THE CARBONIFEROUS RHYNCHONELLID *PUGNOIDES TRIPLEX* (M'COY)

by D. PARKINSON

ABSTRACT. This small shell is described, its variation characteristics studied, and its relative growth features analysed. Although the species displays a fairly wide range of variation, collections from different localities in the D_1 zone have not been found to differ significantly from each other.

WELLER (1914, p. 192) describes *Pugnoides* as follows: 'Shells rhynchonelliform, below medium size, subovate in outline, with the fold and sinus well developed. Both valves marked by rounded or subangular plications which become obsolete in the posterior portion of the shell. Internal characters of both valves essentially as in *Camarotoechia*.'

The genus resembles *Pugnax* in its short costae; it differs from it in internal characters, the most obvious of which is the presence of a median septum in the brachial valve. This feature is absent or obsolescent in *Pugnax*.

Pugnoides triplex (M'Coy)

Plate 76, figs. 1–3.

Diagnosis. Small rhynchonellid, subovate in outline; width a little more than length; median fold on brachial valve with corresponding broad sinus in pedicle valve; costae short, angular to sub-roùnded, three (occasionally two, four, or five) on fold of brachial valve and usually three on flanks; two costae normally in sinus of pedicle valve; umbo of pedicle valve small, pointed, and sub-erect; median septum in brachial valve; dental lamellae in pedicle valve.

Type specimens. M'Coy's original figured type has not been traced. Topotypes are preserved in the British Museum (Natural History) (Pl. 76, fig. 1). These are sandstone casts which according to Davidson (1858–63, p. 104) were found in 'yellow or reddish sandstone forming the base of the Carboniferous system at Kildress in Tyrone'.

M'Coy's figure of '*Atrypa* triplex' (1844, pl. 22, fig. 17) is copied by Davidson (pl. 23, fig. 17). M'Coy describes his species (1844, p. 157) as 'Transversely oval, gibbous, beaks very small, pointed, surface with nine short angular ribs which reach but half way to the beak, front elevated with three of the ridges; the three ridges on each side slightly lower than the mesial ones'. He states that the shell is remarkable for its three equal lobes of three ridges each and comments on its very small size.

Costation. The costae are normally angular to sub-angular. A few specimens have been noted with sub-rounded costae in the ventral sinus which have developed a short median incision near the anterior margin.

Out of 218 shells examined 185 have a tri-costate dorsal fold; there are 10 specimens with only two central costae; 17 specimens have four and 6 specimens have five.

The number of costae on the flanks is less constant, although most shells have three

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on each side. The lateral costae diminish in size posteriorly and where more than three are developed, the fourth is usually not prominent, and if there is a fifth it is short and shows itself as little more than a wrinkling of the lateral margin of the shell.

The tricostate feature of the anterior margin of the dorsal fold develops early in growth, though occasionally the third costa does not appear until later and sometimes not at all. Where there is a fourth costa (Pl. 76) it normally forms in adult individuals as a bifurcation of one of the existing costae. This feature is sometimes seen in the lateral costae, although the usual mode of increase is by addition towards the posterior lateral margin of the shell.

Internal characters. The interior structure, so far as it has been possible to determine it, resembles that of *Camarotoechia* as the genus is interpreted by Weller (1914, p. 175). The hinge plates appear to be simple in outline. Except immediately below the dorsal umbo

TEXT-FIG. 1. Serial sections of a specimen of *Pugnoides triplex* of dimensions $L = 9{\cdot}7$ mm., $W = 10{\cdot}8$ mm., $D = 8{\cdot}0$ mm., taken at 0·3 mm. intervals. ×5.

where they appear to fuse, the hinge plates do not extend beyond the inner surfaces of the septalial plates which connect them to the median septum of the brachial valve. These plates enclose a V-shaped septalium. Anteriorly the median septum breaks away from the septalial plates. The crura are apparently formed by the anterior extensions of the inner margins of the hinge plates. The dental lamellae in the pedicle valve at first diverge both ventrally and anteriorly; they soon become parallel ventrally, but continue to diverge anteriorly. Faint muscle scar impressions have been seen in some individuals.

Text-fig. 1 illustrates serial sections of a specimen collected by Mr. A. Ludford from D_1 reef limestone near the Red Lion Inn, Cauldon, Staffordshire.

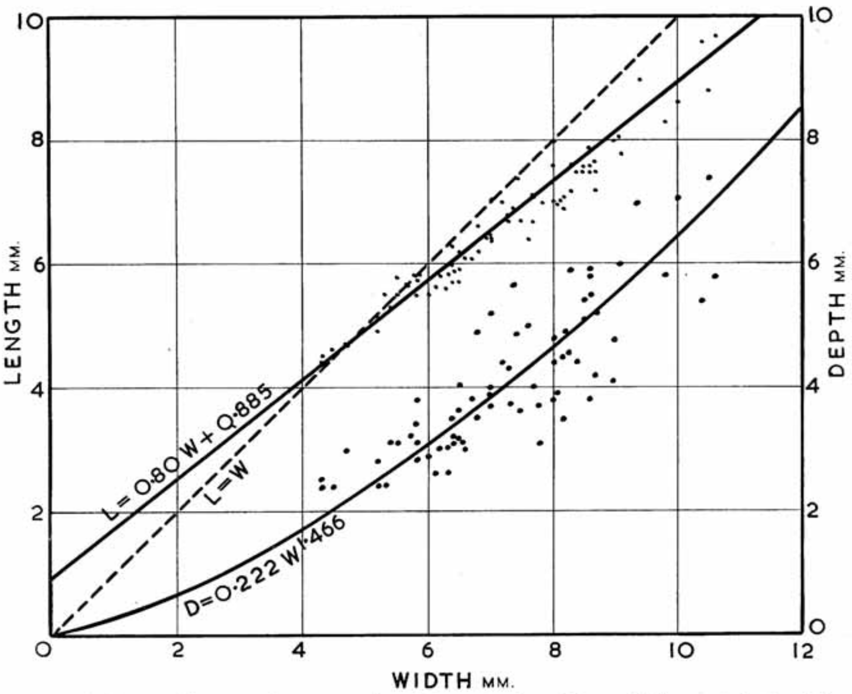
Occurrence. The Kildress sandstone of Co. Tyrone, Northern Ireland, which yielded M'Coy's types is probably of Seminula (S_2) age. (George 1958, p. 282). All the English specimens known to the writer were collected from reef limestone of the Lower *Dibunophyllum* Zone (D_1) in north Staffordshire and Derbyshire. Davidson records and figures '*Rhynchonella pleurodon* var. *triplex*' (p. 105, pl. 23, fig. 16) from the Carboniferous shale near Carluke, Lanarkshire. He also instances its occurrence in 'the shales of the upper portion of the Carboniferous limestone at Settle', in Yorkshire.

Remarks. Davidson confused this species with young specimens of '*Rhynchonella*' *pleurodon* (Phillips). However, the features distinguishing these two variable forms appear to be constant. The costae of *pleurodon* always extend to the posterior margin, whilst those of *triplex* are confined to the anterior part of the shell. In specimens similar in size the costae of *pleurodon* are narrower, closer spaced, and more numerous than those of *triplex*.

Immature specimens of *Pugnax pseudopugnus* D. Parkinson (1954, p. 570) are sometimes difficult to distinguish from *Pugnoides triplex*. Both species have a tricostate dorsal fold, but the internal characters differ markedly. Externally the main distinguishing feature is in the shape of the costae which in *Pugnax pseudopugnus* are more angular, deeper, and more acute than in *Pugnoides triplex*.

VARIATION IN BIOMETRICAL CHARACTERS

Assemblages have been analysed of measurable individuals from four localities: (1) Weaver Hills, north Staffordshire (095462), 72 specimens; (2) *Dielasma* Bed, Treak



TEXT-FIG. 2. Scatter diagrams of a community of *P. triplex* from Weaver Hills, north Staffordshire.

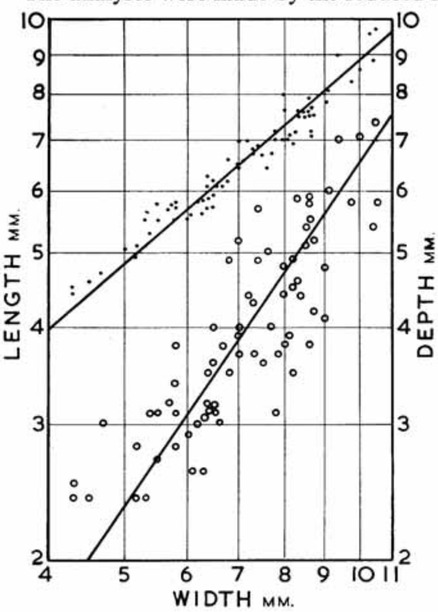
Cliff, north Derbyshire (134832), 28 specimens; (3) Dowel Dale, west Derbyshire (075676), 22 specimens; (4) Narrowdale Hill, north Staffordshire (123574), 28 specimens. Except for Narrowdale the lateral extent of the exposures is only a few feet and the vertical thickness a foot or less. Some of the Narrowdale shells were collected by Mr. A. Ludford and the writer from one thin pocket in the reef limestone; the others, in the British Museum (Natural History), if not from the same bed, were probably obtained from near-by at approximately the same stratigraphical level.

The scatter diagrams (text-figs. 2, 3, 5) indicate the range of variation in the size and shape of the shell. The measurements were made in the conventional directions. The length (L) is the maximum distance in a straight line from the posterior margin at the ventral umbo to the anterior margin; the width (W) is the maximum distance in a straight line perpendicular to the length between the two lateral margins; the depth (D) is the maximum distance through the shell perpendicular to the plane containing the length and width. The thickness (T) is measured centrally in the same plane as the depth. These features should be clear from the figures of Pl. 76 (see also Parkinson 1954, fig. 1, p. 563). In this particular species D is more often than not no greater than T. The sinus is seldom deeper than half a millimetre and there is little to be gained in the statistics by distinguishing between depth and thickness. D is preferred to T because it can be more accurately measured with a dial gauge.

The range of variation, though moderately wide, is about normal for the Carboniferous rhynchonellids. As usual, the L–W scatter is much narrower than those for D–L (not reproduced) and D–W.

RELATIVE GROWTH

The analyses were made by the reduced major axis procedure described by Kermack and Haldane (1950). In text-fig. 2 L is plotted against W and D on an arithmetical grid of the seventy-two specimens from Weaver Hills. The data for L–W were analysed on the assumption of isometry and the relationship was found to be $L = 0{\cdot}80W + 0{\cdot}885$. The line representing this equation fits the data fairly well and shows a uniform increase in length relative to width as the shell grows. It has, of course, to be assumed that the size of the shell is a measure of its age. In specimens with a width greater than 6 mm. the shell is nearly always broader than long. If the prolongation of the growth line to the L axis is justified it further indicates that in the early growth stages L is on average greater than W. At zero width the mean length—if such were physically possible—would be 0·885 mm. But if the fifteen specimens less than 6 mm. wide are considered separately it is found that on the average they are equal in length and width. The calculated mean values of L and W, for W less than 6 mm., curiously enough, happen to give the same figure of 5·253 mm.



TEXT-FIG. 3. Scatter diagrams of the Weaver Hills collection. The equations to the fitted allometric lines (reduced major axes) are $L = 1{\cdot}180\ W^{0{\cdot}876}$ and $D = 0{\cdot}222\ W^{1{\cdot}466}$.

The inference is, on the assumption that growth throughout is isometric, that at first L and W are equal and increase at the same rate, but that later the width begins to increase at a greater rate than the length.

This suggests the probability that differential growth is allometric, i.e. that it accords with the equation $L = \beta W^{\alpha}$ (see Zuckerman *et al.* 1950, for a full discussion), rather than isometric ($L = aW+b$). The data were therefore replotted on a double logarithmic grid. The computed reduced major axis $L = 1{\cdot}180\ W^{0{\cdot}876}$ (or $\log L = 0{\cdot}876 \log W + 0{\cdot}072$) is a satisfactory fit to the scatter in text-fig. 3.

In text-fig. 4 the curves for both isometric and allometric growth are drawn on arithmetical co-ordinates for the early growth stages, together with the line $L = W$, which is never far from the allometric line and meets it a little below 4 mm. (Calculation by putting $L = W$ in the allometric equation shows the two values to coincide at 3·8 mm.)

Although an isometric relationship holds approximately for the L–W scatter, this is not the case for depth–width as can be seen from text-fig. 2, in which a curved line drawn centrally through the points passes through the origin of the graph. This line in fact is derived from the allometric equation $D = 0{\cdot}222\ W^{1{\cdot}466}$ (or $\log D = 1{\cdot}466 \log W - 0{\cdot}653$). The reduced major axis, which is plotted on logarithmic co-ordinates in text-fig. 3, fits the data reasonably well.

The equation for the reduced major axis of the D–L relationship is $D = 0{\cdot}169\ L^{1{\cdot}673}$ ($\log D = 1{\cdot}673 \log L - 0{\cdot}771$). The scatter diagram is not reproduced in the paper.

Similar graphs have been drawn for the samples from the other three localities and analyses carried out. Tests of significance made by the shortened method of Leigh-Dugmore (1953) indicate that the different collections could all belong to the same population. The individual graphs are not reproduced here, but composite scatter diagrams for all the 150 specimens measured are drawn in text-fig. 5. The calculated equations are $\log L = 0{\cdot}830 \log W + 0{\cdot}107$ and $\log D = 1{\cdot}248 \log W - 0{\cdot}478$.

Previous work on differential growth in brachiopods (Parkinson 1952, 1954, 1959; Prentice 1956) has shown that in many instances the values of the allometric growth constants α and β have changed at some stage during growth. In the case of the small shell described here there are no such changes, but it is interesting to consider what might have happened if the shell had grown to a larger size.

Inspection of text-figs. 3 and 5 shows that in each case if the two growth-lines are produced to higher values they will meet at some point which is representative of the width of the shell where length and depth have become equal. The most reliable estimate is obtained by considering the data as a whole, since the differences between the four samples are not statistically significant. The appropriate values can be obtained from the allometric equations representative of the 150 specimens measured:

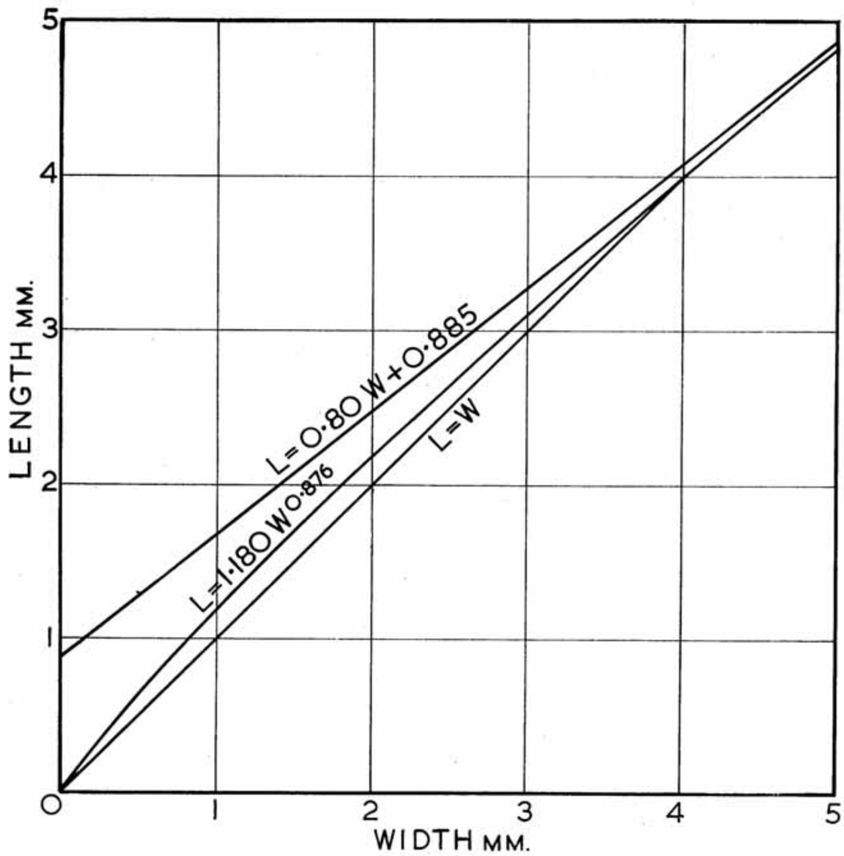
Thus
$$\log D = \log L = 0{\cdot}83 \log W + 0{\cdot}107$$
$$= 1{\cdot}248 \log W - 0{\cdot}478$$
$$\therefore \quad \log W(1{\cdot}248 - 0{\cdot}83) = 0{\cdot}107 + 0{\cdot}478$$

Hence
$$\log W = \frac{0{\cdot}585}{0{\cdot}418} = 1{\cdot}40$$

and
$$\log L = \text{either } (0{\cdot}83 \times 1{\cdot}40) + 0{\cdot}107 = 1{\cdot}269$$
$$= \text{or } (1{\cdot}248 \times 1{\cdot}40) - 0{\cdot}478 = 1{\cdot}269$$
$$\therefore \quad D = L = \text{antilog } 1{\cdot}269 = 18{\cdot}6 \text{ mm.}$$

and
$$W = \text{antilog } 1{\cdot}40 = 21{\cdot}5 \text{ mm.}$$

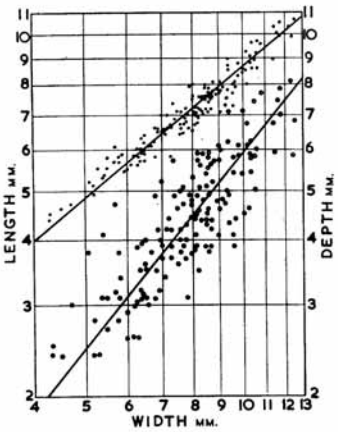
The same result is obtained graphically (text-fig. 6) by finding the point of intersection of the reduced major axes.

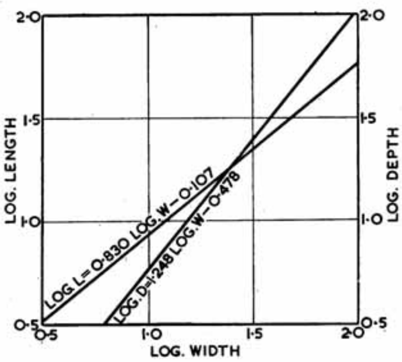


TEXT-FIG. 4. Comparison of the isometric and allometric reduced major axes for the early growth stages of *P. triplex*. Although the departure from isometry for the *L–W* relation is small, allometry gives a truer representation because for small specimens the mean values of *L* and *W* are equal.

This means that if the shell had grown to a size exceeding some 25 mm. in width the depth (and soon the thickness) would have become greater than the length. Since no specimens have been found where the length exceeds 11 mm. the value of 18·6 at which $D = L$ is hypothetical. It is also very approximate because if the Weaver Hills collection is considered separately $D = L$ at a value as low as 13·5 mm. The inference is that the shell would be unlikely to grow much larger without changes in the allometric growth constants α and β, otherwise the shape of old age specimens would be uncharacteristic of the species.

These data serve to illustrate the principle discussed fully elsewhere (Parkinson 1960)





TEXT-FIG. 5. Scatter diagrams of the composite sample of *P. triplex*. The equations to the fitted lines are $L = 1{\cdot}279\ W^{0{\cdot}830}$ and $D = 0{\cdot}333\ W^{1{\cdot}248}$.

TEXT-FIG. 6. Illustrates the changing relative dimensions of the shell with continued growth. Beyond the point of intersection of the reduced major axes the depth becomes greater than the length if the allometric parameters remain constant in value.

that changes in the allometric growth parameters are normally to be expected in the brachiopoda.

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