TAXONOMIC CRITERIA IN THE CLASSIFICATION OF THE PENNSYLVANIAN PRODUCTOID *JURESANIA NEBRASCENSIS*

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ABSTRACT. Biometrical and qualitative analysis of the form of the cardinal process in a sample of 123 brachial valves of *Juresania nebrascensis* (Owen) indicates that this feature is more variable than the size and shape of the valve proper. This relatively greater variability suggests that the form of the cardinal process has only limited value as a taxonomic criterion in the classification of this species.

MOST biometrical studies involving the Brachiopoda have concentrated on the relations between the various overall valve dimensions, especially length, width, and thickness, and have generally ignored for one reason or another the dimensions of the internal features of the valves. Recent discovery of a faunal assemblage containing numerous well-preserved brachial valves of *Juresania nebrascensis* (Owen) presented the opportunity to make both biometrical and qualitative evaluations of the relative significance of external and internal features in the classification of this species. Such a study is especially pertinent in view of the emphasis that has been placed on the form of the cardinal process in productoid taxonomy.

The sample was collected in June and July 1962 from a layer one foot thick of inter-bedded yellowish-brown shale and light gray, crystalline limestone in the upper portion of the Bonner Springs shale (the uppermost unit of the Kansas City group), outcropping in an abandoned quarry near the centre of the $SE\frac{1}{4}$, $SE\frac{1}{4}$, Sec. 7, Eight Mile Grove Twp., Cass Co., Neb., about $1\frac{1}{2}$ miles south-west of the village of Cedar Creek. At this locality the Bonner Springs shale is abundantly fossiliferous, containing trilobites, ostracods, and bryozoa as well as several species of brachiopods. Most of the larger specimens of *J. nebrascensis* had weathered free of the matrix, and so were randomly collected from the surface of the outcrop which extends for about 500 feet along the quarry face. The smaller specimens were picked from bulk samples, which had been boiled to free the valves from the matrix.

Juresania nebrascensis is one of the most common brachiopod species in the Penn-sylvanian system of the northern mid-continent region and is well known to most palaeontologists and stratigraphers familiar with these rocks. The species has been adequately described and illustrated (Dunbar and Condra, 1932, pp. 195–8, pl. 22; Muir-Wood and Cooper, 1960, pls. 79, 80) so neither a formal systematic description nor illustrations of complete specimens are necessary for the purposes of the present paper.

BIOMETRICAL DATA

The sample consists of 123 brachial valves, in various states of completeness, numbered 3300–3422 in the invertebrate palaeontological collection of the University of Nebraska State Museum (UNSM). On all unbroken specimens five dimensions were measured: length (Lbv) and width (Wbv) of the valve, length of the hinge-line (Lhl), length of the cardinal process (Lcp) measured from the hinge-line to the posterior extremity, and width of the cardinal process (Wcp) measured at the widest spread of the myophore lobes. As many of these dimensions as possible were measured on incomplete specimens; all specimens have at least three measurements. Attempts to measure the length and width of the adductor muscle scars proved to be futile since the outline was so indistinct that objective measurements were not possible; therefore, biometrical study of this internal feature was not undertaken.

Table 1 lists the number of specimens on which each dimension could be measured (N), the sample range (OR), sample mean ($\overline{X}$), sample standard deviation (s), and the coefficient of variation (V) for each dimension. Since the values for the sample range indicate that the sample is very heterogeneous with respect to biologic age, biometrical assessment of variability based on univariate analysis is not appropriate (Imbrie, 1956, p. 238). Therefore, bivariate analysis of variability was undertaken; the simplest measures of bivariate variability are the correlation coefficient (r) and the coefficient of relative dispersion about the reduced major axis (D_d; Imbrie, 1956, pp. 239–41). Both these measures have been computed for every pair of dimensions and are listed in Table 2 in order of increasing values of D_d.

TABLE 1. Statistics based on dimensions of brachial valves

	N	OR (mm.)	$\overline{X}$ (mm.)	s (mm.)	V
Wbv	87	7·6–30·0	22·1	5·3	23·98
Lbv	68	6·9–20·4	15·3	2·9	18·95
Lhl	109	6·2–22·8	15·8	3·8	24·05
Lcp	118	0·4–3·4	2·1	0·5	23·80
Wcp	120	0·7–3·4	1·8	0·5	27·77

VARIABILITY

For the purposes of the present paper the term 'variability' refers to the relative spread of the points on a scatter diagram about a line such as the reduced major axis, Bartlett's 'best fit' line (Simpson, Roe, and Lewontin, 1960, pp. 232–7), &c. The sample correlation coefficient (r) and the coefficient of relative dispersion about the reduced major axis (D_d) give good measures of this relative spread if the conditional variances are homogeneous.

In addition to their inappropriateness in heterogeneous samples, as noted above, univariate measures of variability are limited by the fact that they merely express variation in linear dimensions rather than variation in shape. Thus the value of D_d (Table 2) for Lcp–Wcp expresses relative variation in the shape of the cardinal process and the values of D_d for Wbv–Lbv, Wbv–Lhl, and Lbv–Lhl express the relative variation in the

shape of the valve proper. The values of D_d for the paired dimensions involving one dimension of the cardinal process and one dimension of the valve proper, i.e. Lcp–Wbv, Wcp–Lhl, &c., express relative variation in the size of the cardinal process in relation to the size of the valve.

TABLE 2. Total correlation coefficients (r) and coefficients of relative dispersion about the reduced major axis (D_d) for (n) paired dimensions of brachial valves

	n	r	D_d
Wbv–Lbv	67	0·96	6·36
Wbv–Lhl	77	0·92	9·59
Lbv–Lhl	59	0·88	10·68
Lcp–Lbv	65	0·80	12·14
Lcp–Wbv	82	0·79	15·59
Wcp–Lbv	66	0·64	16·29
Lcp–Lhl	104	0·74	17·36
Wcp–Wbv	84	0·65	20·09
Wcp–Lhl	106	0·64	20·44
Lcp–Wcp	117	0·66	20·94

On the basis of the values of D_d (Table 2), the following generalizations concerning variability in the brachial valve of *J. nebrascensis* can be made:

1. The shape of the cardinal process is far more variable than the shape of the brachial valve proper.

2. During growth the size of the cardinal process is only moderately related to the size of the valve proper. In general Lcp is more closely related to the dimensions of the valve than Wcp.

3. Wbv is the one dimension most closely related to all aspects of shell development; Wcp is the least closely related. Wbv–Lbv is the least variable pair of dimensions and should therefore be used in the biometrical discrimination of samples of *J. nebrascensis* from other geographic localities and stratigraphic horizons.

It is important to realize that these generalizations have limitations; they are based on only one sample and apply only to *J. nebrascensis*. To apply them to other productoid species would be an unwarranted extension beyond their intended meaning.

In addition to size and shape, there are two more attributes of the form of the cardinal process that deserve analysis; these are the number of lobes in the myophore and the nature of the shaft. As will be shown below, neither of these attributes is amenable to biometrical analysis, since both undergo progressive change in form during ontogeny. Therefore, this aspect of variability must be approached on a purely qualitative basis.

The shaft may be thought of as consisting fundamentally of two primary lobes extending posteriorly from the hinge-line, approximately in the plane of the valve. The posterior half of each primary lobe bears a groove of variable depth on the dorsal and ventral surfaces, except in very small specimens where the groove is absent on the ventral surface. Typically these grooves join posteriorly to form a prominent narrow incision on the end of the myophore giving it a quadrilobed appearance. In quadrilobed specimens the inner lobe of each primary lobe of the shaft is here termed the inner secondary lobe; the outer lobe is the outer secondary lobe. Such quadrilobate cardinal

processes, with the primary lobes of the shaft separated throughout their entire length, are characteristic of the smaller specimens and comprise about 25 per cent. of the sample.

The most common form of the cardinal process is a variation of the quadrilobed type, which involves an inward twisting of the secondary lobes, especially the inner secondary lobes. This inward twisting generally results in partial or complete fusion of the inner secondary lobes to form a trilobate cardinal process. With only partial fusion the two primary lobes of the shaft remain separate anteriorly, whereas in complete fusion the shaft is one piece, generally with a prominent groove on the ventral surface. With both complete and incomplete fusion the central lobe is usually wider and longer than the lateral lobes and bears a median incision of variable depth on the posterior face. Such trilobate processes, with the inner secondary lobes of the shaft either partially or completely fused, are characteristic of the larger specimens and comprise about 75 per cent. of the sample.

This suggested ontogenetic development from an immature quadrilobate stage to an adult trilobate stage is quite imperfect. The sample contains numerous large quadrilobate specimens as well as several small trilobate specimens. However, the fact that there is a gradational transition from generally small quadrilobate forms to partially fused intermediate trilobate forms and finally to completely fused large trilobate forms supports this suggested ontogeny (Pl. 2, figs. 1–13). During the biometrical portion of this study, an attempt was made to segregate the sample into quadrilobate and trilobate sub-samples to see if this would strengthen the correlations between the dimensions of the cardinal process and the external valve dimensions. This segregation proved to be impossible, since there were so many gradational specimens that could not be objectively placed in either of these groups.

It is perhaps significant to note that there is no evidence that the cardinal process in *J. nebrascensis* conforms to the ontogenetic changes described by Kozlowski (1914, pp. 12–13) and Sarycheva (1949, p. 59). The trilobed form does not arise from a hollow cup or tube.

To explain the cause of variability in fossil animals is largely speculative. None the less it seems quite likely that there must be some relation between the rather spacious umbonal cavity of the pedicle valve in *J. nebrascensis* and the variability of the com-

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EXPLANATION OF PLATE 2

All figures ×3.

Figs. 1–16. *Juresania nebrascensis* (Owen). 1, UNSM 3304, ventral view showing double-shafted cardinal process. 2, UNSM 3303, dorsal view showing double-shafted quadrilobate cardinal process. 3, UNSM 3309, dorsal view of large quadrilobate cardinal process with divergent shafts. 4, 5, UNSM 3330, dorsal and ventral views showing incipient inward twisting of secondary lobes of cardinal process. 6, UNSM 3302, dorsal view showing initial fusion of inner secondary lobes of quadrilobate cardinal process. 7, UNSM 3336, dorsal view showing incomplete fusion of trilobate cardinal process. 8, 9, UNSM 3326, dorsal and ventral views of partially fused trilobate cardinal process. 10, UNSM 3331, dorsal view showing nearly complete fusion of trilobate cardinal process. 11, UNSM 3327, ventral view showing nearly complete fusion of trilobate cardinal process. 12, 13, UNSM 3360, dorsal and ventral views of completely fused trilobate cardinal process. 14, UNSM 3390, ventral view showing additional cardinal process buttress plates. 15, UNSM 3396, ventral view of thickened trilobate cardinal process and inconspicuous alveolus. 16, UNSM 3423, ventral view of thickened trilobate cardinal process and deeply incised adductor muscle scars.

paratively small cardinal process, which only partially fills the cavity when the valves are closed. The size and shape of the cardinal process was apparently not restricted in any way during growth by the size and shape of the umbonal cavity, thereby allowing such great diversity.

In addition to variability resulting from unrestricted growth, there must have been considerable inherent genetic variability in the form of the cardinal process. The sample contains specimens where the cardinal process is not in the centre of the hinge-line, quadrilobate specimens where one shaft is considerably larger than the other, and trilobate specimens where the lobes of the myophore are distinctly asymmetrical. One specimen has an extra pair of buttress plates at the base of the cardinal process (Pl. 2, fig. 14).

TAXONOMIC SIGNIFICANCE OF CARDINAL PROCESS

For many years, brachiopod taxonomists have recognized the importance of the so-called 'stable' internal features in the erection and discrimination of superspecific categories. This has been recently emphasized with regard to the cardinal process in the Productoidea (Muir-Wood and Cooper, 1960, pp. 26–27). The remainder of the present paper consists primarily of an evaluation of the cardinal process as a 'stable' feature in the classification of *J. nebrascensis* proposed by these authors (pp. 255, 266–7).

To properly evaluate the classification of Muir-Wood and Cooper, it is necessary to review briefly the taxonomic history of *J. nebrascensis* and another very similar species, *J. symmetrica* (McChesney). Both these species were originally described over a century ago, and were placed in the genus *Juresania* by Dunbar and Condra (1932). In the classification of the family Productidae used by these authors prime consideration was given to features of ornamentation.

Then in 1954, Stehli subdivided the Productidae and established, among others, the family Echinoconchidae which included the genus *Juresania* (1954, p. 326). Again, prime evidence was placed on ornamental features.

Finally, Muir-Wood and Cooper (1960, pp. 67–69) redefined Stehli's Echinoconchidae, and distributed the genera he included in two new families, the Overtoniidae and the Buxtoniidae, as well as the revised Echinoconchidae. In addition, Muir-Wood and Cooper redefined the genus *Juresania* (pp. 266–7), and created a new genus *Pulcratia* (pp. 249–50) to include some of the species formerly placed in *Juresania*. One result of this revision was to place *J. nebrascensis* in the family Buxtoniidae, and what was formerly *J. symmetrica* (now *Pulcratia symmetrica*) in the family Echinoconchidae.

At both the family and genus levels in the classification of these species, Muir-Wood and Cooper have repeatedly stressed the importance of the cardinal process (pp. 243, 249–50, 255, 267). However, the results of the present study indicate that the form of the cardinal process (form = size+shape+number of myophore lobes+degree of fusion of the shaft) in *J. nebrascensis* is the most variable aspect of the brachial valve. Therefore, the cardinal process cannot be considered a stable internal feature and is not a suitably diagnostic taxonomic criterion for the establishment and recognition of families and genera in the classification of this species. (See Sutton and Summerson, 1943, p. 324; Burma, 1948, p. 753; Mayr, Linsley, and Usinger, 1953, pp. 106, 123–4.)

Nor, at the species level, is the form of the cardinal process a useful taxonomic criterion in the classification of *J. nebrascensis*. The experience of the senior author in identifying

specimens of *J. nebrascensis* and *J. symmetrica* from the Pennsylvanian rocks of eastern Nebraska indicates that the form of the cardinal process is of no value in distinguishing between these two species. The presence of a small pit, or alveolus, near the base of the cardinal process shaft in *J. nebrascensis* and the relatively larger, more deeply impressed muscle scars in *J. symmetrica* have proven to be far more useful than the form of the cardinal process. Unfortunately, neither the alveolus nor the impressed muscle scars can be used with absolute certainty in all cases. (See Pl. 2, figs. 15, 16.)

At just which level in classification the presence of the pit or alveolus near the base of the cardinal process shaft in *J. nebrascensis* should be stressed, must await further study of this and other closely related species. Until such time, the status of the genus *Pulcratia* is uncertain. None the less, it does seem firmly established on the basis of this study and the work of Dunbar and Condra (1932) that *J. nebrascensis* and *J. symmetrica* are closely related and in any classification of productoid brachiopods they should be placed in the same family and perhaps in the same genus.

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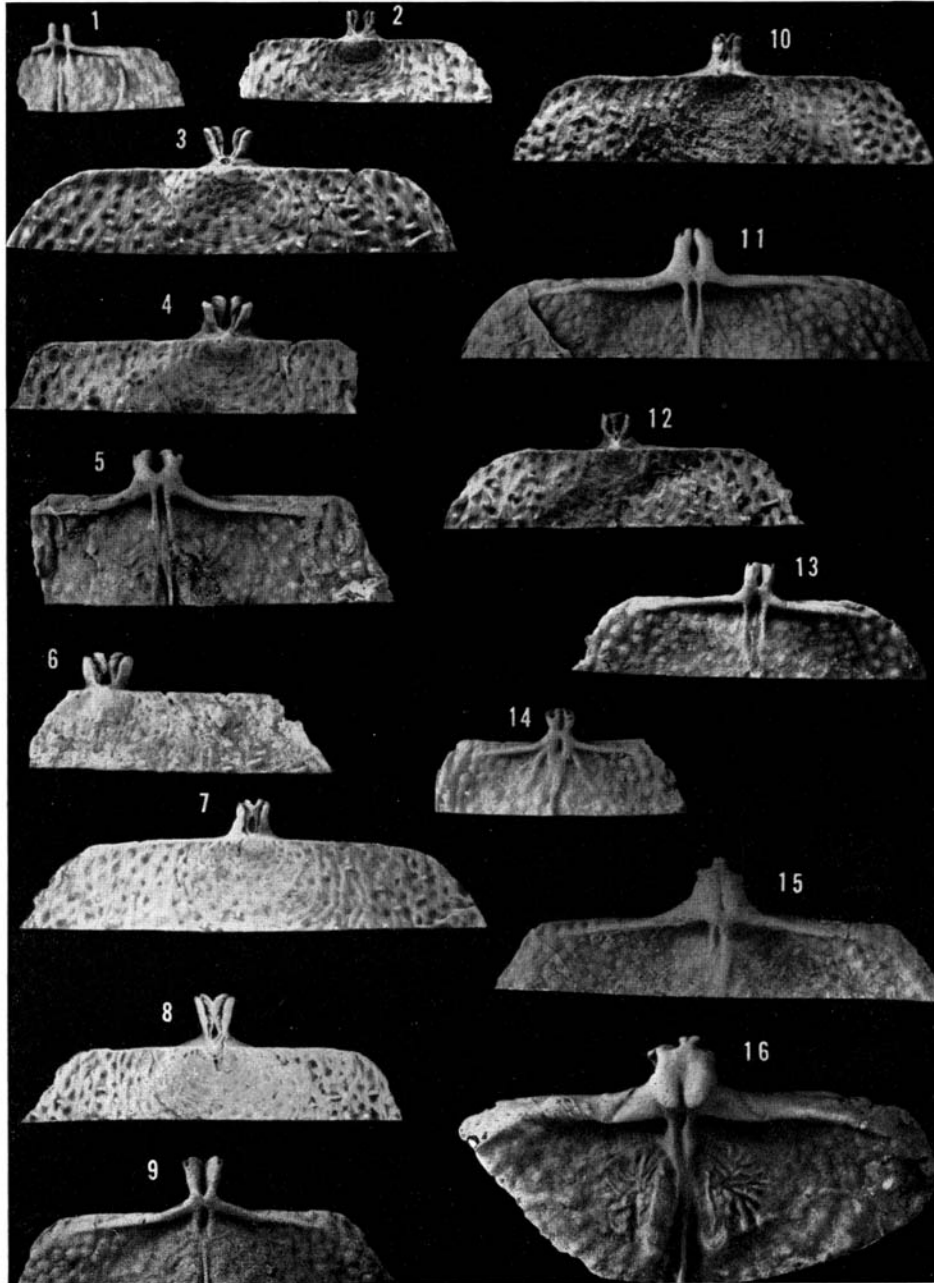
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