# EVOLUTIONARY BRACHIOPOD LINEAGES FROM THE LLANDOVERY SERIES OF EASTERN IOWA

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ABSTRACT. *Stricklandia-Costistricklandia* and *Pentamerus-Pentameroides-Callipentamerus* lineages provide stratigraphical control confirming the repetition of distinct faunas in the lower Silurian Hopkinton Dolomite of eastern Iowa. Traced laterally over the geographical extent of the outcrop area, the lineages also demonstrate that deposition of the Hopkinton Dolomite was phase-like and nearly synchronous. The prominent features that evolved in these brachiopods are the internal, skeletal structures. Changes in the cardinalia of the Iowa stricklandiids correspond to part of the known succession from the Llandovery type district in Wales and from Baltic regions. Variation in the external shell morphology of stricklandiids is interpreted as environmentally induced, and the separation of North American forms into the genera *Microcardinalia* and *Plicostricklandia* on this basis is considered unnecessary. The Iowa Llandovery section documents a previous prediction concerning migration and fusion of the outer plates in the *Pentamerus-Pentameroides* lineage. Pentamerids and stricklandiids formed member populations of 'perched' communities which were intermittently present in platform sea environments. While the illustration of 'insensibly graded' lineages is not possible in a stratigraphical sequence reflecting a history of shifting environments, the progressive changes noted in the Iowa stricklandiids and pentamerids are suggestive of phyletic evolution.

EVOLUTIONARY brachiopod lineages are used for correlating the shelly facies of the Silurian Llandovery Series on a regional and intercontinental basis in the British Isles (Ziegler *et al.* 1968, 1974), Norway (Bassett and Rickards 1971), Estonia (Rubel 1977), and North America (Berry and Boucot 1970; Rickard 1975). Those lineages most widely used are: (1) *Stricklandia-Costistricklandia*, (2) *Eocoelia*, and (3) *Pentamerus-Pentameroides*. In delimiting precise time intervals, the recognition of rapidly evolving lineages has been considered preferable to the Oppelian zone which attempts to group the coincidental ranges of different taxa. The known time ranges of the above lineages are shown in text-fig. 1.

Eocoelia does not occur in the Llandovery section of eastern Iowa or neighbouring areas (text-fig. 2), but the other two lineages are well represented. The *Stricklandia-Costistricklandia* and *Pentamerus-Pentameroides-Callipentamerus* lineages clearly outline the order and timing of depositional events in the Hopkinton Dolomite (text-fig. 3). The evolving structures of the cardinalia in both lineages confirm that the platform communities of Iowa were time-recurrent. From the beginning of the late Llandovery to the start of the Wenlock, the coral–algal community recurred at least four times, the pentamerid community four times, and the stricklandiid community three times. It is believed that the flat-bottomed, platform seas over Iowa supported only a single, ubiquitous community at any given time and that community replacements accompanied minor fluctuations in water depth (Johnson 1975, 1977). Diachronism can be tested by tracing rock units laterally from one locality to another and monitoring the stricklandiid and pentamerid elements. Under this procedure, Bassett and Rickards (1971, text-fig. 1) found a degree of diachronism in some of the
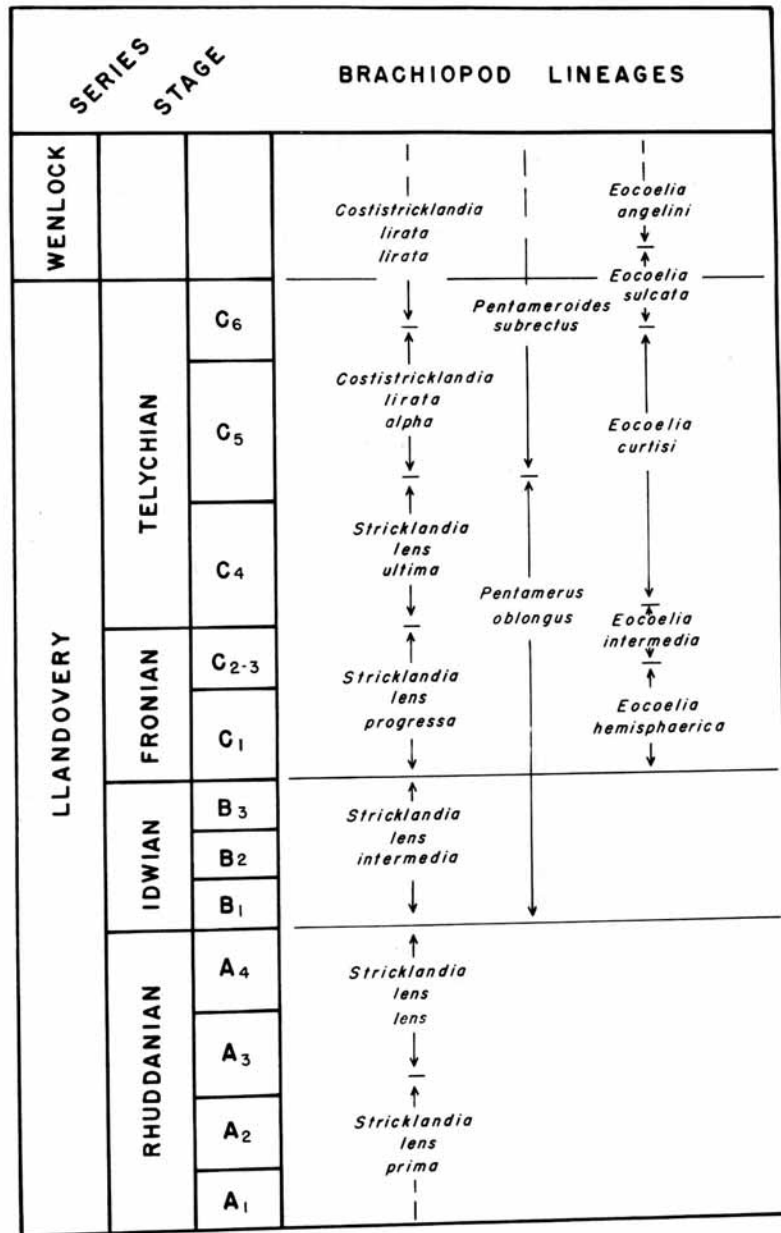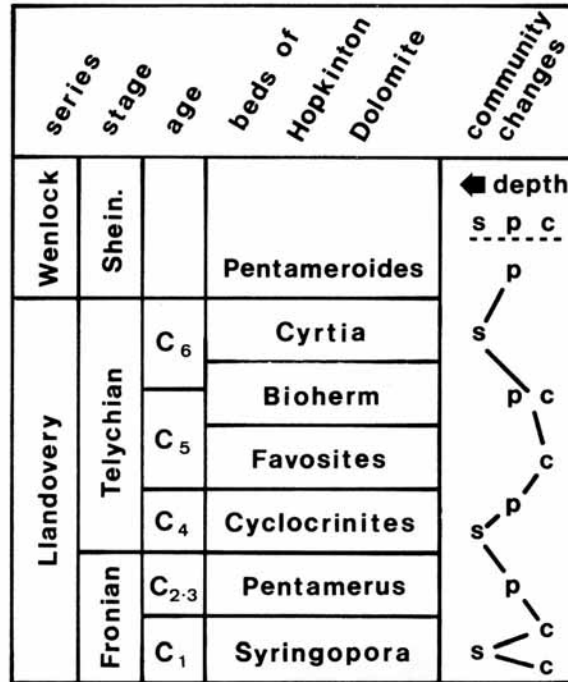
TEXT-FIG. 1. Correlation of brachiopod lineages with the standard stratigraphical sequence at Llandovery, Wales (after Cocks 1971).

classical stages and zones erected for the Silurian of Norway by Kiaer (1908). In the Silurian of Iowa, however, the occurrence of stricklandiid and pentamerid morphotypes is highly consistent within specific rock units. *S. lens progressa*, for example, occurs regularly at a particular level in the *Syringopora* Beds and it can be followed from north-western Illinois for a distance of 200 km across eastern Iowa (text-fig. 2, localities 71, 39, 69, 68, 28, 41, 96). This kind of evidence indicates that the unit-by-unit deposition of the Hopkinton Dolomite was synchronous, or nearly so.
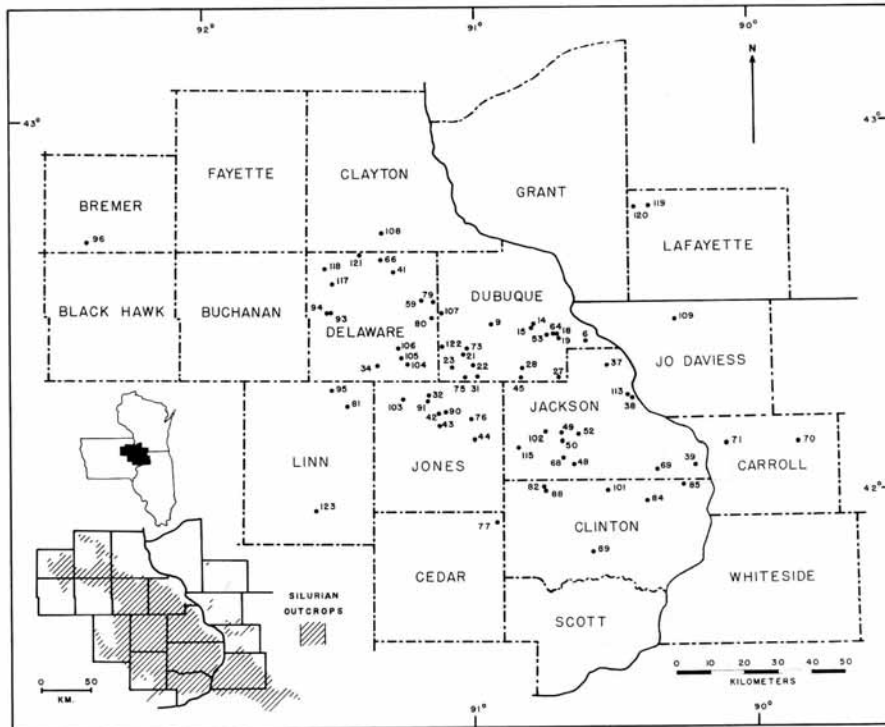
TEXT-FIG. 2. Map of Silurian rock distribution in the tri-state region of Iowa, Illinois, and Wisconsin, showing the location of outcrops examined.

The objective of this paper is to document the Iowa lineages. It will be shown that the stricklandiid lineage of the Iowa Llandovery corresponds precisely to the *Stricklandia lens progressa–S. lens ultima–Costistricklandia* lineage of the type Llandovery district in Wales and the Welsh Borderland. More important, the variation in size and shell shape, thought by Boucot and Ehlers (1963) to distinguish a separate stricklandiid lineage in North America, is interpreted as the result of non-genetic, environmental factors. Refinements in the *Pentamerus–Pentameroides* lineage will be presented and dated with reference to the time standard of the *Stricklandia–Costistricklandia*

series	stage	age	beds of Hopkinton Dolomite	community changes
Wenlock	Shein.		Pentameroides	◀ depth s p c - - - - - - p
Llandovery	Telychian	C₆	Cyrtia	s
		C₅	Bioherm	p c
			Favosites	c
		C₄	Cyclocrinites	p s
	Fronian	C₂·₃	Pentamerus	p
		C₁	Syringopora	s c c

TEXT-FIG. 3. Beds of the Hopkinton Dolomite, showing recurring patterns of community replacement. Key communities include the coral-algal (c), pentamerid (p), and stricklandiid (s) communities (from Johnson 1977).

lineage. These new data should be of value in improving the age assignments of pentamerid-bearing strata where stricklandiids are absent.

Numerical and locality data have been deposited with the British Library, Boston Spa, Wetherby, Yorkshire LS23 7BQ as Supplementary Publication No. SUP 14013 (24 pages).

STRICKLANDIID EVOLUTION

Previous work. The classic contributions on stricklandiid evolution remain those by St. Joseph (1935) and Williams (1951). St. Joseph studied the ribbed stricklandiids of late Llandovery and early Wenlock age, which Amsden (1953) named *Costistricklandia*. Ancestral to *Costistricklandia* are the comparatively smooth-shelled subspecies of *Stricklandia lens*, described by Williams from the Llandovery type area. The morphological details of this sequence have been reviewed recently by Rubel (1977), and confirmed in the Silurian of Estonia. Morphology need not be discussed again here, except to stress that the most prominent evolutionary features involve the internal skeletal structures of the cardinalia (text-fig. 4). Williams (1951, p. 98)
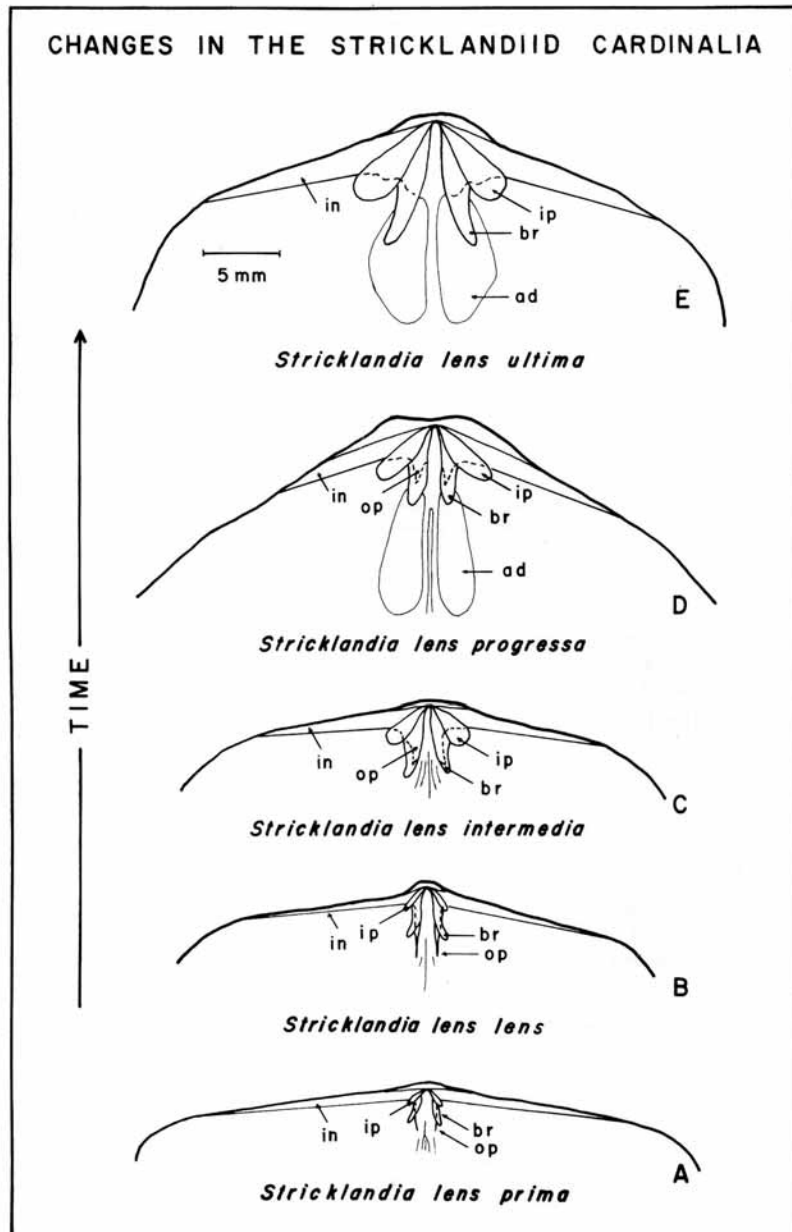
TEXT-FIG. 4. Evolutionary trends in the cardinalia of *Stricklandia*: ad, adductor muscle scar; br, brachial process; in, interarea; ip, inner plate; op, outer plate. The broken lines indicate those parts of the posterior margin of the floor of the valve which are obscured from view by the cardinalia (after Williams 1951).

specifically noted that external features, such as shell shape or length of the hinge-line, are variable and therefore of doubtful systematic value. The systematics of St. Joseph and Williams have stood the test of time and their specific and subspecific nomenclature have remained largely intact. Bassett (1977) and Cocks (1978) have pointed out that under the rules of nomenclature the nominal subspecies of a species should bear the same name as that species, so that *C. lirata typica* of previous usage is properly named *C. lirata lirata*.

Both the smooth-shelled and ribbed forms of stricklandiids are widely known from the Midcontinent region of North America. In their treatment of these, Boucot and Ehlers (1963) erected two additional genera chiefly on the basis of smaller size compared to *Stricklandia* and *Costistricklandia*. They regarded their *Microcardinalia-Plicostricklandia* lineage as generically separate, but phyletically parallel to the *Stricklandia-Costistricklandia* lineage (1963, text-fig. 1). Although these authors acknowledged the occurrences of *S. lens* and *C. lirata* near by in the Northern Appalachians and eastern Ontario, they described the following differences in Midcontinent material (1963, p. 48):

> These mid-continent shells are characterized by never reaching more than about one-third the maximum dimensions achieved by either *Stricklandia* or *Costistricklandia*, and in having relatively much smaller internal structures in both valves than are present in similar sized shells of either *Stricklandia* or *Costistricklandia*.

The species *Microcardinalia triplesiana* was described as having a very short median septum in the pedicle valve and small brachial processes, small inner plates, and no outer plates in the brachial valve.

Later work by Amsden (1966) reported the discovery of a predecessor to *M. triplesiana* in the lower Silurian of Oklahoma. *M. protriplesiana* possesses outer

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EXPLANATION OF PLATE 67

Representative stricklandiids and pentamerids from the Hopkinton Dolomite of Iowa. Internal moulds except for figs. 4, 9, and 11–13.

Figs. 1–4. *Stricklandia lens progressa* Williams. Middle of *Syringopora* Beds. 1, FMNH UC 61426, pedicle valve, ×1. 2, FMNH UC 61488, beak view, ×1. 3, FMNH UC 61209, brachial valve, ×1. 4, impression of the cardinalia from FMNH UC 61209, ×1·5.

Fig. 5. *Callipentamerus corrugatus* (Weller and Davidson). Unnamed rock unit at top of Hopkinton Dolomite. FMNH UC 65538, brachial valve showing much reduced outer plates fused into a cruralium, ×1.

Figs. 6–9. *Stricklandia lens ultima* Williams. Base of *Cyclocrinites* Beds. FMNH UC 62905. 6, pedicle valve, ×1. 7, brachial valve, ×1. 8, beak view, ×1. 9, impression of the cardinalia, ×1·5.

Fig. 10. *Pentameroides subrectus* (Hall and Clarke). Inter-reef facies of Bioherm Beds. FMNH UC 63670, brachial valve showing convergent outer plates fused into a cruralium, ×1.

Figs. 11–13. *Costistricklandia castellana* (White). Inter-reef facies of Bioherm Beds. FMNH UC 63708. 11, brachial valve, ×1. 12, beak view, ×1. 13, pedicle valve, ×1.

Fig. 14. *Pentamerus oblongus* (Sowerby). Base of *Pentamerus* Beds. FMNH UC 65822, brachial valve showing widely spaced, divergent outer plates, ×1.

Fig. 15. *P. oblongus* (Sowerby). Base of *Favosites* Beds. FMNH UC 65850, brachial valve showing narrowly spaced, less divergent outer plates, ×1.

PLATE 67
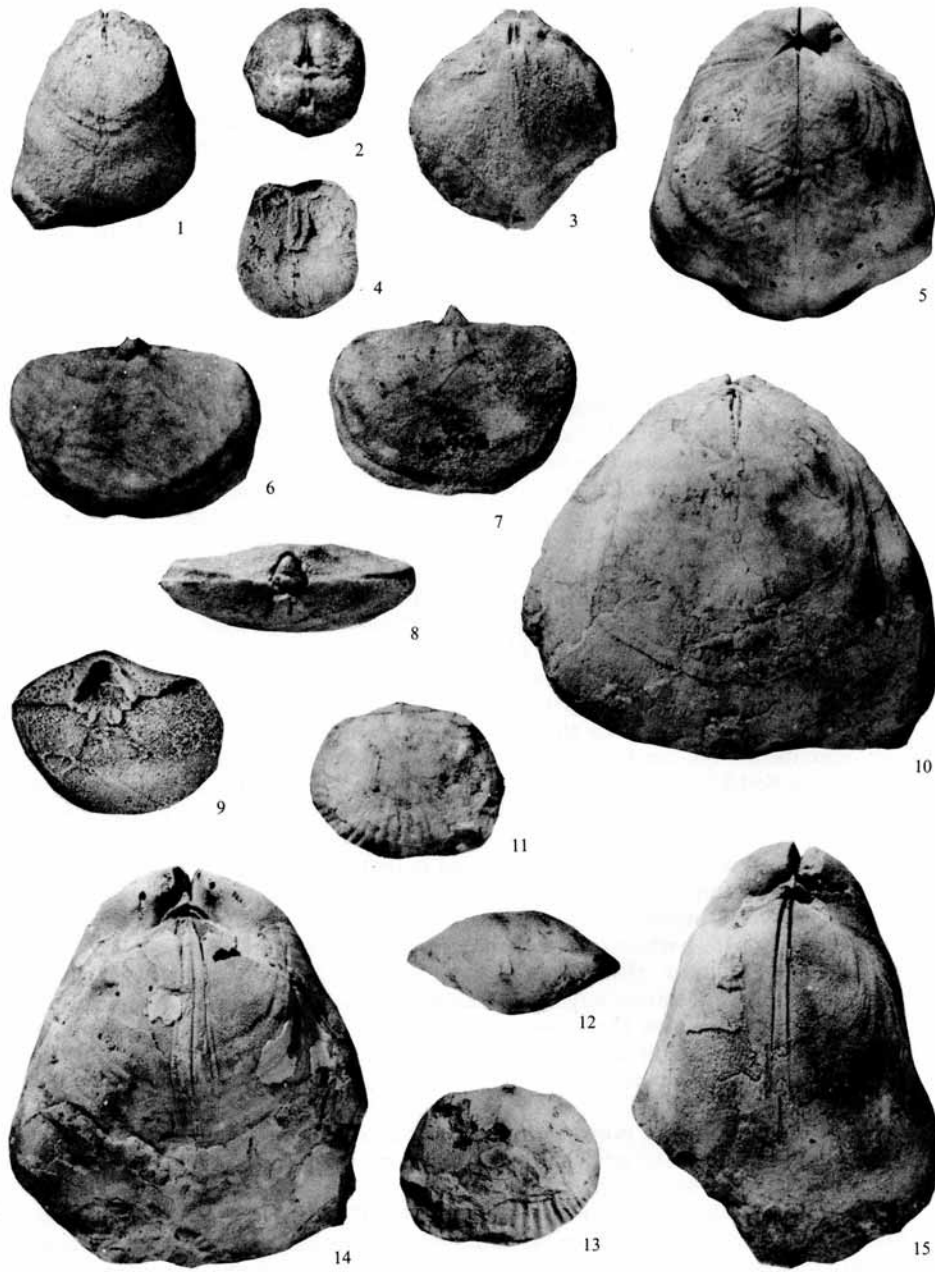
JOHNSON, Silurian Pentameracea

plates, the configuration of which was found to be much like that of *S. lens progressa*. Amsden concluded the following (1966, p. 1015):

> The *Microcardinalia* lineage is presumed to be separate from that of *Stricklandia* and there is, of course, no assurance that the evolution of the two groups proceeded precisely apace. Nevertheless there is a marked similarity between the two phylogenies.

The validity of these two generically separate but phyletically similar stocks was seriously questioned by Cocks and Rickards (1969) when they identified specimens from the lower Silurian of Shropshire, England, that varied in size between *Stricklandia* and *Microcardinalia*. Despite this, the terminology of Boucot and Ehlers appears to have been accepted in North America. Work as recently as that of Chiang (1971) described elements of the *Microcardinalia–Plicostricklandia* lineage from the lower Silurian of south-eastern Ontario.

Iowan occurrences. Stricklandiids occur abundantly at three horizons in the Hopkinton Dolomite of eastern Iowa. They are: (1) the middle of the *Syringopora* Beds; (2) the base of the *Cyclocrinites* Beds; and (3) throughout the *Cyrtia* Beds (see text-fig. 3). Through block samples, large collections of specimens from multiple localities and horizons were obtained and morphologically examined. Also available for comparison were representative collections of stricklandiids obtained by A. M. Ziegler from Wales and the Welsh Borderland. Measurements made on specimens from these collections include: (1) length of the median septum; (2) maximum length; (3) width of the cardinalia; (4) width of the interarea; and (5) height at the distal end of the adductor muscle scar. Casts of the internal structures were also made from selected specimens. The conclusions reached are that the Iowa stricklandiids of each rock unit are uniform in their gross morphology from locality to locality and that they bear a strong resemblance to the morphotypes of Wales and the Welsh Borderland. Specimens from the *Syringopora* Beds (and less commonly from the base of the *Pentamerus* Beds) are considered to be *Stricklandia lens progressa*, whereas those from the *Cyclocrinites* Beds are considered to be *S. lens ultima*. The ribbed stricklandiids from the *Cyrtia* Beds are truly smaller in over-all dimensions than *Costistricklandia*, but should probably be retained in that genus.

In their possession of outer plates, the stricklandiids from the *Syringopora* Beds of the Hopkinton Dolomite are much like the *Microcardinalia pyriformis* of Berry and Boucot (1970, p. 169), which occurs in the Plaines Member of the Kankakee Formation of eastern Illinois. However, the Iowa stricklandiids are particularly large, attaining shell sizes at least as large, if not larger, than *Stricklandia lens progressa* from the type district in Wales. Occasionally the size of *Pentamerus*, they are sometimes found articulated and in a growth position typical of pentamerid brachiopods. Although variation occurs in the stricklandiids of the *Syringopora* Beds, their generally oblong shape (Pl. 67, figs. 1–3) appears to be due to tight packing. Preserved in the umbo-down posture, about 10–12 individuals occupy a 100 cm² area. Under such crowding, the stricklandiid populations easily dominated their contemporaneous fauna by 80% or more.

Like the *M. triplesiana* of Boucot and Ehlers (1963, pp. 51–52), the stricklandiids from the *Cyclocrinites* Beds of the Hopkinton Dolomite lack outer plates. However, they are comparable in shell size to the *Stricklandia lens ultima* from the Welsh

Borderland. Despite variation, the stricklandiids from the *Cyclocrinites* Beds tend to have a bell-shaped profile (Pl. 67, figs. 6, 7) distinct from the elongate form of stricklandiids occurring in the older *Syringopora* Beds. Block samples from the *Cyclocrinites* Beds indicate that these younger stricklandiids only account for 55% or less of their total contemporaneous fauna (Johnson 1977, text-fig. 2). Compared to its predecessor, a wider diversity was attained by the later stricklandiid community, and individual stricklandiids were only loosely packed.

Morphological comparisons. Comparisons for length of the median septum (text-fig. 5) and width of the interarea (text-fig. 6) are made between the smooth-shelled stricklandiids of Iowa and those of Wales and the Welsh Borderland. In each case, the range in variation matches closely. The disparity in size postulated by Boucot and
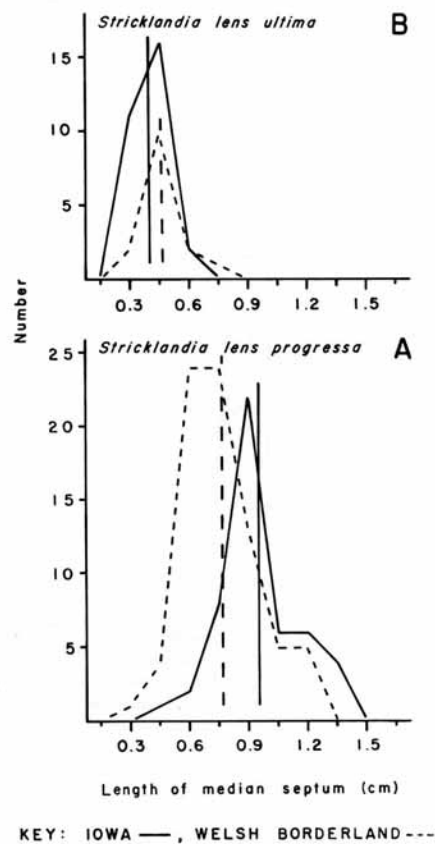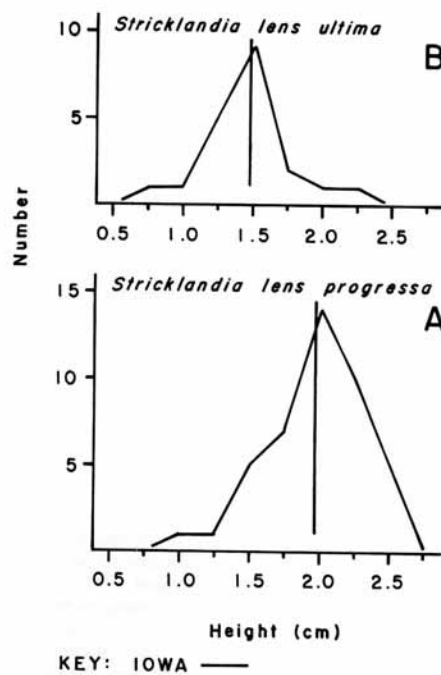

TEXT-FIG. 5. Comparison of the length of the median septum in stricklandiids from Iowa and Wales and the Welsh Borderland. Size class 0·15 cm. A, specimens from the *Syringopora* Beds of the Hopkinton Dolomite in Iowa (locality 85) have slightly longer median septa than specimens from the C₁ beds of the Llandovery district, Wales (locality L-S-B). B, specimens from the *Cyclocrinites* Beds of the Hopkinton Dolomite in Iowa (locality 27) have median septa of the same size as specimens from the Wyche Beds of the Malvern Hills in the Welsh Borderland (locality H-G-F).

KEY: IOWA ——— , WELSH BORDERLAND ---

Ehlers (1963) is not confirmed. Height (text-fig. 7) is plotted for the Iowa stricklandiids alone, because the material from Wales and the Welsh Borderland consisted mostly of disarticulated specimens. It is observed, however, that individuals with a wide interarea are thinner than those with a short interarea. All external features of the stricklandiids are found to be morphologically plastic. Where the typical stricklandiid was confined by tight packing, the median septum lengthened proportionate to the increased shell length and the shell height increased, while the width of the interarea was reduced. Under conditions of loose packing, the morphological relationships were reversed. The result was a limitation on maximum length and thickness, a shorter median septum, and a wider interarea. Not surprisingly, the close agreement in external morphology between the Iowa samples and those from Wales and the Welsh Borderland is related to similar community dominance. In both cases, *Stricklandia lens progressa* dominated contemporaneous faunas to a greater extent than did *S. lens ultima*. Tight packing in stricklandiid populations had the
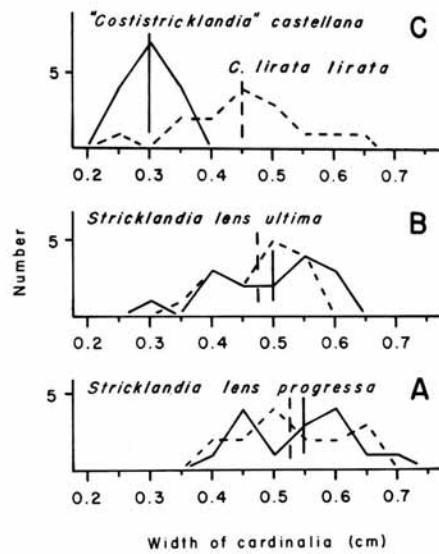

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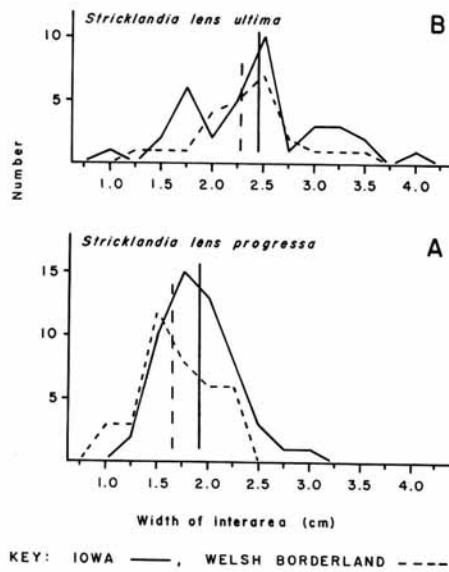
TEXT-FIG. 6. Comparison of the width of the interarea in stricklandiids from Iowa and Wales and the Welsh Borderland. Size class 0·25 cm. A, specimens from the *Syringopora* Beds of the Hopkinton Dolomite in Iowa (locality 85) have interareas of the same size as specimens from the C_1 beds of the Llandovery district, Wales (locality L-S-B). B, specimens from the *Cyclocrinites* Beds of the Hopkinton Dolomite in Iowa (locality 27) have interareas of the same size as specimens from the Wyche Beds of the Malvern Hills in the Welsh Borderland (locality H-G-F).

KEY: IOWA ———

TEXT-FIG. 7. Comparison of shell height (thickness) between stricklandiids from Iowa. Size class 0·25 cm. A, specimens from the *Syringopora* Beds of the Hopkinton Dolomite (locality 85) are thick. B, specimens from the *Cyclocrinites* Beds of the Hopkinton Dolomite (locality 27) are thin.

TEXT-FIG. 8. Comparison of the width of the cardinalia, measured between teeth and sockets, in stricklandiids from Iowa and Wales and the Welsh Borderland. Size class 0·05 cm. A, specimens from the *Syringopora* Beds of the Hopkinton Dolomite in Iowa (locality 85) have cardinalia of the same width as specimens from the C₁ beds of the Llandovery district, Wales (locality L-S-B). B, specimens from the *Cyclocrinites* Beds of the Hopkinton Dolomite in Iowa (locality 27) also have cardinalia of the same width as specimens from the Wyche Beds of the Malvern Hills in the Welsh Borderland (locality H-G-F). C, specimens from the *Cyrtia* Beds of the Hopkinton Dolomite in Iowa (locality 21) have cardinalia which are smaller in width than those of specimens from the Wyche Beds of Old Storridge Common in the Welsh Borderland (locality H-F-B).

effect of limiting faunal diversity, whereas loose packing promoted higher diversity. True to Williams's appraisal (1951) that shell shape and size are of questionable systematic value, the observations on packing and community dominance indicate that ecological factors alone account for these variations.

It now remains to compare the size of the cardinalia in Iowa stricklandiids with those from Wales and the Welsh Borderland. Text-fig. 8 contrasts the width of the cardinalia, as measured between teeth and sockets, for both smooth-shelled and ribbed stricklandiids. In the case of the smooth forms, the three to one disparity in cardinalia size suggested by Boucot and Ehlers (1961, p. 51) is not seen in these data. The ranges in variation for the Iowa samples and those from Wales and the Welsh Borderland match closely (text-fig. 8A, B). However, a significant size difference exists in the comparison of ribbed stricklandiids (text-fig. 8C). The cardinalia of the Iowa sample have only two-thirds the width of the Welsh Borderland sample, yet are proportionately larger in relationship to over-all shell size.

This raises the question of what controls shell size. One possibility is that stricklandiid shell size may be related to water depth. Text-fig. 9 shows the size variation in the width of the interarea between the ribbed stricklandiids from a pentamerid community and a marginal stricklandiid–clorindid community in the Iowa Llandovery. Individuals from the pentamerid community are larger. Although the over-all shell size for the *Plicostsicklandia castellana* of Boucot and Ehlers (1963, pp. 56–57) is much smaller than *Costistricklandia lirata*, a generic distinction on this basis alone seems unwarranted.
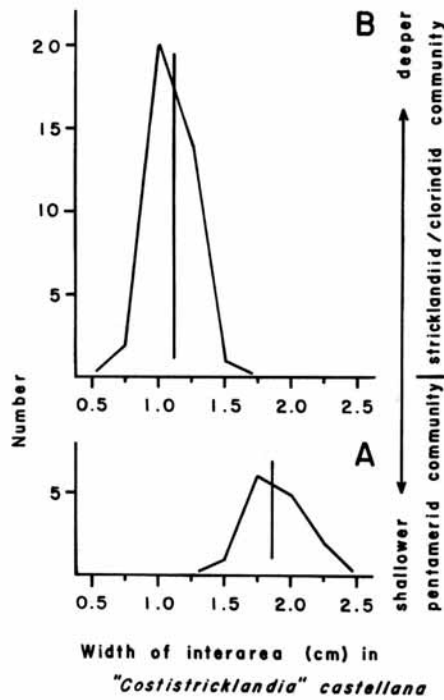
TEXT-FIG. 9. Comparison of width of the interarea in ribbed stricklandiids from the Hopkinton Dolomite of Iowa. Size class 0·25 cm. A, specimens from the inter-reef facies of the Bioherm Beds (locality 50) are large. B, specimens from the *Cyrtia* Beds (locality 21) are smaller.

In distinguishing features of systematic value, it is critical that taxonomists be watchful for morphological variation related to environmental factors. Fürsich and Hurst (1974) reported that a range in shell size in some Silurian brachiopods could be related to overlapping membership in different depth distributed communities. Postulating a more limited food supply in deeper, offshore waters, the authors suggested that brachiopods which decreased in size with water depth were inefficient as food collectors. Those brachiopods exhibiting less change in size were interpreted to have more efficient lophophores. Whatever the cause of size variation in Silurian stricklandiids, the internal skeletal features described by Williams and St. Joseph (text-fig. 4) remain the surest measure of evolutionary change. As suggested by Cocks and Rickards (1969, p. 222), *Microcardinalia* and *Plicostricklandia* are synonyms of *Stricklandia* and *Costistricklandia* respectively.

PENTAMERID EVOLUTION

Previous work. The earliest student of pentamerid evolution was Kiaer (1908, pp. 499–500), working in Norway. He called attention to the gradual increase in the lengths of the spondylium and medium septum in his *Pentamerus borealis*, *P. oblongus*, and *P. gothlandicus* morphological series. Bassett and Cocks (1974, p. 23) pointed out

that the so-called *P. gothlandicus* of Norway is actually a species of *Pentameroides*, not at all like the typical *Pentamerus gothlandicus* of Gotland. Thus, Kiaer's morphological series represents the *Pentamerus–Pentameroides* lineage. This lineage is traditionally considered to reflect the slowest rate of evolution in terms of taxa per unit time, compared with the *Stricklandia–Costistricklandia* and *Eocoelia* lineages (Boucot 1975, text-fig. 18). However, not all potential evolutionary trends have been adequately tested in the *Pentamerus–Pentameroides* lineage. One such trend, predicted by St. Joseph (1938, p. 286), relates to the position of the outer plates, or crural plates, on the brachial valve:

> The distance between the crural-plates in different species of *Pentamerus s. s.* is somewhat variable, and in the later forms in southern Norway (towards the top of zone 7b), they may be close to one another, though never in contact. They unite, however, to form a sessile, or partly elevated cruralium in *Pentamerus* cf. *gotlandicus*, a species which Kiaer considered to have descended from *P. laevis*. It would seem that *Pentamerus* gradually merges into *Pentameroides* through the approximation and final union of the cardinalia.

In the early pentamerid end member, the outer plates are divergent and relatively wide apart. The intermediate form between *Pentamerus* and *Pentameroides* should possess outer plates which are parallel to each other and very closely spaced.

In addition to the Norwegian occurrence, this morphotype has been noticed in pentamerids from the Red Mountain Formation of Alabama (A. M. Ziegler, pers. comm.). Following the merger of the outer plates to form a cruralium in *Pentameroides*, the predictable lineage end member would be reached by gradually decreasing the length of the cruralium. *Callipentamerus corrugatus*, redescribed by Boucot (1964) from the Hopkinton Dolomite of Iowa, fulfils this end member morphotype. Interestingly, the process of merger in the outer plates of the brachial valve is anticipated by a similar fusion arising from dental plates in the pedicle valve. The septum and spondylium duplex are the primary internal skeletal structures in the pedicle valve of pentamerids. These structures are composed of a pair of plates which are fused ventrally to form a septum attached to the valve floor, but separate dorsally to form the spoon-shaped spondylium.

Chiang (1971, text-fig. 5) attempted to monitor the configuration of the outer plates in *Pentamerus oblongus* at stratigraphical intervals through a 7 m section of the Fossil Hill Formation in southern Ontario. The results were contrary to the expected; the maximum width between the outer plates appeared to increase with time, rather than decrease. Chiang (1971, p. 857) concluded that the specimens sampled low in the section were generally smaller than those sampled higher in the section. Thus, the progressive increase in the distance between the outer plates was proportional to the progressive increase in the over-all size of the individuals, and was not indicative of evolutionary change.

Iowan occurrences. Pentamerids occur in profusion at several horizons in the 60 m thick Hopkinton Dolomite. In stratigraphical order from oldest to youngest (text-fig. 3), the pentamerid-bearing layers include: (1) the *Pentamerus* Beds; (2) the middle and top parts of the *Cyclocrinites* Beds; (3) the base of the *Favosites* Beds; (4) the inter-reef facies of the Bioherm Beds; and (5) the *Pentameroides* Beds. The horizons of the *Cyclocrinites* Beds contain '*Pentamerus*' *maquoketa*, locally an extraneous

morphotype ancestral to *Lissocoelina* and *Harpidium* (Boucot 1975, text-fig. 27). All the other horizons yield a range of morphotypes in the *Pentamerus-Pentameroides-Callipentamerus* lineage that illustrates the gradual changes in the cardinalia predicted by St. Joseph (1938).

From horizon to horizon, the pentamerids of the Hopkinton Dolomite are frequently found in their characteristic, umbo-down life position. In sampling the different morphotypes of the *Pentamerus-Pentameroides-Callipentamerus* lineage, this factor was taken advantage of. Most samples were thereby guaranteed to consist of individuals from the same life populations. Collections were made at five horizons. No single outcrop exposes a complete section of the Hopkinton Dolomite, and thus direct evidence of superposition in all five horizons is lacking. A sample interval of about 10 m was based on stratigraphical position relative to known contacts between rock units. In order to test for spatial uniformity in morphotypes along presumed time planes, samples were duplicated from three of the five horizons at additional localities.

Data documenting the decrease in distance between the outer plates are illustrated in text-fig. 10. Each sample consists of fifteen specimens, preserved as internal moulds usually in life position. For every specimen, the distance between the outer plates on the floor of the brachial valve was measured at regular intervals along the length of the structure. This was done by using a vernier calliper under a binocular microscope. The measurements obtained represent an ontogenetic history for each individual, reflecting the development of the outer plates from the juvenile to the mature stage. In each graph (text-fig. 10A–E), the lines represent the growth patterns of the outer plates in fifteen individuals. The points on the lines indicate the intervals at which measurements were made. Three consecutive plots of *Pentamerus oblongus* (text-fig. 10A–C) were made using an interval of 0·5 cm. The plot of *Pentameroides subrectus* (text-fig. 10D) required an interval of 0·25 cm. An interval of 0·10 cm was necessary in plotting the small detail of the outer plates in *Callipentamerus corrugatus* (text-fig. 10E).

The sample plotted in text-fig. 10A was collected from the base of the *Pentamerus* Beds at locality 68 (see text-fig. 2 for all localities and Pl. 67, figs. 5, 10, 14, 15 for representatives of the various morphotypes). The trend of the first graph is consistent, showing the outer plates positioned relatively wide apart and divergent. A duplicate sample from the base of the *Pentamerus* Beds at locality 101 overlaps, but is slightly displaced to the right of this plot (not shown). The sample from the top of the *Pentamerus* Beds at locality 27 (text-fig. 10B) shows a greater variation in the separation of the outer plates. The individuals on the right are more aligned with those of text-fig. 10A. Those on the left, however, possess outer plates slightly less divergent and more closely spaced. The sample in text-fig. 10C was collected up-section, from the base of the *Favosites* Beds at locality 52. The trend is again consistent, showing the outer plates positioned closely together and nearly parallel. A duplicate sample from the base of the *Favosites* Beds at locality 105 plots out more vertically and somewhat to the left (not shown). Higher in the section, *Pentameroides* (text-fig. 10D) from the inter-reef facies of the Bioherm Beds at locality 50 exhibit convergent plates fused into a cruralium. Although there is some variation in the maximum separation of the outer plates, the trend is striking in its sharp inclination to the left. A duplicate
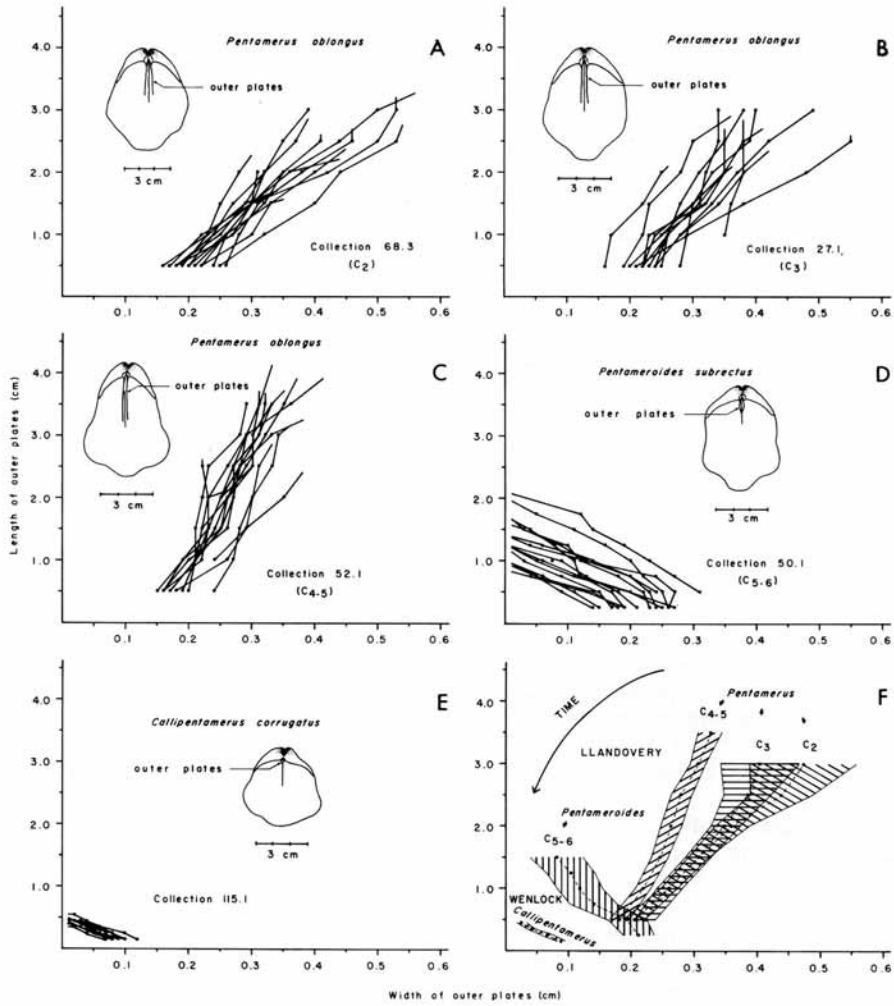
TEXT-FIG. 10. Comparison of the outer plates in an evolutionary sequence of pentamerids from the Hopkinton Dolomite of Iowa. Each line represents a series of measurements made on a single specimen. A, *Pentamerus oblongus* from the base of the *Pentamerus* Beds. B, *P. oblongus* from the top of the *Pentamerus* Beds. C, *P. oblongus* from the base of the *Favosites* Beds. D, *Pentameroides subrectus* from the inter-reef facies of the Bioherm Beds. E, *Callipentamerus corrugatus* from near the top of the Hopkinton Dolomite. F, summary using confidence intervals at the 95% level to define the mean width of the outer plates. Slope to the right or left indicates the degree of plate divergence or convergence, respectively.

sample from locality 45 is in close agreement (not shown). The sample plotted in text-fig. 10E is from the uppermost part of the Hopkinton Dolomite at locality 115. As in *Pentameroides*, the outer plates of *Callipentamerus* are convergent, but their length is greatly reduced.

All trends shown in text-fig. 10A–E are summarized in text-fig. 10F. Confidence intervals at the 95% level define the mean width of the outer plates from morphotype to morphotype. The slope to the right or left indicates the degree of plate divergence or convergence, respectively. Age assignments were refined, in part, on the basis of associated stricklandiid brachiopods. Two fundamental conclusions drawn from this work are: (1) the configuration of the outer plates in pentamerid brachiopods evolved gradually through late Llandovery time; and (2) the pentamerids from particular Iowa units are fairly uniform in the morphology of their outer plates from locality to locality.

STRATIGRAPHICAL VALUE

While the stratigraphical value of the *Stricklandia–Costistricklandia* and *Eocoelia* lineages is widely recognized in Europe and North America, problems remain to be solved with regard to the *Pentamerus–Pentameroides–Callipentamerus* lineage. The transition from *Pentamerus oblongus* to *Pentameroides subrectus* is dated as late Llandovery, but the range of *Pentamerus* is generally extended in the Wenlock (Boucot 1975, text-fig. 27). For example, *P. gothlandicus* occurs close to the base of the Halla Beds of Wenlock age in Gotland (Bassett and Cocks 1974, p. 23). There are two possible interpretations: (1) *Pentameroides* can be regarded as a side branch from the main *Pentamerus* stock, co-existing with *Pentamerus* during the early Wenlock; or (2) all Wenlock occurrences of '*Pentamerus*' can be regarded as homeomorphs of the Llandovery type species, *P. oblongus*. Mixed associations of *Pentameroides* and *Pentamerus* are not reported in the literature. In either case, occurrences of *Pentamerus* in the Llandovery and in the Wenlock must be differentiated if the *Pentamerus–Pentameroides* lineage is to be of significant stratigraphical value.

Proper age identification of *Pentamerus* may be especially difficult in stratigraphical sequences where *Pentameroides* is missing. For example, *Pentameroides* is unknown in the Silurian of Ohio and Indiana, although it occurs near by on the Niagara Peninsula of eastern Ontario, Manitoulin Island, the Upper Michigan Peninsula, eastern Wisconsin, and eastern Iowa. *Pentamerus*, however, does occur in the Cedarville Dolomite of Ohio and in the upper part of the Salamonie Dolomite of Indiana. Berry and Boucot (1970, p. 134) treated these rock units as approximately equivalent in stratigraphical position, assigning a Wenlock age. Caution must be exercised because pentamerids from both formations include morphotypes with outer plates nearly parallel and closely spaced. A thorough programme of sampling would be required to test whether these occurrences are time equivalent to the late Llandovery morphotype anticipating *Pentameroides*. Directly overlying the *Pentamerus* bearing beds of the Salamonie Dolomite in Indiana is the Limberlost Dolomite (Droste and Shaver 1976), separated by an irregular contact. A hiatus between the two formations would provide an explanation for the puzzling exclusion of

Pentameroides in the sequence. The *Pentamerus-Pentameroides-Callipentamerus* lineage in the lower Silurian of eastern Iowa provides a reference. The range of *Pentamerus* requires further investigation, on a case by case basis.

SYMPATRIC OR ALLOPATRIC SPECIATION?

The *Eocoelia*, *Stricklandia-Costistricklandia*, and *Pentamerus-Pentameroides* lineages are generally thought of as examples of phyletic evolution (Boucot 1975, text-fig. 18). If the recurrent community patterns in the Iowa Llandovery sequence are representative, it is likely that the habitat of stricklandiids and pentamerids remained essentially unchanged throughout the early Silurian. Modifications in the cardinalia enabled these brachiopods to become more efficient in their accustomed environments, assuming the structures were adaptive. In terms of habitat, Boucot (1975, pp. 59, 60) believed that the pentamerid brachiopods occupied broad areas, while the stricklandiids and *Eocoelia* may have inhabited a number of smaller, communicating regions. *Eocoelia*, for example, appears to have been restricted to coastal or shelf-margin environments. In any case, the habitat area of these brachiopods is considered to have effectively supported enormous, panmictic populations. If so, then speciation was sympatric (without geographical isolation). Extreme low continentality and the close proximity of Laurentia and Baltica during the Silurian (Ziegler, *et al.* 1977, text-fig. 3) should have promoted sympatric speciation among brachiopod populations in those regions. The observation by J. G. Johnson (1975) that allopatric speciation is the predominant pattern of evolution among Devonian brachiopods, may be explained by the conditions of high continentality prevalent during that time (Ziegler *et al.* 1977, text-fig. 4).

The concept of allopatric speciation was long overdue in its application to the problems of the fossil record (Eldredge and Gould 1972; Gould and Eldredge 1977), but the model does not satisfactorily account for progressive changes demonstrated by the *Eocoelia*, *Stricklandia-Costistricklandia*, and *Pentamerus-Pentameroides* lineages. Some problems are inherent in the documentation of 'insensibly graded' lineages from stratigraphical sequences which accumulated in shallow, platform seas. Difficulties related to environment rather than the imperfection of the geological record were clearly recognized by Darwin (1859, p. 295):

In order to get a perfect gradation between two forms in the upper and lower parts of the same formation, the deposit must have gone on accumulating for a very long period . . . But we have seen that a thick fossiliferous formation can only be accumulated during a period of subsidence; and to keep the depth approximately the same, which is necessary in order to enable the same species to live on the same space, the supply of sediment must nearly have counterbalanced the amount of subsidence.

The orderly succession of depth-associated communities in the Llandovery section of Iowa indicates that the local geological record is reasonably intact. However, stricklandiids and pentamerids do not occur uniformly throughout the 60 m thickness of strata. The evolution of these brachiopods on the platform must be monitored through environmentally appropriate windows framed by shifting conditions of deposition. J. G. Johnson (1974) applied the term 'perched faunas' to depth-associated populations which lived in platform seas. During lower stands in sea level, pentamerid and stricklandiid populations were undoubtedly restricted to the platform margins.

Proponents of allopatric speciation might argue that morphological change was not gradual in the platform populations, but was sporadic, arising in geographically isolated populations at the platform margins. It is not clear, however, that random changes acquired by peripheral populations would consistently follow a unidirectional path of development, as in the case of the pentamerids and stricklandiids. Current weight of opinion in the debate on the tempo and mode of evolution appears to accept that valid examples of phyletic gradualism are uncommon and that they illustrate little more than events of micro-evolution. True or not, such grounds are insufficient cause for the abrogation of the lineage zone in favour of the 'more conservative' Oppelian range zone, as suggested by Eldredge and Gould (1977, pp. 36, 39). As long as lineage zones provide an accurate means of correlation, stratigraphers will continue to refine known lineages and look for new ones.

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