembryonic stages in the development of

the loop of *O. thaynesiana*. Loop terminology in the following discussion is used in the sense of Cooper (1957).

The precentronelliform stage of *O. thaynesiana* is represented here by three specimens, all between 1 and 2 mm in length. In the most paedomorphic of these (USNM 242119; pl. 3, fig. 1), the loop consists only of the descending branches. These are oriented normal to the commissural plane, except at the anterodorsal tips, which are deflected slightly dorsomesially. The descending lamellae diverge anteriorly to about one-fourth valve width, terminating at about two-fifths valve length. There is no anteromedian ridge on the valve floor at this or any subsequent developmental stage. The next precentronelliform specimen (USNM 242120; pl. 3, fig. 2) is more coarsely silicified, but it shows broad descending lamellae, the tips of which have turned not only mesially but ventrally. In lateral view, their growing anterior margins are inclined anteroventrally at about 45°, the same attitude at which the echmidium of the centronelliform stage lies. The entire loop at this stage is concave in ventral view, although the tips of the descending lamellae do not yet meet to form a complete bowl. In the most advanced of the three precentronelliform individuals (USNM 242121; pl. 3, fig. 3), the tips of the descending lamellae are almost in contact. Spines are developed on the dorsal surfaces of the loop even at this early stage. Within this stage no correlation between valve size and level of loop development was discerned, but the precentronelliform stage commonly is completed by the time the dorsal valve has attained a length of 2 mm.

The centronelliform stage is reached very quickly, with little change in the length of the shell, but it is accompanied by a deepening of the ventral valve. A single specimen (USNM 242122; pl. 3, fig. 4) represents this extremely brief developmental stage. No median ventral plate is present; rather the two branches are simply fused. They do not butt squarely but are directed ventromesially, and their ends are broadened anteroventrally to form the echmidium—the tip of which projects ventrally beyond the commissural plane.

The cryptacanthiform stage is represented by three specimens (USNM 242123, 242124, 242125; pl. 3, figs. 5–7) having valve lengths of about 2 mm. In this stage a typical cryptacanthid "ring" or "hood," closed both anteriorly and posteriorly, is not developed. Instead, the growing edges, in the median line, quickly shift from the anteroventrally directed oblique position of the centronelliform stage to a ventrally directed orientation by means of more rapid growth of the dorsal parts of the ascending lamellae. As this growth progresses, the two branches of the loop are joined only proximally, and the distal (anterior) extremities remain separated. At the close of this stage (USNM 242125; pl. 3, fig. 7), the mesial parts of the ventral margin of the ascending lamellae begin to grow anteriorly, subparallel to the commissural plane, and the proximal junction of the descending lamellae is resorbed. At this point the cryptacanthiform stage ends, and the glossothyropsiform stage begins.

The glossothyropsiform stage, present during most of the postembryonic development of *O. thaynesiana*, is initiated

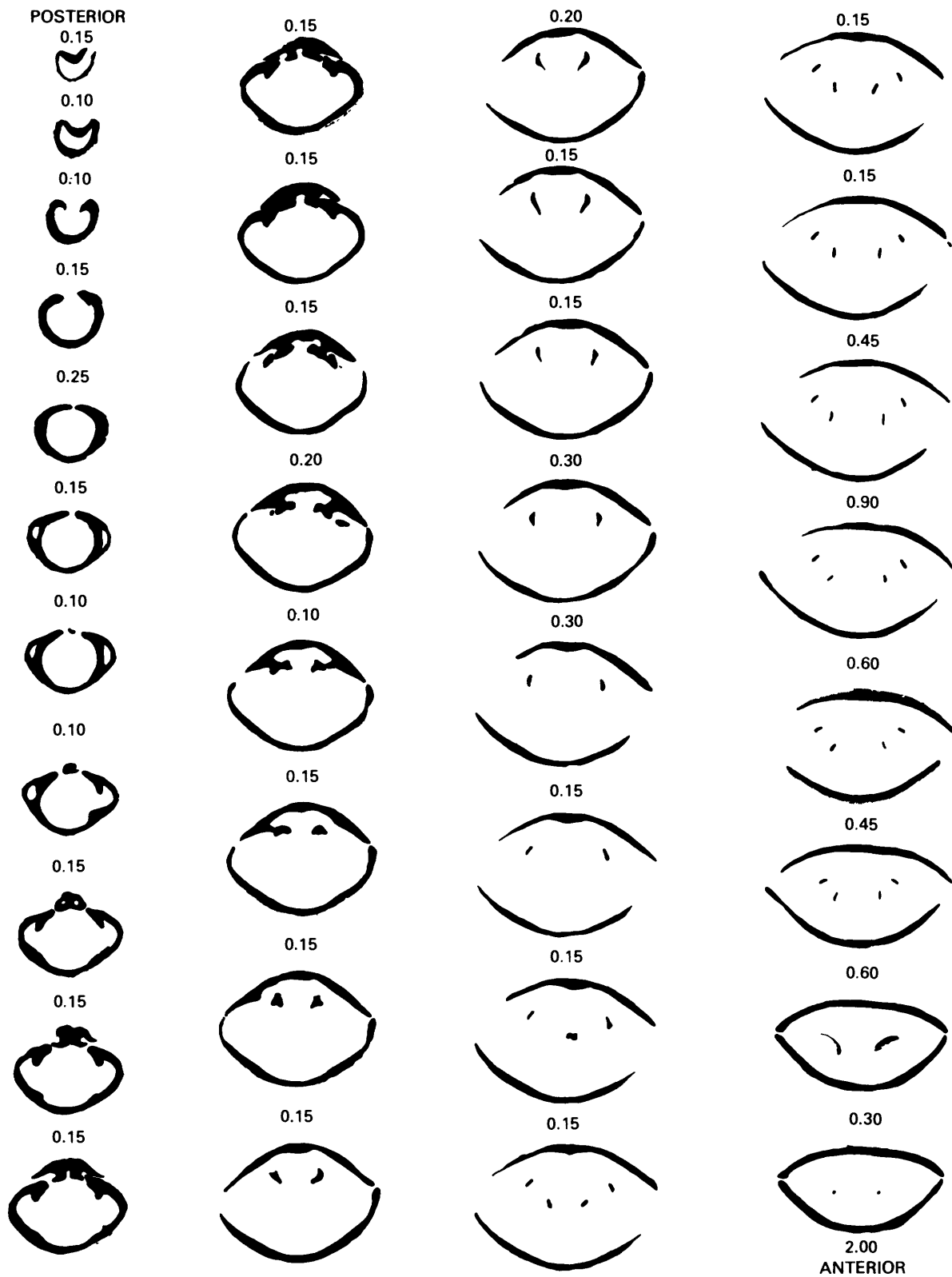


FIGURE 8.—Thirty-five parallel serial sections of a paralectotype specimen (USNM 242139) of *Obnixia thaynesiana* (Girty) from southeastern Idaho (loc. 21). Section planes are oriented normal to the longitudinal axis of the shell. Numbers indicate distance (in millimeters) between successive sections. All sections $\times 4.0$.

at a valve length of about 2.5 mm. It is represented in the present collection by nine specimens, of which six are figured (USNM 242128, 242129, 242131-242134; pl. 3, figs. 8-13). The anterior growth of the ascending lamellae is not so rapid in this stage as that of the descending lamellae, which continue to broaden and grow anteriorly. The junction of the two sets of lamellae becomes increasingly marked, through anterior growth and posterior resorption, so that in the mature glossothyropsiform loop, dorso-ventrally oriented elements in the posteromesial parts of the ascending branches are totally resorbed, and only those parallel to the commissural plane and to the shell's longitudinal axis remain. During this stage the loop grows distally, but the flat surfaces of the descending and ascending lamellae remain essentially parallel. In the adult loop the planar surfaces of all parts of the loop and the crural processes are oriented anteroventrally and (or) laterally (distally).

Superfamily DALLINACEA Beecher, 1893

Family ZEILLERIIDAE Rollier, 1915

Genus PERIALLUS, n. gen.

Etymology of name.—Gr. *periallos* = before all others.

Diagnosis.—Rectimarginate to uniplicate or paraplicate zeilleriids having a distinct pedicle collar, inner hinge plates and (or) septalial plates, and profusely spinose descending lamellae.

Description.—Zeilleriids having smooth unequally biconvex valves, wide ventral umbo, and semierect beak. Anterior commissure variable; rectimarginate in smaller specimens to uniplicate or paraplicate in larger.

Ventral valve having large mesothyridid pedicle foramen and prominent disjunct deltidial plates. Beak broad; beak ridges prominent, sharp, in dorsal view defining large interarea.

Dorsal valve markedly transverse, has small beak and low umbo.

Ventral interior having distinct pedicle collar and strong dental plates. Hinge teeth strong. Muscle scars elongate triangular, commonly extending about one-half valve length.

Dorsal interior having broadly divergent sockets and posterodistally hooked inner socket ridges. Narrow outer hinge plates arising at about midheight of inner socket ridges, directed approximately in plane of commissure. Crural bases with short crural processes; arising from midwidth of hinge plates. Inner hinge plates present or absent; septalial plates variably disposed—vertical, joining valve floor, or dorsomesially directed, forming small septalium. Median septum of variable strength, extending about one-half valve length, present in all observed growth stages. Septal pillar and (or) median septum involvement in loop development not observed. Mature zeilleriiform loop long, commonly about two-thirds valve length; wide, commonly about one-half valve width; composed entirely of primary elements.

Dorsal surface of descending lamellae profusely spinose. Cardinal area not well developed, commonly expressed as low shelf, overhanging umbo.

Type species.—*Periallus woodsidensis*, n. sp.

Occurrence.—*P. woodsidensis*, n. sp., has been recovered from the Woodside Formation in Caribou and Bear Lake Counties, southeastern Idaho, and from the Dinwoody Formation in nearby Wyoming and Montana. A larger form, less confidently assigned to that species, but definitely referable to the genus, comes from the "Ross Fork Limestone Member" of the Thaynes Formation in Caribou County, Idaho.

Comparison.—*Periallus* is easily distinguished from the four known Triassic zeilleriid genera by its rectimarginate to uniplicate or paraplicate anterior commissure. In addition, it differs from *Zeilleria* Rollier, *Aulacothyris* Douville, and *Kolymithyris* Dagens, in bearing a distinct pedicle collar. It differs from both *Zeilleria* and *Woroboviella* Dagens in its long dorsal median septum. *Kolymithyris* is easily distinguished by its thickened cardinalia.

Discussion.—The Zeilleriidae, placed within the Dallinacea following the usage of Dagens (1974), includes those forms in which the loop is not connected to any anteromesial structure in the dorsal valve during ontogeny. Although not even a relatively complete loop development series is available for *Periallus*, the smallest specimens examined (about 2 mm long) show no evidence of such an anteromesial structure.

Dagens (1974) stated that profusely spinose loops are common in Middle Jurassic and younger dallinids but are unusual in the older true zeilleriids. This trait, however representative, cannot be construed as an argument against the assignment of *Periallus* to the Zeilleriidae. That assignment is made on the basis of the basic loop character and diagnostic features of the dorsal cardinalia.

***Periallus woodsidensis*, n. sp.**

Plate 4, figures 1-15.

Terebratula margaritowi Bittner, in Newell and Kummel, 1942, Geol. Soc. America, Bull., v. 53, p. 954, pl. 2, figs. 5a,b (non *T. margaritowi* Bittner, 1899, Comité Géol. St. Petersburg Mém., v. 7, p. 27, 28, pl. 4, figs. 9-15 = *Fletcherithyris* Campbell).

Etymology of name.—*Woodside* = Formation name + *L. -ensis* = at the place of.

Diagnosis.—Small *Periallus*.

Description.—Small smooth unequally biconvex zeilleriid, having a wide ventral umbo and semierect beak. Subtriangular or oval to subpentagonal in outline; commonly widest slightly anterior to midlength; deepest at about midlength. Anterior commissure rectimarginate, uniplicate, or paraplicate. Outermost growth increments commonly imbricate or lamellose.

Ventral valve more convex, having large mesothyridid pedicle foramen and prominent disjunct deltidial plates.

Beak ridges prominent, sharp, defining curved palintrope. Beak wide, large, in dorsal view producing large interarea.

Dorsal valve less convex, markedly transverse, has small beak and low umbo.

Ventral interior having distinct pedicle collar and strong dental plates. Hinge teeth strong, tabular, hooked dorsally, directed anteromesially. Growth traces of hinge teeth present as low ridges on dorsomesial surfaces of dental plates. Muscle scars elongate triangular, commonly extending about one-half valve length.

Dorsal interior having broadly divergent sockets and posterodistally hooked inner socket ridges. Narrow outer hinge plates arising at about midheight of inner socket ridges, directed approximately in plane of commissure. Crural bases have short crural processes directed ventromesially at about 45°, arising from midwidth of hinge plates. Disjunct, narrow, elongate triangular inner hinge plates present or absent, variably expressed, produced mesially in plane of commissure; parallel bordered posteriorly, margins diverging anteriorly. Septalial plates variably expressed: as short vertical apical plates connecting inner hinge plate and crural base to valve floor or as obliquely inclined plates uniting dorsally with low median septum to form septalium. Median septum commonly prominent, extending about one-half valve length, present in all observed growth stages. Neither septal pillar nor median septum involvement in loop development observed. Mature loop zeilleriiform: long, commonly about two-thirds valve length; wide, commonly about one-half valve width, composed entirely of primary elements; having broadly curved anteriorly convergent but widely separated descending lamellae and broad ascending lamellae. Entire dorsal surface of descending lamellae profusely spinose. Cardinal area not well developed, commonly expressed as low transverse bipartite smooth shelf overhanging umbo.

	Holotype		Paratypes	
	USNM 242140	USNM 242141	USNM 242142	USNM 242143
Locality 1				
<i>Measured in millimeters</i>				
Length	5.8	6.5 _b	7.0 _{be}	
Width	5.7	7.2 _h	6.4 _h	
Thickness	2.9	3.7	2.9 _c	
Dorsal valve length	5.0	5.4 _b	5.7 _{be}	7.1
Dorsal valve width				6.8 _h
Loop length				4.8
Loop width				3.6 _h
Distance to crural processes				1.5
Length of ascending lamellae				2.0
Loop depth				0.9
Anterior separation				2.4 _h

Types.—Holotype: USNM 242140; figured paratypes: USNM 242143-242153; measured paratypes: USNM 242141-242143.

Occurrence.—*Periallus woodsidensis* was recovered only from Caribou and Bear Lake Counties, southeastern Idaho, where it occurs in the Woodside Formation (locs. 1, 11; fig. 1; "Fossil Localities Cited in this Report"). Specimens described by Newell and Kummel (1942) as *T. margaritowi*

are here referred to *Periallus* on the basis of the broad ventral beak, rectimarginate to paraplicate commissure, zeilleriid loop, and characteristic septalial plates and median septum. Those specimens were collected from the Dinwoody Formation in the Salt River Range, Lincoln County, Wyo. Newell and Kummel cited the distribution of this form as including southeastern Idaho but did not specify other localities further.

Comparison.—The genus *Periallus* is monotypic. *P. woodsidensis* is easily distinguished from *Obnixia thayne-siana* (Girty) by its rectimarginate to paraplicate anterior commissure and persistent strong dorsal median septum, which commonly extends half the length of the valve. It is very similar to *Fletcherithyris margaritowi* (Bittner), reported from the Induan Stage (*Proptychites* zone) of eastern Siberia (Primor'ye) and from the Olenekian Stage of Mangyshlak, U.S.S.R. (Dagys, 1965). It differs from *F. margaritowi* in bearing a zeilleriiform ("long") rather than a dielasmatic ("short") loop. In view of the recent justified combination of long- and short-looped forms within the Dielasmaticidae (Dagys, 1972, 1974), it may be that the zeilleriids and dielasmaticids represent stocks more closely related than heretofore thought.

Discussion.—The terminology conventionally used (see Campbell, 1965) to describe terebratulid cardinalia is useless to describe *P. woodsidensis* because *P. woodsidensis* has two distinct forms that might logically be termed "inner hinge plates." In the above description, those structures mesial to the crural bases and approximately in the hinge plane are referred to as "inner hinge plates." Those mesial to the crural bases but dorsally joining either a median septum or the dorsal valve floor are termed "septalial plates," following the usage of Dagys (1974). A wide range of variation in dorsal cardinalia is observed in a single population sample of *P. woodsidensis* from locality 1. At the one extreme, apical straight septalial plates extend almost vertically from the crural bases to the valve floor, flanking the median septum, and distinct inner hinge plates are mesial to the growth traces of the crural bases (pl. 4, fig. 12). In contrast (pl. 4, figs. 11, 14), in some forms, inner hinge plates cannot be discerned, and curved septalial plates join either at the valve floor or atop the median septum, in the latter case forming a septalium.

***Periallus* aff. *woodsidensis*, n. sp.**

Plate 4, figures 16-20.

Description.—One specimen has the following measurements (in millimeters):

Locality 35: USNM 242154			
Total length	19.3	Fold height	1.5
Total width	17.9	Distance to crural processes	4.0
Total thickness	8.6 _{be}	Loop length	12.4 _{be}
Dorsal valve length	16.6	Loop width	8.3 _{be}

Types.—Figured and measured specimen: USNM 242154.

Discussion.—Several specimens of *Periallus* questionably assigned to *P. woodsidensis* were recovered from locality 35,

in the "Ross Fork Limestone Member" of the Thaynes Formation, Bingham County, Idaho. Although no complete loop is preserved intact in any of the specimens, one specimen (USNM 242154) contained fragments of the descending and ascending lamellae sufficiently complete to determine the spinose character of the former and the zeilleriid form of the latter. The uniplicate commissure of these forms seems a reasonable outgrowth of the shell form seen in *P. woodsidensis*. The dorsal median septum, however, is not well preserved. The variations in cardinal plate arrangements are similar to those in *P. woodsidensis*, and the larger specimen may represent an adult of that form. The absence of forms intermediate in size and development between the two at any examined locality is the rationale for excluding the above specimens from formal specific status.

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PLATES 1-4

Contact photographs of the plates in this report are available, at cost, from the U.S. Geological Survey
Photographic Library, Federal Center, Denver, Colorado 80225.

PLATE 1

[The object plane parallax for stereo views is 6°]

FIGURES 1-10. *Portneufia episulcata*, n. gen., n. sp. (p. 8).

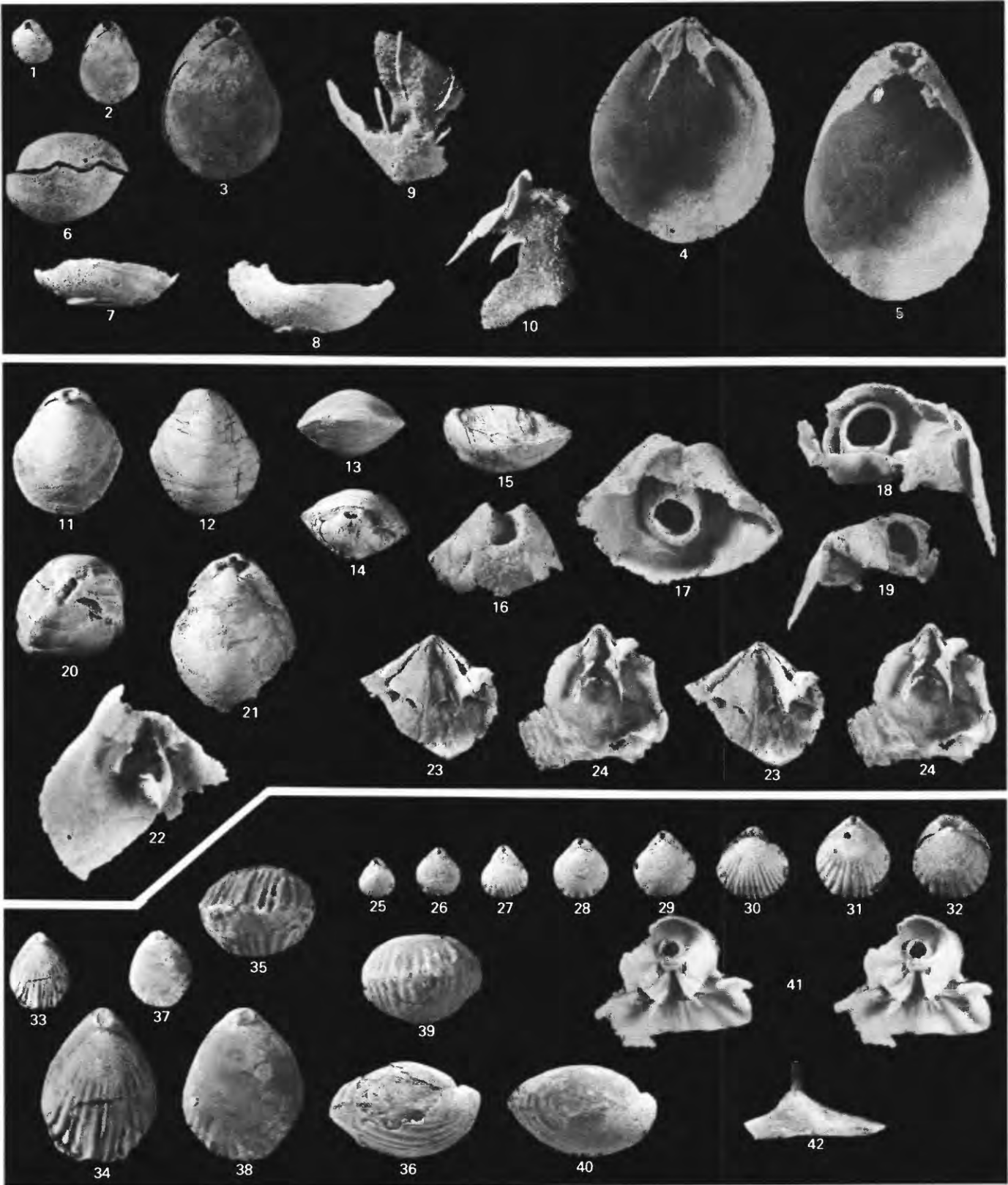
1. Paratype, articulated valves, dorsal view, × 1; showing asymmetric apparent immature individual; USNM 242049; USGS loc. 1271-PC.
 - 2-8. Holotype, separable dorsal and ventral valves;
 2. Articulated valves, dorsal view, × 1, for scale.
 3. Dorsal view, × 2, for comparison.
 4. Dorsal valve, ventral (interior) view, × 3, showing median septum and character of cardinalia.
 5. Ventral valve, dorsal (interior) view, × 3, showing pedicle foramen, deltidial plates, and character of hinge teeth.
 6. Articulated valves, anterior view, × 2, showing episulcate commissure.
 7. Dorsal valve, lateral view, × 2, showing resected beak area at left.
 8. Ventral valve, lateral view, × 2, showing expanded beak area at left.
- Specimens shown in figs. 2-8: USNM 242051; USGS loc. 1271-PC.
- 9, 10. Paratype, fragment containing loop elements, dorsal and ventral views, × 3, showing long descending and ascending lamellae and anteromesially directed crural processes; USNM 242053; USGS loc. 1271-PC.

11-24. *Rhaetina incurvirostra*, n. sp. (p. 9).

- 11-15. Holotype, articulated valves; dorsal, ventral, anterior, posterior, and lateral views, × 1; USNM 242054; USGS loc. 1291-PC.
- 16, 17. Paratype, fragment of ventral valve; ventral view, × 2, showing elongate pedicle foramen; dorsal (interior) view, × 3, showing elongate tubular pedicle collar, concave surface of disjunct deltidial plates, and lack of dental plates; USNM 242058; USGS loc. 1291-PC.
- 18, 19. Paratype, fragment of slightly crushed ventral valve; dorsal view (inverted), × 3, showing relation of hinge tooth to deltidial plates; anterodorsolateral view, × 2, showing relation of pedicle foramen and hinge tooth; USNM 242059; USGS loc. 1291-PC.
20. Paratype, fragment of slightly crushed articulated valves, oblique posterior view, × 1, showing relation of ventral beak to hinge; USNM 242060; USGS loc. 1291-PC.
21. Paratype, nearly complete articulated valves, ventral beak missing, dorsal view, × 1, showing small acute dorsal umbo; USNM 242055; USGS loc. 1291-PC.
22. Paratype, fragment of dorsal valve of apparent immature individual, ventral (interior) view, × 8, showing descending lamella and transverse band; USNM 242056; USGS loc. 1291-PC.
23. Paratype, fragment of dorsal valve, ventral (interior) view (stereo), × 2, showing relation of crural processes, inner and outer hinge plates, and median septum; USNM 242057; USGS loc. 1291-PC.
24. Paratype, fragment of dorsal valve, ventral (interior) view (stereo), × 1.5, showing partial dielasmoid loop with broad descending lamellae and long slender transverse band; USNM 242731; USGS loc. 1291-PC.

25-42. *Vex semisimplex* (White) (p. 10).

- 25-32. Figured specimens, articulated valves, dorsal views, × 1, showing simulated growth series and variation in form and radial ornament; USNM 242071, 242072, 242065, 242073, 242074, 242063, 242069, and 242075; figs. 25, 26, 28, and 29 from USGS loc. 1289-PC; fig. 27 from USGS loc. M-853; fig. 30 from USGS loc. 826-PC; fig. 31 from USGS loc. 1284-PC; fig. 32 from USGS loc. 7813-(Green).
 - 33-36. Paralectotype, articulated valves. (This specimen was serially sectioned parallel to the commissural plane; selected sections appear on pl. 2, figs. 1-5.)
 33. Dorsal view, × 1, for scale.
 34. Dorsal view, × 2, for comparison.
 35. Anterior view, × 2, showing rectimarginate to incipiently unipli-cate commissure.
 36. Lateral view, × 2, showing equibiconvex profile and semierect ventral beak.
- Specimen shown in figs. 33-36: USNM 8190b; USNM loc. 9344.
- 37-40. Lectotype, articulated valves, views and magnifications as in figs. 33-36 above, for comparison; USNM 8190a; USNM loc. 9344.
 41. Figured specimen, Fragment of articulated valves, anteroventral (interior) view (inverted; stereo), × 3, showing pedicle collar, cardinal process, hinge structures, and nature of dorsal cardinalia; USNM 242081; USGS loc. 1284-PC.
 42. Figured specimen, fragment of descending lamellae of dorsal valve, lateral view, × 8, showing elongate crural processes; USNM 242082; USGS loc. 1284-PC.

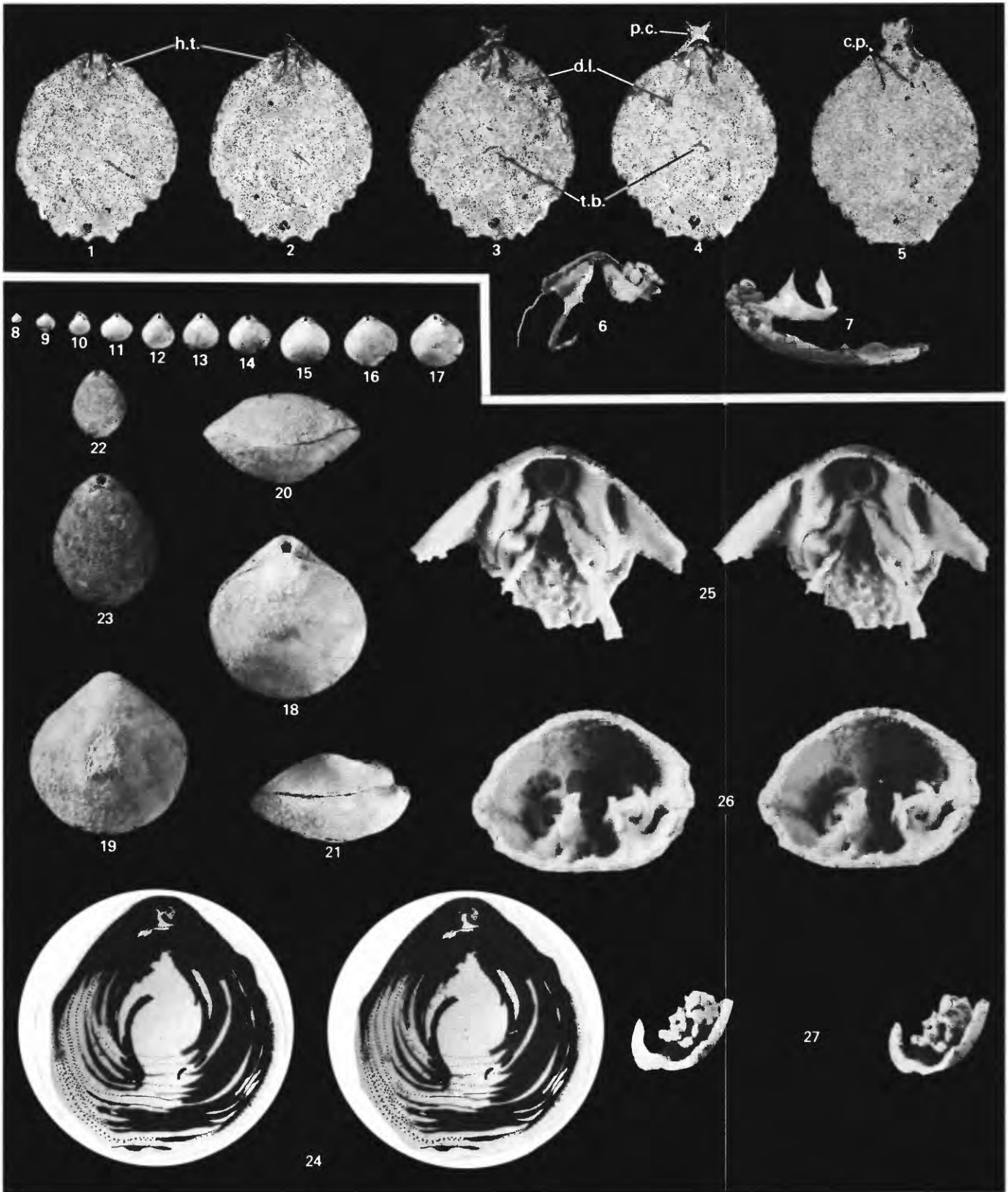


PORTNEUFIA, RHAETINA, AND VEX

PLATE 2

[The object plane parallax for stereo views is 6°]

- FIGURES 1-5. *Vex semisimplex* (White), (p. 10) paralectotype, articulated valves, serial peels parallel to commissural plane (peel interval 0.15 mm) × 3, showing ventral valve pedicle collar (p.c.), hinge teeth (h.t.), dorsal valve crural processes (c.p.), descending lamellae (d.l.), and transverse band (t.b.); sections proceed from dorsal to ventral; USNM 8190b; USNM loc. 9344.
- 6-7. *Plectoconcha aequiplicata* (Gabb) (p. 10), fragment of dorsal valve, ventral (interior) and lateral views, × 3, showing short descending lamellae and wide transverse band of loop, for comparison with figs. 1-5, above; USNM 242083; Leland Stanford Junior University loc. 2532 (Pershing County, Nev., Sonoma Range 1° quad.; sec. 21, T. 28 N., R. 39 E.; Tobin Range, north wall of "Keyhole" Canyon, elev. 6,200 ft; Upper Triassic; Collector: S. W. Muller, August 1941).
- 8-27. *Obnixia thaynesiana* (Girty) (p. 12).
- 8-17. Figured specimens, articulated valves, dorsal views, × 1, simulated partial ontogenetic series, showing size range and variation in shape and form; USNM 242095, 242098, 242100, 242101, 242104, 242105, 242108, 242111, 242115, and 242116; all from USGS loc. 7897 (Green).
- 18-21. Figured specimens, articulated valves, dorsal, ventral, anterior, and lateral views, × 3, showing low beak, rounded beak angles and sulcate anterior commissure of a mature individual; USNM 242116 (same as fig. 17 above); USGS loc. 7897 (Green).
- 22, 23. Lectotype, articulated valves, dorsal views, × 1, for scale, × 2, showing form and outline; USNM 121558; USGS loc. 7406 (Green).
24. Paralectotype, stacked, oriented projections of commissural plane serial peels (peel interval approx. 0.15 mm) of articulated valves, ventral (interior) view (stereo), × 5, showing long anteriorly spinose loop; USNM 242135; USGS loc. 7406 (Green).
25. Figured specimen, fragment of articulated valves, ventral (interior) view (stereo), × 8, showing dental plates and pedicle collar in ventral valve, and lack of prominent median septum or inner hinge plates in dorsal valve; USNM 242136; USGS loc. 7897 (Green).
26. Figured specimen, fragment of articulated valves, anterior (interior) view (dorsal valve down; stereo), × 8, showing tight articulation of recurved hinge teeth and sockets, vestigial apical dorsal median septum, and rudimentary septalial plates; USNM 242137; USGS loc. 7897 (Green).
27. Figured specimen, fragment of articulated valves, anteroventrolateral view (stereo), × 8, showing anterior spines at junction of descending and ascending lamellae of loop; USNM 242138; USGS loc. 7897 (Green).



OBNIxia, PLECTOCONCHA, AND VEX

PLATE 3

[The object plane parallax for stereo views is 6°]

FIGURES 1-13. *Obnixia thaynesiana* (Girty) (p. 12), figured specimens, fragments of articulated valves, dorsal views (stereo), $\times 8$, showing development of glossothyropsiform loop through precentronelliform (figs. 1-3), centronelliform (fig. 4), cryptacanthiform (figs. 5-7), and glossothyropsiform (figs. 8-13) stages; USNM 242119-242125, 242128, 242129, 242131-242134; USGS loc. 7897-(Green).



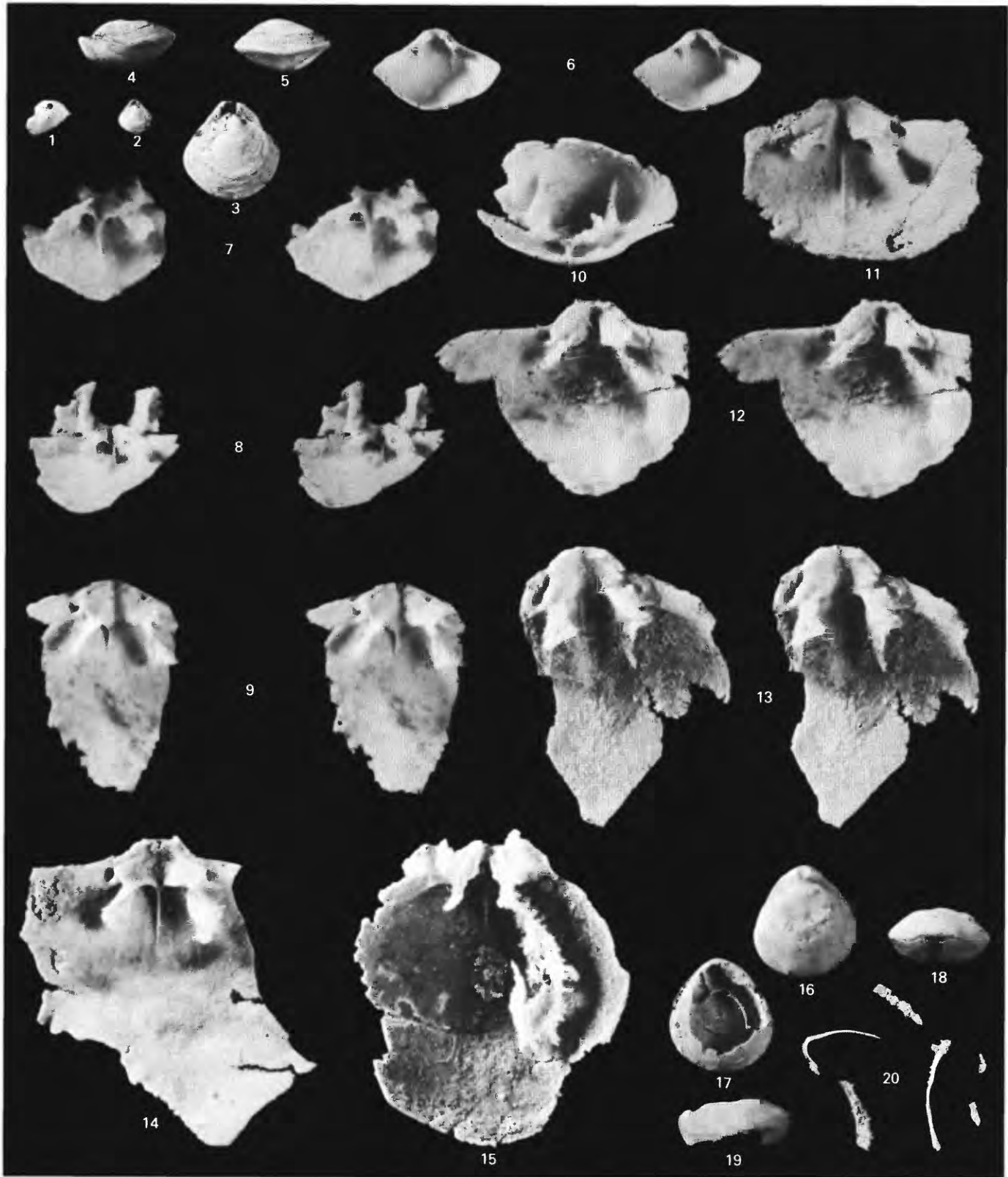
OBNIXIA

PLATE 4

[Unless otherwise noted, the object plane parallax for stereo views is 6°]

FIGURES 1-15. *Periallus woodsidensis*, n. gen., n. sp. (p. 17).

1. Paratype, fragment of articulated valves, dorsal view, $\times 1$, showing small pedicle foramen, wide beak, and well-defined beak ridges; USNM 242144; USGS loc. 76-PC.
 - 2-5. Holotype, articulated valves, dorsal views, $\times 1$, for scale, $\times 3$, showing form and outline; lateral view, $\times 3$, showing profile and form of commissure; anterior view, $\times 3$, showing rectimarginate commissure; USNM 242140; USGS loc. 76-PC.
 6. Paratype, fragment of ventral valve, anterodorsal view (stereo: object plane parallax 3°), $\times 3$, showing dental plates; USNM 242145; USGS loc. 76-PC.
 - 7-9. Paratypes, fragments of articulated valves, anteroventral views (stereo), $\times 8$, showing variation in relationship of septalial plates and median septum in dorsal valve; USNM 242146, 242147, 242149; USGS loc. 76-PC.
 10. Paratype, fragment of articulated valves, anterior view (dorsal valve down), $\times 8$, showing distinct pedicle collar, strong dental plates of ventral valve, and strong median septum in dorsal valve; USNM 242148; USGS loc. 76-PC.
 11. Paratype, dorsal valve, anteroventral view, $\times 8$, showing individual in which septalial plates do not contact median septum; USNM 242153; USGS loc. 76-PC.
 12. Paratype, dorsal valve, ventral view (stereo), $\times 8$, showing differentiation of septalial plates and inner hinge plates; USNM 242150; USGS loc. 76-PC.
 13. Paratype, dorsal valve, ventral view (stereo), $\times 8$, showing high crural processes of mature individual; USNM 242151; USGS loc. 76-PC.
 14. Paratype, dorsal valve, ventral view, $\times 8$, showing septalial plates joining median septum to form septalium; USNM 242152; USGS loc. 76-PC.
 15. Paratype, partial dorsal valve, ventral view, $\times 8$, showing dorsally spinose descending lamella and portion of ascending lamella; USNM 242143; USGS loc. 76-PC.
- 16-20. *Periallus* aff. *woodsidesensis*, n. sp. (p. 18).
- 16-19. Figured specimen, articulated valves, dorsal, ventral (interior), anterior and lateral views, $\times 1$, showing form, outline, and incipient uniplicate commissure; USNM 242154; USGS loc. 7879 (Green).
 20. Figured specimen, fragments of loop, recovered after etching from within the above specimen, various orientations, $\times 2.5$, suggesting that the loop was zeilleriform; USNM 242154; USGS loc. 7879-(Green).



PERIALLUS