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EGBERT G. DRISCOLL,
Wayne State University, Detroit, Michigan

MORPHOLOGY AND EVOLUTION OF CERTAIN PALEOZOIC NUCULANIDAE FROM THE MIDCONTINENTAL UNITED STATES

INTRODUCTION

For over one hundred years certain fossil shells assignable to the family *Nuculanidae* have been reported from the upper Paleozoic strata of the midcontinental United States. The abundance of these shells, particularly in the Pennsylvanian where they often compose a significant portion of the fauna, has led the writer to attempt a reexamination of the group. Names which have previously been applied to these fossils include *Leda bellistriata, Nuculana bellistriata, Nucula arata, Culunana bellistriata,* and *Leda pandoraeformis* among others.

The writer has studied a collection of specimens assembled from various areas and stratigraphic horizons in the midcontinental United States. Three species belonging to the genus *Polidevcia* are redescribed and one species assignable to the genus *Phestia* is reported. A key to the species of *Polidevcia* is presented. Evolutionary trends are discussed. The most significant of these trends in *Polidevcia* are a reduction of the umbonal ridge, a strengthening of the principle internal ridge, and a reduction in the number of concentric ribs.

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ABBREVIATIONS

In reference to particular specimens the following abbreviations are used:

U. M.	University of Missouri
UMMP	University of Michigan, Museum of Paleontology
USNM	United States National Museum
O. S. U.	The Ohio State University

Polidevcia CHERNYSHEV, 1951

Polidevcia CHERNYSHEV, 1943 *(nomen nudum)*
Polidevcia CHERNYSHEV, 1951
Polidevcia SHULGA, 1956
Polidevcia ELIAS, 1957
Culunana LINTZ, 1958
Polidevcia KUMPERA, PRANTL et RŮŽIČKA, 1960
Polidevcia WATERHOUSE, 1965
Culunana McALESTER, 1966
Polidevcia McALESTER, 1966

Type species. By original designation *Leda karagandensis* CHERNYSHEV, 1941.

Polidevcia bellistriata (STEVENS, 1858)

(Pl. 1, Figs. 1—15; Pl. 2, Figs. 1—12; Text-Figs. 1—3)

1858 — *Leda bellistriata* STEVENS, Am. Jour. Sci., 2nd series, v. 25, p. 261, 262.
1858 — *Leda bellistriata* HALL, Rept. Geol. Survey Iowa, v. 1, pt. 2, p. 717, pl. 39, figs. 6a—d.
1898 — *Nuculana bellistriata* WELLER, Bull. U. S. Geol. Survey, 153, p. 380, 381, *in part.*
?1900— *Nuculana bellistriata* BEEDE, Geol. Survey Kansas, v. 6, pt. 2, p. 148, 149.
1915 — *Leda bellistriata* GIRTY, Bull. U. S. Geol. Survey, 544, p. 122—125, pl. 14, figs. 1—9a.
?1922— *Leda bellistriata* MORNINGSTAR, Bull. Geol. Survey Ohio, v. 25, p. 204, 205, pl. 10, fig. 27.
1926 — *Leda bellistriata* BUTTS, Geol. Survey Alabama, Special Rept. no. 14, pl. 66, fig. 10.
1921 — *Leda bellistriata* PLUMMER et MOORE, Univ. Texas Bull. 2132, pl. 7, figs. 1, 5—6a, pl. 14, figs. 13, 14.
1929 — *Nuculana bellistriata* SCHMIDT, Leitfoss. Karbon, p. 47, pl. 11, figs. 11—13.
1931 — *Leda bellistriata* MORSE, Ky. Geol. Survey, Ser. 6, v. 36, p. 315—316, pl. 50, figs. 8—15.
1966 — *Culunana bellistriata* McALESTER, Geol. Soc. Am., Memoir, (in press).

Description. Outline. Anterior margin gently curved in its upper part, more abruptly curved near the anterior extremity of the valves and gently curved in its lower portion to the inferior extreme point where it merges evenly with the lower part of the posterior outline. Lower part of the posterior outline variable; most commonly gently curved from inferior extreme point to rostral extremity but not uncommonly sinuous, being gently convex near the inferior extreme point and the rostral extremity but possessing a gentle concave indentation at a point approximately midway between the two positions. Rostral extremity not commonly preserved; when intact it is variable in outline being sharply rounded or subtruncate. Posterior portion of dorsal outline straight or very slightly concave; more rarely slightly convex; forms angle of approximately 145 ° below beaks with anterior portion of dorsal margin (*dorsal angle* of Kumpera, Prantl et Růžička 1960). Anterior part of dorsal margin short and very nearly straight, merges evenly with upper part of anterior margin. Anterior portion of umbonal outline merges evenly with anterior outline in most specimens but in others these two outlines meet at slight angle giving rise to indented appearance of antero-dorsal portion of shell in lateral view. Posterior portion of umbonal outline drops in sharp concave curve from beak to its intersection with the posterior portion of the dorsal margin.

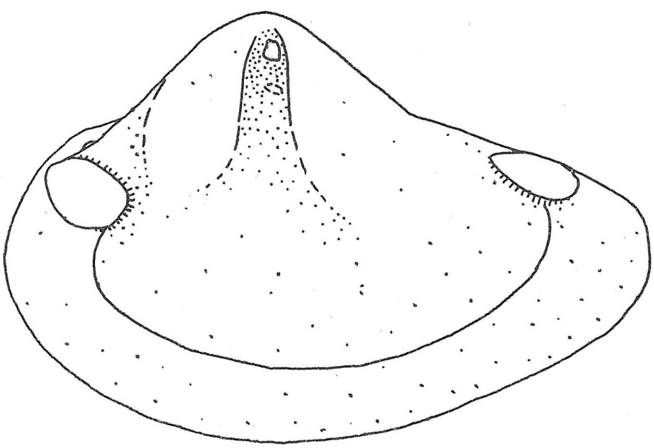
Convexity. Valves moderately to strongly convex. The line of maximum convexity passes from the beaks to the lower part of the anterior outline. The point of maximum thickness lies in the middle third of the valve height. Posterior keel moderate to prominent; acute throughout, most pronounced approximately midway between beaks and posterior extremity, becomes less conspicuous near beaks, merges with general valve convexity at rostral extremity.

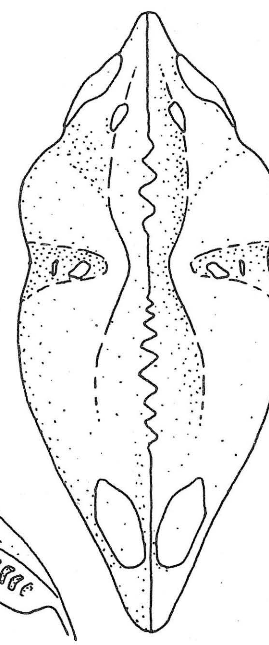
Beaks. Tumid, rounded, contiguous, strongly incurved above the hinge line, distinctly opisthogyrate, situated somewhat anterior to mid-length of the valves.

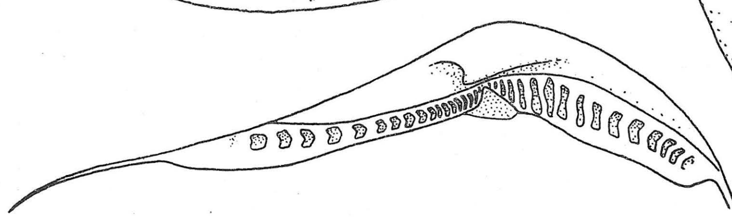
Escutcheon. Long, distinctly depressed, raised along the dorsal margin in the posterior part (Pl. 2, Fig. 4), divided into two parts by a sharp thin rib which begins at the beak of each valve and extends in a curve to a point in the middle third of the elevated dorsal margin. In dorsal view the inner escutcheon (that portion bounded by the sharp thin rib) is lanceolate and, on well preserved specimens, this lanceolate area bears very fine striations which diverge slightly from the dorsal margin posteriorly and are somewhat more pronounced along the posterior edges of the lanceolate area. These striations terminate within the inner escutcheon, not crossing the sharp thin rib. The outer part of the escutcheon bears coarser ribbing which, on most specimens, first appears at the margins of the inner escutcheon, diverges posteriorly toward the margins of the escutcheon, becomes weak or nearly absent over the posterior umbonal ridge, but is continuous with the concentric ribbing of the valve surface. In the outer escutcheon this ribbing forms an obtuse angle with the striae of the inner escutcheon near the beaks but is nearly parallel to the striations in the posterior part of the inner escutcheon. On some specimens the ribbing extends into the inner lanceolate escutcheon.

Lunule. Narrow, shallow, lanceolate and often inconspicuous: bears very fine striations which diverge very slightly from the dorsal margin anteriorly.

Ligament. A number of well preserved specimens show curved lines of elongate perforations which extend subparallel to the sharp thin rib separating the inner and outer escutcheonal areas and subparallel to the margins of the lunule. These are thought to be terminal points of the horny process (Sorgenfrei 1936). They become larger and more widely separated anteriorly and posteriorly from the beaks. Near the beaks the line of perforations lies upon the rib defining the inner escutcheon but it is progressively further outside this rib in a posterior direction and the position of the perforations is not believed to be in any way controlled by the position of the rib. Anteriorly the lines of perforations are very nearly coincident with the margins of the lunule. In 10 specimens examined the lunules showed a maximum of 10 perforations per valve and a minimum of 6. Escutcheons showed a maximum of 18 per valve and a minimum of 7. Perforations are arranged alternately between the valves, not directly opposite one another, and the positions of perforations correspond to the apices of the sockets, each perforation being located directly above the termination of a dental socket. This relationship accounts for the curved nature of the line of perforations as well as for the fact that they become more widely separated as distance from the beaks is increased.







TEXT FIG. 1. Idealized lateral view of internal mold of *Polidevcia bellistriata*. Primarily based on hypotype O. S. U. 19794 from the Kanwaka Shale.
TEXT FIG. 2. Idealized dorsal view of internal mold of *Polidevcia bellistriata*. Note pattern of accessory muscle scars and distribution of internal ridges. Primarily based on hypotype O. S. U. 19794 from the Kanwaka Shale.
TEXT FIG. 3. Idealized drawing of the dentition of *Polidevcia bellistriata*. Note that dentition is continuous above triangular resilifer. Primarily based on hypotype U. M. 16172 from the Graford Formation.

H i n g e . Taxodont dentition. Anteriorly hinge plate extends from below beak to just beyond anterior extremity of lunule and is slightly convex upward. Posterior hinge plate somewhat longer, extending from below beak to just beyond posterior extremity of inner escutcheon and being slightly concave upward. Teeth closely spaced below beaks, becoming more widely separated anteriorly and posteriorly. Teeth immediately anterior to beak straight but become cheveron-shaped on more anterior portions of the hinge plate with the apex directed toward the beaks. Posterior teeth cheveron-shaped with apex directed toward beaks. Triangular resilifer present below beaks (Text-Fig. 3, Pl. 1, Fig. 12). Teeth become greatly reduced above resilifer but dentition is continuous along entire hinge plate.

M u s c l e s c a r s . Posterior adductor muscle scar sub-oval, wider posteriorly than anteriorly, elongate in an anterior-posterior direction, placed immediately adjacent to keel, but not extending onto that structure, anterior extremity of scar situated near posterior extremity of dentition, anterior border of scar deeply incised into shell. Anterior adductor scar subcircular, adjacent to anterior margin of shell immediately below anterior extremity of hinge plate, posterior border of scar deeply incised into shell (Text-Figs. 1, 2; Pl. 1, Figs. 1—3, 12).

P a l l i a l l i n e . Extremely weak, even on well preserved specimens the pallial line cannot be traced throughout its course.

I n t e r n a l r i d g e s . Principal internal ridge (*umbonal ridge* of Kumpera, Prantl et Růžička 1960) is high and sharply defined in umbonal region, becomes broader and lower as it extends ventrally and curves posteriorly, merges with valve convexity near pallial line, ridge not prominent on small specimens. A second less prominent but still conspicuous internal ridge extends from the umbonal region to the base of the anterior adductor scar. A third weakly developed internal ridge is commonly observed in the posterior end of the valves. This ridge, or weak fold, is most pronounced below the posterior adductor scar, disappearing as it is traced anteriorly toward the umbo.

A c c e s s o r y m u s c l e s c a r s . Arrangement of accessory muscle scars is shown in Text-Figs. 1, 2.

S u r f a c e s c u l p t u r e . Regular, narrow, closely spaced concentric ribs cover the surface of the valves, imbricate from below upward, parallel to the valve margins. Over the umbonal ridge (*keel* of Kumpera, Prantl et Růžička 1960) concentric ribs become much reduced or, less commonly, disappear entirely. On most specimens at least some of the ribs may be traced over the umbonal slope onto the outer part of the escutcheon. No concentric sculpture present internally (Pl. 1, Fig. 5).

R e m a r k s . Table 1 outlines the characteristics which may be used to distinguish *Polidevcia bellistriata* from *P. arata* and *P. pandoraeformis.* Text-Fig. 2 illustrates the accessory muscle scars of *P. bellistriata.* Two scars are present on the umbonal portion of the principal internal ridge, the more dorsal being the larger and more pronounced. These are thought to represent the points of attachment of the dorsomedian and ventromedian muscles (Driscoll 1964). The elongate and oval scars located near the dorsal margin posteriorly represent the posterior re-

TABLE 1

Polidevcia bellistriata	*Polidevcia arata*	*Polidevcia pandoraeformis*
No keel anterior to beaks.	Slight keel anterior to beaks.	No keel anterior to beaks.
Lunule weak, not distinct anteriorly.	Lunule clearly defined, shorter than in *P. bellistriata.*	Lunule weak.
Concentric ribs numerous, parallel to valve margins.	Concentric ribs strong, not parallel to valve margins.	Concentric ribs numerous, parallel to valve margins.
Rib dividing inner and outer escutcheon weak, joins dorsal margin in middle 1/3 of distance from beak to rostral extremity.	Rib dividing inner and outer escutcheon strong, joins dorsal margin in middle 1/3 of distance from beak to rostral extremity.	Ridge dividing inner and outer escutcheon weak, joins dorsal margin about 1/3 of distance from beaks to rostral extremity.
Anterior dorsal margin curved evenly into anterior margin.	Obtuse angle between anterior part of dorsal margin and dorsal part of anterior margin.	Anterior dorsal margin curved evenly into anterior margin.
Markedly opisthogyrate.	Slightly opisthogyrate or nearly orthogyrate.	Strongly opisthogyrate.
Internal ridges strong.	Internal ridges strong.	Internal ridges weak.
Valves strongly convex.	Valves strongly convex.	Valves weakly convex.
Umbonal ridge moderate.	Umbonal ridge moderate.	Umbonal ridge very sharp.
Inner escutcheon striated.	Inner escutcheon striated.	Inner escutcheon striated, with a series of warps above teeth.

tractor muscles and the single pair of accessory muscle scars found near the anterior dorsal border represent either the anterior protractor or anterior retractor muscles, probably the former. Two small weak accessory scars found just posterior to the principal internal umbonal ridge in the umbonal region are thought to be related to activity other than foot movement.

Occurrence. *Polidevcia bellistriata* occurs throughout the Pennsylvanian System but has not been reported from older rocks. It is most plentiful in the Pennsylvanian of Oklahoma but has been reported from widely separated areas of the United States where Pennsylvanian strata outcrop.

Branson (1930, p. 43) has commented that "Typical specimens of *L. bellistriata* occur in the Rex Chert member of the Phosphoria Formation in the Fort Hall Indian Reservation, Idaho." I have examined a single silicified specimen from this locality (U. M. 5273). This Lower Permian specimen is assignable to *Polidevcia bellistriata* and represents the highest reported stratigraphic occurrence of the species.

Types. Stevens' primary types are lost. Topotype material collected by James Murphy from the Brush Creek Limestone at Summit Cut, Summitville, Columbiana County, Ohio is available. From this material the writer here designates as neotype a complete specimen, O. S. U. 19791 (Pl. 1, Figs. 13—15). Hypotypes from the same locality consist of a right valve, O. S. U. 19792 (Pl. 1, Fig. 4) and a left valve, O. S. U. 19793 (Pl. 1, Fig. 9). Three hypotypes examined by Charles Butts (1926) are figured (Pl. 2, Figs. 1—12). One of these, USNM 47156, was previously figured by Butts (1926, Pl. 66, Fig. 10).

Additional hypotypes include a well preserved left valve showing a resilifer from the Pennsylvanian Graford Formation, U. M. 16172 (Pl. 1, Figs. 10—12), a whole specimen from the same locality, U. M. 16175 (Pl. 1, Figs. 5—8), and a well preserved internal mold from the Kanwaka Shale, Shawnee Group of Osage Co., Oklahoma, O. S. U. 19794 (Pl. 1, Figs. 1—3).

Polidevcia arata (HALL, 1852)
(Pl. 3, Figs. 1—14)

1852 — *Nucula arata* HALL, *in* STANSBURY, Exploration and Survey of the Valley of the Great Salt Lake of Utah, ... U. S. 32nd Cong. Spec. Sess., Executive No. 3, p. 413, Pl. 2, figs. 5a—b.
1869 — *Leda bellistriata* ? *SAFFORD,* Geology of Tennessee, p. 444.
1871 — *Leda bellistriata* ? WINCHELL, Proc. Am. Philo. Soc., v. 11, p. 256.
1884 — *Nuculana bellistriata* WHITE, 13th Ann. Rept. Dept. Geol. and Nat. Hist. Indiana, 1883, p. 146, Pl. 31, figs. 8, 9.
?1888— *Nuculana bellistriata* KEYES, Proc. Acad. Nat. Sci. Phila., p. 233.
?1894— *Nuculana bellistriata* KEYES, Missouri Geol. Survey, v. 5, p. 122, PL. 45, figs. 4a—b.
1896 — *Nuculana* aff. *bellistriata* SMITH, Proc. Am. Philo. Soc., v. 35, no. 152, p. 245.
1909 — *Leda bellistriata* GRABAU et SHIMER, North American Index Fossils, Invertebrates, v. 1, p. 401, text-figs. 512a, b.
1898 — *Nuculana bellistriata* WELLER, U. S. Geol. Survey, 153, p. 380, 381 *in part.*
1958 — *Culunana bellistriata* LINTZ, Jour. Paleontol., v. 32, p. 107—108, Pl. 16, figs. 16, 17.

Description. Outline. Anterior margin gently curved in its upper part, more abruptly curved near the anterior extremity, being bluntly pointed on some specimens and evenly and gently curved in its lower portion to the inferior extreme point where it merges evenly with the lower part of the posterior outline. Posterior part of dorsal outline evenly and gently curved in most specimens, occasionally sinuous with gentle concave indentation in the area corresponding to the ventral extremity of the principal internal ridge. Rostral extremity sharply rounded. Posterior portion of the dorsal margin straight or slightly concave, possessing a small but distinct convex bulge at the point where the rib separating the inner and outer escutcheon meets the dorsal margin. Posterior portion of the dorsal margin forms angle of approximately 155° with the anterior part of the dorsal margin immediately below beaks (*dorsal angle* of Kumpera, Prantl et Růžička 1960). An obtuse angle is present in the outline where the anterior portion of the dorsal margin joints the anterior outline. Anterior portion of umbonal outline meets anterior part of dorsal outline at an obtuse angle, never merges evenly. Posterior portion of the umbonal outline extends in gentle concave curve from beaks to its intersection with the posterior part of the dorsal margin.

Convexity. Valves moderately to strongly convex. Line of maximum convexity extends from beaks to the lower part of the anterior outline. The point of maximum thickness is variable but lies in the middle third of the valve, most commonly in the upper part of the middle third. Posterior keel prominent from rostral extremity to rib separating inner and outer escutcheon, most pronounced near this rib, weak within the inner escutcheon, merges with general valve convexity at the rostral extremity.

Beaks. Tumid, rounded, contiguous, strongly incurved above the hinge line, very slightly opisthogyrate or nearly orthogyrate, situated approximately 2/5 of the total valve length from the anterior extremity.

Escutcheon. Long, distinctly depressed, raised along the dorsal margin in the middle and posterior part (Pl. 3, Fig. 7), divided into two parts by a sharp thin rib which begins at the beak of each valve and extends in a curve to a point in the middle third of the elevated dorsal margin (Pl. 3, Fig. 5). Keeled dorsal margin often sharply raised where intersected by this rib. In dorsal view the inner escutcheon (that portion bounded by the sharp thin rib) is lanceolate. The inner escutcheon is striated and the outer escutcheon is ribbed, the pattern of striations and ribs being identical to that found in *Polidevcia bellistriata* but varying in strength from specimen to specimen.

Lunule. Narrow, shallow, lanceolate and depressed; bears very fine striations extending subparallel to the dorsal margin. Lunule border well defined on most specimens.

Ligament. Lines of elongate perforations subparallel to the lunule and inner escutcheon are thought to be present. These are believed to be terminal points of the horny process (Sorgenfrei, 1936). On no specimen are they well preserved and they have only been observed with certainty bordering the escutcheon.

Hinge. Taxodont dentition. No specimens with well preserved dentition available. Posteriorly hinge plate extends to just beyond posterior extremity of inner escutcheon. Presence of resilifer suspected but not confirmed in this species.

Muscle scars. No specimens illustrate well preserved interiors. Both the adductor and accessory muscle scar patterns appear, from poorly preserved material, to be similar to those found in *Polidevcia bellistriata.*

Internal ridges. Strong internal ridges are present in very nearly the same positions as in *P. bellistriata.*

S u r f a c e s c u l p t u r e. Strong, regular, concentric, flat-topped ribs cover the surface of the valves, but disappear posteriorly before reaching the umbonal ridge (*keel* of Kumpera, Prantl et Růžička 1960). In cross-section ribs are more abruptly rounded on dorsal edge and merge more evenly with general valve convexity on ventral edge; separated by gentle concave rib-interspaces (Pl. 3, Fig. 4). Ribbing is very nearly parallel to valve margins but a slight angular relationship is universally present; a few more ribs being present on posterior portions of the shell and intersecting the ventral valve margin at an angle of only slightly less than 180°. Extremely fine growth lines, parallel to the valve margins, present on well preserved specimens. These show a small-angle relationship to ribbing and are best preserved in the rib interspaces.

R e m a r k s. Table 1 outlines the characteristics which may be used to distinguish *Polidevcia arata* from *P. bellistriata* and *P. pandoraeformis.*

O c c u r r e n c e. *P. arata,* though less abundant than *P. bellistriata,* is plentiful throughout the Pennsylvanian System of the central United States. From the collections at hand it is clear that the geographic distribution of the species extends from central Texas through Oklahoma, Missouri, Illinois and into Indiana. The stratigraphic range of *P. arata* includes a considerable part of the Pennsylvanian. From the limited collections studied no precise stratigraphic limits may be ascertained, However, the range of *P. arata appears* to be more restricted than that of *Polidevcia bellistriata;* no specimens of *P. arata* from above the Missourian or below the Des Moinian have been found in the collections examined (Text-Fig. 11).

T y p e s. The writer here designates as neotype a complete, well-preserved specimen from the Coal Measures, Vermilion Co., Indiana, USNM 145985 (Pl. 3, Figs. 11—14). This specimen was previously a hypotype figured by White (1884, Pl. 31, figs. 8, 9). Three hypotypes are also designated, USNM 145986 from the Coal Measures, Henry Co., Missouri (Pl. 3, Figs. 8—10) and UMMP 50293 and 50294 from the Middle Palo Pinto limestone, Palo Pinto Co., Texas (Pl. 3, Figs. 1—7).

Polidevcia pandoraeformis (STEVENS, 1858)

(Pl. 4, Figs. 14—15)

1858 — *Leda pandoraeformis* STEVENS, Am. Jour. Sci., p. 262.
1862 — *Leda bellistriata* WINCHELL, Proc. Acad. Nat. Sci. Phila., p. 419.
1865 — *Leda bellistriata* WINCHELL, Proc. Acad. Nat. Sci. Phila., p. 128.
1965 — *Polidevcia pandoraeformis* DRISCOLL, Paleontographica Americana, p. 79, Pl. 10, figs. 16—34.

D e s c r i p t i o n. O u t l i n e. Anterior outline of umbonal margin continuous with anterior margin; forms a broad, even, sweeping outline from beaks around anterior margin and ventral part of posterior margin to porterior rostral extremity. Outline bluntly pointed anteriorly. Between the inferior extreme point and the rostral extremity outline is evenly and gently curved, no concave indentation being uresent. Rorstral extremity roundly subtruncate. Posterior portion of the dorsal outline is concave upward, concavity becoming greater near beaks. Posterior portion of umbonal outline forms curve, concave upward, from beaks to near rostral extremity, where it joins the posterior part of the dorsal outline. Concavity of posterior umbonal outline only slightly greater than that of posterior portion of dorsal outline.

Convexity. Valves moderately convex. The line of maximum convexity passes from the beaks to near the inferior extreme point. The point of maximum thickness lies in the middle third of valve height. Posterior keel moderately prominent. Umbonal ridge extremely sharp.

Beaks. Contiguous, incurved above the hinge line, strongly opisthogyrate, situated near the mid-length of the valves.

Escutcheon. Long, corresponds to entire posterior area above the umbonal slopes, divided into two parts by a thin rib beginning at the beak of each valve and extending in a curve to a point on the dorsal margin approximately one-third of the distance from the beaks to the rostral extremity. In dorsal view the inner escutcheon (that portion bordered by the thin rib) is lanceolate and striated. The outer escutcheon is ribbed. Ribbing and striations have a pattern similar to that present in *Polidevcia bellistriata.* Inner escutcheon of well preserved specimens shows a series of weak but regular warps which correspond to the positions of the teeth immediately below.

Lunule. Narrow, elongate, lanceolate, not well preserved on specimens studied.

Ligament. Curved lines of perforations subparallel to the inner escutcheon are present. Similar perforations may be present near lunule borders but were not observed. These perforations are believed to be terminal points of the horny process (Sorgenfrei 1936). They become larger and more widely spaced posteriorly. Near the beak the perforations lie upon the narrow rib defining the inner escutcheon but posteriorly they are situated just outside this rib. The two specimens showing escutcheonal perforations have 9 and 10 such points. Preservation is not perfect in either specimen and these perforation counts must be regarded as minimum estimates.

Hinge. Taxodont dentition. Anterior hinge plate slightly convex upward, extends from beak approximately half the distance to the anterior extremity. Posterior hinge plate longer, extending posteriorly about half the distance from the beaks to the posterior rostral extremity, concave upward. Teeth closely spaced near beaks, becoming more widely separated anteriorly and posteriorly. Teeth immediately anterior to beaks straight but become cheveron-shaped on more anterior portions of the hinge plate, and strongly cheveron-shaped on the posterior hinge plate. In both cases the cheveron apices point toward the beaks. Small triangular resilifer present immediately below beaks. Poor preservation makes it uncertain whether teeth terminate at resilifer or are reduced and pass above resilifer.

Muscle scars. Posterior adductor scar elongate, wider posteriorly than anteriorly, situated on umbonal slope, with anterior extremity of scar just posterior to posterior extremity of dentition. Anterior border of scar sharply incised into shell, postero-ventral border slightly scalloped. Weak, irregular ridges subparallel to umbonal slope cover scar. Anterior adductor scar weak, not clearly defined on specimens studied.

Pallial line. Very weak, cannot be clearly traced on specimens examined.

Internal ridges. All internal ridges weak. Principal internal ridge (*umbonal ridge* of Kumpera, Prantl et Růžička 1960) is a very weak, broad swelling extending ventrally, curving posteriorly, and merging with the general valve convexity near the pallial line. A second narrower ridge extends in an antero-ventral direction from the umbonal region. A third internal ridge or fold, the most pronounced in this species, is present in the posterior end of the valves. It extends from below the posterior adductor scar anteriorly and toward the umbo but merges with the general valve convexity a short distance anterior to the posterior adductor scar.

Accessory muscle scars. In the umbonal region ill-defined accessory muscle scars are present on and near the principal internal ridge. Near the anterior extremity of dentition a thin, elongate scar is present adjacent and parallel to the hinge line. This is thought to represent anterior protractor muscles.

Surface sculpture. Regular, narrowly spaced concentric ribs, parallel to the valve margins cover the surface of the valve from beak to ventral margin but are greatly reduced or disappear entirely as they approach the antero-dorsal margin and the postero-dorsal margin. They do not extend over the umbonal slope. Concentric ribs are somewhat variable in shape, appearing as imbricate from below upward on some specimens and as simple acute ridges on others. No concentric sculpture present internally.

Remarks. Table 1 outlines the characteristics which may be used to differentiate *Polidevcia pandoraeformis* from *P. bellistriata* and *P. arata*.

Occurrence. *P. pandoraeformis* is known only from the Mississippian Coldwater Shale and Marshall Sandstone of Michigan.

Types. A lectotype and several hypotypes of this species have ben designated by the writer (1965, p. 80). They are held by the Museum of Paleontology, University of Michigan. The lectotype, UMMP 44059, is figured here (Pl. 4, Figs. 14—15).

UNASSIGNED SPECIES

A number of reported occurrences of *"Leda bellistriata"*, *"Nucula bellistriata"*, *"Nuculana bellistriata"*, *"Leda arata"* and *"Nucula kazanensis"* are found in the literature but are not included in synonymy with any of the three species of *Polidevcia* here described. The specimens upon which these reports are based are too poorly preserved, or too poorly described and illustrated, to allow proper identification. I believe that these forms may be assigned to *Polidevcia* but that any attempt at specific determination from the literature is useless. I have been unable to locate the specimens upon which these reported occurrences were based.

Polidevcia spp. cf. *P. bellistriata, P. arata, P. pandoraeformis*

1860 — *Nucula (Leda) kazanensis* SWALLOW et HAWN, trans. Acad. Sci. St. Louis v. 1, p. 190. *Non N. kazanensis* VERNEUIL, 1845.
1866 — *Nucula kazanensis* GEINITZ, Carb. und Dyas in Nebraska, p. 20, 21, Pl. 1, figs. 33, 34.
1875 — *Leda bellistriata* TOULA, Sitz-Ber. k. Akad. Wiss. Wein, v. 1, Abth., Maiheft, p. 558, 559, Pl. 3, fig. 8.
1887 — *Nuculana bellistriata* HERRICK, Bull. Denison Univ., v. 2, p. 40, Pl. 4 fig. 26
1903 — *Nuculana cf. bellistriata* JAKOWLEW, Mem. Com. Geol., h. s. 4, p. 10.
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1932 — *Leda bellistriata* FEDOTOV, Transactions of the United Geological and Prospecting Service of the U. S. S. R., Fas. 103, p. 28, 29, Pl. 2, figs. 1, 2.
1951 — *Leda bellistriata* CHOW, Pennsylvania Topographic and Geologic Survey, Bull. G 26, p. 25, Pl. 3, fig. 3.

In 1908 Beede and Rogers (p. 368, 380, Pl. 42) listed, but did not describe or figure, *Nuculana bellistriata* from various horizons in the coal measures of Kansas, and in 1915 Mather (p. 212—214, Pl. 15, Fig. 19) reported the occurrence of *Leda bellistriata* in the Hale Formation at Fayetteville, Arkansas. I am unable to determine whether these forms should be assigned to *Polidevcia* or *Phestia.*

Meek (1872, p. 206, Pl. 10, Figs. 11a, b) reported the occurrence of *Nuculana bellistriata* var. *attenuata.* The writer has examined Meek's primary types. These are small, poorly preserved and have few distictive characters. Their general form indicates that they do not belong to any of the species of *Polidevcia* considered here. The types are figured for comparison (Pl. 4, Figs. 1—8).

Phestia CHERNYSHEV, 1951

Phestia CHERNYSHEV, 1943 *(nomen nudum)*
Phestia CHERNYSHEV, 1951.
Phestia SHULGA, 1956
Phestia ELIAS, 1957
Phestia KUMPERA, PRANTL et RŮŽIČKA, 1960.
Phestia McALESTER, 1966.
Type species. By original designation *Leda inflatiformis* CHERNYSHEV, 1939.

Phestia ginnyi sp. n.

(Pl. 4, Figs. 9—13; Text - Figs. 4, 5)

Leda bellistriata BRANSON, E. B., 1916, p. 659, Pl. 3, figs. 9—12.
Leda bellistriata BRANSON, C. C., 1930, p. 43, Pl. 10, figs. 15—20.
Nuculana bellistriata BRANSON, C. C., 1948, p. 633, *in part.*

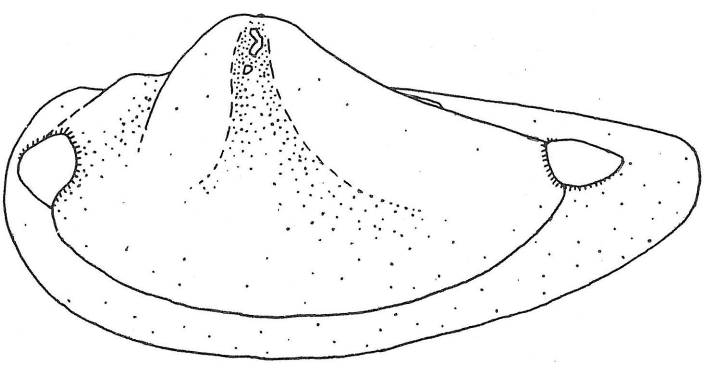
Description. Outline. Anterior margin gently curved in its upper part, more abruptly curved around anterior extremity of shell, and evenly and gently curved throughout its lower portion into the lower part of the posterior outline. Lower part of posterior outline evenly curved from inferior extreme point to posterior extremity of valve; not sinuous. Posterior extremity of valve is abruptly rounded or subtruncate. Posterior portion of dorsal outline variable; straight, slightly concave or slightly convex, forms angle of approximately 145° with anterior portion of dorsal margin below beaks. Umbonal outlines meet dorsal margin anteriorly and posteriorly at slight angle; do not merge evenly with either the anterior or posterior dorsal outline.

Convexity. Valves moderately convex. Line of maximum convexity passes from beak to lower part of anterior margin. Point of maximum thickness liesin the middle third of valve height. Posterior keel weak to moderate, most pronounced approximately midway between beaks and posterior extremity, merges with general valve convexity posterior to this point.

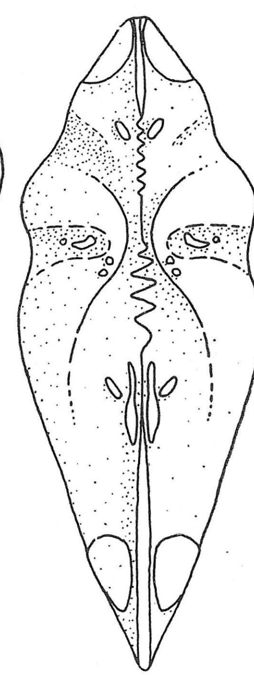
Beaks. Tumid, not contiguous, orthogyrate or slightly opisthogyrate, situated slightly anterior to mid-length of valves.

Escutcheon. Poorly defined, slightly depressed areas on both sides of the keel extend from beaks approximately midway to posterior valve extremity but do not appear to represent a true escutcheon.

Lunule. No true lunule present although a weak, poorly defined depression exists anterior to beaks.



TEXT FIG. 4. Idealized lateral view of internal mold of *Phestia ginnyi* sp. n. Primarily based on holotype, U. M. 5283, from the Phosphoria Formation of Wyoming.



TEXT FIG. 5. Idealized dorsal view of internal mold of *Phestia ginnyi* sp. n. Note accessory muscle scar pattern and distribution of internal ridges. Primarily based on holotype, U. M. 5283, from the Phosphoria Formation of Wyoming.

L i g a m e n t . Probably internal; no specimens allow detailed examination of hinge line; presence of resilifer not confirmed.

H i n g e . Taxodont dentition; teeth extending from approximately midway between beaks and posterior extremity to approximately midway between beaks and anterior extremity; closely spaced below beaks, more widely separated anteriorly and posteriorly.

M u s c l e s c a r s . Posterior adductor muscle scar oval-shaped, elongate in an anterior-posterior direction, posterior part situated immediately adjacent to keel, diverges from keel anteriorly, anterior border of scar deeply incised into shell, posterior border less so. Anterior adductor scar subcircular, adjacent to antero-dorsal margin of valve, posterior border of scar more clearly defined than anterior border (Text-Fig. 5).

P a l l i a l l i n e . Moderately well defined; entire.

I n t e r n a l r i d g e s . Principal internal ridge (*umbonal ridge* of Kumpera, Prantl et Růžička 1960) sharply defined in umbonal region, becomes broader and lower as it extends ventrally and curves posteriorly, merges with general valve convexity before reaching pallial line. A second weak internal ridge extends from umbonal region to anterior adductor scar.

A c c e s s o r y m u s c l e s c a r s . Dorsomedian and ventromedian scars clearly defined on well preserved specimens; dorsomedian scar being the larger. An accessory muscle scar is present adjacent to hinge line just posterior to anterior adductor scar (Text-Fig. 5).

S u r f a c e s c u l p t u r e . Unknown; specimens preserved as internal molds or, rarely, as possible composite molds (McAlester 1962) preserving little of the external ornamentation.

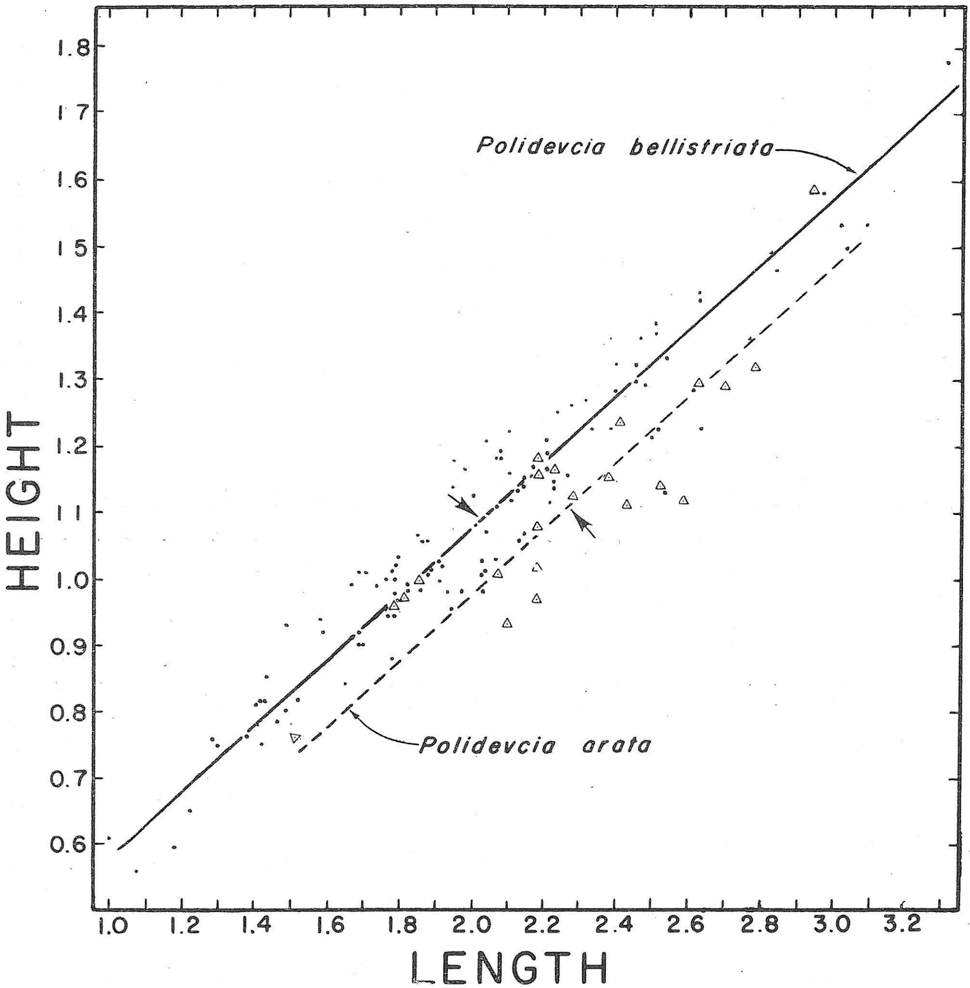
O c c u r r e n c e . *Phestia ginnyi* is known to occur only in the Phosphoria Formation of Wyoming.

T y p e s . The holotype of *Plestia ginnyi* is here designated as U. M. 5283 (Pl. 4, Figs. 9—11). This specimen, from the Pustula Member of the Phosphoria Formation, Big Popo Agie Canyon, Wyoming, is an internal mold which was previously designated as a hypotype of *Leda bellistriata* by Branson (1930, p. 43, Pl. 10, Fig. 15). Two figured paratypes from the same locality are here designated U. M. 16173 and 16174. Unfigured paratypes include 62 topotype specimens, U. M. 752.

STATISTICAL TREATMENT

249 specimens of nuculanids from widely separated stratigraphic and geographic localities in the United States were examined. All specimens had previously been assigned to *Nuculana bellistriata* (STEVENS) either in publications or for the purposes of museum classification. 160 of the specimens were found to belong to *Polidevcia bellistriata* (STEVENS), 36 to *Polidevcia arata,* 12 to *Polidevcia pandoraeformis,* and 41 to *Phestia ginnyi.*

On all specimens examined five measurements were attempted: length, height, width, the length-parallel distance from the anterior extremity to a point directly below the beaks, and the number of concentric ribs in a distance of 0.5 cm. The count of concentric ribs was



TEXT FIG. 6. Growth lines of *Polidevcia bellistriata* and *P. arata.* Dots indicate specimens of *P. bellistriata*; triangles *P. arata.* Reduced major axes are plotted for each set of specimens. Both growth lines have the form y = ax + b. For *P. bellistriata* a = .495; b = .088. For *P. arata* a = .488; b = .009. Coefficient of correlation for *P. bellistriata* sample .953; for *P. arata* .887. Arrows indicate joint means. Numerical scales in centimeters.

made near the widest part of the shells immediately below the beaks (Text-Fig. 9).

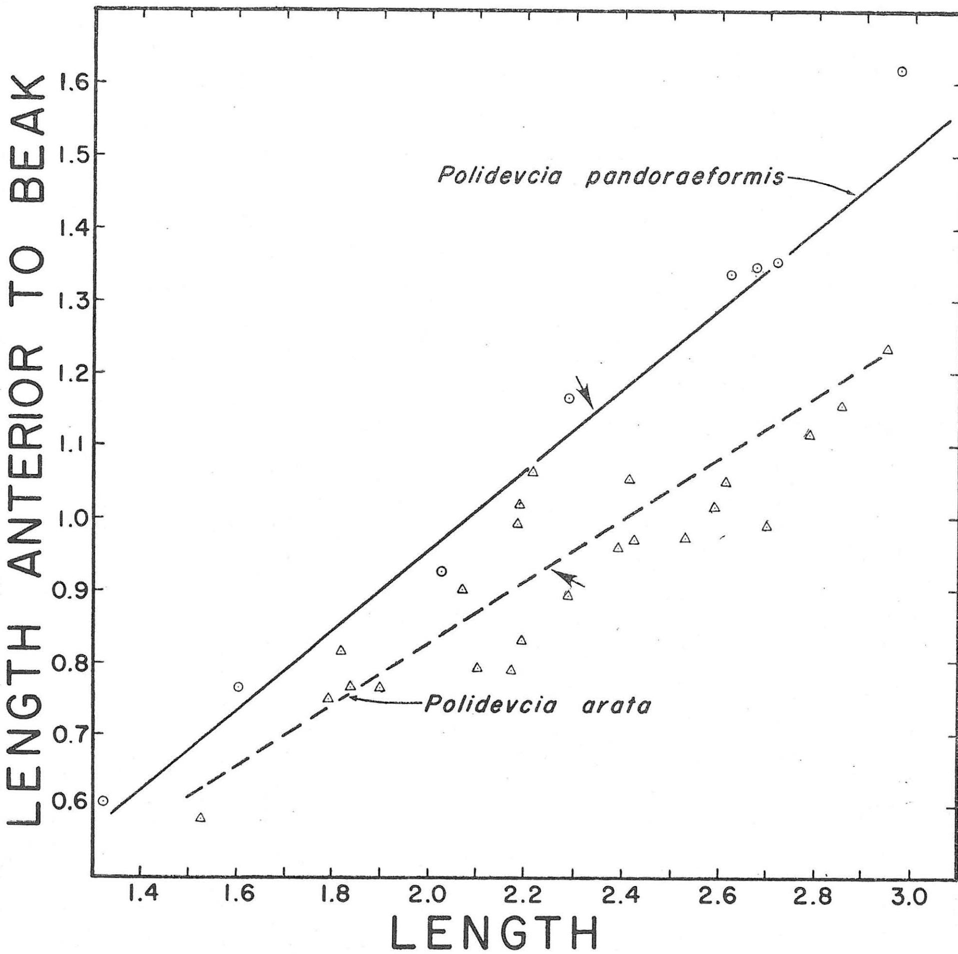
The two genera and four species discussed in this paper were tentatively separated on the basis of general shape, size, the number of concentric ribs per unit height, and the characteristics outlined in Table 1. In order to test the validity of the species and, if valid, to characterize the morphologic variation, the mean and standard deviation of each measured variable was determined. These are shown in

TABLE 2

	P. bellistriata			*P. arata*			*P. pandoraeformis*			*Phestia ginnyi*		
	N	Mean	S. D.	N	Mean	S. D.	N	Mean	S. D	N	Mean	S. D.
Length	126	2.03	0.44	23	2.25	0.35	9	2.34	0.58	41	0.67	0.20
Height	154	1.12	0.22	29	1.09	0.20	11	1.24	0.29	41	0.43	0.13
Width	121	0.82	0.17	22	0.87	0.13	—	—	—	37	0.29	0.09
Length Ant. to beaks	153	0.90	0.17	29	0.90	0.17	11	1.08	0.31	41	0.29	0.11
Ribs/ 0.05 cm.	137	20.19	3.95	35	11.69	2.18	6	22.50	4.46	—	—	—

TABLE 3

Variable pairs	*P. belli-striata*		*P. arata*		*P. pandorae-formis*		*Phestia ginnyi*	
	N	r	N	r	N	r	N	r
Length — Height	125	.953	22	.887	9	.962	41	.979
Length — Width	102	.868	—	—	—	—	37	.936
Length — Length Ant. to beaks	124	.924	22	.897	9	.943	41	.962
Length — Ribs/.05 cm.	—	—	—	—	5	.896	—	—
Height — Width	121	.920	22	.745	—	—	37	.950
Height — Length Ant. to beaks	153	.929	28	.934	11	.954	41	.949
Height — Ribs/.05 cm.	—	—	—	—	5	.916	—	—
Width — Length Ant. to beaks	121	.868	22	.749	—	—	37	.926
Width — Ribs/.05 cm.	—	—	—	—	—	—	—	—
Length Ant. to beaks — Ribs/.05 cm.	—	—	—	—	5	-.813	—	—



TEXT FIG. 7. Growth lines of *Polidevcia pandoraeformis* and *P. arata.* Circles indicate specimens of *P. pandoraeformis*; triangles *P. arata.* Reduced major axes are plotted for each set of specimens. Both growth lines have the form y = ax + b. For *P. pandoraeformis* a = .555; b = —.160. For *P. arata* a = .427; b = —.0.33. Coefficient of correlation for *P. pandoraeformis* sample .943; for *P. arata* .897. Arrows indicate joint means. Numerical scales in centimeters.

Table 2. The coefficient of correlation for all pairs of variables was determined. Those showing a coefficient of correlation better than ± .700 are shown in Table 3.

The high negative correlations of length, height, width, and length anterior to the beaks to the number of concentric ribs per 0.5 cm. shown for *Polidevcia pandoraeformis* indicate that the concentric ribs become more widely separated as size of the shell increases. The same characteristic was shown in other species of *Polidevcia* to a lesser degree.

Statistical discrimination between the lines of relative growth of length and height for the various species was attempted with the formulae described by Imbrie (1956, p. 235—238). Table 4 summarizes the results. A z value greater than 1.96 indicates that the probability of the difference being due to chance is less than 0.05. If z = 2.58, the probability of the difference being due to chance is 0.01.

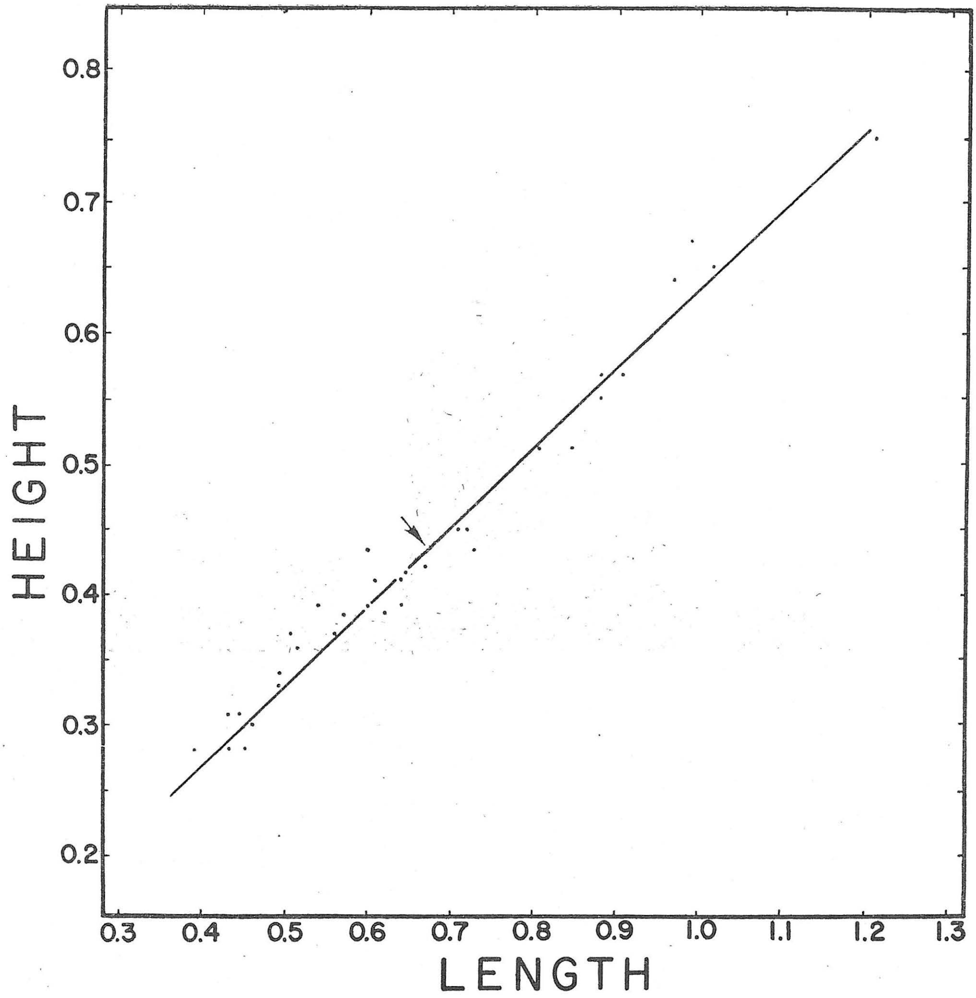
Examination of Table 4 indicates very substantial differences between the relative growth lines of *Phestia ginnyi* (Text-Fig. 8) and of all species of *Polidevcia.* Testing the slopes of the height-length growth lines shows that P < .01 between *Phestia ginnyi* and *Polidevcia bellistriata* and that P < .05 between *Phestia ginnyi* and *Polidevcia arata*

TABLE 4

Species	Variable pairs	Slope z	P	Position z	P
Polidevcia bellistriata — Polidevcia arata	Height - Length	0.14	>.05	2.78	<.01
Polidevcia bellistriata — Polidevcia pandoraeformis	Height - Length	0.74	>.05	0.11	>.05
Polidevcia bellistriata — Phestia ginnyi	Height - Length	5.21	<.01	5.29	<.01
Polidevcia arata — Polidevcia pandoraeformis	Height - Length	0.65	>.05	1.96	.05
Polidevcia arata — Phestia ginnyi	Height - Length	2.52	<0.5	3.22	<.01
Polidevcia pandoraeformis - Phestia ginnyi	Height - Length	1.66	>.05	3.14	<.01
Polidevcia arata — Polidevcia pandoraeformis	Length anterior to beaks - Length	1.74	>.05	2.73	<.01
Polidevcia bellistriata — Polidevcia pandoraeformis	Length anterior to beaks - Length	2.74	<.01	1.34	>.05

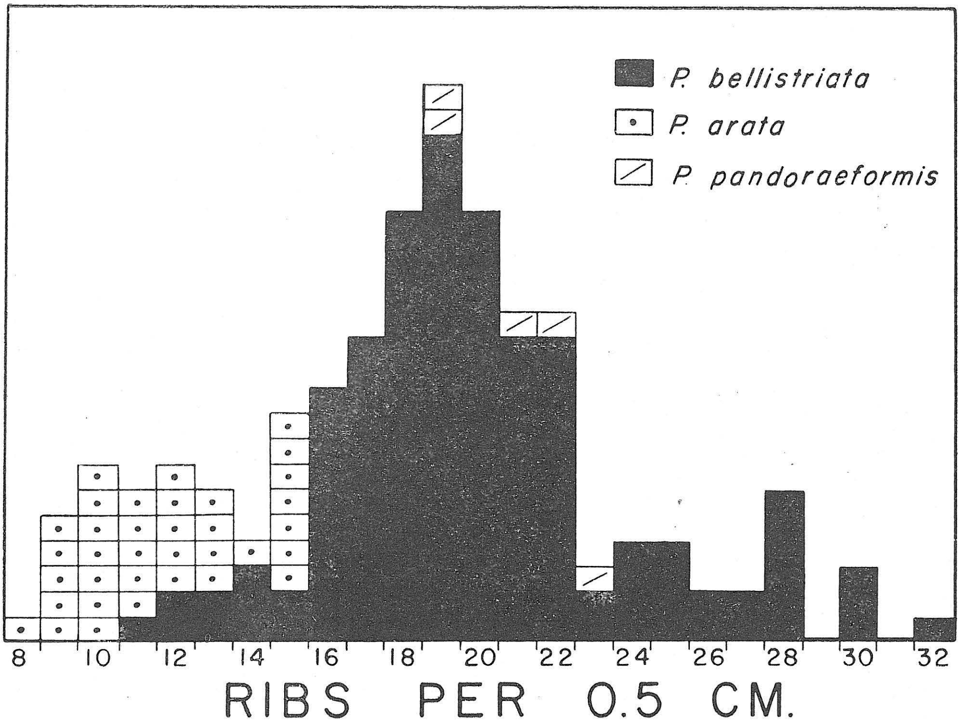
but that P > .05 between *Phestia ginnyi* and *Polidevcia pandoraeformis.* Testing the position of the height-length growth lines shows that P < .01 between *Phestia ginnyi* and all three species of *Polidevcia.*

The differences between relative height-length growth lines are less between species of *Polidevcia.* A probability of < .01 is found in testing the position of the growth lines of *Polidevcia bellistriata* and *P. arata.* Text-Fig. 6 illustrates this relationship. Tests of both the slopes and positions of the relative height-length growth lines of *P. bellistriata* and *P. pandoraeformis,* and *P. pandoraeformis* and *P. arata* indicate



TEXT FIG. 8. Growth line of *Phestia ginnyi.* Reduced major axis is plotted. Growth line has the form y = ax + b. a = .619; b = 0.21. Coeficient of correlation is .979. Arrow indicates joint means.

a probability of .05 or greater that the difference arose by chance. This probability level is not acceptable for statistical discrimination. In order to provide more convincing evidence of the presence of distinct species the relative length anterior to the beaks to total length growth lines of *P. arata* and *P. pandoraeformis* and of *P. bellistriata* and *P. pandoraeformis* were tested. The position of the two lines is significantly different in *P. arata* and *P. pandoraeformis* (Text-Fig. 7). The slope is significantly different in *P. bellistriata* and *P. pandoraeformis.*



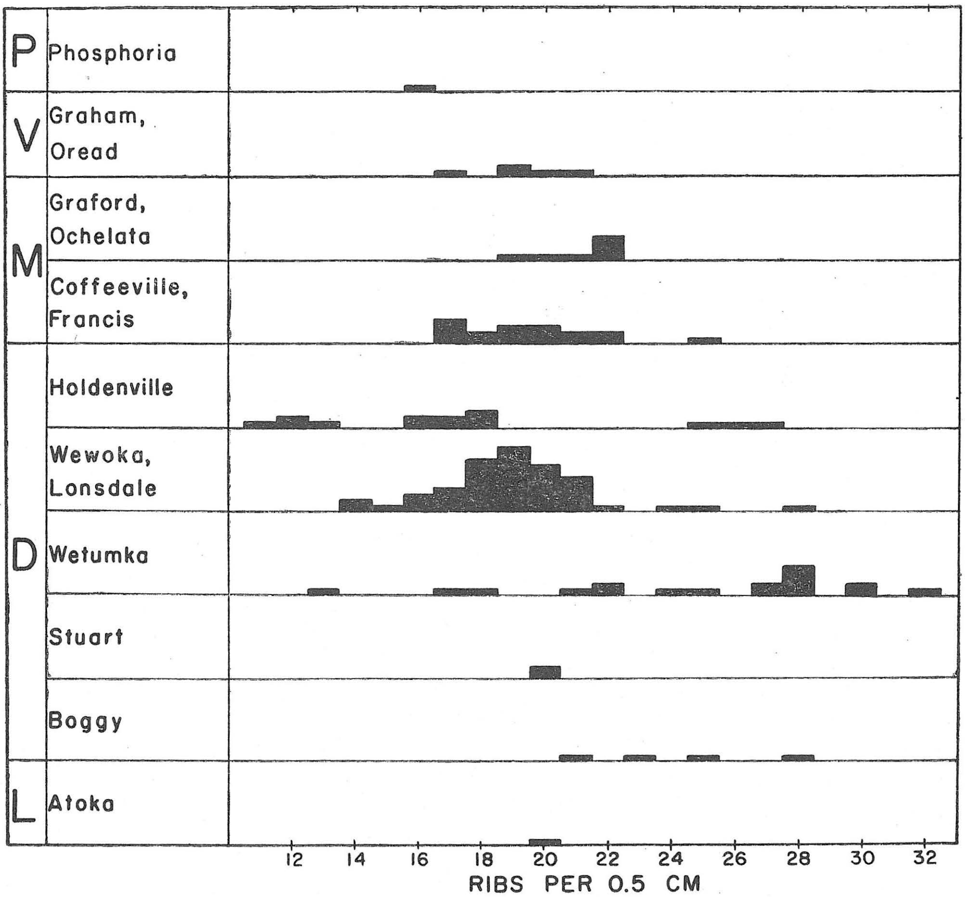
TEXT FIG. 9. Histogram illustrating the number of ribs per 0.5 centimeters in three species of *Polidevcia*. Rib counts were made on 134 specimens of *P. bellistriata*, 35 specimens of *P. arata* and 5 specimens of *P. pandoraeformis*.

REMARKS ON EVOLUTION

Kumpera, Prantl et Růžička (1960, p. 76, 77) have commented that the keel (*umbonal ridge* of present paper) becomes less acute in stratigraphically higher forms of *Polidevcia*. This suggestion is supported by the presence of an extremely sharp umbonal ridge in the Mississippian form *P. pandoraeformis* and the more evenly rounded umbonal ridges of *P. bellistriata* and *P. arata* from Pennsylvanian strata.

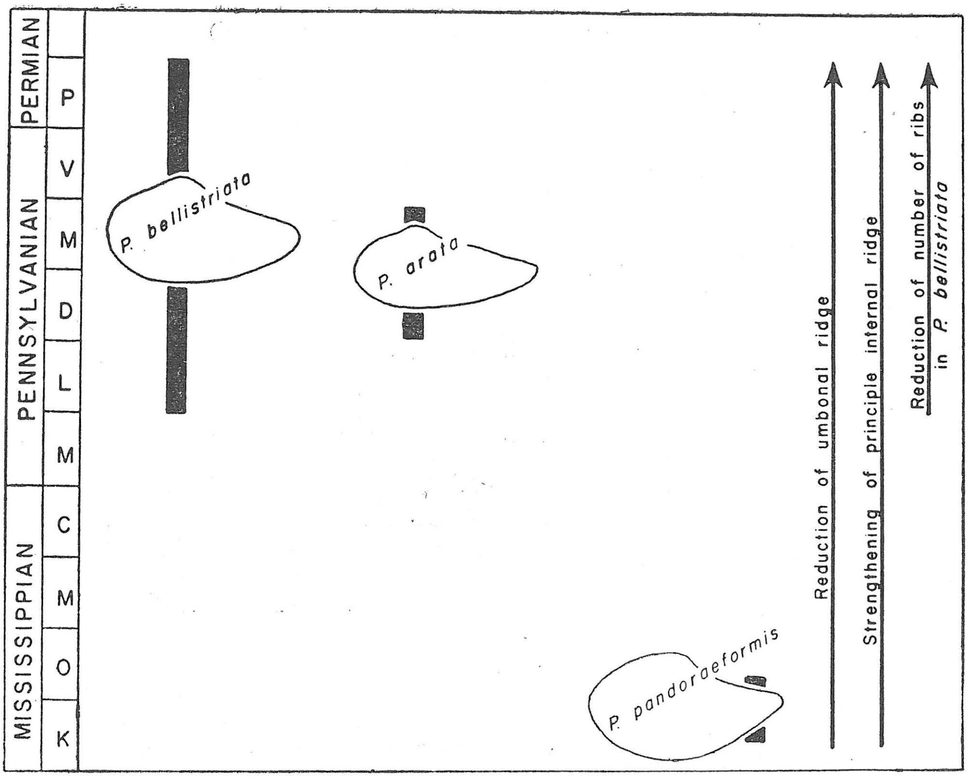
The same authors further suggested (1960, p. 32) that the umbonal ridge (*principal internal ridge* of present paper) is less well developed in older specimens and becomes more pronounced in stratigraphically higher forms. The species examined here support this observation. *P. pandoraeformis* (Mississippian) has a weakly developed principal internal ridge whereas *P. arata* (Pennsylvanian) and *P. bellistriata* (Pennsylvanian and Lower Permian) illustrate strong development of this feature (Text-Fig. 11).

Few specimens from the highest and lowest stratigraphic occurrences of *Polidevcia bellistriata* are present in the collections studied. Those



TEXT FIG. 10. Rib counts on 116 specimens of *Polidevcia bellistriata* from various stratigraphic horizons in the Pennsylvanian and Permian. Specimens from the Des Moines and Missouri Series are much more common in the collections studied than those from higher or lower strata. There is some indication that the number of ribs decreases in stratigraphically higher forms.

specimens available suggest a possible reduction in the number of concentric ribs in stratigraphically higher forms. This relationship is illustrated in Text-Fig. 10.



TEXT FIG. 11. General stratigraphic range of three species of *Polidevcia.* Evolutionary trends are noted on right. Letter designations in the Mississippian indicate Kinderhook, Osage, Meramec, and Chester; in the Pennsylvanian, Morrow, Lampasas, Des Moines, Missouri and Virgil; in the Permian, Phosphoria.

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PLATE 1

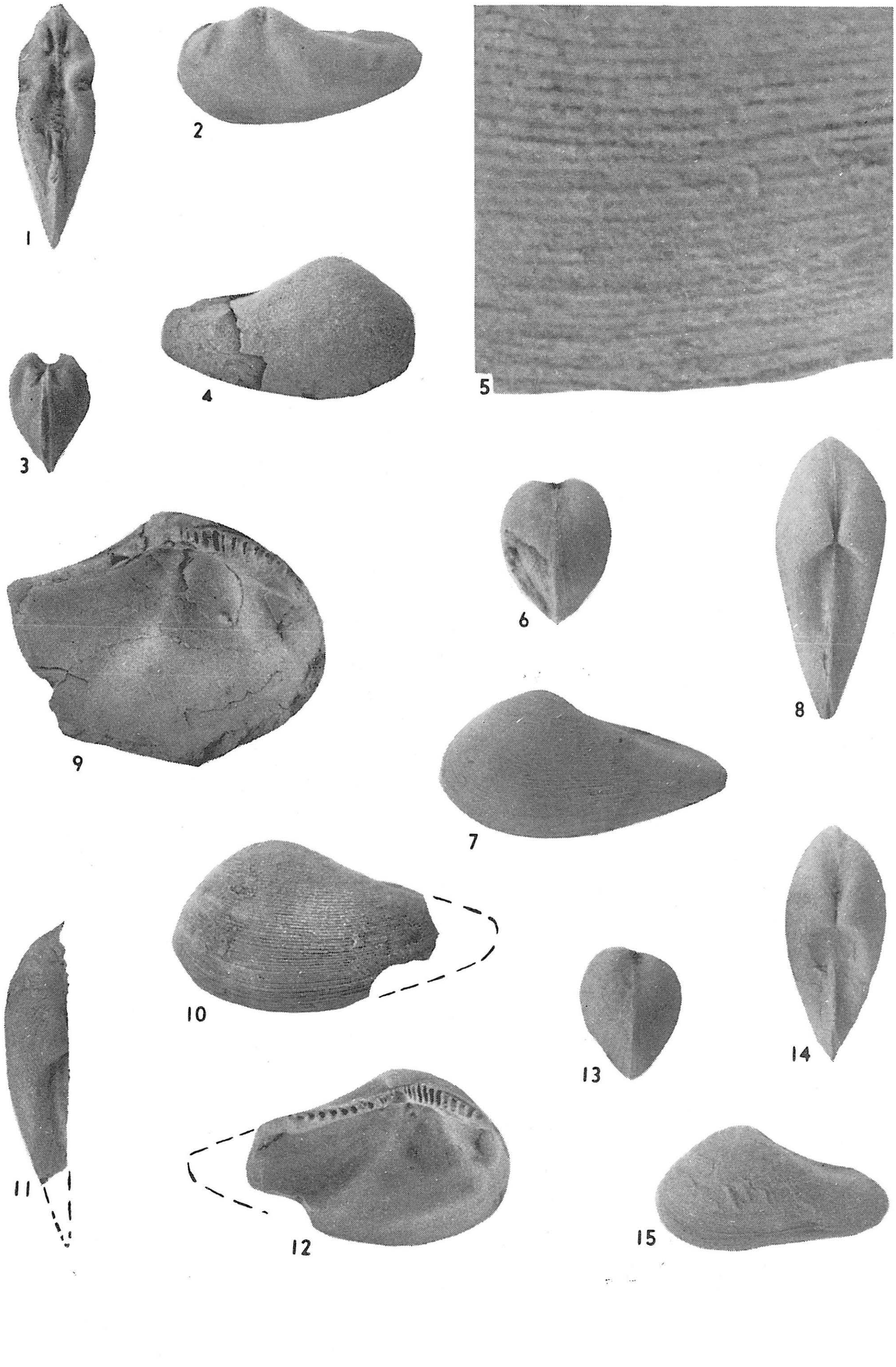
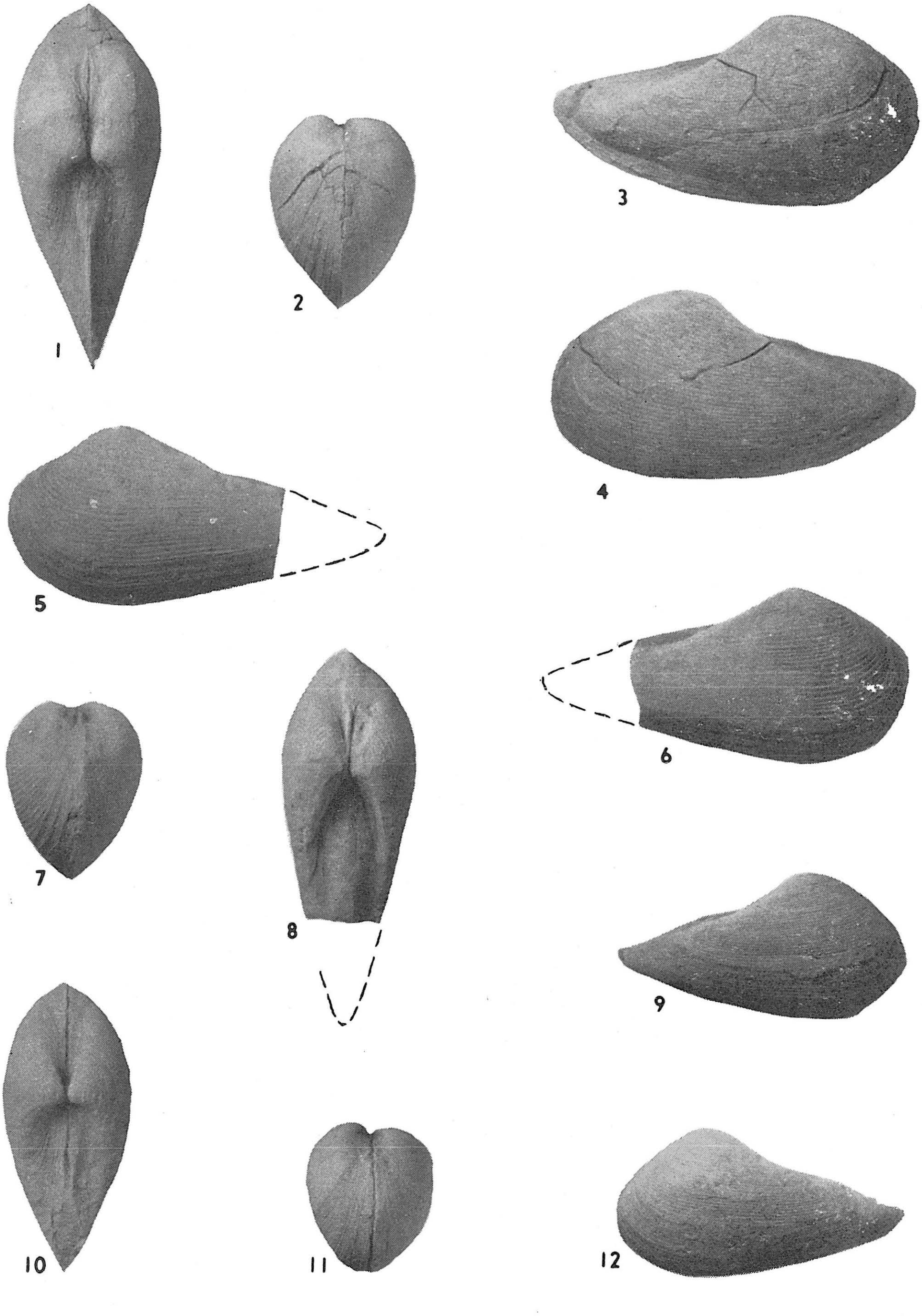


PLATE 2



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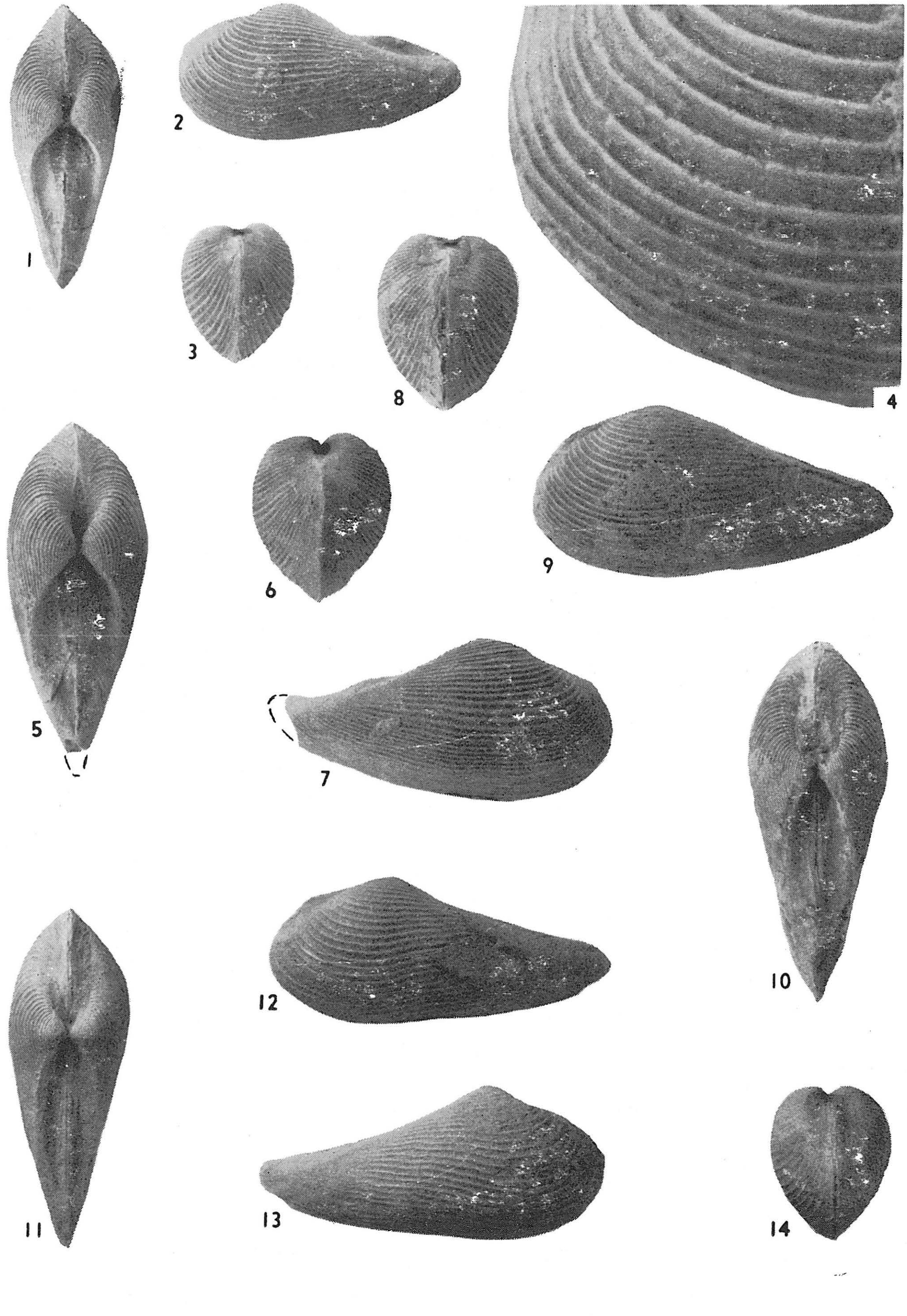
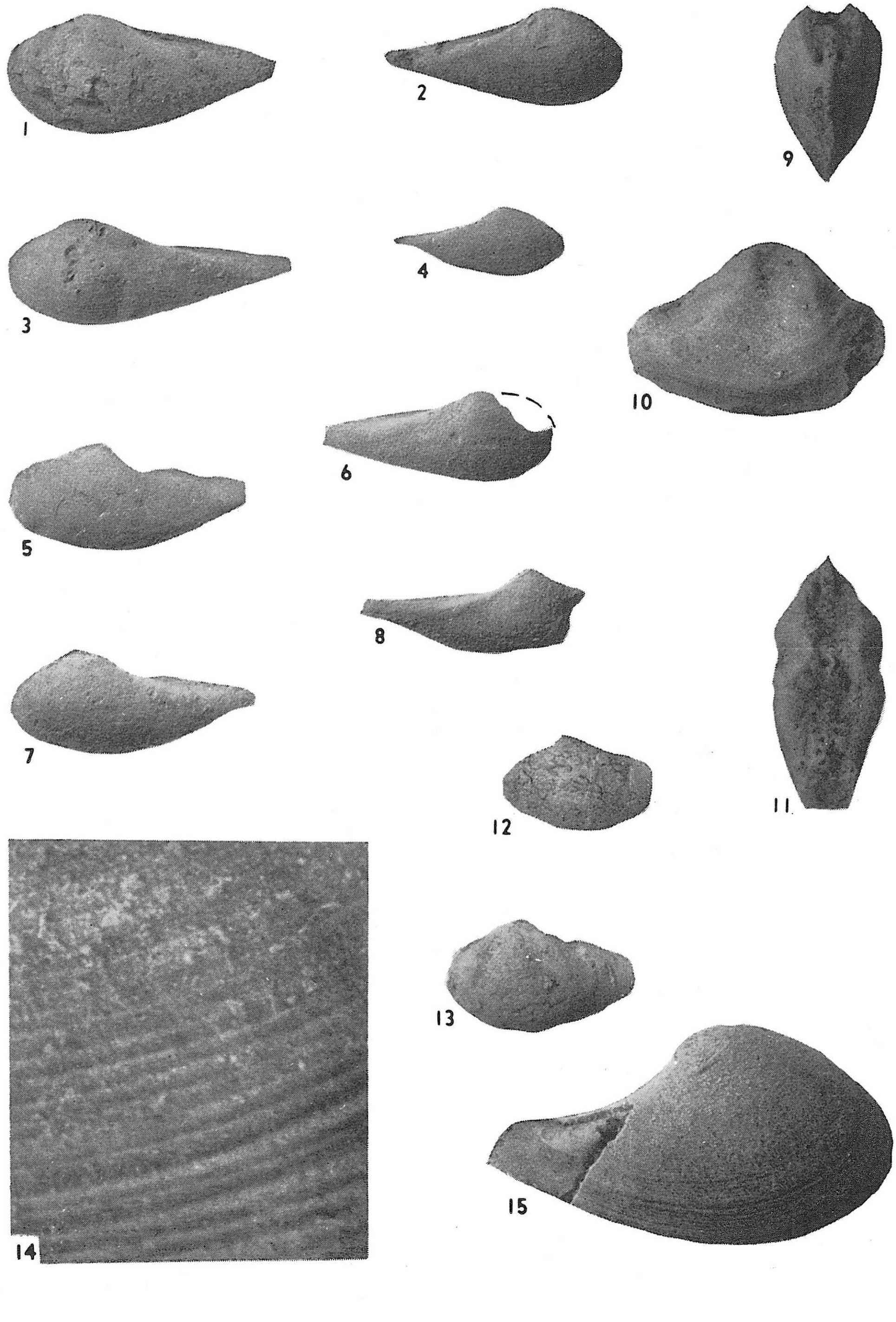


PLATE 4



EXPLANATION OF PLATES

PLATE 1

Figs. 1—3. *Polidevcia bellistriata* (Stevens), hypotype, O. S. U. 19794, an internal mold from the Kanwaka Shale, Shawnee Group of the NE 1/4, Sec. 32, T24N, R9E, Osage Co., Oklahoma. Fig. 1, dorsal view; fig. 2, left lateral view; fig. 3, anterior view. All ×2. Note internal ribs and accessory musculature.

Fig. 4. *Polidevcia bellistriata* (Stevens), hypotype and topotype, O. S. U. 19792, from the Brush Creek Limestone, Conemaugh Series of Summit Cut, Summitville, Columbiana Co., Ohio. Right lateral view. ×2. Note that the internal mold partially visible in the figure is free of the shell and allows comparison of external and internal morphologic features.

Figs. 5—8. *Polidevcia bellistriata* (Stevens), hypotype, U. M. 16175, from the Graford Formation at Kyle Mountain, Palo Pinto Co., Texas. Fig. 5, surface ornamentation along ventral margin. ×10. Note that concentric sculpture paralels ventral margin. Fig. 6, anterior view, ×2; fig. 7, left lateral view, ×2; fig. 8, dorsal view, ×2.

Fig. 9. *Polidevcia bellistriata* (Stevens), hypotype and topotype, O. S. U. 19793, from the Brush Creek Limestone, Conemaugh Series at Summit Cut, Summitville, Columbiana C., Ohio. View of hinge line and interior of broken valve. ×4. Note internal ridges.

Figs. 10—12. *Polidevcia bellistriata* (Stevens), hypotype U. M. 16172, from the Graford Formation at Kyle Mountain, Palo Pinto Co., Texas. Fig. 10, left lateral view; fig. 11, dorsal view; fig. 12, internal view. All ×2. Note that dentition passes above triangular resilifer.

Figs. 13—15. *Polidevcia bellistriata* (Stevens), neotype and topotype, O. S. U. 19791 from the Brush Creek Limestone, Conemaugh Series at Summit Cut, Summitville, Columbiana Co., Ohio. Fig. 13, anterior view; fig. 14, dorsal view; fig. 15, left lateral view. All ×2.

PLATE 2

Figs. 1—4 *Polidevcia bellistriata* (Stevens), hypotype, USNM 47157 from the Pennsylvanian rocks at Springfield, Illinois. This hypotype is one of those reported by Butts (1926). Fig. 1, dorsal view; fig. 2, anterior view; fig. 3, right lateral view; fig. 4, left lateral view. All ×2.

Figs. 5—8. *Polidevcia bellistriata* (Stevens), hypotype, USNM 47158 from the Pennsylvanian rocks at Peoria, Illinois. This hypotype is one of those reported by Butts (1926). Fig. 5, left lateral view; fig. 6, right lateral view; fig. 7, anterior view; fig. 8, dorsal view. All ×2.

Figs. 9—12. *Polidevcia bellistriata* (Stevens), hypotype, USNM 47156 from the Pennsylvanian strata of Montgomery Co., Illinois. This hypotype was figured by Butts (1926, pl. 66, fig. 10). Fig. 9, right lateral view; fig. 10, dorsal view; fig. 11, anterior view; fig. 12, left lateral view. All ×2.

PLATE 3

Figs. 1—4. *Polidevcia arata* (Hall), hypotype, UMMP 50293 from the middle Palo Pinto Limestone, Pennsylvanian, of Palo Pinto Co., Texas. Fig. 1, dorsal view; fig. 2, left lateral view; fig. 3, anterior view. All ×2. Fig. 4, view of antero-ventral margin, ×10. Note that concentric ornamentation is not parallel to shell margin.

Figs. 5—7. *Polidevcia arata* (Hall), hypotype, UMMP 50294 from the middle Palo Pinto Limestone, Pennsylvanian, of Palo Pinto Co., Texas. Fig. 5, dorsal view; fig. 6, anterior view; fig. 7, right lateral view. All ×2.

Figs. 8—10. *Polidevcia arata* (Hall), hypotype, USNM 145986 from the Coal Measures of Henry Co., Missouri. Fig. 8, anterior view; fig. 9, left lateral view; fig. 10, dorsal view. All ×2.

Figs. 11—14. *Polidevcia arata* (Hall), neotype, USNM 145985 from the Coal Measures of Vermilion Co., Indiana. This specimen was previously a hypotype figured by White (1884, pl. 31, figs. 8, 9). Fig. 11, dorsal view; fig. 12, left lateral view; fig. 13, right lateral view; fig. 14, anterior view. All ×2.

PLATE 4

Fig. 1. *Nuculana bellistriata* var. *attenuata* Meek, holotype, USNM 6491 from the Rockford Limestone at Nebraska City, Nebraska. Left lateral view. ×2.

Figs. 2—8. *Nuculana bellistriata* var. *attenuata* Meek, seven different paratypes, USNM 6491, from the Rockford Limestone at Nebraska City, Nebraska. ×4.

Figs. 9—11. *Phestia ginnyi* sp. nov., holotype, U. M. 5283, an internal mold from the Phosphoria Formation, Pustula Member at Big Popo Agie Canyon, Wyoming. Fig. 9, anterior view; fig. 10, right lateral view; fig. 11, dorsal view. All ×4. Note internal ridges and accessory muscle scars.

Figs. 12—13. *Phestia ginnyi* sp. n., paratypes, U. M. 16172 and 16173 respectively, from the lower Phosphoria Formation at Big Popo Asie Canyon, Wyoming. All ×4.

Figs. 14—15. *Polidevcia pandoraeformis* (STEVENS), lectotype, UMMP 44059 from the Marshall Sandstone at Mosherville, Michigan. Fig. 14, surface sculpture on exterior of valve, ×10. Fig. 13, right lateral view, ×2.