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ART. I.—*The Morphogenesis of Platystrophia. A Study of the Evolution of a Paleozoic Brachiopod*; by EDGAR ROSCOE CUMINGS.

FEW fossils present features of as great interest and importance, both to geologists and zoologists, as the Brachiopoda, and among them, few are as familiar as the genus *Platystrophia*, the “*Orthis lynx*” of collectors. Wherever Ordovician rocks are exposed the geologist may expect to meet with this ubiquitous and characteristic genus. The regularity with which it turns up in collections from new localities is little short of amazing, and perhaps, if familiarity breeds contempt, accounts for the indefinite and hazy notions current as to its real history and the interrelations of its component elements.

The writer has made an attempt in a preliminary paper to obtain some measure of the variability of *Platystrophia* and out of that study has grown a deeper interest in this form and a deeper insight into its history. The present study is based upon the method of investigation of post-embryonic growth stages, which we owe to Alpheus Hyatt and his able exponents of the present day, Beecher, Jackson, Smith and others. I have endeavored to make full use of specimens representing all stages of growth and all the elements of the range and distribution of *Platystrophia*. The mere study of growth stages has not been deemed adequate unless supplemented by series of adults; and it is hoped that in this way is escaped the error of depending on one class of evidence. That this method thus supplemented has proved potent in discovering unsuspected relationships among the members of a genus which has attracted widespread attention for nearly a century, will be evident to those who follow the present discussion to its close.

The order of presentation is, first, the development of *Platystrophia* under the heads *Nepionic*, *Neanic*, *Ephebic* and

*Gerontic*\* stages: second, a critical discussion of the several adult types variously known as species and varieties of *Platystrophia*; and third, a general résumé and discussion of the history of the genus and the laws of its evolution.

The material used in this investigation belongs in part to the author's collection, which contains several thousand specimens coming from every division of the Cincinnati Group of the Ohio Valley. In addition the Yale Museum contains, besides many specimens from Cincinnati and vicinity, specimens from the Trenton of New York, Kentucky, Tennessee, and Minnesota; from the Galena of Minnesota; from the Clinton of New York and Kentucky; from the Silurian (Niagara) of Anticosti and the Island of Gotland; and from the Ordovician of Wessenberg, Russia. Mr. P. E. Raymond very kindly gave me a series of specimens from the lower Trenton of Crown Point, New York; and Mr. C. J. Sarle of Rochester, N. Y., loaned me a series from the Clinton of that vicinity. Dr. J. M. Clarke loaned for study specimens from the Ryedorph conglomerate (basal Trenton) in the vicinity of Albany, N. Y. Mr. Chas. Schuchert of the U. S. National Museum loaned specimens from his private collection and the collection of the museum, representing the following localities and horizons: St. Petersburg, Russia (Ordovician); Gotland, Sweden (Silurian); Gasport and Lockport, N. Y., Eaton and Dayton, Ohio, and Osgood, Indiana (all Silurian). Prof. R. T. Jackson of Harvard University with great kindness allowed me to study their unrivalled collection of *Platystrophia*, containing many thousand specimens from Cincinnati, Ohio (Ordovician). Dr. G. F. Matthew sent me for study his types of *Orthas lenticularis* from St. John, N. B. To Prof. H. S. Williams of Yale University the writer is indebted for opportunity to examine material from the Ordovician of Arkansas, and for suggestions which his wide acquaintance with kindred subjects renders of especial value. To Prof. C. E. Beecher, who has afforded me every facility and encouragement during the prosecution of this work, the author is under deep and lasting obligations.

#### *Development of Platystrophia.*†

I. *Nepionic stages*.—The youngest individuals seen (fig. 1), have a breadth of 1<sup>mm</sup> and a length of 0.66<sup>mm</sup>. They represent an early nepionic stage. They are markedly transverse,

\* For a classification of the stages of growth and decline as applied to the Brachiopoda, the reader is referred to Beecher's paper on the Development of the Brachiopoda, this Journal, vol. xlv, 1892, pp. 150-154, pl. i. The substitution of the forms *Nepionic*, *Ephebic* and *Gerontic* for *Nealogic*, *Ephebotic* and *Geratologic* is in accordance with present usage. See Hyatt, Phylogeny of an Acquired Characteristic, Proc. Am. Phil. Soc., xxxii, pp. 390-397. See also Proc. Bos. Soc. Nat. Hist., vol. xxvi, pp. 93-108.

† Schlotheim's original description of *Terebratulites* (= *Platystrophia*) *bifurcatus* is so difficult of access that it is here quoted in full:

having an index\* of 1.5, and the greatest breadth about one-third of the way from the beaks to the front margin. The posterior margin (cardinal line) is straight, and the anterior semielliptical. The greatest height is at the beaks, which project slightly beyond the area, but are not incurved. The area is considerably less than the width of the shell at the hinge; and the large foramen is about equally shared by the two valves. At the apex of the ventral foramen is a small callosity. No deltidium was observed.

*Ventral valve.*—In the initial specimens, this valve, for about half the distance from the beak to the front margin, is without longitudinal markings of any sort; but shows a number of very faint concentric lines. The anterior half of the

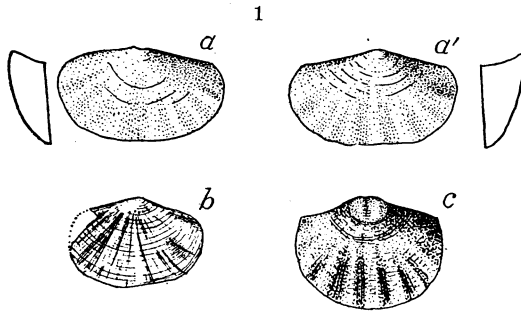


FIG. 1. *a*, Nepionic stage of *Platystrophia*, from specimen obtained at Vevay, Indiana. *a*, dorsal valve, showing median sinus and four plications on either side, profile to left; *a'*, ventral valve showing median fold and four plications on either side, profile to right;  $\times 22$ . *b*, *c*, *Orthis lenticularis* var. *lynceoides* Matthew: figures of the types; *b*, ventral valve of a transverse individual showing bifurcation of several plications toward the anterior margin; *c*, ventral valve of a narrower individual with very strong plications. The umbonal region is exfoliated. *a*, Author's collection.

valve is thrown into nine low rounded plications. One of these occupies the median line, originates nearer the apex, and is slightly more prominent than the others, thus forming a median fold. Toward the front margin the plications are very faintly crenulated by obscure concentric lines.

“22. *Terebratulites biforatus*

“Ein freyes ganz vollständig, mit versteinelter Schaafe erhaltenes Exemplar, aus dem südlichen Frankreich. Vielleicht gleichfalls aus Kreide-lagern der Champagne. (1 ex.)

“Mit ganz gleichen, breiten, länglichrunden Halften, deren Schnäbel gleichförmig gewölbt und auf beyden Seiten durchbohrt sind. Die Oberschaafe mit einer breiten concaven Rückenfurche, die untere Hälfte mit convex hervorstehenden Rücken. Beyde Hälften gleichförmig der Länge nach gestreift, mit ziemlich tiefen zwischenfurchen. Ausserordentlich selten.”

Die Petrefactenkunde auf ihrem jetzigen Standpunkte, etc., Gotha, 1820. p. 265.

No figure is given.

\* Breadth divided by length = shell index.

*Dorsal valve*.—As in the ventral valve the posterior half is smooth, with faint concentric lines. The anterior half is occupied by eight plications. The depression (sulcus) between the two inner ones is deeper and broader than between the others, giving the effect of a median sinus corresponding to the large median plication or fold of the ventral valve. The convexity of the dorsal valve is nearly as great as that of the ventral.

*Comparison with nepionic stages of other Orthidæ*.—At the stage represented by the youngest specimens of *Platystrophia* (1<sup>mm</sup> broad), *Dalmanella* (*testudinaria*, *elegantula*) and *Rhipidomella hybrida*\* have twelve plications on each valve, which arise very close to the apex. The valves are convex, though the dorsal usually has a sinus (sometimes conspicuous) toward the front. The areas are high and well developed, not, however, extending to the cardinal extremities. The ventral area is noticeably higher than the dorsal. The delthyria in both valves are large and open.

*Bilobites* at this stage has nine plications on the ventral valve, one of which lies at the bottom of a shallow median sinus. These originate, as in *Platystrophia*, about half-way from the beaks to the front margin. The areas are high and the delthyria large and open. The relative convexity of the two valves is almost exactly the same as in *Platystrophia*.†

*Hebertella* at 1.4<sup>mm</sup>, the youngest stage yet seen, has eighteen plications which originate very near the beak. The valves are both convex, the ventral being considerably higher. The areas are high and about perpendicular to the plane of separation of the valves.

All the young *Orthidæ* seen, with the exception of *Bilobites*, have noticeably transverse shells:‡ but in all other respects, except the index, the young *Bilobites* most closely resembles the nepionic *Platystrophia*.

*Comparison with adult stages of other Orthidæ*.—There are no adult *Orthidæ* in the Ordovician with which it is possible to compare the nepionic shell of *Platystrophia*.§ Wysogorski has suggested the derivation of the genus from the *Orthis calligramma* group.¶ His views are based entirely upon adult characters of both groups. He says (loc. cit.) "In both groups the

\* For the development of *Dalmanella elegantula* and *Rhipidomella hybrida* see Beecher and Clarke, Mem. N.Y. State Museum, i, 1889, pp. 13-18.

† For the development of *Bilobites*, see Beecher, this Jour. xlii, July, 1891, pp. 51-56.

‡ The index of *Dalmanella* is 1.33 or more, and of *Hebertella* 1.43. That of *Bilobites* is only 1.13 (Beecher's figures).

§ *Orthis lapworthi* Davidson, from the Llandeilo—Middle Caradoc of England, comes the nearest, and is probably an almost lineal descendant of *Orthis lenticularis* of the Upper Cambrian.

¶ Zur Entwicklungsgeschichte der Brachiopodenfamilie der Orthiden im ostbaltischen Silur. Sonder-Abdruck aus der Zeitschrift d. Deut. Geol. Ges. Jahrg., 1900, Heft 2, p. 14.

muscular impressions are the same; many individuals of the *Orthis calligramma* group manifest a tendency to form a sinus, which in *Platystrophia* is so strongly developed that with the corresponding fold of the dorsal valve it constitutes a chief characteristic of this subgenus." It is only necessary to state that the presence of a sinus in the ventral valve of adult Brachiopoda is so nearly universal as to be of little use in tracing phylogenies. As a matter of fact the *nepionic* shell of *Platystrophia* has the sinus in the dorsal valve and the fold on the ventral. Though this feature also characterizes many specimens of *O. calligramma*, nevertheless the fact that a dorsal sinus is a nepionic feature of such widely separated forms as *Dalmanella*, *Rhynchonella*, *Rhynchotreta*, *Rhynchospira*, *Cælospira*, *Atrypa*, etc., renders this character of little significance in indicating a common origin of *O. calligramma* and *Platystrophia*.

The ancestors of *Platystrophia* are scarcely to be sought in the Ordovician, since the genus is already represented in the lower beds of this system.\* In the Upper Cambrian, however, we meet with a form that possesses in the adult practically all of the nepionic characters of *Platystrophia*. This form is *Orthis lenticularis* Wahlenberg sp., a widely distributed and highly variable species, found in the Lingula-flags of Wales, the Alum schists of Scandinavia, and the equivalent formations of Canada.† Through the kindness of Dr. G. F. Matthew I have obtained for examination the types of his var. *lyncoioides* of this species, from the Upper Cambrian of St. John, N. B. These are shown in fig. 1, *b* and *c*.‡ The contour of fig. 1*b* is precisely

\* *Platystrophia* has several times been stated to occur in the Chazy of this country. (see Hall and Clarke, Pal. N. Y., viii, pt. i, p. 202.—Winchell and Schuchert, Geol. Minnesota, iii, pp. 456, 457.—Schuchert, Bull. U. S. G. S., No. 87, p. 309; Proc. U. S. National Museum, vol. xxii, 1900, p. 151 (Birdseye).—Ruedemann, Bull. N. Y. State Museum, No. 49, Dec., 1901, p. 92). I am unable to find any original reference in the literature to its occurrence in rocks of this age. Messrs. Ami, Whiteaves, and W. Billings of Ottawa, Canada, inform me that the museum of the Canadian Survey contains no Chazy specimens; and that they are not aware that the species has ever been found in that series. Mr. Billings suggests that it may have been found in rocks formerly held as Chazy, but now known to be of later age. Mr. McBride of Montreal writes that there are no Chazy specimens in the museums at Montreal and that he does not know of the occurrence of *Platystrophia* in the Chazy. Mr. Seely, who is familiar with the Chazy, writes to the same effect. It is very probable therefore that the form is not known to occur below the Trenton in this country.

† For synonymy and descriptions of this species see Davidson, Silurian Brachiopoda, 1869, pp. 230-232:—Matthew, Trans. Roy. Soc., Canada, ix, 1891, Sec. iv, pp. 46-49. Wysogorski (Entwicklungsgeschichte, p. 8, footnote 1) places *O. lenticularis* in the genus *Orthis* emend. Wysog., which includes the impunctate *Orthis*.

‡ These two specimens are figured by Matthew (op. cit., pl. xii, fig. 10). His fig. 10*b* represents the same individual as our fig. 1*b*. It should be noted that all the plications reach the front margin and several of them bifurcate, giving, as shown in our figure, several additional plications at that point.

like that of the nepionic *Platystrophia* (fig. 1a')—a ventral valve in both cases. *O. lynceoides* also has a strong median plication and about four weaker ones on either side. The posterior half of the valve is devoid of longitudinal markings, but possesses concentric lines. The beak is well elevated, though the area is not exposed in any of Dr. Matthew's specimens. As shown in Davidson's figures of *O. lenticularis* the area is high and the foramen large and triangular.\* Our fig. 1c indicates that the ventral muscular impression is about the same as in other primitive *Orthidæ* (*Platystrophia*, *Plectorthis*, etc.).

The name which Dr. Matthew has given this pretty little variety of *Orthis lenticularis* indicates, as he also expressly states, that he considered it as a possible ancestor of *Platystrophia*. My own conclusion to the same effect was reached independently through a comparison of the nepionic *Platy-*

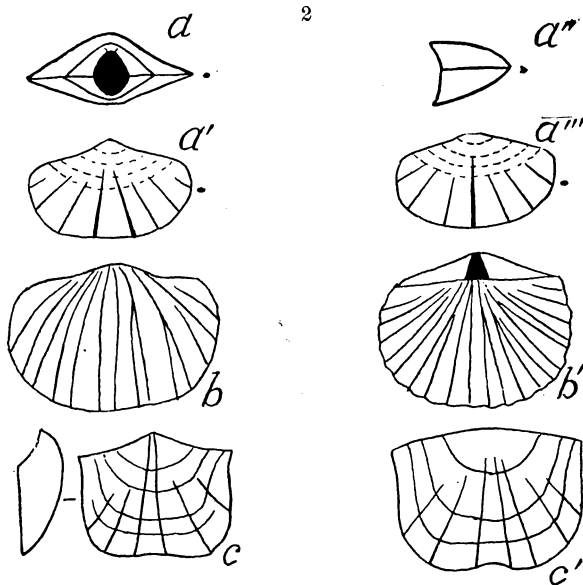


FIG 2. *a*, *a'*, *a''*, *a'''*, posterior, ventral, profile and dorsal outline views of the nepionic *Platystrophia*; actual size shown by small figures to the right. *b*, *b'*, ventral and dorsal views of *Orthis Hicksii*, after Davidson. *c*, *c'*, ventral and dorsal views of *Orthis salemensis*, after Walcott.

*strophia* with Davidson's figures of *O. lenticularis*. Aside from the strong resemblances pointed out above, the wide distribution, great abundance, and high variability of this species make it an ideal ancestral type. It may very well have produced, on the one hand, the pauciplicate group, *Platystrophia*,

\* Silurian Brachiopoda, 1869, pl. xxxiii, fig. 26a.

*Orthis* s. s. *Dinorthis*, *Plectorthis*, etc.; and on the other the multiplycate group *Hebertella*, *Dalmanella*, etc.

In the Middle Cambrian, *Orthis Hicksii* Salter,\* fig. 2*b*, has many of the nepionic characters of *Platystrophia* and may be the ancestor of *Orthis lenticularis*.

The Lower Cambrian furnishes very few Brachiopods of an Orthid aspect: but *O. salemensis* Walcott,† an outline figure of which is given here (fig. 2*c*), again strongly suggests the nepionic shell of *Platystrophia*. In the present state of our knowledge of Cambrian forms it is perhaps unsafe to speculate far in regard to phylogenies of any sort; nevertheless I am inclined to believe that some such form as *O. salemensis* constitutes the final link between the *Orthidæ* and the primitive Brachiopoda of the type of *Kutorgina cingulata*.

II. *Neanic stages*.—The specific characters of *Platystrophia* do not begin to appear until the shell has reached a breadth of 3<sup>mm</sup> or more. At about this size, the demarcation of the true fold and sinus, which began at a little over 2<sup>mm</sup>, has produced a noticeable sinuosity of the margin (as viewed from the front). At the bottom of the sinus is a single plication—the same that formed the ventral fold of the nepionic shell. On either side of the sinus are four or five plications (including the ones immediately bounding it). The dorsal valve has the two median plications slightly elevated, forming a fold; and the sulcus between them represents the continuation of the median dorsal sinus of the nepionic shell. (These stages are shown in fig. 3, IV, V.)

A little later (fig. 3, VI), usually at about the breadth of 4<sup>mm</sup>, two additional plications make their appearance in the sinus at its front margin, one on either side of the primary plication. In the dorsal valve at this stage the two plications of the fold are each seen to bifurcate, giving four in all. The typical number of plications of the fold and sinus of *P. lynx* are now present, though the lateral slopes still possess only five or six. Further increase in the number of plications of the slopes takes place by addition at the cardinal angles, and never (with the rarest exceptions) by bifurcation of those already formed, or by implantation between them. In a shell of 6 or 7<sup>mm</sup> breadth it is usually possible to determine the variety, therefore the neanic period may be said to cease at that size.

In well preserved material it is possible to study the neanic stages at the beaks of adult specimens; and these stages and those immediately following (early ephebic) are of the utmost importance in tracing lines of descent within the genus. Three

\*Davidson, Silurian Brachiopoda, 1869, p. 230.

†Tenth Ann. Rep., U. S. G. S., 1891, p. 612, pl. 72, fig. 6.

of the species which are here recognized as belonging to *Platystrophia* are marked by important differences at this stage.

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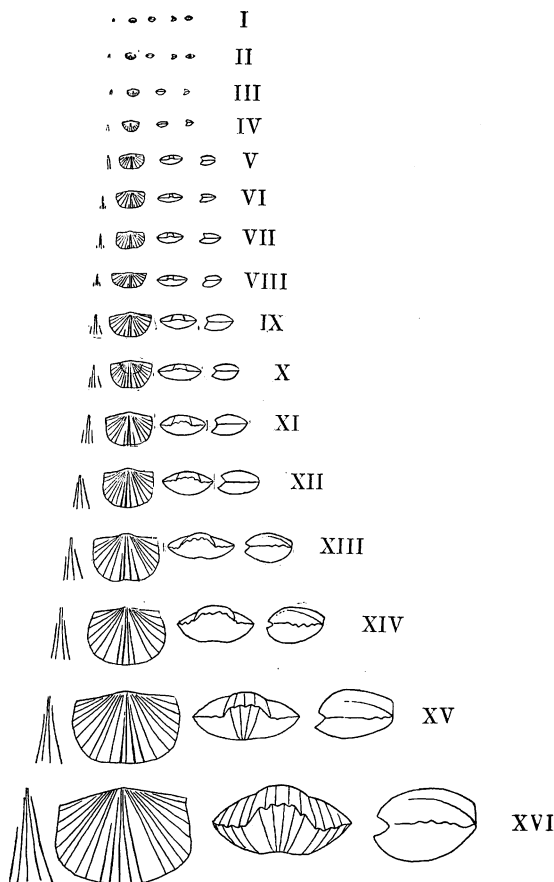


FIG. 3. Series of specimens of *Platystrophia lynx* from Vevay, Indiana, showing change in contour, profile, and convexity of shell with advancing growth. I, specimen 1<sup>mm</sup> broad, nepionic stage, natural size, same specimen as fig. 1a. V, beginning of neanic stage, in which the dorsal fold and ventral sinus become defined. The early ephebic stages are represented by numbers XI to XVI, the latter being a nearly adult individual, possessing four plications in the sinus. The method of origin of the plications of the sinus is shown to the left of each row. All natural size. Author's collection.\*

\*In all the outline figures in this paper the lines correspond to the depressions between plications, and the interspaces to the plications themselves.



The above described mode of origin of the plications of the fold and sinus applies to all American Ordovician forms, with the exception of some from the basal Trenton. It does not apply to Upper Silurian forms nor does it seem to apply to Ordovician forms of the Russian Province. Though I have not been able to obtain specimens of Upper Silurian forms of *Platystrophia* in the nepionic stage, nevertheless several adult individuals from the Island of Gotland are so perfectly preserved that even the nepionic stages can be studied at the beaks. In the Gotland specimens, precisely as in the Ordovician specimens just described, there is at first a median ventral fold and a median dorsal sinus. A little later the ventral fold becomes depressed between the two adjacent plications of the valve, and this median plication of the ventral sinus thus formed, immediately bifurcates, making the two main plications of the sinus of all Upper Silurian forms. On the dorsal valve the two plications bounding the median sinus become elevated, and a third is implanted between them, making the three main plications of the dorsal fold of all Upper Silurian forms. All the Russian Ordovician forms studied also belong to this type, as will be shown in a later paragraph.

An examination of thousands of specimens of American Ordovician forms, and scores of specimens of Silurian forms reveals no real exception to the above described modes of origin of the plications of the fold and sinus.\* Yet some confusion seems to exist on this very point.

In the *Geology of Minnesota*, vol. iii, p. 456, occurs the following statement in regard to the development of *Platystrophia*: "The writers [Winchell and Schuchert] regret their inability to secure very young specimens of this species for the purpose of determining the ancestors or line of development. In several immature individuals it has been observed that in the early nealagic [neanic] stage the beaks are strongly elevated, probably erect, and each has a very large open delthyrium, surface smooth at first, but gradually developing eight plications and a mesial sinus in each valve. The sinus in the dorsal valve is bounded by two elevations which become plications, and between them is soon developed a single costa which immediately bifurcates. The four plications increase in strength and become strongly elevated as they proceed to the anterior margin, producing the conspicuous fold of the valve."

With the first part of this statement my observations are in full accord. In regard to the origin of the plications,

\* Some specimens from the basal Trenton, to be described later, are of the Upper Silurian type.

however, it is necessary to state that the method they describe has only been observed in an occasional specimen of Upper Silurian (biplicate)\* type and therefore does not apply to any of our Ordovician *Platystrophias* above the basal Trenton. In no case have I seen a mesial sinus in both valves, at any stage in development. The true method of origin of the plications in American Ordovician forms was pointed out by Hall in 1847.†

It remains to note some apparent exceptions to the above rule in regard to American Ordovician forms. Very rarely in the Cincinnati group an individual of *Platystrophia costata*‡ occurs with three full plications on the fold and two in the

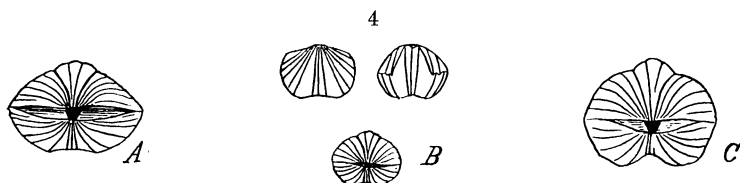


FIG. 4. A and C, specimens of a pauciplicate *lynx* from Cincinnati, Ohio, in which the third plication of the sinus is suppressed, causing the shell to simulate *P. dentata*, shown at B. In C the lateral plication of the sinus is clearly seen to be implanted; and less clearly though just as certainly in A. In *P. dentata* as shown in B (a specimen from Russia) the primary plication of the sinus bifurcates. A and C from the Dyer collection, Museum of Comparative Zoology, Harvard University. B from collection of the U. S. National Museum.

sinus. In the Dyer collection at Harvard, which contains several thousand specimens of this variety, I noticed perhaps half a dozen such individuals. In the majority of these the type is manifestly triplicate, since the second plication of the sinus is implanted at the side of the primary and does not originate by the bifurcation of the primary. The third plication is simply suppressed. I saw but two individuals (fig. 4, A and C) in which the primary plication seemed to bifurcate, and even here a close inspection of the beak shows that the second plication is really implanted.

Another apparent exception is that of the type in which there is but one plication in the sinus. A careful examination

\* It is convenient to speak of forms of *Platystrophia* having two main plications in the sinus, originating as just described the Silurian type, as biplicate. Those having three characteristic plications, as in nearly all American Ordovician forms, are similarly called triplicate; and those having but one plication in the sinus, uniplicate.

† Pal. N. Y., vol. i, 1847, pp. 133-134.

‡ The American form known as *dentata* Meek, and *crassa* James, has been shown to be the same as *costata* Pander. See this Journal, July, 1902, p. 14, footnote.

of numerous individuals has, however, demonstrated the fact that even this type is fundamentally triplicate.\* The details of this point will appear later. Suffice it to say that here again the secondary plications have been suppressed. They may often be seen more or less distinctly in the rostral region, but fade out toward the front. With the one exception, therefore, noted above, all the Ordovician forms of this country belong fundamentally to the triplicate type.

*Comparison with adult stages of other Orthidæ.*—The early neanic shell with one plication in the sinus and five on each lateral slope is strikingly suggestive of the var. *costata* of Russia and the lower part of the Cincinnati group of this country. As just pointed out, however, the latter is evidently derived from a triplicate type such as we find abundantly represented in the Trenton. Practically any group of *Platystrophia* may produce an occasional uniplicate individual. Fig. 15f shows it in the normal *costata*; fig. 15a in the var. *laticosta*. In the *lynæ* group it is extremely rare. Only one example has come to my notice. Theoretically there should be a uniplicate *Platystrophia* in the lowest Ordovician. If this stage was passed before any definite differentiation of the fold and sinus took place, then some of the small *Orthidæ* of the Calciferous and Chazy come very near the requirements. Otherwise I know of no form corresponding to the theoretical uniplicate type.†

In some respects the adult *Plectorthis plicatella* resembles the neanic *Platystrophia*. If the sinus and fold be disregarded (and in some Trenton forms these are surprisingly inconspicuous), the neanic *Platystrophia* is almost a *Plectorthis*. There is little doubt that when the nepionic shell of *Plectorthis* is discovered it will be found to be quite indistinguishable from the nepionic shell of *Platystrophia*, since the two groups present at the beaks almost identical characters. *Plectorthis* appears in American faunas in the Black River formation,‡ and *Platystrophia*, as we have seen, in the basal Trenton. *Plectorthis* may therefore represent an offshoot from the *Platystrophia* group near its initiation or, as sug-

\* For the uniplicate European forms I cannot speak. From what I can infer from a careful study of their range and variation, they also probably sprang from a triplicate or biplicate type. This subject will be discussed more in detail later.

† I have gone over the large collections in the Yale Museum, from Crown Point and other well known localities of Chazy and Calciferous fossils. No doubt the connecting form between *Orthis lenticularis* and *Platystrophia* will come to light when much more complete investigations of these old Ordovician rocks are made.

‡ Mr. P. E. Raymond figures and describes specimens of *Plectorthis plicatella* from the Black River limestone of Crown Point, N. Y. (Bull. Am. Paleontology, No. 14, 1902, p. 88, pl. 19, figs. 5, 6.)

gested above, it may have been separately derived from the *Orthis lenticularis* stock.

III. *Ephebic stages*.—The ephebic stages begin with the assumption of characters of lowest taxonomic rank (varietal) (see fig 3; XI–XVI). During these stages there is no marked change in the number of plications, though these may be added, or in the case of the fold and sinus, subtracted, until the final assumption of gerontic characters. The convexity of the valves increases progressively, and the incurvature of the beaks becomes more and more pronounced. The pedicle often

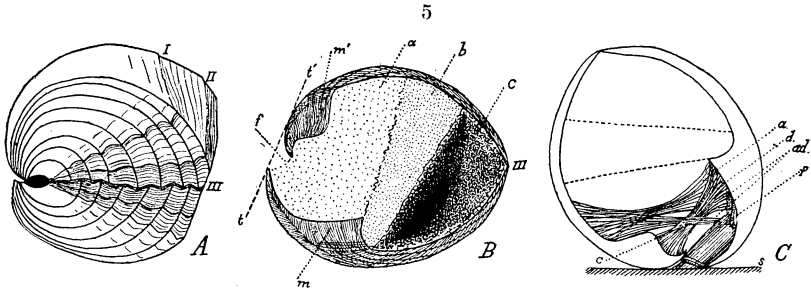


FIG. 5. Very large senile individual of *Platystrophia lynx* from the upper Lorraine of Vevay, Indiana;  $\times \frac{1}{2}$ . A, profile; B and C, sections in the median plane. Normal adult growth was attained at varix No. I. The successive additions of shell substance are shown in B, and the probable musculature in C. The pedicle has entirely abandoned its original foramen and encroaches on the umbonal region of the ventral valve; the apex of the dorsal valve lies in the ventral delthyrium. The shell was partially infilled with very fine silt, probably while still standing in its natural position, with the shell resting on the plane *tt'(s)*. *f*, pedicle passage; *mm'*, muscular platforms of dorsal and ventral valves respectively; *a*, *b*, oxidized and unoxidized portions of infiltrated material; *c*, cavity lined with small crystals of calcite; C, *a.*, adductor muscle; *d.*, diductor; *ad.*, adjusters; *p.*, pedicle; *c.* position of hinge axis. Author's collection.

encroaches on the apex of the ventral valve, even sometimes in early ephebic stages. All, or any of these changes may affect any one of the forms under which *Platystrophia* is known. Other modifications affecting the ephebic stages can more conveniently be discussed under the heads of these various forms.

IV. *Gerontic stages*.—Old age manifests itself in *Platystrophia* by increasing gibbosity, thickening of the shell, pronounced growth varices, and obsolescence of plications, and at times by marked changes in the contour of the shell (shell index). Though senile individuals are met with in all the types of *Platystrophia*, *lynx* and *acutilirata* afford the best examples of it, and in many specimens from the upper range of these species senescence begins early in the ontogeny.

Of these gerontic modifications, the thickening of the shell and obsolescence of plications are the most important. The former character is well shown in fig. 14, and the latter in fig. 12. The thickening of the valves is responsible for the increasing incurvature of the beaks. In extreme cases (fig. 5 *A*) this causes the pedicle to encroach on the ventral beak to such an extent as to completely abandon its normal foramen, which is invaded by the dorsal beak.

Fig. 5 represents the largest specimen of *P. lynx* seen. *C* shows it in its natural position during life with an indication of the musculature. This individual is decidedly senile, complete ephebic growth having terminated at the varix No. *I*, though the amount of thickening of the shell is not as great as in many smaller individuals (cf. fig. 5 *B* and fig. 14 *B*).

*Platystrophia acutilirata* presents even more extreme gerontic modifications than *P. lynx*. The greatest gibbosity seen in any group occurs here, and the amount of change in the shell index is truly remarkable. It will be more convenient, however, to discuss the details of these changes due to senescence under the heads of the several species and varieties of *Platystrophia*.

#### *Platystrophia lynx*.\*

The species commonly known in this country as *Platystrophia lynx* is beyond any question the most abundant and widespread Ordovician member of the genus, and also bears the greatest resemblance to the species commonly known as *Platystrophia biforata* (Schlotheim). Hall † does not attempt to distinguish between them. Davidson ‡ says in regard to the British specimens, "We certainly have the type *biforata* and the variety *lynx*, but these two seem so intimately connected that I have combined them under Schlotheim's single designation [*biforata*]." According to von Buch, § *lynx* has four plications in the sinus and on the fold || and nine on each side. Schlotheim's *biforatus*, he says, is "very nearly related" to *lynx*. The former has five plications in the sinus and nine on each side and is broader than *lynx*. According to de Verneuil ¶ "The *S. [Spirifer] biforatus* proper seems to be rare; we have, as had Eichwald, a single specimen very poorly preserved. His came from Reval and ours from the neighbor-

\* Eichwald, Skizze von Podolien, 1830, p. 202.

† Pal. N. Y., i, 1847, p. 132.

‡ Silurian Brachiopoda, 1871, p. 271.

§ Essai d'une classification et d'une description des Delthyris, etc., Mem. Soc. Géol. France, iv, 1840, pp. 190, 191.

|| He certainly was mistaken in either the number on the fold or in the sinus. There is always one more on the fold.

¶ Géol. de la Russie, 1845, pp. 136, 137.

hood of St. Petersburg. The beaks, as in most *Spirifers* from the latter locality, are small, appressed and render it difficult to view the double area" (p. 136). Of *lynæ* he says, "This variety differs from *S. [Spirifer] biforatus* only in the less number of plications in the sinus . . . . M. Eichwald says he found it in the drift near Grodno, with two plications in the sinus, three on the fold and eleven on the sides" (p. 137).\*

So far as concerns the characters mentioned above as distinctive of *lynæ* and *biforata*, it must be admitted that none of them are of any value. *Platystrophia lynæ* has all the way from one to seven plications in the sinus and may have from six to twelve on either side; and varies in shell index between the limits of 1.0 and 1.8.†

It is altogether likely that the *biforatus* type does not occur in American upper Ordovician faunas; and the same may be true of Eichwald's species, *lynæ*. The latter certainly and Schlotheim's species in all probability, came from Russia. In regard to *biforatus*, von Buch (loc. cit.) says, it "very likely came from the north and not from France." With our present knowledge of the species we may be sure it did not come from France, at least, if it is an Ordovician type at all. It may very likely have been obtained in the same manner as *P. lynæ* from glacial pebbles.‡

I have before me specimens of the *lynæ*, *biforata*, and *dentata* types from the Ordovician of Russia. All of these show a peculiarity that I have never seen in an American so-called *biforatus* or *lynæ*, from beds of equivalent age, namely, the presence at the beaks of three plications on the fold and two in the sinus. This peculiarity, as has been pointed out, invariably characterizes Silurian forms both American and foreign.§

Figures 6, 4*b* and 21*e*, are of these Russian types; and show the number and arrangement of the plications of the fold and sinus. Fig. 21*e*, of the ventral valve of a specimen of *P.*

\* The shell index of *biforatus* given by deVerneuil is 1.5 : that of *lynæ* 1.3.

† Schuchert says (Bull. U. S. G. S. No. 87, 1897, p. 308), "Individuals of a stratum . . . are fairly constant in form, size, and plications, and it is this limited constancy that has served in many of the following species [*biforata*, *lynæ*, *laticosta*, *acutilirata*, *crassa*]." Even this "limited constancy" can scarcely be found in many localities, for I have seen several of the varieties together in a single slab of limestone.

‡ It should be remembered that Schlotheim distinctly states that his "one example" of *Terebratulites biforatus* came from Southern France. Either he was mistaken or this type is a Mesozoic *Spiriferina*!

§ Mr. A. F. Foerste (Bull. Dennison University, i, 1885, p. 80) was the first to call attention to the fact that Silurian forms have an odd number of plications on the fold and an even number in the sinus, while the reverse is true of Ordovician forms. While this is not strictly true, it is true that the Silurian forms have at the beak, without exception, three on the fold and two in the sinus.

*biforata* from Wesenberg,\* Russia, shows five plications in the sinus. To the left is shown the arrangement of these plications. At the apex there is a single plication which immediately bifurcates. Then a plication is implanted between the two thus formed, and immediately bifurcates giving four plications. Between the two last formed is now implanted

6

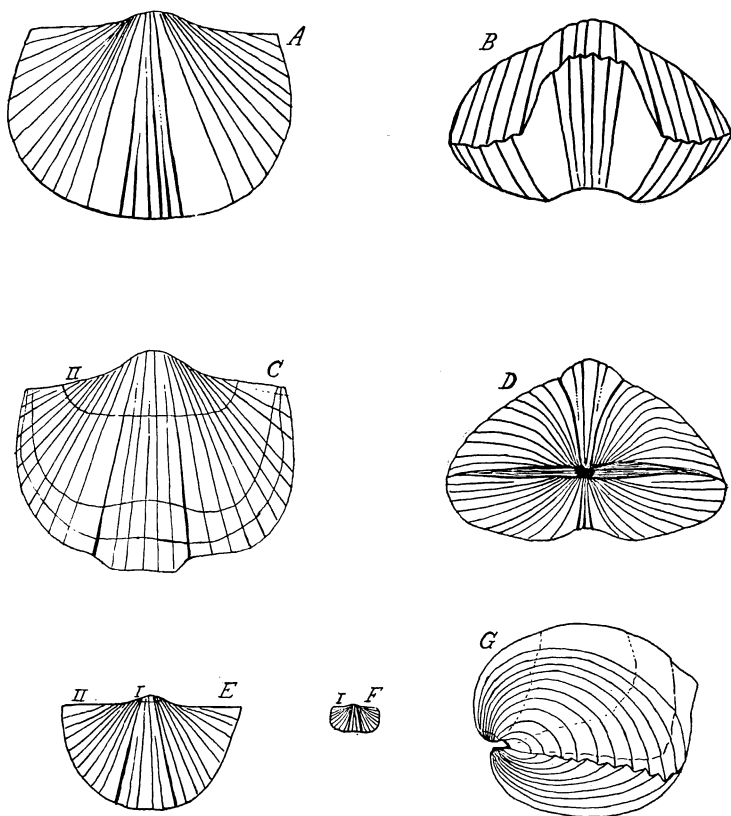


FIG. 6. *Platystrophia biforata* (*P. lynx* of authors) from Pulkowa, Russia. A-D ventral, anterior, dorsal, and posterior views; E, stage II. (see C) drawn separately; F, stage I. (see E) drawn separately; G, profile, showing strong incurvature and great size of dorsal valve.† Collection U. S. National Museum.

another plication, making five. Fig. 21e', of the dorsal valve of the same specimen, shows six plications on the fold, which as seen in the diagram to the left originate as follows: first, two

\* This specimen and the next to be described were labeled by F. Roemer.

† All figures natural size unless otherwise stated.

appear at the apex; between these, one is implanted and almost immediately bifurcates; and between these two, another is implanted and bifurcates, making six in all.

Another specimen of *P. biforata* from Wesenberg, Russia, has four plications in the sinus and five on the fold, but they originate in precisely the same way. The last plication added on the fold does not, however, bifurcate; and the unpaired median plication of the sinus is wanting.

In a specimen from Pulkowa, Russia (near St. Petersburg), labeled *P. lynx*, there are (fig. 6) six plications on the fold and five in the sinus. These originate as follows: In the sinus one plication appears at the apex and immediately bifurcates. Each of the two thus formed bifurcate, and the one to the left bifurcates again, giving five in all. On the fold two plications appear at the apex and one more is almost immediately implanted between them. Each of these three now bifurcate, giving, at the front margin, six plications. The specimen therefore belongs to the same type (biplicate) as the Wesenberg specimens. It is impossible to make sure from the literature of the Russian *Platystrophia* whether this peculiarity characterizes all Russian forms. According to Wysogorski,\* who is very familiar with the *Orthis* of the Baltic-Province, "the form from the Upper Silurian of Gotland is characterized by smaller size [than the Russian form] while in other respects it agrees with *Platystrophia biforata* Schloth." I have examined some thirty specimens of the Gotland form and these invariably have three plications on the fold and two in the sinus. If Wysogorski has taken this peculiarity into consideration, his statement is strong evidence, in support of that afforded by the Russian specimens which I have examined, as to the bipligate character of all these Russian types. None of the earlier authors shed any light on this point. De Verneuil gives several excellent figures of the *lynx*, *dentata* and *chama* (= *costata*) types and mentions a *lynx* from Grodno with two plications in the sinus. In his figures of *lynx* four plications are shown on the fold but their mode of origin cannot be made out, though they are all shown to originate closer to the apex than is common in our American *lynx*, and even closer than in the *lynx* from Cincinnati, Ohio, figured on the same plate. Whenever four plications are present on the fold of biplicate types, they certainly come in closer to the apex than the four plications of triplicate types. Nevertheless, such evidence as afforded by the figures in question cannot be considered as of any particular value.

Davidson's figures and descriptions of British Ordovician

\* *Entwicklungsgeschichte*, p. 15.



specimens leave us almost equally in the dark on this point.\* Fig. 12 of *biforata* certainly seems to be of the triplicate type, the same as our Trenton and Cincinnati *lynæ*. The var. *fissicostata*, on the other hand, is more probably of the biplicate type; as are certainly all the Wenlock forms figured. On the whole, it seems quite likely that the majority of Russian, if not of all European Ordovician forms of *Platystrophia*, belong to the biplicate type. *In this country, however, the biplicate type is absolutely restricted to the Silurian and basal Trenton.*†

This difference in the mode of origin of the plications of the fold and sinus is of fundamental importance. It has been shown that in nepionic stages of all forms, whether American or European, Ordovician or Silurian, there is a median plication or fold on the ventral valve and a median sulcus or sinus on the dorsal valve. This nepionic ventral fold becomes the primary plication of the ventral sinus of later stages. In triplicate and uniplicate types this primary plication remains simple; but in biplicate types it bifurcates near its point of origin, i. e., in an early neanic stage. Such a difference characterizing so early a stage of the shell certainly *points to the origin of the peculiarity very early in the history of the genus*; and it is consequently very significant that the only place where the two types, biplicate and triplicate, are associated together in American faunas, is in the basal Trenton of the Hudson-Champlain area.‡ The question whether there is a similar association of the two forms in the early Russian deposits cannot with the material at present available be definitely settled.

*Platystrophia* seems to have made its appearance in Russian seas at fully as early an epoch as in American. Wysogorski states that it occurs first in the Echinosphærites limestone.§ Schmidt lists *P. lynæ* from Erras, Reval and Odensholm in beds from the "vaginatum" limestone to the Borkholm.|| Wl.

\* Silurian Brachiopoda, 1871, pp. 268-273, pl. xxxviii, figs. 11-25.

† These basal Trenton forms from the Hudson-Champlain area will be described under the *biforata* type, to which they belong. The fact that they are of the biplicate type, taken in connection with the further fact, brought out by Ruedemann, of the general European aspect of the Lower Ordovician faunas of the Hudson Valley area, is certainly in striking accord with the evidence already adduced as to the predominance of the biplicate type of *Platystrophia* in European faunas. See also Ulrich and Schuchert, Bull. N. Y. Mus. No. 52, 1902, pp. 633-663.

‡ An apparent exception to this statement has been discussed under the subject of neanic stages.

§ Entwicklungsgeschichte, pp. 14, 15.

|| Untersuchung über die Sil. Form. von Ehstland, etc. Archiv. für die Naturkunde Liv-, Ehst.- und Kurlands, 1ter ser., 2ter Band, 1858, p. 213.

Lamansky cites *Platystrophia biforata* from the "planilimbata" limestone.\* As to the correlation of these beds with American strata there is unfortunately no unanimity of opinion. Schmidt is disposed to consider the Echinosphærites limestone as the equivalent of the Quebec Group of this country; and the vaginatum as equivalent to our Black River formation.† In Kayser's *Lehrbuch der Geologie* (1891) the Echinosphærites limestone is placed higher than the Trenton and the vaginatum as equivalent to the Trenton.‡ The planilimbata limestone would then be about equivalent to our Black River. Substantially the same correlation is given by Neumayr§ and by de Lapparent.|| It seems probable, therefore, that the first appearance of *Platystrophia* in Europe was at least as early as in this country, and perhaps earlier: and since it was during this early Ordovician epoch that the two main types of the genus were being differentiated, we may expect to find both in the European as well as in the American deposits of that age.

From the above discussion it appears that there existed after the early Ordovician two distinct types of *Platystrophia*, one of which (the triplicate) characterized the American Ordovician, and the other (the biplicate) the European Ordovician and the Silurian of both America and Europe. Both of these types or species include several varieties. It is also evident that the terms *lynæ* and *biforata* have been very loosely applied to both of these types. Since the term *lynæ* has become so strongly associated with the American group of shells (triplicate type), I propose to limit the term to such American Ordovician shells. It is impossible to say whether the type of *P. biforata* is biplicate or triplicate. The presumptions are strongly in favor of its being biplicate. I, therefore, propose to restrict the term to biplicate forms such as the Wesenberg specimen above described. It will then include Ordovician forms of Europe, and Clinton forms of both Europe and America. For the biplicate shells with few plications such as are found in Gotland, the Wenlock of England, and Anticosti, the term *dentata* will be used. Further details of the species *biforata* and *dentata* will be given later.

*Derivation of Platystrophia lynæ*.—According to the above interpretation and restriction of *P. lynæ*, this form probably

\* Neue Beiträge zur vergleichung des Ost-Baltischen und Scandinavischen Unter-Silurs. Centralblatt für Min. Geol. und Pal., Neues Jahrb., 1901, No. 20, pp. 611-618.

† Quar. Jour. Geol. Soc., xxxviii, 1882, pp. 520, 521; Archiv. Liv., Ehst.-und Kurlands, 1ter ser., 2ter Bd., 1858, p. 48.

‡ Op. cit., p. 64.

§ Erdgeschichte, 1895, vol. ii, p. 98.

|| Traité de Géologie, 1900, p. 824.

stands nearer the radical stock than any other. The case in which the nepionic ventral fold remains simple and unmodified throughout the life of the individual certainly must be considered as more primitive than the case in which the nepionic fold bifurcates. It is known that in nepionic and early neanic stages of brachiopods, plications are added by implanta-

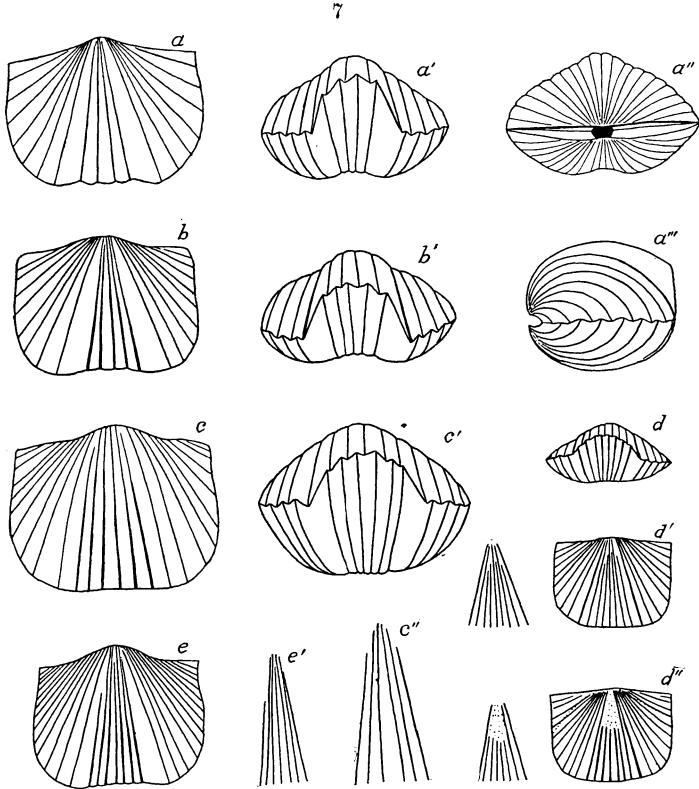


FIG. 7. *Platystrophia lynx* from Vevay, Indiana, showing variation in number of plications of fold and sinus. *a a'''*, ventral, anterior, posterior and profile views of a normal individual with the normal number, three in sinus and four on fold; *bb'*, ventral and anterior views of individual with four plications in sinus, the fourth originating by bifurcation of the left lateral; *cc'*, ventral and anterior views of individual with five plications in sinus, the two additional plications are implanted, *c''*, diagram showing method of origin of plications; *ee'*, individual with six plications in sinus; *dd'* (with diagrams to left of *d'* and *d''*), individual with seven plications in sinus; *d'*, dorsal; *d''*, ventral views. Author's collection.

tion except in highly accelerated types. We must believe, therefore, that a tendency of the primary plication of the

sinus to bifurcate manifested itself as an adult character in the ancestors of *Platystrophia biforata*, and that, subsequently, acceleration crowded back the point of bifurcation into early neanic stages.

The most primitive *Platystrophia* should, as stated in another place, be uniplicate, and it was from such a uniplicate stock that both *P. lynx* and *P. biforata* were derived. The fact that in *lynx* there is no modification of the fold and sinus until an *advanced* neanic stage, while in *biforata* such modification takes place, as explained, at an *early* neanic stage, indicates that *lynx* is nearest to this primitive *Platystrophia*. *P. lynx* certainly stands as the radical of all our Ordovician forms above the basal Trenton.

*Variation of Platystrophia lynx*.—This subject has already been investigated quantitatively and the results published.\* As that investigation applied to specimens from the Middle Cincinnati group only, there is considerable to add in regard to Trenton forms and especially in regard to some highly accelerated forms from immediately beneath the Clinton limestone at Richmond and other localities in Indiana. The Vevay material, quantitatively studied, included the varieties *laticosta* and *costata*, which were shown to pass by insensible gradations into the normal *lynx* type.†

The *lynx* group of the Trenton varies extensively in contour and number of plications, as has often been pointed out.‡ Fig. 8 shows the contour of a series of sixteen specimens, taken at random, from Trenton Falls' material. The index here varies from 1.2 to 1.82, the average being 1.42 and the largest class 1.4. The angle between the hinge line and lateral line of the shell (cardinal angle) varies from 80° to 110°; the number of plications on the ventral valve from 17 to 24, and the number in the sinus from 2 to 6. No. 32, fig. 8, is a composite of Nos. 1-16 inclusive and shows the normal Trenton Falls' type of shell. This shell has a cardinal angle of 90°, with very slight auriculation.§

\* Cumings and Mauck, A Quantitative Study of Variation in the Fossil Brachiopod *Platystrophia lynx*. This Journal, July, 1902, pp. 9-16.

† Mr. F. W. Sardeson has expressed the opinion that all the so-called varieties of *Platystrophia* in the Cincinnati group are distinct.

A careful study and measurement of over 2,000 individuals and inspection of some 8,000 others, has failed to establish a specific distinctness. See Sardeson, Am. Geol., vol. xix, 1897, p. 109. Compare also Williams, Geol. Biology, pp. 315, 321.

‡ See especially Hall, Pal. N. Y., vol. i, 1847, pp. 133, 134. Winchell and Schuchert Geol. Minn., iii, 1893, pp. 456, 457.

§ When there is any auriculation of the cardinal extremity the measurement is made between the hinge line and a line tangent to the cardinal extremity and the lateral margin, as shown in fig. 8 bis.

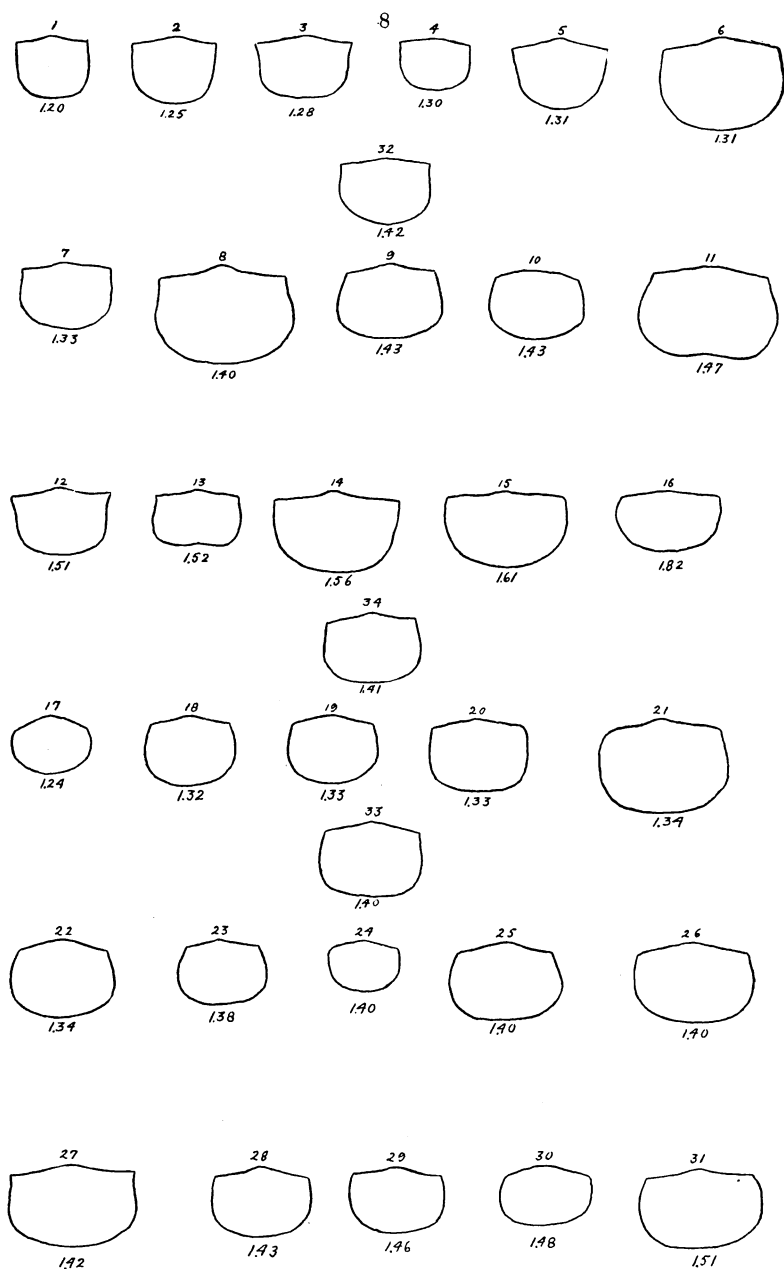


FIG. 8. *Platystrophia lynx*. 1-16, from Trenton Falls, N. Y.; 32, composite of 1-16; 17-31, from Colby County Kentucky (Trenton); 33, composite of 17-31; 34, composite of 1-31; Shell index given below each figure. All natural size. Collection Yale Museum.

Nos. 17-31 inclusive, fig. 8, represents the contours of a series of specimens from the Trenton of Kentucky (Colby Co.). Here the index varies from 1.24 to 1.51; the average being 1.4 and the largest class 1.4. The cardinal angle varies from  $90^{\circ}$  to  $112^{\circ}$  (in a specimen from Harrodsburgh, Mercer Co., Ky., the cardinal angle is  $120^{\circ}$ ). The number of plications varies from 17 to 27; the number in the sinus from 3 to 5. No. 33, fig. 8, is a composite of Nos. 17-31 inclusive. This

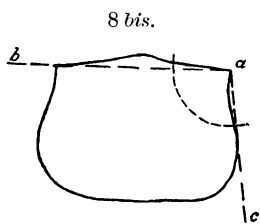


FIG. 8 bis. Diagram showing method of obtaining cardinal angle *bac*.

normal shell of the Kentucky group has an index of 1.40 and a cardinal angle of  $95^{\circ}$ . No. 34, fig. 8, is a composite of Nos. 32 and 33, and has an index of 1.41 and an angle of  $93^{\circ}$ . The great similarity of the New York and Kentucky forms is apparent.

Very few specimens from the Trenton of Minnesota have been studied, but these show no departure from the above type. The specimens from the Galena of Minnesota are however more like the

Cincinnati group *lynx*.

In brief, the Trenton shell is rather transverse, slightly shorter on the hinge than farther forward; valves about equally convex, never extremely gibbous; plications about 22, of which three or four are in the sinus, four or five on the fold. The sinus is never as profound as in the varieties *costata*, *laticosta* and *acutilirata*.

The Trenton forms just described are from the middle and upper part of the series. Some specimens from Montreal, Canada, loaned me by Mr. Chas. Schuchert, are of a somewhat different and more primitive type. These latter (fig. 9) have

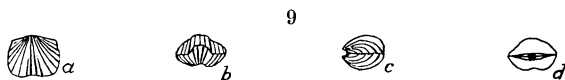


FIG. 9. *Platystrophia lynx*, small pauciplicate form from the lower Trenton at Montreal, Canada. *a*, ventral; *b*, anterior; *c*, profile; *d*, posterior views. Schuchert collection.

but 4-7 plications on the slopes; the shell is narrowest at the hinge-line and considerably less transverse than the Trenton Falls type (the index is 1.23 in the specimen figured, which is about an average individual). The second and third plications of the sinus arise about  $4^{\text{mm}}$  from the beak. These shells strongly suggest the small pauciplicate form found at the base of the Lorraine at Cincinnati, Ohio.\* As to the exact age of the beds from which these specimens came it is impossible to say. In

\* See Winchell and Schuchert, Geol. Minn., iii, 1893, p. 456.

the section at Montreal, given in the Geology of Canada, "*Orthis lynx*" is listed from the first, second, and fourth divisions of the section; that is from the lower 150 ft. of the formation. The chances are that the present specimens are from the lowest of these divisions, or less than 10 ft. above the Black River formation.\* These small shells may therefore represent the immediate ancestors of the normal Trenton form above described.

The small pauciplicate *P. lynx* (fig. 9 bis) from the lower Lorraine at Cincinnati, is of interest as the immediate progenitor of *P. costata* and probably also of *P. laticosta*. It occurs, associated with the uniplicate form (*costata*), often in clusters, one of which is shown in fig. 9 bis. This specimen has the shells in their natural position, with the beaks very closely appressed to the surface of support.

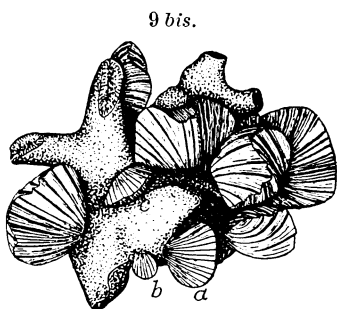


FIG. 9 bis. Cluster of *Platystrophia lynx*, pauciplicate form, on a colony of *Constellaria constellata*. All the individuals are in their natural position with the beaks closely appressed to the surface of support. *a* and *c*, *Plectorthis plicatella*; *b*, *Zygospira modesta*. Collection of the Museum of Comparative Zoology, Harvard University.

The question arises whether this form of *P. lynx* is not an unmodified descendant of the Montreal type just described. This is certainly possible if not probable. The occurrence of an occasional individual with few plications among the normal *P. lynx* of the middle and upper Trenton suggests, on the other hand, that these lower Lorraine forms may have originated as a variant of the latter. For convenience this form of *P. lynx* may very well be called *pauciplicata*. It seems, as stated above, to represent the initiation of a tendency that afterwards in *P. laticosta* and *P. costata* assumed considerable importance.

In American literature the Trenton shells have often been referred to the species *biforata*. I have already pointed out the fact that this type is not represented in American Ordovician deposits above the basal Trenton. The large form from the Cincinnati group universally known as *Platystrophia lynx* probably differs from the Russian *lynx* and is identical with our Trenton forms. In the interval between the Trenton and Lorraine the typical *lynx* changed surprisingly little. Fig.

\* Geol. of Canada, 1863, pp. 137-138.

10, *a*, is drawn from an individual which departs very little from the normal form of the Lorraine.\* Fig. 10, *b*, is an average specimen from Trenton Falls, N. Y., enlarged to the same size. The two shells have the same index, nearly the same number of plications, and differ little in contour. The cardinal angle of the Lorraine specimen is  $89^\circ$ , that of the Trenton Falls specimen  $96^\circ$ . The latter is more gibbous. It would

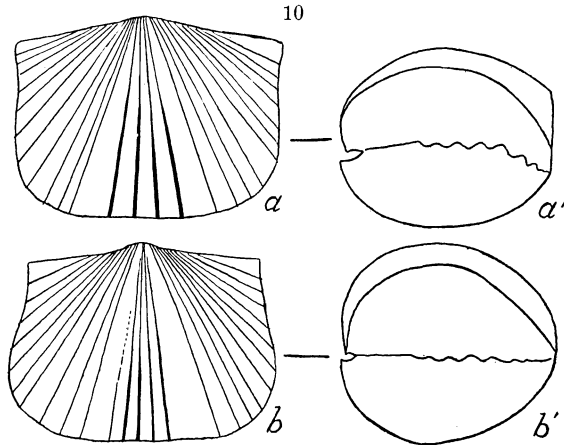


FIG. 10. *Platystrophia lynx*. *aa'*, normal Lorraine type from Vevay, Indiana, natural size; *bb'*, normal Trenton type from Trenton Falls, N. Y.;  $\times 2\frac{1}{2}$ . *a*, author's collection; *b*, collection of Mr. Wm. L. Porter.

be possible to select plenty of adult individuals from the Trenton and Lorraine that except for size would present no appreciable differences. The slight change of the average shell index (from 1.4 in the Trenton specimens to 1.3 in the Lorraine (Vevay) specimens) is due solely to the more robust growth of the latter, which always have the higher index in early ephelic stages (see fig. 13). It will be shown later that the extreme manifestation of this tendency produces in the upper Lorraine a shell of very low index; while the latest representatives of *lynx*, now to be described, have again a very high index.

In the extreme upper part of the Ordovician (Madison beds) of Richmond, Weisburg and Laurel, Indiana, the writer found a variety of *Platystrophia lynx* which is of exceptional interest (fig. 11). As is well known, the so-called Richmond beds (*Rhynchotrema* zone) contain exclusively the variety *acutilirata* associated almost constantly with *Hebertella occidentalis*. At about 50 ft. below the Clinton at Laurel and about 13 ft.

\* This specimen is from Vevay, Indiana.



to 15 ft. at Richmond, comes in a large and decidedly transverse variety of *P. lynx* associated with *Hebertella sinuata*.\* This association is a point of great importance since it shows that these two forms of *Platystrophia* and *Hebertella*, so constantly met with together in the Lorraine, have lived on together at some point through the *Rhynchotrema* hemera† and here under a recurrence of suitable conditions reappear, the former with some modification, the latter with scarcely any.‡

This form of *Platystrophia lynx* has eight to eleven plications on the lateral slopes, and the index may be as great as 1.9.

11

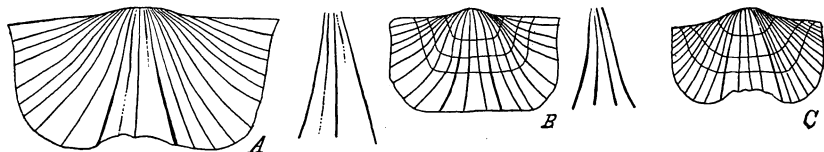


FIG. 11. A, *Platystrophia lynx* from 12 ft. below the Clinton at Richmond, Indiana: dorsal valve showing obsolescence of both lateral plications toward the anterior margin. B, dorsal valve of another individual from the same horizon and locality showing complete reduction of the fourth plication. C, specimen of *P. acutilirata* from the extreme Upper Ordovician at Weisburg, Indiana, showing the similarity of this retrogressive form to *P. lynx*. Author's collection.

A number of individuals (5 out of 100) show a reduction of the lateral plications of the fold and sinus. Fig. 11, A, shows a reduction of both lateral plications of the fold. On the anterior portion of the fold, the one to the right has completely vanished and the one to the left is very faint and does not reach the margin. All four plications are about normal on the posterior portion of the fold. Another specimen, fig. 11, B, has three plications on the fold. The only indication of the fourth is the abnormal breadth of the right hand plication at the umbonal region.

That such a tendency to eliminate plications should affect 5 individuals out of 100, while in the Lorraine not more than one *P. lynx* out of a thousand exhibits anything analogous, is certainly not without profound significance. There are in the

\* These beds are exposed at Richmond near the point where the "Boston Pike" crosses Elkhorn Creek, S.E. of the city. The ledge of Clinton 12 ft. thick forms a fall. Immediately below the Clinton is 4 ft. of clay and below this, limestone layers alternating with shale. *Platystrophia lynx* is found in large numbers in the limestone for some distance down the creek.

† Buckman's term, or some other equally unequivocal, is needed in a case like this where the lifetime of a species is referred to. See Quar. Jour. Geol. Soc., xlix, 1893, p. 481.

‡ The *Rhynchotrema* zone does not contain any specimens of *Hebertella sinuata* except at its very base.

present collection two specimens of *Platystrophia lynx* from Vevay, Indiana, both of which have three plications on the fold : One individual has four in the umbonal region ; and the other never developed but three\* at any stage. The first has an abnormally low index (1.1) and bears every evidence of lateral cramping during growth. This would account for the failure

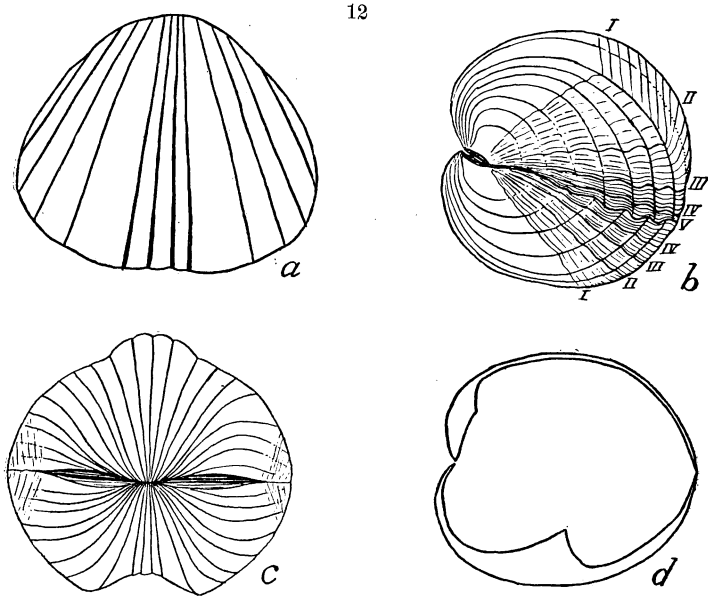


FIG. 12. Markedly gerontic individual of *Platystrophia lynx* from the "lynx beds" of Cincinnati, Ohio. Normal adult growth ceased at varix No. I. Note the very large cardinal angle ( $125^{\circ}$ ), extreme gibbosity, and obsolescence of the lateral plications. Dyer collection, Museum of Comparative Zoology, Harvard University.

of the fourth plication. The early growth stages of the second specimen also show an abnormally low index and the failure to develop the full number of plications is therefore probably due to the same cause. The Richmond shells, on the other hand, are very transverse at all stages, especially so in the adult. The correct explanation of the obsolescence of plications in this type, as well as in the *laticosta* and *costata* types where it is still more pronounced, is probably to be sought in a readjustment of the brachia, producing an elevation and narrowing of the fold. This subject will be more fully discussed in a later paragraph.

\* Both are strictly of the triplicate type.

*Gerontic stages of Platystrophia lynx.*

—The gerontic stages of this species are alluded to above. In the "lynx beds" at Cincinnati, Ohio, there is a veritable race of gerontic individuals. Fig. 12 represents one of these (from the Dyer collection of Harvard). The hinge-line is relatively very short, the cardinal angle being  $125^{\circ}$ . The vertical diameter exceeds the longitudinal in the ratio of 102 to 100. The shell index is 1.16; so that the three dimensions of length, breadth, and height are nearly equal. This extreme gibbosity, combined with so short a hinge-line, produces the peculiar effect seen in fig. 12, *a*; that is, though a similar view of *P. lynx* usually shows all the plications of the slopes, in this case only five out of eight are visible on each slope. Normal adult growth was reached at the varix numbered *II*. After this point the increase was mainly in a direction at right angles to the plane of separation of the valves. This has produced such a degree of incurvature of the beaks that the delthyria are completely concealed, and since there is in this individual no encroachment of the pedicle upon the ventral beak, this organ must have been reduced to very small dimensions or possibly have ceased to function at all. The changing contour of another individual, in which gerontic stages are initiated early in the ontogeny, is shown in fig. 13, of a specimen from Vevay, Indiana. *b-g* show these successive stages separately drawn.

The initiation of gerontic stages early in ontogeny is clearly indicative of the paracme of this type of *Platystrophia*. One of the most extreme manifestations of senescence is the obsolescence of the plications; yet in the present group this begins comparatively early (fig. 12, *b I*) and in later stages the 1st, 2d, 3d and 4th plications from the cardinal angle have completely disappeared and the shell is non-plicate, except at the front margin; and even here the plications are inconspicuous.

\* See Nickles, Jour. Cin. Soc. Nat. Hist., vol. xx, No. 2, Jan. 1902, pp. 85, 86.

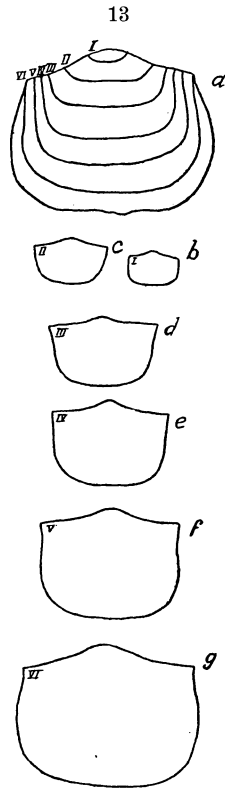


FIG. 13. *Platystrophia lynx* from the upper Lorraine, Vevay, Indiana, showing growth varices (*I-VI*) of a gerontic individual and the successive stages drawn separately (*b-g*). Author's collection.

ous. Another feature indicative of extreme senescence is the thickening of the shell. This has advanced to such an extent in many specimens from the "lynx beds" that the space available for the lodgment of the internal organs of the animal is less than in earlier growth stages. In one specimen, fig. 14, *C*, there is a very exceptional thickening of the ventral valve over the anterior margin of the ovarian region. In all cases of great thickening of the shell the muscular pit of the ventral valve is profound and the shell substance at its bottom is often so thin as to be translucent. Fig. 14, *B*, shows one of the most massive shells seen. This shell is 12<sup>mm</sup> thick at the anterior rim of the muscular pit. Six laminae parallel to the outer surface of the shell (corresponding to as many strong growth varices) indicate the successive additions to the shell substance. After the first (lowest) of these no forward growth took place, and there was a progressive reduction in the amount of room inside the shell.

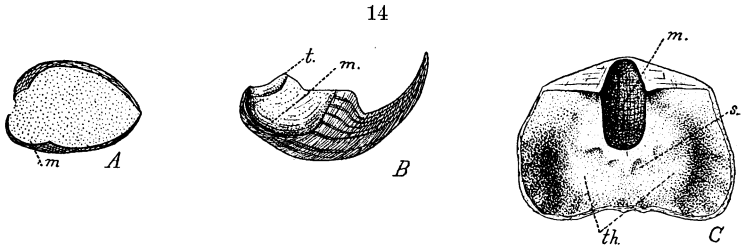
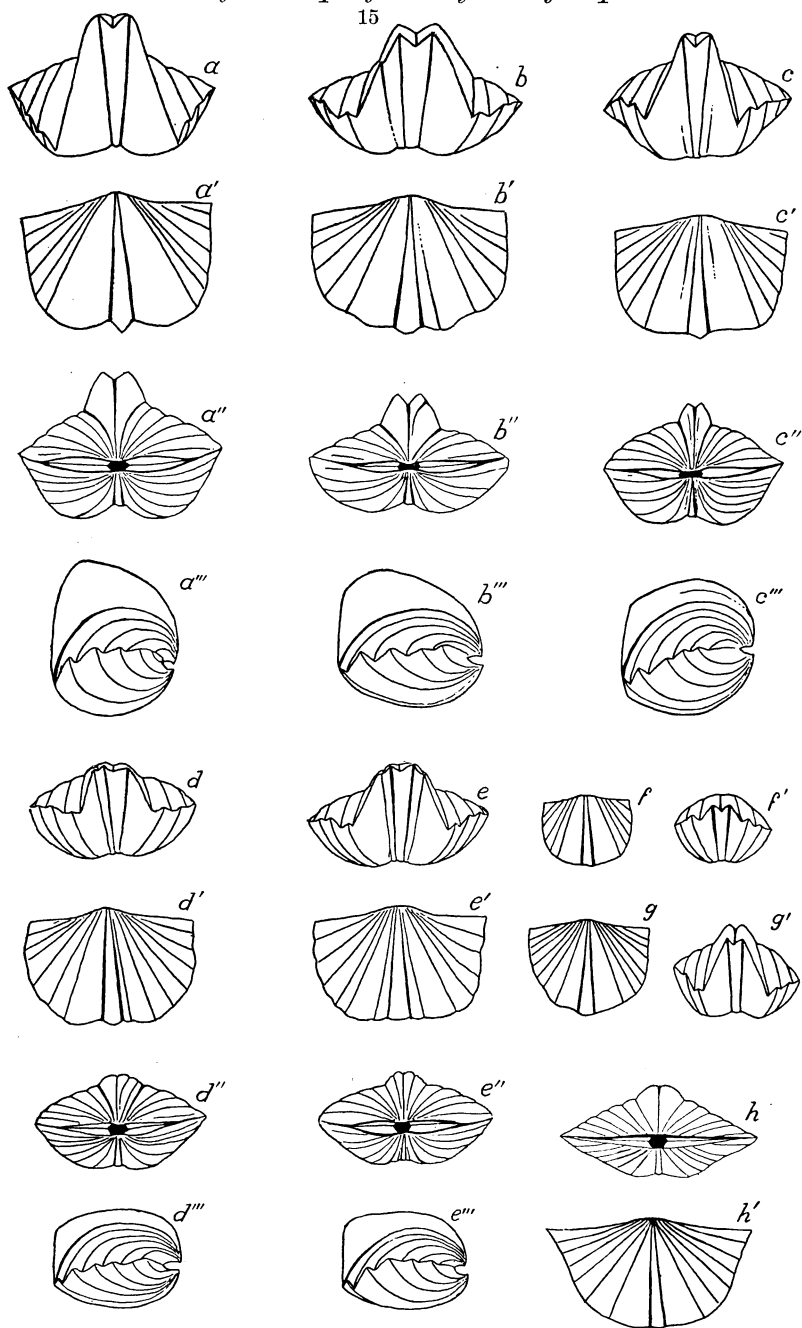


FIG. 14. *Platystrophia lynx*. *A*, from Vevay, Indiana; *B* and *C*, from Cincinnati, Ohio, all slightly reduced. *A*, normal adult individual cut antero-posteriorly in the median plane to show normal thickness of valves; *m*, muscular platform of ventral valve. *B*, extremely senile and greatly thickened ventral valve, showing lamination of shell substance and six successive additions on its inner surface after normal adult growth had been attained; *t*, tooth; *m*, muscular pit; *C*, greatly thickened ventral valve, interior view showing profound muscular pit, *m*; vascular impressions, *s*; and abnormal thickening in the ovarian region, *th*. *A*, author's collection; *B*, collection of Yale Museum; *C*, Dyer Collection, Museum of Comparative Zoology, Harvard University.

There is no evidence that this gerontic type of *lynx* extended its range beyond the "lynx beds," or that it produced any radical from which a new orthid stock sprang. It seems to have become extinct. The succession, so far as concerns the remain-

FIG. 15. *a-e*, *Platystrophia lynx* var. *laticosta* from the Lorraine, Vevay, Indiana. *a-a'''*, anterior, ventral, posterior, and profile views of the form *unicostata*, in which the lateral plications of the fold and sinus are completely lost; *b-b'''*, same of an individual which has one lateral plication feebly developed; *c-c'''*, same of an individual in which the lateral plications of fold and sinus are present only in the umbonal region; *d-d'''*, individual with one complete lateral plication; *e-e'''*, normal *laticosta* type. *f-f'*, tracing from Pander's figure of *P. costata*; *g-g'*, tracing from Meek's figure of *P. dentata*; *h-h'*, tracing from deVerneuil's figure of *P. chama*. *a-e*, author's collection.



(See bottom of page 28 for description.)

der of the Ordovician of this country was, as we shall see, taken up and passed on by the *laticosta* and *costata* types.

The fact that a more nearly normal form of *lynæ* survived to the close of the Ordovician (Madison beds) has already been pointed out. This form seems to represent the final expression of the type—a shell, primitive in many respects, though of large size; and undergoing a last attempt to accommodate itself to changing conditions.

*Platystrophia laticosta*.\*—This is one of the most interesting and one of the least understood types of *Platystrophia*. It seems to be confined to American faunas, and occurs here only in the Cincinnati group of the Ohio valley, where it ranges through the Lorraine and reappears at the base of the Richmond formation.

Meek† has admirably described this variety and little can be

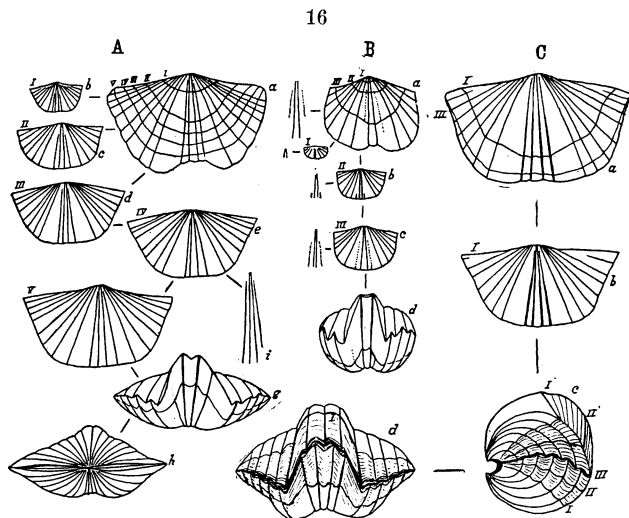


FIG. 16. A and C, *Platystrophia laticosta* from Vevay, Indiana;  $\times \frac{2}{3}$ . B, *P. costata* from Cincinnati, Ohio;  $\times \frac{2}{3}$ . A, shows growth stages I-V separately drawn (b-f), and anterior (g) and posterior (h) views: note the disappearance of the right hand plication of the sinus after stage V. B, shows the initiation of a second and third plication in the sinus at stage II (a, b) and their disappearance at stage III (a, c). C, is a gerontic individual of *P. laticosta*; note the increase of the cardinal angle after stage I, and the reduction in the height of the fold, and strong growth varices (c, d). A and C, author's collection; B, Yale collection.

added in regard to its adult characters. Its minute study, based upon hundreds of individuals, has, however, developed unsuspected relationships, which I shall now point out. Fig. 15 gives

\* James, Cat. L. Sil. Foss. Cincinnati Group, 1871, p. 10.

† Pal. Ohio, i, 1873, p. 116, pl. 10, fig. 4. *P. chama* deVerneuil (not *P. costata* Pander) may be related to *P. laticosta*.

some idea of the variation of *laticosta*; *e* is a normal individual with one large (median) and two small (lateral) plications in the sinus. *a* has but one plication in the sinus and the fold is extremely elevated. *b* to *d* are intermediate between these two. In seeking the derivation of this type as in other types of *Platystrophia* the growth stages are of paramount importance. In fig. 15, *c*, are shown two lateral plications in the sinus originating at the usual distance from the beak but disappearing a little over half way from the beak to the front margin. Fig. 16, *A*, shows the inception of this process of reduction of the lateral plications of the sinus. Here only one plication is affected, and that only near the front margin. Fig. 16, *B*, shows the same tendency in *P. costata*.

Considering now the growth varices (fig. 16) it is evident that *laticosta* becomes progressively more transverse during ephebic stages, while *costata* becomes progressively less transverse; the early stages of the two being identical and also identical with the early stages of *P. lynx*. In *P. laticosta* the cardinal angle is progressively 72°, 73°, 63°, 68°, and 70°, returning thus in gerontic stages to near the angle of an early ephebic stage. In *costata* (fig. 16. *B*) the angle changes from 95° to 78° to 82° to 99° in the fully adult stage, while in gerontic stages it may be as much as 113°. The largest angle seen in any stage of *laticosta* was 95°. Both *laticosta* and *costata* are therefore derived from a primitive *lynx* by a reduction of the number of plications, and an elevation of the fold. The relation of *laticosta* to *costata* is not a linear one; but after the establishment of a pauciplicate stock like the young of both (see ante), a divergence occurred, one branch taking the direction of an elongate narrow type (*costata*) and the other the direction of a transverse acuminate type with extremely high fold (*laticosta*).

The above mentioned uniplicate *laticosta* (fig. 15, *a*) is found in the Upper Lorraine and is not to be confused with *P. costata*. The former has an exceptionally high fold but the same contour as a normal *laticosta*, from which variety it is derived, and with which it is connected by every possible gradation. If it is desired to distinguish this form from *P. laticosta*, it may conveniently receive the name of *unicostata*.\*

In the *Dalmanella Meeki* zone which intervenes between the Lorraine and Richmond beds, no specimens of *Platystrophia* occur, except at the very top of the zone where the typical

\*The *dentata* and *crassa* of American authors undoubtedly include these two forms *costata* and *unicostata*. The former term will be shown to apply only to certain foreign and Upper Silurian biplicate types. Since the term *crassa* confuses two distinct forms it had better be abandoned altogether, especially since the form to which it was intended to apply is the *costata* of Pander.

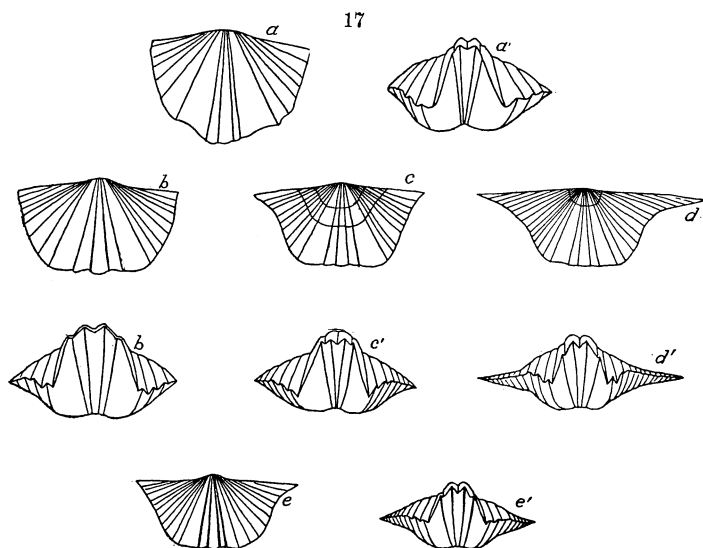


FIG. 17. Group of *Platystrophia acutilirata* from the base of the *acutilirata* zone (Lower Richmond) Tanner's creek, Indiana, with forms transitional to *P. laticosta* from the same zone. *aa'*, *P. laticosta*, after Meek; *bb'*, *P. laticosta*, Tanner's creek, lower Richmond; *cc'*, intermediate *acutilirata* type; *dd'*, very mucronate *acutilirata*; *ee'*, normal *acutilirata*. Author's collection.

*laticosta* again makes its appearance. Within the next 20 ft. of strata this *laticosta* is modified into a typical *acutilirata*. Fig. 17 will make this clear. *The transition has been noted in so many individuals, from so many different localities, that there can be no doubt as to the correctness of this view of the relationship of these two forms.* If any additional evidence were needed, it is furnished by a study of the early stages of *acutilirata* and by the general angularity and high fold of the latter species; as well as by the absence of the *laticosta* type from the *Rhynchotrema* zone, where *acutilirata* abounds.

Few individuals of *laticosta* present pronounced gerontic modifications. Such changes when they do occur produce a shell of extreme gibbosity, and with a large cardinal angle (from  $65^{\circ}$  to  $74^{\circ}$  in one specimen), so that the contour of the shell approaches that of *P. lynx*. Fig. 16, *C*, illustrates this. Normal growth ceased at stage *I*; the fold subsequently becomes lower relative to the size of the shell (cf. stages *I* and *II*), and the frontal profile becomes regularly curved instead of being truncated as in ephebic stages (cf. fig. 16, *Cc*, with fig. 15, *e'''*); so that the profile also resembles that of a gerontic



*P. lynx*. In fact the gerontic *laticosta*, in almost every feature in which it departs from the normal adult type of the variety, approaches *P. lynx*.

In another place\* I have pointed out the intimate connection between *Platystrophia laticosta* and *P. lynx*. The examination of many thousands of specimens of these forms has failed to bring to light any character which does not show transitional stages from one to the other. The relatively greater strength and smaller number of the plications of *laticosta* is its most constant character, and with this is usually combined auriculation and prolongation of the cardinal extremities: the latter character is, however, by no means uncommon in *P. lynx*. It seems best therefore, to the writer, to consider *laticosta* as a variety of *lynx*, transitional between it and the species *acutilirata*.

For comparison with the uniplicate *laticosta* I have inserted (fig. 15, *h*) figures of *P. chama* traced from deVerneuill's figures.† That author says (op. cit.) he succeeded in obtaining a complete series of transitional forms between the small narrow type of *chama* (= *costata* Pander) and the acuminate type figured. As I have not seen any specimens of *P. chama*, deVerneuill's statement must be taken as indicating the relation of these two forms; though I strongly suspect that *chama* may bear no closer relation to *costata* Pander than does the uniplicate *laticosta*. The latter may, indeed, be the form to which it more nearly corresponds.

*Platystrophia acutilirata*.‡—Another type, found only in American faunas, is *Platystrophia acutilirata* Conrad, which is confined to the Richmond beds of the Cincinnati group.§ This species presents the most remarkable similarity to a *Spirifer* of any of the types of *Platystrophia*. The breadth may become as much as three times the length; and the cardinal extremities are frequently as acuminate as those of an average *Spirifer mucronatus*,|| yet between these extreme forms

\* This Journal, July, 1902, p. 14.

† Géol. de la Russie, 1845, pl. v. figs. 1b, 1c.

‡ Conrad, Jour. Acad. Nat. Sci., Philadelphia, viii, 1842, p. 260.

§ Keyes lists this form from the Hudson shales (Cincinnati) of Louisiana, Missouri. As he gives no figure or description, it is uncertain whether his specimens are really referable to *acutilirata* or belong to the acuminate type of *lynx*. See Keyes, Geol. Missouri, vol. v, Paleontology, 1894, p. 66.

|| Prof. H. S. Williams has called my attention to the fact that Atwater's specimen of *S. pennatus* came from a locality in Ohio to which examples of *Platystrophia acutilirata* might have been transported by streams. While I do not believe that *Spirifer pennatus* is a *Platystrophia acutilirata*, the possibility of this being the case together with the total inadequacy of Atwater's description and figures, would seem to warrant abandoning his name altogether and returning to the well known name of *mucronatus* for this species of *Spirifer*. See Atwater, this Journal, ii, 1820, p. 244, pl. I, figs. 2, 3.

and a normal *P. laticosta* there is, as above stated, *every possible gradation*, as there is between the latter and *P. lynx*.\*

*P. acutilirata* presents considerable variation, chiefly, however, in becoming first progressively more and more acuminate, and second in becoming, in the upper part of its range, retrogressively less and less acuminate. The shell index varies in progressive series from less than 1.6 to more than 2.7 and in retrogressive series from the latter figure to 1.4. The number of plications varies from 18 or 19 to 37 or 38, of which three are almost invariably in the sinus (four on the fold).† The cardinal angle varies in progressive series from 80° to 40° and in retrogressive series from 40° to 90°, which is very nearly the normal angle for *P. lynx*. These changes may frequently be noted in a single individual. Fig. 18, *e*, shows a retrogressive individual from the upper Richmond beds of Richmond, Indiana.‡ This specimen is inequilateral through inequality of growth and not as a result of deformation after fossilization. Such lack of symmetry is frequently met with among these retrogressive individuals. The early ephebic stage (*I*) is almost identical with such a form as fig. 17, *b*. The normal *acutilirata* stage is shown at *II* (fig. 18, *d*, illustrates the same thing). The cardinal angle here changes from 76° in stage *I*, to 50° in stage *II*, back to 77° in the final stage (using the right-hand angle in each case). Fig. 18, *f* to *k* with the degrees marked to the right, indicate the changes for other individuals. Fig. 18, *k*, represents a specimen from the lower part of the range of *acutilirata*.§ Here all the stages are progressive,

\* Prof. D. W. Dennis has called attention to the change from narrow to greatly extended forms of *P. acutilirata* in traversing the Richmond section from the foot to the head of the gorge of the Whitewater river. He did not, however, recognize the relation of *acutilirata* to *laticosta*. Dr. Dennis also calls attention to the variation of *Hebertella* in the same section. I have already mentioned the presence of *H. sinuata* in the upper part of the Richmond section. This species is also found at the base of the Richmond beds and is there modified into the variety *occidentalis*. The latter is not however modified back into a *sinuata* but this form comes in suddenly at the top of the section. See Proc. Ind. Acad. Sci., 1898, pp. 288, 289.

† Meek says the breadth is "sometimes twice, or even, in extreme cases, three times the length of the valves;" and that there are "on each side of the mesial fold and sinus from 11 to 18 [plications], making the entire number about 26 to 40 on each valve." I see no reason to doubt his extreme figures. See Meek, Pal. Ohio, vol. i. 1873, p. 119.

‡ The retrogressive forms of *acutilirata* figured in this paper are nearly all from the falls of the west fork of the Whitewater river, one mile N.W. of Richmond. These beds come stratigraphically immediately below those of Elk Horn creek, mentioned above as containing a peculiar type of *P. lynx*. The latter beds are not exposed on the west fork. Fig. 11, *c*, is from equivalent strata just south of Weisburg Station, Ind.

§ This specimen is from Tanners creek, Dearborn Co., Indiana, one mile S.E. of Weisburg. It is associated with *Prasopora hospitalis*, *Batostoma varians*, *Leptaena rhomboidalis*, *Strophomena planumbona*, *Rafinesquina alternata*, a very convex form, and a very large form, *Hebertella sinuata*, *Streptelasma corniculum*, etc., etc.

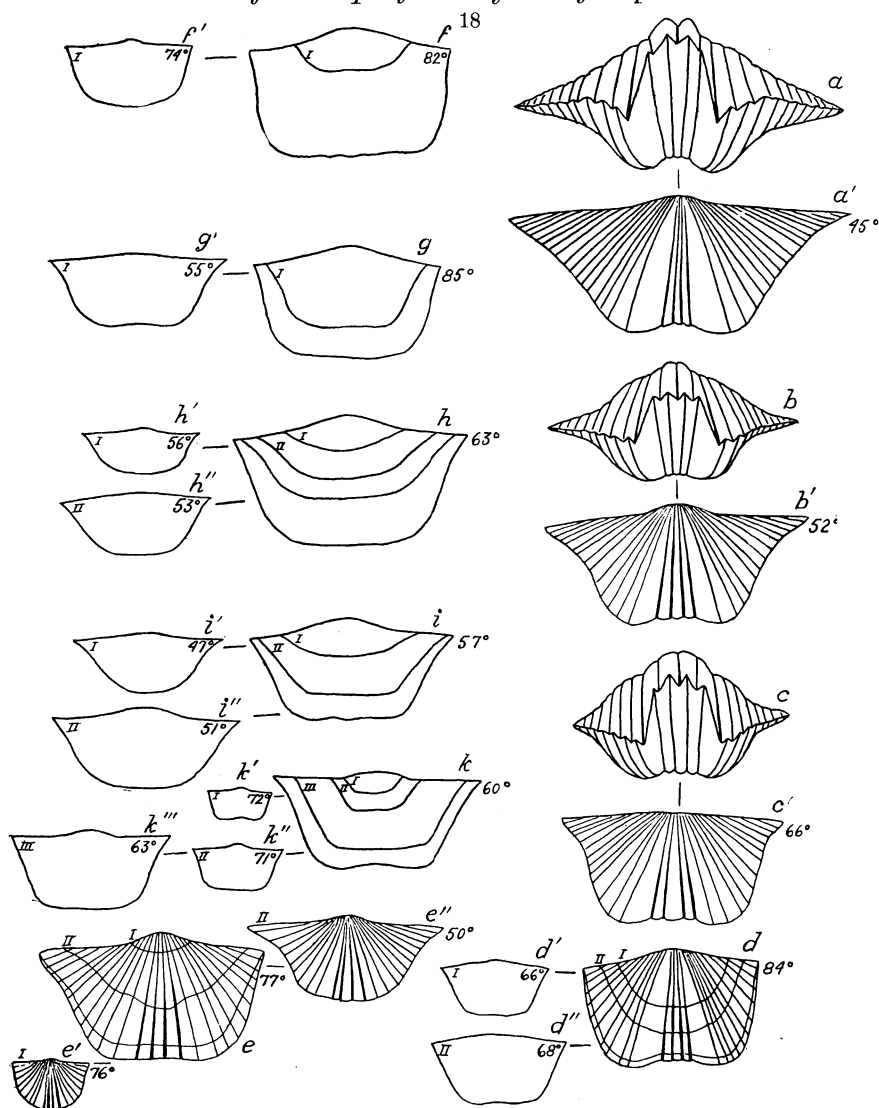


FIG. 18. *Platystrophia acutilirata* from Richmond, Indiana. *a-a'*, anterior and ventral views of a very mucronate individual; *b b'*, an intermediate form; *c-c'*, narrower, very gibbous form; *d-d'*, retrogressive type with stages *I* and *II* drawn separately to the left; *e-e''*, a similar individual showing asymmetrical growth and great increase of the cardinal angle in late growth stages; *f, g, h, i*, outlines of other retrogressive individuals showing increase of the cardinal angle in late growth stages; *k-k'''* an individual from the base of the *acutilirata* zone showing progressive decrease in the cardinal angle. Specimens *a-i* are from the upper part of the *acutilirata* zone. Author's collection.

i. e. the individual becomes more and more acuminate throughout its ontogeny. What is true of this individual is true of practically every individual from the same horizon.

*Platystrophia acutilirata* presents the most profound gerontic modifications of any member of the genus; and gives rise in even greater degree than *P. lynx* to what may almost be termed a phylogerontic group of shells representing the parame of the *laticosta* line, of which as we have seen *acutilirata* is but an extreme manifestation. Though *P.*

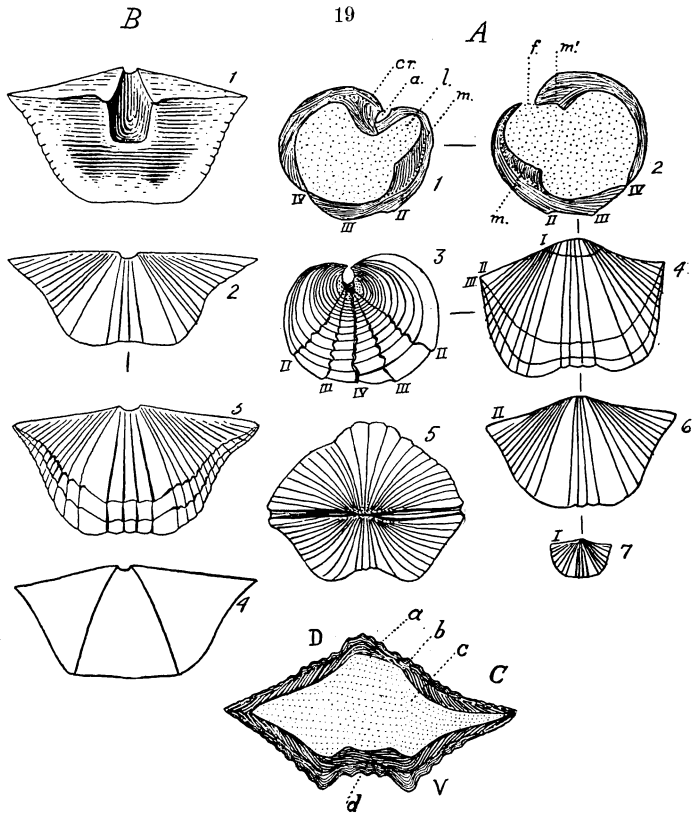


FIG. 19. Senile individuals of *Platystrophia acutilirata* from the upper Richmond of Richmond, Indiana. A, an extremely gibbonous and greatly thickened shell; 1 and 2, median sections showing thickening and reduction of body cavity; 3, 4, 5, profile, ventral, and posterior views showing pronounced varices II, III, IV; 6 and 7, stages II and I separately drawn. B, another individual; 1, interior showing profound muscular pit; 2, stage represented by first growth varix; 3, ventral valve showing strong varices; 4, stage represented by second varix. C, another individual cut transversely in the dorso-ventral plane to show thickening of shell. cr., crura; a., area; mm', ventral and dorsal muscular platforms; f, pedicle foramen; d, ventral muscular platform. Author's collection.

*acutilirata* is a much smaller shell than *P. lynx* of the Lorraine, yet the thickening of the shell in gerontic stages is greater both relatively and absolutely. The acuminate cardinal extremities are so thickened that this region of the shell becomes practically filled up with shelly deposit. The thickening of the central and anterior region of the shell is very great (fig. 19, *A*, 1 and 2), so that the actual room left for the lodgment of the soft organs of the animal is less than in unthickened shells of a much lower index, and less both relatively and absolutely in gerontic stages than in ephebic stages of the same individual. Fig. 19, *C*, of a vertical section from cardinal angle to cardinal angle of a markedly senile individual, will make this plain. The convexity (vertical diameter) of the shell is also considerably greater than in any other type of *Platystrophia*, the height being in extreme cases 1.5 greater than the length, while in *P. lynx* the extreme is 1.04 or height and length nearly equal, and in *laticosta* 1.14. The changes in contour due to senescence are profound, as has already been pointed out. Fig. 19, *A*, represents a shell in which normal growth was attained at the varix numbered *II*. The cardinal angle at this stage is  $58^{\circ}$ . In the latest stage it is  $79^{\circ}$ , and in the early stage represented at *I*, it is  $76^{\circ}$ . Here is a total change of  $39^{\circ}$ .

The retrogressive series mentioned above is produced by the acceleration of gerontic stages, till in such individuals as fig. 11, *C*, from the extreme upper Richmond beds at Weisburg, Indiana, the acuminate or normal *acutilirata* stages come on near the beaks and the adult has the outlines of a normal *lynx*. In fact, the resemblance between this shell and the true *lynx* of the same horizon is so striking, that only by a study of the stages indicated by the growth varices can they be distinguished.

Whether any Silurian Orthid was derived from *Platystrophia acutilirata* is impossible at present to determine. Certainly none of the Silurian forms of *Platystrophia* bear any close relation to this type, since they are as persistently biplicate as the latter is persistently triplicate. To be sure, many individuals from the upper Richmond beds have one or other of the secondary plications of the fold and sinus originating very near the apex, as we should expect from the marked acceleration of these shells in nearly every particular; but I have never seen a specimen in which the lateral plications manifested any tendency to disappear, nor in which there is even a suggestion of a biplicate type. The form seems to have perished very soon after its assumption of retrogressive characters. Indeed, the coming in of a strongly molluscan fauna in these late Ordovician beds seems to indicate some radical change in con-

ditions and this may account for the sudden decline and extinction of *acutilirata*.

As to the taxonomic value of the term *acutilirata* the writer is of the opinion that the form should certainly be considered as a species, although, as pointed out, it is perfectly connected by intermediate forms with *P. laticosta*. It is not, however, except in a very limited zone associated with the latter variety; and it represents such a remarkable distinctness and completeness of history after its initiation, that no one need confuse it with any other member of the genus.\*

*Platystrophia costata*.†—It will not be necessary to enter here into the question of the synonymy of this type. DeVerneuil's objection to Pander's name was based upon the pre-occupation of the term *costata* by *Spirifer costatus* Sowerby. Since the latter is a true *Spirifer* we must return to Pander's name for the present form.

*Platystrophia costata* (= *P. dentata* Meek; *P. crassa* James) makes its appearance in American faunas in the lower Lorraine of the Ohio Valley; and is the well known variety with a rather small, gibbous shell having one plication in the sinus and five or six on the lateral slopes. The derivation of this type has been discussed at sufficient length under the head of neanic stages of *Platystrophia*. It comes from a normal triplicate type by the dropping out of both secondary plications of the fold and sinus.

Under *P. laticosta*, mention was made of a uniplicate form of that variety. Doubtless the latter has usually been confused

\*It may seem to be doing violence to taxonomy to distinguish a form at one stage of its history as a *variety* and at another stage as a *species under a distinct name*; nevertheless, I believe we must be prepared to take this step, since we must certainly find as the investigation of fossils becomes more minute and precise that cases such as this of *Platystrophia laticosta* and *P. acutilirata* are by no means exceptional. In this connection I may quote a passage from a timely article by Mr. O. F. Cook on categories of species (Am. Nat., vol. xxxiii, 1899, p. 292). He is comparing existing species to islands and bodies of land more or less separated from each other in "the sea of non-existence." He says, speaking of incipient species, "Although the designation by name of the various prominences or arms of a diversified island [which is gradually sinking] is desirable, even before the expected separation occurs, the prophetic tendency should, in the interest of historical accuracy, be curbed to the extent of distinguishing in category between groups which are already segregated in nature and those which are not, . . . by treating them as already distinct we ignore the existence of intermediate forms and proceed as though degree of apparent difference were an index of segregation or a taxonomic substitute for it." He suggests the use of the term *subspecies* for all such non-segregated groups or *incipient species*. In this sense *P. laticosta* would be a subspecies of *P. lynx*; and *P. acutilirata* the completely segregated group or species. I have retained the more usual designation of variety for the former.

†Pander, Beiträge zur Geognosie des russischen Reiches, 1830, p. 96, pl. 11, fig. 3.—De Verneuil, Géol. de la Russie, 1845, p. 140.—Sowerby, Trans. Geol. Soc. Lond., 2d ser., vol. v, pl. 55, figs. 5-7.

with *P. costata*. The two are, however, easily distinguished and, besides, have a different range.\* *P. costata* is, moreover, derived from *P. lynx* and not from *P. laticosta*, as is the case with the other form.

*Platystrophia costata* presents well characterized gerontic stages (fig. 16, B). These are marked by extreme gibbosity and great breadth anterior to the hinge-line so that the cardinal angle may be as great as  $113^{\circ}$ . Where the secondary plications of the sinus and fold are faintly marked in ephebic stages, they are almost sure to become obsolete in gerontic stages. The thickening of the shell does not become pronounced as in *lynx* and *acutilirata*.

The *costata* and *laticosta* types seem to have been produced simultaneously from the same pauciplicate *lynx* stock. The former did not survive the Middle Ordovician either in this country or in Europe;† but from it sprang the only genus, so far as at present known, that can be traced to the *Platystrophia* group as a radical stock. From a study of the young of *Bilobites*, Beecher‡ concluded that it was probably derived from the *Platystrophia* group. This conclusion has since been called in question by Wysogorski,§ who maintains that the punctate character of *Bilobites* removes it from the "*Orthis* group," in which he places *Platystrophia*, and relates it to the "*Dalmanella* group." It is well known, however, that punctate and impunctate shells occur in a variety of diverse groups of Brachiopods, and that the early members of a group may be impunctate, while the later members are punctate.||

The resemblance of the early nepionic stages of *Bilobites* to the nepionic stages of *Platystrophia* has already been pointed out. The similarity between a late nepionic stage of *Bilobites* and the adult *Platystrophia costata* amounts

\**Platystrophia cypha* James is doubtless this form of *P. laticosta*. He mentions the extremely high fold and one strong plication of the sinus. The writer has never seen as many plications as he records (22 to 26), but doubtless in the upper part of its range (his specimens are from Warren Co., Ohio), the form developed a larger number of plications. See James, Cin. Quar. Jour. Sci., i, 1874, p. 20.

† See Wysogorski, *Entwicklungsgeschichte*, p. 15.

‡ This Jour., vol. xlii, July, 1891, p. 54.

§ *Entwicklungsgeschichte*, p. 9, footnote 1.

|| The early Spirifers are impunctate; but in the Ostiolati *S. plenus* is punctate. Among the derived genera several are punctate, viz., *Syringothyris*, *Cyrtina*, *Spiriferina*. Among the *Rhynchonellidae* all the earlier forms are impunctate, but *Rhynchopora* of the Carboniferous is punctate, though in all other respects it agrees with the earlier *Rhynchonellids*. Among the *Athyridae*, *Hindella*, *Caelospira*, etc., of the Silurian are impunctate, while *Eumetria*, *Hustedia*, etc. of the Carboniferous, are strongly punctate; *Rhynchospira* is sparsely punctate. The *Atrypidae* are impunctate. Among the Terebratulacea, nearly all are conspicuously punctate, but in the early genera, *Rensselæria* and *Amphigenia*, the punctation is incomplete. See Hall & Clarke, Pal. N. Y., viii, pt. 2, 1893.

In *Hebertella* the early species are impunctate or superficially punctate: the upper Richmond form is more clearly punctate.

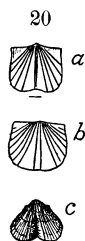


FIG. 20.—*a*, Young stage of *Bilobites varicus*, drawn from the beak of an adult individual,  $\times 4$ ; *b*, small specimen of *Platystrophia costata*, natural size; *c*, adult *Bilobites varicus*, natural size.

almost to identity in everything except size. Fig. 20, *a*, is drawn from the ventral beak of an adult *Bilobites varicus* from the Lower Helderberg of New York; and fig. 20, *b*, is a small individual of *P. costata*, from Cincinnati, Ohio. An examination of several hundred individuals of *B. varicus* has shown that there is invariably present, in well preserved material, a median plication at the apex of the ventral sinus\* (fig. 20, *a*). This plication very soon becomes obsolete, so that the greater portion of the sinus is without plication of any kind. Clearly such a vestigial character is not without significance. The median plication of the sinus of uniplicate and triplicate types of *Platystrophia* is a character that is never absent whatever other modifications may affect the shell; the presence of this persistent character in a derived genus is to be expected, and affords, together with the evidence from development, a virtual demonstration of the derivation of *Bilobites* from *Platystrophia*. Moreover, since the *costata* and *unicostata* types of the latter genus present the most profound modifications of fold and sinus, and since this extreme elevation of the fold must have been related to a marked separation of the brachia and the latter character have been responsible for the production of a bilobate shell, we are justified in considering either *costata* or *unicostata* as the ancestor of *Bilobites*. *P. costata* is preferred because of its wide distribution and greater abundance. It would be interesting to know in what province the early stages in the evolution of *Bilobites* were passed. No trace of the genus has so far been found in the late *Ordovician*. It is extremely rare in the late Clinton and Niagara of this country; but occurs somewhat abundantly in the equivalent formations of the Island of Gotland. Since *P. costata* is abundant in the European province, we may look there rather than in America for the transitional forms to *Bilobites*.†

The taxonomic value of the term *costata* need not detain us long. De Verneuil regards *P. chama* as a variety of *P. bifurcata* (?), and in this country the form is also usually placed as a variety. It has been shown that there are in the Cincinnati group abundance of transitional forms between *costata* and the

\* This characterizes all the other species of *Bilobites* as well.

† Mr. C. J. Sarle of Rochester, N. Y., has found a form of *Bilobites*, similar to *B. verneuiliana*, in the Clinton of Rochester, N. Y., where, in one layer, it occurs rather abundantly.



pauciplicate *lynæ*. For the European form I can not speak. It may even prove to be distinct from ours, though it certainly seems to be identical. The wide distribution of *costata* would seem to entitle it to rank as a species, yet the evidence at present available is rather in favor of regarding it as a variety of *P. lynæ*, the differentiation of which began quite early in the history of the genus.

*Platystrophia biforata*.—The reasons for considering this species as distinct from American Ordovician forms of *Platystrophia* have already been stated, and the main features of the type described. Little can be added in regard to the foreign forms. The Russian *biforata* occurs in beds as low as the Trenton, and in this country, a shell of quite similar aspect, and of unquestioned biplicate type, is found in the Trenton of the Lake Champlain region\* associated with the normal *lynæ* type.† This association is of great interest since it shows that the differentiation of these two species was going on in the early Ordovician, and also that there was free intercommunication between the American and European Province at that time.‡ The total absence of *biforata* from American deposits throughout the remainder of the Ordovician might also indicate a closure of this avenue of communication early in that period.§

In the Clinton of this country we again meet with a biplicate *Platystrophia* strikingly similar to the Russian *P. biforata*. The writer has examined about 50 individuals from Rochester and Gasport, N. Y., Dayton, Ohio, Irvine, Kentucky, and Richmond, Indiana. These present considerable variation, mainly in the number of plications, which may be all the way from 16 or 18 to 46 on the valve, a greater range than in any other type (see fig. 21).

\* Mr. P. E. Raymond sent me specimens from the Crown Point section. The species occurs there in the upper part of the section. All the specimens sent may be of the biplicate type, although several have three plications in the sinus. The exfoliation at the beaks renders it impossible to make sure to which type the latter belong. Billings figures a Canadian *Platystrophia* with rounded cardinal angles and four plications in the sinus, two of which appear to arise at the apex. This specimen is very similar to several of the Crown Point forms, and may very likely belong to the same type. See Raymond, Bull. Am. Pal., No. 14, 1902, pp. 27, 28; and Billings, Geol. Canada, 1863, p. 167, fig. 149 a.

† Some specimens collected at Ft. Cassin, Vt., by Mr. H. M. Seeley, are clearly referable to *P. lynæ*.

‡ See Frech, Lethæa geognostica, Theil I, Lethæa Paleozoica, 1897, 2, p. 100. Ruedemann, Bull. N. Y. St. Mus., No. 42, vol. 8, 1891, pp. 561-564; Ibid., No. 49, 1901, pp. 104-107 and footnote p. 107. Ulrich and Schuchert, Bull. N. Y. St. Mus., No. 52, 1902, pp. 633-663.

§ Cf. Dana, Man. Geol. 4th ed., 1894, p. 536.—Ruedemann, Am. Geol., June, 1897, pp. 367-391.

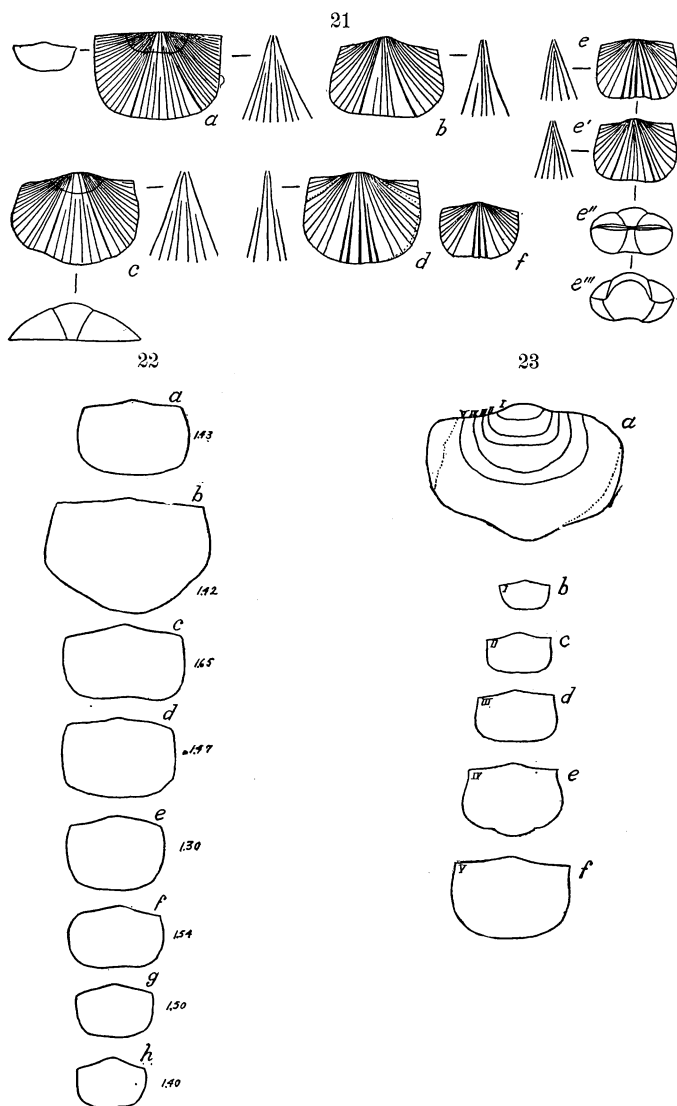


FIG. 21. *a, b, c, d, f, Platystrophia biforata* from the Clinton of Rochester, N. Y.; *a, b, c*, dorsal and *d, f*, ventral valves: adjacent diagrams show method of origin of plications of fold and sinus. *e, P. biforata* from Wesenberg, Russia (Ordovician); *e*, ventral; *e'*, dorsal; *e''*, posterior; *e'''*, anterior views. *a, b, c, d, f*, collection of Mr. C. J. Sarle, Rochester, N. Y.; *e*, Yale Collection.

FIG. 22. Series of Clinton *Platystrophia biforata* showing variation in outline and index. Value of index given to right of each shell. Collection of Mr. C. J. Sarle, Rochester, N. Y.

FIG. 23. Specimen of *Platystrophia biforata* from the Clinton of Gasport, N. Y., showing growth varices I-V and the stages separately drawn (*b-f*). Collection U. S. National Museum.

The number of plications in the sinus varies from two to nine (three to ten on the fold), which is also a greater range than observed in any other type. All except the primary plications originate at a considerable distance from the beak. The amount of variation in the shell index and contour (fig. 22) is less than in the *lynæ* type, and the sinus is never profound. The average index is about 1.4, or very near that of the Trenton *lynæ*. The cardinal angle is difficult to determine with accuracy owing to the worn condition of most of the specimens; but is scarcely ever less than 90° and may be considerably over 100°. The dorsal valve is usually considerably more convex than the ventral, especially in the umbonal region, but the incurvature of the beaks is not as great as in *lynæ*. Internally *biforata* has the dental sockets more deeply excavated and the crura more prominent. The muscular scars have not been observed.

The British types of *Platystrophia* have given the writer considerable trouble because of the general absence of specimens of that province from American collections. The figures and descriptions given by Davidson and others throw very little light upon the subject. All their Wenlock examples certainly belong to the *dentata* type, as is pointed out later, but the position of the *Ordovician* forms cannot be determined. The var. *fissicostata* McCoy,\* judging from the figures given by Davidson†, strongly resembles our Clinton forms. It has, according to McCoy, "four ribs on the rostral part of the mesial furrow, the two outer of which usually branch at four or five lines from the beak, the others branch irregularly lower down once or twice; lateral ribs varying from six to fifteen within three or four lines from the beak, branching irregularly, some into two, others into four, with age; surface crossed towards the margin with sharp striæ of growth. This variety does not seem to have been noticed either in Russia or America, yet it is extremely common in our old rocks . . . ." This variety, according to Davidson, "abounds in the Caradoc" at numerous localities and in the Coniston, etc. Now, the only American type known to the writer that ever has bifurcating plications is the *biforata* of the Clinton, in which group this peculiarity is common.‡ Again, the presence of "four ribs on the rostral part of the mesial furrow" is a character absolutely unknown in the *lynæ* type, but common in the *biforata* type. On the whole, it seems likely that *fissicostata* is a true *biforata* similar to

\* British Pal. Foss., 1852, pp. 192, 193.

† Silurian Brachiopoda, 1871, pl. xxxviii, figs. 15-17, 19.

‡ Mr. Foerste has already called attention to this fact. Bull. Dennison University, I, 1885, p. 80.

our Clinton forms.\* The derivation of *P. biforata* has been discussed at some length in connection with *P. lynx*. It is plain that we must look to European deposits for the fullest light on this point. I am convinced that whatever new evidence arises will be found to support the position taken here, that *P. lynx* is really the more primitive. The history of the species after its reappearance in our Clinton faunas is not as fully understood as could be wished, owing to the small amount of careful stratigraphic work that has been done on this series of rocks. Too much emphasis can not be laid on the necessity of *accurate, detailed, and comprehensive* work of this sort. Nevertheless the main features outlined above are not likely to be modified by future investigations.

To *Platystrophia biforata* is here assigned the rank of a species occupying the same position of prominence in relation to the European and Silurian faunas that *P. lynx* does in relation to the American Ordovician faunas. So far as is now known, the type did not survive the Clinton.†

*Platystrophia dentata*.‡—So much confusion exists in this country in regard to this type of *Platystrophia* that it will be necessary to enter somewhat in detail into the question of synonymy.

In 1830 Pander described and figured *Porambonites dentata*, *P. costata*, *P. brevis*, and *P. recta*. The affinities of the last two are uncertain, but the first two represent very characteristic and widely distributed types of *Platystrophia*. *P. dentata*, according to both the figures and description given by Pander, has two plications in the sinus (three on the fold) and about five on each side. The sinus is deep, the contour of the shell rounded, and the profile plump, or even gibbous. This form was refigured and described by deVerneuill,§ who says that it passes by insensible gradations into *biforata* on the one hand and *chama* (= *costata*) on the other. Davidson|| placed *dentata* in the synonymy of *biforata*. In 1873 Meek¶ described under this name a form which he says is "referred in Mr. James's list to *O. [Orthis] dentata* of Pander." In regard to this, Mr. James\*\* says, the specimens "were wrongly put up

\* According to Schmidt, *fissicostata* occurs in Russia at Muddis, Koil, Lyckholm, and Hohenholm, in the Lyckholm beds, which are equivalent in age to the upper part of our Cincinnati group. See Schmidt, Archiv. für die Naturkunde Liv-, Ehst.- und Kurlands, 1ter ser, 2ter Band, 1te Lieferung, 1858, p. 213.

† *Delthyris brachymota* Hall (Geol. 4th Dist. N. Y., 1843, p. 71) is a *P. biforata* of the Clinton type.

‡ Pander, Beiträge zur Geognosie des russischen Reiches, 1830, p. 96, pl. 11, figs. 4 a-e.

§ Géol. de la Russie, 1845, p. 138, pl. iii, fig. 5 a-f.

|| Silurian Brachiopoda, 1871, p. 268.

¶ Pal. Ohio, i, 1873, p. 117.

\*\* Cin. Quar. Jour. Sci., i, 1874, p. 21.

for Mr. Meek, Pander's *O. dentata* not being sent." It seems that Meek received the labeled specimens from James. The latter further says: "I now propose the above name [*crassa*] for the shell described by Meek [as *dentata* Pander]." Meek (loc. cit.) expresses grave doubts as to the identity of the form with Pander's species. He says: "I doubt very much, however, whether it agrees with that variety [*dentata*], which is described by McCoy, from British specimens, as having constantly two plications in the sinus." Nevertheless, Miller\* subsequently referred the form to *dentata* without further remark. It is known now that Meek's *dentata* is the same as *crassa* James; and it has been pointed out that both are the same as *costata* Pander. The name *crassa* therefore lapses into the synonymy of *costata*.

*Platystrophia dentata* Pander is a perfectly distinct type found in the Ordovician of Russia and the Niagara of both Europe and America. To this type belong the Anticosti and Gotland forms, as well as the Niagara form of Kentucky and Indiana.

In regard to the variation of *P. dentata*, there is little to be said. Shaler's measurements of a series of twenty shells from Anticosti (which are now before me) show but little variation, and the same is true of the Gotland specimens, about thirty of which I have measured. There is also scarcely any variation in number of plications. One specimen from Gotland has three instead of two in the sinus, though only two start at the beak. The Kentucky specimens figured by Nettleroth also have at the front margin more than the usual number of plications in the fold and sinus,† but otherwise closely resemble the Gotland form.

As to the derivation of *P. dentata*, the same argument that derives the closely related *P. biforata* from a primitive unipliicate stock holds in the present case. *P. dentata* was derived from such a primitive stock, probably at about the same time with *P. biforata*, and by the same process of acceleration of the point of bifurcation of the primary plication of the sinus. The transitional stages are to be sought in Russian deposits, since *dentata* is absent from the American Ordovician.

In Niagara time the species spread westward into Gotland, and from there into England and Ireland and the Gulf of St.

\* Cin. Quar. Jour. Sci., vol. ii, 1875, p. 27.

† On the Anticosti form see Shaler, Bull. Mus. Comp. Zool., iv, 1865, p. 67, and Brachiopoda of the Ohio Valley, p. 44. This is the form to which he gave the name *regularis*. On the Kentucky form see Nettleroth, Kentucky Fossil Shells, 1889, p. 35, pl. 29, figs. 18, 19.

Lawrence.\* By another route the form reached the Mississippi area of this country, where it is very poorly represented.†

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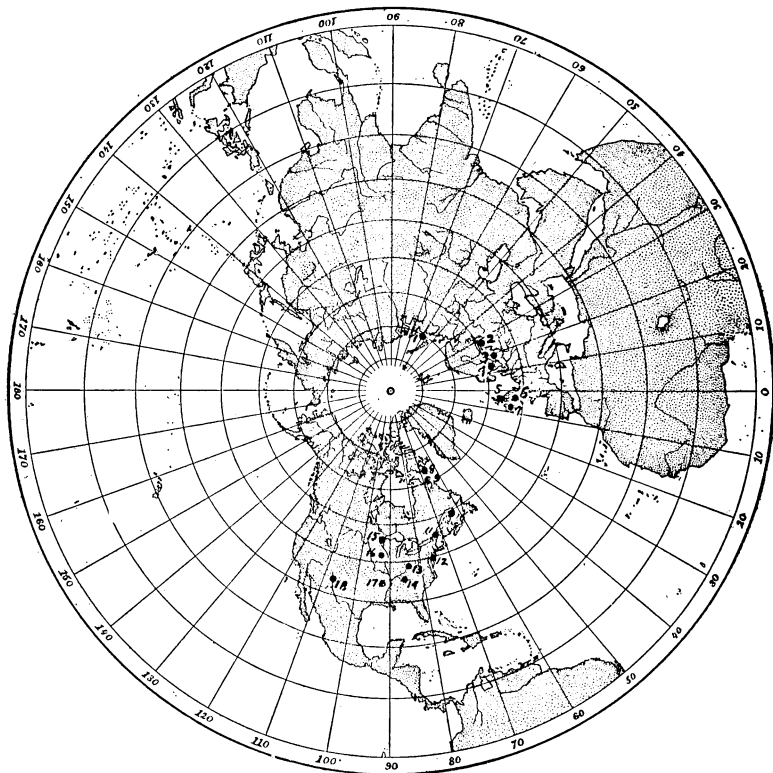


FIG. 24.—Map showing distribution of *Platystrophia*. 1, Khabarova; 2, Russian Province; 3, Island of Gotland; 4, West Gotland; 5, Scotland; 6, Wales; 7, Ireland; 8, Baffinland; 9, Akpatok Island; 10, Anticosti; 11, New York—Canadian Ordovician province; 12, New Jersey; 13, Cincinnati region; 14, Tennessee region; 15, Minnesota; 16, Missouri; 17, Arkansas; 18, New Mexico. Stereographic projection, after Penfield.

\* *Platystrophia* occurs in the Wisby (Unter-Mergel) formation of Gotland (Schmidt), associated with *Bilobites biloba*, *Rhipidomella hybrida*, *Strophomena depressa*, *Rhynchotreta cuneata*, etc., and in the lower part of the Middle Gotland formation. These beds are equivalent, according to Lindström, to the Wenlock of Britain (Niagara of this country). See Schmidt, Archiv. Liv.-, Ehst.- und Kurlands, ser. i, ii, 2, 1854, pp. 426, 453, 454; and Lindström, Of. Sven. Vet. Akad., xvii, 1860, p. 381; Neues Jahrbuch f. Min. Geol. u. Pal., 1888, i, pp. 147-164.

† An occasional individual from the Clinton of Rochester, N. Y., presents somewhat the appearance of *P. dentata*, but with a larger number of plications and a shallower sinus. They are probably the young of *P. biforata*.

From the Niagara of Osgood, Indiana, I have a single specimen (Schuchert collection) which is identical with the neanic stage of the Gotland form. It may be an immature individual.

The presence of the Gotland type of *Platystrophia dentata* in the Niagara of the Ohio valley is of interest in connection with the strong resemblance of the Silurian faunas of the Chicago area to the Gotland faunas, pointed out by Weller,\* and indicates a westward movement of the latter through the Hudson Bay route during Silurian time. In this connection it is also to be noted that the *Platystrophia* of the Wenlock of England and Ireland, judging from Davidson's figures,† is of the same type as that of Anticosti, that is, larger and less angular than the Gotland form. The relations of these several geological provinces will be readily understood by reference to the map, fig. 24. The extremely small size and simplicity of the Gotland and Osgood specimens is of special interest. Some of the former have in the adult but four plications on the lateral slope, and are therefore strictly comparable to the neanic stage of the normal Ordovician types. Such a complete return to the primitive type is rarely seen (see No. 16, and xix, fig. 27).

*Platystrophia dentata* is fully entitled to rank as a species, although in the Ordovician deposits of Russia, according to de Verneuil, it is connected by intermediate forms with *P. biforata*. Its distinctness and wide distribution during the Silurian are facts of greater import than the presence of such linking forms in the Ordovician.‡

*Abnormal and Pathologic Types.*—No truly pathologic shells of this genus have come to the writer's notice, with the exception of a series of specimens submitted by Mr. Charles Schuchert of the U. S. National Museum. These shells, two of which are shown in fig. 25, are from the Richmond beds of Waynesville, O. They are all small, frequently distorted, as in fig. 25, *a*; and show a pronounced tendency to obsolescence of the plications at varying stages of growth. In fig. 25, *a*, this tendency does not manifest itself till late in the ontogeny, after the formation of a very conspicuous growth varix. In fig. 25, *b*, the plications become obsolete a short distance from the apex of the beak, and farther forward regain nearly their normal strength.

\* Jour. Geol., vi, 1898, p. 697. Cf. Dana, Man. Geol., 4th ed., 1894, p. 536. De Lapparent, Traité Géol., 1900, pp. 809, 823 (Maps).

† Silurian Brachiopoda, 1869, pl. xxxviii, figs. 11, 20, 24.

‡ It may be well when these early linking forms of *P. biforata* and *P. dentata* are more carefully studied to distinguish them by a varietal or sub-specific name, as I have done in the case of *P. laticosta*.

It is rather difficult to assign these shells to any one of the common types of *Platystrophia*. From their occurrence and association, as well as from the aspect of the early ontogenetic stages, it seems almost certain that they are pathologic individuals of the *acutilirata* group. The individual shown in fig. 25, *a*, certainly presents every appearance of a normal *acutilirata*, up to the formation of the first strong growth varix. When normal growth was interrupted the shell reverted to a simpler, more primitive type, so that the later stages are strongly suggestive of *P. lynæ*. The obsolescence of plications which, we have seen, characterizes gerontic stages only of normal shells, here affects ephebic stages as well, and to a profound degree. In both cases it is the direct result of the failing vitality of the organism. In the former case, however, the failure is a normal phase of ontogeny; in the latter, it is due to the stress of an adverse environment, to which the organisms attempted, with varying success, to adjust themselves.\*

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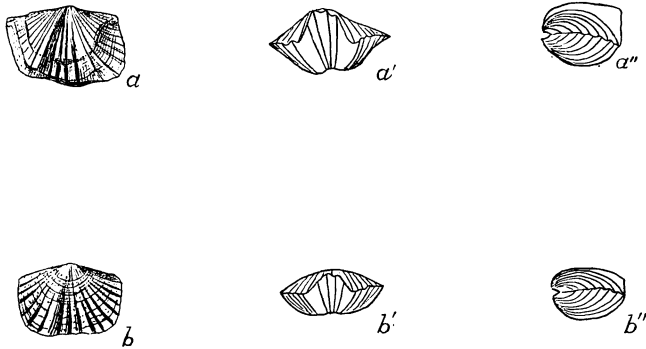


FIG. 25.—Pathologic individuals of the *acutilirata* type from Waynesville, O. In *a* the shell is greatly distorted owing to irregularity of growth, and the plications are obsolescent near the lateral margins. In *b* the plications become nearly obsolete a short distance from the beak and then continue with nearly normal strength to the margins. Schuchert collection.

\* This subject has been ably discussed by Hyatt. Genesis of the Tertiary species of *Planorbis* at Steinheim, Anniversary Mem. Bos. Soc. Nat. Hist., 1880, p. 15.

[To be continued.]