FUSELLA M'COY 1844, A PROBLEMATIC BRACHIOPOD GENUS FROM THE LOWER CARBONIFEROUS

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ABSTRACT

The genus *Fusella* is redescribed and assigned to the subfamily Strophopleurinae. Related or similar species are discussed.

INTRODUCTION

THE GENUS name *Fusella*, first published in 1844 by M'Coy for small transversely fusiform spiriferide brachiopods, has been poorly known and ill-used for about one hundred and thirty years. We redescribe the type specimen of the type species, *F. fusiformis* (Phillips), and other conspecific and congeneric material in the hope of establishing the genus *Fusella* on a more stable basis. Silicified specimens of *F. rhomboidea* (Phillips) allow the description of interiors believed to be closely comparable to those of *F. fusiformis*. The genus is formally redescribed and we discuss both its position within the Spiriferacea and those species which, in the past, have been assigned to *Fusella*.

SYSTEMATICS

Superfamily **SPIRIFERACEA** King 1846

Family **MUCROSPIRIFERIDAE** Pitrat 1965

Subfamily **STROPHOPLEURINAE** Carter 1974

DIAGNOSIS (emended). Small to medium very transverse Mucrospiriferidae with simple lateral costae and lirate, subimbricate micro-ornamentation. Fold and sulcus commonly non-costate, with or without median rib and groove ; sulcus bounding ribs commonly accentuated, as are corresponding dorsal grooves. Ventral interarea large and denticulate. Dental plates short or buried by shell thickening. Dorsal sockets small and closely set ; cardinal process commonly medially supported by short ridge ; shell substance impunctuate.

DISCUSSION. Recently Carter (1974) proposed a classification of the Spiriferidae which involved the erection of the Strophopleurinae. Into this subfamily he placed '*Strophopleura* Stainbrook, 1947 ; *Alispirifer* Campbell, 1961 ; *Acuminothyris* Roberts, 1963 ; *Voiseyella* Roberts, 1964 (= *Amesopleura* Carter, 1967) ; ? *Eleutherokomma* Crickmay, 1950 ; ? *Pterospirifer* Dunbar, 1955 ; ? *Celsifornix*' Carter (1974 : 677). This subfamily corresponds partially with a new taxon of the authors' which was in script form at the time of Carter's 1974 publication. We accept

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Carter's subfamily but emend its taxonomic position and, importantly for the purpose of this paper, add the genus *Fusella* as a firm member of the subfamily. We believe that *Alispirifer* Campbell doubtfully belongs here but would suggest the inclusion of *Brachythyrina* Frederiks 1929 and *Paeckelmanella* Likharev 1934. Roberts (1971) placed *Voiseyella* in the Mucrospiriferidae but the above grouping within the Strophopleurinae removes *Fusella* and *Brachythyrina* from the Spiriferidae. *Alispirifer*, *Paeckelmanella* and *Pterospirifer* are removed from the Licharewiinae and *Eleutherokomma* from the Acrospiriferinae of the Treatise (Williams *et al.* 1965) classification.

Ivanova (1972 : 315) proposed the family Paeckelmanellidae for *Paeckelmanella*, *Alispirifer*, *Spiriferinaella* and *Pterospirifer*. The family was placed, with some reservation, in the Syringothyridacea, within the suborder Spiriferidina, but neither a full diagnosis nor a discussion was provided. Carter's subfamily, here used, partially equates with Ivanova's family, as can be seen from the generic constituents. Ivanova, Carter and we ourselves all agree that the taxon containing *Paeckelmanella* – and we believe *Fusella* – belongs within the Spiriferidina, but at family levels of classification there is no agreement ; Ivanova placed the mucrospiriferids within the new suborder Delthyrididina whereas most previous authors placed them in the Spiriferidina.

Genus ***FUSELLA*** M'Coy 1844

Type species. *Spirifera fusiformis* Phillips 1836 : 210 ; pl. 9, figs 10, 11. By original designation of M'Coy (1844 : 132).

Diagnosis. Small (commonly less than 30 mm wide) strongly transverse shells with pointed extremities. High, variably concave, denticulate ventral interarea extending full width of shell. Lateral profile subcircular. Ventral sulcus bordered by pair of prominent ribs, dorsal fold variably developed. Lateral ribbing weak to moderately developed. Dental plates close together within sulcus, subparallel and with callosity filling apex of delthyrium in large specimens. Crural bases converge to valve floor posteriorly. Shell impunctate.

Discussion. Although M'Coy (1844) was reasonably precise, for that date, in his description of *Fusella*, the name has been ill-used ever since. This is because there is only one well-known specimen of the type species *F. fusiformis* in existence and from this it is impossible to learn any detailed information about the internal morphology. It is this species which M'Coy specified as the type of his new 'subgenus' *Fusella*, characterized as follows.

> 'Shell elongate transversely, fusiform, cardinal area wide, much curved ; beaks incurved. This group would embrace these little *Spirifers* of the mountain limestone which have a perfectly fusiform outline, the depth being equal to the length, and the sides cylindrical ; the cardinal area is extremely wide in proportion to their size and is always hollowed or much curved, thus contrasting with the narrow, flat area of the typical *Spirifers* while the strongly incurved beaks distinguish them from the *Cyrtiae*. It would include the *S. bicarinata*, *S. rhomboides*, &c. &c.' (1844 : 132).

M'Coy's description stressed the incurved nature of the ventral umbo, which leads to the belief that he had not seen Phillips' actual specimen of *F. fusiformis* in which the ventral interarea is almost flat, only being concave medially, close to the umbo. The umbo projects beyond the hinge line by no more than 1·5 mm ; Waterhouse (1970 : 3) is in error in writing that the 'umbo extended 2·5 mm beyond the hinge', probably because he took his measurement from his published illustrations which are at almost twice the stated magnification. M'Coy's description may therefore have been influenced by specimens from the Cork area of Ireland best assigned to *F. rhomboidea* (Phillips). This suggestion is further supported by the size quoted by M'Coy for *F. fusiformis*, viz. 'length four lines, width one inch three lines, depth four lines[1]' (1844 : 132), a width which is somewhat greater than that of the type specimen of *F. fusiformis*.

A review of the confused use of the name *Fusella* was published by Waterhouse (1970). He redescribed the type specimen, from the Gilbertson Collection in the British Museum (Natural History), and compared it with various other species in an attempt to suggest its affinities. He concluded that *Unispirifer* Campbell 1957, with which *Fusella* has sometimes been synonymized, was distinctive and we agree with this view. Waterhouse thought that the shell substance of *F. fusiformis* was punctate, leading him to discard species such as *Spirifer rhomboidea* Phillips as being closely related, but to the conclusion that *Fusella* was 'probably related to members of the Syringothyrididae' (1970 : 6). Both optical and scanning electron-microscope studies of the type specimen and second undoubted specimen of *F. fusiformis* show that the shell is not endopunctate but quite normal for impunctate spiriferaceans (Pl. 1, figs 20, 21).

Thomas (1971) is one of the latest of several palaeontologists to say that it seemed inadvisable to use the generic name *Fusella* until the type specimen was adequately known from topotypic material. Had the name fallen from use this would be a sensible suggestion but in view of its continued appearance in the literature, commonly quite incorrectly, it is desirable to further Waterhouse's contention that it should become a well-known genus in its own right. Following the Russian lead when Ivanova (1960) placed *S. tornacensis* de Koninck within *Fusella* some palaeontologists, such as Carter (1967), have placed species in *Fusella* which differ widely from *F. fusiformis*. Within their concept the genus is relatively less wide, very much longer and has a strongly uniplicate anterior commissure. Carter (1971) described the genus *Mirifusella*, said to be 'most similar to *Fusella* M'Coy', but in fact differing considerably in outline and internal features. We have, therefore, a situation in which some palaeontologists advise the suppression of the name *Fusella* and others use this name, at times quite incorrectly. Because of this confusion it is desirable to correct the use of *Fusella* to the best of our ability, even if this is done without resort to additional genuine topotypic material. In the collections of the British Museum (Natural History) there exists one specimen clearly conspecific with the type specimen of *F. fusiformis*. This second specimen is in the Davidson Collection (B 7379) and came from Dovedale, Derbyshire (Pl. 1, figs 5–7). The ventral umbo has been broken from this specimen and it is possible to see that the

[1] A line or ligne is one twelfth of an inch (=2·1167 mm).

dental plates did not extend anterodorsally to support completely the teeth and delthyrial margin near the hinge line. Unfortunately searches in the Derbyshire or Bolland and Clitheroe areas have failed to reveal additional specimens. The information on internal morphology of *Fusella* is, therefore, mainly based upon the silicified Fermanagh specimens collected by Brunton and assigned to *F. rhomboidea* (Phillips), a species believed to be closely related to *F. fusiformis* and which originally also came from Bolland (Pl. 1, figs 13–19).

In the last twelve years two genera have been proposed which are probably synonymous with each other and also are closely related to *Fusella*. These are *Voiseyella* Roberts 1964, with type species *Strophopleura anterosa* Campbell 1957 from the Lower Carboniferous of the Werria Basin, New South Wales, Australia, and *Amesopleura* Carter 1967, with type species *Spirifer novamexicana* Miller 1881 from the Lower Carboniferous (Osagian) of New Mexico. Both these authors thought that *Spirifer mundula* Rowley 1893 should probably be placed in their genus. Subsequently Roberts (1971) has placed *Amesopleura* into synonymy with *Voiseyella*. Having inspected Roberts' 1964 material from the Greenhills area of New South Wales and Carter's 1967 material from the Lake Valley region of New Mexico we agree with this synonymy. The question then arises as to the relationship of *Voiseyella* with *Fusella*. Neither Roberts nor Carter compared their genera with *Fusella*, although the former (1971) discussed the relationship of *Fusella* with *Unispirifer* and the latter placed his new species *llanoensis* (1967) within his concept of *Fusella*. These genera are clearly quite closely related ; their dimensions, outlines and profiles are very similar, as is the form of ribbing. The most important difference, and that which prevents the synonymy of *Voiseyella* within *Fusella*, is that the dental plates of *Voiseyella* diverge from the umbo following the ribs bordering the sulcus whilst those of *Fusella* are unusual in remaining subparallel within the confines of the ventral sulcus (Pl. 1, fig. 19) ; they do not follow the borders of the sulcus, as in many spiriferaceans. (The dental plates of *V. novamexicana* also follow the ribs bordering the ventral sulcus.)

In view of the varied use of the name *Fusella*, and despite the redescription by Waterhouse (1970), it seems desirable to provide a description of *F. fusiformis* based upon the type specimen and second specimen in the Davidson Collection.

Fusella fusiformis (Phillips)

Pl. 1, figs 5–12

1836 *Spirifera fusiformis* Phillips : 217 ; pl. 9, figs 10, 11.
1849 *Spirifera fusiformis* Phillips ; Brown : 108 ; pl. 51, figs 4, 5.
1858 *Spirifera fusiformis* Phillips ; Davidson : 56 ; pl. 13, figs 15, 15a.
1970 *Fusella fusiformis* (Phillips) ; Waterhouse : 3 ; figs 1A–F.

TYPE SPECIMEN. The single specimen described and figured by Phillips (1836) in the Gilbertson Collection, British Museum (Natural History), B 249, from Bolland, Yorkshire.

DIMENSIONS. Width (incomplete) 22·6 mm. Mid-point to ear of more complete side 13·8 mm. Length 8·2 mm. Thickness 8·2 mm. Angle of sulcus 33°. An estimate of the complete width of the shell is about 28 mm.

Diagnosis. Small transversely narrowly rhombic shells as long as thick and about three and a third times as wide as long. High ventral interarea with only slightly projecting umbo. Ribbing weakly developed and dorsal median fold prominent only anteriorly ; dorsal umbo medially sulcate. Dental plates short and subparallel, diverging anteriorly less than the angle of sulcus.

Description. The tip of the right side of the shell is missing and sediment obscures two thirds of the interarea. The external surface has been deeply exfoliated in patches, especially on the ventral valve. Elsewhere the shell is somewhat eroded and on only one small area in the ventral sulcus is primary shell preserved. Thus details of external ornamentation cannot be given, nor is it possible to count the number of ribs with certainty other than on the left half of the dorsal valve where there are ten or eleven simple costae. Within the more deeply exfoliated secondary fibrous shell of the ventral valve short radially arranged traces of mantle canals are visible. Growth lines are clearly seen, especially on the dorsal valve (about 4 per mm at the side of the fold) and indicate a fusiform shape throughout ontogeny ; they became more prominent anteriorly. The ventral interarea is vertically grooved by flexures in the secondary fibres (Pl. 1, figs 10, 21) which formed a delicate denticulation of the hinge line at the inner surface. (When covered by primary shell this feature would not be visible.) The ventral sulcus is prominent but the expected dorsal fold is virtually lacking although its position is marked by a pair of bordering ribs more prominent than the others. There is a dorsal median depression which becomes shallower and less well defined anteriorly from the umbo. The anterior commissure is uniplicate. No internal structures can be seen in the specimen although the exfoliation of the ventral umbo shows the secondary fibres to be bent along lines interpreted as the bases of the dental plates. If this is correct, it can be said that the dental plates are positioned on the borders of the ventral sulcus at a distance of 2 mm from the umbo but anteriorly remain subparallel and thus within the diverging sulcus. (This is the same as is seen in the Fermanagh silicified material assigned to *Fusella*.)

The second specimen, from Dovedale (B 7379, Pl. 1, figs 5–7), is smaller than the holotype and in that it too has lost its right tip and ventral umbo it is less well preserved (half width 11·3 mm, length *c.* 6·3 mm, thickness 6·1 mm). The dorsal fold is slightly developed anteriorly, resulting in a rather more prominent uniplication of the anterior commissure than in the holotype. The broken ventral umbo allows it to be seen that the dental plates are short for they did not reach anteriorly to the plane of fracture. It is impossible to measure the angle of divergence of the ventral sulcus but an estimate of the delthyrial angle, based on the remaining dorsal half of the interarea, is 30°. As in the holotype, the dorsal umbo is unusually shaped with a shallow V-shaped groove about 1 mm long terminating anteriorly on the pair of large ribs bordering the fold. Inspection of the visible surfaces shows that the shell structure of both specimens is fibrous with no sign of endopunctation.

Discussion. It is unfortunate that *F. fusiformis* is a rare species in rocks of low to mid Viséan age. If it were not for the second conspecific specimen from Dovedale we might have considered the type specimen to be a freak. Indeed it is possible

that the presence of a reasonably developed dorsal fold is more characteristic ; this feature is better developed on the Dovedale specimen and it is unusual for a uniplicate spiriferacean not to have a better developed fold. Growth lines show that even at a dorsal valve length of 2·5 mm the commissure was uniplicate. The amplitude of the uniplication is 3·0 mm on the type specimen and 3·2 mm on the Dovedale specimen. The growth lines also show that these shells grew with a fusiform shape virtually throughout their postembryonic ontogeny ; a growth line about 1 mm from the dorsal umbo indicates that the valve width at that stage was 4 mm.

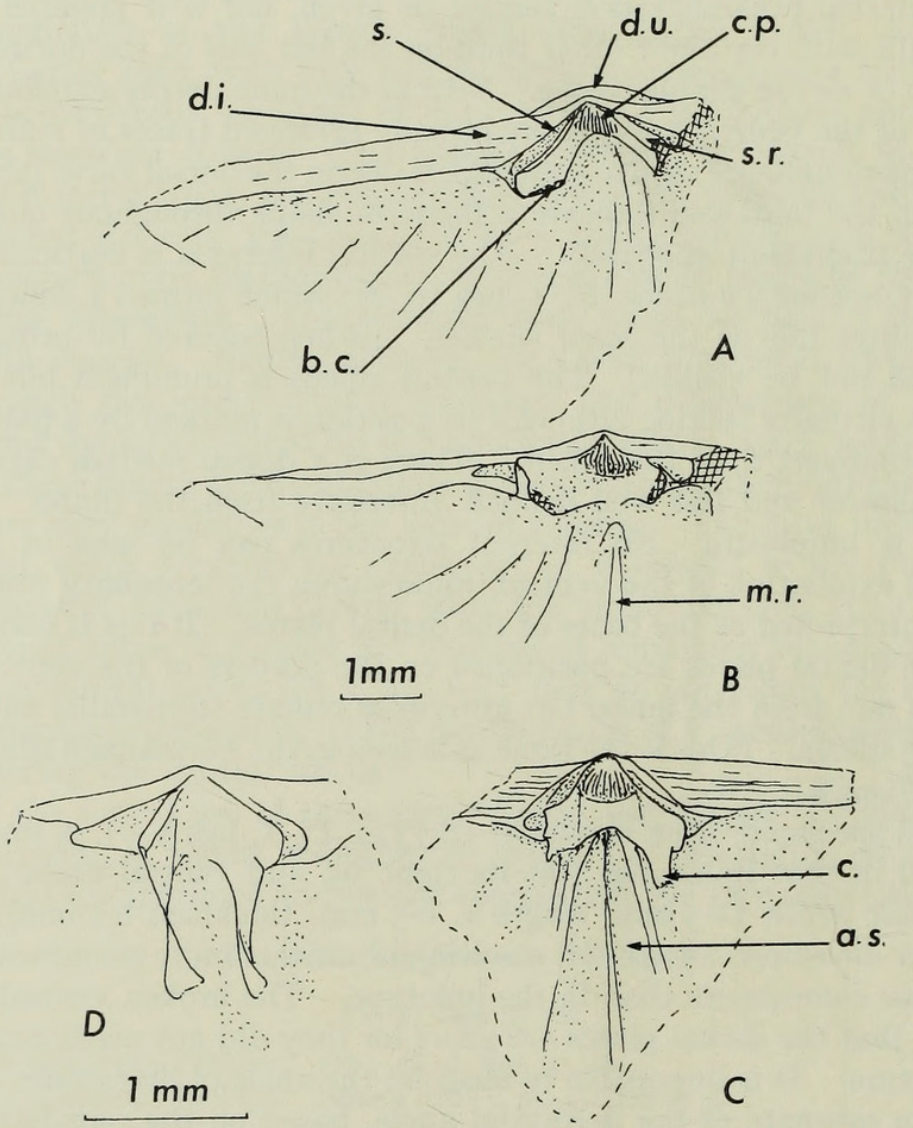

FIG. 1. Camera-lucida drawings of silicified dorsal valve interiors of *F. rhomboidea* (Phillips) from the Viséan of Co. Fermanagh, Ireland. A, B, dorsal and posterodorsal views of a nearly fully developed valve ; C, dorsal view of part of a fully developed valve ; D, dorsal view of a juvenile valve at twice the magnification. Note the posteriorly narrow sockets which, in adult shells, remained functional only anteriorly. Cross shading denotes broken shell material. a.s. – adductor muscle scar ; b.c. – broken stump of the crus ; c. – crus ; c.p. – cardinal process ; d.i. – dorsal interarea ; d.u. – dorsal umbo ; m.r. – median ridge (dividing the adductor scars) ; s. – socket ; s.r. – socket ridge, which merges dorsally with the crural base. (See also Pl. 1, fig. 18.)

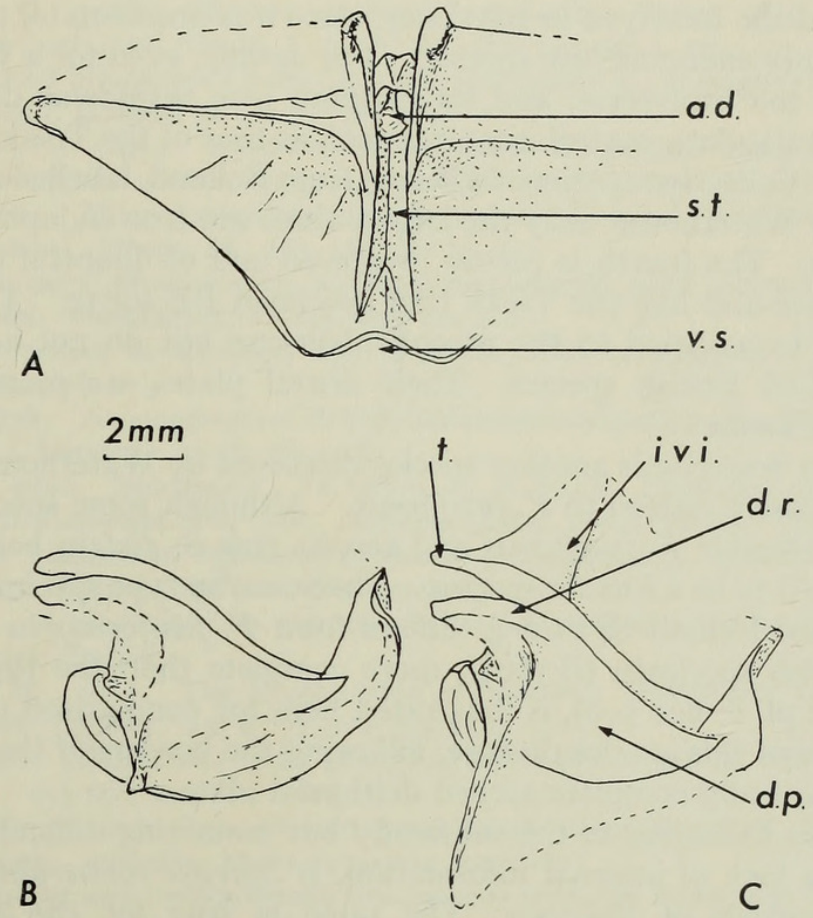

FIG. 2. Camera-lucida drawings of a silicified ventral valve of *F. rhomboidea* (Phillips) from the Viséan of Co. Fermanagh, Ireland. A, posterior view; B, lateral view; C, ventrolateral view. a.d. – apex of the delthyrium, filled by secondary shell material; d.p. – dental plate; d.r. – dental ridges bordering the interior surfaces of the edges of the delthyrium. Anteroventrally these ridges are supported by the dental plates which buttress across the ventral shell cavity. i.v.i. – internal surface of the ventral interarea; s.t. – secondary shell thickening between the dental plates; t. – tooth; v.s. – ventral sulcus. (See also Pl. 1, fig. 19.)

In the British Isles the species most closely resembling *F. fusiformis* is *F. rhomboidea* (Phillips), the type specimen of which also came from Bolland (Pl. 1, figs 13–17). This species is a constituent of the silicified brachiopod faunas being studied by Brunton (1966, 1968) from Ireland but as yet has not been redescribed except briefly by Brunton & Champion (1974). Other than *F. rhomboidea* there are several species mentioned by Waterhouse (1970), some of which he believed may belong to *Fusella*. It was his mistaken belief that *F. fusiformis* was endopunctate which led him to discard species like *rhomboidea, convoluta* (Phillips) and *trigonalis* (Martin) as being closely related. For the same reason Waterhouse related *Fusella* to *Syringothyris*, in particular some specimens believed to be *S. cuspidatus* (J. Sowerby). He figured (1970 : fig. 2, A–F) a specimen named '*Spirifer cuspidatus* (Phillips)' from Treak Cliff, Derbyshire, in the British Museum (Natural History) collections (BB 40831). This specimen belongs neither to the species *cuspidatus* (first described by Martin in 1809 but ascribed to J. Sowerby (1816) by Muir-Wood

when she selected the lectotype in 1951) nor, since it is impunctate, to *Syringothyris* which includes only endopunctate species. The outline, even for a young specimen of *cuspidatus*, is too transverse, and furthermore true *cuspidatus* does not have a sulcate fold or denticulate ventral interarea such as that of the Treak Cliff specimen. Of the Gilbertson Collection specimens (B 297) from Bolland, labelled as *S. cuspidatus* and discussed by Waterhouse, only the largest three are true endopunctate *Syringothyris cuspidatus*. The fourth is poorly preserved and of doubtful affinity but the fifth is impunctate and like the Treak Cliff specimen BB 40831. These specimens should probably be assigned to the Strophopleurinae but do not accord with any presently described British species. Their dental plates are more like those of *Voiseyella* than *Fusella*.

Spirifer distans Sowerby is another species discussed by Waterhouse (1970) in the belief that it is closely related to *F. fusiformis*. Although some specimens assigned to *distans* may resemble *F. fusiformis* and despite true *S. distans* being impunctate, we do not believe it to be a *Fusella* species. The Sowerby type specimen of *S. distans*, from near Dublin, Ireland (B 61009), differs from *F. fusiformis* in external shape and a second Irish specimen (B 7664), more complete than the type refigured by Davidson (1858 : pl. 8, figs 5–8), is illustrated here for comparison (Pl. 1, figs 1–4). The dental plates of this species diverge, following the borders of the ventral sulcus, and there is an apically complete arched delthyrial plate.

Another species belonging in the subfamily but remaining difficult to assign to a genus, through a lack of internal information, is *Spirifer roemerianus* de Koninck, from the Tournaisian of Belgium. The same is true for the species *Spirifer triangularis* J. de C. Sowerby, placed in *Fusella* by Muir-Wood in 1951. This species is larger than *F. rhomboidea* and differs in having a high carinate fold and prominent ventral median rib in the sulcus. *Spirifer convoluta* Phillips is another extremely transverse species but it reaches much larger dimensions (at least 80 mm wide) than *F. fusiformis*. Its interior is unknown so the generic assignment is doubtful, but if it were to be included within *Fusella* the diagnosis of that genus would require emendation to include species at this size. *Spirifer bicarinata* M'Coy was one of the species M'Coy mentioned originally as being in *Fusella*. Other than by M'Coy's description and incomplete figure, *S. bicarinata* is virtually unknown ; the type specimen seems to be lost and it is unwise to continue using the name.

In conclusion, therefore, we assign *Fusella* to the Strophopleurinae and in addition to the type species, *F. fusiformis* (Phillips), we include *F. rhomboidea* (Phillips) and doubtfully *F. trigonalis* (Martin), *F. triangularis* (J. de C. Sowerby), *F. roemerianus* (de Koninck) and *F. convoluta* (Phillips) within this genus. *Strophopleura* probably evolved from the Mucrospiriferidae in the Upper Devonian and gave rise to the Tournaisian *Voiseyella* and *Acuminothyris* and to the Viséan *Fusella* ; from this the Carboniferous to Lower Permian genus *Brachythyrina* may have evolved, and also the northern Permian genera *Paeckelmanella* and *Pterospirifer*.

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PLATE 1

The specimens are all housed in the BM(NH) and those in Figs 1–19 were coated with ammonium chloride sublimate before being photographed. The prints are not retouched.

Spirifer distans J. de C. Sowerby

FIGS 1–4. Viséan of Millicent, Co. Kildare, Ireland. Viewed anteriorly, posteriorly, dorsally and from the left side. × 1. B 7664.

Fusella fusiformis (Phillips)

FIGS 5–7. Viséan of Dovedale, Derbyshire. Viewed anteriorly, posteriorly and dorsally. The arrow on Fig. 7 indicates the region illustrated in Fig. 20. × 2. B 7379. Davidson Collection.

FIGS 8–12. Holotype, figured by Phillips, from Bolland, Yorkshire. Viewed anteriorly, dorsally, posteriorly (the arrow indicates the region enlarged in Fig. 21), ventrally and from the left side. × 1·5. B 249. Gilbertson Collection.

FIG. 20. Exfoliated standard secondary fibres from the position marked on Fig. 7. The posterior dorsal margin is to the top and the mid-line to the right. Scanning electron micrograph, × 210.

FIG. 21. Exfoliated secondary fibres of the ventral interarea of the holotype (see Fig. 10) showing the flexures resulting in a fine denticulation at the commissure. Scanning electron micrograph, × 140.

Fusella rhomboidea (Phillips)

FIGS 13–17. Lectotype, figured by Phillips, from Bolland, Yorkshire. Viewed ventrally, anteriorly, posteriorly, dorsally and from the right side. × 1; Figs 15, 17 × 2. B 236. Gilbertson Collection.

FIGS 18–19. Silicified specimens from the Upper Viséan of the Sillees river, Co. Fermanagh, Ireland (see Brunton 1966 for locality details). Fig. 18, mature dorsal valve interior (see also Fig. 1A–D, p. 280), × 4. BB 61611. Fig. 19, young ventral valve interior looking posteriorly (see Fig. 2A–C, p. 281), × 3. BB 61612.


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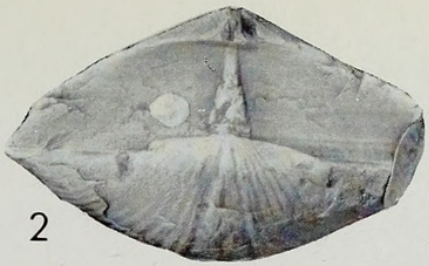
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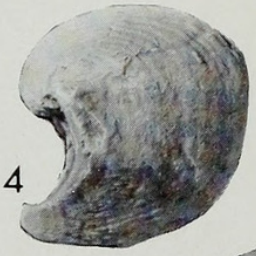
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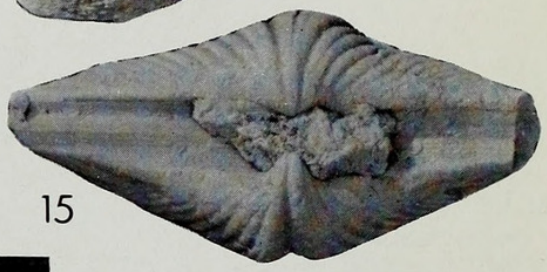
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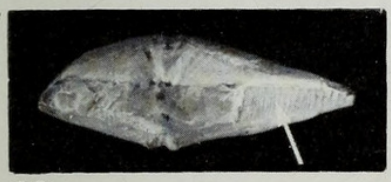
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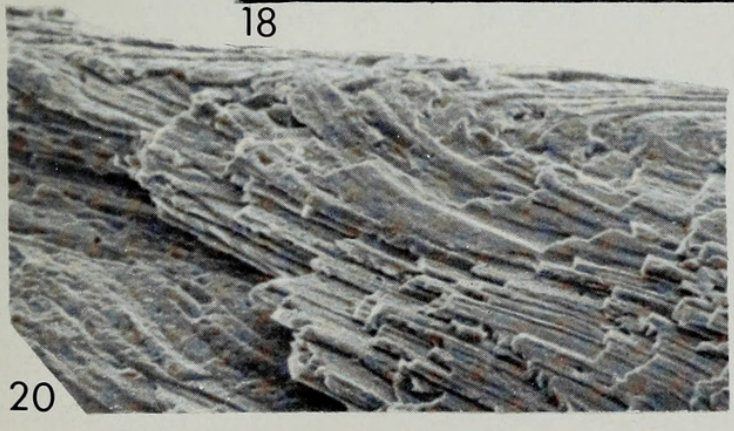
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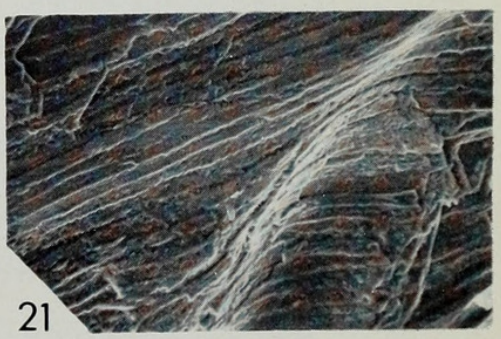
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