A NEW GENUS OF CARBONIFEROUS SPIRIFERID BRACHIOPOD FROM SCOTLAND

by MARIE LEGRAND-BLAIN

ABSTRACT. The microsculpture and vascular markings of the classical species *'Spirifer' trigonalis* are described, mainly from Scottish Brigantian (late Viséan) specimens. The genus *Angiospirifer* and subfamily Angiospiriferinae are created. *Angiospirifer* is related to the genus *Brachythyrina*, which became widespread during the upper Carboniferous.

CARBONIFEROUS spiriferids present unusual systematic difficulties, especially when specimens have a simple external shape and ornamentation, and when the microsculpture and internal features become taxonomically important. Among upper Palaeozoic spiriferids, in addition to the dental plates, the mantle canals are important taxonomic and evolutionary features (Ivanova 1960, 1971; Lazarev and Poletaev 1982). However, good internal surfaces or moulds are needed for such observations: in consequence, mantle canals are unknown on many of the long-established Dinantian species that were collected from limestone facies.

'S.' trigonalis (Martin, 1809) *sensu* Muir-Wood 1956, a species often cited from the Eurasian and North African Carboniferous, has been studied in detail by Dunlop (1961), so its biometry and shell structure are well established. This paper adds to Dunlop's study by researching the microsculpture and mantle canals of *'S.' trigonalis*: a species previously attributed to a variety of genera, but here assigned to a new genus, *Angiospirifer*.

SYSTEMATIC PALAEONTOLOGY

Genus ANGIOSPIRIFER nov.

Type species. Spirifer trigonalis (Martin, 1809) *sensu* Muir-Wood 1956; Brigantian, Scotland.

Derivatio nominis. From the Greek word *aggeion* (= vessel): a reference to the development of the vascular markings.

Diagnosis. Shell of trigonal shape, megathyrid to slightly brachythyrid; lateral ribs conspicuous, rarely divided, median sinus and fold costate; sub-imbricated micro-lamellae bearing faint radial tubercles; adminicula short, intra-sinal; elongated apical callosity located between apex and muscle scar; genital markings surrounding the apical-muscular area; vascular markings roughly reticulated, developed on adult interior lateral ventral region.

Description of the type species: S. trigonalis

The type specimen of the species *trigonalis* is a neotype, proposed by Muir-Wood to the International Commission on Zoological Nomenclature (1956, p. 112). It bears British Museum (Natural History) number BB 7340; and is figured by Davidson (1858, pl. 5, fig. 33; 1863, pl. 50, fig. 4) and Dunlop (1961, pl. 64, figs. 1–3). The locality 'Cousland, near Dalkeith, Midlothian', is a well-known old quarry in the North Greens Limestone and underlying shales (Wilson 1974, locality 32; P. Brand, pers. comm.), of upper Brigantian age (George *et al.* 1976, fig. 14J). The lost original specimens described by Martin came from a different locality: 'Derbyshire', with an imprecise age of Asbian to Brigantian. So, the neotype choice may have alterated the original sense of the species *trigonalis*.

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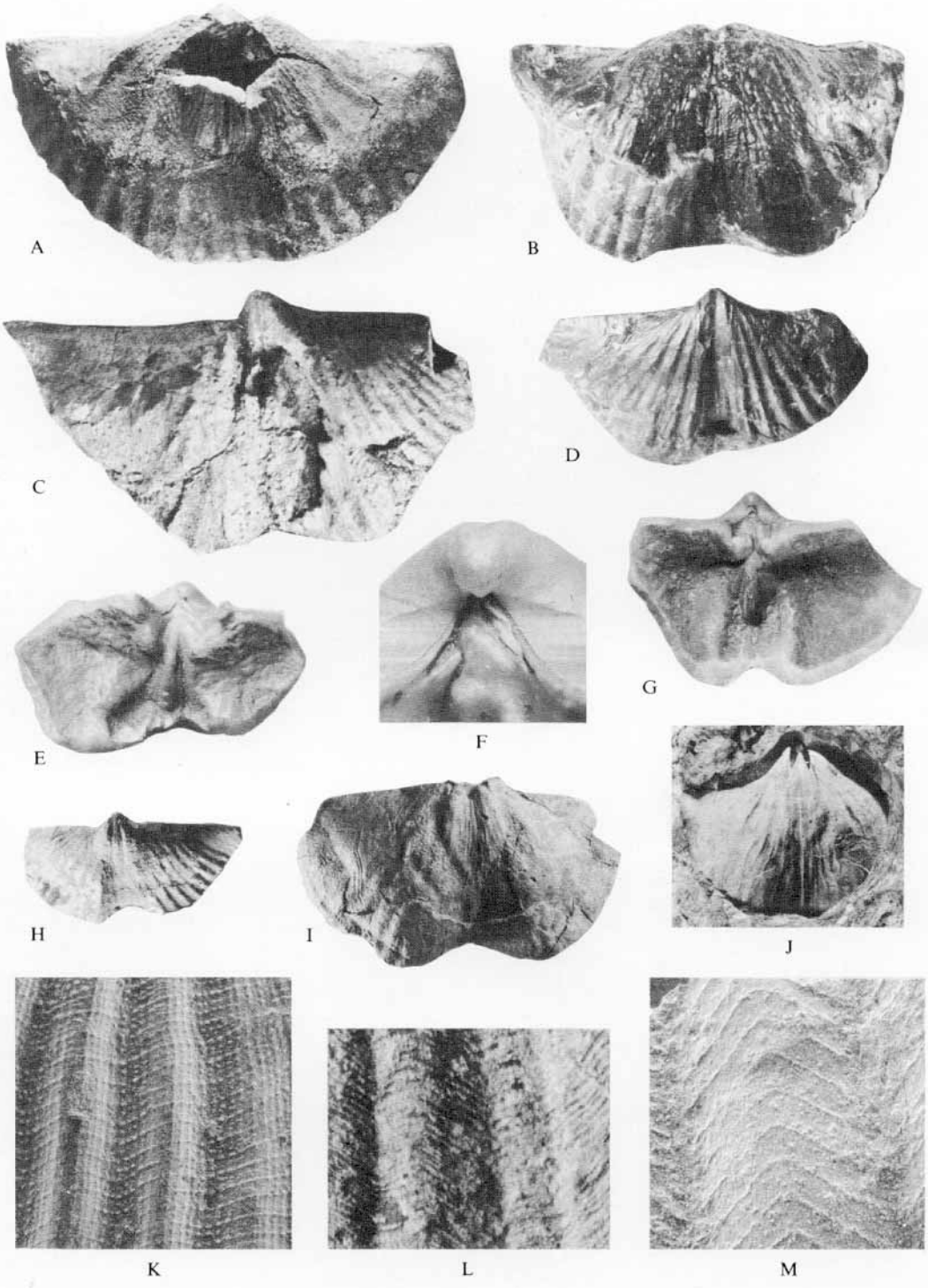
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Newly collected topotypes would have provided the firmest basis for this study, but they proved impossible to obtain. P. Brand (British Geological Survey, Edinburgh) recently visited Cousland quarry and found it partly filled. Some specimens collected from Cousland have been examined in the British Geological Survey, Edinburgh (EV 517–519, 524, B 1735^{D}, B 1787^{D}, T 3277), but they are poorly preserved.

On the other hand, D'Arcy quarry, 4 km S-SW of Cousland in the North Greens Limestone (Wilson 1974, locality 31), has yielded good specimens (British Geological Survey, Edinburgh, T 3278; text-fig. 1C, M). In addition the *S. trigonalis* material described by Dunlop (1961) is from another Scottish locality: Brockley, near Coalburn, Lanarkshire. This locality is 65 km SW from Cousland, in the Douglas Main Limestone, at the base of the lower Limestone group, and a little below the *stratum typicum* (George *et al.* 1976, fig. 14B). Dunlop (1961) has established statistically that the Brockley spiriferid population belongs to the species *trigonalis*. I have collected extra specimens from this locality (text-fig. 1B, D). Therefore, in the absence of good *trigonalis* topotypes, D'Arcy and Brockley specimens may be used. In both localities the shells are preserved in shaly limestones, those from D'Arcy being rather fragile and distorted. Internal moulds have been prepared by partly removing the shell material with needles (text-fig. 2A, D, F).

Other specimens are natural internal moulds from outside Scotland: British Geological Survey no. RV 733, figured in Burgess and Holliday (1979, pl. 6, fig. 14) and herein (text-fig. 1A), from the Pendleian of Cumbria; British Museum (Natural History), Gilbertson Collection no. B 244, figured by Waterhouse (1970, pl. 2, figs. G–J), from an unknown locality, probably Bolland, Yorkshire; B.M.(N.H.) nos. BD 2062–2063 (text-fig. 1E, F, G), from the late Dinantian of Alnwick, Northumberland. These latter specimens show apical interiors.

Morphological terms. Most morphological terms are in current use, as in Williams and Rowell (1965). Some less common terms not cited by Dunlop (1961) are listed in Table 1.

Biometry. The Brockley population has been studied statistically by Dunlop (1961, p. 480, text-fig. 1, tables 1, 2). Some specimens from D'Arcy attain 42 mm in width, whereas the Brockley shells never exceed 39·3 mm wide. The external variability of *A. trigonalis* is important, and more so than previously recognized. The neotype is decidedly narrower than the largest members of these populations (maximum width 27·8 mm; hinge width 24·9 mm; length 24 mm; thickness 18·2 mm).

TEXT-FIG. 1A–G, M., *Angiospirifer trigonalis* (Martin, *sensu* Muir-Wood). A, British Geological Survey, Keyworth, RV 733; natural internal mould of adult specimen, formerly figured by Pattison *in* Burgess and Holliday (1979, pl. 6 fig. 14). Knucton Shell Beds, Pendleian, Coldberry Gutter (Cumbria), × 2. B, British Museum (Nat. Hist.) BD 1700, prepared internal mould of adult pedicle valve collected by the author. Douglas Main Limestone of Lower Limestone Group, Brigantian, Brockley (Lanarkshire), × 2. C, British Geological Survey, Edinburgh, T 3278-1, prepared internal mould of adult pedicle valve. North Greens Limestone of Lower Limestone Group, Brigantian, D'Arcy quarry (Midlothian), × 2. D, B.M.(N.H.) BD 1701, prepared internal mould of young pedicle valve collected by the author. Same locality as B, × 2. E, F, B.M.(N.H.) BD 2062, adult pedicle valve; Carboniferous Limestone (Brigantian), Alnwick (Northumberland). E, interior, showing delthyrium, elongated apical callosity, muscle scar, × 2. F, fragments of stegidial plates, × 5. G, B.M.(N.H.) BD 2063, pedicle valve interior. Same locality as E and F, × 2. M, B.G.S., Edinburgh, T 3278-2, external microsculpture. Same locality as in C, × 20. H and K, *Anthracospirifer pellaensis* (Weller); H, B.M.(N.H.) BD 1703, prepared internal mould of adult specimen given to the author by Dr. G. A. Cooper; Pella beds, Meramecian, 2 miles S of Pella (Iowa, USA), × 1. K, B.M.(N.H.) BD 1704, external microsculpture of specimen given to the author by Dr. A. S. Horowitz; Pella Formation, Meramecian, Mahaska quarry (Iowa, USA), × 10. I, J, L, '*Parachoristes*' (*sensu* Lazarev and Poletaev 1982). I, J, Cayton Gill beds, Kinderscoutian, Ripley, Harrogate (N. Yorkshire). I, B.G.S. Keyworth, 50261, natural internal mould of adult pedicle valve, formerly figured as '*Spirifer α*' by George (1932, text-fig. 8), × 1. J, B.M.(N.H.) BD 1702, natural mould of rather young pedicle valve collected by the author, × 1. L, B.M.(N.H.) BD 1705, external microsculpture of specimen collected by the author. Oued el Hamar Formation, upper Bashkirian, Oued Tagnana section, loc. ML 290, 15 km W-NW. of Béchar (Algeria), × 10.

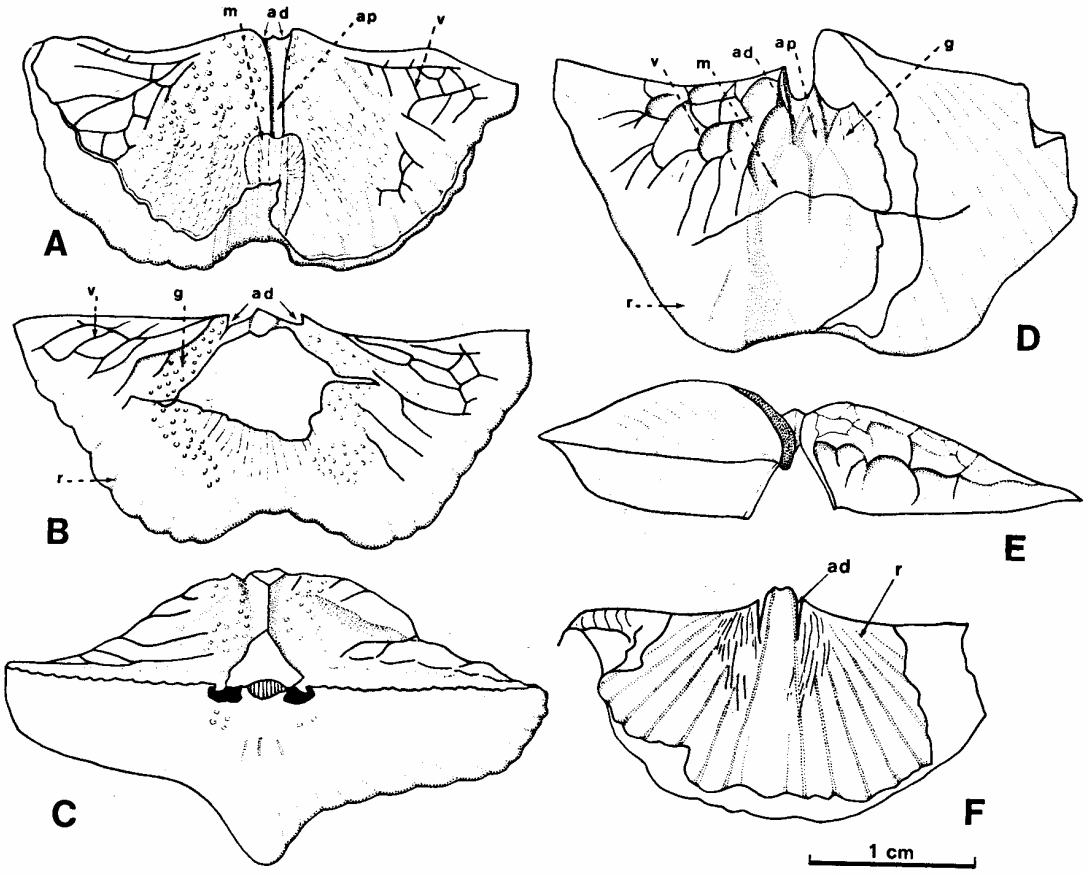
TABLE 1. Morphological terms not cited in Dunlop (1961) or differently interpreted, and their equivalents in the literature

Terms and their authors (when post *Treatise*, 1965)	Definitions	Equivalents in: (1) Dunlop 1961; (2) Vandercammen 1959, 1962; (3) Lazarev and Poletaev 1982
Adminicula	Ventral parts of dental plates, joining to the bottom of the pedicle valve	(1) dental plates
Apical callosity	Secondary thickening inside the umbo of the pedicle valve	(1) 'ventral septum'
Delthyrial plate	Transverse plate connecting the two dental plates in their apical part, below the interarea level	
Genital markings	Radial ridges or pits on inside of shell within genital areas	(2) gonoglyphe (3) alveolate vascular system
Stegidial plates: Cowen 1968; Grant 1976	Pairs of laminate plates making up the delthyrial cover, forming a convex arch above the interarea level; they are fragile and rarely entirely preserved	(1) a part of the 'delthyrial plate' (2) plaques deltidiales
Tabellae: Waterhouse 1968	Dorsal supporting plates, called crural plates by some authors	(1) crural plates
Vascular markings	Impressions of mantle canals on shell interior	(2) angioglyphe (3) pinnate, ramified, reticulate vascular system

Microsculpture. The neotype exhibits fine but worn concentric lamellae. Davidson (1863, pl. 50, fig. 9*a*) figured the microsculpture of a specimen from Barrhead, Renfrewshire, Scotland. This specimen is not preserved in the British Museum collections. However, Davidson's observation is confirmed on specimens from D'Arcy (text-fig. 1M). The concentric lamellae are variously spaced (4–10 per mm) and are slightly raised and imbricated, like a tiled roof; their anterior borders display a festoon aspect, due to fine tubercles being arranged regularly in radial rows. Sometimes, traces of these tubercles form very fine radial lirae.

Delthyrium and stegidial plates. Dunlop (1961) described the area and delthyrial structures. None of the Scottish specimens displays externally preserved stegidial plates, but fragments of these structures are seen on specimens from Alnwick (text-fig. 1F) and on B.M.(N.H.) B 244 (Waterhouse 1970, fig. 2J). Stegidial structures are found on apical sections of Brockley specimens, as described below.

Internal moulds and surfaces (text-figs. 1A–G, 2). On adult internal moulds the adminicula appear as extremely short apical incisions, close to each other and within the sulcus. A narrow median apical callosity forms a depression that runs from the inter-adminicular region to the posterior end of the muscle scar; its length and shape are very variable, from short rhombic form (text-fig. 2D) to an elongate septum-like shape (text-figs. 1G, 2A). The muscle scar is moderately to slightly depressed into the shell substance, pyriform, and more or less separated from the apex, occurring either just in front of the adminicular distal extremities (text-fig. 2D) or at some distance from them (text-fig. 2A). The genital markings surround the region of the muscle scar and apical callosity, extending up on to the inside of the interarea on both sides of the delthyrium (text-fig. 2C). This area bears small pits which may be arranged in an indistinct radial pattern. The vascular markings, around the genital area, extend over the whole posterolateral interior surface, including the lateral regions of the interarea. Two distinct canals run from the tops of lateral apical cavities towards the lateral extremities. They widen, divide into transverse canals, and form a rough reticulation upon the insides of the interarea



TEXT-FIG. 2. *Angiospirifer trigonalis* (Martin, *sensu* Muir-Wood), internal moulds. A, British Museum (Nat. Hist.) BD 1700, adult pedicle valve. Douglas Main Limestone, Brigantian, Brockley (Lanarkshire). B, C, British Geological Survey, Keyworth, RV 733, adult specimen, broken in the ventral muscular area. Knucton Shell Beds, Pendleien, Coldberry Gutter (Cumbria). B, ventral view. C, dorsal view. D, E, British Geological Survey, Edinburgh, T 3278-1, adult pedicle valve. North Greens Limestone, Brigantian, D'Arcy Quarry (Midlothian). D, ventral view. E, dorsal view. F, B.M.(N.H.) BD1701, young pedicle valve. Same locality as in A. ad = adminicula or their internal moulds; ap = apical callosity; g = genital markings; m = muscle scar; r = external ribs on their internal moulds; v = vascular markings.

and ears. Other radial canals extend from the lateral parts of the genital area, to branch and anastomose together (text-fig. 2A, B, D). The shape of the external ribs is seen internally only anteriorly. Brachial valve internal moulds (text-fig. 2C) display short thick tabellae; the cardinal process and muscle scar are poorly preserved; reduced genital markings appear on both sides of the muscle area.

A young pedicle valve, 25 mm wide, with a shell thickness of 0·4 mm, shows internally the external ribs pattern within 7 mm of the apex (text-figs. 1D, 2F). The adminicula are represented by two slender incisions, 2 mm apart and 2·4 mm long; their apical parts are extra-sinal, whereas their distal extremities coincide with the sinal borders. There is no apical callosity. The muscle scar is hardly distinguishable, but posteriorly it projects to between the adminicula, whereas its anterior border

seems to extend beyond them. The genital and vascular markings are not differentiated. Lateral to the adminicula, thin radiating canals run in different directions from the external ribs.

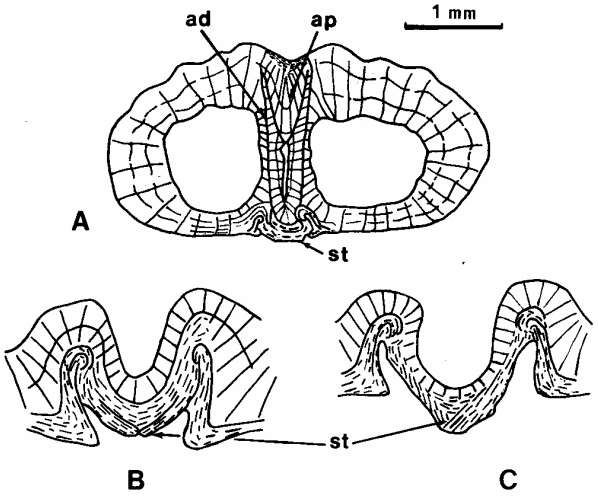
On another young pedicle valve, 41 mm wide and 1 mm thick (T 3278-3, not figured), the external ribs are seen internally after one third of the length of the valve. Already the muscle scar is located anterior of the apex, from which it is separated by a median callosity 4 mm long. The genital and vascular markings are again poorly differentiated.

The characteristic adult pattern of genital and vascular markings appears on the pedicle valves when the shell, in the posterior region, is at least 2 mm thick. Thus the ontogeny of *A. trigonalis* is characterized by a rapid forward migration of the muscle scar; the development of the vascular markings is linked with a thickening of the shell in the whole posterolateral ventral region.

Apical sections of pedicle valves. Apical sections have been described by Dunlop (1961, text-figs. 4*e–f*, 7*e*, 12*a–e*; pl. 65, fig. 7), and again here (text-fig. 3A–C). The dental plates are well developed, made of two distinctive parts: 1, short converging dental 'flanges' bordering the delthyrium; 2, long parallel or slightly diverging adminicula. Both parts are made of tertiary columnar shell, on both sides of a slender median fibrous layer (Vandercammen and Plodowski 1967). The 'median septum' of Dunlop (1961, text-figs. 4*d*, 12*a*, *d*, *e*) corresponds mainly to the median apical callosity, posterior to the muscle scar. The growth surfaces (as seen in sections, e.g. Dunlop 1961, text-fig. 12*e*) show that there is no fibrous layer such as occurs in true septa. On the other hand, in the umbo infilling, the 'V' structure called a septum by Dunlop (1961, text-fig. 12*a*), resembles a recrystallization figure ('faux coussinet septal' of Vandercammen and Plodowski 1967). The 'delthyrial plate' described by Dunlop poses a problem: its anterior part is convex, protruding above the level of the interarea. In fact, it is *pro parte* a stegidial cover, as is strongly suggested by sections exhibiting paired but unequally developed plates (text-fig. 3B, C). A true single internal delthyrial plate is restricted to the top of the delthyrial cavity, but on most adult specimens it is obliterated by the umbonal infilling and recrystalization.

Remarks. The species *trigonalis* has been attributed in the literature to several spiriferid genera: to *Spirifer* by most authors in the past, and by Dunlop (1961); to *Fusella* by Buckman (1906), Beznosova (1959), and (with some uncertainty) Brunton and Rissoné (1976); to ?*Anthracospirifer* by Thomas (1971); and to ?*Unispirifer* by Afanas'eva (1975).

Spirifer Sowerby 1816 attains a greater size than *Angiospirifer*, and has frequently divided radial ribs and a microsculpture of radial lirae; vascular markings are absent or reduced to fine and short canal traces. *Fusella* M'Coy 1844 has dental plates comparable to those of *Angiospirifer*, being



TEXT-FIG. 3. *Angiospirifer trigonalis* (Martin, *sensu* Muir-Wood), transverse sections of pedicle valves showing structures reinterpreted from Dunlop (1961). A, Dunlop's text-fig. 12*e*. B, Dunlop's text-fig. 11*e*. C, Dunlop's text-fig. 11*g*. Douglas Main Limestone, Brigantian, Brockley (Lanarkshire). ad = adminicula or their internal moulds; ap = apical callosity; st = stegidial plates.

positioned within the sinus (Brunton and Rissoné 1976, fig. 2A). The muscle scars are indistinguishable, the median callosity is restricted to the tip of the umbo, and the vascular markings are reduced. A further important difference is the virtual absence of ribbing in the ventral sulcus of *Fusella*. *Unispirifer* Campbell 1957 has an ornamentation of finer and more numerous ribs than on *Angiospirifer* and a microsculpture of radial lirae. Its adminicula diverge and surround the posterior part of the muscle scar and the vascular markings are not differentiated. *Anthracospirifer* Lane 1963 has the same external shape and ornamentation as *Angiospirifer*, but it differs in: *a*, its microsculpture, with radial lirae as prominent as the concentric lamellae, forming a characteristic reticulation (text-fig. 1K; Sutherland and Harlow 1973, pl. 16, fig. 10); *b*, the position of the ventral muscle scar, which on adult internal moulds creates a strong apical relief (text-fig. 1H; Sutherland and Harlow 1973, pl. 16, fig. 4); *c*, the adminicula, which diverge around the posterior part of the muscle scar, in an extra-sinal position; *d*, the vascular markings, which seem to be absent. In the pedicle valve of *Anthracospirifer* the posteriorly thickened shell thins rapidly towards the margins, so that the internal surface shows the external ribbing. *Prochoristitella* Legrand-Blain 1968 resembles *Angiospirifer* by the position of the adminicula, apical callosity, and muscle scar; however, the microsculpture differs from that of the latter genus by better development of the radial lirae; mantle cavities are reduced. *Brachythyrina* Fredericks 1929 has the same shape and ornamentation as *Angiospirifer*. Its apical callosity, muscle scar, and mantle canals are comparable, but *Angiospirifer* is distinguished by possessing adminicula. Choristitids, like *Angiospirifer*, are provided with slightly diverging or parallel adminicula, and reticulate vascular markings (Lazarev and Poletaev 1982, pl. 1, figs. 4, 5): this pattern is well exhibited on British specimens from the Kinderscoutian Cayton Gill beds (text-fig. 1I, J). The choristitid microsculpture, seldom figured in Russian literature, is not preserved on the Cayton Gill material. On Algerian Bashkirian specimens (text-fig. 1L) the microsculpture is rather similar to that of *Angiospirifer*, although the concentric lamellae are more closely spaced. The differences between choristitids and *Angiospirifer* are: *a*, the radial ribs are generally more slender and bifurcating in choristitids; *b*, the adminicula are longer and the apical callosity reduced or absent; *c*, the vascular markings are more extensive, especially in the anterior part of the pedicle valve, and their reticulation is more delicate than in *Angiospirifer*. Finally, the genus *Subspirifer* Shan and Zhao 1981, which resembles *Angiospirifer* by shape and costation, differs by its smooth dorsal fold. Its microsculpture is unknown and its internal structure inadequately figured.

Generic composition

It is difficult to assign with certainty species of the broad *trigonalis* group to *Angiospirifer*. Some of the '*trigonalis*' specimens widely cited in the Eurasian and North African Carboniferous may not belong to *Angiospirifer*. For example, '*Spirifer trigonalis*' from Silesia (Zakowa 1958, pl. 3, fig. 9; 1966, pl. 15, figs. 3, 6) of probable Asbian age, displays a prominent apical muscle scar and pinnate mantle canals; it is probably not congeneric. The species *bisulcatus* Sowerby, sometimes considered synonymous with *trigonalis*, does not belong to *Angiospirifer*, since the syntypes in the Sowerby Collection, examined in the British Museum (Natural History), have a lirate microsculpture.

Some Serpukhovian Russian species, described by Semikhatova (1941) as '*trigonalis* group', may be true *Angiospirifer*: their adminicula show a tendency towards reduction and the muscle scar is located far from the apex (*S. gamma* Semikhatova, 1941, pl. 5, figs. 14*b*, 16*b*). The microsculpture of the species *parabisulcatus* Semikhatova is identical to that of *A. trigonalis* (Ivanova 1971, text fig. 4; pl. 1, fig. 4). The assignment of these species to *Angiospirifer* should be checked by observations of the vascular markings.

In addition the present author is currently investigating several undescribed *Angiospirifer* species in the upper Viséan and Serpukhovian of the northern Algerian Sahara.

Phyletic and systematic position of the genus Angiospirifer

The evidence of reticulate vascular markings as early as the upper Viséan is a significant feature for the phyletic trends of Spiriferidae. Ivanova (1972) pointed that the complex choristitid canal system evolved from a spiriferid stock. In the diagram of Lazarev and Poletaev (1982), such a development

was recorded only from Bashkirian choristitids, and regarded as an important criterion for distinguishing lower and upper Carboniferous Spiriferids. There is now evidence for the existence of reticulate vascular markings as early as the end of lower Carboniferous, both in *Angiospirifer* and in *Brachythyrina* (*Anthracothyrina*) Legrand-Blain, 1984. These taxa are related to each other, displaying a reduction in their dental plates (studied in some Russian species of the *trigonalis* group by Yanichewsky (1935), Semikhatova (1941), and observed also in Algerian species). On the other hand, *Angiospirifer* is a possible ancestor of choristitids. The origin of *Angiospirifer* should be sought in pre-Brigantian specimens, probably among the genera *Unispirifer* or *Prochoristitella.*

Placing *Angiospirifer* within its correct position and amongst the spiriferids is currently impossible. Ivanova (1972) attaches importance to the canal system which characterizes the families Brachythyrididae and Choristitidae. The existence in *Angiospirifer* of a denticulate interarea separates it from the Brachythyrididae. The Choristitidae of Ivanova (1972) have well-developed adminicula, so it is impossible to include both *Angiospirifer* and *Brachythyrina* in that family.

Carter (1974) distinguished many subfamilies in the Spiriferidae, but without considering the mantle canals. He doubtfully placed *Brachythyrina* in the Prospirinae (the microsculpture of which is lirate). His sub-family Choristitinae includes several genera characterized by numerous divided ribs.

Brunton and Rissoné (1974), followed by Waterhouse (1981), placed *Fusella* and *Brachythyrina* in the subfamily Strophopleuridae, which they considered as belonging to the family Mucrospiriferidae, and not Spiriferidae. In my opinion the sinal costation of *Angiospirifer* is strongly different from the ornamentation of Mucrospiriferids.

Thus, since *Angiospirifer* does not fit into existing families, I propose a new sub-family, belonging to the family Spiriferidae King 1846 *sensu* Carter 1974.

Subfamily ANGIOSPIRIFERINAE nov.

Diagnosis. Transverse shape; ribs not numerous, sometimes dividing; microsculpture sub-imbricated; adminicula short or lacking; apical callosity and vascular markings more or less developed.

Genera included. Angiospirifer gen. nov.; *Brachythyrina* Fredericks, 1929; *Prochoristitella* Legrand-Blain, 1968; *Kinghiria* Litvinovitch, 1969; ?*Quizhouspirifer* Xian, 1979; ?*Subspirifer* Shan and Zhao, 1981.

Stratigraphic range. Lower Carboniferous (Viséan) to lower Permian.

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