New interpretations of the phylogeny and taxonomy of delthyridoid spiriferids (Brachiopoda, Lower and Middle Devonian)

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A new phylogeny is introduced for Lower and Middle Devonian delthyridoid spiriferids with plicated fold and sulcus and bifurcating and trifurcating ribs. The new interpretation is based on side-by-side comparison of the type species of the genera with special focus on the micro-ornamentation and the style of ribbing, especially in the sulcus. During the revision of this group the following taxa are proposed: Multispiriferidae fam. nov., Ovetensispirifer novascotianus gen. et sp. nov., Turcispirifer turciae gen. et sp. nov.; three taxa are described in open nomenclature: gen. nov. A, ?Turcispirifer sp. A, and Ovetensispirifer cf. ovetensium. In the systematic part, each genus is described including its type species of the studied group. Emended diagnoses from family to species level are given. As a consequence of this study, the geographic distribution of the taxa of each evolutionary branch emphasizes the endemicity present during Early Devonian time and its decline at the beginning of the Middle Devonian. However, on the other hand, faunal pathways are shown from Western Europe to Nova Scotia, from North Africa over Turkey to Eastern Asia and to Arctic Canada, and probably from Venezuela to North Africa.

Delthyridoid spiriferids are an important tool for Devonian biostratigraphy and have been studied for almost two centuries. However, their systematics and their relationships to different faunal provinces during the Early Devonian are still a matter of debate. The systematics and phylogenetic interpretations introduced in this work are an attempt to elucidate the relationships between delthyridoid spiriferids showing the characters of the plicated fold and sulcus as well as bifurcation and trifurcation of ribs. Previous phylogenetic analyses are in most cases based on comparisons of literature. Bad illustrations and poor understanding of language used in original publications complicated the work. The result is often an erroneous report of the same genus from different faunal provinces (e.g., Solle 1953, 1971; Boucot 1959; Wang & Rong 1986). Nevertheless, phylogenetic studies restricted to certain areas of one faunal province are of importance for consideration of global connections and evolutionary lineages for certain genera (e.g., Gourvennec 1989, Carls et al. 1993, Jansen 2001a).

In the first edition of the Treatise on Invertebrate Paleontology, Pitrat (1965) tried to establish systematics for the whole group of spiriferids and spread the genera considered in the present work through the whole Delthyridoidea Phillips, 1841 and Cyrtioidea Frederiks, 1924. In the following years several new taxa were established. Carter et al. (1994) published the preliminary version of the revised Treatise on Invertebrate Paleontology and made an attempt to revise the systematics of spiriferid delthyridoid brachiopods. Since its publication this work has been considered controversial in several ways and is characterised by certain mistakes in the diagnoses of genera, resulting in erroneous taxonomy (e.g., Jansen 2000, 2001a, b; Schemm-Gregory 2007, 2008c, in press). Most of these errors were unfortunately adopted in the next Treatise on Invertebrate Paleontology edition (Johnson & Hou 2006, Gourvennec & Carter 2007). Further works that do help to clarify the systematics and the palaeobiogeographical relationships of spiriferids on a global scale are, for example, Boucot (1975), Boucot & Blodgett (2001), and Talent et al. (2001).

In this work genera from different regions, North America, Europe, North Africa, Central Asia, and South China (Fig. 1), are compared side-by-side for the first time and are,
where necessary, revised. Emended and new diagnoses are given for the taxa studied. As a result, unravelling the taxonomy has led to a systematics more complicated than that given in the last Treatise on Invertebrate Paleontology (Johnson & Hou 2006, Gourvennec & Carter 2007) with the relationships of the evolutionary branches showing an independent development for each branch during the Early Devonian and migration tendencies since the Late Emsian.

For stratigraphic assignment of Lower Devonian faunas, different subdivisions of the Devonian stages are used. In Europe and North Africa the brachiopods studied occur in neritic facies and correlation is based on the regional stages ‘Siegenian’ and ‘Emsian’ in their classical sense. For eastern North America the regional division into ‘Oriskanian’ and ‘Onondagan’ is used, although these units are still not confidently correlated to the GSSP (= Global Boundary Stratotype Sections and Points). In all other regions, if not indicated, the stages ‘Pragian’ and ‘Emsian’ are used in the GSSP sense (Gradstein et al. 2004).

Material and methods

The material is preserved as internal or external moulds of single or articulated specimens, and also as articulated or single shells. Fragments of shell material have been treated with formic acid to study micro-ornamentation impressions. Latex casts of external and internal moulds were made to study the shell morphology of the specimens. Drawings were done with the help of a camera lucida. Measurements were taken with digital calliper and rounded to 0.1 mm. Specimens were coated with magnesium oxide prior to photographing.

Institutional abbreviations

AMNH: American Museum of Natural History, New York City, USA; D: Centre des Sciences de la Terre, Lyon, France; DEVEC-TR: General Directorate of Mineral Research and Exploration, Ankara, Turkey; FMNH PE: The Field Museum of Natural History, Chicago, USA; GZG.INV.: Geowissenschaftliches Zentrum der Universität Göttingen, Museum, Germany; IPB: Institut für Paläontologie, Universität Bonn, Germany; IV: National Geological Museum of China, Beijing, PR China; MB.B.: Museum für Naturkunde Berlin, Germany; Mbg.: Institut für Geologie und Paläontologie, Philipps Universität Marburg, Germany; MCZ: Museum of Comparative Zoology/Harvard University, Cambridge, Massachusetts,
USA; NHM: The Natural History Museum, London, UK; NIGP: Nanjing Institute of Geology and Palaeontology, Nanjing, PR China; NS: Geological Museum of Ministry of Geology and Mineral Resources, Beijing, PR China; NYSM: New York State Museum, Albany, USA; PC: private collection of Prof. Dr. Peter Carls, Technische Universität Braunschweig, Germany; PMO: Palaeontological Museum, Oslo, Norway; PZ: Museo del Departamento de Palaeontología de la Universidad Zaragoza, Spain; SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; SKGS: South Kazakhstan Geological Survey, Tashkent; UA: University of Alberta, Canada; USNM: Smithsonian Institution/National Museum of Natural History, Washington DC, USA; YPM: Peabody Museum/Yale University, New Haven, USA.

**Important morphological features**

For a reasonable and probable reconstruction, morphological features have to be considered in relation to their importance. Some characters were created at the beginning of the evolutionary development of the group and did not change through the phylogeny of a certain group whereas others appeared several times in certain branches and/or were lost after a while. To judge the value of each morphologic character in the delthyridoid spiriferids a careful study of extensive material was made. In the following section, certain morphologic characters important for the interpretation of the phylogeny are briefly described.

**Micro-ornamentation.** – Two types of micro-ornamentation, fimbriate and capillate, are present in the material studied (Fig. 2). Fimbriate micro-ornamentation consists of rows of micro-spines at the edge of each growth lamella whereas capillate micro-ornamentation shows capillae on the surface that are crossed by the growth lamellae. In some genera micro-spines are also developed in capillate micro-ornamentation. All fimbriate genera studied in this work show single rows of micro-spines at the edge of each growth lamella (Fig. 3) and are considered to be the root of the spiriferids studied (see section Phylogenetic interpretations and palaeobiogeography).

**Ribs.** – The radial ridges of the coarse ornamentation are described in this work as ribs. According to Williams & Brunton (1997), ribs describe any ornament of radial ridges;
costae, however, is the term for “first-formed radial ridges on external surface of brachiopod shell” (Williams & Brunton 1997, p. 427) or coarse ribs in general, costellae are fine ribs, and capillae very fine ribs. A third term for characterizing coarse ornamentation is plication. Plications are major undulations of the commissure that are reflected on the shell interior. As the differentiation between costa, costella, and capillae is subjective and these terms are often used in different senses, the neutral term ‘ribs’ is used in this work.

To describe bifurcation and trifurcation patterns, ribs of first, second, and third order are distinguished. Ribs of first order are the main ribs before multiplication; those of second order have bifurcated or trifurcated ribs for the first time, whereas third order ribs have multiplied twice during ontogeny. The style of ribbing is different in each taxon on the external surface either on flanks and/or in sulcus and on the fold (Fig. 4). For certain taxa no adequate or well-enough preserved material was available to give a reliable number of ribs on flanks. After all the number of ribs on flanks varies strongly during ontogeny due to the multiplication.

Dividing ribs in the sulcus. – The scheme of dividing ribs in the sulcus can also be used as a tool for determination at genus level (Fig. 5). Important characters are the median rib in the sulcus and the growth stage in which furcation occurs, as well as the rib that is dividing.

Development of secondary shell material. – Some genera of spiriferids are characterized by strong development of secondary shell material in the apical region, probably to stabilize the life position of the upwards-oriented anterior margin of the shells (Jansen 2001a). As a result, the ventral muscle field is deeply impressed in the shell material and the dental plates are embedded into shell material and may not be preserved on the internal mould (e.g., Costispirifer).
In genera that do not show much development of secondary shell material, the dental plates leave long and mostly thin slits on either side of the filling of the ventral muscle field on the internal mould. Strong development of secondary shell material in the dorsal apical region results in free exposed cardinalia whereas in taxa with less development of secondary shell material the cardinalia are hidden beneath the filling of the dorsal umbo on the internal mould.

**Crural plates.** – Crural plates are connected with the dorsal valve floor. However, until they are completely embedded into shell material several crural stages are visible (see Gourvennec 1989, p. 29, fig. 16). Juvenile specimens have to be studied to see if the crural plates are free lying and if they become embedded during ontogeny. The presence or absence of crural plates is a genus level character.

**Delthyrium, deltidial lamellae, and deltidium.** – The Delthyridoidea are characterised by an open delthyrium that may be restricted by a pair of deltidial lamellae. The thickness and orientation of these lamellae is regarded as a taxonomically important character (Schemm-Gregory in press). The deltidial lamellae can also be fused in the apical region forming a small deltidium.

**Ctenophoridium and notothyrial shelf.** – The term ctenophoridium describes the dorsal diductor field and consists of lamellae orientated in longitudinal direction. Some authors (e.g., Gourvennec 1989, Jansen 2001a) regard the number of these lamellae as an important character for systematic description, but in most cases, the preservation of internal moulds is quite poor and the lamellae are abraded, which can give the wrong impression of their number. Nonetheless, the number of lamellae indicates tendencies in phylogeny. The ctenophoridium can be supported by a notothyrial shelf. Presence or absence of the notothyrial shelf is an important character. The absence of the shelf results in an orientation of the surface of the ctenophoridium perpendicular or oblique to the commissural plane whereas its presence is seen in a ridge on the internal mould posterior and/or beneath the filling of the dorsal umbo on the internal mould. If the ctenophoridium lies on this ridge, it is oriented parallel to the commissural plane.

**Phylogenetic interpretations and palaeobiogeography**

The root of the delthyridoid spiriferids probably lies in the fimbriate Howellella (Iberohowellella) Carls, 1985, as already discussed by Carls et al. (1993), from which Vandercammenina Boucot, 1975 separated. Vandercammenina, especially the early form V. sollei Carls, 1986 shows few ribs in the sulcus and on the fold and clearly developed crural plates. Later in the evolutionary lineage of Vandercammenina the number of ribs in sulcus and fold increases. Especially in the type species, V. trigeri (de Verneuil, 1850), a development of secondary shell material in the dorsal apical region can be noted resulting in embedded crural plates. During the Siegenian, Struveina Boucot, 1975 separated from Vandercammenina, a genus characterized by bifurcation and trifurcation of ribs on the flanks as well as in the sulcus and on the fold but also in the lack of crural plates in all of its species. *Fimbrispirifer* Cooper, 1942 has been found at the beginning of the Eifelian in North America. This genus is interpreted, even though crural plates are present, as being a descendant from the North African/European *Struveina* rather than from *Vandercammenina* because of the strong bifurcation and trifurcation of ribs. Migration of *Fimbrispirifer* might have been possible with sea-level rise at the beginning of the Eifelian (Johnson et al. 1985). *Struveina* became extinct during Emsian time in the classical German sense; *Vandercammenina* during the Eifelian.

Another lineage arising from the African forms of *Vandercammenina* is represented by the new genera described...
Table 1. Comparison of the fimbriate genera studied with ribbed fold and sulcus and bifurcating and trifurcating ribs on flanks, fold, and in sulcus

<table>
<thead>
<tr>
<th></th>
<th>Fimbrispirifer</th>
<th>Struveina</th>
<th>Vandercammenina</th>
<th>Ovetensispirifer</th>
<th>Turcispirifer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coop., 1942</td>
<td>Boucot, 75</td>
<td>Boucot, 1975</td>
<td>gen. nov.</td>
<td>gen. nov.</td>
</tr>
<tr>
<td>septal pillow</td>
<td>–</td>
<td>–</td>
<td>small</td>
<td>large +</td>
<td>+</td>
</tr>
<tr>
<td>dental plates</td>
<td>divergent</td>
<td>divergent</td>
<td>divergent</td>
<td>divergent</td>
<td>almost parallel</td>
</tr>
<tr>
<td>ventral muscle field</td>
<td>weakly impressed</td>
<td>weakly impressed</td>
<td>moderately impressed</td>
<td>strongly impressed</td>
<td>weakly impressed</td>
</tr>
<tr>
<td>median rib in sulcus</td>
<td>+</td>
<td>+/-</td>
<td>–</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>notothyrial shelf</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>lacking or indicated</td>
<td>indicated in some cases</td>
</tr>
<tr>
<td>dental sockets</td>
<td>thin</td>
<td>thick</td>
<td>thin</td>
<td>thick</td>
<td>thin</td>
</tr>
<tr>
<td>brachiophores</td>
<td>thin, small</td>
<td>thick, small</td>
<td>thin, small</td>
<td>thin, long</td>
<td>thin, ?</td>
</tr>
<tr>
<td>crural plates</td>
<td>+</td>
<td>–</td>
<td>+/-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>bifurcation of costae on flanks</td>
<td>+</td>
<td>+</td>
<td>rarely</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>trifurcation of costae on flanks</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>deltidium</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>geographic occurrence</td>
<td>eastern North America</td>
<td>Europe</td>
<td>North Africa, Europe</td>
<td>Europe</td>
<td>Turkey, ?Morocco</td>
</tr>
<tr>
<td>stratigraphic occurrence</td>
<td>Emsian to Lower Givetian</td>
<td>Lower Siegenian to Middle Eifelian</td>
<td>Lower Siegenian to Middle Eifelian</td>
<td>Siegenian</td>
<td>Siegenian to ?Emsian</td>
</tr>
</tbody>
</table>

Here, Ovetensispirifer and Turcispirifer. They are interpreted as being descendents of Vandercammenina because of the presence of crural plates and fimbriate micro-ornamentation and the absence of bifurcating ribs on the flanks. Ovetensispirifer appears during the early Siegenian in the Iberian Chains (Spain) and Nova Scotia (Canada), probably also in the Istanbul Basin, Turkey (U. Jansen, pers. comm. 2008); Turcispirifer appears in Turkey and probably in Morocco during the Siegenian. The vandercammeninid ancestor of Ovetensispirifer might be close to V. sollei because of the small number of ribs in the sulcus and the development of crural plates that both, Ovetensispirifer and V. sollei show. Ovetensispirifer novascotianus sp. nov. from Nova Scotia clearly shows a faunal relationship to Ovetensispirifer ovetensis from the Iberian Chains and the Armorican Massif (France) of the Rhenish-Bohemian Region during Siegenian time based on its strong development of secondary shell material in the apical region of both valves and the elevated internal mould of the ventral muscle field. Additional brachiopods that occur together with O. novascotianus in North America are Crassirensellaeria sp. and ?Brachyspirifer aff. crassicosta (Boucot 1960a, b), but these forms are related to taxa occurring in the Ardenno-Rhenish Mountains (Belgium, Germany) of the Rhenish-Bohemian Region. Species of Turcispirifer found in Turkey show faunal affinities to North African faunas of Early Devonian age (Schem-Gregory et al. 2008a, b) whereas affinities between Turkey and Central Europe (e.g., de Verneuil 1869, Paeckelmann & Sieverts 1932) turn out to be suspect. Recent studies on the palaeogeography of the Rhec Ocean show that faunal exchange seems to have been more plausible between the Istanbul Basin (present day Turkey), which was then situated at the southern margin of Baltica, and North Gondwana (present day North Africa) than between the Istanbul Basin and Avalonia (present day Central Europe) (U. Linneman, pers. comm. 2008). Table 1 shows the morphological comparison of fimbriate genera discussed.

The Asian Emsian (sensu GSSP; Gradstein et al. 2004) forms that are characterised by a capillate micro-ornamentation, and in some genera also with micro-spines of different length, probably developed out of the Turkish Turcispirifer with slow-eastwards migration. The group around Borealispirifer Hou & Su in Su & Hou, 1993 that appears in Central and East Asia during the Emsian in GSSP sense shows relatively narrow ribs, but has bifurcation and trifurcation on the flanks as well as in the sulcus and on the fold. However, the Turkish forms show only bifurcation of ribs in the sulcus and on the fold. The occurrence of capillae with micro-spines is interpreted as a development from fimbriate to capillate micro-ornamentation. During the Early Emsian Elymospirifer Wang in Wang et al., 1974, a South Chinese and Taimyr form, probably evolved out of Borealispirifer and gave rise to the Late Emsian Perryspirifer Jones & Boucot, 1983, which possibly migrated further eastwards with the sea-level rise at the Early/Late Emsian boundary interval (Johnson et al. 1985) from South China to the Canadian Arctic Islands.

The morphology of the European genus Multispirifer Kaplun, 1961 is quite distinct from all other genera studied in this work. A possible phylogenetic link to a potential ancestor is still missing. Its origin from an early Siegenian
form of *Vandercammenina* might be a reasonable possibility. The phylogenetic lineage of this genus is characterized by large forms with ‘bundled’ ribs, cardinalia situated on an elevated shelf, and a capillate micro-ornamentation that can also show micro-spines and is considered in this work to be an isolated evolutionary branch. *Multispirifer* became extinct before the Early Emsian in the classical German sense. However, this interpretation is still a matter of debate.

The family Costispiriferidae shows a capillate micro-ornamentation without micro-spines and is interpreted to have evolved from early forms of *Vandercammenina*. The reason for the restricted appearance of Costispiriferinae in North America and the local appearance of Multiplicatispiriferinae in Morocco remains speculative and is probably the result of incomplete preservation. However, relationships between the Anti-Atlas (Morocco) and the Appalachian Chain (eastern North America) have already been discussed, e.g., Michard (1976). *Multiplicatispirifer weisbordi* (Harris in Liddle et al., 1943) from Venezuela might represent the phylogenetic link between *Costispirifer* Cooper, 1942 and *Multiplicatispirifer* Schemm-Gregory, 2008c. In the present state of research, it is assumed that Multiplicatispiriferinae evolved out of Costispiriferinae and Schemm-Gregory (2008c) provided an attempt to reconstruct their phylogenetic relationships and migration pathways. Table 2 shows a morphological comparison of the discussed capillate genera. The interpretation of the discussed phylogenetic relationship is shown in Fig. 6.

### Table 2. Comparison of the capillate genera studied with ribbed fold and sulcus and bifurcating and trifurcating ribs on flanks, fold, and in sulcus

<table>
<thead>
<tr>
<th>Costispiriferidae</th>
<th>Elymospideridae Johnson &amp; Hou in Carter et al., 1994</th>
<th>Multispiriferidae fam. nov.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Costispirifer</em> Cooper, 1942</td>
<td><em>Elymospifer</em> Wang in Wang et al., 1974</td>
<td><em>Multispirifer</em> Kaplan, 1961</td>
</tr>
<tr>
<td><em>Multiplicatispirifer</em> gen. nov.</td>
<td><em>Perryspirifer</em> Jones &amp; Boucot, 1983</td>
<td></td>
</tr>
<tr>
<td><em>Borealispirifer</em> Hou &amp; Su in Su &amp; Hou, 1993</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>gen. nov. A</em></td>
<td></td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Outline</th>
<th>Megathyrid</th>
<th>Megathyrid</th>
<th>Megathyrid</th>
<th>Megathyrid</th>
<th>Megathyrid</th>
<th>Megathyrid</th>
<th>Brachythrid</th>
</tr>
</thead>
<tbody>
<tr>
<td>Septal pillow</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>+</td>
<td>?</td>
<td>?</td>
<td>+</td>
</tr>
<tr>
<td>Dental plates</td>
<td>Divergent</td>
<td>Divergent to almost parallel</td>
<td>Divergent</td>
<td>Divergent</td>
<td>Divergent</td>
<td>Almost parallel</td>
<td>Divergent</td>
</tr>
<tr>
<td>Ventral muscle field</td>
<td>Strongly impressed</td>
<td>Weakly impressed</td>
<td>Moderately impressed</td>
<td>Strongly impressed</td>
<td>Weakly impressed</td>
<td>Strongly impressed</td>
<td>Strongly impressed</td>
</tr>
<tr>
<td>Median open in sulcus</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Notothyrial shelf</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>+</td>
</tr>
<tr>
<td>Dental sockets</td>
<td>Thin, small</td>
<td>Thick</td>
<td>Thin</td>
<td>Thin</td>
<td>Thin</td>
<td>?</td>
<td>Thick, long</td>
</tr>
<tr>
<td>Brachiophores</td>
<td>Thin, small</td>
<td>Thick, small</td>
<td>Thin, small</td>
<td>Thin, long</td>
<td>?</td>
<td>?</td>
<td>Thick, long</td>
</tr>
<tr>
<td>Crural plates</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Bifurcation of costae on flanks</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Trifurcation of costae on flanks</td>
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<td>–</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Deltidium</td>
<td>+</td>
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<td>?</td>
<td>?</td>
<td>+</td>
</tr>
<tr>
<td>Geographic occurrence</td>
<td>Eastern North America</td>
<td>North Africa</td>
<td>Taimyr, South China</td>
<td>Canadian Arctic Islands</td>
<td>Kazakhstan, northern China</td>
<td>Northern China</td>
<td>Central Europe</td>
</tr>
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<td>Stratigraphic occurrence</td>
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<td>Emsian</td>
<td>Lower Emsian</td>
<td>Upper Emsian</td>
<td>Lower Emsian</td>
<td>Lower Emsian</td>
<td>Siegenian</td>
</tr>
</tbody>
</table>

**Systematic palaeontology**

Order *Spiriferida* Waagen, 1883
Suborder *Delthyridina* Ivanova, 1972
Superfamily *Delthyridoidea* Phillips, 1841
Family *Fimbrispiriferidae* Pitrat, 1965

*Type genus.* – *Fimbrispirifer* Cooper, 1942.

*Emended diagnosis.* – Shells with ribbed fold, sulcus, and flanks; ribs multiply by bifurcation and trifurcation; crural plates variably present. Micro-ornamentation fimbriate with single rows of micro-spines on the edge of each growth lamella.
Geographic and stratigraphic occurrence. – Eastern and central North America, North Africa, Western and Central Europe, Turkey; Siegenian to lower Givetian (middle Lower Devonian to upper Middle Devonian).


Remarks. – The Bultynckia is raised to family level as published in the former Treatise on Invertebrate Paleontology (Pitrat 1965). The consideration that the Bultynckia is a subfamily of the Hysterolitidae Termier & Termier, 1949 is erroneous as the Hysterolitidae are defined as having a smooth fold and sulcus, occasionally with a median furrow or rib as already pointed out in (Schemm-Gregory in press). The distinct scheme of ribbing on flanks, fold, and sulcus in comparison to other delthyridoid spiriferids (Fig. 5) justifies the family following also the intention of other authors (Termier & Termier 1949).

Discussion. – The genus Bultynckia García-Alcalde, 2004 is excluded from the Bultynckidae due to its style of ribbing. It shows bifurcating of ribs only on flanks at the anterior margin and only in some cases a rib on the walls of the sulcus. Furthermore, the fold and sulcus are rather flat on its top or bottom, sometimes showing a very coarse median rib or a broad, but shallow furrow that shows a very different style from the scheme of ribbing on the sulcus and fold of the genera of Bultynckidae considered in this work. García-Alcalde (2004) discussed the differences of Bultynckia with Vanderacammenina, Struveina, Fimbrispirifer, and Multispirifer. Until further material can be studied Bultynckia is referred to the Paraspiriferinae Pitrat, 1965, as was the suggestion of García-Alcalde (2004).

Genus Fimbrispirifer Cooper, 1942

Type species. – Spirifer venustus Hall, 1860, p. 62.

Emended diagnosis. – Medium to large, biconvex to ventriconvex. Ventral interarea curved and apsacine. Fold, sulcus, and flanks with numerous bifurcating ribs; ribs on flanks may also trifurcate. Ribs and furrows are rounded in cross section. No deltidium, dental plates short and wedge-like. Crural plates present, notothyrial shelf and septal pillow lacking. Micro-ornamentation of closely spaced, zigzag concentric growth lamellae with single rows of micro-spines at their edges.

Species assigned. – Spirifer venustus Hall, 1860, Spirifer divaricatus Hall, 1867, Spirifer grieri Hall, 1867, Fimbrispirifer tricostatus Fagerstrom, 1961.

Remarks. – Cooper (1942, p. 231) originally defined Fimbrispirifer by its fimbriate micro-ornamentation (Fig. 2A), however, on most of the material, including the holotype of the type species, the micro-ornamentation is not preserved. Thus, various authors assigned spiriferids to Fimbrispirifer emphasizing their bifurcating ribs and ribbed fold and sulcus rather than by the micro-ornamentation, which is only preserved in rare cases (e.g., Amsden 1963, Brice 1982). Havlíček (1959) defined Fimbrispirifer by simple and bifurcating ribs and ribs on flanks, fold, and in sulcus with a fimbriate micro-ornamentation. Later, Boucot (1975) separated the genera Vanderacammenina and Struveina from Fimbrispirifer based on the absence and presence of crural plates and the style of ribbing. In the present work, the concept of Boucot (1975) is followed and according to his and my own studies, “Fimbrispirifer” charybdis (Barrande, 1879) has to be excluded from Fimbrispirifer due to the lack of multiplying ribs. However, “Fimbrispirifer”-like forms are reported from the upper Eifelian beds from Skaly (Holy Cross Mountains, Poland: Halamski 2004, p. 207) but have not been considered here.

Discussion. – Fimbrispirifer differs from Struveina in its shorter dental plates, a narrower ctenophoridium, delicate cardinalia, and distinct crural plates which are always lacking in Struveina.

In contrast to Vanderacammenina, Fimbrispirifer shows a thin ctenophoridium. The ctenophoridium in Vanderacammenina is broader. Fimbrispirifer always has crural plates whereas in Vanderacammenina the crural plates are either embedded into secondary shell material or indicated.
by a broad and rounded indentation beneath the filling of the ventral muscle field on the internal mould (Fig. 7; Gourvennec 1989, pl. 6, figs 22, 23). The ribs of Fimbrispirifer are bifurcating and trifurcating on the flanks, in Vandercammenina they bifurcate on the flanks only in very few specimens. Vandercammenina has in contrast to Fimbrispirifer no median rib in the sulcus.

The dental plates in Turcispirifer are long, thin, and oriented almost parallel to each other whereas they are small and divergent in Fimbrispirifer. A notothyrial shelf is always lacking in Fimbrispirifer, in Turcispirifer it can be indicated in some cases. Turcispirifer shows no bifurcation on its flanks whereas Fimbrispirifer shows bifurcating and trifurcating ribs on its flanks. Ovetensispirifer differs from Fimbrispirifer in having much more secondary shell material developed in its apical region of both valves, a deeply embedded ventral muscle field, and longer dental plates. Ribs of Ovetensispirifer are bifurcating in the sulcus and on the fold in adult stages. The growth lamellae of Ovetensispirifer are at a greater distance from each other than growth lamellae in Fimbrispirifer.

Geographic and stratigraphic occurrence. – Eastern and central North America; Emsian to lower Givetian (upper Lower Devonian to upper Middle Devonian).

**Fimbrispirifer venustus (Hall, 1860)**

Figures 2A, 4A, 5, 7

1860 *Spirifer venustus* n. sp. – Hall, p. 82.

**Holotype.** – Articulated shell, designated as lectotype by Jones & Boucot (1983), stored under inventory number USNM 39489. Length 27.8 mm, width 41.8 mm, and thickness 24.4 mm. A plaster cast of the holotype is stored under inventory number SMF 66613.

**Type horizon and locality.** – Beechwood Limestone, Hamilton Group, Givetian (upper Middle Devonian); Lebanon, Kentucky, USA.

**Material.** – Locality and stratum: Lebanon, Kentucky, USA; Beechwood Limestone. 1 articulated specimen: USNM 39489 (holotype), 1 internal mould of articulated specimen USNM 39489a (paratype). Locality and stratum: abandoned quarry 2.5 km SSE of Ragland, Alabama, USA; Ragland Sandstone. 1 fragment of an external ventral mould: USNM 108217.

**Emended diagnosis.** – Shells medium-sized to large, transverse, and ventribiconvex in longitudinal section; megathyrid without mucronations. Fold and sulcus conspicuous with ribs bifurcating and trifurcating on flanks. Crural plates strong and well developed. Brachiophores and dental sockets delicate. Notothyrial shelf lacking. Growth lamellae at short distance to each other.

moderately high. Coarse ornamentation: ribs unequally bifurcating and trifurcating on the posterior half of the flanks at the same growth stage. Each rib multiplies only once (Fig. 4A). Sulcus with median furrow. Ribs bifurcating to median from the sulcus bordering ribs always at the same growth stage (Fig. 5). Ribs on the fold bifurcating from the most lateral rib to median or from the first pair of rib to lateral. Ribs on fold and in sulcus are of same size as ribs on the flanks. All ribs fine, separated by fine furrows. Ribs and furrows rounded to angular in cross section. Micro-ornamentation: fimbriate, with single rows of micro-spines on the edge of each growth lamella. Growth lamellae well developed and close to each other. Interior of ventral valve: filling of the umbo extends to posterior over the hinge line. Almost no development of secondary shell material in apical region. Lateral apical cavities are clearly separated by dental plates from the central apical cavity. Fillings of the lateral apical cavities reaching to posterior over the hinge line almost as far as the internal mould of the ventral muscle field. Muscle field not embedded into shell material. Free portions of dental plates thin and moderately long. Ribs well impressed on the internal mould, bifurcation and trifurcation of ribs visible. Interior of dorsal valve: notothyrial shelf lacking. Ctenophoridium small, situated anterior of the hinge. Crural plates strong and long. Crural bases preserved as free lamellae or lacking. Dental sockets thin, long, and almost parallel to the hinge line. Brachiophores thin and small. Myophragm weakly developed, leaving a fine furrow in the anterior half of the internal mould. Adductor scars not preserved. Fold moderately elevated and rounded on top. Ribs well impressed on the internal mould, bifurcation and trifurcation of ribs visible.

Geographic and stratigraphic occurrence. – Eastern North America; lower Givetian (upper Middle Devonian).

Figure 8. Vandercammenina parcefurcatus (Spiestersbach, 1915). Locality: Railway cut near Gummersbach, Bergisches Land (Rheinisches Schiefergebirge, Germany). Stratum: lower Selscheid Beds, Eifelian (lower Middle Devonian). • A, B – GZG.INV. 15222, internal dorsal mould (× 1.0). Plan (A) and oblique posterior (B) views. • C-E – GZG.INV. 15223, internal dorsal mould. Plan (C) and oblique posterior (D) views (× 2.0) and plan (E) view (× 1.0).

Genus Struveina Boucot, 1975

Type species. – Spirifer Daleidensis Steininger, 1853, p. 71.

Emended diagnosis. – Medium-sized to large spiriferids with bifurcating and trifurcating ribs on sulcus, fold, and flanks. Ribs are rounded, furrows are angular to rounded in cross section. Crural plates and notothyrial shelf always lacking.


Species excluded. – Spirifer parcefurcatus Spiestersbach, 1915.

Remarks. – The species parcefurcatus Spiestersbach, 1915 (Fig. 8) is excluded from Struveina due to the presence of well developed crural plates preserved as long slits on the internal dorsal mould and rare occurrence of bifurcating ribs on its flanks. A few specimens from the Selscheid Beds (lower Eifelian, lower Middle Devonian) of the material from Thienhaus (1940, GZG.INV. 15222–15226) and Schmidt & Trunko (1965, GZG.INV. 15215–15221) show 1 or 2 bifurcating ribs next to the sulcus. The illustrated paratype by Spiestersbach (1915, pl. 14, fig. 10), a dorsal internal mould, shows weakly indicated crural plates and bifurcation of the first pair of ribs. Further material of this taxon from the lower Eifelian of the Sauerland region (Germany) has been studied by the present author in the collection of the Geowissenschaftliches Zentrum der Universität Göttingen, Museum. In this work the species parcefurcatus is assigned to the genus Vandercammenina.

Discussion. – Struveina differs from Vandercammenina in possessing regular bifurcating and trifurcating ribs on its flanks, a median rib in the sulcus, a median furrow on the fold, strong dental sockets, and strong brachiophores. Crural plates are never preserved in Struveina, in Vandercammenina indentations above the cardinalia are interpreted as remains of crural plates, in some specimens crural plates are well preserved leaving long and thin slits on the dorsal internal mould.

The dental plates in Struveina are divergent whereas they are oriented almost parallel in Turcspirifer. Struveina has no crural plates which are long and thin in Turcspirifer. The ribs on the flanks are bifurcating and trifurcating in Struveina, in Turcspirifer they never bifurcate on flanks. Struveina lacks a septal pillow and a notothyrial shelf, both characters are developed in Turcspirifer, although in the latter only indicated in some cases.

Ovetensispirifer has a stronger development of secondary shell material in the apical region, strong dental plates,
and crural plates. The latter are always lacking in Struveina. Struveina shows bifurcation and trifurcation of ribs in sulcus, on fold, and on flanks whereas Ovetensispirifer shows bifurcation of ribs only in the sulcus and on the fold.

The comparison of Struveina with Fimbrispirifer is described above.

Geographic and stratigraphic occurrence. – Western and Central Europe (Germany, Spain, Belgium, France, England); Lower Siegenian boundary (according to Carls 1987) to Middle Eifelian (middle Lower Devonian to lower Middle Devonian).

Struveina daleidensis (Steininger, 1853)
Figures 2B, 4B, 5, 9

1853 Spirifer Daleidensis Steininger; Steininger, p. 71.
1889 Spirifer Daleidensis Steininger, 1853. – Kayser, p. 27, pl. 16, fig. 10.
1900 Spirifer Daleidensis Steininger, 1853. – Scupin, pp. 75, 76, pl. 7, fig. 10.
1963 Fimbrispirifer daleidensis (Steininger, 1853). – Van-dercammen, pp. 29–35, pl. 2, figs 14–16, pl. 3, figs 1–12.

Holotype. – Ventral internal mould stored in the Steininger collection as inventory number MB.B. 2031.1. It is illus-
trated by Kayser (1889, p. 27, pl. 16, fig. 10). Width 36.0 mm and length 32.6 mm. A plaster cast of the holotype is stored under inventory number SMF 19239.

**Type horizon and locality.** – Wiltz Formation (Upper Em-
bifurcating or intercalating. Sulcus conspicuous to inconspicuous. Micro-ornamentation fimbriate with narrow micro-spines on the edge of each growth lamellae. Growth lamellae developed at regular distances. Interior of the ventral valve variable. Crural plates free lying or completely embedded into secondary shell material.

[After Carls, unpubl.; from Gourvennec 1989, p. 94; translated and modified from Jansen 2001a, p. 287.]


Species excluded. – *Vandercammenina ovetensium* Carls, 1986.

Remarks. – Boucot et al. (1958) reported a new unnamed spiriferid genus from the Lower Devonian of Nova Scotia. Later, Boucot (1960a, b) discussed the relationship of further material to the Rhenish species *Vandercammenina bischofi* (Giebel, 1858). Part of the material was studied by the present author in the Museum of Comparative Zoology/Harvard University and has been assigned to the new genus *Ovetensispirifer*, see discussion below.

Discussion. – *Vandercammenina* differs from *Turcispirifer* in lacking or having a smaller septal pillow, the lack of a median rib in the sulcus, and of a notothyrial shelf. *Vandercammenina* in the gerontic stage rarely shows bifurcating ribs on the flanks whereas in *Turcispirifer* ribs never bifurcate on the flanks.

The species *ovetensium* is excluded from *Vandercammenina* and erected as type species of the new genus *Ovetensispirifer* due to its strong development of secondary shell material in the apical region and the resulting strongly embedded ventral muscle field. *Vandercammenina* shows little development of secondary shell material in the apical region and a gently embedded ventral muscle field. *Ovetensispirifer* is strongly dorsiiconvex, the sulcus shows steep flanks, is flat at the base, and its anterior margin is defined by a long sulcus tongue. The sulcus of *Vandercammenina* is rounded at its base, shows shorter and oblique flanks, the sulcus tongue is short, and its anterior margin rounded. The specimen illustrated by Gourvennec (1989, pl. 7, fig. 12) shows a well developed septal pillow. The etenophoridium of *Ovetensispirifer* lies further to the posterior than in *Vandercammenina*. *Ovetensispirifer* always shows clearly developed crural plates, which may be absent or only weakly indicated in *Vandercammenina*.

The comparison of *Vandercammenina* with *Fimbri-spirifer* and *Struveina* is described above.

Geographic and stratigraphic occurrence. – Europe, North Africa; Lower Siegenian boundary (according to Carls 1987) to Middle Eifelian (middle Lower Devonian to lower Middle Devonian).

**Vandercammenina trigeri** (de Verneuil, 1850)

Figures 2C, 4C, 5, 10

1850 *Spirifer Trigeri* de Verneuil; de Verneuil, p. 781.
2007 *V. trigeri* (de Verneuil, 1850). – Jansen et al., tab. 1, fig. 4.19.

Further synonymy see Jansen (2001a, p. 288).

Lectotype. – Articulated shell stored under inventory number D210, illustrated by Gourvennec (1989, pl. 6, figs 1–5). Holotype 47.1 mm wide and 35.5 mm long.

Type horizon and locality. – Néhou Formation, Lower Siegenian (middle Lower Devonian); Néhou, abandoned quarry at the Lande du Parc/Manche (Armorican Massif, France).

Material. – Locality and stratum: Assa 1, east of Assa (southern Anti-Atlas Mountains, Morocco). Assa Formation (Rich 1), Lower Siegenian (middle Lower Devonian). 1 ventral internal mould: SMF 59180; 2 dorsal internal moulds: SMF 59181, 59184; 2 ventral shells: SMF 59180, 59183; 2 dorsal shells: SMF 65198, 65398. Locality and stratum: 1 km S of Modorry, 3.3 km W of Mezquita (eastern Iberian Chains, Spain); Nogueras Formation, upper d2c beta, upper Lower Siegenian (middle Lower Devonian). 1 articulated shell: SMF 59452 (illustrated by Carls et al. 1993, pl. 36, fig. 60).

Diagnosis. – Shells medium-sized without mucronations. Sulcus with 8 ribs on average, median rib in sulcus lacking, instead with median furrow. About 20 simple ribs on each flank. Sulcus conspicuous. Sulcus bordering ribs not weakened and not included into the sulcus. Ventral interarea aspalcine and curved. Hardly any development of secondary shell material in apical region. Free portions of dental
plates long, thin, and divergent. Lamellae of ctenophoridium partly dichotomous and subparallel to each other. [Translated from Jansen 2001a, p. 289.]

Description. — Form and size: shells medium-sized, megathyrid without mucronations, some specimens show the development of small ears. Biconvex to ventribiconvex in longitudinal section, outline subelliptical to subquadrangular. Exterior of ventral valve: ventral interarea moderately high, apsacline and curved. Delthyrium open, deltoidal lamellae clearly developed, deltidium lacking. Exterior of dorsal valve: interarea moderately low, anacline to orthocline. Notothyrium open and with chilidial lamellae. Coarse ornamentation: ribs on flanks simple, only in some specimens sporadic bifurcation of ribs is seen at the anterior margin of the flanks (Fig. 4C). Up to 22 ribs are present on each flank of the ventral valve. Sulcus without median rib. Ribs in sulcus multiply by bifurcation from the sulcus bordering rib on the flanks of the sulcus, bifurcation on each side parallel at the same growth stage (Fig. 5). Up to 8 ribs present in sulcus in adult specimens. Micro-ornamentation: fimbriate micro-ornamentation with single rows of micro-spines at the edge of each growth lamella. Similar to the micro-ornamentation of Struveina (Fig. 2C). Growth lamellae at a moderate distance from each other. Interior of ventral valve: filling of the umbo extending to posterior over the hinge line. Hardly any development of secondary shell material in apical region. Lateral apical cavities are clearly separated by dental plates from the central apical cavity. Fillings of the lateral apical cavities reaching as far to the posterior as the hinge line on the internal mould of the ventral muscle field. A small septal pillow is developed beneath the posterior end of the ventral muscle field. Ventral process broad,
leaving a clear indentation on the internal mould at the posterior end of the muscle field. A short and weakly developed myophragm develops out of the ventral process leaving a fine furrow through the posterior half of the ventral muscle field on the internal mould. Ventral muscle field only weakly embedded into shell material, always wider than long, and with 2 to 3 impressions of ribs on the internal mould. Diductor scars not preserved. Adductor field elongate and impressed into the internal mould. Muscle bounding ridge often lacking, in some specimens weakly developed leaving an almost inconspicuous furrow on the internal mould. Free portions of dental plates thin and long, situated between the third and fourth rib on the internal mould. Sulci without impression of median rib. Sulcus bordering ribs not weakened and not included into the sulcus. 4 to 6 impressions of ribs in the sulcus and 13 to 15 impressions of ribs on each flank preserved. No gonoglyphs and no impressions of growth lamellae preserved. Interior of dorsal valve: filling of the dorsal umbo extends gently above the hinge line and overhangs above the cardinalia. Notothyrial shelf lacking. Ctenophoridium situated posterior to the dental sockets. Median process almost unrecognisable rounded in cross section. Brachiofores not curved over top. Impressions of ribs as on the internal mould of ventral valve. Growth lamellae are not impressed.

Geographic and stratigraphic occurrence. – Central, South, and Southwest Europe, North Africa; Siegenian (middle Lower Devonian).

Genus Ovetensispirifer nov.

Type species. – Vandercammenina ovetensium Carls, 1986, p. 35.

Derivation of name. – After the type species ovetensium.

Diagnosis. – Medium-sized to large shells, dorsibiconvex in longitudinal section with 1 median and 2 lateral ribs in the sulcus bifurcating in adult stage, and numerous simple ribs on flanks. Sulcus and fold weakly defined; sulcus bounding ribs often included in the sulcus. Strong development of secondary shell material in apical region of both valves. Large septal pillow. Free portions of dental plates wedge-like and short. Crural plates well developed, dental sockets coarse. Notothyrial shelf lacking.


Discussion. – The genus Ovetensispirifer is erected due to its strong morphological differences from Vandercammenina (see above). The rare bifurcation of ribs, the strong development of secondary shell material in the apical region of both valves, style of ribbing of ribs in sulcus, and the development of crural plates in comparison to Vandercammenina justify the establishment of a new genus.

Turcspirifer differs from Ovetensispirifer in hardly any development of secondary shell material in the apical region of both valves, long and slender dental plates, longer crural plates, and the lack of an embedded ventral muscle field. The comparison of Ovetensispirifer with Fimbri spirifer, Struveina, and Vandercammenina is described above.

Geographic and stratigraphic distribution. – Armorican Massif, Iberian Chains (southern Europe), ?Istanbul Region (Turkey); Siegenian to Emsian in the classical German sense (middle to upper Lower Devonian).

Ovetensispirifer ovetensium (Carls, 1986)

Figures 2E, 4D, 5, 11, 12

1969 Fimbrispirifer sp. Carls, p. 311 (Horizon MS 11).
1969 Fimbrispirifer cf. bischofi. – Carls, p. 312 (Horizon MS 12a).
1971 Fimbrispirifer charybdis (Barrande, 1879). – Bul- tyck & Soers, p. 9 (Couche 3 = Horizon MS 11).
1980 Vandercammenina sp. X. – Carls & Heddebaut, p. 219, pl. 32, figs 5–9.
1986 Vandercammenina ovetensium Carls; Carls, pp. 35, 36, pl. 1, fig. 2.
1987 Vandercammenina ovetensium n. sp. nom. nud. – Carls, p. 115.

Holotype. – Ventral internal mould with fragmentary corresponding external mould stored under inventory number PZ 102 (figured by Carls 1986, pl. 1, fig. 2). Width 35.7 mm and length 24.8 mm.

Type horizon and locality. – Fossiliferous marl, bed 1 m below the middle limestone bed of the Horizon MS 11 (= Ce3 after Bultynck & Soers 1971) of the Cercadillo Formation (Lower Siegenian sensu Carls 1987); east slope of the Valley Arroyo del Agua (= W side of S Cabeza Gorda), 4.2 km WSW Riba de Santiuste, 3.2 km SE Alcolea de las Peñas, topographical mapsheet 434 (Barahona) 1 : 50 000, Guadalajara Province (Spain).

Diagnosis. – Ovetensispirifer with 3 ribs in sulcus and 4 ribs on fold, short dental plates, and 2 impressions of ribs on the internal mould of ventral muscle field.

Description. – Form and size: shells medium-sized, megathyrid without mucronations, and subelliptical in outline; equibiconvex to dorsibiconvex in longitudinal section. Exterior of ventral valve: ventral interarea moderately high, apsacline, and curved. Delthyrium open, deltial lamellae clearly developed, deltadium lacking. Exterior of dorsal valve: dorsal interarea low, anacline, and curved. Notothyrium not recognisable. Coarse ornamentation: ventral and dorsal valves are covered by numerous fine ribs with furrows of same size. Ribs are angular to rounded in cross section and do not bifurcate on flanks (Fig. 4D), furrows are angular in cross section. Lateral ribs in sulcus and on fold bifurcate once in adult stage (Fig. 5). Usually 3 ribs in the sulcus and 4 ribs on fold, in gerontic stage 5 ribs in sulcus and 6 ribs on fold. Growth lamellae are rarely developed at the anterior margin. Micro-ornamentation: fimbriate with single rows of micro-spines at the edge of each growth lamella. Similar to the micro-ornamentation of Struveina (Fig. 2E). Growth lamellae of moderate distance to each other. Interior of ventral valve: filling of the umbo extending clearly to posterior over the hinge line. Beneath the ventral muscle field a long septal pillow is developed that is medially grooved on the internal mould. Ventral process small leaving only a shallow indentation on the internal mould, hardly dividing the posterior end of the ventral muscle field. Out of the ventral process develops a faint myophragm leaving a furrow in the posterior half of the ventral muscle field. Strong development of secondary shell material in the apical region resulting in a strongly embedded ventral muscle field. Fillings of the lateral apical cavities hardly extend posteriorly over the hinge line, but point ventrally in an apical direction. Ventral muscle field with 2 very weak impressions of ribs. Adductor scars elongate and elliptical in outline, posterior and anterior pairs hardly differentiable. Diductor scars preserved as longitudinal striae in the.
anterior half of the impression of the ventral muscle field. Dental plates short and wedge-like. Out of the dental plates extends a fine muscle bounding ridge leaving a shallow furrow on the internal mould that diminishes in the gerontic stage. A platform is developed at both sides of the ventral muscle field due to the development of secondary shell material. On this platform, gonoglyphs are sometimes preserved as small pointed cones on the internal mould (Fig. 12F, K). Sulcus weakly defined, however, sulcus bordering ribs included into the sulcus. Sulcus rounded in cross section. Bifurcation of ribs is not impressed on the internal mould, neither growth lamellae. Interior of dorsal valve: filling of the umbo extending very little posteriorly over the hinge line. Ctenophoridium broad. Notothyrial shelf lacking or indicated. Dental sockets long, rounded in cross section, and pointing in an apical direction almost to the posterior end of the ctenophoridium. Brachiophores thin and not curved above the dental sockets. Crural bases are not preserved. Crural plates long and thin, reaching to the floor of the shell. Dorsal median process broad and thick leaving deep broad indentation on the internal mould. Gonoglyphs in the lateral environment of the dorsal umbo preserved as small tubercles on the internal mould. Impressions of adductor field not preserved. Fold moderately elevated. Fold bordering furrows wider than furrows on fold and on flanks. Impressions of bifurcating ribs on the fold. Impressions of growth lamellae not preserved.

Discussion. – Ovetensispirifer ovetensium is smaller than O. novascotianus, has 2 ribs less in the sulcus, and 2 impressions of ribs on each side of the internal mould of the ventral muscle field whereas O. novascotianus has 4 to 5 impressions of ribs on the internal mould of the ventral muscle field. A morphological comparison of taxa of Ovetensispirifer is given in Table 3.

Geographic and stratigraphic occurrence. – Armoricain Massif and Iberian Chains (Western Europe); Siegenian (middle Lower Devonian).

Ovetensispirifer cf. ovetensium (Carls, 1986)

Figures 13, 14

2002 huge Vander camar menina. – Carls & Valenzuela-Ríos, p. 320.

Locality. – Miguel Chico, NW Santa Cruz, Guadarrama (Iberian Chains, Spain).

Material. – 4 ventral internal moulds with corresponding external mould: PC 444, 448–450; 3 ventral internal moulds: PC 442, 445, 447; 1 ventral external mould: PC 443; 1 dorsal internal mould with corresponding external mould: PC 446; 3 dorsal internal moulds: PC 440, 441, 443.

Description. – Form and size: shells medium to large-sized, megathyrid without mucronations but sometimes small ears are developed. Equibiconvex to strongly dorsibiconvex in longitudinal section, subelliptic to semicircular in outline. Exterior of ventral valve: interarea high, apsacline to almost catacline, and curved with impressions of transverse growth lamellae. Delthyrium open, deltoidal lamellae thin and not fused in the posterior part, deltidium lacking (Fig. 14C, D). Exterior of dorsal valve: interarea low and anacline to almost orthocline.

Table 3. Comparison of Ovetensispirifer ovetensium, O. cf. ovetensium and O. novascotianus

<table>
<thead>
<tr>
<th></th>
<th>O. ovetensium</th>
<th>O. cf. ovetensium</th>
<th>O. novascotianus</th>
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</thead>
<tbody>
<tr>
<td>size</td>
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<td>outline</td>
<td>no development of ears</td>
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<td>ribs in sulcus on internal mould</td>
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<td>5–6</td>
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<tr>
<td>ribs on fold on internal mould</td>
<td>4–6</td>
<td>not countable</td>
<td>7–8</td>
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<td>impression of ribs on the internal mould of the ventral muscle field</td>
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<td>not countable</td>
<td>3–4</td>
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<td>notothyrial shelf</td>
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<td>Nova Scotia (Canada)</td>
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<td>Upper Siegenian</td>
<td>Siegenian to ?Emsian</td>
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Notothyrium open, chilidial lamellae very thin. Coarse ornamentation: flanks are covered by numerous thin and simple ribs separated by furrows of the same size. Ribs and furrows are rounded to angular in cross section. Sulcus with median rib and fold with median furrow. Ribs on fold and in sulcus are thinner than on the flanks. Bifurcation of ribs in the sulcus occurs once or twice, the first time in the posterior third of the shell, the second time only in the gerontic stage. Bifurcation of ribs on fold corresponds to bifurcation of ribs in sulcus (Fig. 14Q).

Micro-ornamentation: fimbriate as in *O. ovetensium*. Interior of ventral valve: filling of the ventral umbo extending posteriorly over the hinge line. Strong development of secondary shell material in apical region. A large septal pillow is situated beneath the ventral muscle field from which it is separated by a strong contraction on the internal mould. It is bordered on each side by a subdeltidial furrow that leaves a distinct ridge on the internal mould. Ventral process moderately developed leaving a shallow indentation in the posterior part of the ventral mus-
Morphological terms of *Ovetensispirifer cf. ovetensium* (Carls, 1986). • A – PC 447. Ventral internal mould, plan view. Dental plates, ventral process, septal pillow, myophragm, gonoglyphs, and muscle bounding ridge are preserved as negative forms. • B, C – dorsal internal moulds, plan (B: PC 440) and oblique posterior (C: PC 446) views. Dental sockets, crural plates, lateral furrows, myophragm, and brachiophores are preserved as negative forms.

Remark. – The stratigraphic distribution of *O. cf. ovetensium* is certain for the d3c Top sensu Carls (1996) of the...
Santa Cruz Formation. In the lowermost part of the Mari-
posas Formation fragments that can be possibly assigned O. cf. ovetensium were found, however, the material is not sufficiently preserved to allow a definite determination as O. cf. ovetensium. Therefore the range of O. cf. ovetensium into the lowermost part of the Emsian in the classical Ger-
mansen sense remains speculative.

Discussion. – The main difference between O. ovetensium and O. cf. ovetensium is the size of the shells and the stra-
tigraphic distribution. In the material studied, specimens of the type species are relatively smaller and differ from O. cf. ovetensium in a more transverse outline and sometimes a notothyrial shelf which is always lacking in O. cf. ovetensium. A detailed description of O. cf. ovetensium is cur-
cently in preparation (P. Carls, pers. comm. 2008). There-
fore, open nomenclature is chosen.

Geographic and stratigraphic distribution. – Guadarrama (Spain); d3c Top sensu Carls (1996), Santa Cruz Forma-
tion to ?lowermost Mariposas Formation (Upper Siegenian; Upper Emsian in the classical German sense, mid-
to ?upper Lower Devonian).

Ovetensispirifer novascotianus gen. et sp. nov.
Figures 15, 16

1958 “Spirifer” n. gen. et n. sp. – Boucot et al., pp. 857, 858, pl. 1, figs 4–9.
1960a “Spirifer” cf. “S.” bischofi. – Boucot, pl. 68, fig. 10.

Holotype. – Ventral internal mould stored under inventory number MCZ 191917. Width 50.6 mm and length 42.5 mm.

Type horizon and locality. – ‘Nictaux iron ore beds’ (~ Oriskany Formation), ~ Pragian, middle Lower Devo-

Material. – Locality and stratum: see type horizon and loca-
ty. 10 ventral internal moulds: MCZ 191917 (holotype),

Ovetensispirifer cf. ovetensim (Carls, 1986). Locality: Miguel Chico, NW of Santa Cruz, Guadarrama (Iberian Chains, Spain). Stratum: d3c Top (Upper Siegenian, middle Lower Devonian). All figures are at original size (~ 1.0), unless otherwise stated. • A–D – PC 447. Internal ventral mould and latex cast of it. Plan (A) and oblique lateral (B) views of the mould, plan (C) and oblique lateral posterior view (D) of latex cast; note teeth, dental plates, and delthyrium (D); scale bar 5 mm. • E–H – PC 446. Internal dorsal mould with corresponding external mould. Plan view on external mould (E), posterior (F), oblique posterior (G), and plan (H) views of internal mould; note cardinalia (G); scale bar 5 mm. • I–J – PC 448. Internal ventral mould. Plan (I) and anterolateral (J) views; note septal pillow and gonoglyphs. • K, L – PC 444. Internal ventral mould. Anterolateral (K) and plan (L) views. • M, N – PC 443. Internal dorsal mould and latex cast of it. Oblique posterior view on internal mould (M) and plan view on latex cast (N). • O, P – PC 444. Internal dorsal mould. Plan (O) and oblique posterior (P) views; note cranial plates (P). • Q–S – PC 449. Internal ventral mould with corre-

Figure 14. Ovetensispirifer cf. ovetensim (Carls, 1986). All figures are at original size (~ 1.0), unless otherwise stated. • A–D – PC 447. Internal ventral mould and latex cast of it. Plan (A) and oblique lateral (B) views of the mould, plan (C) and oblique lateral posterior view (D) of latex cast; note teeth, dental plates, and delthyrium (D); scale bar 5 mm. • E–H – PC 446. Internal dorsal mould with corresponding external mould. Plan view on external mould (E), posterior (F), oblique posterior (G), and plan (H) views of internal mould; note cardinalia (G); scale bar 5 mm. • I–J – PC 448. Internal ventral mould. Plan (I) and anterolateral (J) views; note septal pillow and gonoglyphs. • K, L – PC 444. Internal ventral mould. Anterolateral (K) and plan (L) views. • M, N – PC 443. Internal dorsal mould and latex cast of it. Oblique posterior view on internal mould (M) and plan view on latex cast (N). • O, P – PC 444. Internal dorsal mould. Plan (O) and oblique posterior (P) views; note cranial plates (P). • Q–S – PC 449. Internal ventral mould with corre-

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Coarse ornamentation: ventral and dorsal valves are covered by 13 to 18 or more fine ribs with furrows of same size. Ribs are broad, angular to rounded in cross section, and do not bifurcate on flanks (Fig. 16S, T), furrows are narrow and angular in cross section. Sulcus with 3 or 5, in gerontic stage 7 ribs, and with median rib. Fold with median furrow and with 4 to 6, in gerontic stage 8 ribs. Bifurcation of ribs in fold and sulcus at first at the very posterior end and later at about half of valve length. Growth lamellae not preserved. Micro-ornamentation: not preserved in the material studied. Interior of ventral valve: filling of the umbo clearly extending posteriorly over the hinge line. Beneath the ventral muscle field a thick septal pillow is developed that is mediadly broadly indented by the ventral process on the internal mould (Fig. 16G). Ventral process small leaving only a shallow indention on the internal mould, strongly dividing the posterior end.

Figure 15. Morphological terms of Ovetensispirifer novascotianus sp. nov. • A – MCZ 191917. Ventral internal mould, plan view. Dental plates, ventral process, septal pillow, ventral myophragm, and muscle bounding ridge are preserved as negative forms. • B, C – MCZ 191916. Dorsal internal mould, plan (B) and oblique posterior (C) views. Dental sockets, crural plates, lateral furrows, dorsal myophragm, remain of crural plates, and brachiophores are preserved as negative forms.

Figure 16. Ovetensispirifer novascotianus sp. nov. Locality and stratum (A–T): Nictaux Falls, ca 40 km NE of Annapolis, Annapolis Co., Nova Scotia, Canada; ‘Nictaux iron ore beds’. Locality and stratum (U–V): Torbrook, ca 45 km NE of Annapolis, Nova Scotia, Canada; Torbrook Sandstone. Both Oriskanian (~Pragian, middle Lower Devonian). All figures are at original size (×1.0). • A – MCZ 191917. Internal ventral mould. Plan view. • B–D – MCZ 191929. Internal ventral mould and latex cast. Posterior view on internal mould (F) and view on apical region of latex cast (G). • H, I – MCZ 191916. Internal dorsal mould. Plan (H) and (I) oblique posterior views. • J–L – MCZ 191928. Internal ventral mould. Lateral (J), plan (K) and oblique posterior (L) views. • M–O – MCZ 191961. Internal dorsal mould and latex cast of it. Plan (M) and oblique posterior (N) views on internal mould and plan view on latex cast (O). • P – MCZ 191925. Internal ventral mould. Plan view (P). • Q – MCZ 191920. Internal ventral mould. Plan view (Q). • R – MCZ 191921. Internal ventral mould. Plan view (R). • S, T – MCZ 191915. Fragment of internal ventral mould and latex cast. Plan views on latex cast (S) and internal mould (T). • U – MCZ 191896. Internal ventral mould. Plan view (U). • V – MCZ 191894. Locality: see Fig. 16U, internal dorsal mould. Plan view (V).
of the ventral muscle field. Out of the ventral process develops a faint myophragm which leaves a furrow in the posterior third of the ventral muscle field on the internal mould. Ventral muscle field strongly embedded due to the development of secondary shell material in the apical region. Internal mould of ventral muscle field strongly elevated and with 4 to 5 impressions of ribs. Adductor scars elongate but only hardly preserved. Diductor scars preserved as longitudinal striae at the very anterior margin of the impression of the ventral muscle field, in one specimen radial striae are preserved in the centre of the impression of the ventral muscle field. Dental plates short to long and thin, teeth not preserved. Out of the dental plates comes a shallow muscle bounding ridge leaving a weak furrow on the internal mould. Gonoglyphs are preserved as small tubercles next to the muscle field on the internal mould (Fig. 16G). Flanks anterior of the ventral muscle field covered by 12 impressions of thin ribs that are rounded to angular in cross section. Furrows broad and shallow, flat on bottom in cross section. Sulcus weakly defined and rounded in cross section with 5 to 7 impressions of ribs including the median rib. Bifurcation of ribs and growth lamellae not impressed on the internal mould. Interior of dorsal valve: filling of the umbo extending posteriorly very little over the hinge line. Ctenophoridium broad and bordered by a pair of weakly developed and faint lateral furrows (Fig. 16N). Notothyrial shelf indicated. Dental sockets long, thin, and rounded in cross section, and pointing in an apical direction almost to the posterior end of the ctenophoridium. Brachio phores broad and not curved above the dental sockets. Crural bases are not preserved. Crural plates long and broad, reaching to the floor of the shell, and not embedded into secondary shell material in adult stages. Dorsal median process broad and short leaving deep shallow indention on the internal mould. Adductor field subelliptical in outline and situated on the fold. Fold moderately to highly elevated and with impressions of 4 ribs that bifurcate in the posterior end. 10 to 12 impressions of ribs per flank. Impressions of ribs start almost at hinge line. Ribs and furrows angular in cross section. Gonoglyphs and impressions of adductor field and of growth lamellae not preserved.

Discussion. – The Nictaux Falls iron ore beds and their fauna have been known for 140 years (e.g., Dawson 1868). Since Dawson’s account the brachiopods have been determined by comparison with the European Rhenish fauna but a systematic revision using modern character analysis was still missing. Boucot et al. (1958) examined the iron ore mineralogical properties and proposed a Siegenian age for the fauna. Even though most of the fauna is tectonically deformed and the micro-ornamentation is not preserved owing to metamorphism, most of the specimens show the characteristic features of Ovetens spirifer, e.g., the large, strongly elevated, and impressed ventral muscle field, the crural plates, and the scheme of ribbing in the sulcus, so that a determination even to species level is possible.

Geographic and stratigraphic occurrence. – See type locality and type horizon.

Genus Turcispirifer nov.

Type species. – Turcispirifer turciae gen. et sp. nov.

Derivation of name. – Genitive form of turcus (= adj., latinization for Turkish).

Diagnosis. – Medium to large-sized specimens with simple ribs on flanks and bifurcating ribs on fold and in sulcus. Crural plates present. Dental plates long, thin, and almost parallel to each other. Hardly any secondary shell material in apical region. Septal pillow present. Cardinalia delicate, notothyrial shelf lacking to weakly indicated in some specimens.

Type horizon and locality. – Kartal Formation (probably Siegenian, middle Lower Devonian); Roumeli His sar, in the Valley Baltaliman and one of its branches, ca 9 km west of Istanbul on the European side of the Bosphorus in the Istanbul Basin (Northwest Turkey).

Species assigned. – Turcispirifer turciae gen. et sp. nov. and ?Turcispirifer sp. A described in this work.

Discussion. – The comparison with Fimbrispirifer, Struvicinina, Vandercammenina, and Ovetenspirifer is described above.

Geographic and stratigraphic occurrence. – Turkey, ?Morocco; Siegenian to ?Emsian in the classical German sense (middle to upper Lower Devonian).

Turcispirifer turciae gen. et sp. nov.

Figures 2D, 4E, 5, 17, 18

1869 Spirifer trigeri de Verneuil, 1850. – de Verneuil, pp. 41–43, pl. 21, figs 1b, ?7.
1900 Spirifer Trigeri de Verneuil, 1850. – Kayser, pp. 31, 37, pl. 1, figs 1, 2.
1916 Spirifer trigeri de Verneuil, 1850. – Hüffner, pp. 304, 305, 330, pl. 30, fig. 1.
1932 Spirifer trigeri de Verneuil, 1850. – Paeckelmann & Sieverts, pp. 66, 67, pl. 3, figs 4, 5.

Holotype. – Internal mould of dorsal valve, stored under inventory number NYSM 17694.
Derivation of name. – Genitive form of Turcia (= latinization for Turkey) where the type locality is situated.

Type horizon and locality. – See genus.

Material. – Locality and stratum: see type locality. 1 internal mould of articulated shell: NYTSM 17693; 1 internal dorsal mould: NYTSM 17694, holotype; 3 ventral internal moulds: NYTSM 17690–17692. Locality and stratum: outcrops along the forest road east of Dallm lake, 3 km S of Korucu village ca 8 km NE of Silê district at the coast of the Black Sea (Northwest Turkey); Kartal Formation, Siegenian to ?Emsian (middle to ?upper Lower Devonian). The Korucuköy Section is described in Gedlık et al. (2005). 1 articulated specimen: DEVEC-TR KO II Ma 9 (1); 2 ventral external shells: SMF 66614, DEVEC-TR KO II Ma 9 (2); 1 internal ventral mould: DEVEC-TR KO II Ma 8 (1); 2 internal dorsal moulds: SMF 66615, DEVEC-TR KO II Ma 8 (2). Locality: between Pendik and Kartal on the Asian side of the Bosphorus (NE side of the Sea of Marmara). 2 plaster casts of ventral internal moulds: Mbg. 5130 (original illustrated by Kayser 1900, pl. 1, fig. 1), Mbg. 5131 (mentioned by Kayser 1900, p. 31); 1 ventral external shell: Mbg. 5132. Locality: Pendik on the Asian side of the Bosphorus (NE side of the Sea of Marmara). 1 ventral external shell: Mbg. 5133. 1 dorsal external shell: Mbg. 5134. Locality: Kartal on the Asian side of the Bosphorus (NE side of the Sea of Marmara). 1 ventral external shell: Mbg. 5135. Locality: Büyük Bakkalköy NE of Kartal on the Asian side of the Bosphorus (NE side of the Sea of Marmara). 1 ventral external shell: Mbg. 5136.

Remarks. – Specimens studied are from museum collections where the exact horizon from where the material was sampled was not given on the label. Provenance might be either the Kartal or Pendik Formation.

Diagnosis. – See genus which is at present monospecific.

fine slits on the internal mould. Dental sockets thin, long, rounded in cross section, and situated almost parallel to the hinge line. Outline of adductor field not recognisable. Dorsal myophragm fine and short. Fold moderately high with median furrow and in the posterior part with bifurcating ribs. Ribs fine and rounded in cross section. Furrows narrower than ribs and rounded to angular in cross section. Impressions of 20 ribs on flanks are countable.

Description of paratypes. – Form and size: shells medium-sized and megathyrid. Ventribiconvex to equi-biconvex in longitudinal section, outline semielliptic. Small ears developed. Exterior of ventral valve: ventral interarea high, anascline to almost catacline, and curved. Delthyrium open with a pair of fine deltildial lamellae that are not combined to form a deltium. Sulcus inconspicuous. Exterior of dorsal valve: dorsal interarea lower than ventral interarea, anascline to almost orthoclone. Notothyrium open, chilidial lamellae very thin. Fold moderately elevated, inconspicuous, only recognisable by bifurcating ribs. Coarse ornamentation: ribs very fine and rounded in cross section. They are separated by smaller furrows that are angular in cross section. Flanks are covered by simple ribs (Fig. 4E). In the sulcus ribs are bifurcating in the posterior part. Sulcus with 10 to 16 ribs at the anterior margin. Median rib lacking (Fig. 5). On the fold all ribs bifurcate once. Micro-ornamentation: fimbriate with single rows of narrow micro-spines situated at the edge of each growth lamella (Fig. 2D). Growth lamellae of moderate distance to each other. Interior of ventral...
valve: filling of the apical cavities extending posteriorly over the hinge line until almost the posterior margin of the internal mould of the ventral muscle field. Hardly any secondary shell material developed in apical region. Septal pillow small, separated by a small contraction on the internal mould of the ventral muscle field. Ventral process small leaving a thin short indentation on the internal mould of the ventral muscle field. Ventral muscle field broad, elongated, not impressed into shell material, and extending shortly to posterior over the hinge line. Adductor scars preserved as radial impressions on the internal mould, anteriorly they are striated in a longitudinal direction. Adductor scars elongated and thin, completely surrounded by adductor scars, posterior and anterior pairs are hardly distinguishable. Muscle bounding ridge thin and hardly recognisable leaving a fine furrow on the internal mould. Free portions of dental plates thin and moderately long, reaching to about half of the length of the ventral muscle field. Teeth not preserved. Gonoglyphs preserved as small tubercles with elliptical outline on the internal mould situated in the lateral surrounding area of the ventral muscle field (Fig. 18F). Sulus of internal mould inconspicuous and without impression of median rib. Impressions of bifurcation of ribs in the sulcus not preserved. Impressions of numerous fine and simple ribs on flanks. Impressions of growth lamellae are impressed at the anterior margin of the internal mould. Interior of dorsal valve: filling of dorsal muscle field extending posteriorly over the hinge line. Ctenophoridium thin and with at least 25 very fine undulating lamellae. Notothyrial shelf lacking. Crural plates clearly developed, leaving long, fine slits on the internal mould. Dental sockets long, triangular in outline, rounded in cross section, and situated almost parallel to the hinge line. Brachiophores thin and not curved above the dental sockets. Adductor scars not impressed. Dorsal myophragm short reaching 1/5 to 1/4 of valve length. Fold moderately high with at least 12 impressions of ribs that are fine and rounded in cross section. Furrows on the internal mould are narrower than ribs and rounded to angular in cross section. At least 26 impressions of ribs on each flank.

Geographic and stratigraphic occurrence. – Northwest Turkey; Kartal and Pendik formations, Siegenian to ?Em- sian in the classical German sense (middle to ?upper Lower Devonian).

?Turcísípirifer sp. A

Figures 19, 20

?1964 Fimbrisípirifer (?) trigeri (de Verneuil, 1850). – Drot, pp. 63, 64, pl. 5, fig. 2a–c.


Material. – 1 internal mould of articulated specimen: SMF 65225; 1 posterior part of a ventral internal mould: SMF 65226.

Description. – Form and size: shells medium-sized, megathyroid without mucronations, ventribiconvex in longitudinal section, and semieelliptical in outline. Reconstructed size of internal mould of articulated specimen (SMF 65225): length 29.1 mm and width 47.1 mm. Exterior of ventral valve: interarea high, apsacline, and curved without impressions of growth lamellae. Delthyrium open, deltidial lamellae and deltúdium lacking. Exterior of dorsal valve: interarea low and anacline to almost orthocline. Notothyrium open, chilidal lamellae not preserved. Coarse ornamentation: ribs fine as in Turcísípirifer turciae, impressions of bifurcating ribs in sulcus and on fold preserved on the internal moulds, however, external moulds and shell material are lacking in the material. Micro-ornamentation: not preserved in the material studied. Interior of ventral valve: filling of the ventral umbo extending posteriorly over the hinge line. Hardly any development of secondary shell material in apical region. Septal pillow clearly developed posteriorly beneath the ventral muscle field. It leaves a distinct and long ridge on the internal mould and is clearly separated from the muscle field by a strong contraction of the internal mould. Ventral process very small, leaving a hardly recognisable groove on the internal mould. A moderate myophragm develops out of the ventral process through the whole muscle field leaving a distinct furrow on the internal mould. Ventral muscle field elongate, extends posteriorly over the hinge line, and always longer than wide. Adductor scars are preserved as striae in longitudinal direction, adductor scars are not recognisable on the internal mould. Muscle bounding ridge not preserved. Free portions of dental plates long, thin, slightly divergent in anterior direction, and gently curved towards the centre at their anterior margin. Gonoglyphs are not preserved. Sulcus moderately deep and inconspicuous. Impressions of ribs numerous, fine, and rounded in cross section but hardly recognisable on the internal mould. Impressions of ribs in the sulcus of the internal mould are bifurcating, at least 12 to 14 ribs at anterior margin, and are separated by narrow furrows that are angular to rounded in cross section. Interior of dorsal valve: ctenophoridium bordered by strongly developed lateral furrows that are angular in cross section and preserved as distinct rims on the internal mould. Lamellae of ctenophoridium at least 11 and widely spaced. Notothyrial shelf and crural plates lacking. Small depressions above the dental sockets on the internal mould (Fig. 20E) are interpreted as remains of crural plates. Dental sockets thin...
and rounded in cross section. Brachiophores short, thin, and pointing in apical region. Median process very weak. Dorsal myophragm short and very fine. Adductor field slightly embedded into shell material. Anterior and posterior pairs not distinguishable. Adductor scars in posterior region radially striated on the internal mould. Fold inconspicuous and moderately elevated. Impressions of fine ribs on flanks and fold in the anterior two thirds of the internal mould that are separated by finer furrows.

Discussion. – The lack of micro-ornamentation and external surface does not allow a definite determination at the genus level, thus open nomenclature is chosen. The internal moulds of ?Turcispirifer sp. A most closely resembles Turcispirifer turciae sp. nov., but the different locality and their probably slightly older stratigraphic assignment argue for another species. Furthermore, the specimens from Morocco have a wider ventral muscle field than T. turciae, a shallower sulcus, and weaker impressions of ribs on the internal mould. The crural plates of T. turciae are more clearly developed than in ?Turcispirifer sp. A.

Geographic and stratigraphic distribution. – Southern Anti-Atlas, Dra Valley, Morocco; Mersâ-Akhsâï Formation (Rich 2), mid- to Upper Siegenian (middle Lower Devonian).
Family Costispiriferidae Termier & Termier, 1949
[ex subfamily Costispiriferinae Termier & Termier, 1949]

**Diagnosis.** – Shells with numerous fine and low ribs separated by narrow furrows. Ribs on flanks are simple, ribs on fold and sulcus bifurcate or intercalate. Micro-ornamentation capillate without micro-spines.

**Remarks.** – The Costispiriferinae are lifted to family level (Schemm-Gregory 2008c) because of its style of ribbing and capillate micro-ornamentation. In the last Treatise on Invertebrate Paleontology (Johnson & Hou 2006, Gourvennec & Carter 2007), they were regarded as a subfamily of the Acrospiriferidae Termier & Termier, 1949, which is erroneous as the Acrospiriferidae are characterised by fimbriate micro-ornamentation (Jansen 2000, 2001a, b; Schemm-Gregory 2007, 2008a, b).

**Discussion.** – Costispiriferidae as well as Elymospiriferidae Johnson & Hou in Carter et al., 1994 and Multispiriferidae fam. nov. are characterised by capillate micro-ornamentation with and without micro-spines whereas Fimbrispiriferidae have a fimbriate micro-ornamentation. The ribs of Costispiriferidae are lower and rounded in cross section, in Fimbrispiriferidae ribs are rounded to angular in cross section and more elevated.

Costispiriferidae differ from Elymospiriferidae in possessing simple ribs on the flanks whereas ribs of Elymospiriferidae bifurcate and trifurcate on the flanks and are separated by deeper and wider furrows. Costispiriferidae and Elymospiriferidae are both capillate, but Costispiriferidae never show micro-spines at the edge of growth lamellae. Crural plates are well developed in Elymospiriferidae but never in Costispiriferidae. Specimens of Costispiriferidae are in general larger than specimens of Elymospiriferidae. Furthermore, Elymospiriferidae differ from all other families discussed in the development of coarse deltidial lamellae that extend clearly to the posterior.

Multispiriferidae fam. nov. have coarser and ‘bundled’ ribs with remarkably wider furrows than Costispiriferidae. In Costispiriferidae the ribs are never ‘bundled’ and also very closely situated to each other. Ribs of Multispiriferidae bifurcate several times during ontogeny whereas ribs of Costispiriferidae bifurcate once. Costispiriferidae are in outline rather subcircular whereas Multispiriferidae are transverse, always wider than long, and subelliptical. In contrast to Costispiriferidae, Multispiriferidae have a septal pillow and a notothyrial shelf but lack a median rib in the sulcus. The cardinalia of Multispiriferidae are situated on an elevated shelf that is more or less in the same plane as the interarea (compare also Boucot 1975, p. 365). The micro-ornamentation of Multispiriferidae is capillate with curved capillae and shows clearly developed micro-spines at the edge of each growth lamellae developing out of the capillae (Fig. 2F). Micro-spines are always lacking in the capillate micro-ornamentation of Costispiriferidae.

**Geographic and stratigraphic distribution.** – North America and North Africa; Oriskanian (~ Pragian) to Emsian in the classical German sense (middle to upper Lower Devonian).

Subfamily Costispiriferinae Termier & Termier, 1949

**Type genus.** – Costispirifer Cooper, 1942.

Genera assigned. – At present only the type genus Costispirifer Cooper, 1942.

Genera excluded. – Cumberlandina Boucot, 1975.

Discussion. – Cumberlandina Boucot, 1975 is excluded from Costispiriferinae because of the lack of bifurcating ribs on the flanks as well as on the sulcus and fold, and also by the presence of a stegidium, one of the characteristic morphological features of the Mucrospiriferidae Boucot, 1959 (A.J. Boucot, pers. comm. 2007). Concerning this remarkable difference, I recommend placing Cumberlandina into the family Mucrospiriferidae Boucot, 1959, following the author’s intention and in contrast to Johnson (1970) and Johnson & Hou (2006) in the Treatise on Invertebrate Paleontology.

Geographic and stratigraphic occurrence. – North America and Venezuela; Oriskanian (~ Pragian) to ?Emsian (middle to upper Lower Devonian).

Genus Costispirifer Cooper, 1942

Type species. – Spirifer arenosus var. planicostatus Swartz, 1929, p. 56.

Diagnosis. – Fold and sulcus inconspicuous with bifurcating ribs. Simple ribs on flanks. Without septal pillow, notothyrial shelf, and crural plates.

Species assigned. – Spirifer arenosus Conrad, 1839 (= Spirifera superba Billings, 1874), Spirifer unicus Hall, 1860, Spirifer billingsianus Miller, 1889, Spirifer arenosus var. planicostatus Swartz, 1929, Spirifer dobbinensis Merriam, 1940.

Remarks. – Careful restudy of material from C. arenosus and C. superbus shows that these taxa are conspecific. The differences proposed by Billings (1874) in the height of ventral area, depth of the sulcus, respectively, and elevation of fold between these two species are ontogenetic features. The “large undivided rib along the mesial line of both valves” (Billings 1874, p. 46) in C. superbus could not be found, instead the median rib in the sulcus of the material studied was bifurcating.

In the following, C. arenosus is described as the characteristic representative of this group. The author of this work studied various extensive collections of the eastern North American Devonian brachiopods and could not find any representative of the type species C. planicostatus. As representatives of C. arenosus are present in all collections studied yielding material of Oriskanian age from North America, it seems to be more reasonable to describe this taxon with respect to further study on Costispirifer and for understanding the phylogenetic interpretation of this study.

Discussion. – Costispirifer differs from Multiplicatispirifer in the arrangement of capillae of the micro-ornamentation. In Multiplicatispirifer they are pseudoradially arranged, diverging from the furrows and concavely curved outwards to the top of the ribs whereas in Costispirifer capillae are strictly radially arranged and extend linearly. Ribs in Multiplicatispirifer bifurcate on flanks, fold, and in sulcus in Costispirifer they only bifurcate in sulcus and on fold. Secondary shell material is very thick in the apical region of Costispirifer whereas hardly any is developed in Multiplicatispirifer.

Geographic and stratigraphic occurrence. – See subfamily.

Costispirifer arenosus (Conrad, 1839)

Figures 2G, 4F, 5, 21, 22

1839 Delthyris arenosus Conrad; Conrad, p. 65.
1860 Spirifer arenosus Conrad, 1839. – Hall, pp. 425–427, pl. 98, figs 1–8, pl. 99, figs 1–10, pl. 100, figs 1–8.
1874 Spirifera superba Billings; Billings, pp. 45, 46, pl. 3, figs 3, 3a, 3b.
1909 Spirifer arenosus Conrad, 1839. – Clarke, p. 83, pl. 19, figs 1–4.

Type. – A holotype was not designated in the original description by Conrad (1839). It is strongly desirable to see where all of the original material is stored in order to define a lectotype. I could only visit and study the collection housed in the New York State Museum, Albany, in the American Museum of Natural History, New York City, and in the Peabody Museum of Natural History/Yale University, New Haven but not the collection housed in the Chicago Field Museum, Chicago.

Type horizon. – Oriskanian (~ Pragian, middle Lower Devonian).

Material. – Locality: Clarence, New York, USA. 1 ventral internal mould: NYSM 1904. A plaster cast of this mould is stored under inventory number SMF 22366. Locality: Schoharie, New York, USA. 1 ventral internal mould: AMNH FI 34840; 1 dorsal internal mould: AMNH FI 34840. A plaster cast of this mould is stored under in-

Remarks. – Stratum of all specimens Oriskanian (~ Pra- gian, middle Lower Devonian).

Figure 21. Morphological terms of Costispirifer arenosus (Conrad, 1839). • A – NYSN 1904. Ventral internal mould, plan view. Dental plates, ventral process, and muscle bounding ridge are preserved as negative forms. • B, C – SMF 66617. Plaster cast of dorsal internal mould, plan (B) and oblique posterior (C) views. Dental sockets, lateral furrows, brachiophores, and myophragm are preserved as negative forms.

Diagnosis. – Shells megathyrid without mucronations, sometimes small ears developed. Delthyrium large. Ribs in sulcus and on fold bifurcating. Teeth short and knob-like, brachiophores curved over dental sockets.

Description. – Form and size: shells large-sized and me- gathyrid, without mucronations but often with development of little ears. Ventribiconvex to mostly equibiconvex in longitudinal section, outline semicircular. Exterior of ventral valve: ventral interarea high, apsacline, and straight or curved. Delthyrium broad and open. Deltidial lamellae broad and fused to build a deltium in the apical part of the delthyrium. Transverse growth lamellae of the
interarea weakly preserved even on silicified shells. Sulcus shallow, inconspicuous, and rounded to flat in cross section. Exterior of dorsal valve: dorsal interarea low and anacline to almost orthocline. Notothyrium open with thin chilidial lamellae. Fold inconspicuous, faintly elevated, and almost flat on top. Coarse ornamentation: complete shell covered with more than 20 fine ribs that are angular to rounded in cross section. Ribs are separated by finer furrows that are angular in cross section. Ribs on flanks are simple (Fig. 4F). Bifurcation of ribs is visible in the posterior part of sulcus and fold. Ribs in sulcus and on fold somewhat smaller than on flanks. Sulcus with median rib that may bifurcate once. One pair of ribs is intercalated in the posterior part of the sulcus between the lateral ribs of the sulcus and the median rib (Fig. 5). The median rib on the fold bifurcates and a new rib is intercalated. Micro-ornamentation: capillate with capillae radially arranged, rarely interrupted by growth lamellae (Fig. 2G). Growth lamellae well developed at anterior margin. Interior of ventral valve: Filling of the ventral umbo extends posteriorly over the hinge line. At the bottom of the central apical cavity no septal pillow and no deltidial plate are developed. A small ventral process constricts the posterior end of the ventral muscle field leaving a small indentation on the internal mould. Out of the ventral process extends a fine myophragm leaving a fine furrow through the whole impression of the muscle field on the internal mould. The ventral muscle field is broad and pyriform in outline and always longer than wide. It is strongly impressed in the shell due to the strong development of secondary shell material in the apical region. Adductor and diductor scars are clearly differentiable. Diductor scars impressed, long and thin, situated on either side of the myophragm. Posterior and anterior adductor pairs not distinguishable. Diductor scars preserved as longitudinal and radial striations on the impression of the ventral muscle field; longitudinal and straight striations especially present at the anterior margin, radiate striations in the central part of the impression of the ventral muscle field. Long and wedge-like dental plates describing the lateral boundary of the ventral muscle field in younger specimens. In adult and gerontic stages, dental plates very short or even lacking due to the development of secondary shell material; sometimes only preserved as small slits or shallow indentations on the internal moulds. Out of the dental plates originates the muscle bounding ridge that can be very coarse in gerontic stage leaving a deep and broad furrow on the internal mould. Teeth short and knob-like. Lateral of the ventral muscle field a platform is built almost perpendicular to the commissural plane due to the development of secondary shell material. Gonoglyphs are preserved as small, low, and round bumps widely situated on each side in the surrounding area of the ventral muscle field, mainly on the platform, a few occur also just anterior of the platform. Impressions of ribs are anterior of the platform and the ventral muscle field. They are stronger on the flanks than in the sulcus. Interior of dorsal valve: filling of the dorsal umbo extends a little posteriorly over the hinge line. Beneath the dorsal umbo lies the broad ctenophoridium that shows up to 12 lamellae. Notothyrial shelf lacking. Dental sockets cone-shaped and rounded in cross section, situated almost parallel to hinge line, and pointing in an apical direction. Brachiophores thin and curved over the dental sockets. Crural plates lacking, crural bases preserved as free lamellae. Dorsal median process hardly developed. A short and very fine myophragm separates the whole adductor field. Adductor field impressed into shell material with ‘mushroom’-like outline and situated on the fold and in the posterior half also lateral of it. Adductor scars preserved as longitudinal striations on the internal mould. A very fine muscle bounding ridge defines the outline of the muscle field leaving a fine furrow on the internal mould. A short, low platform is developed on both sides of the adductor field in gerontic stage. A few gonoglyphs in the form of small, low, and round bumps are

Figure 22. Costispirifer arenosus (Conrad, 1839). All figures are at original size (× 1.0), unless otherwise stated. • A–E – YPM 601203. Articulated specimen with weathered shell. Locality and stratum: Allegany County, Cumberland/Maryland (USA); Ridgeley Member, Oriskany Sandstone, Oriskanian (~ Pragian, middle Lower Devonian). Ventral (A), dorsal (B), posterior (C), anterior (D), and lateral (E) views. • F, G – YPM 402946. Articulated specimen. Locality and stratum: See Fig. 22A–E. Ventral (F) and dorsal (G) views. • H – SMF 66617. Locality and stratum: Schoharie, New York; Oriskany Sandstone, Oriskanian (~ Pragian, middle Lower Devonian). Plaster cast of internal dorsal mould, original unnumbered USNM, Boucot collection. Plan view. • I, J – YPM 601360. Ventral shell. I. Plan view (I) on ventral interior and detailed view (J) on delthyrium, deltidial lamellae, and deldium (× 3.0). Scale bar represents 5 mm. • K–M – YPM 601362. Dorsal shell. Locality and stratum: See Fig. 22A–E. Plan view on dorsal exterior (K) and interior (L), detailed view (M) on cardinalia (× 3.0). Scale bar represents 5 mm. • N, O – YPM 402935. Articulated specimen with weathered shell. Locality and stratum: See Fig. 22A–E. Ventral (N) and dorsal (O) views. • P, Q – YPM 402894. Articulated specimen with weathered shell. Locality and stratum: See Fig. 22A–E. Ventral (P) and dorsal (Q) views. • R – SMF 66616. Locality and stratum: Clarence, New York; Oriskanian (~ Pragian, middle Lower Devonian). Plaster cast of ventral valve with weathered shell, original NYSM 1904. Plan view. • S – YPM 601359. Ventral shell. Locality and stratum: See Fig. 22A–E. Plan view on ventral interior. • T – YPM 221342. Locality and stratum: Beach shingle, Percé Rock, Percé, Gaspé East County, Québec (Canada); Oriskanian (~ Pragian, middle Lower Devonian). External dorsal valve. Plan view. • U – YPM 221339. Locality and stratum: See Fig. T. External ventral valve. Plan view. • V – YPM 221310. Locality and stratum: small quarry beside road a few hundred metres W of house of Joseph Gave, about 1 km NW of Grande Grève, Gaspé East County, Québec (Canada); Grande Grève Lime- stone, Oriskanian (~ Pragian, middle Lower Devonian). External dorsal valve. Plan view. [Remark: T–V – all specimens belong to the rejected species C. superbus (Billings, 1874).]
situated with wide interspaces on this platform above the dental sockets and brachiophores. Fold inconspicuous and hardly elevated compared to the flanks. Top of fold broadly rounded to almost flat. Impressions of ribs preserved only in the anterior half of the internal mould. Impressions of bifurcation of ribs on the fold hardly preserved. Impressions of growth lamellae well developed close to the anterior margin of the internal mould.

**Geographic and stratigraphic occurrence.** – Eastern North America (New York, Maryland, Canada); Oriskany Sandstone, Ridgeley Member, ?Onondaga Limestone, Grande Grève Limestone, Oriskanian (~Pragian) to ?Emsian (middle to ?upper Lower Devonian).

**Diagnosis.** – Large and in longitudinal section ventribiconvex spiriferids with fine bifurcating ribs on flanks, sulcus, and fold. Sulcus inconspicuous. Septal pillow present. Dental plates long and thin. Micro-ornamentation capillate consisting of capillae and fila. Capillae pseudoradially arranged and concavely curved outwards, diverging from the costal furrows towards the top of the ribs.

**Species assigned.** – *Multiplicatispirifer foumzguidensis Schemm-Gregory, 2008c, Spirifer weisbordi Harris in Lidell et al., 1943.*

**Geographic and stratigraphic occurrence.** – Anti-Atlas Mountains, Dra Valley, Morocco; ?Venezuela; Lower/Upper Emsian boundary interval in the classical German sense (upper Lower Devonian); Slope of the hill ‘El Háidoúriya’, section Foum Zguid III. Detailed description see Jansen (2001a) and Jansen et al. (2004).

**Material.** – 1 articulated internal mould with corresponding ventral external mould: SMF 66484a, b (holotype); 4 articulated specimens: SMF 66485–66488; 20 ventral internal moulds: 66489, 66491–66501, 66502/1, 66502/3, 66503–66505/1; 5 dorsal internal moulds: SMF 66506–66510; 2 ventral external moulds: 66502/2, 66505/2; 1 fragment of a ventral internal mould: SMF 66512.

**Description.** – See genus which is at present monospecific.

**Type horizon and locality.** – Unit 16 of section Foum Zguid III sensu Jansen (2001a), respectively, Unit 9 sensu Jansen et al. (2004), Mdaouer-el-Kbîr Formation, Lower/Upper Emsian boundary interval in the classical German sense (upper Lower Devonian); Slope of the hill ‘El Háidoúriya’, section Foum Zguid III. Detailed description see Jansen (2001a) and Jansen et al. (2004).

**Diagnosis.** – See genus which is at present monospecific.

**Type species.** – *Multiplicatispirifer foumzguidensis Schemm-Gregory, 2008c.*

**Description.** – Form and size: shells large-sized, ventribiconvex in longitudinal section, brachythryrid without mucronate cardinal extremities, and semielliptical in outline. Exterior of ventral valve: ventral interarea high, apsacine, and curved. Delthyrium open, but constricted by thin deltoidal lamellae that do not build a deltiodium. Exterior of dorsal valve: dorsal interarea low, anacline, and curved. Notothyrium open, chilidial lamellae not developed. Coarse ornamentation: surface covered by numerous fine, bifurcating ribs on flanks as well as on sulcus and fold that are separated by more narrow furrows. Furrows and ribs are rounded in cross section. Ribs bifurcate at different growth stages (Fig. 4G). Sulcus inconspicuous, broad, and deep with median costa bifurcating for the first time in the posterior part. Sulcus at base rounded in cross section. Median rib in sulcus bifurcates followed by an intercalation of a new rib, etc. (Fig. 5). Fold inconspicuous, flattened on top, and moderately elevated. Growth lamellae very fine and mostly only weakly preserved. Micro-ornamentation: capillate with fila; ribs and furrows are covered with very fine capillae that multiply by intercalation. Capillae are pseudoradially arranged and even concavely curved outwards diverging from the costal furrows to the top of ribs (Fig. 2F). Interior of ventral valve: ventral muscle field extending posteriorly over the hinge line. Lateral apical cavities are weakly constricted by secondary shell material, extending also posteriorly over the hinge line and reaching almost as far as the ventral muscle field. A septal pillow is developed beneath the ventral muscle field, clearly bordered to the anterior by a distinct groove on
the internal mould. Both sides of the septal pillow are bordered by a thin subdeltidial furrow on the internal mould. Ventral process weakly developed leaving a very small groove on the internal mould. A thin myophragm extends from the ventral process leaving a thin furrow through the whole ventral muscle field on the internal mould. The ventral muscle field is thin, elongate, and not impressed into shell material.

Figure 23. Morphological terms of Multiplicatisspirifer foumzguidensis (Schemm-Gregory, 2008c). • A – SMF 66489. Ventral internal mould, plan view. • B, C – SMF 66484a (holotype). Internal mould of articulated specimen, plan (B) and oblique posterior (C) views on dorsal valve. Dental plates, ventral process, septal pillow, muscle bounding ridge, ventral and dorsal myophragms, dental sockets, brachiophores, and lateral furrows are preserved as negative forms.

No ribs are impressed on the internal mould of the ventral muscle field. Diductor scars preserved as subradial striae on the internal mould; at the anterior margin of the ventral muscle field striae in longitudinal direction are impressed. Adductor scars elongate, posterior and anterior pairs clearly differentiable. Both are clearly impressed into the internal mould. Muscle bounding ridge absent or weakly developed, in a very few specimens leaving a fine furrow on the internal mould. Free portions of dental plates long and very thin, situated on the lateral border of the sulcus, leaving divergent slits on the internal mould. Gonoglyphs are not preserved. Sulcus inconspicuous, at base rounded to flattened in cross section, and with median rib. Impressions of ribs weakly developed, in most cases only peripherally preserved. Bifurcation of ribs faintly impressed on the internal mould. Furrows are finer than ribs. Impressions of growth lamellae
recognisable at the anterior margin. Interior of dorsal valve: filling of the umbo extends posteriorly over cardinalia and for a short distance over the hinge line. Hardly any secondary shell material developed in apical region. Notothyrial shelf lacking. Ctenophoridium situated beneath the filling of the umbo, covered by 24 to 31 lamellae and bordered by two fine and thin furrows leaving a small ridge on either side on the internal mould. Dorsal median process weakly developed, situated dorsally of the ctenophoridium. It is followed by a fine myophragm that extends through the entire muscle field. Dental sockets cylindrical, thin, long, and almost parallel to hinge line. Brachiophores long and thin, pointing in an apical direction. Crural bases not recognisable. Outline of adductor field ‘teardrop’-like, inconspicuously defined. In a few places elongate striae are impressed on the internal mould. Adductor scars situated on the fold and also in the posterior part lateral of it. Fold moderately elevated and with median furrow. Ribs impressed at the anterior two thirds of the dorsal internal mould on the flanks and on the fold. Bifurcation of ribs hardly recognisable. Go noglyphs are not preserved. Impressions of growth lamellae preserved at the anterior margin.

**Stratigraphic and geographic occurrence.** – See type horizon and type locality.

**Discussion.** – The genus *Multiplicatispirifer* was described as monospecific, however, in the J.M. Bowen collection at the Natural History Museum, an external ventral valve was found that could be determined as *?Multiplicatispirifer weisbordi* (Fig. 24). This specimen was found in the Sierra de Perijá, Venezuela, and is the only find of a representative of *Multiplicatispirifer* outside of North Africa. Even though the micro-ornamentation and internal features are unknown it can be considered as belonging to *Multiplicatispirifer*. It differs from *M. foumzguidensis* in gently coarser ribs and a shallower and broader sulcus. The ribs in the sulcus of *?M. weisbordi* are gently finer than ribs on the flanks whereas ribs on sulcus and on flanks are of same size in *M. foumzguidensis*. The occurrence of *?M. weisbordi* in Venezuela which belongs together with eastern North America to the Eastern American Realm verify the argumentation for a pathway between America and North Africa around the Siegenian/Emsian interval (Michard 1976, Schemm-Gregory 2008c).

**Family Elymospiriferidae Johnson & Hou in Carter et al., 1994**

**Type genus.** – *Elymospirifer* Wang in Wang et al., 1974.


**Remarks.** – As well as the Costispiriferidae, the Elymospiriferidae are characterised by a capillate micro-ornamentation and its assignment to the Acrospiriferidae is rejected. Their differences in style of ribbing, development of their ventral muscle field and the weaker development of secondary shell material compare to some taxa of the Costispiriferidae, their clear development of crural plates, and the capillate micro-ornamentation with micro-spines versus the capillate micro-ornamentation without micro-spines of the Costispiriferidae justify the raising to family level.

**Discussion.** – The genus *Multispirifer* Kaplun, 1961 is removed from the Elymospiriferidae because of its more transverse outline and the development of mucronate ex-
tremities, and is here assigned to a new family Multispiriferidae. The coarse-ornamentation in multispiriferidids with its bifurcating and trifurcating ‘bundled’ ribs of unequal size depending on growth stage is different from the bifurcating and sometimes trifurcating ribs in the Elymospiriferidae, which show almost the same size at every growth stage. The cardinalia in Multispiriferidae are very coarse and clearly developed; in Elymospiriferidae the cardinalia are somewhat smaller, finer, and mostly overhung by the filling of the dorsal umbo. In Multispiriferidae the cardinalia are situated on an elevated ‘shelf’ as discussed above. The micro-ornamentation of Multispiriferidae consists of capillae with larger micro-spines than in Elymospiriferidae. The relationship to the family Costispiriferidae is described above.

**Geographic and stratigraphic occurrence.** – Kazakhstan, Taimyr, China; Canadian Arctic Islands; Pragian to Eifelian (middle Lower Devonian to lower Middle Devonian).

**Genus Elymospirifer Wang in Wang et al., 1974**

**Type species.** – *Indospirifer kwangsiensis* Hou, 1959, p. 458.

**Emended diagnosis.** – Medium to large-sized shells, equi-biconvex to mostly ventribiconvex in longitudinal section, subrectangular in outline. Ventral interarea curved and apsacline. Ribs and furrows are rounded in cross section. Micro-ornamentation of variably developed radial striations interrupted by fine and narrow growth lines, short rounded micro-spines may be present at the edge of the growth lamellae. Dental plates long. Hardly any development of secondary shell material in apical region. Crural plates short.

**Species assigned.** – At present only the type species *Indospirifer kwangsiensis* Hou, 1959.

**Discussion.** – Jones & Boucot (1983) separated *Elymospirifer* from the Fimbrispiriferidae due to the lack of micro-spines and the presence of capillae. However, on some *Elymospiriferidae*, either in *Elymospirifer* or in *Perryspirifer* (type species: *Spirifer scheii* Meyer, 1913) (Fig. 25), short and rounded micro-spines are developed at the end of the capillae pointing in an anterior direction.

In contrast to *Elymospirifer*, *Perryspirifer* is characterised by the lack of crural plates, however, Brice (1982, pl. 17, fig. 11) shows that slits after crural plates or at least remains of crural plates can be found on dorsal internal moulds. In *Elymospirifer*, the crural plates are well developed. The apical region of *Perryspirifer* consists of a strong development of secondary shell material, in

![Figure 25. Morphological terms of *Perryspirifer scheii* (Meyer, 1913). Ventral internal mould, UA 3939, figured by Jones & Boucot (1983, fig. 8Z), plan view. Dental plates, ventral process, myophragm, gonoglyphs, and muscle bounding ridge are preserved as negative forms.](image-url)
able to *Borealispirifer* belong to more than one genus, e.g., comparing the low curvature and the strong development of secondary shell material. One example is given in gen. nov. *A maximus* (Zhang, 1983) (Fig. 27) with little secondary shell material and the strongly biconvex curvature of *B. bifurcatus* (Hou & Su in Su & Hou 1993, pl. 1, fig. 2), plan view. Dental plates, myophragm, gonoglyphs, and muscle bounding ridge are preserved as negative forms.

**Geographic and stratigraphic occurrence.** – Taimyr and Autonomous Region Guangxi, South China; Lower Emsian (upper Lower Devonian).

1959 *Indospirifer kwangsiensis* Hou; Hou, pp. 458, 459, pl. 3, fig. 5.


1986 *Elymospirifer kwangsiensis* (Hou). – Wang & Rong, pp. 199, 200, pl. 73, figs 1–15, pl. 74, figs 1–12, pl. 75, figs 1–13, pl. 77, figs 1–12, pl. 95, fig 10, text-figs 103–105.

**Holotype.** – Articulated specimen, figured by Hou (1959, pp. 458, 459, pl. 3, fig. 5) and stored under inventory number IV 426 [IV02960]. The holotype is 40.3 mm wide, 25.4 mm long, and 21.8 mm thick.

**Type horizon and locality.** – Yukijang Formation, Lower Emsian (upper Lower Devonian); Liujiang Section, Liujiang, Autonomous Region Guangxi, South China.

**Material.** – Locality and stratum: see type horizon and locality. 3 articulated specimens: IV 426 [IV02960], SMF 66618, unnumbered specimen in the Biological Collection.
of USNM (a plaster cast of this specimen is stored under inventory number SMF 66620).

**Diagnosis.** – See genus which is at present monospecific.

**Description.** – Form and size: shells transverse and brachythryid without mucronations. Outline subelliptical to subtriangular. Equibiconvex to ventribiconvex in longitudinal section. **Exterior of ventral valve:** ventral area apsacilne, moderately to very high, and strongly curved. Deltidial lamellae well developed, clearly extending posteriorly and fused in the posterior part to form a small deltium. Sulcus broad, deep, and in cross section rounded to almost flat at its base with moderately steep flanks. **Exterior of dorsal valve:** dorsal interarea low and ortho- cline. Notothyrium and chilidial lamellae not visible. Dorsal shell strongly convex in longitudinal section. Fold gently elevated compared to neighbouring flanks. **Coarse ornamentation:** first to third pair of ribs of flanks bifurcating, rarely trifurcating in the anterior half. In a few specimens more laterally situated ribs also bifurcate (Fig. 4H). Sulcus with median rib. Sulcus bordering ribs are the coarsest ribs of the ventral valve. Bifurcation of ribs occurs only in the sulcus bordering ribs into the sulcus (Fig. 5). Fold with median furrow. Bifurcation of ribs on fold from the bordering ribs to median, rarely bifurcation from median pair of ribs on fold (Wang & Rong 1986, pl. 75, fig. 11). Ribs of second order smaller than those of first order on flanks, on fold, and in sulcus. Growth lamellae well developed at anterior margin. **Micro-ornamentation:** capillate, sometimes micro-spines pointing anteriorly on the edge of each growth lamella (Wang & Rong 1986, pl. 75, figs 10, 13 and studied by the present author on the holotype) (Fig. 2H). **Interior of ventral valve:** Filling of ventral umbo extends posteriorly over the hinge line. Almost no development of secondary shell material in the apical region. Fillings of lateral apical cavities reaching almost to the posterior margin of the ventral muscle field. Ventral process very small leaving a fine indentation on the internal mould. No septal pillow developed. Ventral muscle field elongated and thin. Anterior margin of muscle field inconspicuous, neither a muscle bounding ridge nor muscle scars preserved. Dental plates long and thin. Teeth small and knob-like. Impressions of ribs well developed, starting almost at the posterior end of the internal mould. Bifurcation of ribs not preserved, instead impressions of ribs seem to multiply by intercalation. **Interior of dorsal valve:** ctenophoridium thin. Notothyrial shelf lacking. Crural plates long and moderately thick. Dorsal median process very small. Out of it extends a very fine and short myophragm to anterior. Outline of the adductor field inconspicuous. Impressions of ribs similar to those in ventral valve.

**Geographic and stratigraphic occurrence.** – See genus.

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**Genus Perryspirifer Jones & Boucot, 1983**

**Type species.** – *Spirifer scheii* Meyer, 1913, p. 25.


**Species assigned.** – At present only the type species *Perryspirifer scheii* Meyer, 1913 (= *Perryspirifer pseudoscheii* Brice, 1982, *Perryspirifer fascicostatus* Brice, 1982).

**Discussion.** – Jones & Boucot (1983) have statistically studied about 1,000 specimens of *Perryspirifer* from the Canadian Arctic Islands and proved that this species shows a lot of intraspecific variability in morphologic features, e.g., number of plications or size of shells. I follow the intention of these authors and include *P. pseudoscheii* and *P. fascicostatus* into *P. scheii*. 
Geographic and stratigraphic occurrence. – Canadian Arctic Islands; upper Lower Emsian to Eifelian (upper Lower Devonian to lower Middle Devonian).

**Perryspirifer scheii** (Meyer, 1913)

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1913 Spirifer scheii Meyer; Meyer, pp. 25, 26, pl. 5, fig. 7, pl. 6, fig. 1a–c.


1982 *Fimbrispirifer 'pseudoscheii* Brice; Brice, pp. 73–77, fig. 23, pl. 18, figs 1–3, 6–8.

1982 *Fimbrispirifer fascicostatus* Brice; Brice, pp. 77–81, fig. 24, pl. 18, figs 4–5, pl. 19, figs 1–7, 9.


**Lectotype.** – Articulated shell selected by Brice (1982, p. 72, pl. 17, figs 1a–e) and stored under inventory number PMO A18820. The lectotype is 40.8 mm wide, 27.5 mm long, and 26.3 mm thick.

**Type horizon and locality.** – Blue Fiord Formation, Upper Emsian (Upper Lower Devonian); southeast of Ellesmere Island, Arctic Canada.

**Material.** – Observations are made based on descriptions and figures illustrated by Brice (1982) and Jones & Boucot (1983).

**Diagnosis.** – See genus which is at present monospecific.


**Geographic and stratigraphic occurrence.** – Eids to Bird Fiord formations, upper Lower Emsian to Eifelian (Upper Lower to lower Middle Devonian).

**Genus Borealispirifer** Hou & Su in Su & Hou, 1993

**Type species.** – *Eospirifer (Multispirifer) bifurcatus* Kaplun, 1961, p. 91.

**Diagnosis.** – Medium of large-sized, strongly biconvex, with slightly acute cardinal angles. Ventral interarea low. Fold and sulcus broad and not sharply bounded. Flanks with bifurcating ribs. Dental plates intrasinal. Rare development of secondary shell material in apical region. Vesticial crural plates present.


**Species excluded.** – *Borealispirifer maximus* (Zhang, 1983).

**Discussion.** – The species *maximus* was excluded from *Borealispirifer* due to its differences in curvature and development of secondary shell material. It is erected as the type species of gen. nov. A., which is less convex, very transverse, and equiconvex in longitudinal section, whereas taxa of *Borealispirifer* are equibiconvex to dorsoconvex in longitudinal section and less transverse. The new genus shows strong development of secondary shell material in the apical region, *Borealispirifer* has hardly any development of secondary shell material in apical region. The ventral muscle field of gen. nov. A is more elongated than the ventral muscle field in *Borealispirifer*.

The comparison of *Borealispirifer* with *Elymospirifer* and *Perryspirifer* is described above.

**Geographic and stratigraphic occurrence.** – Kazakhstan and northern China; Pragian to Lower Emsian (middle to upper Lower Devonian).

**Borealispirifer bifurcatus** (Kaplun, 1961)

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1961 *Eospirifer (Multispirifer) bifurcatus* Kaplun; Kaplun, pp. 91, 92, pl. 14, figs 1–4.


1991 *Multispirifer bifurcatus* (Kaplun, 1961). – Kaplun & Krupchenko, pl. 34, figs 4a, b.

1991 *Multispirifer pseudodivaricatus* Kaplun; Kaplun & Krupchenko, pp. 140–142, pl. 33, figs 1–4, pl. 34, figs 1–3.


**Holotype.** – Ventral internal mould stored in the SKGS under inventory number Bala well collection No. 1, specimen 320. The holotype is 39 mm wide and 24.5 mm long.

**Type horizon and type locality.** – Sardzhal beds, Upper Emsian (Upper Lower Devonian); northern Balkhash Lake, Kazakhstan.

**Material.** – Observations were made using the description and figures illustrated by Kaplun (1961), Kaplun & Krupchenko (1991), and Hou & Su (in Su & Hou 1993).
**Diagnosis.** – Medium to large-size shells, mostly dorsibiconvex in longitudinal section, and with bifurcation of ribs on flanks, fold, and in sulcus. Hardly any shell material developed in the apical region.

**Description.** – Form and size: shells medium-sized, equibiconvex to dorsibiconvex in longitudinal section, and subelliptical in outline. Brachythryid without mucronations. **Exterior of ventral valve:** ventral interarea low, apsacline, and curved. Delthyrium open with clearly developed deltoidal lamellae. Sulcus shallow, inconspicuous, and rounded in cross section. **Exterior of dorsal valve:** dorsal interarea very low and anacline to orthocline. Fold high, inconspicuous, and rounded in cross section. **Coarse-ornamentation:** 9 to 17 primary ribs on flanks that bifurcate and trifurcate in the anterior half of the shell. Fold and sulcus ribbed with 6 to 9 bifurcation ribs. **Micro-ornamentation:** capillae radially straight, forming small nodules with growth lamellae. **Interior of ventral valve:** filling of the umbo extends posteriorly over the hinge line. Fillings of the lateral apical cavities almost reaching as far posteriorly as the filling of the ventral umbo due to weak development of secondary shell material in apical region. Ventral muscle field broad, pyriform, without impressions of ribs, and weakly embedded into shell material. Ventral process small leaving a small indentation at the posterior margin of the muscle field on the internal mould. Out of the ventral muscle extends a fine myophragm preserved as a thin furrow through the whole muscle field. Diductor field preserved as radial striations in the anterior half of the muscle field impression which completely encloses the adductor field. Adductor field elongate, situated on each side next to the myophragm, and weakly embedded into shell material. Free portions of dental plates long leaving thin slits on the lateral margin of the muscle field of the internal mould. In gerontic stage, dental plates may be embedded into secondary shell material. A muscle bounding ridge defines the anterior margin of the muscle field preserved as a clearly developed furrow on the internal mould. Impressions of growth lamellae preserved in rare cases at the anterior margin. **Geographic and stratigraphic occurrence.** – See type horizon and type locality.

**Genus nov. A**


**Diagnosis.** – Strongly transverse specimens with bifurcating and trifurcating ribs on flanks, fold, and in sulcus. Both valves almost flat in transverse section. Strong development of shell material in apical region. Ventral muscle field narrow, elongate, and embedded in shell material.

**Species assigned.** – At present only the proposed type species gen. nov. A. maximus (Zhang, 1983).

**Remarks.** – The outline of the new genus and the strong development of secondary shell material, as well as the thin and elongated ventral muscle field plead for the erection of a new genus. However, it was not possible to study the type material from Kazakhstan, therefore, open nomenclature is chosen.

**Geographic and stratigraphic occurrence.** – Eming County, Junggar, Xinjiang, PR China; Mengelu and Zuo-mubasite formations, Emsian (upper Lower Devonian).

**Gen. nov. A maximus (Zhang, 1983)**

**Figures 5, 27**

1983 **Fimbrispirifer maximus** Zhang; Zhang, p. 349, pl. 97, fig. 5.  

**Type horizon and type locality.** – Mengkelu Formation, Emsian (upper Lower Devonian); Eming County, western Junggar, Xinjiang, PR China.

**Material.** – Description made using the account and figures of Hou & Su in Su & Hou (1993).

**Diagnosis.** – See genus which is at present monospecific.

**Description.** – Form and size: shells medium to large-sized, equibiconvex to ventribiconvex in longitudinal section, strongly transverse, and subelliptical in outline. Both valves flattened. Brachythryid without mucronations. **Exterior of ventral valve:** ventral interarea low, apsacline, and curved. Sulcus shallow, inconspicuous, and rounded in cross section. **Exterior of dorsal valve:** dorsal interarea orthocline to anacline. Fold low, inconspicuous, and rounded in cross section. **Coarse-ornamentation:** flanks, sulcus, and fold covered by fine, bifurcating...
ribs separated by narrower furrows. Bifurcation in general in the posterior part of the shell. Fold with median furrow. Sulcus with median rib (Fig. 5). Micro-ornamentation: according to Hou & Su in Su & Hou (1993, p. 143), Zhang (1983, p. 349) described the micro-ornamentation as fimbriate, consisting of lines of micro-spines at the edge of each growth lamella. Interior of ventral valve: filing of the ventral umbo extending gently posteriorly over the hinge line. Ventral muscle field strongly embedded into shell due to strong development of secondary shell material in apical region. Ventral muscle field elongated, longer than wide, and diamond-shaped. Myophragm fine, reaching through the posterior half of the muscle field. Ventral muscle field smooth, without any impressions of ribs. Free portions of dental plates short, leaving short, thin slits, or even only indentations, on either side of the impression of the ventral muscle field on the internal mould. Muscle bounding ridge clearly developed, leaving a coarse furrow on the internal mould that is sharply converging to anterior in the impression of the sulcus. Gognoglyphs coarse and embedded into the shell, preserved as elongated tubercles on the surface of the internal mould in the lateral environment of the ventral muscle field. Impressions of ribs preserved in the anterior third of the internal mould. Bifurcation of ribs not visible. Impressions of growth lamellae at the anterior margin.

Stratigraphic and geographic occurrence. – See genus which is monospecific.

Family Multispiriferidae fam. nov.

Type genus. – Multispirifer Kaplun, 1961.

Diagnosis. – Large spiriferids with mucronations. ‘Bundled’ ribs that anteriorly bifurcate and trifurcate on flanks, fold, and sulcus. Cardinalia large and coarsely developed, situated on an elevated platform in the same plane with the dorsal interarea. Crural plates lacking, moderate development of secondary shell material in apical region. Micro-ornamentation capillate, some specimens showing marginal, long micro-spines at the edge of each growth lamella.

Geographic and stratigraphic occurrence. – Germany and Belgium; Middle Siegenian (middle Lower Devonian).

Genus Multispirifer Kaplun, 1961

Type species. – Spirifer solitarius Krantz, 1857.

Diagnosis. – See family.

Species assigned. – Only the type species Multispirifer solitarius (Krantz, 1857).

Geographic and stratigraphic occurrence. – See family.

Multispirifer solitarius (Krantz, 1857)

Figures 2I, 4I, 5, 29

1857 Spirifer solitarius n. sp. Krantz; Krantz, pl. 9, fig. 1a [non 1b].
1900 Spirifer solitarius Krantz, 1857. – Scupin, pp. 11, 12 [215, 216], pl. 1 [24], figs 1, 2a–d.
1961 Eospirifer (Multispirifer) aff. solitarius. – Kaplun, pp. 89, 90, pl. 8, figs 6–9.

Holotype. – Ventral internal mould designated by monotypy stored under inventory number IPB A. Krantz, No. 5a, A. Krantz collection (illustrated by Krantz 1857, pl. 9, fig. 1a). Width 65.0 mm and length 37.5 mm.

Type horizon and locality. – Middle Siegen Beds (middle Lower Devonian); abandoned quarry close to Menzenberg (TM Königswinter 5309) near Bad Honnef (Middle Rhine area, Germany).

Material. – Locality and stratum: different localities in the Rheinisches Schiefergebirge, Germany; Middle Siegen beds, mid-Siegenian (middle Lower Devonian). 7 ventral internal moulds with corresponding external mould: Mbg. 3976; SMF XVII 820c, XVII 820d, XVII 1725a, 66337; 4 ventral internal moulds: SMF XVII 820b, XVII 820c, 66337, 66608; 2 ventral external mould: IPB AS Krantz Nr. 5a (holotype); SMF 66609; 2 dorsal internal moulds with corresponding external mould: SMF XVII 820c; 6 dorsal internal moulds: Mbg. 3978; SMF XVII 820c, 66611, 66339; 4 dorsal external moulds: Mbg. 3979, SMF 66610, 66612, 66336.

Diagnosis. – See subfamily.

Description. – Form and size: shells large, transverse, outline subelliptical, and brachythryid with mucronations; almost equibiconvex to gently ventribiconvex in longitudinal section. Exterior of ventral valve: ventral interarea high, cataclinal, and often curved, mostly with strong and transverse growth lamellae. Delthyrium open, often with clearly developed deltoidal lamellae that form a small
deltidium in the apical part. Sulcus always with median rib, ribs of third order may be developed. Exterior of dorsal valve: dorsal interarea low, strongly curved, and anacline, but clearly catacline in the lower part. Fold often with median furrow. Ribs of third order may be developed on fold. Coarse ornamentation: ribs of first order begin at the apex, ribs of second order develop by bifurcation anterior of the ventral muscle field on the internal mould. Ribs of first order strong, ribs of second order smaller and weaker, those of third order developed only in sulcus or on fold, in juvenile specimens angular becoming rounded in adult stage in cross section. Ribs of second and third order are clearly smaller and finer than ribs of first order giving them the characteristic ‘bundled’ appearance. 5 to 8 ribs of first order on each flank, including ribs of second order, number may reach 18. Fine growth lamellae in anterior part of both valves. At the middle of shell length the ribs of first order bifurcate or trifurcate. Trifurcation only on the first 4 pairs of ribs next to sulcus and fold, ribs of second order weaker than the ribs of first order (Fig. 4I). Ribs of third order may also develop in sulcus and on fold. Bifurcation on fold and in sulcus on the inner side of the lateral ribs of sulcus and fold (Fig. 5). Micro-ornamentation: capillate with tendency to development of long marginal micro-spines at the edge of each growth lamellae (Fig. 2I). Interior of ventral valve: filling of the ventral umbo extends gently posteriorly over the hinge line. Ventral process small, in juvenile specimens often very sharp, in geronic stage often blurred leaving a round indentation on the internal mould. A well developed septal pillow is situated below the ventral process and is laterally bordered by a pair of small ridges after the deltidiad lamellae. Lateral apical cavities filled by secondary shell material. Ventral muscle field gently embedded into shell, elongate, and subtrapeziform to subtriangular in geronic stage. Ventral median septum lacking or weakly developed. Impressions of 1 to 2 ribs on the ventral muscle field. Diductor scars radially arranged. Adductor scars thin and elongated, hardly recognisable on internal mould. Muscle bounding ridge very weakly developed, often only recognisable in juvenile specimens and diminishing in adult specimens. Free portions of dental plates

Figure 29. Morphological terms of Multispirifer solitarius (Krantz, 1857). A – SMF 66337. Ventral internal mould, plan view. Dental plates, ventral process, septal pillow, myophragm, and muscle bounding ridge are preserved as negative forms. B, C – SMF 66639. Dorsal internal mould, plan (B) and oblique posterior (C) views. Dental sockets, brachiophores, lateral furrows, median process, and muscle bounding ridge are preserved as negative forms.
wedge-like and embedded into secondary shell material, in juvenile specimens dental plates often thin and longer than in adult stages. Gonoglyphs rarely and only weakly preserved lateral of the ventral muscle field. Sulcus always with median rib. Impressions of ribs of second and rarely third order starting from the flanks of the sulcus bordering ribs. Sulcus bounding ribs not weakened, the first 2 or 3 pairs of ribs remarkably coarser than the following lateral pairs. Impressions of ribs of first order on the internal mould 4 to rarely 5 with ribs of second order often 8, in rare cases more than 10. Ribs of second order only weakly developed on the internal mould and much weaker developed than ribs of first order. Ribs in juvenile specimens angular in cross section and strongly elevated, in adult stages lower and rounded in cross section due to development of secondary shell material. Multiplication of ribs only anterior of the muscle field impressed on the internal mould. Visceral impressions arranged as radial striae on the surface of the internal mould, mostly lateral of the anterior margin of the muscle field. Interior of dorsal valve: internal mould transverse and without mucronations. Dorsal adductor field embedded into shell material. Cardinalia clearly visible and situated on an elevated shell that is more or less in the same plane as the interarea. Ctenophorium situated on a notothyrial shelf and laterally bordered by a pair of furrows leaving a distinct rim on the internal mould that is angular to rounded in cross section. Dental sockets thin and rounded in cross section. Brachiophores low and very thin pointing apically. Crural plates and free portions of crural bases absent, weak indentations lateral of the adductor field may represent remains of crural plates. Median process coarse leaving a deep and coarse furrow on the internal mould that is flattened at its base on the internal mould separating the posterior part of the adductor field. A short myophragm extends out of the adductor field that can be large in rare cases. Dorsal adductor field 'mushroom'-shaped in outline and bordered anteriorly by a fine muscle bounding ridge that leaves a weak furrow on the internal mould. Anterior and posterior pair of adductors clearly differentiable. The posterior pair consists of a 'hippodrome'-like field on each side situated on the fold and the first pair of ribs that may also reach into the second pair of furrows. The posterior adductors are elongated and longer than the anterior adductors. Adductor field situated on the fold, its posterior end is embedded into secondary shell material building two 'horn'-like structures pointing in a posterior direction on the internal mould. Adductors are sometimes impressed as radial striations on the internal mould. Impressions of ribs present anterior of the muscle field but weaker than on the ventral valve consisting almost only of ribs of first order. Striations of visceral impressions preserved in a few specimens. Gonoglyphs preserved as little transverse ridges on the internal mould which are pointing in a lateral direction.

Remarks. – Kaplun in Kaplun & Krupchenko (1991) erected the genus Multispirifer with its European type species M. solitarius and new taxa from Kazakhstan. Hou & Su (in Su & Hou 1993) realised that the Kazakhstan forms had nothing to do with the European Multispirifer and erected the genus Borealispirifer with the type species B. bifurcatus from Kazakhstan. Talent et al. (2001) considered Kaplun’s (1961) taxa of Borealispirifer as species of Struveina, which is erroneous because the two genera possess different micro-ornamentation, capillate versus fimbriate, respectively. In this work, Multispirifer is considered as an isolated branch of delthyridoid spiriferids that is restricted to the Middle Siegenian of Belgium and Germany.

Geographic and stratigraphic occurrence. – See family.

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