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# A TOURNAISIAN BRACHIOPOD FAUNA FROM SOUTH-EAST WALES

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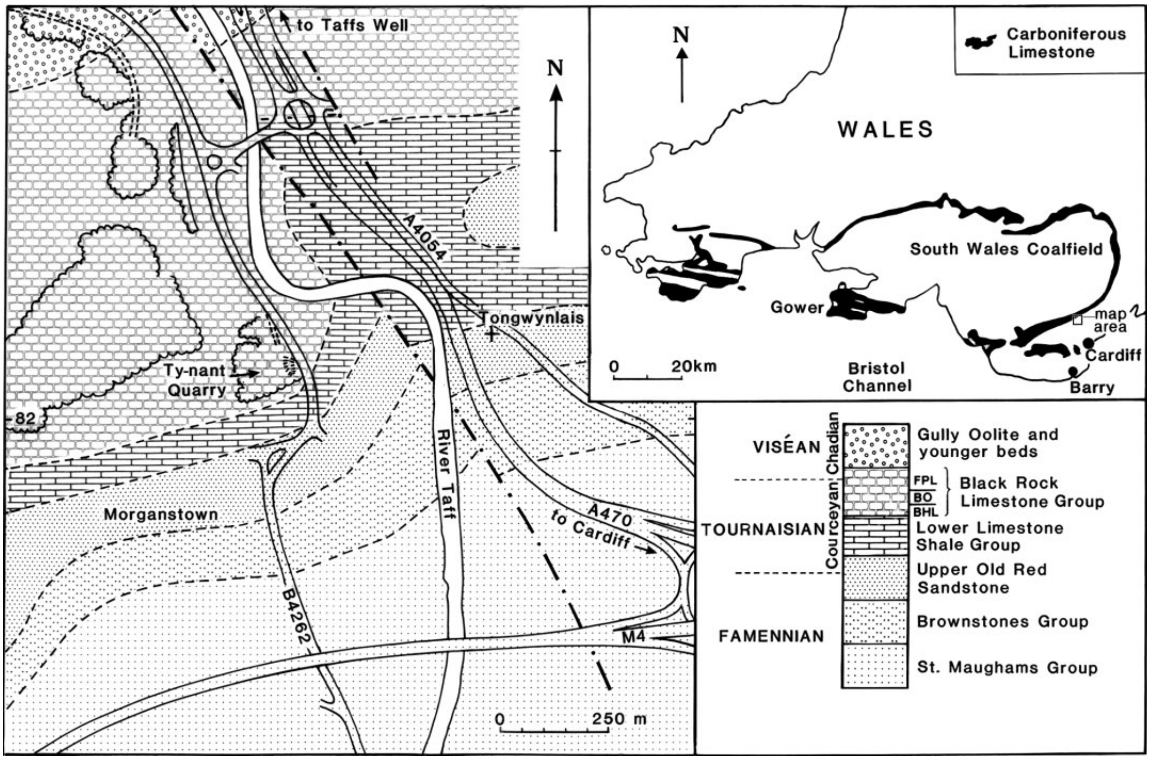
**Abstract:** An exceptionally preserved fauna within dolomites of the Friars Point Limestone Formation includes the most diverse brachiopod assemblage yet described from the Tournaisian of the British Isles, and the first from Wales. Each of the 16 brachiopod genera includes a single species, of which four are new (*Schellwienella cheuma*, *Schuchertella subcrona*, *Composita ptygmation*, *Fusella extrata*). Associated fossils are corals (one species), bryozoans (two species) and crinoids (one species). Spiriferoideans and schizophorides are numerically dominant, indicative of level-bottom, inner mid-ramp biotopes. Biogeographical comparisons reflect the cosmopolitanism of early Carboniferous brachiopod generic assemblages. Taxonomic comparisons involve selection of lectotypes for *Syringothyris exoleta* North, 1920, *Syringothyris cyrtorhyncha* North, 1920, *Tylothyris laminosa beta* North, 1920, and *Tylothyris laminosa gamma* North, 1920.

**Key words:** Brachiopoda, Carboniferous, Tournaisian, Wales

Lower Carboniferous (Dinantian) rocks crop out extensively across South Wales, mostly as carbonate ramp facies (Wright 1986) that make up a thick succession known traditionally as the Carboniferous Limestone. The limestones form a distinct topographical and structural rim around the northern, eastern and southern flanks of the South Wales coalfield basin (Text-fig. 1), with considerable attentuation and interruption both to the north and the east. For a summary of the distribution and variations in sequences in the region, see George (1974, pp. 89–101), George *et al.* (1976, pp. 17–22, fig. 5) and Wright (1986, 1987). The facies across South Wales extend into the Bristol-Mendips area as part of an originally continuous palaeogeographical province referred to as the South-West Province of the British Isles (George 1954). Throughout this province faunas and algal floras are generally common to abundant through considerable thicknesses of strata. Brachiopods and corals are among the most diverse components of the preserved macrofaunas.

Despite the long history of investigation of the lower Carboniferous in South Wales, extending back well over 150 years and in which numerous invertebrate shelly fossils have been recorded in stratigraphical reports, there have been remarkably few systematic accounts and illustrations of the faunas. For the brachiopods, individual specimens from the area have been used in a limited number of more widespread analyses of generic or higher taxonomic groups, but apart from the summary notes appended to the paper on Gower by Dixon and Vaughan (1911), we know of no other publication that deals with the taxonomy of macrofaunas as a whole for any district in the area.

The reason for this lack of primary taxonomic knowledge is mainly preservational. In the limestones, shell fabrics are generally recrystallised or neomorphosed to varying degrees, often heavily so. As a result they are difficult to extract from resistant beds in a sufficiently complete and detailed state as to permit accurate identification, particularly of internal structures. This problem is compounded in the eastern and north-eastern outcrop areas by the progressively intense effect of dolomitisation (e.g. Bhatt 1976; Hird *et al.* 1987; Waters and Lawrence 1987, p. 24), which commonly obliterates original bedding structures and destroys or severely alters the fossils. Identifications quoted in faunal lists from the region are therefore commonly tentative at best, as are conclusions drawn from them. Sevastopulo and Nudds (1987, p. 39) emphasised the need for 'fresh systematic study to realise [the] biostratigraphical potential' of the brachiopods in these sequences. We have recently begun to try to improve the taxonomic database for the earlier Dinantian (Tournaisian) successions in south-eastern Wales by re-examining existing collections and by identifying those sections from where it might be possible to extract relatively well-preserved populations of brachiopods that do permit detailed study. Increased resolution should improve the utility and potential for biostratigraphical correlation, palaeoecological analysis and assessment of biogeographical



**TEXT-FIG. 1.** Location and summary of stratigraphy at Ty-nant Quarry and the adjacent area. FPL, Friars Point Limestone; BO, Brofiscin Oolite; BHL, Barry Harbour Limestone.

relationships in what is one of the important developments of lower Carboniferous rocks in the British Isles.

This paper describes an exceptionally well-preserved fauna in the dolomite belt immediately to the north of Cardiff in south-east Wales. It is from the large, now disused Ty-nant Quarry cut into the south-east corner of Garth Hill on the west side of the gorge of the River Taff some 500 m directly west of the village church at Tongwynlais (National Grid Reference ST 1272 8210; Text-fig. 1). Almost everywhere throughout this immediate area faunas are mostly obliterated by the dolomitisation (e.g. Bhatt 1976, p. 58), but from one level at Ty-nant material is preserved in fine detail as moulds and casts that allow internal and external morphology to be studied closely and illustrated as a standard for comparision of other faunas in the region. Mould preservation is rare at any level throughout the South Wales lower Carboniferous. The fine preservation and abundance of some taxa allows us to demonstrate a range of morphological variation in certain diagnostic features that has not been appreciated previously. As a result of the increased rigour of taxonomic discrimination it is also possible now to make clearer comparisons with contemporaneous faunas from other parts of Britain and elsewhere, to which some of the South Wales taxa have been assigned in the past, and thus to assess biogeographical relationships more effectively.

## STRATIGRAPHY

The succession at Ty-nant was first discussed by Dixey and Sibly (1918, p. 138), who commented on the well-preserved brachiopod/coral fauna in one band within the dolomites. They correlated the beds with an horizon in $Z_2$ or at the base of $\gamma C_1$ in the zonal system of Vaughan (1905). As a result of Geological Survey mapping, this part of the succession was long referred to lithologically as part of the Main Limestone division of the lower Carboniferous (e.g. Strahan 1909, p. 19; Strahan and Cantrill 1902, p. 22; 1912, p. 21; Squirrell and Downing 1969, fig. 4, pp. 60, 64, 73). The dolomitised limestones overlying the Lower Limestone Shales throughout the whole of the east crop of South Wales were subsequently assigned to a single, Rudry Formation by George *et al.* (1976, pp. 21, 79, fig. 5).

Re-mapping and description of the Cardiff district then demonstrated, however, that the term Rudry Formation is unnecessary here (Waters and Lawrence 1987, p. 25, fig. 8), where the widely recognised Black Rock Limestone Group embraces three formations at the base of the former Main Limestone. All three formations are present in the section at Ty-nant Quarry (Waters and Lawrence 1987, p. 38). Unfortunately, the band of reddish-purple dolomite from which our fauna comes has long since been quarried away, but Dixey and Sibly (1918, p. 138) recorded that it was from the crinoidal dolomites at the top of the quarry, indicating unequivocally that it was within the lower–middle part of the Friars Point Limestone Formation. The lithology and faunal preservation support this lithostratigraphical assignment as there is no trace of either the oolites diagnostic of the underlying Brofiscin Oolite Formation or the silicification common in the Barry Harbour Limestone Formation now exposed at the base of the quarry.

### *Correlation*

The Black Rock Limestone Group is of Courceyan–early Chadian age in the Regional Stage nomenclature of George *et al.* (1976). On a regional basis the lower–middle beds of the Friars Point Limestone span parts of the *Zaphrentites delanouei–Caninophyllum patulum* coral assemblage biozones of Ramsbottom and Mitchell (1980) and are within the *Pseudopolygnathus multistriatus-Polygnathus mehli* conodont zonal interval of Varker and Sevastopulo (1985). These data place the Ty-nant fauna within the mid–upper part of the Tournaisian Series, probably close to the Tn2/Tn3 boundary of Belgian notation (i.e. close to the Hastarian-Ivorian Stage boundary; Conil *et al.* 1977).

## SYSTEMATIC PALAEONTOLOGY

Morphological terminology and systematic classification mainly follow Williams *et al.* (1997–2002), with the exception that classification of the Spiriferida follows Carter *et al.* (1994). Unless noted otherwise, all specimens described and illustrated are housed in the Department of Geology, National Museum of Wales. All dimensions are in millimetres: lv, maximum (sagittal) length of ventral valve; ld, maximum length of dorsal valve; w, maximum width; hw, hinge width; lmv, length of ventral muscle field; lmd, length of dorsal muscle field; est, estimated measurement. Because most specimens are from Ty-nant Quarry (locality details on Text-fig. 1), locality information in plate captions, text-figure captions and running text is given only for specimens that are not from Ty-nant.

### Superfamily STROPHOMENOIDEA King, 1846
### Family RAFINESQUINIDAE Schuchert, 1893
### Subfamily LEPTAENINAE Hall and Clarke, 1893

### Genus LEPTAGONIA M'Coy, 1844

*Type species. Producta analoga* Phillips, 1836; from the lower Carboniferous (probably Pendleside Limestone Group, Viséan) of Bowland [Bolland], Yorkshire, England.

### *Leptagonia* sp.
Plate 1, figures 5, 9

*Material.* One ventral interior, one dorsal interior, two dorsal exteriors.

### *Description*

*Exterior.* Transversely semi-elliptical with maximum width at the straight hinge; cardinal angles weakly subrounded, probably as very short ears although only one poor example is preserved. Lateral and anterior margins smoothly curved. Ventral umbonal area weakly convex, ventral beak low, short, only just projecting posterior to the hinge, dorsal umbo very faintly concave. Ventral and dorsal discs almost flat, dorsal disc with low, broad, rounded, peripheral rim dying out posterolaterally, ventral rim low, sharp, dropping abruptly to anterior margin. Ventral interarea highly apsacline, delthyrium broad, triangular, delthyrial angle about 120 degrees, apparently filled in its posterior half by a weakly concave pseudodeltidium. Notothyrium with slender chilidium folded down centrally between the cardinal process lobes. Ornament poorly preserved but with > 15 low, rounded regularly spaced rugae that extend anteriorly at least just over the dorsal rim and are deflected at cardinal extremities. Rounded costellae apparently present originally.

*Ventral interior.* Ventral muscle field strongly impressed, transversely subdiamond shaped, about 75 per cent as long as wide, raised anteriorly and anterolaterally on a low pseudospondylium with a high, slender rim that merges smoothly posteriorly with the bases of the dental plates. Teeth laterally triangular with posterodorsally directed faces set slightly below the level of the hinge, anterior faces thickly rounded and merge with the stout dental plates that are contiguous with the walls of the deep delthyrial cavity; inner faces of teeth and dental plates weakly grooved below the hinge; denticular cavities deep. Diductor scars large, fan shaped, grooved and striated radially, separated throughout their length by the adductor scars. The adductors occupy a maximum of 25 per cent of the width of the muscle field and are raised on a strong rounded ridge that rises and widens anteriorly from the floor of the delthyrial cavity to overhang the anterior margin of the pseudospondylium. The ridge is bisected longitudinally by a slender myophragm originating posteriorly as a low swollen process. The base of the adductor ridge extends slightly anterior to the pseudospondylium as a rounded buttress onto the floor of the valve. Rugae impressed weakly internally.

*Dorsal interior.* Cardinalia and dorsal muscle field raised on a low, flattened to weakly concave pad. Cardinal process lobes stout, elongated with smoothly rounded attachment faces, divergent at about 120 degrees from one another, merging smoothly distally into the muscle pad. Sockets long, triangulate with weakly concave floor, bounded anteromedially by steep wall of muscle pad which projects slightly ventrally as a slender plate. There is a relatively large alveolus directly anteromedial to the process lobes. Muscle field rounded, divided longitudinally by a shallow furrow; anterolateral margins weakly flabellate, with large scars divided into at least three by low swellings of the muscle pad. Rugae impressed as in ventral valve.

*Remarks.* Dinantian *Leptagonia* from many areas of Britain and more widely throughout the world have commonly been referred to as *L. analoga*, but until recently the true identity of this type species of the genus has remained obscure so that the name has simply been used as a 'blanket' to cover a diverse group of taxa. Dixey and Sibly (1918, p. 137, loc. 5) identified *L. analoga* in contemporaneous strata only a short distance to the west of Ty-nant. Brunton's designation (1968, p. 29, pl. 3, figs 26–27) of a lectotype for *L. analoga*, from the Viséan of Bolland in Yorkshire, and his redescription of the species, together with the further revision of British material by Brand (1972), allows the Ty-nant specimens to be distinguished clearly as a separate taxon, although we consider that the limited material warrants no more than open nomenclature. Externally the two are similar in outline, convexity and number of rugae, but the ventral muscle fields are quite different by comparison with the specimen in Brunton's (1968) plate 3, figure 28 from Redesdale in Northumberland (Phillips 1836, p. 215 reported Redesdale as one of the original localities for *L. analoga*); in our material the ventral muscle field is distinctly transverse and diamond shaped (Pl. 1, figs 8–9), but in the Redesdale Viséan *analoga* it is subcircular and in the absence of evidence to the contrary from a range of material in which to assess possible variation we take this marked difference as being of taxonomic value. The Ty-nant material is similar to Tournaisian specimens from Belgium figured by Demanet (1934, pl. 5, figs 10, 12–13; as *analoga*), which also have a distinctly diamond-shaped ventral muscle platform, as do approximately contemporaneous specimens from as far afield as Australia (Thomas 1971, pl. 18, figs 3, 5); there is almost certainly a spectrum of species involved in these early Dinantian complexes, but they require further study in order to assess their relationships with true *analoga* based on a range of morphological features in addition to the obvious differences in ventral musculature.

### Superfamily CHONETOIDEA Bronn, 1862
### Family RUGOSOCHONETIDAE Muir-Wood, 1962
### Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

### Genus RUGOSOCHONETES Sokolskaya, 1950

*Type species. Orthis hardrensis* Phillips, 1841; from the lower Carboniferous (Dinantian, upper Viséan, Brigantian) of Hardrow [Hardraw], Yorkshire, England.

### *Rugosochonetes vaughani* Muir-Wood, 1962
Plate 1, figures 10–12; Plate 2, figures 1–9

*v.1962 *Rugosochonetes vaughani* Muir-Wood, p. 72, pl. 8, figs 4–6 [see also for synonymy].
1972 *Rugosochonetes vaughani* Muir-Wood; Brand, p. 95, pl. 7 [name only].

*Material.* Two ventral interiors, one dorsal interior.

#### *Description*

Shell small–medium, dorsal valve very weakly concave, ventral valve moderately convex but flattening posterolaterally. Outline transversely subelliptical, hinge straight, cardinal margins obtusely rounded, maximum width close to mid-length. Ventral interarea plane, apsacline. Delthyrium relatively wide, apparently open, apical angle about 35 degrees. No hinge spines observed in the Ty-nant material. Ornament impressed through valves to internal surface preserves very fine, branching capillae over the whole shell with about 20–25 ribs in a 5-mm arc close to the anterior margin.

*Ventral interior.* Teeth tabular in section, rounded distally and flat dorsally, originating under interarea. A low, short, slender median ridge/myophragm abuts against the underside of the interarea and decreases in height anteriorly, occupying only about 20 per cent of the valve length; beyond that point a barely discernible myophragm is traceable in 22.9G.50.1, but is better preserved in 84.13G.34, extending to about 80 per cent of the valve length (cf. Pl. 1, figs 10–11 and Pl. 2, figs 1–2). Low, weakly divergent accessory septa are present to about 70 per cent of the valve

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**EXPLANATION OF PLATE 1**

Figs 1–4. *Rhipidomella michelini* (Léveillé 1835). 1–2, 84.14G.6, ventral internal mould and latex cast; × 3. 3–4, 84.14G.3, ventral internal mould and latex cast; × 2.

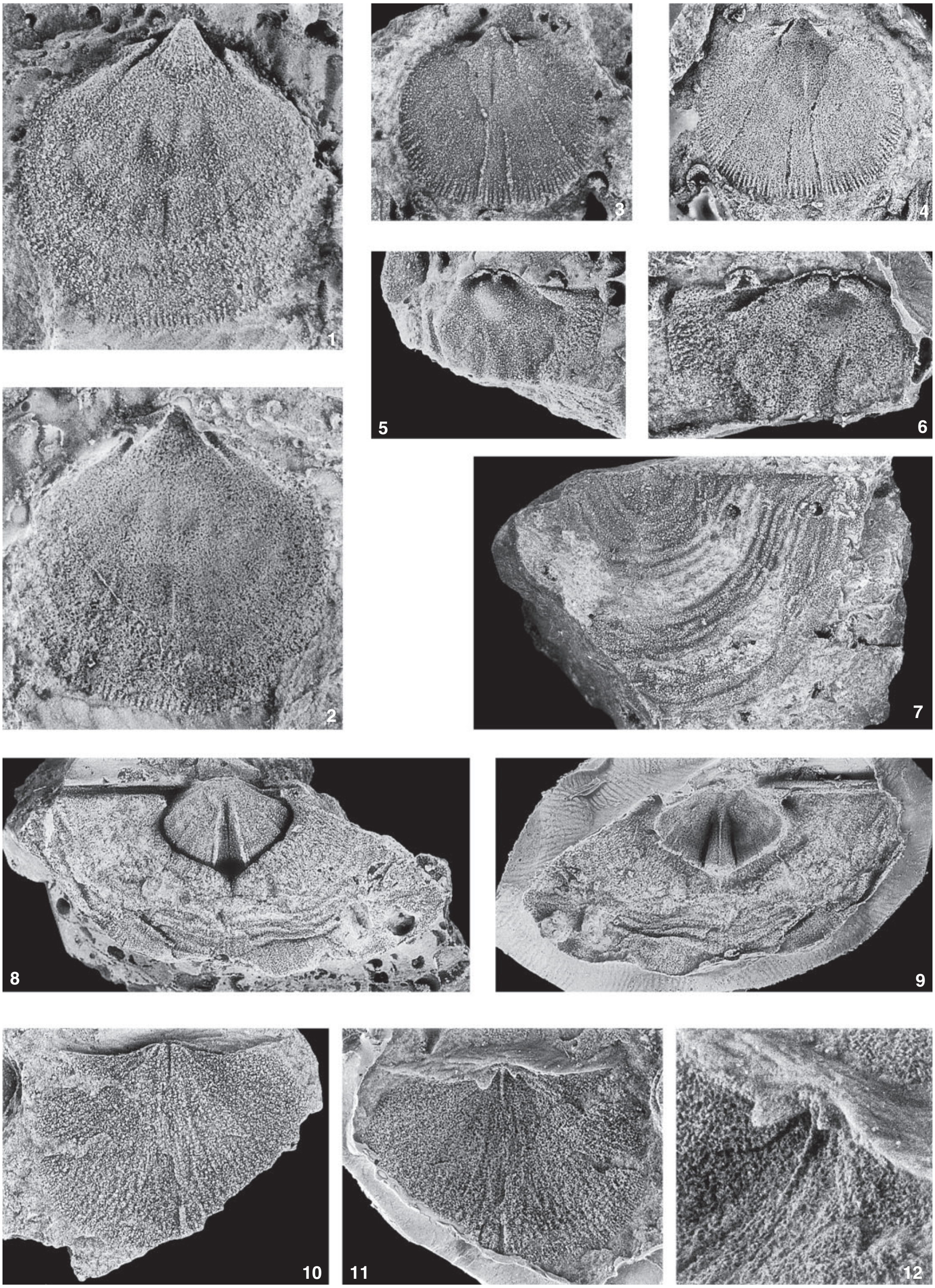
Figs 5–9. *Leptagonia* sp. 5–9, 57.421G60.3, dorsal internal mould, × 2, and latex cast, × 3. 7, 57.421G81.1B, dorsal external mould; × 1·5. 8–9, 84.13G.54, ventral internal mould and latex cast; × 2.

Figs 10–12. *Rugosochonetes vaughani* Muir-Wood, 1962. 22.9G50.1, ventral internal mould and latex cast, × 2; oblique-lateral view of delthyrial cavity and hinge teeth, × 5.

length. Musculature weakly impressed, confined within a shallow, triangulate depression. Internal shell surface weakly papillose.

*Dorsal interior.* The single, poorly preserved dorsal interior has a small but distinct cardinal process pit, shallow elongate sockets and rounded socket ridges divergent at about 150

PLATE 1



BASSETT and BRYANT, Tournaisian brachiopods degrees from one another. Anderidia short and slender, divergent at about 45 degrees from one another. Very faint myophragm present anterior to the process pit. Cardinal process and musculature not preserved. Internal surface papillose as in ventral valve.

*Remarks.* Notwithstanding the sparsity of specimens and detail in our Ty-nant material, there is no reason to doubt that it is conspecific with *R. vaughani* as defined and identified by Muir-Wood (1962, p. 72) from contemporaneous and closely adjacent Tournaisian levels in other areas of South Wales, the Bristol-Mendip district and Ireland. We have compared our material with a very well-preserved set of samples (over 700 specimens; Pl. 2, figs 4–9), including silicified material from the Black Rock Limestone Group of Friars Point at Barry (ST 1075 6644; Waters and Lawrence 1987, pp. 30–34, fig. 12); this fauna is being described separately by CB.

*R. vaughani* is similar to the Viséan type species *R. hardrensis* in general characters of size, outline, convexity and fine capillation (see Muir-Wood 1962, pp. 65–68; Brand 1970, pp. 106–107, pl. 7), but *vaughani* differs in having a lower spine angle (30–40 degrees in Barry populations compared with 45–50 degrees in *hardrensis*), in having less widely divergent and shorter anderidia, more widely divergent socket plates, and a less extended ventral median ridge.

## Subfamily PLICOCHONETINAE Sokolskaya, 1960

### Genus PLICOCHONETES Paeckelmann, 1930

*Type species. Chonetes buchiana* de Koninck, 1843; from the 'lower Carboniferous limestone' (Viséan) at Visé, Belgium.

### *Plicochonetes elegans* (de Koninck, 1847)
Plate 2, figures 10–15

1847 *Chonetes elegans* de Koninck, p. 220, pl. 20, fig. 13*a–e*.

v.1962 *Plicochonetes elegans* (de Koninck) Muir-Wood, p. 82, pl. 15, figs 7–9.

*Material.* One ventral interior.

*Description.* Valve small–medium (l, 10·1; w, 14·6 est), strongly and evenly convex centrally, flattened posterolaterally at the alate extemities. Maximum width at the straight hinge, alae only slightly rounded; outline subtriangulate, lateral margins very weakly concavo-flexed, convergent to smoothly rounded anterior margin. One probable short spine preserved in original orthomorph oblique orientation. Interarea flat, weakly apsacline, delthyrium relatively wide with weakly curved margins and a very small apical plate/pseudodeltidium.

Teeth small, subtriangular, no dental plates. Posterior wall of delthyrial cavity subvertical, slightly swollen as a relatively wide, flattened callist. From the base of the callist a short, relatively stout, tear-shaped, tapering septum extends anteriorly just beyond the level of the teeth, and from the end of the septum a low, rounded, slender but distinct myophragm extends almost to the anterior margin of the valve. Musculature indistinct but seemingly with a pair of slender, lanceolate, tapering diductor scars flanking the myophragm along its posterior third.

Valve interior divided into three distinct, tiered levels. A deep, subcircular hollow occupies the median half of the valve, presumably corresponding closely with the extent of the visceral area; subvertical arcuate walls curve anterolaterally from below the teeth to define this central region. A steep, curved crescentic terrace is then present in the mid width of each half of the valve, extending laterally from the delthyrial margins to the mid point of the hinge and curving anterolaterally to anteriorly. The third level occupies the posterolateral thirds of the valve as shallow triangular hollows forming the alate hinge extremities.

Faint impressions of the external ornament impressed on the internal mould surface indicate a relatively fine costellation.

*Remarks.* Although based only on a single specimen, our identification of *P. elegans* from Ty-nant is supported by comparison with material from elsewhere in the region, including approximately coeval or only slightly younger beds in the Black Rock Limestone Group near Wenvoe to the west of Cardiff (Pl. 2, figs 13–15); in overall features of morphology and convexity the Wenvoe specimens are inseparable, and have at least

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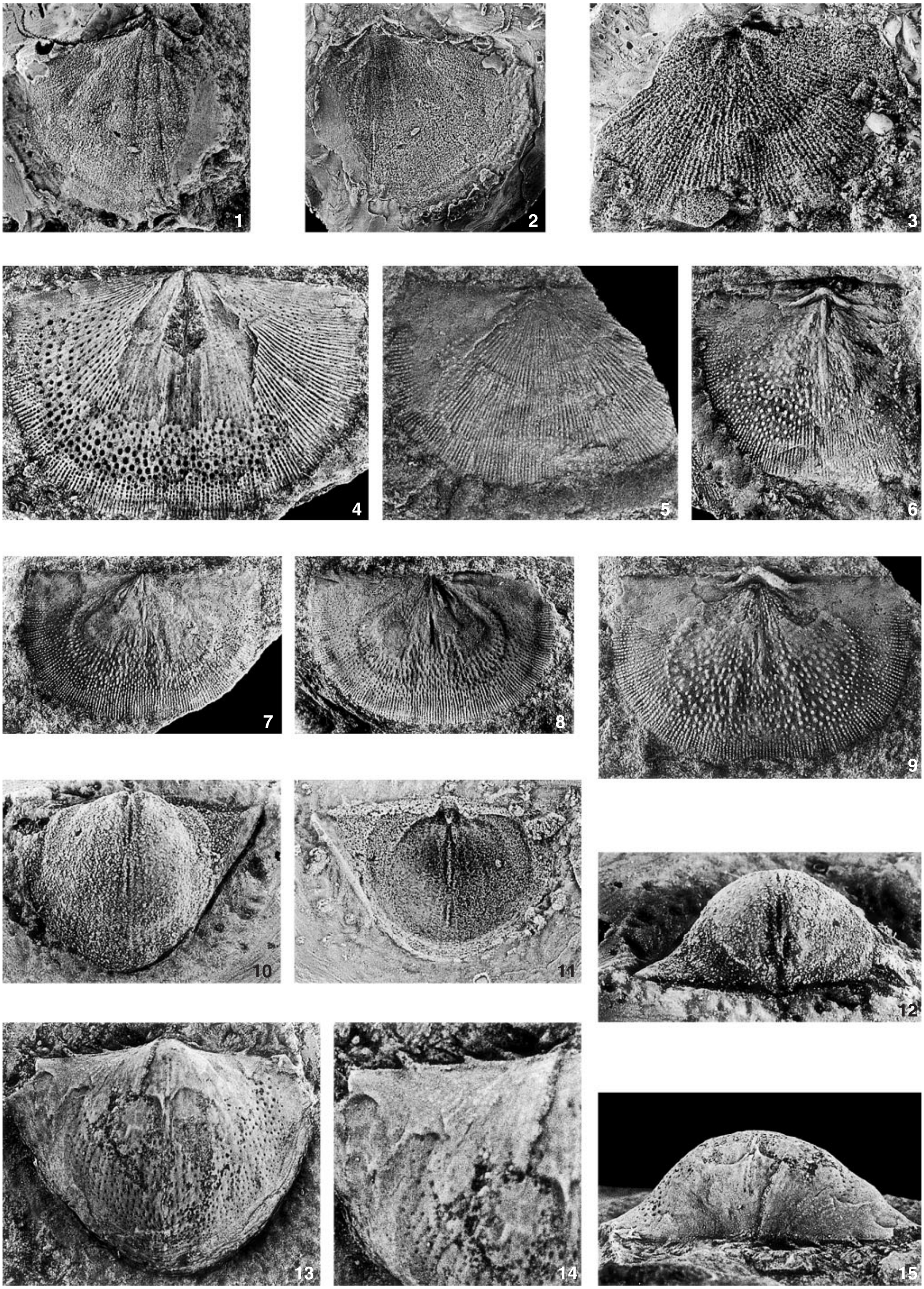
## EXPLANATION OF PLATE 2

Figs 1–9. *Rugosochonetes vaughani* Muir-Wood, 1962. 1–2, 84.13G.34, ventral internal mould and latex cast; × 1·5. 3, 84.13G.5, latex cast of dorsal interior; × 4. 4, 90.48G.1, ventral exterior with hinge spines on exfoliated shell medianly; × 3. 5, 90.48G.2, dorsal exterior; × 3. 6, 90.48G.3, dorsal interior; × 3. 7–8, 90.48G.4a-b, ventral interior and counterpart impression; × 2. 9, 90.48G.5, dorsal interior; × 3. 5–9 are from the Black Rock Limestone Group at Friars Point, Barry.

Figs 10–15. *Plicochonetes elegans* (de Koninck, 1847). 10–12, 19.205GR.1, ventral internal mould, latex cast and posterior view of mould; × 3. 13–15, 20.362.G58, ventral exterior, × 3; detail of spines, × 5; and posterior view, × 3, Black Rock Limestone Group, probably Friar's Point Limestone, Alp's Quarry, Wenvoe, South Glamorgan (ST 129 742).

four short hinge spines present on either wide of the umbo. As in the type material of *P. elegans* (de Koninck 1847, pl. 20) from the Tournaisian of Belgium, and material figured by Muir-Wood (1962, pl. 15) from the same region, this species has finer costellation and is somewhat more convex ventrally than the type spe-

PLATE 2



BASSETT and BRYANT, *Plicochonetes*, *Rugosochonetes* cies of the genus *P. buchianus* from Viséan horizons (e.g. Brunton 1968, pl. 9, figs 27–32) and from *P. stoddarti* named by Vaughan (1911, p. 381; see also Muir-Wood 1962, pl. 15, figs 10–11; Davidson 1863, pl. 55, fig. 12) from the Tournaisian of the Bristol district, both of which are coarsely costellate to costate; there is no indication of such coarse ribbing impressed on the internal surface of our material.

### Superfamily PRODUCTOIDEA Gray, 1840
### Family BUXTONIIDAE Muir-Wood and Cooper, 1960
### Subfamily TOLMATCHOFFIINAE Sarycheva, *in* Sarycheva *et al.* 1963

### Genus MARGINATIA Muir-Wood and Cooper, 1960

*Type species. Productus fernglenensis* Weller, 1909; from the lower Carboniferous [Fern Glen Formation, Mississippian Osagean (Tournaisian–Viséan)] of Fern Glen, St. Louis County, Missouri, USA.

### *Marginatia* sp.
### Plate 5, figures 4–7

*Material.* One ventral interior.

*Description.* The outline of the visceral disc is not preserved fully, but it appears to have been originally slightly transverse, with weakly rounded lateral and anterior margins, about 85 per cent as long as wide. Disc convex, somewhat swollen at the smooth umbo, with the low, bluntly rounded beak extending posterior to the cardinal margin. Convexity decreases on the disc laterally and anteriorly, with the posterolateral areas becoming very weakly concave. Cardinal margin straight, ears small, rounded. No sulcus present. The valve is sharply geniculate, probably originally through about 140–150 degrees (now slightly crushed and sheared). Trail relatively long, preserved length some 140 per cent that of the disc, probably with subparallel margins.

Sculpture reticulate on the disc; costellae low, rounded, equally spaced, increasing by intercalation and bifurcation. Close to 20 ribs present in a 10-mm arc at the 15-mm growth stage. Rugae slightly more prominent than costellae, becoming stronger in the anterior half of the disc. Low nodes present at the intersection of costellae and rugae. Trail costellate only, with subparallel ribs subequally spaced throughout and similar in strength and amplitude to those at the periphery of the disc. There is no apparent increase in costellae on the trail. Coarse spine bases preserved on trail, scattered randomly (Pl. 5, fig. 7); disc apparently without spines except possibly for a few disposed posterolaterally close to the hinge (Pl. 5, fig. 6); nodose intersections of costellae and rugae were possibly also originally spinose.

Musculature not preserved on the mould. Short, widely divergent dental plates are present.

*Discussion.* The adoption of a scheme involving tribes in productide classification (Brunton *et al.* 1995 and in Williams *et al.* 2000) conveys to us no advantage in elucidating evolutionary relationships; in any case, the hierarchical position of *Marginatia* is not affected whether in a subfamily/tribe structure or an equally weighted family/subfamily system, so for the sake of uniformity in this paper we follow the discrimination of the tolmatchoffiine and buxtoniine buxtoniids at the subfamily level as set out, for example, by Lazarev (1990, pp. 107–108).

Although present only as a single, moderately preserved ventral mould, we see no reason to doubt the assignment of our Ty-nant specimen to *Marginatia*. The absence of costellae on the umbo, the restriction of rugae to the visceral disc, sparsity of spines on the disc and random occurrence on the trail are all characteristic features of early members of the genus. The superficially similar *Antiquatonia* generally has stronger ribbing and reticulation and has distinctive rows of spines on a ridge up the ventral flanks and along the hinge (Muir-Wood and Cooper 1960, p. 263). The general external morphology of *Tolmatchoffia* Frederiks, 1933 is also similar to *Marginatia*, but the type species *T. robusta* (Tolmatchoff, 1924) from the Tournaisian of the Kuznetsk Basin, Russia, differs most notably in having well-developed costellation present already from the protegular nodes (e.g. Sarycheva *et al.* 1963, pls 21–22).

Muir-Wood and Cooper (1960) apparently overlooked Muir-Wood's (1928, p. 65) species '*Productus*' *vaughani* in their major review of all then-known productid taxa, but we agree with Sarycheva *et al.* (1963, pp. 188, 193) and Roberts (1971, p. 122) that it belongs in *Marginatia*; the type material is from Tournaisian beds in the Bristol district, which are only very slightly older than the Ty-nant horizon, and is closer to our specimen in overall morphology than any other known species, including the distinctive sparse array of spines on the ventral postero-

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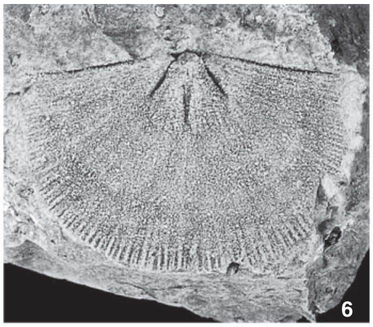
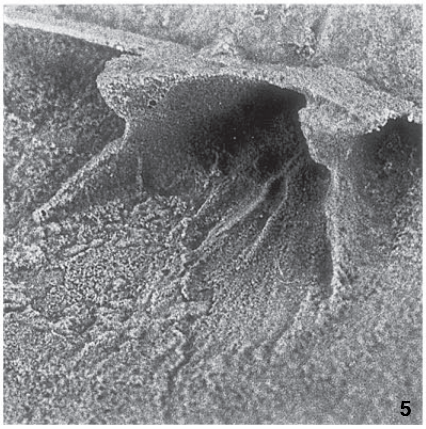
## EXPLANATION OF PLATE 3

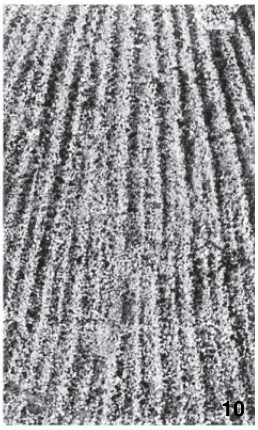
Figs 1–12. *Schellwienella cheuma* sp. nov. 1–5, holotype, 84.14G.2, ventral internal mould, × 1; details of musculature, × 3; and details of latex cast of muscle field and dental plate system, × 3. 6–7, 84.13G.4, ventral internal mould, × 1·5; latex cast of muscle field, × 4. 8–10, 22.9G52.2, ventral external mould and latex cast, × 1·5; detail of median ornament from latex cast, × 5. 11–12, 22.9G52.1, ventral internal mould and latex cast; × 1.

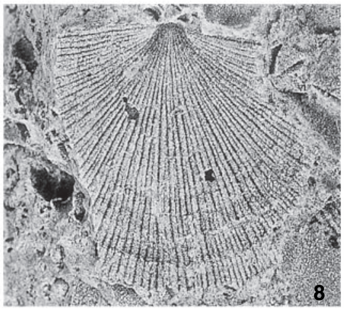
lateral flanks. However, according to Muir-Wood (1928, p. 66) the costellae in *vaughani* increase by bifurcation and intercalation over the whole shell, whereas there is no rib increase on the trail of our specimen (Pl. 5, fig. 7); should future finds from the Tournaisian in the vicinity of Ty-nant suggest that this is a variable feature, then it is

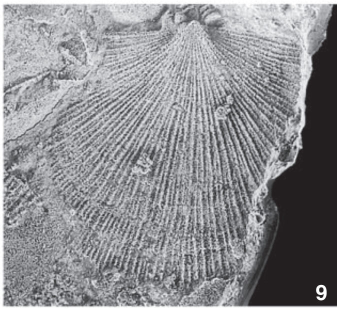
PLATE 3

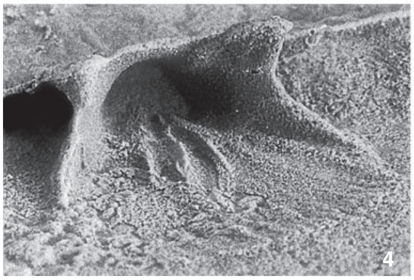


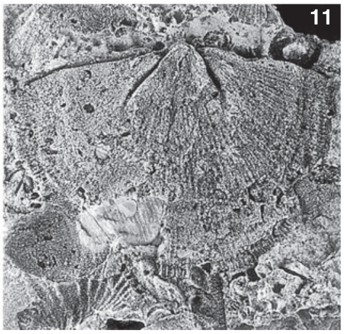












BASSETT and BRYANT, *Schellwienella*

most probable that the specimen described here belongs to *M. vaughani*.

Otherwise, there are also close similarities with other approximately contemporaneous species such as *M. deruptoides* Sarycheva from the Kuznetsk Basin, Siberia, and *M. mimica* Roberts from the Bonaparte Gulf Basin of north-western Australia; a discussion of comparisons within this group is given by Roberts (1971, p. 122). A group of North American taxa centred around the type species *M. fernglenensis* (Weller) and *M. burlingtonensis* (Hall) typically has somewhat coarser ornament and a variably developed ventral sulcus (e.g. see Weller 1909, 1914; Carter 1987). We can confirm the wider presence of *Marginatia* in South Wales, where specimens from Hastarian beds at Freshwater West, Pembrokeshire (Pl. 5, figs 8–12) have ornament and sulcation more reminiscent of the *burlingtonensis* group than our *Marginatia* sp. Note that the Freshwater species has sparse, coarse spines along the ventral hinge margin (Pl. 5, figs 11–12), a feature that the preservation does not allow us to confirm in the Ty-nant specimen, although from the comparative discussion by Roberts (1971, p. 122) this would appear to be a variable character in *Marginatia*.

### Superfamily ORTHOTETOIDEA Waagen, 1884

*Discussion.* Our fauna includes two genera assigned here to this superfamily: *Schellwienella* and *Schuchertella*. Because we regard the Pulsiidae and Schuchertellidae as objective synonyms (see discussion below), we do not follow here the family groupings of Williams and Brunton (in Williams *et al.* 2000) in classification of the Orthotetoidea; in our view the relationships require further investigation.

Williams (in Williams *et al.* 1965, p. 404; also in Williams *et al.* 2000, p. 644) discussed the confused and unsatisfactory classification of these and related strophomenide genera, and they were included in the 1965 'Treatise' within a superfamily Davidsoniacea. Most subsequent authors then followed this superfamilial nomenclature until Copper (1978, p. 306) suggested that the nominate genus *Davidsonia* is an atrypide. This view was challenged by Johnson (1982), who concluded instead that *Davidsonia* is a strophomenide, but sufficiently different to warrant isolation in a monogeneric Davidsoniacea. Meanwhile, Cooper and Grant (1974, pp. 255–257) recognised three superfamilies within this group of strophomenides: Davidsoniacea, Orthotetacea and Derbyiacea (their Davidsoniacea is essentially the impunctate group renamed as Fardeniacea by Johnson). Both *Schuchertella* and *Schellwienella* fall within the Orthotetacea as restricted by Cooper and Grant, and we agree that features of the cardinalia justify separation of this superfamily from the Derbyiacea. In a later paper, Cooper and Dutro (1982) reverted to including *Schuchertella* again in the Davidsonacea without comment. Williams and Brunton (1993) then clarified relationships within this group via a study of shell structure and we adopt their suprageneric classification here (also Williams and Brunton in Williams *et al.* 2000), with the exception that we continue to recognise the Pulsiinae at the subfamily level within the schuchertellids rather than as a separate family.

### Family SCHUCHERTELLIDAE Willams, 1953
### Subfamily PULSIINAE Cooper and Grant, 1974
### [= SCHELLWIENELLINAE McIntosh, 1974]

*Remarks.* Cooper and Grant (1974, pp. 256, 260) defined their new subfamily Pulsiinae for schuchertellids with dental plates, embracing two genera, *Schellwienella* and *Pulsia*. In the same year, McIntosh (1974, p. 204) also proposed a new subfamily Schellwienellinae to include *Schellwienella*, *Pulsia* and *Orthotetella*; she also used the presence of dental plates as one of her diagnostic characters. The two suprageneric group names are thus essentially objective synonyms, and we here use the Pulsiinae within the Schuchertellidae as it has priority. Cooper and Grant's monograph was published on 16 April 1974 (*Smithsonian Year* 1974, p. 333], whilst McIntosh's paper did not appear until part 3 of the *Scottish Journal of Geology* for 1974, dated 18 October. We follow Williams and Brunton (in Williams *et al.* 2000) in excluding the Permian genus *Orthotetella* from the Pulsiinae, since we regard its features of the

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**EXPLANATION OF PLATE 4**

Figs 1–7. *Schellwienella cheuma* sp. nov. 1–3, 84.15G.1, dorsal external mould and latex cast, × 1·5; detail of ornament from latex cast; × 5. 4–7, 84.13G.17, dorsal internal mould, × 1·5; with latex cast of cardinalia showing normal, oblique-anterior, and posterior views, × 5.

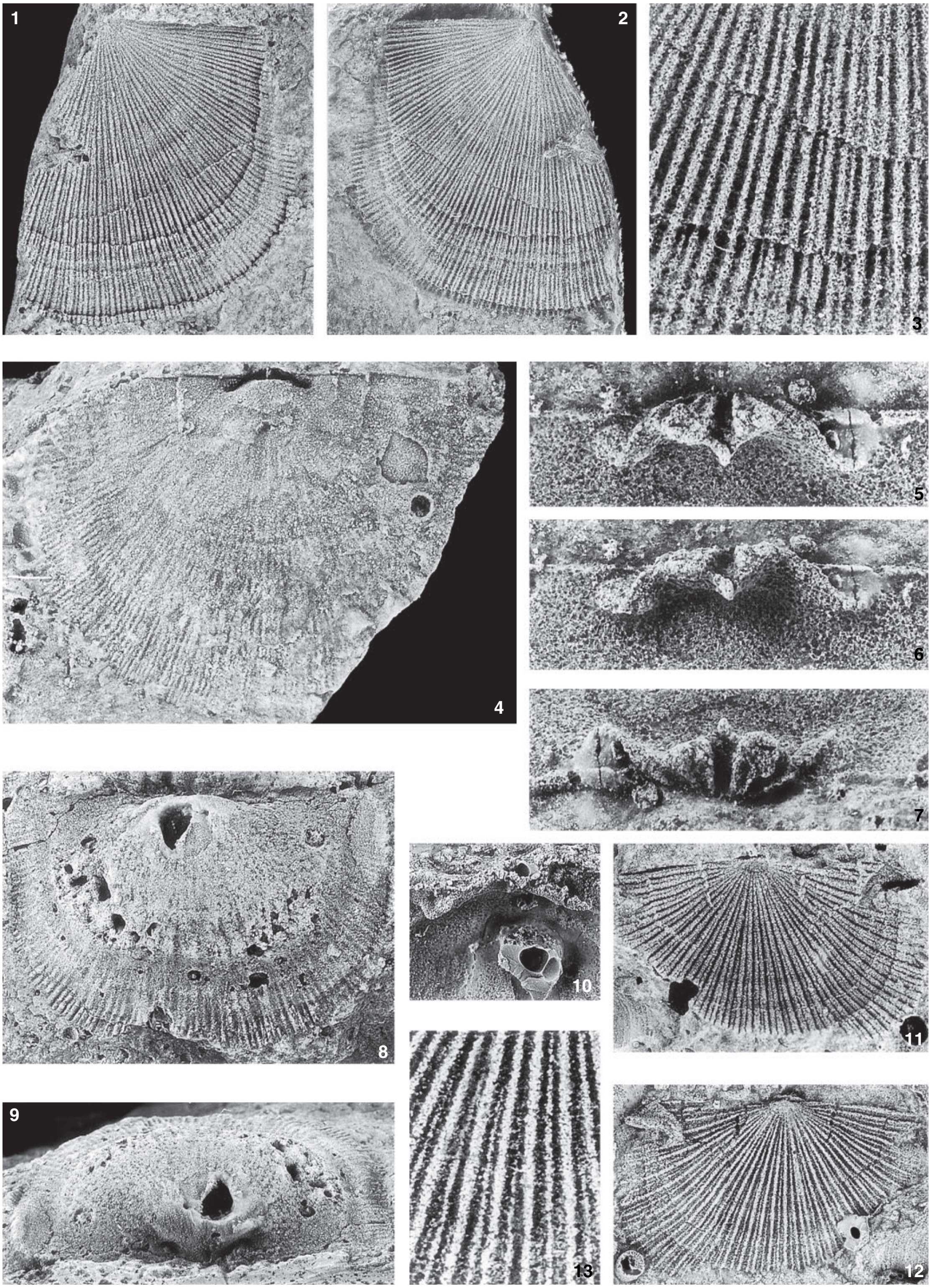
Figs 8–13. *Schuchertella subcrona* sp. nov. 8–10, 84.13G.16, dorsal internal mould and posterior view, × 1·5; with latex cast of cardinalia, × 3. 11–13, 84.13G.37, dorsal external mould and latex cast, × 2; detail of ornament from latex cast, × 5.

cardinalia to be sufficiently different to warrant familial separation as detailed by Cooper and Grant (1974, pp. 256, 285).

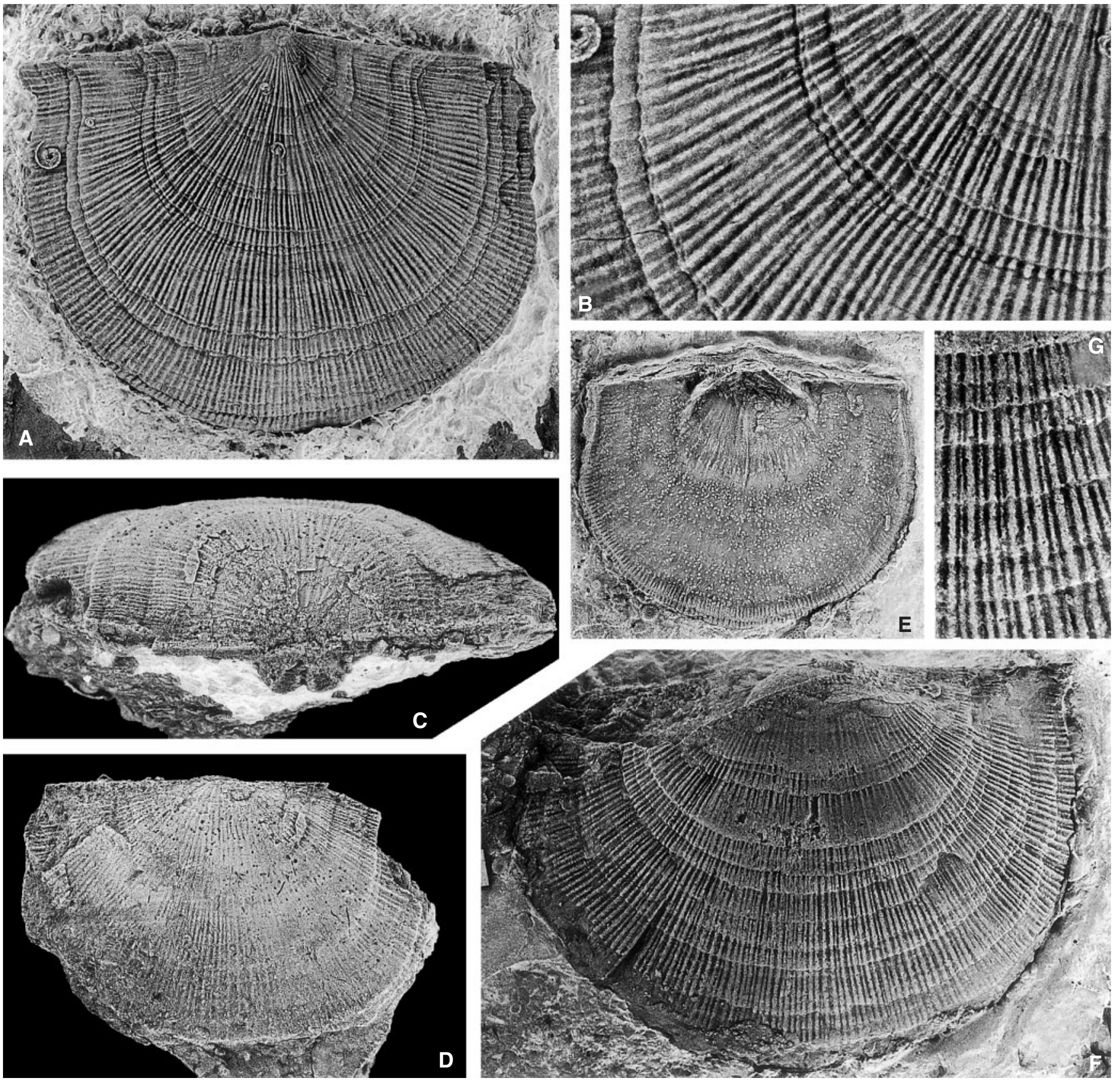
### Genus SCHELLWIENELLA Thomas, 1910

*Type species. Spirifera crenistria* Phillips, 1836; from the lower

PLATE 4



BASSETT and BRYANT, *Schellwienella*, *Schuchertella*



**TEXT-FIG. 2.** *Schellwienella aspis* Smyth, 1930. A–B, holotype, Trinity College Dublin T191/1086, ventral exterior, × 1·5, and detail of ornament, × 3·5. C–D, syntype, Trinity College Dublin F194/1086, dorsal posterior view of cardinal process, × 2, and normal view of dorsal valve, × 1·5. E, syntype, Trinity College Dublin F193/1086, ventral interior, × 1·5. F–G, syntype, Trinity College Dublin F192/1086, dorsal exterior, × 1·5, and detail of ornament, × 3. Carboniferous, Courceyan, all from Hook Head, County Wexford, Eire.

Carboniferous (Pendleside Limestone Group, Viséan) of Bowland [Bolland], Yorkshire, England.

### *Schellwienella cheuma* sp. nov.
### Plate 3; Plate 4, figures 1–7

v.1918 *Schellwienella* cf. *crenistria* [Phillips]; Dixey and Sibly, p. 138 *pars*.

*Derivation of name.* Greek, *cheuma*, a stream, referring to the type locality at Ty-nant, which is the Welsh for 'house by the stream'.

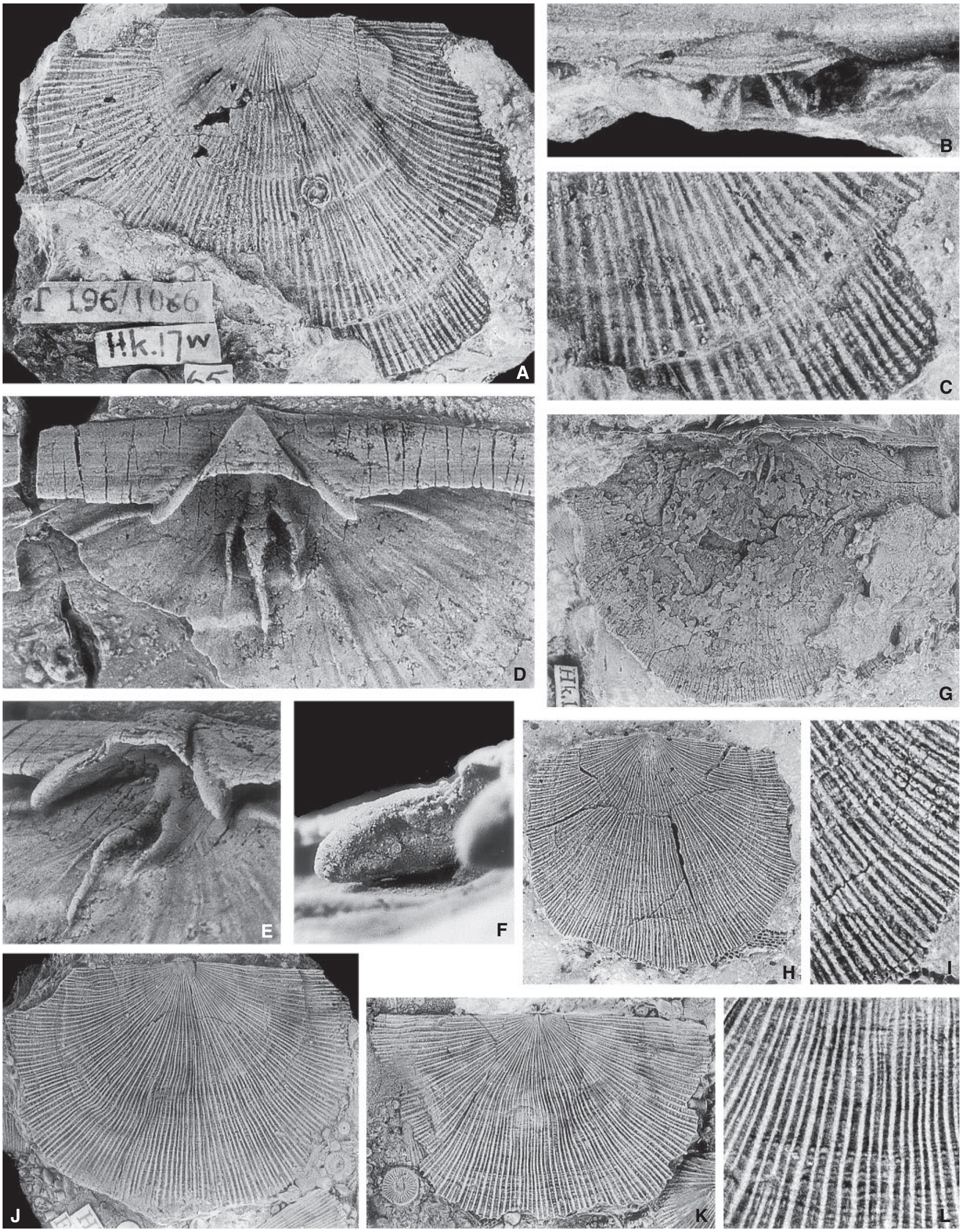
*Holotype.* Ventral valve interior, 84.14G.2; Pl. 3, figs 1–5.

*Paratypes.* Two ventral interiors (84.13G.4; 22.9G.52.1), one dorsal interior (84.13G.17), two ventral exteriors (22.9G.52.2; 84.15G.1).

*Diagnosis.* Ventral muscle field triangular, dental plates long. Deltidium large, almost flat. Notothyrial platform downfolded between process lobes. Multicostellate.

### *Description*

*Exterior.* Shells initially transversely semicircular, becoming subcircular to subquadrate at maturity, maximum length up to about 80–85 per cent of maximum width. Cardinal margin straight to weakly triangulate, lateral margins straight or weakly flexed, anterolateral and anterior margins smoothly



**TEXT-FIG. 3.** *Brochocarina wexfordensis* (Smyth, 1930). A–C, holotype, Trinity College Dublin T196/1086, dorsal exterior, × 1·5, posterior view, × 5, and detail of ornament, × 3. D–F, syntype, Trinity College Dublin F199/1086, ventral interior with detail of hinge area structures and musculature, normal and oblique-anterior views, × 3; note the unsupported teeth in F, × 10. G, syntype Trinity College Dublin F198/1086, ventral interior, × 1. H–I, syntype, Trinity College Dublin F197/1086, ventral exterior, × 1, and detail of ornament, × 3. J, syntype, Trinity College Dublin F200/1086, dorsal exterior, × 1. K–L, syntype, Trinity College Dublin F200/1086, dorsal exterior, × 1, and detail of ornament, × 3. Carboniferous, Courceyan, all from Hook Head, County Wexford, Eire.

curved. Maximum width close to mid length. Dorsal valve moderately and evenly convex; ventral valve resupinate, weakly convex at umbo, flattening laterally and anteriorly to become flat or weakly concave. Umbones low, ventral beak projected only minimally beyond the hinge. Ventral interarea large, plane, apsacline. Delthyrium sealed completely by a large, triangular, very weakly convex deltidium. Chilidium small, apparently leaving the notothyrium open anteriorly to expose the attachment faces of the cardinal process lobes.

Shell sculpture multicostellate, fine, with 23–25 equally spaced, rounded costellae in a 10-mm arc at the 10-mm growth stage. There is almost no size differentiation between different orders of costellae. Faint, lamellose fila are present.

*Ventral interior.* Delthyrial cavity large, deep. Teeth large with elongated-triangular, flat dorsal faces, supported to their mid length by upright dental plates (Pl. 3, figs 4–5), which extend anterolaterally to mid length of the muscle field. Denticular cavities deep and cut well back under the interarea and proximal parts of the teeth. Throughout its width the interarea projects well forward over the cardinal margin.

Muscle field large, triangulate with straight to slightly flexed lateral margins and weakly rounded posterior margin, unbounded by ridges in its anterior half; the scars occupy almost 33 per cent of the valve width and up to almost 50 per cent of the length. Diductor scars large, triangular, completely surrounding the adductor scars and scored with low attachment ridges around the anterior periphery. Adductor scars lanceolate, confined at maturity almost entirely within the posterior half of the muscle field and extending anteriorly only just beyond the limit of the dental plate extensions; adductors bounded laterally by slender, weakly curved ridges and at maturity there is also a slender, median longitudinal ridge to produce a distinctive trifid ridge system as in the holotype (Pl. 3, figs 2–5); these ridges fuse anteriorly as a low platform forming the anterior extremity of the adductor field, although there is a faint trace of the extension of the median ridge beyond the platform to bisect the diductor scars anteromedially.

*Dorsal interior.* Socket plates very weakly curved (Pl. 4, figs 5–7), divergent at about 130 degrees from one another, fused medially with cardinal process lobes. Notothyrial cavity deep, excavated below the cardinal process and with vertical walls laterally below the socket plates. Sockets large, shallow, flat floored, triangular, merging smoothly into the valve floor laterally. Notothyrial platform broad. Cardinal process bilobed with a medially grooved attachment face to each lobe. The lobes are stout, triangular, with faces directed posteroventrally; they are separated medially by a deep, wide groove whose floor is downfolded strongly into the notothyrial cavity (Pl. 4, fig. 6).

Musculature unclear but probably confined within a faint depression extending only just beyond the anterior limits of the socket plates.

*Remarks.* This species incorporates some of the material identified by Dixey and Sibly (1918) as *Schellwienella* cf. *crenistria* (see synonymy). Other material has been identified commonly as *crenistria* from many areas in the lower Carboniferous of Britain elsewhere, but although it is the type of the genus it remains very poorly known. Thomas (1910, pp. 103, 126) pointed out that the name has been used very loosely and that various genera are probably involved, and these comments still hold true. From comparison with Phillips's original illustration (1836, pl. 9, fig. 6) we judge that *S. crenistria s.s.*, of Viséan age, differs from *S. cheuma* in having a strongly convex deltidium, a more strongly convex dorsal valve, more rounded shell margins and coarser, more widely spaced radial sculpture. Details of the interior of *S. crenistria s.s.* remain obscure and await confirmation based on re-investigation of topotype material. Externally, *S. cheuma* compares most closely with *Schellwienella aspis* (Smyth, 1930) from approximately contemporaneous rocks of Hook Head, Co. Wexford, Ireland (Smyth 1930, p. 553, pl. 15, figs 1–4; Text-fig. 2 herein), especially in general outline, convexity and multicostellate ribbing. Some specimens in the type lot of *S. aspis*, including the holotype (Text-fig. 2A), have distinctly alate cardinal extremities, which are not present in *S. cheuma*, but it is possible that such features are variable within a population and of limited taxonomic value. The convex deltidium of *aspis* contrasts with the almost flat structure in *cheuma*. Internally the two species are markedly different in the configuration of the ventral muscle field, which is subrounded in *aspis* (Text-fig. 2E) and distinctly triangular in *cheuma* (Pl. 3, figs 1–7). The Ty-nant species also has more slender, less widely divergent, upright dental plates, that support

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## EXPLANATION OF PLATE 5

Figs 1–3. *Schuchertella subcrona* sp. nov. 1–2, 84.13G.47, ventral internal mould, × 1·5; and detail of muscle area, × 3. 3, 30.260G16, ventral internal mould; × 1.

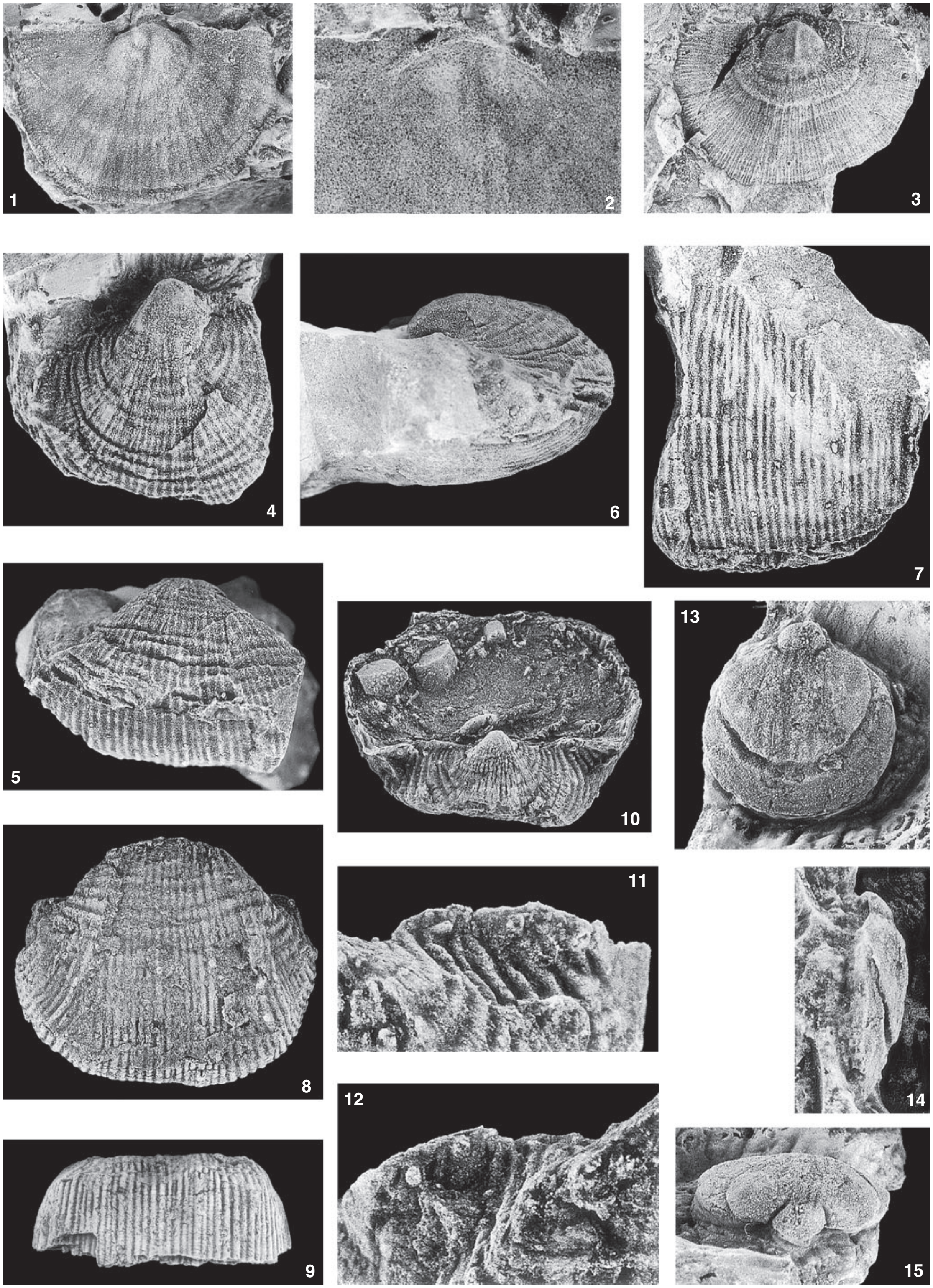
Figs 4–7. *Marginatia* sp. 84.13G.53, ventral internal mould in normal, oblique lateral and anterior views; × 2.

Figs 8–12. *Marginatia* cf. *burlingtonensis* Hall, 1858. 45.288G27.3, ventral exterior, × 1·75; anterior, × 1·5; posterior, × 1.75 and detail of spines on right and left of hinge line, × 5. Carboniferous, Courceyan, Freshwater West, Pembrokeshire.

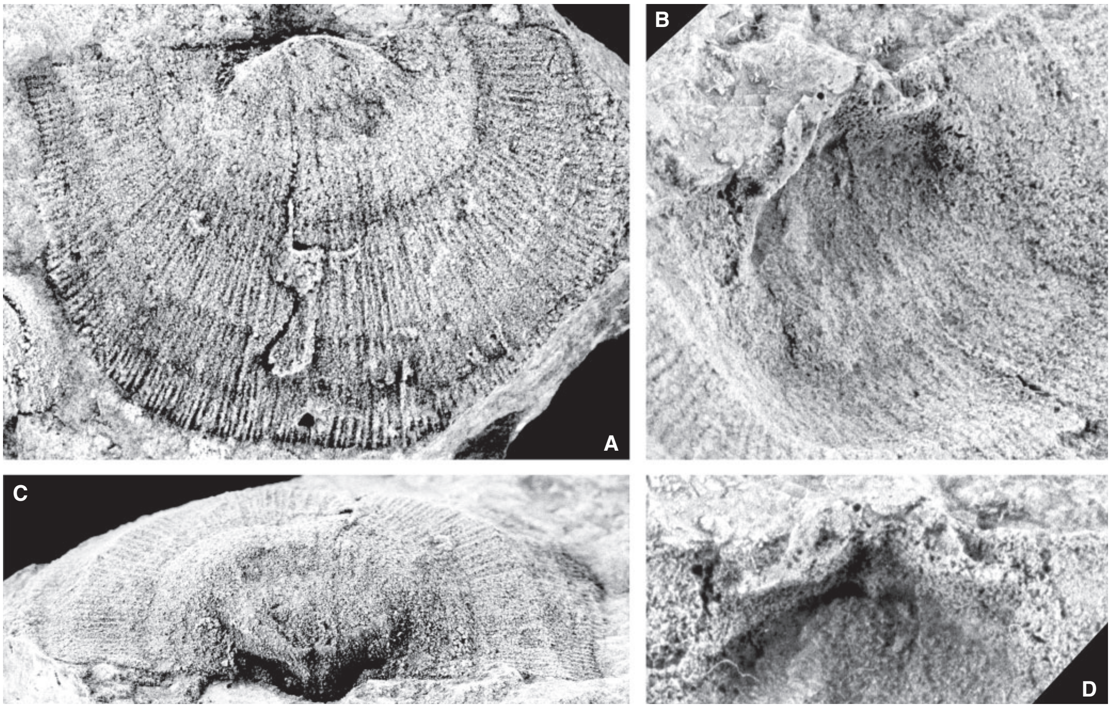
Figs 13–15. *Composita ptygmation* sp. nov. 84.13G.15A, ventral internal mould showing normal, lateral and posterior views; × 2.

more clearly differentiated teeth than in *aspis* (Pl. 3, figs 4–5). The three ridges characteristic of the ventral adductor field in *S. cheuma* are not present in *aspis*, where there is instead a single, slender, rounded myophragm extending anteriorly to the margin of the diductor scars (Text-fig. 2E).

PLATE 5



BASSETT and BRYANT, Tournaisian brachiopods



**TEXT-FIG. 4.** *Schuchertella subcrona* sp. nov. Holotype, 78.20GR3982, dorsal internal mould in dorsal and posterior views, × 1·5, with enlarged detail, × 2, of the structure of the cardinalia.

Note that the trifid ventral ridges of *S. cheuma* are very similar to those recorded originally as a diagnostic character of the genus *Brochocharina* Brunton, 1968, now assigned to the family *Orthotetidae* (in Williams *et al.* 2000, p. 652); this character is clearly more widespread within the Orthotetoidae. *Brochocharina* is distinguished from *Schellwienella* especially in lacking dental plates, with the teeth extended as long dental ridges which are unsupported anteriorly above the floor of the valve (cf. Pl. 3, figs 1, 4 and Text-fig. 3E–F).

### Subfamily SCHUCHERTELLINAE Williams, 1953

### Genus SCHUCHERTELLA Girty, 1904

*Type species. Streptorhynchus lens* White, 1862; from the uppermost Devonian (Louisiansa Limestone, Famennian) of Burlington (Iowa), Clarkesville (Missouri) and Hamburg (Illinois), USA.

### *Schuchertella subcrona* sp. nov.

Plate 4, figures 8–13; Plate 5, figures 1–2; Text-fig. 4

*Derivation of name.* From the Welsh word *cron*, referring to the subrounded outline of the relatively large muscle fields.

*Holotype.* Dorsal internal mould, 78.20GR3982; Text-figure 4.

*Paratypes.* Two ventral internal moulds: 84.13G.47, 30.260G16; Plate 5, figures 1–3.

*Diagnosis.* Dorsal muscle field relatively large, confined in a distinct subrounded concave hollow. Socket plates robust, weakly curved.

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**EXPLANATION OF PLATE 6**

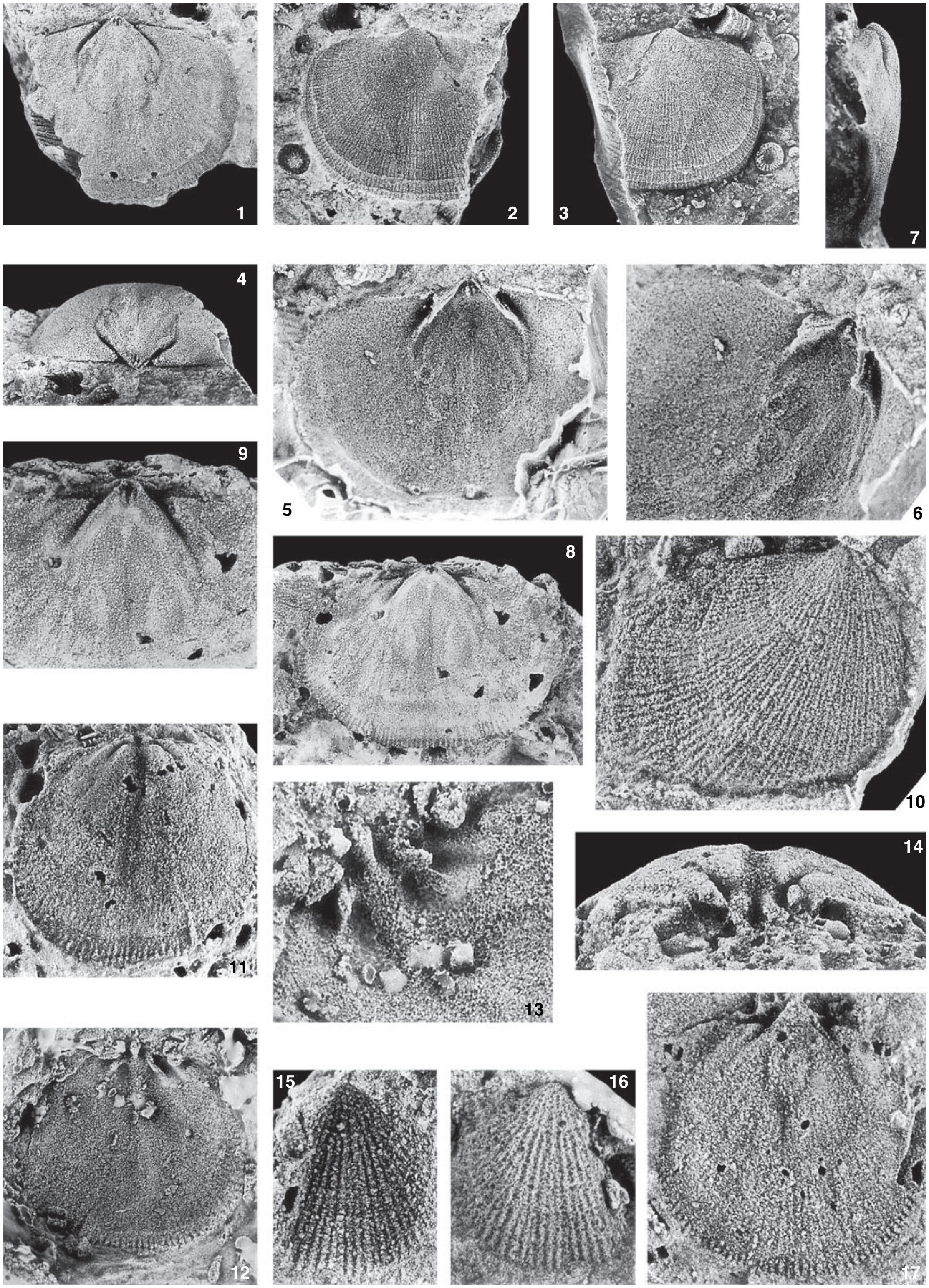
Figs 1–10. *Schizophoria resupinata* (Martin, 1809). 1–6, 84.13G.40A,B, dorsal internal and external moulds, × 2; external latex cast, × 2; posterior view of mould, × 2; latex cast of mould, × 3; and oblique-lateral view of cast, × 4. 7, 57.421G60.2, lateral view of ventral internal mould; × 2. 8–9, 84.13G.29, dorsal internal mould, × 2; and detail of posterior, × 3. 10, 84.13G.33, latex cast of ventral exterior; × 4.

Figs 11–17. *Rhipidomella michelini* (Léveillé, 1835). 11–14, 57.421G60.1, dorsal internal mould and latex cast, × 3; oblique-lateral detail of cardinalia and posterior view of mould, × 5. 15–16, 84.13G.47, ventral external mould and latex cast; × 5. 17, 84.14G.5, ventral internal mould; × 3.

### Description

*Exterior*. Transversely oblong to semicircular, maximum length about 70–74 per cent maximum width, cardinal margin straight with tiny alae in earlier growth stages but cardinal angles becoming obtusely rounded at maturity, lateral and anterior margins gently and smoothly curved; hinge width approximately 95 per cent of maximum width. Deltidium and chili-

PLATE 6



BASSETT and BRYANT, *Rhipidomella, Schizophoria* dium present but obscure on mould material. Subequally biconvex to dorsibiconvex, curvature smooth or with both valves somewhat inflated initially and then flattened out to form a rim from about the mid point of growth. Umbones obscure, beaks low, not projected beyond the hinge. A broad, weak sulcus may be developed anteromedially in the ventral valve.

Shell sculpture subequally parvicostellate, fine, with 22–23 rounded costellae in a 10-mm arc at the 10-mm growth stage. Ribs increase mostly by insertion and are equally spaced throughout growth, separated by slightly wider, flat, relatively deep interspaces. Very fine, slightly lamellose growth fila present across both the costellae and the interspaces, tending to be slightly more prominent on the former to give the shell an imperceptibly scabrous appearance.

*Ventral interior.* Teeth small, elongate-rounded, dental plates lacking but with rudimentary bases merging anterolaterally into short, slender, subrounded, weakly curved ridges that bound the muscle field posteriorly; the ridges diverge anterolaterally from one another at 125–130 degrees. Small, relatively deep, rounded to ovoid denticular cavities present. Delthyrial cavity broad, shallow, with posterior wall rising subvertically to abut against the base of the deltidium.

Muscle field subrounded, occupying 25–30 per cent of the valve width and about 30 per cent of the length, widest in its posterior half at the extremities of the posterolateral bounding plates. A low, narrow, rounded ridge bisects the muscle field longitudinally and becomes obscure before the anterior margin. Diductor scars large, semicircular to suboval, unbounded laterally and anteriorly but defined by confinement in shallow depression in the valve floor. Adductor scars obscure but probably restricted as slender lanceolate impressions adjacent to the median ridge.

*Dorsal interior.* Socket plates weakly curved, well developed, suspended from the cardinal margin well above the valve floor, divergent at about 130 degrees from one another, fused medially with cardinalia and the base of the chilidium, which is downfolded between the process lobes. Sockets relatively large, ovoid.

Notothyrial cavity wide and deep with a subvertical posterior wall. Muscle field large, weakly impressed but within a distinct concave hollow, unbounded by ridges, extending anteriorly for about 25 per cent of valve length. Adductor scars suboval, separated by a broad, flat, low ridge.

*Remarks.* The structure of the cardinalia and the absence of dental plates identify this material as *Schuchertella*. The general morphology does not compare closely with any formally described species, and the distinctive nature of the large, rounded dorsal muscle field suggests that the Ty-nant taxon is a new species. It possibly embraces some of the specimens listed by Dixey and Sibly (1918, p. 138) as *Schellwienella* cf. *crenistria*, although this name fairly certainly also covered mostly what we describe above as *Schellwienella cheuma* sp. nov.

Internally there is some resemblance of *S. subcrona* to *Serratocrista* Brunton, 1968, but the latter is readily identified externally by its distinctive spinose costellation.

### Family RHIPIDOMELLIDAE Schuchert, 1913
### Subfamily RHIPIDOMELLINAE Schuchert, 1913

### Genus RHIPIDOMELLA Oehlert, 1890

*Type species. Terebratula Michelini* Léveillé, 1835; from the lower Carboniferous (Dinantian) of Belgium/northern France [exact horizon and locality uncertain]

### *Rhipidomella michelini* (Léveillé, 1835)
Plate 1, figures 1–4; Plate 6, figures 11–17

1835 *Terebratula Michelini* Léveillé, p. 39, pl. 2, figs 14–17.
v.1918 *Orthis michelini* [(Léveillé)]; Dixey and Sibly, p. 138.
1934 *Rhipidomella michelini* (Léveillé); Demanet, p. 37, pl. 2, figs 1–9 [see also for earlier synonymy].
v.1968 *Rhipidomella michelini* (L'Eveillé) (*sic*); Brunton, p. 17, pl. 3, figs 1–25.

*Material.* Three ventral interiors, one dorsal interior, one dorsal exterior.

*Remarks.* Although the material available from Ty-nant is limited there is no reason to doubt its identity with

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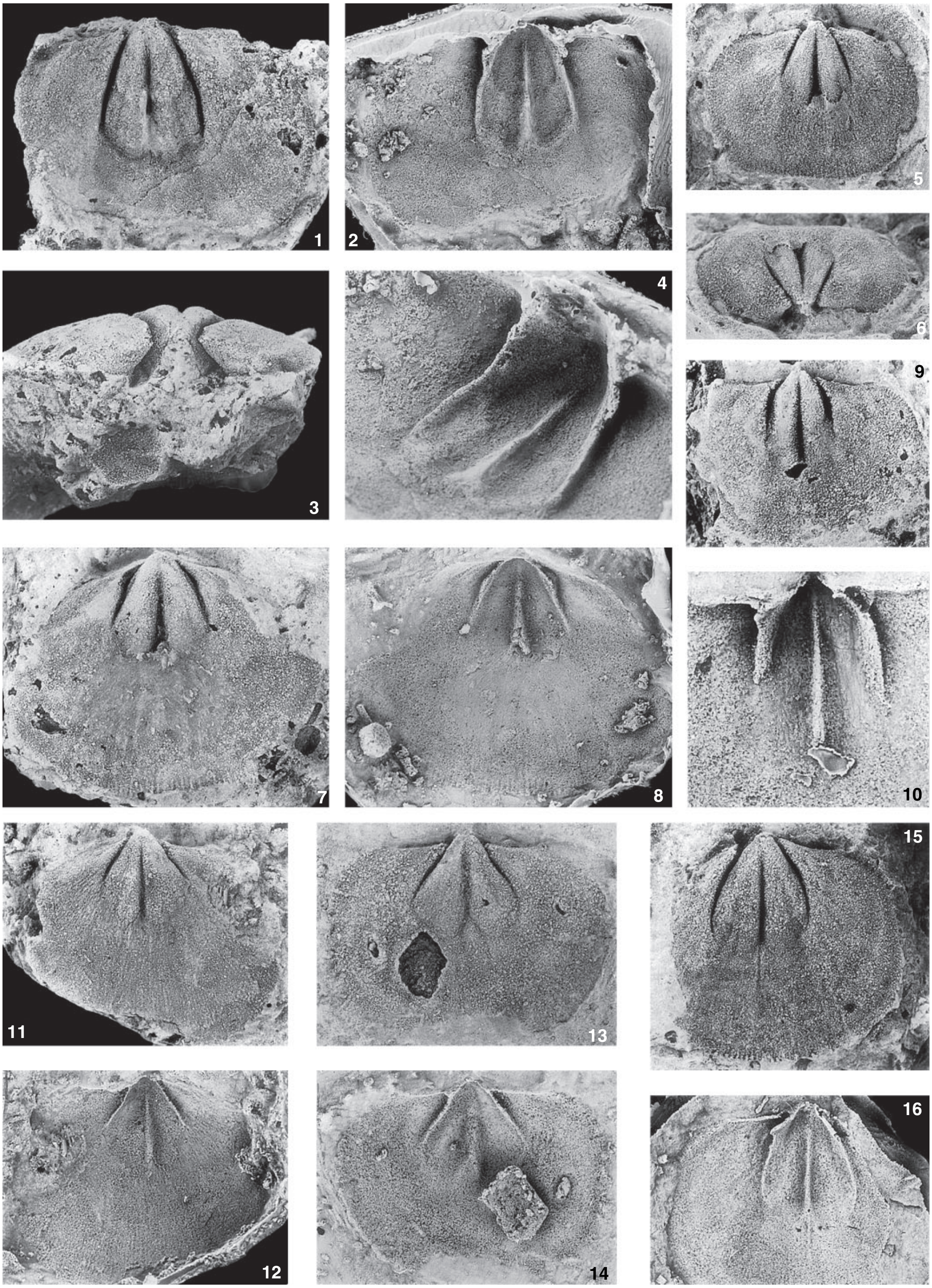
**EXPLANATION OF PLATE 7**

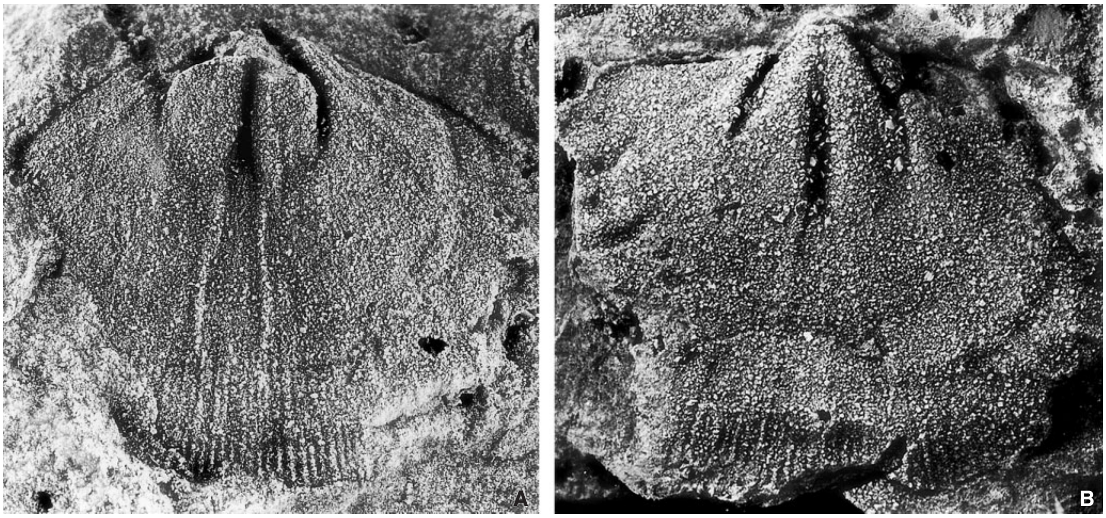
Figs 1–16. *Schizophoria resupinata* (Martin, 1809). 1–4, 84.13G.24, ventral internal mould, latex cast, posterior view of mould, × 2; and oblique view of posterior morphology, × 3. 5–6, 84.13G.41A, ventral internal mould and posterior view; × 2. 7–8, 84.13G.5, ventral internal mould and latex cast; × 2. 9–10, 84.13G.37, ventral internal mould, × 2; and latex cast, × 4. 11–12, 57.421G60.2, ventral internal mould and latex cast; × 2. 13–14, 84.13G.34, ventral internal mould and latex cast; × 2. 15–16, 84.13G.41B, ventral internal mould, × 1·75; and latex cast, × 1·5.

this species, which has been quoted as occurring in the Dinantian over wide areas. Léveillé's (1835) very generalised original illustrations give little clue as to the true identity of the species, but our specimens fit within the variation of material described subsequently by Demanet (1934) from the type area, and also within more recent

PLATE 7



BASSETT and BRYANT, *Schizophoria*



**TEXT-FIG. 5.** *Schizophoria resupinata* (Martin, 1809). Two ventral internal moulds displaying fine preservation of the *vascula media*. A, 30.260G16; B, 84.13G.19; both × 4.

descriptions such as that by Brunton (1968) based on Viséan material from Ireland. The single Ty-nant dorsal valve exterior is slightly more convex than the ventral valves, which show weak anterior sulcation typical of the species. The ventral diductor scars become increasingly flabellate with growth, whilst the adductor scars are distinctly oval and with only a relatively slender septum anteriorly.

### Superfamily ENTELETOIDEA Waagen, 1884
### Family SCHIZOPHORIIDAE Schuchert, 1929

### Genus SCHIZOPHORIA King, 1850

*Type species. Conchyliolithus Anomites* (*resupinatus*) Martin, 1809, pl. 49; from the Lower Carboniferous (Viséan) of Dovedale, Derbyshire.

### *Schizophoria resupinata* (Martin, 1809)
### Plate 6, figures 1–10; Plate 7; Text-figures 5–7

1809 *Conchyliolithus Anomites* (*resupinatus*) Martin, pl. 49, figs 13–14.
1850 *Schizophoria resupinata* (Martin) King, p. 106.
1968 *Schizophoria resupinata* (Martin); Pocock, p. 80, pl. 18, fig. 7, text-figs 13–15 [see also for earlier synonymy].
1968 *Schizophoria resupinata* (Martin); Brunton, pl. 2, figs 1–6.
1976 *Schizophoria* (*Schizophoria*) *resupinata* (Martin) Lazarev, p. 99, fig. 58, pl. 2, figs 3–4; pl. 3, figs 1–5.
1989 *Schizophoria* (*Schizophoria*) *resupinata* (Martin); Zakowa, p. 103.

*Material.* 86 ventral valves, 62 dorsal valves.

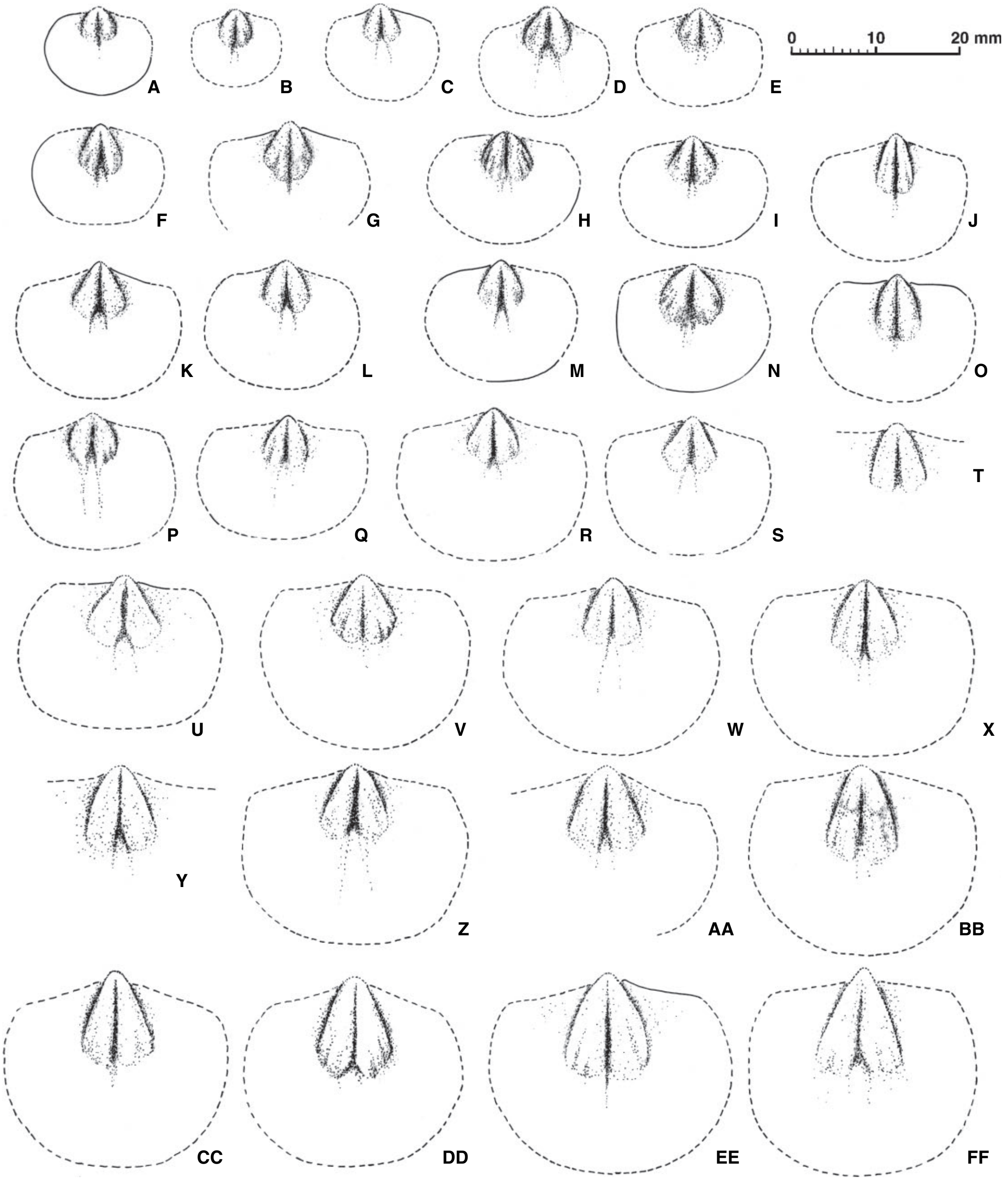
### *Description*

*Exterior.* Dorsibiconvex with relatively weak ventral curvature generally only about 50–60 per cent of dorsal curvature. Ventral valve of some specimens has a very shallow, flattish sulcus occupying somewhat more than the median 30 per cent of the anterior half of the shell, dorsal sulcus narrower and more pronounced but never strong; anterior commissure rectimarginate to weakly unisulcate. Shell outline transversely suboval to subcircular. Hinge line straight, occupying about 65–80 per cent of the maximum shell width, which is close to mid length; cardinal angles obtuse and well rounded, lateral and anterior margins smoothly and uniformly curved.

Ventral interarea flat, weakly apsacline, delthyrium open with an apical angle close to 90 degrees. Dorsal interarea short, somewhat obscure but apparently strongly anacline; notothyrium wide with a rounded apex, apical angle up to 100 degrees.

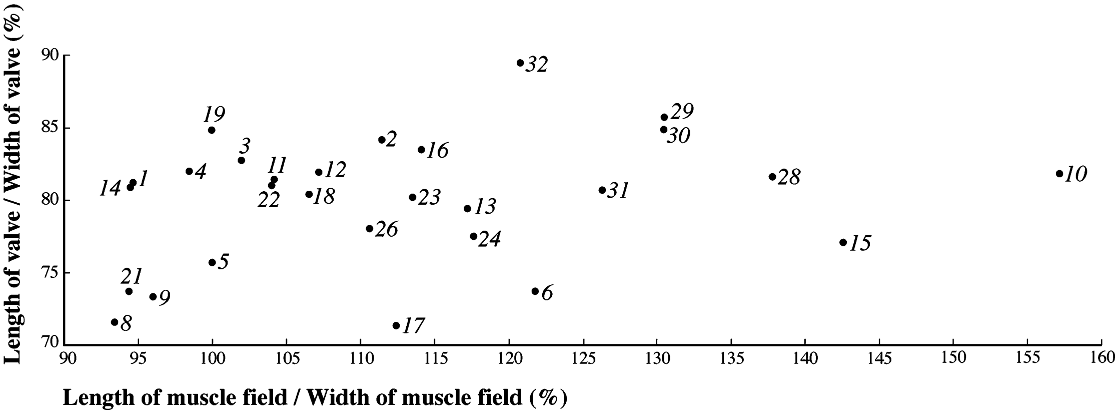
Ornament multicostellate with about 20–25 costellae in a 5-mm arc throughout the length of the valves; in places the ribs thicken slightly at the occasional growth lamellae, possibly representing the infill of aditicules.

*Ventral interior.* Teeth deltidiodont, relatively small, tabular in lateral view, varying from pointed to subrounded at their distal extremities, lateral cavities shallow and barely excavated below the interarea. Delthyrial chamber small. Dental plates short, slender, divergent from one another at close to 90 degrees and divergent ventrally onto the valve floor where they merge smoothly with the well-developed lateral bounding ridges of the muscle field. In overall pattern the muscle field is consistently well impressed and elongate-triangular cordate in outline (Pl. 7; Text-figs 5–6), but in detail there is considerable variation in relative proportion of the scars, the disposition and divergence of the bounding ridges, the degree of flabellation, and the nature of the median ridge. Some of the variation takes place through ontogeny, but for the most part it is



**TEXT-FIG. 6.** Ontogenetic variation in the ventral musculature of *Schizophoria resupinata* (Martin, 1809); see text for discussion. Drawn from internal moulds in the population at Ty-nant.

random (e.g. Text-fig. 7). Throughout growth the muscle field consistently occupies approximately the central third of the valve width, but there is an increase in relative length of the muscle field from about 33 to 50 per cent of valve length with growth (Text-fig. 6). The large diductor scars are consistently elongate-arcuate but vary in disposition from being essentially subparallel through growth, with a persistently narrow median ridge, to becoming splayed anteriorly where the ridge then bifurcates and the muscle scars become flabellate; in most specimens the median ridge increases slightly in height anteriorly. Slender subparallel to weakly divergent vascula media extend from the centro-anterior terminations of the muscle field (Text-figs 5–6). Valve margins crenulated by the impress of the external ornament.



**TEXT-FIG. 7.** Graphical plot of muscle field dimensions relative to overall valve size in the 32 specimens of *Schizophoria resupinata* illustrated in Text-figure 6, demonstrating random variation through ontogeny.

*Dorsal interior.* Notothyrial chamber with a steep posterior wall. Cardinal process small, simple, set directly on the valve wall, slender posteriorly but expanding distally as a faint lobe. Fulcral plates small, flat, merging smoothly medially with small, distally pointed brachiophores. Brachiophore plates relatively long, slender, divergent dorsally onto the valve floor and widely divergent at close to 90 degrees from one another. Muscle field weakly impressed, large elongate-suboval, occupying the median third of the valve and close to 50 per cent of valve length, contained within a shallow hollow, bounded by the brachial plates in its posterior half but unbounded anteriorly. Individual scars not well differentiated, divided medially by a faint, relatively broad, flattened ridge.

*Dimensions of figured specimens*

| | lv | ld | w | hw | lmv | lmd |
|---|---|---|---|---|---|---|
| Ventral interiors | | | | | | |
| 84.13G.24 | 19·0 | – | 26·4 est. | – | 11·3 | – |
| 84.13G.41A | 10·2 | – | 15·85 | 12·0 | 10·3 | – |
| 84.13G.41B | 21·2 | – | 28·0 est. | 19·6 est. | 10·7 | – |
| 84.13G.5 | 20·1 | – | – | – | 8·7 | – |
| 84.13G.37 | 13·9 | – | 20·0 est. | 12·8 est. | 6·5 | – |
| 57.421.G60.2 | 17·5 | – | 19·2 est. | – | 7·55 | – |
| 84.13G.34 | 18·0 | – | 24·3 | 14·6 | 8·2 | – |
| Dorsal(?) exterior | | | | | | |
| 84.13G.33 | – | – | 18·8 est. | 10·0 est. | – | – |
| Dorsal interior and exterior | | | | | | |
| 84.13G.40a,b | – | 13·3 | 16·4 est. | 12·6 est. | – | 7·4 |
| Dorsal interior | | | | | | |
| 84.13G.29 | – | 13·2 | 20·5 est. | 15·7 | – | 8·3 |

*Remarks.* This is the most common species in the Ty-nant fauna. Variation in British and related European Carboniferous species of *Schizophoria* has been discussed in considerable detail by a number of authors, including recognition of a number of species or subspecies separate from the widely identified *S. resupinata* (e.g. see Brunton 1968; Pocock 1968; Zakowa 1989 for summaries of earlier studies). We cannot readily identify our Ty-nant specimens within any of these other taxa so we adopt the conservative stance of incorporating our population within a somewhat variable morphological plexus of *resupinata* itself. The demonstrable random variation that we see, for example, in ventral musculature within the Ty-nant population certainly spans a range reported in other nominal species and suggests that the plasticity of such characters should be assessed very closely before separating stocks under separate names. The ribbing strength of our material accords well with that of the '*resupinata* group' as discussed by Brunton (1968, p. 10), as does the disposition of the dental plates. At the same time, we do note some differences of potential taxonomic significance, such as the presence of a trilobed cardinal process in gerontic specimens assigned to *resupinata s.s.* (e.g. Brunton 1968, pl. 2, figs 5–6), whereas in our material the process is rather delicate and with only a single lobe. The higher energy environments in the sequences from which the types of *resupinata* come could equally well be a factor in the development of more robust structures through ontogeny, and we again lean on the side of taxonomic

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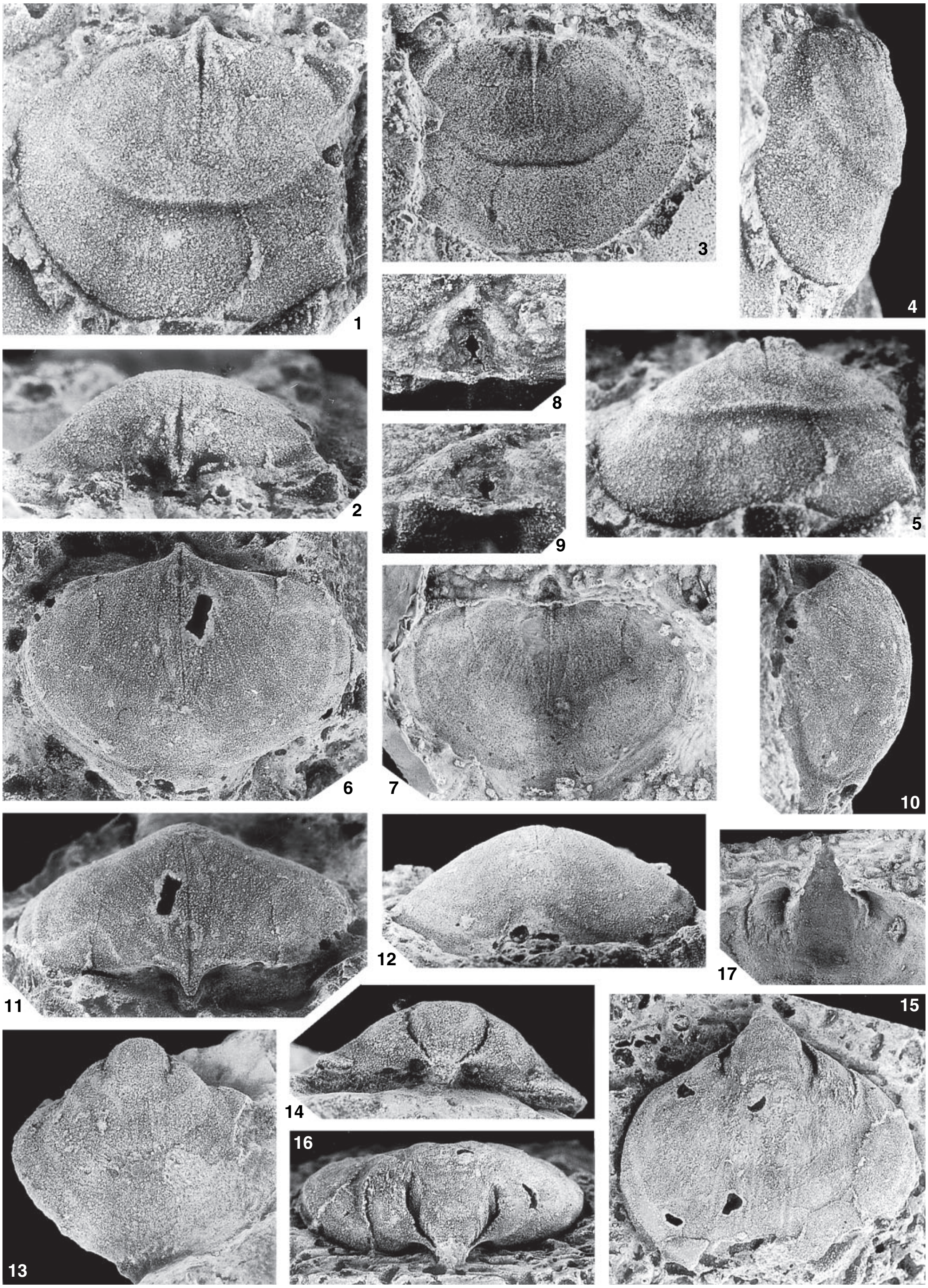
## EXPLANATION OF PLATE 8

Figs 1–17. *Composita ptygmation* sp. nov. 1–5, holotype, 57.421G79, dorsal internal mould, × 3; posterior view and latex cast, × 2; lateral and anterior views, × 3. 6–12, 84.13G.8, dorsal internal mould and latex cast, × 2; normal and anterior-oblique view of latex cast of cardinal plate, × 5; lateral, posterior and anterior views of mould, × 2. 13–14, 84.13G.6, ventral internal mould and posterior view; × 2. 15–17, 84.13G.1, ventral internal mould, posterior view, and latex cast of posterior structures; × 2.

conservatism in assessing the finer preservation of such features in the Ty-nant population from relatively low-energy environments.

As a final comment on this taxon, there is no doubt that it belongs to *Schizophoria* (*Schizophoria*), and is thus certainly within the *resupinata* group, rather than the sub-

PLATE 8



BASSETT and BRYANT, *Composita*

genera *S*. (*Paraschizophoria*) or *S*. (*Pocockia*) as recognised by Lazarev (1976, pp. 110, 112; see also Harper 2000, pp. 840–842).

### Superfamily ATHYRIDOIDEA Davidson, 1881
### Family ATHYRIDIDAE Davidson, 1881
### Subfamily ATHYRIDINAE Davidson, 1881

### Genus COMPOSITA Brown, 1849

*Type species. Spirifer ambiguus* J. Sowerby, 1822; from the lower Carboniferous (Dinantian, Viséan, probably Brigantian, Monsal Dale Limestones Formation), west of Bakewell, Derbyshire, England.

### *Composita ptygmation* sp. nov.
### Plate 8; Plate 9, figures 10–13

*Derivation of name.* Diminutive of the Greek *ptygma* (anything folded), referring to the weak dorsal fold.

*Holotype.* Dorsal interior, 57.421G.79; Plate 8, figures 1–5.

*Paratypes.* Two ventral interiors (84.13G.1 and 6) and two dorsal interiors (84.13G.8 and 13a,b).

*Diagnosis.* Transversely elliptical to semicircular with a weak, uniplicate, uniformly rounded dorsal fold developed only anteriorly. Cardinal plate wide and almost flat with a straight anterior margin. Ventral muscle field weakly flabellate.

#### *Description*

*Exterior.* Transversely suboval to subpentagonal, maximum length varying from about 68 to 91 per cent of maximum width (mean 79·5 per cent in the type series), with the latter close to or slightly posterior to mid length. Hinge very short, confined within the span of the teeth and sockets in the median 30–35 per cent of the shell. Posterolateral margins weakly curved, lateral and anterolateral margins smoothly rounded or with a distinct shoulder at the maximum width in the more pentagonal individuals; anterior margin only weakly curved or even slightly invaginated as in the holotype. Subequally biconvex; dorsal curvature uniform sagitally, ventral curvature slightly inflated medially in posterior half of the valve but sloping away fairly sharply both laterally and posterolaterally. Dorsal and ventral beaks not incurved over the hinge, ventral umbo slightly swollen. Dorsal valve with a weak, gently rounded fold developed only anterior to the mid length, forming less than 50 per cent of the width at the anterior margin where it makes only a slight dorsal deflection; ventral valve with a complementary flattish to very gently rounded shallow sulcus, also developed only anteriorly. No trace of sculpture preserved, apart from widely spaced growth ridges, some of which mark points of changing convexity.

*Interior.* Delthyrial chamber deep with a subvertical posterior face, dental plates outwardly curved and weakly flabellate, dropping abruptly to the floor of the valve, supporting small, bluntly triangular teeth and bounding deep lateral cavities that are excavated well under the cardinal margin. At their bases the dental plates merge into short muscle-bounding ridges. Ventral muscle field confined mostly within delthyrial cavity, occupying only about 30 per cent of valve width, unbounded anterolaterally and anteriorly; adductor scars broad and occupying the flattened median half of the muscle field, bounded laterally by the diductor scars which lie on the lateral slopes of the delthyrial cavity. There was probably a large pedicle callist. Faint traces of vascula media are visible along the length of the sides of the sulcus.

Notothyrial chamber deep, excavated well under the cardinal margin, with a steep posterior face. Dental sockets deep, excavated partly under the cardinal margin, suspended high above the valve floor on downward-concave fulcral plates (Pl. 9, fig. 11). Excavated along the cardinal margin above each dental socket is a shallow, slender, elongated groove that must have acted as an accessory socket and whose anterior margins form low outer socket ridges. Inner socket ridges strong, elevated well above the cardinal plate, divergent at about 120 degrees to one another and with tops convergent ventromedially relative to their bases. Cardinal plate perforated posteromedially, almost flat with a straight anterior margin, supported laterally by curved inner walls of the fulcral plates and extending freely well anterior to the cardinal margin. Outer hinge plates, crural bases and inner hinge plates fused. Crura not preserved.

Dorsal muscle field relatively long and slender, confined to median 15–20 per cent of valve width and extending anteriorly to 50–60 per cent of the length, bisected longitudinally posteriorly by a low, slender, hastate, rounded ridge which arises in the notothyrial chamber and tapers anteriorly to a fine myophragm. Posterolateral adductors small, confined to subrounded hollows below the walls of the valve, laterally bounding the larger scars that lie either side of the ridge/myophragm throughout their length, fairly well impressed in longitudinal hollows posteriorly

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**EXPLANATION OF PLATE 9**

Figs 1–8. *Eomartiniopsis* sp. 58.464G349, steinkern in dorsal, ventral, posterior and anterior views, and dorsal latex cast, × 1·5; detail of latex cast of posterior structures in normal, × 3 and in oblique-lateral views, × 2; and lateral view of mould, × 1·5.

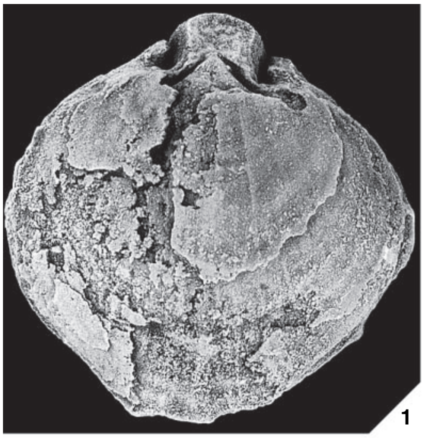
Figs 9–14. *Composita ptygmation* sp. nov. 84.13G.18A,B, dorsal internal mould, anterior view and latex cast, × 2; oblique-lateral detail of cardinal plate and sockets, × 4; latex cast of conjoined mould, × 2; posterior view of mould; × 3.

but only faintly impressed throughout most of their length as lanceolate (Pl. 8, fig. 8) to tear-shaped (Pl. 8, fig. 1) scars with barely discernible margins; very small adjustor scars are apparent at the anterior margin of the delthyrial chamber.

*Dimensions of figured specimens*

| | | l | w |
|---|---|---|---|
| Dorsal interior | 57.421.G79 (holotype) | 14·85 | 21·0 (est.) |
| Dorsal interior | 84.13G.8 (paratype) | 19·25 | 27·15 |

PLATE 9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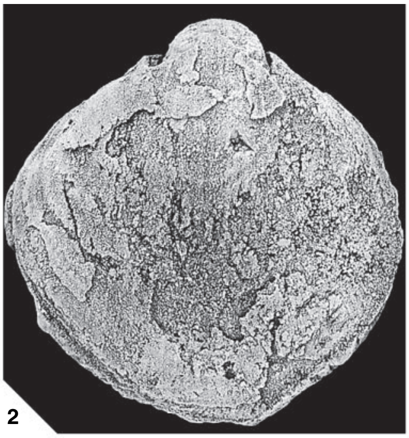
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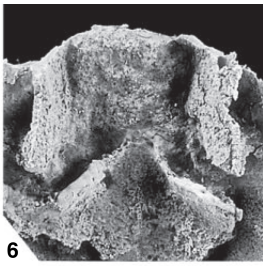
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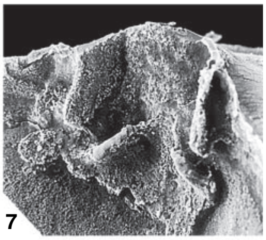
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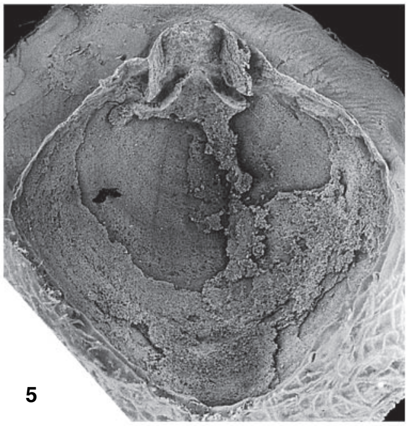
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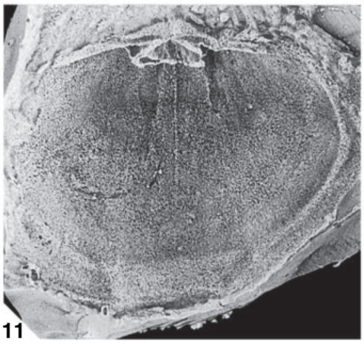
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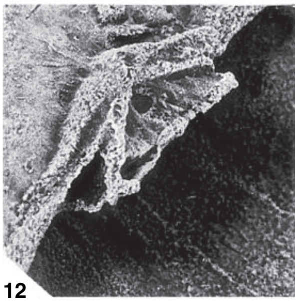
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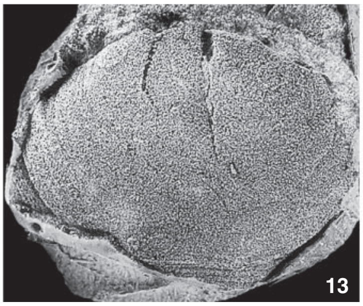
9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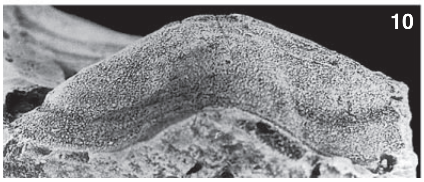
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14

BASSETT and BRYANT, *Composita*, *Eomartiniopsis*

| | | | |
|---|---|---|---|
| Dorsal interior | 84.13G.18a (paratype) | 19·0 | 31·0 (est.) |
| Ventral interior | 84.13G.6 (paratype) | 17·85 | 22·60 |
| Ventral interior | 84.13G.1 (paratype) | 21·10 | 22·65 |

*Remarks.* The smooth shell, dorsal fold and ventral sulcus, and the distinctive posteromedially perforated apical plate in this species are typical features of *Composita*. The only other British Carboniferous species referred confidently to this genus is *C. ambigua* (J. Sowerby, 1822), which has been reported widely previously in many faunal lists dealing with Dinantian stratigraphy. The types of *C. ambigua* are from probable uppermost Viséan strata in Derbyshire (Brunton 1980, p. 230, figs 26–28). *C. ptygmation* is readily distinguished from *C. ambigua* by its more transverse outline with a weaker fold and sulcus, curved margins of the slightly flabellate ventral muscle field, and especially by its distinctive triangular, flat cardinal plate with a straight anterior margin.

### Superfamily MARTINOIDEA Waagen, 1883
### Family MARTINIIDAE Waagen, 1883
### Subfamily EOMARTINIOPSINAE Carter, *in* Carter *et al.* 1994

### Genus EOMARTINIOPSIS Sokolskaya, 1941

*Type species. Eomartinopsis elongata* Sokolskaya, 1941; from the lower Carboniferous (Tournaisian, Upa limestones) of the Moscow Basin, Russia.

### *Eomartiniopsis* sp.
Plate 9, figures 1–8

*Material.* One steinkern.

## *Description*

*Exterior.* Shell relatively large (l, 36·15; w, 36·3; t, 22·7), subcircular, rotund, subequally biconvex. Posterior region of both valves slightly inflated, dorsal valve with smoothly rounded fold anteriorly occupying median third of the shell, ventral valve with complementary shallow sulcus. Maximum width of shell at mid length, hinge short, occupying less than 50 per cent of maximum width. Posterolateral margins smoothly curved as distinct shoulders, anterolateral margins equally curved, anterior margin only weakly curved, anterior commissure broadly uniplicate.

Interareas lacking, ventral beak blunt, apparently erect, dorsal beak small, weakly incurved just over the hinge line. Details of delthyrium and notothyrium not preserved.

Very faint traces of radial ornament and concentric growth lines are preserved on the mould.

*Ventral interior.* Median septum absent. Dental plates well developed, slightly sinuous, aligned oblique-medially onto the valve floor, comprising well-differentiated ventral adminicula and dental flanges. Teeth small. Musculature not preserved but clearly confined originally within the deep, flattish-floored hollow between the dental plates.

*Dorsal interior.* Cardinalia short, crural bases are weakly curved divergent plates, slightly swollen distally, fulcral plates very weak, sockets very shallow. No cardinal process (or ctenophoridium) preserved, no musculature preserved.

*Remarks. Eomartiniopsis* remains a relatively poorly known genus, despite having been reported in lower Carboniferous faunas across wide areas (e.g. Sokolskaya 1941; Carter 1967, 1988, 1999; Roberts 1971). Our single specimen from Ty-nant is assigned to the genus, with some uncertainty, mainly on the basis of its distinct fold and sulcus, short crural plates and absence of a median septum. Of other martiniid genera reported from the British Isles, *Martinia* is easily distinguished in lacking dental plates and crural plates, in *Martiniopsis* a fold and sulcus are weak or absent and the crural plates are long and slender, and *Merospirifer* has weak costae and a ventral median septum (see also discussion by Brunton 1984, pp. 95–97).

### Family SPIRIFERIDAE King, 1846
### Subfamily PROSPIRINAE Carter, 1974

### Genus UNISPIRIFER Campbell, 1957

*Type species. Spirifera striato-convoluta* Benson, Dunn and Brown, 1920; from the lower Carboniferous (Lower Burindi Group, middle–upper Tournaisian) in the 'Shelly Ridge' of Watts, Babbinboon, New South Wales, Australia.

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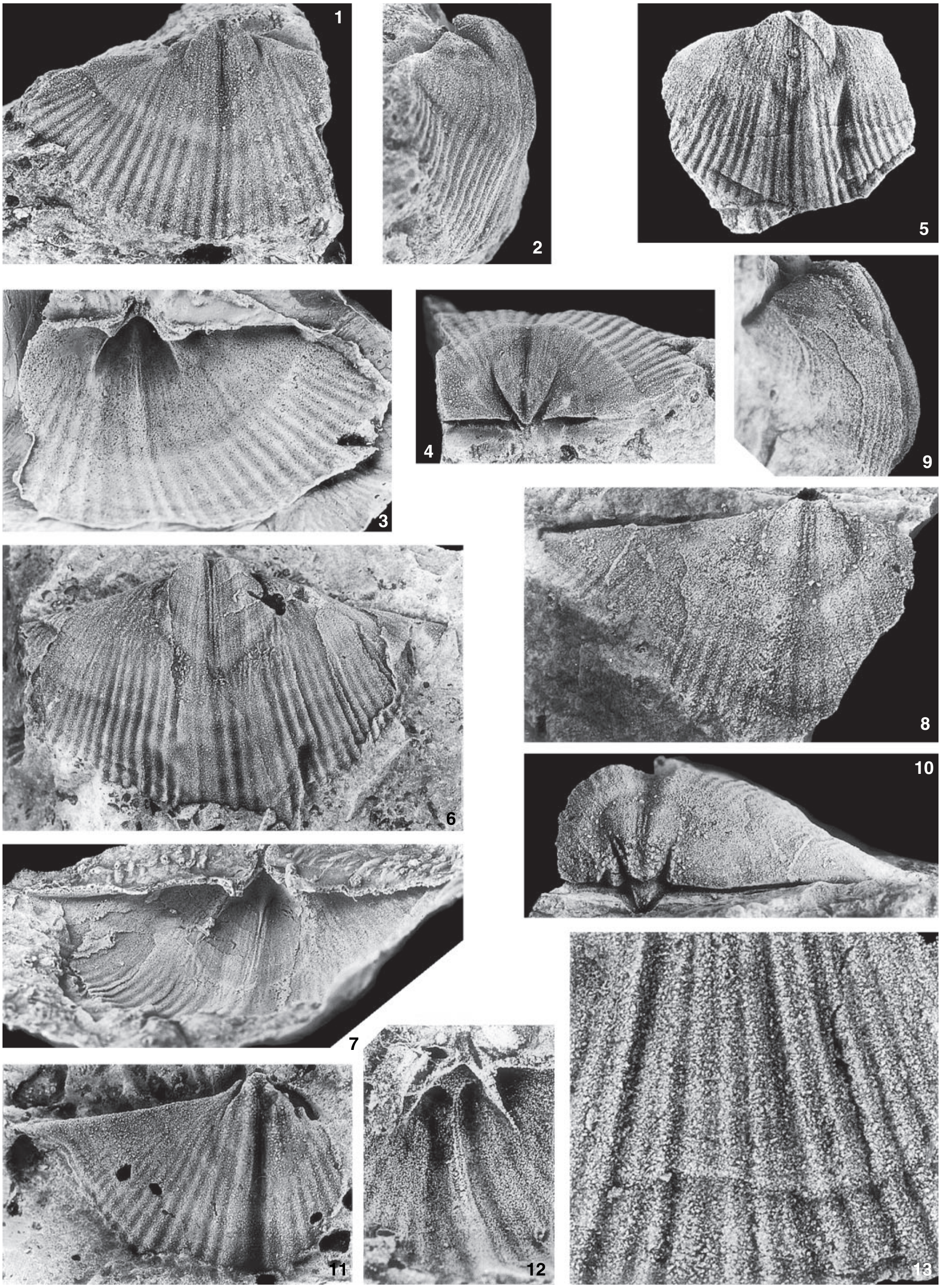
**EXPLANATION OF PLATE 10**

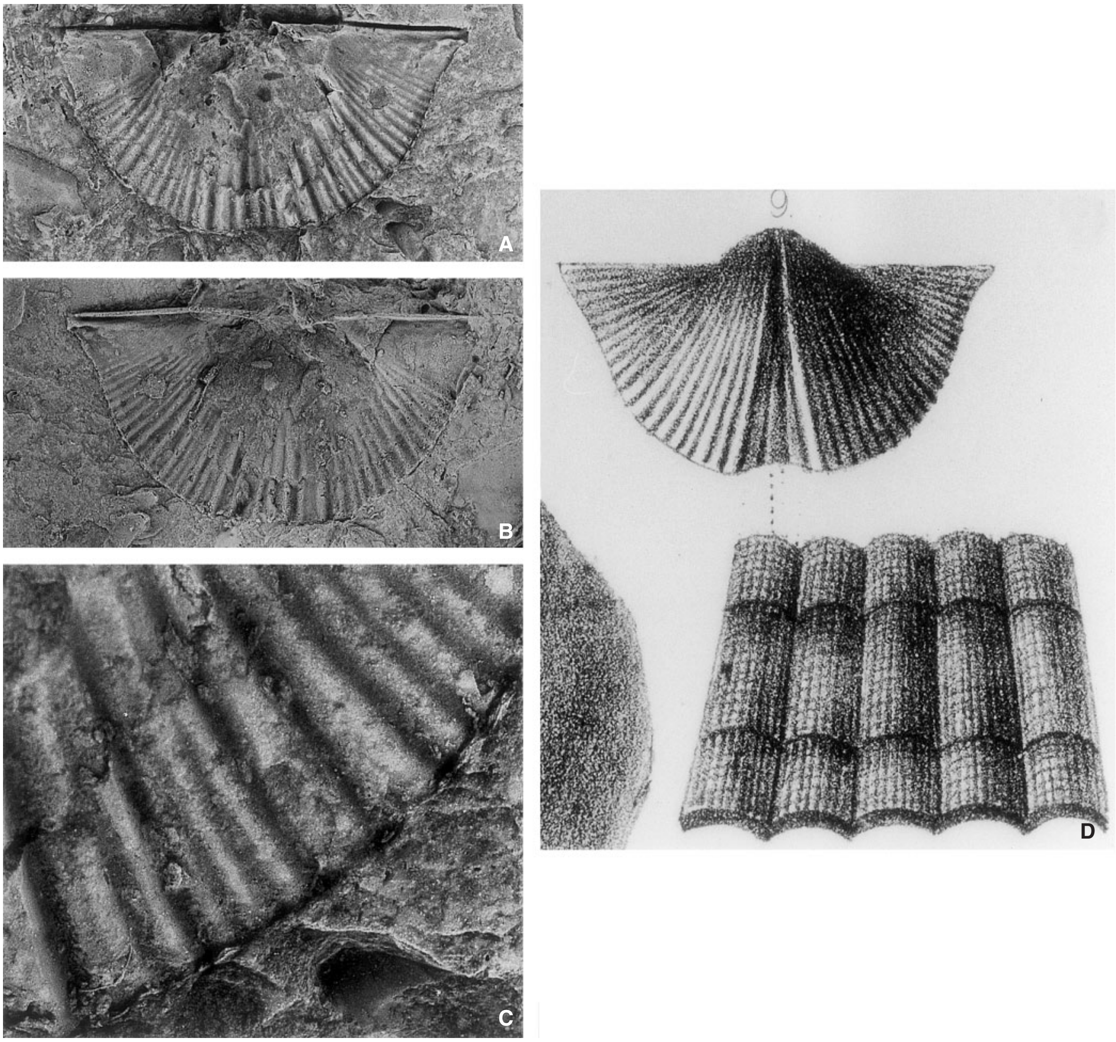
Figs 1–13. *Unispirifer* cf. *clathratus* (M'Coy, 1844). 1–4, 84.13G.49, ventral internal mould in normal, and lateral views, latex cast, and posterior view of mould; × 2. 5, 84.13G.2, ventral internal mould; × 1·5. 6–7, 22.9G51.2, ventral internal mould and latex cast; × 1·5. 8–10, 57.421G81.1, ventral internal mould in normal, lateral and posterior views; × 2. 11–12, 84.13G.35, ventral internal mould, × 3; and latex cast of posterior structures, × 5. 13, 84.13G.31, detail of dorsal mould showing bifurcating costellae on fold; × 5.

*Remarks*. We follow Carter (1974, p. 680; 1987, p. 72; 1988, p. 63) and Carter *et al*. (1994, p. 343) in including *Unispirifer* within the Prospirinae. Maxwell (1961, pp. 89–91), Roberts (1971, p. 208) and Thomas (1971, pp. 68–70)

PLATE 10



BASSETT and BRYANT, *Unispirifer*



**TEXT-FIG. 8.** *Unispirifera clathratus* (M'Coy, 1844). A–C, National Museum of Ireland F7453, lectotype, ventral internal mould and latex cast, × 2, with detail of ornament on the cast, × 9; Carboniferous, Dinantian, Lisnapaste, Ballintra, Co. Donegal. D, M'Coy's original illustration of *Spirifera clathrata* (1844, pl. 19, fig. 9).

discussed the differences between *Unispirifer* and *Prospira*, which we accept here in maintaining the identity and close relationship of both genera.

### *Unispirifer* cf. *clathratus* (M'Coy 1844)

Plate 10; Plate 11, figures 1–11; Plate 12, figures 7–16

v* cf.1844 *Spirifera clathrata* M'Coy, p. 130, pl. 19, fig. 9.
v. cf.1858 *Spirifera striata* (Martin); Davidson, p. 19 *pars*, pl. 3, figs 6, 6a only [ = M'Coy's *clathrata*], *non* pl. 2, figs 12–21, *non* pl. 3, figs 2–4.
v. cf.1904 *Spirifer bisulcatus* Sowerby [group] Mutation B′ (= *Spirifer* aff. *clathratus*, McCoy); Vaughan, p. 125, pl. 2, fig. 3a–c.
v. cf.1905 *Spirifer* aff. *clathratus* M'Coy; Vaughan, p. 300, pl. 26, fig. 5.

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## EXPLANATION OF PLATE 11

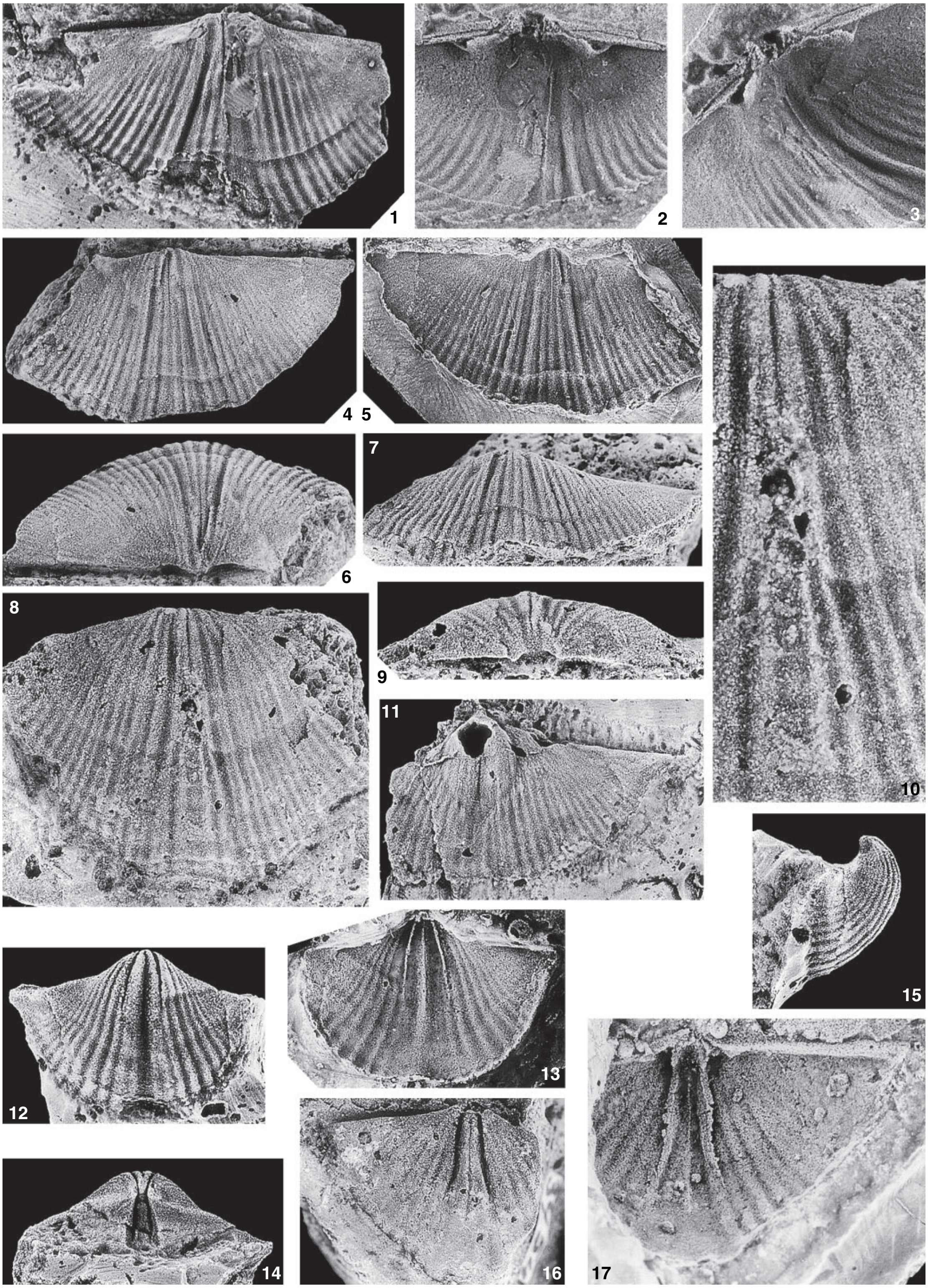
Figs 1–11. *Unispirifer* cf. *clathratus* (M'Coy, 1844). 1–3, 57.421G81.2, dorsal internal mould, × 1·5; and latex cast in normal and oblique-lateral views of posterior structures, × 2. 4–7, 84.13G.31, dorsal internal mould and latex cast, with posterior and anterior views of mould; × 1·5. 8–10, 84.13G.43, dorsal internal mould in normal and posterior views, × 2; with detail of costellae from median part of mould, × 5. 11, 84.13G.14, ventral internal mould; × 1·5.

Figs 12–17. *Fusella extrata* sp. nov. 12–15, holotype, 84.13G.50, ventral internal mould, latex cast, posterior and lateral views of mould; × 2. 16–17, 84.13G.33, dorsal internal mould, × 2; and latex cast, × 3.

v. cf.1915 *Spirifer clathratus* M'Coy; Vaughan, p. 41, pl. 6, fig. 5, *non* figs 4, 6 [= *tornacensis* de Koninck].

cf.1957 *Unispirifera clathratus* (McCoy); Campbell, p. 67 [name only].

## PLATE 11



BASSETT and BRYANT, *Fusella*, *Unispirifer*

*Material.* Seven ventral interiors, three dorsal interiors.

*Remarks.* Numerous specimens from various parts of the world and various stratigraphical horizons within the Carboniferous have long been identified as '*Spirifer clathratus*', following its original description by M'Coy (1844) from 'Carboniferous Slate' at Lisnapaste, Ballintra, Co. Donegal in Ireland. The name has persisted despite the fact that soon after his original definition, M'Coy formed the opinion that *clathrata* was a synonym of '*Spirifera striata* (Martin, 1809)' (see Davidson 1858, pp. 19, 21), and it was also considered subsequently to be synonymous with other species such as '*Spirifera bisulcata*' (J. Sowerby, 1825) (e.g. Davidson 1861, p. 221).

Uncertainty as to the true identity and relationships of *clathratus* has continued until now, partly because M'Coy's original material has been thought to be lost and thus unavailable for comparative examination. In this regard the name '*Spirifer tornacensis* de Koninck, 1883' has been applied not uncommonly to early Carboniferous British spiriferids following its detailed description based on abundant material from beds regarded as generally contemporaneous in Belgium; even here, however, the confusion has been heightened by the fact that some authors have discussed the possible synonymy of *clathratus* and *tornacensis* (e.g. Vaughan 1915, p. 41). Vaughan stated that M'Coy's type specimen is lost, but Mr Nigel Monaghan recently discovered a single specimen in the M'Coy collection at the National Museum of Ireland which is from Lisnapaste and is a syntype of *clathratus*. The original description states that the species 'grows much larger than the specimen figured', indicating that M'Coy had at least two or more syntypes available. This syntype (NMI F7453), which we here designate as the lectotype, is a poorly preserved mould of a ventral valve interior, with the musculature and denticular detail damaged and obscure (Text-fig. 8). This is presumably the same specimen as that discussed by Sartenaer and Plodowski (1996, p. 61) and which they differentiate from *tornacensis* 'on account of its external shape, its smaller size, and its very irregular costation' (see also discussion below). Sartenaer and Plodowski (1996, p. 61) doubted that this specimen is a M'Coy type; while it may not necessarily be an originally figured specimen (and given the generality of mid nineteenth century illustrations it is impossible to be certain), there is no reason from the accompanying documentation to doubt that it is a syntype. From an immediate standpoint, however, this nicety is irrelevant, as we agree completely with Sartenaer and Plodowski that at the specific level *clathratus* (and therefore our cf. *clathratus*) has nothing in common with *tornacensis*.

According to Mr N. Monaghan (*in litt.* 1993), the type locality at Lisnapaste for *clathratus* is a roadside exposure south of a bridge at Irish Map Grid G944716, in beds mapped as Ballyshannon Limestone (George and Oswald 1957) of early Viséan age (Chadian–Arundian) (George *et al.* 1976, fig. 15; Sevastopulo 1981, p. 158). Unfortunately, because of the poor preservation of the specimen, it is not possible here to resolve the detailed questions of synonymy and relationships touched on above, and such matters will require the collection of topotypes, which is beyond the scope of this paper. However, we can conclude that our material from Ty-nant is more similar to the lectotype of *clathratus* than to other named species.

The transverse shell with a long alate hinge, and the pattern of costal bifurcation in *clathratus* (Text-fig. 8) identify it clearly within *Unispirifer*, as recognised originally by Campbell (1957, p. 67). M'Coy's original illustration (1844, pl. 19, fig. 9; Text-fig. 8D herein) shows a strongly clathrate pattern of capillae and fila on the costae, which are not preserved on the lectotype (Text-fig. 8C), but this is probably because of its preservation; such ornament is also not preserved on our material.

Sartenaer and Plodowski defined a new genus, *Atylephorus*, to accommodate *tornacensis*, differing from *Unispirifer* mostly in details of size, ornamentation and differentiation of the fold and sulcus. Some of the generic differences may be somewhat finely drawn, but we do not have sufficient other comparative material to comment further; suffice it to say that the specific distinctness of *tornacensis* is now well confirmed by Sartenaer and Plodowski. Thus, *A. tornacensis* differs from *U. clathratus* (and our cf. *clathratus*) in being considerably larger at maturity, more strongly biconvex, and much more finely ribbed with more numerous medial and lateral bifurcations; the ventral muscle field of *tornacensis* is more slender and elongated than the rounded pattern in cf. *clathratus* (e.g. see de Koninck 1887, pl. 25, figs 1–13). The other species confused previously with

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## EXPLANATION OF PLATE 12

Figs 1–6. *Tylothyris laminosa laminosa* (M'Coy, 1841). 1–4, 84.13G.52, dorsal internal mould and latex cast, × 3; latex cast of cardinal area, × 5; and posterior view of mould, × 3. 5–6, 84.14G.1, dorsal internal mould and latex cast; × 2.

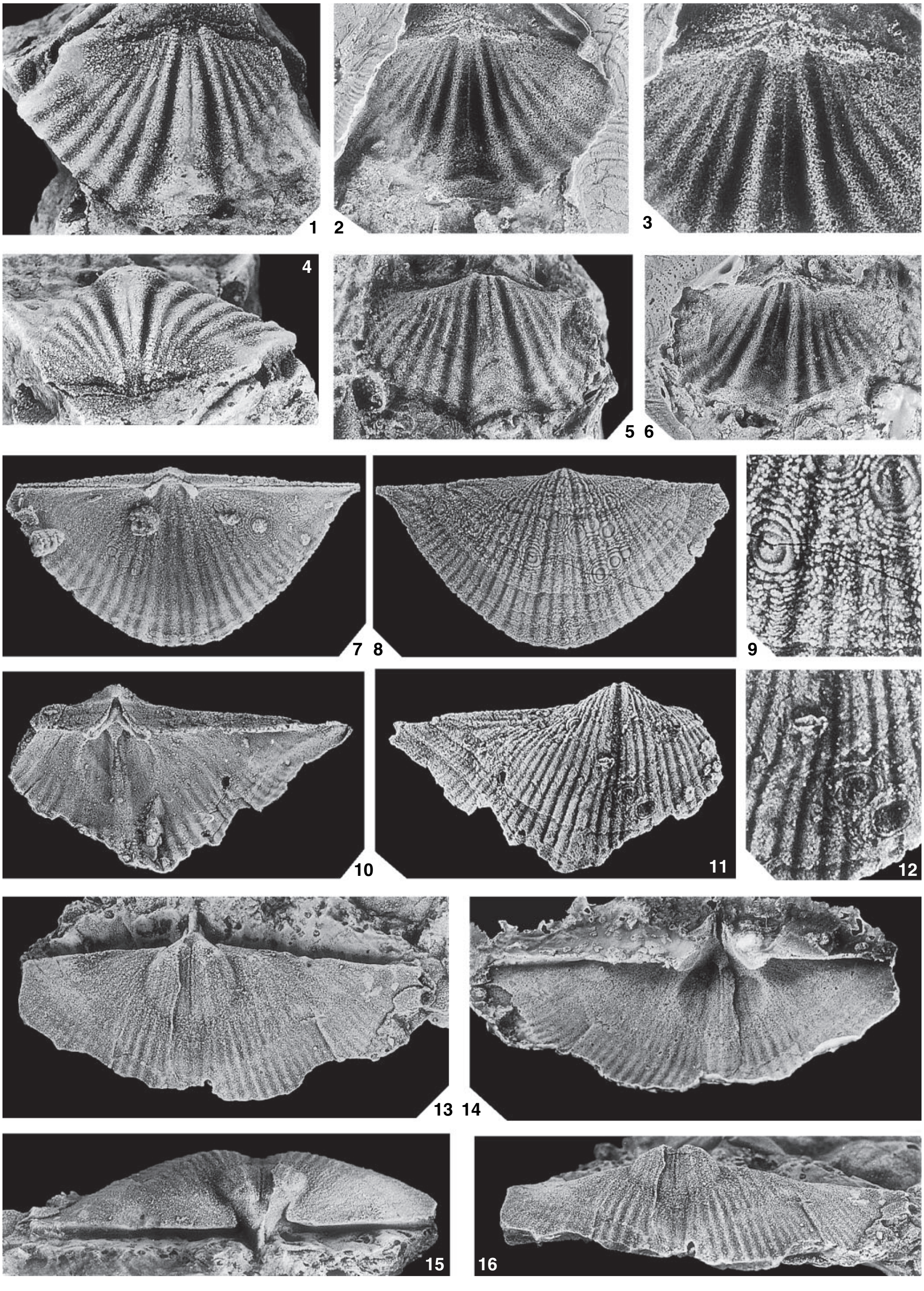
Figs 7–16. *Unispirifer* cf. *clathratus* (M'Coy, 1844). 7–9, 90.48G.6, interior and exterior of dorsal valve, × 2; with detail of external ornament on fold distorted by beekite rings, × 5; Barry Island, South Glamorgan. 10–12, 90.48G.7, interior and exterior of ventral valve, × 2; and detail of ornament in the sulcus, × 4; Barry Island. 13–16, 57.421G79, ventral internal mould and latex cast, posterior and anterior views of mould; × 1·5.

*clathratus* (*striata* and *bisulcata*; see above) belong to *Spirifer s.s.*, typified by their large size, obtusely rounded cardinal extremities and strong fold and sulcus.

### *Description*

*Exterior.* Widely transverse with a length/width ratio of 48–60 per cent, cardinal extremities mucronate to subalate; hinge long,

PLATE 12



BASSETT and BRYANT, *Tylothyris*, *Unispirifer* straight, forming point of maximum shell width. Posterolateral extremities weakly flexed at cardinal extremities, shell outline subelliptical to subtriangular with smoothly curved lateral and anterior margins. Subequally weakly to only moderately biconvex, flanks tending to become slightly flatter posterolaterally; ventral umbo only weakly inflated, dorsal umbo not raised above convexity of flanks. Dorsal fold narrow, subrounded to flattened, in some specimens barely raised above lateral areas, widening only a little but evenly anteriorly to occupy < 20 per cent of the valve width at the anterior margin, not forming an anterior tongue; complementary ventral sulcus generally more distinct but never deep. Anterior commissure weakly uniplicate.

Ventral interarea weakly concave, apsacline. Delthyrium wide with curved margins, rounded to subangular apically and with a depressed apical plate. Dorsal interarea short, anacline, notothyrium wide with weakly curved margins and rounded apex.

Ornament moderately coarsely costellate, with almost straight ribs originating mostly at the umbones and increasing only occasionally by bifurcation (e.g. Pl. 10, fig. 13). Ribs strong, rounded and equally spaced with subequally sized rounded interspaces. On the fold there are almost invariably four initial ribs increasing by bifurcation to six at about mid length in mature specimens. In the sulcus there is a complementary pattern of three ribs increasing by bifurcation up to seven. Growth lines widely spaced, occasionally strong.

*Ventral interior.* Delthyrial cavity deep with a steep posterior face, occupied by a strong pedicle callist extending up into the delthyrium. Teeth relatively large, extended laterally along the hinge, anterior faces curved and with dorsal faces hollowed out. Dental plates strong, short, extending anteriorly into slender curved ridges that bound the muscle field in its posterior half.

Muscle field large, deeply impressed, subcircular to slightly longitudinally suboval, occupying some 20 per cent of valve width and 25 per cent of the length. Posteriorly there is a wide, tapering, flat triangular median platform (e.g. Pl. 10, fig. 12; Pl. 12, fig. 10) at the anterior end of the delthyrial cavity, which passes into a slender, low myophragm aligned along the centre of the ridge reflecting the external sulcus. Slender, lanceolate adductor scars are confined along the ridge adjacent to the myophragm. Diductor scars large, suboval, almost unconfined by bounding ridges anteriorly. No details of vascularia preserved.

*Dorsal interior.* Notothyrial cavity shallow, with no trace of ctenophoridium. Outer socket ridge coincident with the margin of the interarea. Sockets deep, elongate, narrow, aligned subparallel to the hinge margin. Crural plates well developed. Inner socket ridges strong, slightly swollen distally and somewhat sinuous in some specimens. Musculature hardly preserved, but in some specimens there is a slender myophragm extending for almost the whole length of the valve from the notothyrial cavity almost to the anterior margin (e.g. Pl. 11, figs 2–3, 5).

*Remarks.* Despite the generally fine preservation of the specimens from Ty-nant, most are not generally sufficiently completely preserved to allow accurate measurements of dimensions. However, magnifications quoted in the plates are accurate to within < 5 per cent of error.

### Superfamily PAECKELMANELLOIDEA Ivanova, 1972
### Family PAECKELMANELLIDAE Ivanova, 1972
### Subfamily STROPHOPLEURINAE Carter, 1974

### Genus FUSELLA M'Coy, 1844

*Type species. Spirifer fusiformis* Phillips, 1836; from the lower Carboniferous (probably Pendleside Limestone Group, Viséan) of Bowland [Bolland], Yorkshire, England.

### *Fusella extrata* sp. nov.
Plate 11, figures 12–16; Plate 13, figures 1–16

*Derivation of name.* Latin *extra*, besides or outside; referring to the position of the dental plates bordering or outside the ventral sulcus.

*Holotype.* Ventral internal mould 84.13G.50; Plate 11, figures 12–15.

*Paratypes.* Seven ventral moulds (19.205GR.1, 18.13G.34, 84.14G.7, 84.14G.7b, 84.13G.10, 84.13G.51, 84.13G.44) and eight dorsal moulds (19.205GR1, 84.13G.33, 84.15G.2, 84.14G.8, 84.15G.3, 84.15G.3b, 22.9G51.1, 22.9G52.1).

*Diagnosis.* Mucronate but not widely alate; weakly ventribiconvex. Ventral interarea high, incurved. Concentric

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## EXPLANATION OF PLATE 13

Figs 1–16. *Fusella extrata* sp. nov. 1–2, 19.205GR.1a, ventral internal mould and latex cast; × 3. 3, 84.15G.2, dorsal internal mould; × 2. 4–5, 84.14G.8, dorsal internal mould and latex cast; × 3. 6–9, 84.13G.44, ventral internal mould, × 2; latex cast of teeth and muscle field, × 3; lateral and posterior views of mould, × 2. 10–12, 19.205GR.1b, ventral internal mould and latex cast, × 3; oblique-lateral view of posterior structures, × 8. 13–14, 84.13G.34, ventral internal mould and interarea; × 4. 15–16, 84.14G.7, ventral internal latex cast and posterior view of mould; × 4.

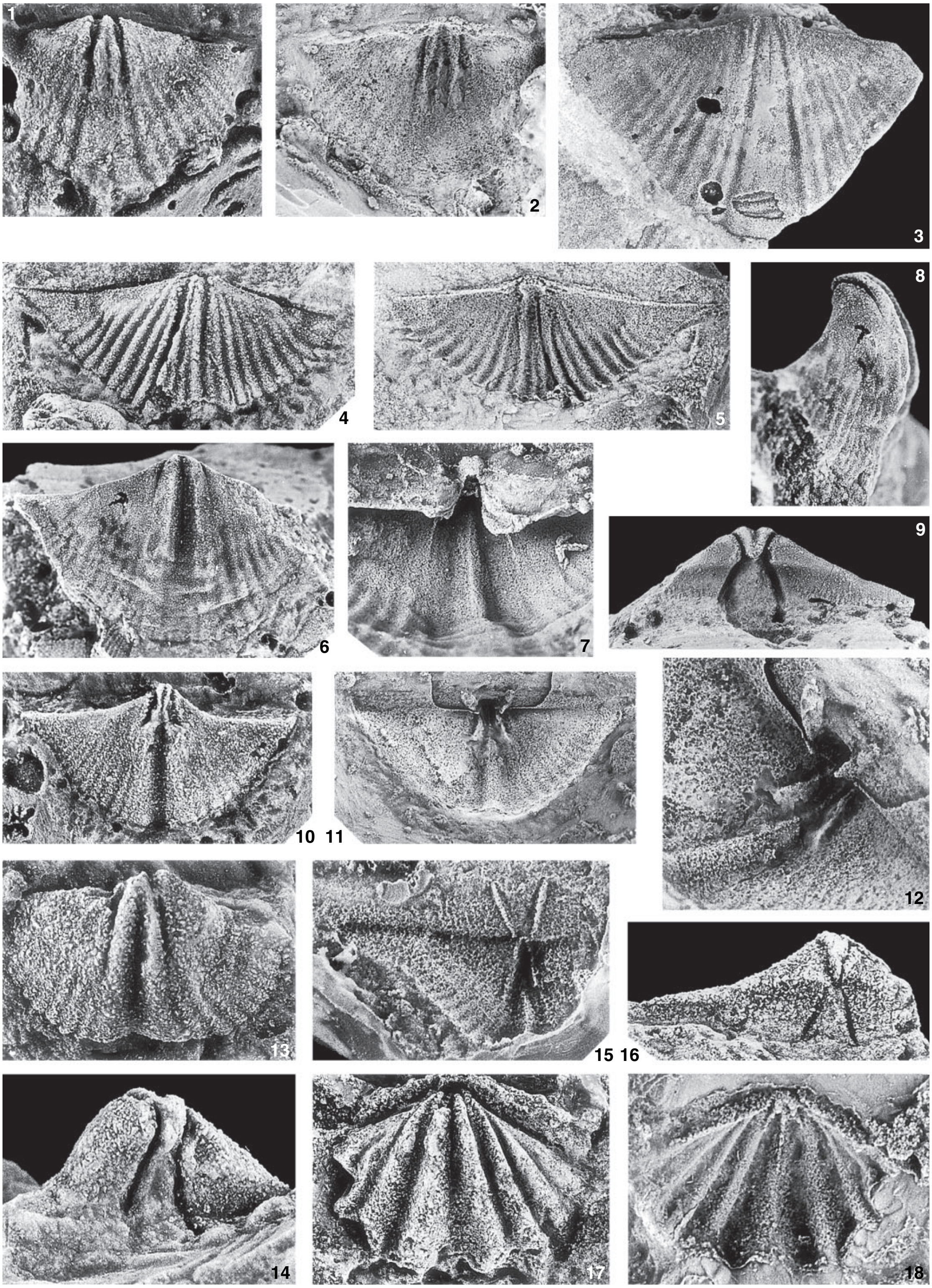
Figs 17–18. *Spiriferellina* sp. 84.14G.5, ventral internal mould and latex cast; × 4.

ornament not lamellose. Dental plates/adminicula slender, long, extending outside sulcus boundaries. Dorsal adminicula and myophragm long, slender.

### *Description*

Slightly ventribiconvex, somewhat fusiform but mostly mucronate as opposed to pronouncedly alate. Outline laterally subtriangular,

PLATE 13



BASSETT and BRYANT, *Fusella*, *Spiriferellina* cardinal extremities subrounded to subangular. Maximum width at the straight to weakly curved hinge. Anterolateral and anterior margins smoothly curved in suboval form, flexed only at posterolateral extremities. Anterior commissure weakly uniplicate with a narrow ventral sulcus and dorsal fold; these structures are persistently narrow throughout the shell length.

Ventral beak high, not inflated, incurved but not crossing the distinctly concave, apsacline interarea. Dorsal interarea short, anacline, umbo obscure. Delthyrium relatively narrow with weakly curved margins, no apical structures. Notothyrium small with gently curved margins.

Ornament of fairly strong rounded costae, equally spaced, generally simple but with occasional branching on the lateral slopes. Costae on the dorsal fold originate at the umbo as a pair but bifurcate close to mid length. Sulcus bounded by a branching pair of costae on each side, defining the sulcal margin. Mature specimens have traces of four or more ribs in the sulcus. Lateral slopes each generally with up to ten costae, rarely more. Irregular concentric growth lines occur but no micro-ornament is present.

*Ventral interior.* Teeth deltidiodont, extended laterally along the hinge, supported by receding dental plates whose bases extend anteriorly as fine ridges reaching to about mid valve length. Initially these adminicula run along the margins of the sulcus, but in some mature specimens the ridges extend outside the margins of the sulcus (e.g. Pl. 11, fig. 13; Plate 13, fig. 7). Muscle field long and narrow, confined within the limits of the plates. In some specimens there is a weak myophragm along the crest of the central sulcal ridge in the posterior half of the shell.

*Dorsal interior.* Cardinalia weak, with poorly defined, small crural plates and very shallow sockets. A pair of prominent adminicula, subparallel to weakly divergent, extend from the crural bases to about the mid length of the valve, flanking the narrow median sulcal groove in which the poorly defined muscle field is confined posteriorly. A slender myophragm extends along the centre of the groove, extending in some specimens beyond the mid valve length.

*Dimensions of figured specimens*

| | | l | w |
|---|---|---|---|
| 84.13G.50 | Ventral valve (holotype) | 11·5 | 22·8 |
| 84.13G.33 | Dorsal valve (paratype) | 14·3 | 24·0 est. |
| 19.205GR1a | Dorsal valve (paratype) | 8·3 | 14·0 |
| 84.15G.2 | Dorsal valve (paratype) | 16·5 | 30·8 est. |
| 84.13G.44 | Ventral valve (paratype) | 15·1 | 27·8 |
| 19.205GR1 | Ventral valve (paratype) | 7·3 | 14·8 |
| 84.14G.7 | Ventral valve (paratype) | 7·0 | 18·6 |

*Discussion.* As discussed by Brunton and Champion (1974) and Brunton and Rissoné (1976), problems of interpreting *Fusella* stem from its original ill-definition and continued difficulties in understanding the affinities of the type species. Nevertheless, these authors made a clear case for retaining the validity of the genus and this new species from Ty-nant fits closely within it. The two other British species discussed by Brunton and Champion (1974) and Brunton and Rissoné (1976), *Fusella fusiformis* (Phillips) and *Fusella rhomboidea* (Phillips), both differ from *F. extrata* in being strongly transverse with extended alae. In *F. rhomboidea* the ribs are fewer and stronger and the dorsal fold commonly has a low median rib. In *F. fusiformis* the dorsal fold is very low and has a median groove.

### Superfamily DELTHYRIDOIDEA Phillips, 1841
### Family MUCROSPIRIFERIDAE Boucot, 1959
### Subfamily TYLOTHYRIDINAE Carter, 1972

### Genus TYLOTHYRIS North, 1920

*Type species. Spirifer laminosa* M'Coy, 1841; from the lower Carboniferous (Tournaisian, Courceyan–Chadian, Hook Head Formation) of Hook Head, Ireland.

### *Tylothris laminosa laminosa* (M'Coy, 1841)

Plate 12, figures 1–8; Plates 14–15; Plate 16, figures 1–6

1841 *Spirifera laminosa* M'Coy, p. 26.
v.1920 *Tylothyris laminosa* (M'Coy) North, p. 197, pl. 13, fig. 16.
v.1920 *Tylothyris laminosa* (M'Coy) mut. $\gamma$ North, p. 200, pl. 13, figs 1–2, 12–13.
v.1984 *Tylothyris laminosa* (M'Coy); Brunton, p. 77, figs 108–119 [see also for earlier synonymy]

*Material.* Twenty-eight ventral valves and 17 dorsal valves.

*Remarks.* This well-known species has been described in considerable detail by North (1920) and Brunton (1984)

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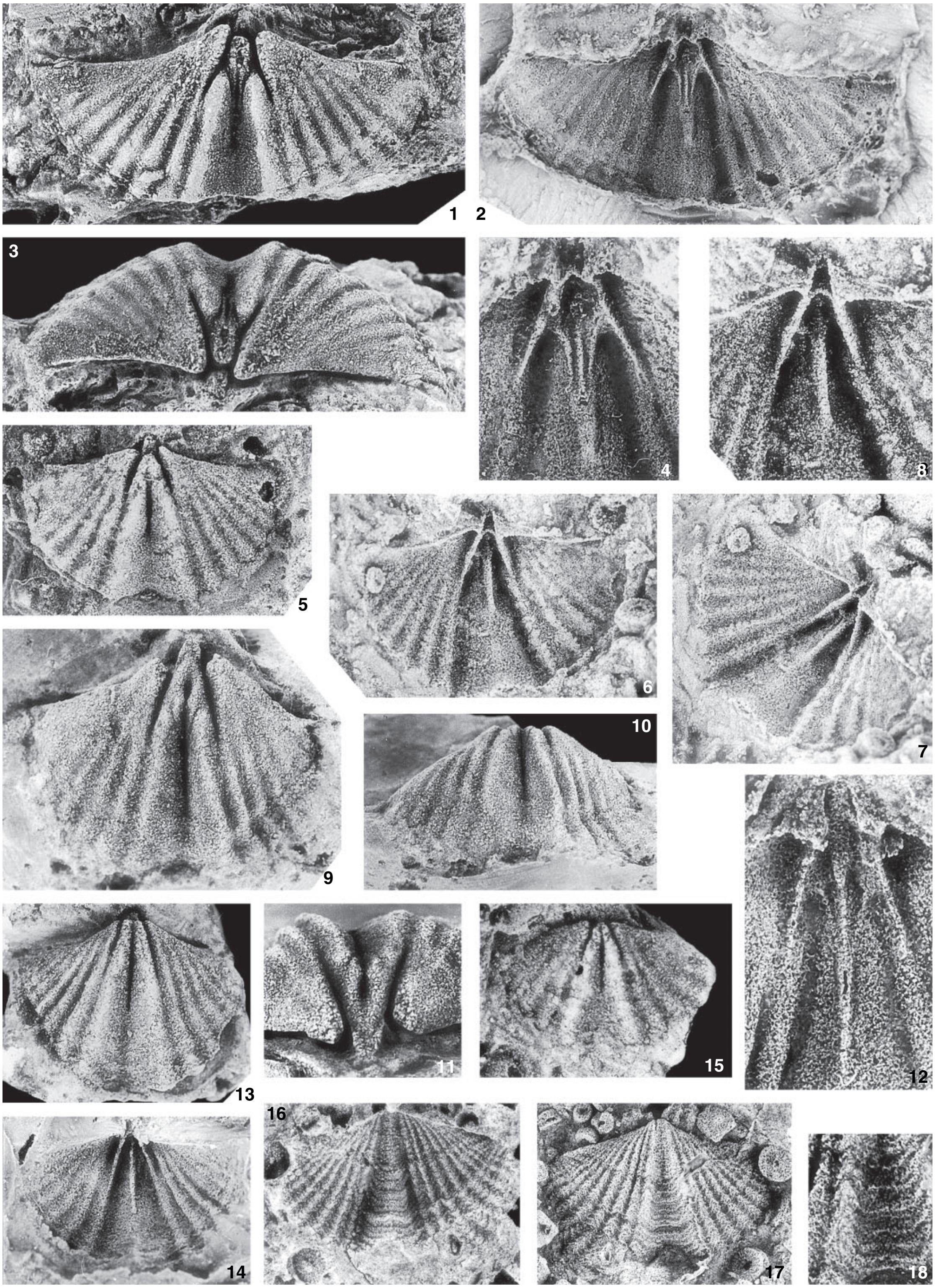
**EXPLANATION OF PLATE 14**

Figs 1–18. *Tylothyris laminosa laminosa* (M'Coy, 1841). 1–4, 84.13G.21, ventral internal mould, latex cast, posterior view of mould, × 3; detail of posterior structures, × 5. 5–8, 22.9G49.3, ventral internal mould, latex cast, oblique-lateral view of latex cast, × 3; and detail of posterior, × 5. 9–12, 84.14G.4, ventral internal mould, anterior view, × 2·5; posterior view, × 3; and detail of posterior structure, × 5. 13–14, 84.13G.12, ventral internal mould and latex cast; × 3·5. 15, 22.9G49.3, ventral internal mould; × 3. 16–18, 22.9G50.2, ventral external mould, latex cast, × 2; and detail of ornament in sulcus, × 5.

and our large population from Ty-nant conforms in all aspects. There is thus no need to repeat such descriptive information here. The range of variation is fully illustrated in Plates 12 and 14–16. As noted by Brunton (1984, p. 79), the supposed 'holotype' of the species selected by North (1920, p. 198) is in fact a neotype.

PLATE 14



BASSETT and BRYANT, *Tylothyris*

North (1920, p. 199) recognised two 'mutations' of *T. laminosa*, essentially as subspecies. He clearly stated (p. 200) that mutuation *gamma* was the typical form of the species, so that as noted in synonymy already by Brunton (1984, p. 77) this in fact is a junior synonym of *T. laminosa s.s.* (i.e. *T. laminosa laminosa*). For purposes of nomenclatorial formality we here select the specimen figured by North on his plate 13, figure 2 as the lectotype of *T. laminosa* mut. *gamma*, refigured here on Plate 16, figures 3–5. North's originals of his plate 13, figures 1 and 12 are refigured here on Plate 16, figures 6 and 8–9, respectively; they are syntypes of *T. laminosa* mut. *gamma*.

North's principal criteria (1920, p. 199, fig. 4) for separating his *Tylothyris laminosa* mut. *beta* from *gamma* were smaller size and a less elevated ventral interarea. The differences in fact are very slight, and we here provisionally synonymise the two forms. All North's material of *beta* is in the National Museum of Wales (Cunnington Collection; see Text-fig. 9). As lectotype of *T. laminosa beta* we select 22.9G78·3, figured on Text-figure 9A–C; all other specimens on Text-figure 9 are syntypes.

Brunton (1984, p. 83) noted that North's subdivision of what he named *Tylothyris subconica* (Martin, 1809) into two subspecies, *T. subconica subconica* and *T. subconica castletonensis*, might belong to other genera, possibly *Syringothyris* or *Pseudosyrinx*; analysis of such possible relationships is beyond the scope of this paper, but the two named subspecies are illustrated for comparison on Text-figure 10. The specimen named by North (1920, p. 203) as the holotype of *T. subconica subconica* is not from the original Martin collection, and should thus be identified as a neotype (19.246G4; see Text-fig. 10A–G).

### Superfamily SYRINGOTHYRIDOIDEA Frederiks, 1926
### Family SYRINGOTHYRIDAE Frederiks, 1926
### Subfamily SYRINGOTHYRIDINAE Frederiks, 1926

### Genus SYRINGOTHYRIS Winchell, 1863

*Type species. Spirifer carteri* Hall, 1857 [*pro Syringothyris typa* Winchell, 1863]; from the lower Carboniferous (Tournaisian, Kinderhook, Waverly Group, probably Logan Formation, Byer Member) of Licking County, Ohio, USA.

### *Syringothyris* cf. *exoleta* North, 1920
Plate 17, figures 6–11

1918 *Syringothyris* cf. *cuspidata* [Martin]; Dixey and Sibly, p. 138.
v*1920 *Syringothyris cuspidata* mut. *exolata* North, p. 185, text-figs 1d, 3e–f, pl. 11, figs 4–5.

*Material.* One ventral interior, one dorsal interior.

*Discussion.* North (1920) recognised that the commonly quoted species *Syringothyris cuspidata* (Martin, 1809) could be fairly readily subdivided into a number of taxa, some of which he named as new species and others as 'mutations' of *cuspidata*. Vandercammen (1955) later identified one of the North species (*Syringothyris elongata*) in Tournaisian rocks of Belgium, but otherwise North's separate taxa have hardly been mentioned or used in systematic studies. Because we have direct access to North's collections, we are able to make some comments on the different taxa, but it is beyond the scope of this paper to attempt a full revision. From Ty-nant there are only two specimens of *Syringothyris*, which we judge to be closest to *S. cuspidata* mut. *elongata* North. We regard this taxon as being specifically distinct from *S. cuspidata* itself and identify the Ty-nant specimens as *S.* cf. *exoleta*. We designate specimen 20.474G3 as the lectotype of *S. exoleta*, the 'typical example' illustrated by North (1920, pl. 11, fig. 4a–b) and re-figured here on Plate 17, figures 1–5, from Sutton in Glamorgan.

*Description of Ty-nant specimens.* Valves relatively large, about twice as wide as long, subequally biconvex. Maximum width at the hinge, cardinal extremities only slightly alate, lateral margins evenly curved anteromedially, anterior margin only weakly curved, with broadly uniplicate commissure. Dorsal umbo slightly inflated, median fold present from the posterior margin, rounded throughout and widening rapidly to occupy about 25 per cent of the valve width at the anterior margin. Ventral valve with complementary sulcus. Fold and sulcus smooth, flanks bearing numerous strong, rounded costae about 2 mm wide anteriorly and evenly spaced.

Delthyrium and notothyrium wide with rounded apices, other details obscure on the mould material.

Ventral interior obscure, but with slender dental plates/adminicula extending a short distance anteriorly fairly close alongside the ridge formed by the external sulcus. Outer socket ridges

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**EXPLANATION OF PLATE 15**

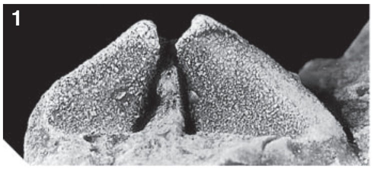
Figs 1–19. *Tylothyris laminosa laminosa* (M'Coy, 1841). 1, 57.421G60.3, interarea on ventral mould; × 3. 2–3, 57.421G60.1, ventral external latex cast, × 2; and detail of ornament, × 5. 4–6, 22.9G50.3, dorsal external mould, latex cast, × 2; and detail of ornament, × 5. 7–9, 57.421G60.3, dorsal external mould, latex cast, × 2; and detail of ornament, × 5. 10–12, 84.13G.11, dorsal internal mould, latex cast, × 2; and detail of cardinalia, × 5. 13–14, 22.9G50.5, dorsal external mould and latex cast; × 2. 15–16, 22.9G50.1, latex cast of dorsal external mould, × 2; and detail of ornament, × 5. 17–18, 22.9G54, dorsal internal mould and anterior view; × 2. 19, 57.421G60.2, posterior view of dorsal internal mould; × 3.

disposed along hinge line, sockets long, widening anterolaterally, relatively deep, inner socket ridges disposed at about 120 degrees to one another. Other internal features not known.

*Dimensions of figured specimens*

| | l | w | t |
|---|---|---|---|
| Dorsal internal mould | 26·2 | 58·8 est. | – |

PLATE 15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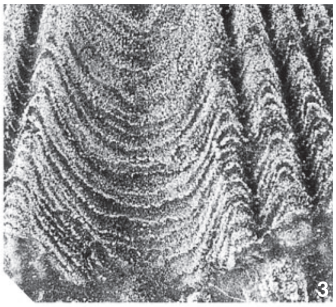
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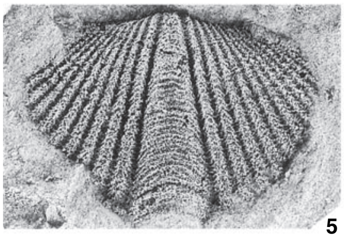
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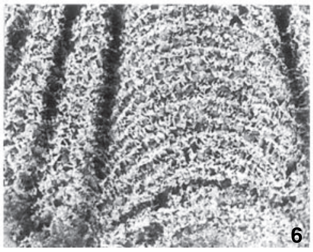
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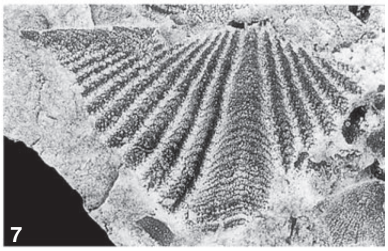
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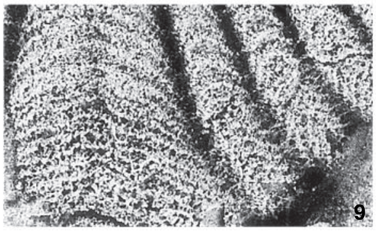
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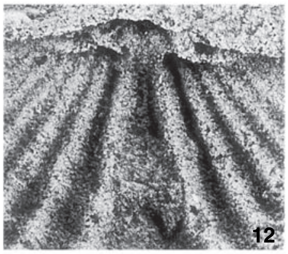
10


11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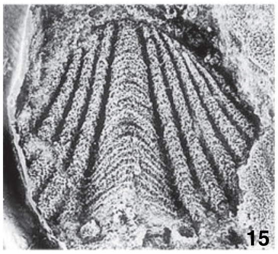
13


14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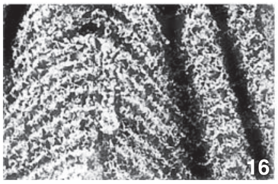
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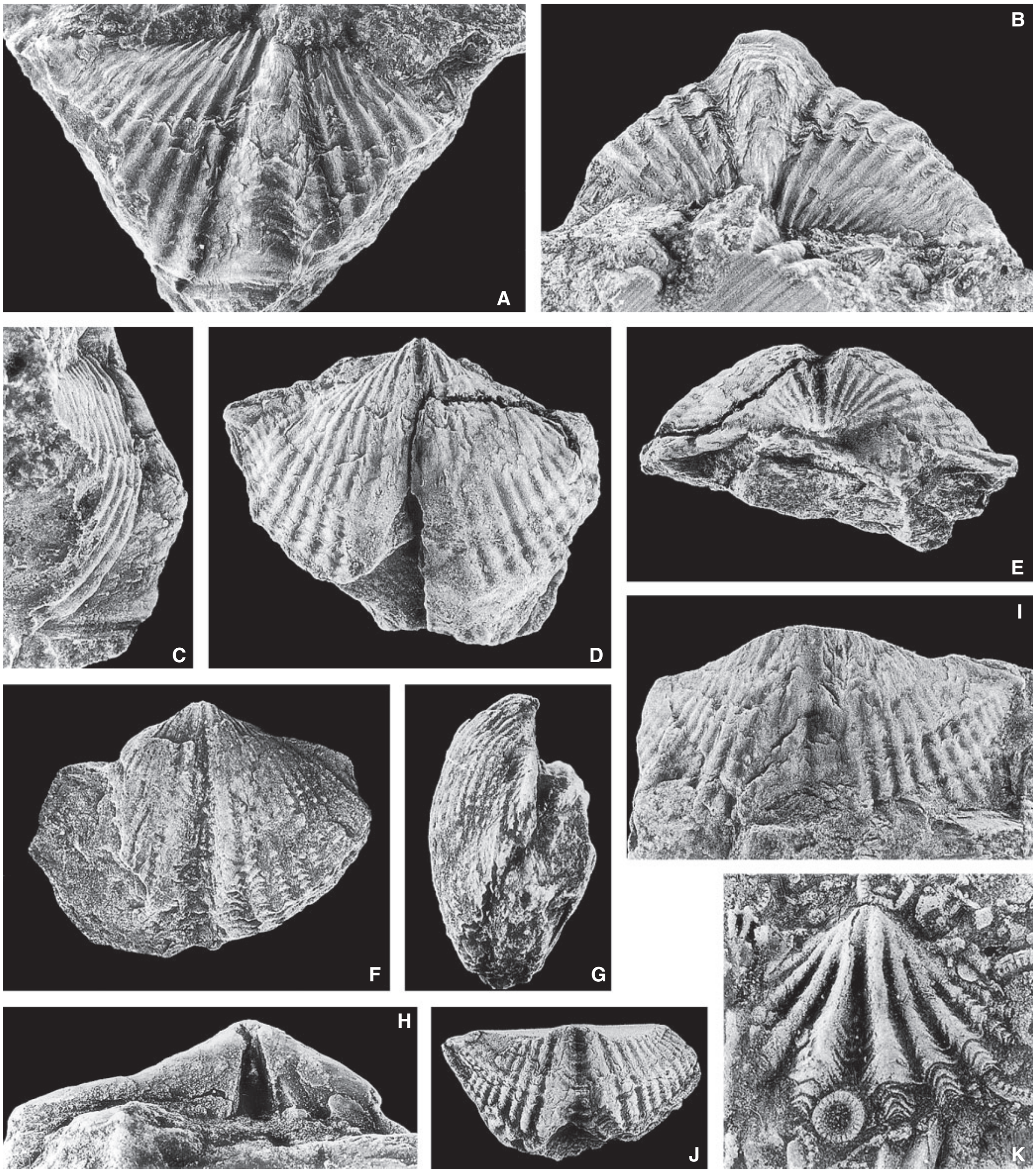
17


18


19

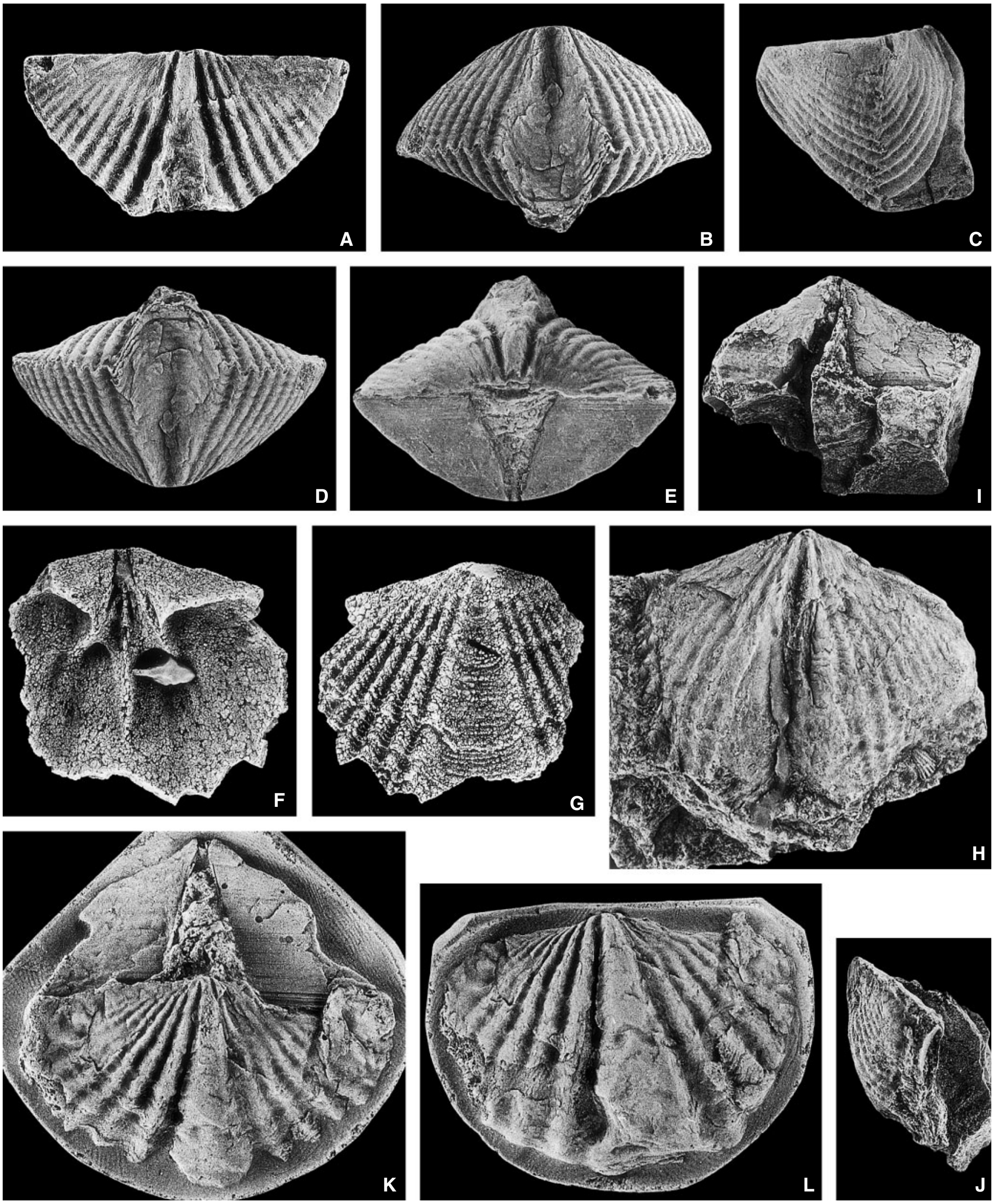
BASSETT and BRYANT, *Tylothyris*



**TEXT-FIG. 9.** *Tylothyris laminosa* (M‘Coy, 1841) *beta* North, 1920. A–C, lectotype, 22.9G78.3, dorsal exterior with posterior and lateral views; × 2. D–E, 22.9G78.4, ventral exterior and posterior; × 2. F–H, 22.9G78.1, ventral exterior and lateral views, × 2; and posterior view of interarea, × 3. I, 22.9G77, ventral exterior after sectioning of apex; × 2. J, 22.9G78.2, ventral exterior with apex removed; × 2. A–J all from Carboniferous, Courceyan, top of Lower Limestone Shales, Coed-y-Gareg, Upper Neath Valley, Mid-Glamorgan. K, 57.421G50, ventral exterior, × 5; Carboniferous, Courceyan, Howle Hill, Mitcheldean, Gloucestershire.

| | | | |
|---|---|---|---|
| 84.13G.35 | | | |
| Ventral internal mould | 26·1 | 52·3 | – |
| 57.421G33 | | | |
| Conjoined valves, lectotype | 35·0 | 72·5 | 40·1 |
| 20.474G3 | | | |

*Remarks.* Of North’s (1920) other new taxa, the closest to *S. exoleta* is *S. cyrtorhyncha*, both having large, flat ventral interareas that become weakly concave apically, and similarly convex ventral valves. We select as lectotype of *S. cyrtorhyncha* specimen 20.474G4 (North 1920, pl. 11, fig. 6), from Mitcheldean Quarry, Gloucestershire, refigured here on Text-figure 11A–C. The specimen of *cyrtorhyncha* that North cited and figured as an example of the species (1920, p. 184, pl. 22, fig. 3a–b) is lost. The holotype of *S. principal-*



**TEXT-FIG. 10.** A–G, *Tylothyris subconica subconica* (Martin, 1809) North, 1920. A–E, neotype, 19.246G4, conjoined valves in dorsal, ventral, lateral, anterior and posterior views, × 1·5; Carboniferous, Brigantian, Attermire, Yorkshire. F–G, 20.474G9, ventral interior and exterior, × 2; Carboniferous, Brigantian, Waterhouses, Staffordshire. H–J, *Tylothyris subconica* cf. *castletonensis* North, 1920, 22.9G70, ventral exterior, × 1·5; posterior and lateral views, × 1; Carboniferous, Brigantian, Park Hill, Derbyshire. K–L, *Tylothyris subconica castletonensis* North, 1920, plaster casts of specimens in the Natural History Museum. K, 22.9G60.1, dorsal exterior with ventral interarea, × 1·5; Carboniferous, Brigantian, Wetton, Staffordshire. L, 22.9G60.2, dorsal exterior, × 1·5; Carboniferous, Brigantian, Wetton, Staffordshire.

*is* North (1920, pl. 11, fig. 2) from Howle Hill, is 20.474G2, refigured here on Text-figure 11D–F. A syntype of *S. principalis* is figured on Text-figure 11G–I. *S. principalis* is readily distinguished from *S. exoleta* by its considerably smaller maximum size, completely flat ventral interarea, acutely angled delthyrium, and in having markedly finer costation.

### Superfamily SPIRIFERINOIDEA Davidson, 1884
### Family SPIRIFERINIDAE Davidson, 1884

### Genus SPIRIFERELLINA Frederiks, 1919

*Type species. Terebratulites cristatus* Schlotheim, 1816; from the Permian (Zechstein) of Glücksbrunnen, Thuringia, eastern Germany.

### *Spiriferellina* sp.
Plate 13, figures 17–18

*Material.* One ventral internal mould.

*Remarks.* Endopunctae typical of *Spiriferellina* and related genera are not preserved in the dolomitic matrix of any of our mould material from Ty-nant, and in this single internal mould there is no preservation of the equally typical micro-ornament of pustules and microspines. Nevertheless it has an otherwise typical morphology for the genus in its small size (l, 8·8; w, 10) with eight strong angular plications. Internally there are very slender dental plates set along the crest of each of the first submedial plicae forming the inner expression of the exterior interplications. The median septum is short and slender, extending from the delthyrial cavity onto the central ridge of the valve floor.

The lateral margins of the specimen appear not to be completely preserved and the original outline was probably slightly more transverse than is apparent in Plate 13, figures 17–18. From the number and general character of the plications we consider the specimen to be close to *Spiriferellina octoplicata* (J. de C. Sowerby, 1827). The plications of *S. insculpta* (Phillips 1836) as described by Brunton (1984) appear to be broader and less angular. The Ty-nant specimen may be close to forms described by North (1920, p. 217) as *S. octoplicata* mut. *delta* Vaughan (see Text-fig. 12A herein).

North (1920), Campbell (1959), Logan (1964), Brunton and Champion (1974) and Brunton (1984), among many others, made fundamental contributions to the understanding of this group of endopunctate brachiopods, including genera such as *Punctospirifer* North, 1920. Material in the North Collection includes a wide range of specimens that illustrate many points in understanding these discussions, and comparative taxa of particular relevance to such understanding are illustrated on Text-figures 12–14.

### Superfamily DIELASMATOIDEA Schuchert, 1913
### Family CRANAENIDAE Cloud, 1942
### Subfamily CRANAENINAE Cloud, 1942

### Genus CRANAENA Hall and Clarke, 1893

*Type species. Terebratula romingeri* Hall, 1863, p. 297; from the Hamilton Group (Middle Devonian) of Michigan and Iowa, USA.

### *Cranaena*? sp.
Text-figure 15

*Material.* One ventral interior.

*Description.* Valve moderately and uniformly convex along its sagital length, but becoming flattened to weakly concave along the flanks. The specimen is broken but was probably elongate oval in outline, with the fairly straight posterolateral margins divergent at almost 80 degrees to one another. Palintrope short, rounded. Delthyrial margin curved.

Teeth very small, supported by short dental plates set closely adjacent to the walls of the delthyrial cavity. Bases of dental plates produced anteriorly as slender, weakly divergent ridges extending to about 25 per cent of the valve length. Posterior wall of delthyrial cavity vertical. Musculature not impressed but probably confined within the shallow depression between the bounding ridges.

*Remarks.* The assignment of this specimen to *Cranaena* is tentative but not without reason. In the absence of any shell to determine the shell fabric and of any definitive dorsal structures it is not possible strictly to confirm even that it is a terebratulide. But it certainly differs from any other species in the Ty-nant fauna, and in the ventral morphology it is very similar to specimens of *Cranaena* from the Black Rock Limestone Group at Barry, which

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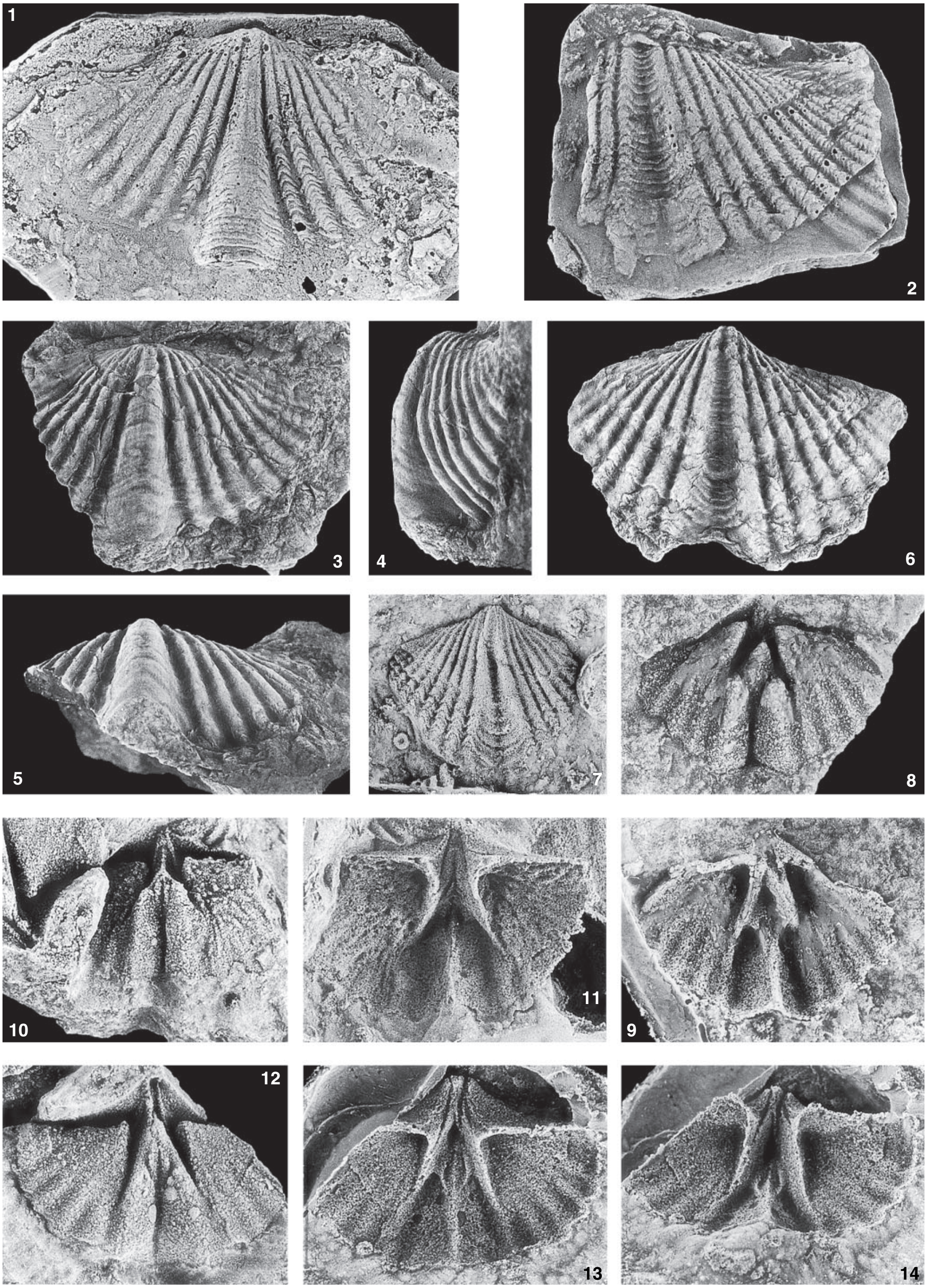
#### EXPLANATION OF PLATE 16

Figs 1–2. *Tylothyris laminosa laminosa* (M‘Coy, 1841) 22.9G.71, 22.9G.72, dorsal external plaster cast, × 2, and ventral external plaster cast, × 2, of specimen in The National Museum Ireland, Dublin; Carboniferous, Courceyan, Hook Head, County Wexford, Eire.

Figs 3–14. *Tylothyris laminosa gamma* North, 1920. 3–5, lectotype, 19.246G3, dorsal exterior, lateral and posterior, × 2; Courceyan, Alps Quarry, Wenvoe, Glamorgan. 6, 20.474G5, ventral exterior, × 2; Courceyan, Twyn-yr-odin, Glamorgan. 7, 57.421G55.1, ventral exterior; × 2. 8–9, 20.474G7, ventral internal mould and latex cast; × 3. 10–11, 57.421G55.2, ventral internal mould, × 3; and latex cast, × 5. 12–14, 57.421G55.2, ventral internal mould, latex cast and anterior-oblique view of latex cast; × 3. 7–14 all from Courceyan, Collafield, Littledean, Gloucestershire.

have all the definitive attributes of that genus. *Cranaena* is a not uncommon genus in lower Carboniferous successions in many parts of the world (e.g. Cloud 1942; Stehli 1965; Carter 1967, 1987; Roberts 1971; Carter and Poletaev 1998), but these records from South Wales represent its first recognition in the British Isles. Brunton (1982) has reviewed the taxonomy and distribution of other British Dinantian terebratulide genera.

PLATE 16



BASSETT and BRYANT, *Tylothyris*

## ECOLOGY AND BIOGEOGRAPHY

Of the 16 brachiopod genera recorded here from the Ty-nant fauna, *Schizophoria* (48 per cent) and wide-hinged spiriferides (mostly *Tylothyris*, *Unispirifer*, *Fusella*; 30 per cent) together make up almost 80 per cent of the total known specimens. In this pattern of relative abundances within suprageneric groupings there is a close comparison with the Benthic Assemblage (BA) structure established by Boucot (1975) as part of a world-wide marine Silurian–Devonian community framework. Spiriferides are consistently dominant members of BA3 in the mid part of the ecological spectrum, interpreted as being in an environment with low water energy with medium- to high-diversity faunas. The common presence of dalmanellides (i.e. *Schizophoria*) at Ty-nant suggests a setting in the inner part of BA3 towards the 'margin' with BA2. Such an interpretation is also supported by the presence of athyrides and chonetides (*Composita*, *Rugosochonetes*), which are generally more common in BA2 environments.

Lithofacies at Ty-nant equally support a relatively low-energy setting. The purple-red dolomites and dolomitic siltstones show no evidence of structures of high water energy. We conclude therefore that our fauna was established in the inner part of the early Carboniferous South Wales mid-ramp environment on a level subtidal bottom, with few or no intervals of high energy water. In the Boucot (1975) model this would suggest a maximum subtidal depth of 200 feet (60 m).

The accompanying fauna at Ty-nant is remarkably limited in diversity by comparison with the brachiopods, restricted to sparse camerate crinoids, rugose corals and trepostome bryozoans (see Pl. 18). Although dolomitisation has destroyed some of the fine detail in this material, preservation is generally good, for example with crinoid material being preserved without complete disarticulation, again indicative of a low-energy environment.

*Biogeography.* Reconstructions of early Carboniferous palaeogeography place southern Britain straddled across or close to the equator (e.g. Scotese and McKerrow 1990, fig. 17). This was an interval of prolonged cosmopolitanism, and with regard to brachiopods there was consistent interplay between the main continental blocks from which faunas have been described; all were in an equatorial to tropical/subtropical position. Thus, there are no endemic genera identified in the Ty-nant brachiopod fauna. Migration patterns related to climate have been discussed by Kelley *et al.* (1990). Taxonomic linkages of the Ty-nant genera with faunas from other regions are documented in the bibliographic references cited throughout this paper.

*Acknowledgements.* Dr John Nudds (formerly Trinity College, Dublin), Mr Nigel Monahan (National Museum of Ireland, Dublin) and Dr Sarah Long (Natural History Museum, London) kindly gave access to and/or loaned collections under their care for comparative purposes. Dr Howard Brunton (formerly The Natural History Museum) was most helpful in discussing and giving advice on many matters related to Carboniferous brachiopods. Our thanks are also extended to many other colleagues who provided information and publications at various times. Reviews of the manuscript by Drs Long and Brunton are much appreciated.

## REFERENCES

BENSON, W. N., DUN, W. S. and BROWNE, W. R. 1920. The geology and petrology of the Great Serpentine Belt of New South Wales. *Proceedings of the Linnean Society of New South Wales, Section B*, **45**, 337–374, pls 18–24.

BHATT, J. J. 1976. Geochemistry and petrology of the Main Limestone Series (Lower Carboniferous), South Wales, U.K. *Sedimentary Geology*, **15**, 55–86.

BOUCOT, A. J. 1959. Brachiopods of the Lower Devonian rocks at Highland Mills, New York. *Journal of Paleontology*, **33**, 727–769, pls 90–103.

—— 1975. *Evolution and extinction rate controls*. Developments in Palaeontology and Stratigraphy, 1. Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York, xv + 427 pp.

BRAND, P. J. 1970. Scottish Carboniferous chonetoids. *Bulletin of the Geological Survey of Great Britain*, **31**, 89–137, pls 7–13.

—— 1972. Some British Carboniferous species of the brachiopod genus *Leptagonia* McCoy. *Bulletin of the Geological Survey of Great Britain*, **39**, 57–79.

BRONN, H. G. 1862. *Die Klassen und Ordnungen der Weichtiere (Malacozoa), Vol. 3, Part 1.* Leipzig and Heidelberg, 518 pp., 44 pls.

BROWN, T. 1849. *Illustrations of the fossil conchology of Great Britain and Ireland*. Smith, Elder, London, viii + 274 pp., 115 pls.

BRUNTON, C. H. C. 1968. Silicified brachiopods from the Viséan of County Fermanagh (II). *Bulletin of the British Museum (Natural History), Geology*, **16**, 1–70, 9 pls.

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### EXPLANATION OF PLATE 17

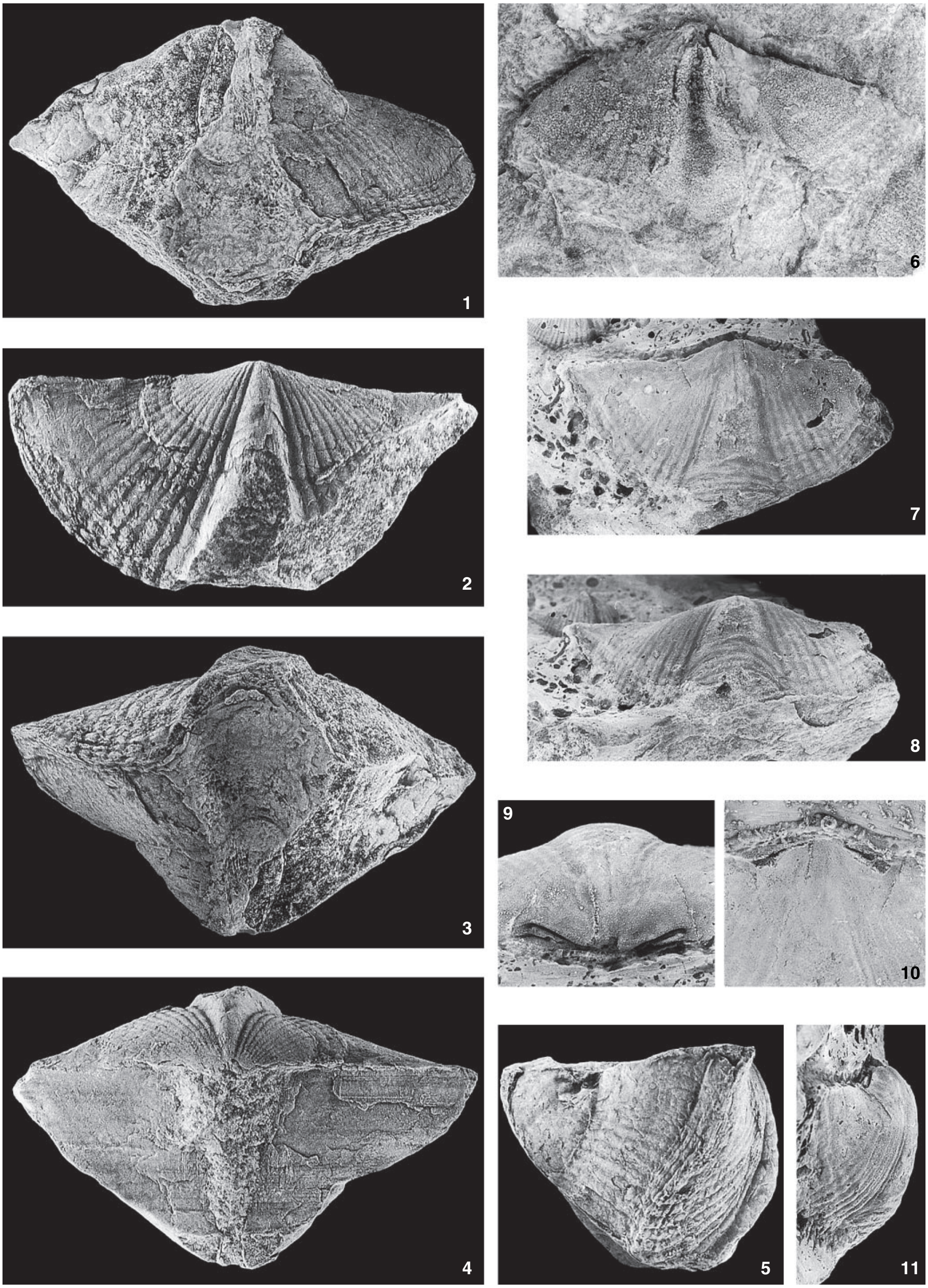
Figs 1–5. *Syringothyris exoleta* North, 1920. Lectotype, 20.474G3, ventral, dorsal, anterior, posterior and lateral views of conjoined valves; × 1; Black Rocks, near Sutton, Glamorgan.

Figs 6–11. *Syringothyris* cf. *exoleta* North, 1920. 6, 57.421G33, ventral internal mould; × 1·5. 7–11, 84.13G.35, dorsal internal mould in normal, anterior, × 1, and posterior views, × 1·5; latex cast of posterior structures, × 1·5; and lateral view of mould, × 1.

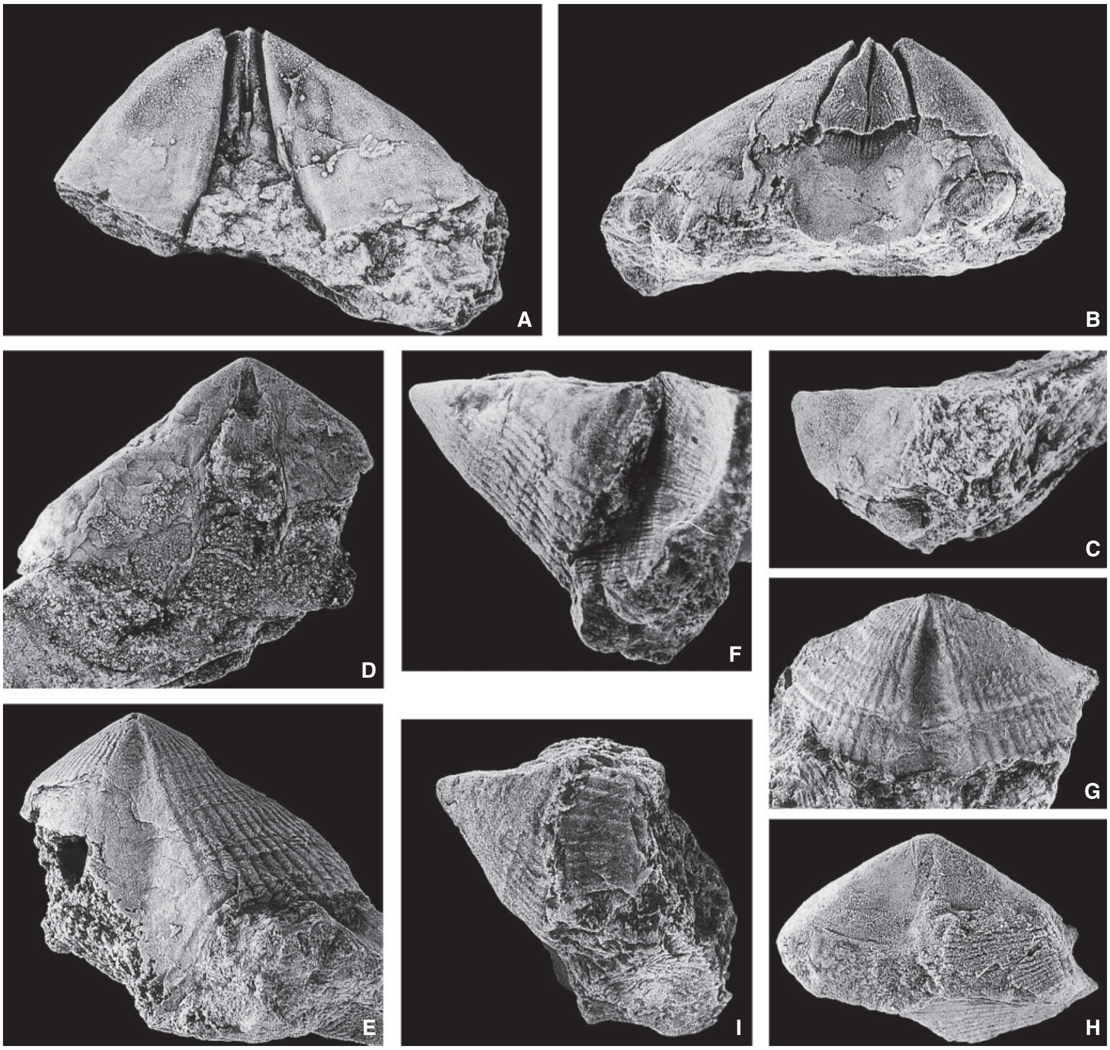
—— 1980. Type specimens of some Upper Palaeozoic athyridide brachiopods. *Bulletin of the British Museum (Natural History), Geology*, **34**, 219–234.

—— 1982. British Dinantian (Lower Carboniferous) terebratulid brachiopods. *Bulletin of the British Museum (Natural History), Geology*, **36**, 45–57.

## PLATE 17



BASSETT and BRYANT, *Syringothyris*



**TEXT-FIG. 11.** A–C, *Syringothyris cuspidata* (Martin, 1809) *cyrtorhyncha* North, 1920, lectotype, 20.474G4, ventral internal mould showing interarea with syrinx, and lateral view, × 1; Carboniferous, Courceyan, Mitcheldean Quarry, Gloucestershire. D–I, *Syringothyris principalis* North, 1920. D–F, 20.474G2, holotype, ventral valve showing interarea and ventral and lateral views, × 1·5; Carboniferous, Courceyan, Howle Hill, Mitcheldean District. G–I, 20.474G1, syntype, ventral exterior with posterior and lateral views, × 1·5; Carboniferous, Courceyan, Trot's Corner, Mendip Area.

—— 1984. Silicified brachiopods from the Viséan of County Fermanagh, Ireland (III). Rhynchonellids, spiriferids and terebratulids. *Bulletin of the British Museum (Natural History), Geology*, **38**, 27–130.

—— and CHAMPION, C. 1974. A Lower Carboniferous brachiopod fauna from the Manifold Valley, Staffordshire. *Palaeontology*, **17**, 811–840, pls 107–111.

—— LAZAREV, S. S. and GRANT, R. E. 1995. A review and new classification of the brachiopod order Productida. *Palaeontology*, **38**, 915–936.

—— and RISSONÉ, A. 1976. *Fusella* M'Coy 1844a, problematic brachiopod genus from the Lower Carboniferous. *Bulletin of the British Museum (Natural History), Geology*, **27**, 275–284.

CAMPBELL, K. S. W. 1957. A Lower Carboniferous brachiopod-coral fauna from New South Wales. *Journal of Paleontology*, **31**, 34–98, pls 11–17.

—— 1959. The type species of three Upper Palaeozoic punctate spiriferoids. *Palaeontology*, **1**, 351–363, pls 58–60.

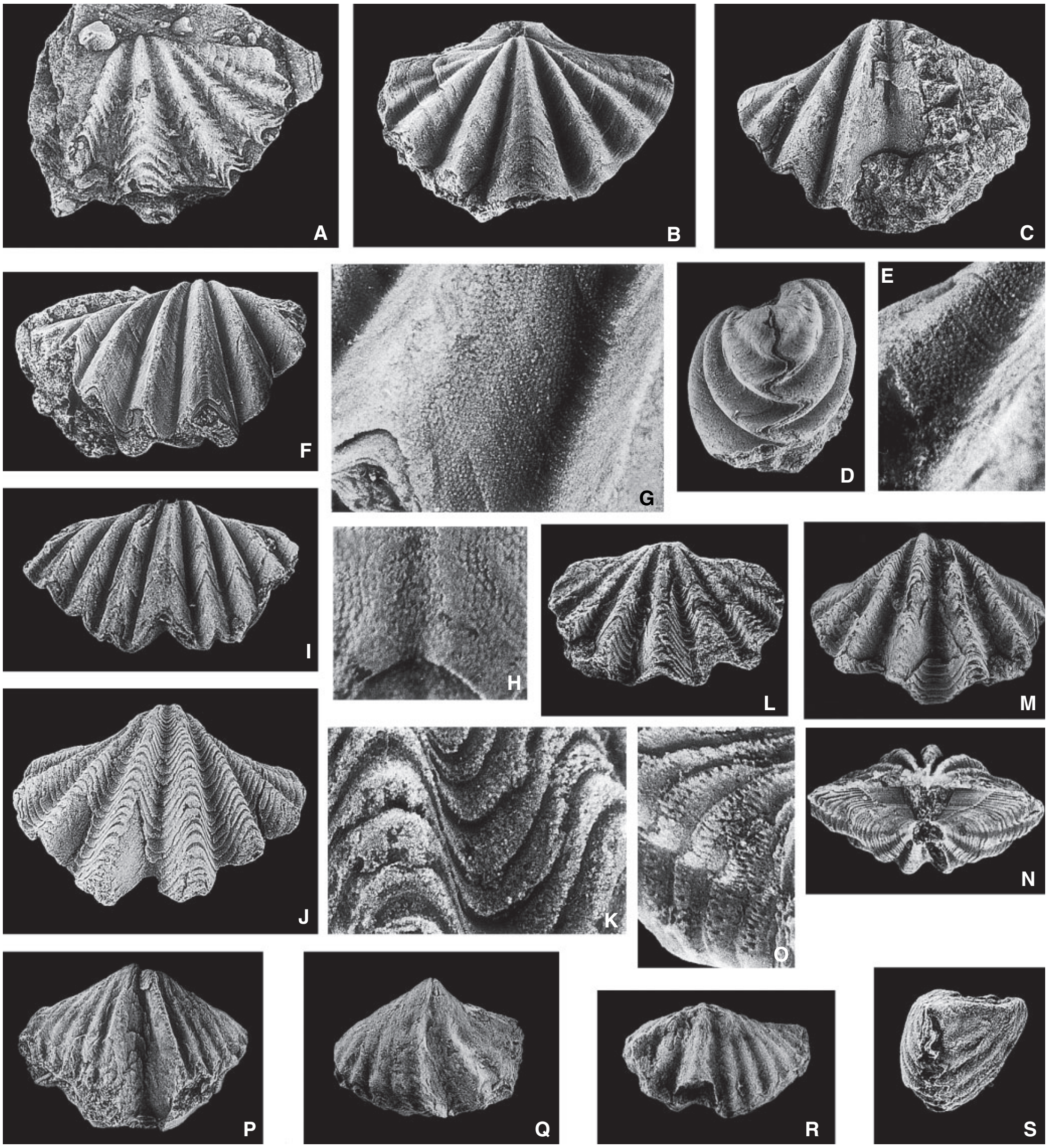
CARTER, J. L. 1967. Mississippian brachiopods from the Chappel Limestone of central Texas. *Bulletins of American Paleontology*, **53**, 249–488, pls 13–45.

—— 1972. Two new genera of lamellose spiriferacean brachiopods. *Journal of Paleontology*, **46**, 729–734, pl. 1.

—— 1974. New genera of spiriferid and brachythyridid brachiopods. *Journal of Paleontology*, **48**, 674–696, pls 1–4.

—— 1987. Lower Carboniferous brachiopods from the Banff Formation of Western Alberta. *Bulletin of the Geological Survey of Canada*, **378**, 1–183, pls 1–29.

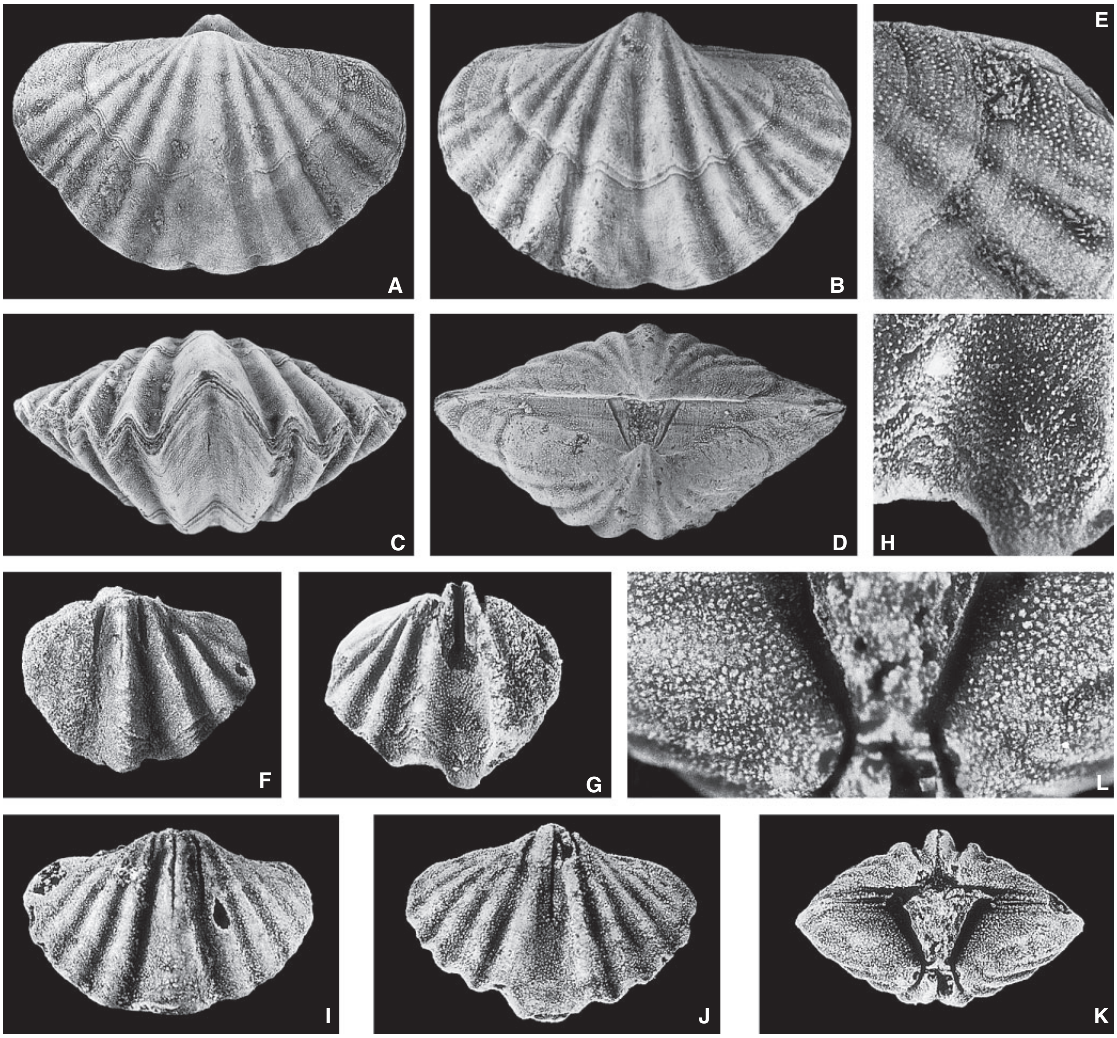
—— 1988. Early Mississippian brachiopods from the Glen Park Formation of Illinois and Missouri. *Bulletin of the Carnegie Museum of Natural History*, **27**, 1–82.



**TEXT-FIG. 12.** *Spiriferellina octoplicata* (J. de C. Sowerby, 1827) *delta* Vaughan, 1915. A, 20.474G6, dorsal exterior, × 4; Barry, South Glamorgan; figured North 1920, plate 13, figure 9. B–I, *Spiriferellina octoplicata octoplicata* (J. de C. Sowerby). B–E, 19.246G10, conjoined valves, dorsal exterior, ventral exterior, lateral, × 2, and detail of ornament, × 10; Carboniferous, Brigantian, Parkhill, Derbyshire. F–H, 22.9G1.1, dorsal exterior, × 2, with details of pustulose ornament, × 10 and × 14.5; Carboniferous, Brigantian, Treak Cliff, Castleton, Derbyshire. I, 22.9G1.4, dorsal exterior, × 2; Carboniferous, Brigantian, Treak Cliff, Castleton, Derbyshire. J–K, *Spiriferellina insculpta* (Phillips, 1836), 57.421G74, ventral exterior, × 2, and detail of ornament showing pustules, × 10; Carboniferous, Brigantian, Treak Cliff, Castleton, Derbyshire. L–O, *Spiriferellina octoplicata* (J. de C. Sowerby, 1827), 57.421G72.1, conjoined valves, dorsal, ventral, posterior, × 2, and detail of ornament on ventral valve, × 12; Carboniferous, Treak Cliff, Derbyshire. P–S, *Spiriferellina perplicata* North, 1920, topotypes. P, 22.9G6.1, ventral, exterior; × 2. Q–S, 22.9G6.3, conjoined valves, ventral exterior, dorsal and, lateral views, × 2; Carboniferous, Treak Cliff, Castleton, Derbyshire.

—— 1999. Tournaisian (early Osagean) brachiopods from a bioherm in the St. Joe Formation near Kenwood, Oklahoma. *Annals of the Carnegie Museum*, **68**, 91–149.

—— JOHNSON, J. G., GOURVENNEC, R. and HOU HONG-FEI 1994. A revised classification of the spiriferid brachiopods. *Annals of the Carnegie Museum*, **63**, 327–374.



**TEXT-FIG. 13.** A–E, *Spiriferina walcotti* J. de C. Sowerby, 1823, 57.421G155.2, conjoined valves, dorsal exterior, ventral exterior, posterior, and anterior, × 2; with details of pustulose ornament on dorsal valve, × 5; Jurassic, Lower Lias, Radstock, Somerset. F–H, *Spiriferellina cristata* Schlotheim, 1816, 57.421G103.1, conjoined valves in dorsal and ventral views, × 4; with detail of pustules on ventral sulcus, × 10; Permian, Humbleton Hill, Durham. I–L, *Spiriferellina multiplicata* (J. de C. Sowerby, 1829), 57.421G102.1, steinkern with dorsal internal, ventral, and posterior views, × 4, and detail of pustulose ornament on ventral valve, × 12; Permian, Sunderland.

—— and POLETAEV, V. I. 1998. Atokan (late Bashkirian or early Moscovian) brachiopods from the Hare Fiord Formation of Ellesmere Island, Canadian Arctic Archipelago. *Annals of the Carnegie Museum*, **67**, 105–180.

CLOUD, P. E. 1942. Terebratuloid Brachiopoda of the Silurian and Devonian. *Special Paper of the Geological Society of America*, **38**, i–xi + 1–182, pls 1–26.

CONIL, R. *et al.* 1977. Nouvelle charte stratigraphique du Dinantien type de la Belgique. *Annales de la Société Géologique du Nord*, **96**, 363–371.

COOPER, G. A. and DUTRO, J. T. Jr 1982. Devonian brachiopods of New Mexico. *Bulletins of American Paleontology*, **82** and **83** (no. 315), 1–215, pls 1–45.

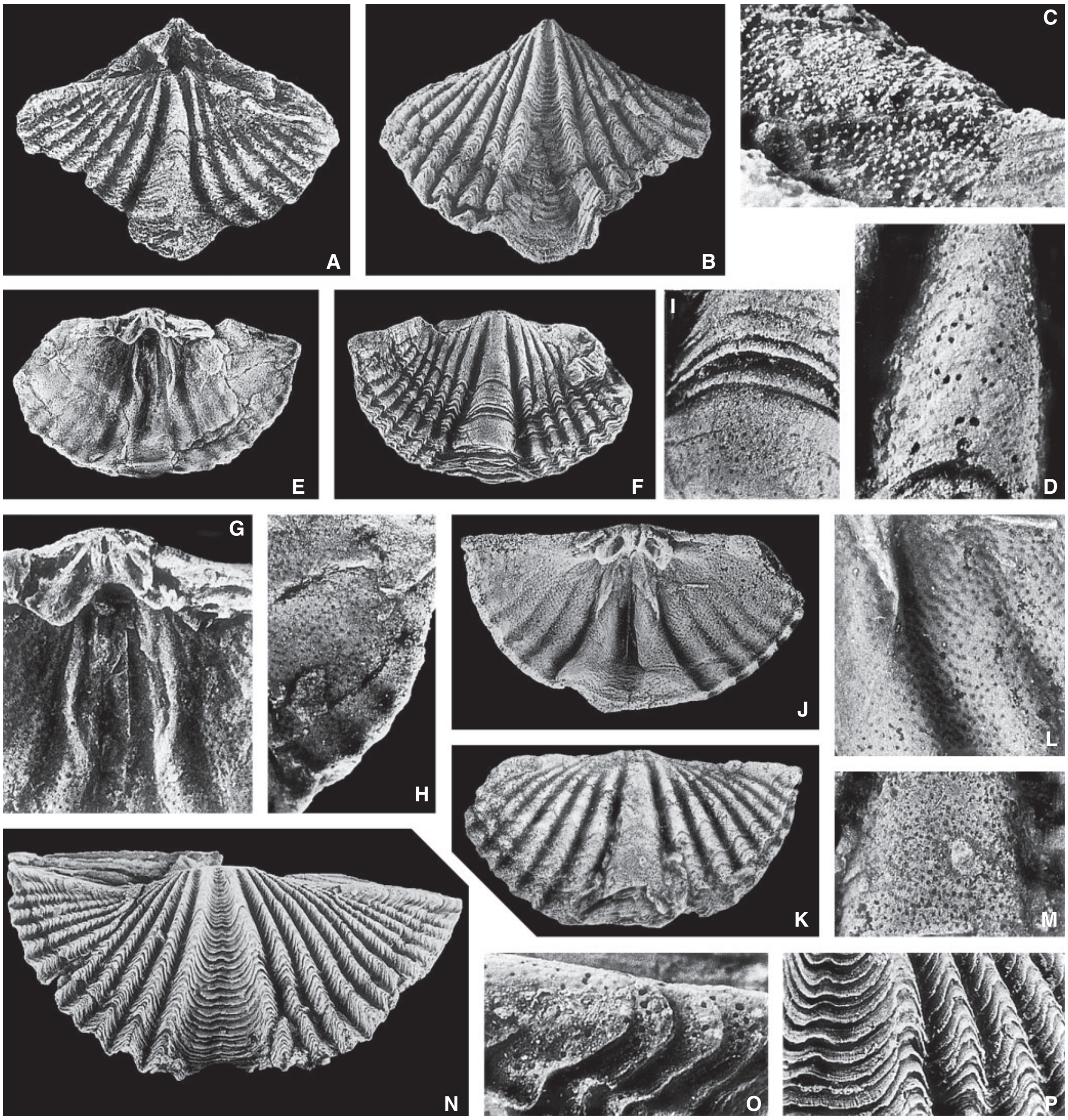
—— and GRANT, R. E. 1974. Permian brachiopods of West Texas, II. *Smithsonian Contributions to Paleobiology*, **15**, 233–793, pls 24–191.

COPPER, P. 1978. Devonian atrypoids from western and northern Canada. *In* STELCK, C. R. and CHATTERTON, B. D. E. (eds). Western and Arctic Canadian biostratigraphy. *Special Paper of the Geological Association of Canada*, **18**, 289–317, pls 1–7.

DAVIDSON, T. 1858–63 A monograph of the British fossil Brachiopoda. Vol. II, Part V, Nos. 1–5. The Carboniferous Brachiopoda. *Palaeontographical Society [Monograph]*, London, pp. 1–280, pls 1–55. [Publication Nos. 42, 46, 54, 55, 59].

—— 1881. On genera and species of spiral-bearing Brachiopoda, from specimens developed by the Rev. Norman Glass. *Geological Magazine, New Series, Decade 2*, **8**, 1–13, 15 text-figs.

DEMANET, F. 1934. Les brachiopodes du Dinantien de la Belgique, Vol. 1. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, **61**, 1–116, pls 1–10.



**TEXT-FIG. 14.** A–M, *Punctospirifer scabricosta redesdalensis* North, 1920; all topotypes. A–D, 22.9G42.1, conjoined valves in dorsal exterior and ventral exterior views, × 2; with details of pustulose ornament on ventral area and dorsal fold, × 12. E–I, 22.9G42.2, dorsal interior and exterior, × 3; with details of musculature and cardinalia, × 8; with detail of internal punctation, × 10, and pustules on external fold, × 9. J–M, 57.421G151, dorsal valve interior and exterior, × 3; with detail of internal punctation and on external fold, × 10. N–P, *Punctospirifer scabricosta* North, 1920. 22.9G85, ventral valve exterior, × 2; with detail of punctation, × 12, and ornament, × 5. All specimens are from Carboniferous, Asbian, Redesdale, Northumberland.

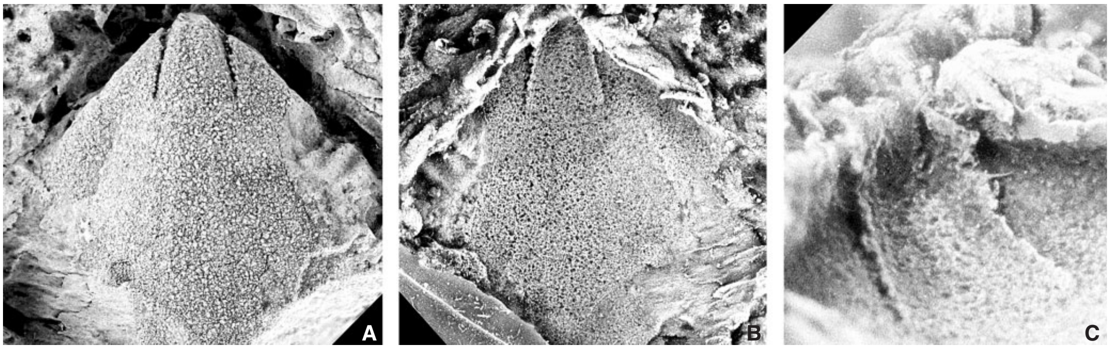
DIXEY, F. and SIBLY, T. F. 1918. The Carboniferous Limestone Series on the south-eastern margin of the South Wales Coalfield. *Quarterly Journal of the Geological Society of London*, **73**, 111–164, pls 12–16.

DIXON, E. E. L. and VAUGHAN, A. 1911. The Carboniferous succession in Gower (Glamorganshire), with notes on its fauna and conditions of deposition. *Quarterly Journal of the Geological Society of London*, **67**, 477–571, pls 38–41.

FREDERIKS, G. H. 1919. Palaeontological studies. 2. On the Upper Carboniferous spiriferids of the Urals. *Bulletin du Comité Géologique, Saint Pétersbourg*, **38**, 295–324.

—— 1926. Table for determination of the genera of the family Spiriferidae King. *Izvestiya Akademii Nauk SSSR, Seriya 6*, **20**, 393–423. [In Russian].

—— 1933. Paleontological notes. 4. On some upper Palaeozoic brachiopods of Eurasia. *Materialy Tznigni, Paleont. i Stratigr.*, **2**, 24–32. [In Russian].



**TEXT-FIG. 15.** *Cranaena* sp. 84.13G.44, internal mould of ventral valve and latex cast, × 4; with oblique view of dental plate morphology on the cast, × 8.

GEORGE, T. N. 1954. Pre-Seminulan Main Limestone of the Avonian Series in Breconshire. *Quarterly Journal of the Geological Society of London*, **110**, 283–322, 1 pl.

—— 1974. Lower Carboniferous rocks in Wales. 85–115. *In* OWEN, T. R. (ed.). *The Upper Palaeozoic and post-Palaeozoic rocks of Wales*. University of Wales Press, Cardiff, 426 pp.

—— JOHNSON, G. A. L., MITCHELL, M., PRENTICE, J. E., RAMSBOTTOM, W. H. C., SEVASTOPULO, G. D. and WILSON, R. B. 1976. A correlation of Dinantian rocks in the British Isles. *Geological Society, London, Special Report*, **7**, 1–87.

—— and OSWALD, D. H. 1957. The Carboniferous rocks of the Donegal Syncline. *Quarterly Journal of the Geological Society of London*, **113**, 137–183.

GIRTY, G. H. 1904. New molluscan genera from the Carboniferous. *Proceedings of the United States National Museum*, **27**, 721–736, pls 16–18.

GRAY, J. E. 1840. *Synopsis of the contents of the British Museum*. Forty-second edition. London, 370 pp.

HALL, J. 1857. Descriptions of Palaeozoic fossils. *New York State Cabinet of Natural History, Annual Report*, **10**, 41–186.

—— 1863. Descriptions of new species of Brachiopoda from the Upper Helderberg, Hamilton, and Chemung groups. *New York State Cabinet of Natural History, Annual Report*, **16**, 48.

—— and CLARKE, J. M. 1892–95. *Palaeontology: Volume 8. An introduction to the study of the genera of Palaeozoic Brachiopoda. Part 2*. Geological Survey of the State of New York, 317 pp.

HARPER, D. A. T. 2000. Dalmanellidina. 782–844 *In* WILLIAMS, A., BRUNTON, C. H. C., CARLSON, S. J., *et al.* 1997–2002 (see below).

HIRD, K., TUCKER, M. E. and WATERS, R. A. 1987. Petrography, geochemistry and origin of Dinantian dolomites from south-east Wales. 359–377. *In* MILLER, J., ADAMS, A. E. and WRIGHT, V. P. (eds). *European Dinantian environments*. John Wiley and Sons, Chichester, x + 402 pp.

IVANOVA, YE. A. 1972. Main features of spiriferid evolution (Brachiopoda). *Paleontologicheskii Zhurnal*, **1972**, 28–42. [In Russian].

JOHNSON, J. G. 1982. *Davidsonia* and Davidsoniacea, Devonian strophomenid brachiopods. *Journal of Paleontology*, **56**, 973–976, pl. 1.

KELLEY, P. H., RAYMOND, A. and LUTKEN, C. B. 1990. Carboniferous brachiopod migration and latitudinal diversity: a new palaeoclimatic method. 325–332. *In* McKERROW, W. S. and SCOTESE, C. R. (eds). *Palaeozoic palaeogeography and biogeography*. Memoir of the Geological Society of London, **12**, 435 pp.

KING, W. 1846. Remarks on certain genera belonging to the Class Palliobranchiata. *Annals and Magazine of Natural History*, **18**, 26–42.

—— 1850. A monograph of the Permian fossils of England. *Palaeontographical Society [Monograph]*, London, xviii + 1–258, pls 1–28. [Publication no. 5].

KONINCK, L. G. DE 1843. *Description des animaux fossiles qui se trouvent dans le terrain Carbonifère de Belgique*. Liège, iv + 650 pp., 55 pls.

—— 1847. Monographie des genres *Productus* et *Chonetes*. *Mémoires de la Société Royale des Sciences de Liège*, 1–246, pls 1–20.

—— 1883. Sur le *Spirifer mosquensis* et sur ses affinities avec quelques autres espèces du même genre. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, **2**, 371–395, pls 13–15.

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## EXPLANATION OF PLATE 18

Figs 1–5. Camerate crinoid indet. 1–3, 58.464G59.1,2, external mould and latex cast, × 3; mould of calyx, × 2. 4–5, 84.13G.39, external mould and latex cast; × 2.

Figs 6–8. *Sychnoelasma konincki* (Milne-Edwards and Haime, 1851). 6, 84.13G.16, latex cast of calyx; × 2. 7–8, 84.13G.30a, internal mould showing cardinal fossula on the convex side of calyx, transverse and lateral views; × 2.

Fig. 9. *Fenestella* sp. 5, 84.13G.42, external mould; × 6.

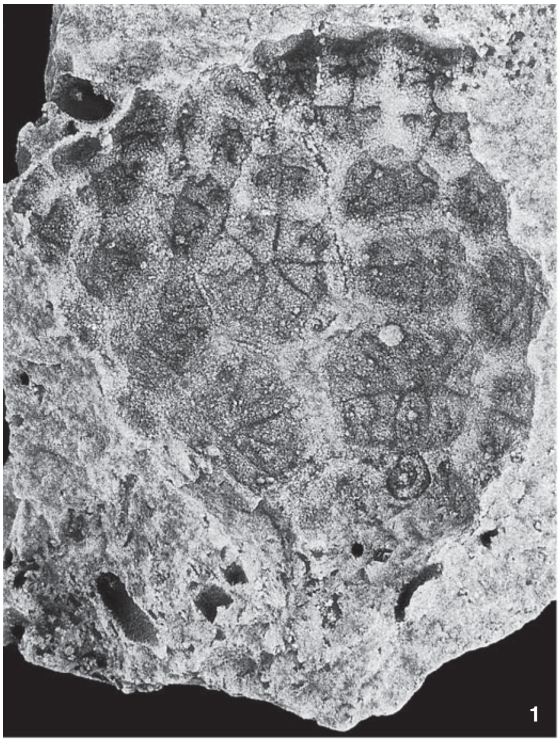
Fig. 10. Trepostome bryozoan indet., 84.13G.7, external mould; × 5.

—— 1887. Faune du Calcaire Carbonifère de la Belgique. Sixième Partie. Brachiopodes. *Annales du Musée Royal d'Histoire Naturelle de Belgique*, **14**, 1–154, pls 1–37.

LAZAREV, S. S. 1976. Morphology and evolution of brachiopods (of the superfamily Enteletacea). *Transactions of the Institute of Paleontology, Academy of Sciences of the USSR*, **154**, 1–167, pls 1–15. [In Russian].

—— 1990. Evolution and systematics of productids. *Akademiya Nauk SSSR, Trudy Paleontologicheskogo Instituta*, **242**, 1–174, pls 1–40. [In Russian].

## PLATE 18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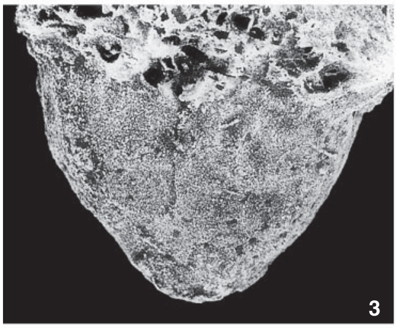
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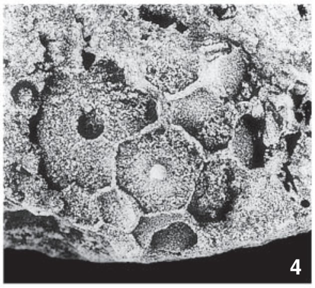
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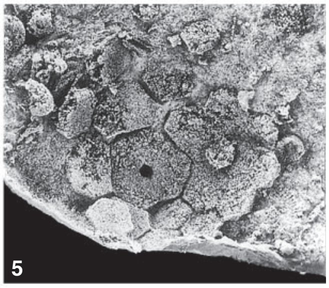
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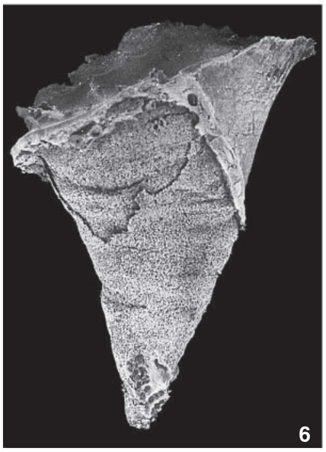
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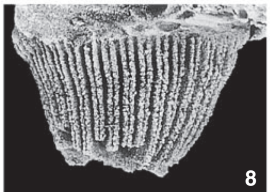
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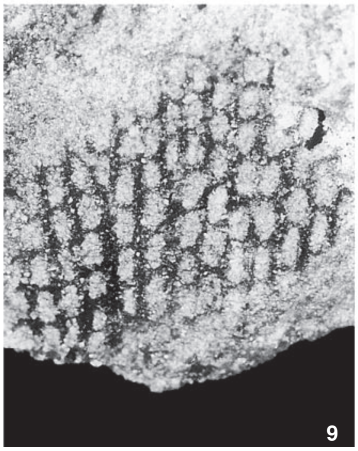
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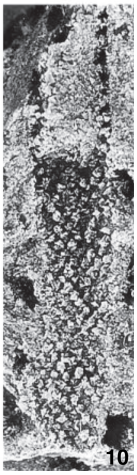
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BASSETT and BRYANT, Tournaisian fauna

LÉVEILLÉ, C. 1835. Aperçu géologique de quelques localités tres riches en coquilles sur les frontières de France et de Belgique. *Memoires de la Société Géologique de France*, **2**, 29–40, pl. 2.

LOGAN, A. 1964. An Indo-Pacific spiriferinid from the Triassic of northeastern British Columbia. *Bulletin of Canadian Petroleum Geology*, **12**, 692–718.

MARTIN, W. 1809. *Petrificata derbiensia: or figures and descriptions of petrifactions collected in Derbyshire.* Wigan, 28 pp., 52 pls.

MAXWELL, W. G. H. 1961. Lower Carboniferous brachiopod faunas from Old Cannindah. *Queensland Journal of Paleontology*, **35**, 82–103, pls 19–20.

M'COY, F. 1841. *A catalogue of the Museum of the Geological Society of Dublin.* Dublin, 28 pp.

—— 1844. *A synopsis of the characters of the Carboniferous Limestone fossils of Ireland.* Williams and Norgate, London, 274 pp., 29 pls.

McINTOSH, M. J. 1974. Some Scottish Carboniferous davidsoneacean brachiopods. *Scottish Journal of Geology*, **10**, 199–221, pls 1–6.

MUIR-WOOD, H. M. 1928. The British Carboniferous Producti. II. *Productus* (*sensu stricto*); *Semireticulatus* and *Longspinus* groups. *Memoirs of the Geological Survey of Great Britain, Palaeontology*, **3**, 1–217, pls 1–12.

—— 1962. *On the morphology and classification of the brachiopod suborder Chonetoidea*. British Museum (Natural History), London, 132 pp., 16 pls.

—— and COOPER, A. G. 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). *Memoir of the Geological Society of America*, **81**, 1–447, pls 1–135.

NORTH, F. J. 1920. On *Syringothyris* Winchell, and certain Carboniferous Brachiopoda referred to *Spiriferina* d'Orbigny. *Quarterly Journal of the Geological Society of London*, **76**, 162–227, pls 11–13.

OEHLERT, D. P. 1890. Note sur différents groupes établis dans le genre *Orthis* et en particulier sur *Rhipidomella* Oehlert (= *Rhipidomys* Oehlert, olim). *Journal de Conchyliologie, Series 3*, **30**, 366–374.

PAECKELMANN, W. 1930. Die Brachiopoden des deutschen Underkarbons. 1. Die Orthiden, Strophomeniden und Choneten des Mittleren und Oberen Unterkarbons. *Abhandlungen der Preussischen Geologischen Landesantalt, Neue Folge*, **122**, 143–326, pls 9–24.

PHILLIPS, J. 1836. *Illustrations of the geology of Yorkshire, Part 2. The mountain limestone district.* London, 253 pp., 25 pls.

—— 1841. *Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon and West Somerset*. Longman, Brown, Green and Longmans, London, 231 pp., 60 pls.

POCOCK, Y. P. 1968. Carboniferous schizophoriid brachiopods from Western Europe. *Palaeontology*, **11**, 64–93, pl. 18.

RAMSBOTTOM, W. H. C. and MITCHELL, M. 1980. The recognition and division of the Tournaisian Series in Britain. *Journal of the Geological Society of London*, **137**, 61–63.

ROBERTS, J. 1971. Devonian and Carboniferous brachiopods from the Bonaparte Gulf Basin, northwestern Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics*, **122**, 1–319, pls 1–59 [2 vols].

SARTENAER, P. and PLODOWSKI, G. 1996. Restatement of the late Tournaisian *Spirifer tornacensis* de Koninck, 1883 on the base of the original collection. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, **66**, 53–71.

SARYCHEVA, T. G., SOKOLSKAYA, A. N., BEZNOSOVA, G. A. and MAKSIMOVA, S. V. 1963. Carboniferous brachiopods and palaeogeography of the Kuznetsk Basin. *Akademiya Nauk SSSR, Trudy Paleontologicheskogo Instituta*, **95**, 1–547, pls 1–64. [In Russian].

SCHLOTHEIM, E. F. VON 1816. Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. *Denkschriften Koniglichen Akademie der Wissenschaften zu München, Mathematisch-Physikalisch Klasse*, **6**, 13–36.

SCHUCHERT, C. 1893. A classification of the Brachiopoda. *American Geologist*, **11**, 141–167.

—— 1913. Class 2. Brachiopoda. 355–420, text-figs 526–636. *In* ZITTEL, K. A. VON. *Textbook of Palaeontology, Vol. 1* (translated and edited by EASTMAN, C. R.). Second edition. Macmillan & Co., London.

—— 1929. Classification of brachiopod genera, fossil and recent. 10–25. *In* SCHUCHERT, C. and LEVENE, C. M. *Animalia pars 42. In* POMPECKJ, J. F. (ed.). Fossilium Catalogus, Vol. 1. Junk, Berlin.

SCOTESE, C. R. and McKERROW, W. S. 1990. Revised world maps and introduction. 1–21. *In* McKERROW, W. S. and SCOTESE, C. R. (eds). *Palaeozoic palaeogeography and biogeography*. Memoir of the Geological Society of London, **12**, 435 pp.

SEVASTOPULO, G. D. 1981. Lower Carboniferous. 147–171. *In* HOLLAND, C. H. (ed.). *A geology of Ireland.* Scottish Academic Press, Edinburgh, x + 335 pp.

—— and NUDDS, J. R. 1987. Courceyan (early Dinantian) stratigraphy of Britain and Ireland: coral and conodont zones compared. *In* BRENCKLE, P. L., LANE, H. R. and MANGER, W. L. (eds). Selected studies in Carboniferous paleontology and biostratigraphy. *Courier Forschungsinstitut Senckenberg*, **98**, 39–46.

SMYTH, L. B. 1930. The Carboniferous rocks of Hook Head, County Wexford. *Proceedings of the Royal Irish Academy*, **39**, B, 523–566, pls 15–20.

SOKOLSKAYA, A. N. 1941. Lower Carboniferous and Devonian–Carboniferous brachiopods of the Moscow Basin (Tschernyschino, Upa and Melevka-Burajevnia beds). Part 1. Spiriferidae. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR*, **12**, 1–138, pls 1–12. [In Russian, English summary].

—— 1950. Chonetidae of the Russian Platform. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR*, **27**, 1–108, pls 1–13. [In Russian].

—— 1960. Subfamily Chonetacea. 221–223. *In* SARYCHEVA, T. G. (ed.). *Principles of Paleontology. Bryozoa, Brachiopoda*. Academy of Sciences, USSR, Moscow. [In Russian].

SOWERBY, J. and SOWERBY, J. C. DE 1812–46 *The mineral conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the earth.* Seven volumes. Pls 1–383 (1812–22) by J. Sowerby; pls 384–648 (1823–46) by J. de C. Sowerby. London.

SQUIRRELL, H. C. and DOWNING, R. A. 1969. The geology of the South Wales Coalfield, Part I. The country around Newport, Monmouthshire. Third edition. *Memoirs of the Geological Survey of Great Britain*, Sheet 249, 1–333.

STEHLI, F. G. 1965. Paleozoic Terebratulida. 730–762. *In* WILLIAMS, A., ROWELL, A. J., MUIR-WOOD, H. M., *et al.* 1965 (see below).

STRAHAN, A. 1909. The geology of the South Wales Coalfield, Part I. The country around Newport, Monmouthshire. Second edition. *Memoirs of the Geological Survey of Great Britain*, Sheet 249, 1–115.

—— and CANTRILL, T. C. 1902. The geology of the South Wales Coalfield, Part III. The country around Cardiff. First edition. *Memoirs of the Geological Survey of Great Britain*, Sheet 263, 1–149.

—— —— 1912. The geology of the South Wales Coalfield, Part III. The country around Cardiff. Second edition. *Memoirs of the Geological Survey of Great Britain*, Sheet 263, 1–157.

THOMAS, I. 1910. The British Carboniferous Orthotetinae. *Memoirs of the Geological Survey of Great Britain, Palaeontology*, **1**, 83–134, pl. 13.

THOMAS, G. A. 1971. Carboniferous and early Permian brachiopods from western and northern Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics*, **56**, 1–277, 31 pls.

TOLMATCHOFF, I. P. 1924. Lower Carboniferous fauna from the Kuznetsk coal basin. *Materialy po Obshchei Prikladnoi Geologii*, **25**, 1–320, pls 1–5. [In. Russian].

VANDERCAMMEN, A. 1955. A propos des perforations du test de *Syringothyris* et des genres voisins. *Publications pour l'Etude de la Paléontologie et de la Stratigraphie Houillères*, **21**, *Hors Série*, 387–393, pls A–B.

VARKER, W. J. and SEVASTOPULO, G. D. 1985. The Carboniferous System: Part 1. Conodonts of the Dinantian Subsystem from Great Britain and Ireland. 167–189. *In* HIGGINS, A. C. and AUSTIN, R. L. (eds). *A stratigraphical index of Conodonts*. Ellis Horwood, Chichester, 263 pp.

VAUGHAN, A. 1904. Notes on the corals and brachiopods obtained from the Avon section and preserved in the Stoddart collection. *Proceedings of the Bristol Naturalists' Society, New Series*, **10**, 90–134, pls 1–2.

—— 1905. The palaeontological sequence in the Carboniferous Limestone of the Bristol area. *Quarterly Journal of the Geological Society of London*, **61**, 181–307, pls 22–26.

—— 1911. *In* REYNOLDS, S. H. and VAUGHAN, A. Faunal and lithological sequence in the Carboniferous Limestone Series (Avonian) of Burrington Combe (Somerset). *Quarterly Journal of the Geological Society of London*, **67**, 342–392, pls 28–31.

—— 1915. Correlation of Dinantian and Avonian. *Quarterly Journal of the Geological Society of London*, **71**, 1–52, pls 1–7.

WAAGEN, W. H. 1883. Salt Range fossils, Part 4 (2), Brachiopoda. *Palaeontologia Indica, Series 13*, **1**, fasc. 2, 391–546, pls 29–49.

—— 1884. Salt Range fossils, Part 4 (2), Brachiopoda. *Palaeontologia Indica, Series 13*, **1**, fasc. 3, 547–610, pls 50–57.

WATERS, R. A. and LAWRENCE, D. J. D. 1987. The geology of the South Wales Coalfield, Part III. The country around Cardiff. Third edition. *Memoirs of the Geological Survey of Great Britain*, Sheet 263, 1–114.

WELLER, S. 1909. The fauna of the Fern Glen Formation. *Bulletin of the Geological Society of America*, **20**, 265–332.

—— 1914. The Mississippian Brachiopoda of the Mississippi Valley basin. *Illinois State Geological Survey, Monograph*, **1**, 1–508, pls 1–83 [bound as separate Atlas].

WHITE, C. A. 1862. Description of new species of fossils from the Devonian and Carboniferous rocks of the Mississippi Valley. *Proceedings of the Boston Society of Natural History*, **9**, 8–33, 5 text-figs.

WILLIAMS, A. 1953. North American and European stropheodontids: their morphology and systematics. *Memoirs of the Geological Society of America*, **56**, 1–67, pls 1–13.

—— and BRUNTON, C. H. C. 1993. Role of shell structure in the classification of the orthotetidine brachiopods. *Palaeontology*, **36**, 931–966, pls 1–5.

—— —— CARLSON, S. J. *et al.* 1997–2002. *In* KAESLER, R. L. (ed.). *Treatise on invertebrate palaeontology, Part H, Brachiopoda, Revised*. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, Vol. 1 (1997), Introduction, i–xx + 1–539; Vols 2–3 (2000), Linguliformea, Craniiformea, and Rhynchonelliformea, i–xxx + 1–423, i–ii + 424–919; Vol. 4 (2002), Rhynchonelliformea (part), i–xxxix + 921–1688.

—— ROWELL, A. J., MUIR-WOOD, H. M. *et al.* 1965. *In* MOORE, R. C (ed.). *Treatise on invertebrate paleontology, Part H, Brachiopoda*. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, xxxii + 927 pp.

WINCHELL, A. 1863. Description of the fossils of the Yellow Sandstones lying beneath the Burlington Limestone at Burlington, Iowa. *Proceedings of the Academy of Natural Sciences of Philadelphia, Series 2*, **15**, 2–25.

WRIGHT, V. P. 1986. Facies sequence on a carbonate ramp: the Carboniferous Limestone of South Wales. *Sedimentology*, **33**, 221–241.

—— 1987. The evolution of the early Carboniferous Limestone province in southwest Britain. *Geological Magazine*, **124**, 477–480.

ŻAKOWA, H. 1989. Orthid brachiopods from the Upper Visean (Carbonifeorus of the Świętokrzyskie Mts., Poland. *Acta Palaeontologica Polonica*, **34**, 91–124, pls 1–8.