On the genus *Acrospirifer* Helmbrecht et Wedekind, 1923 (Brachiopoda, Lower Devonian)

(Contributions to Lower Devonian brachiopods from the Rheinisches Schiefergebirge and adjacent areas, 1)

O rodu *Acrospirifer* Helmbrecht et Wedekind, 1923 (Brachiopoda, spodní devon)

(3 plates)

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Numerous Devonian spiriferid species with strongly plicate shells distributed almost worldwide have been assigned to the taxon *Acrospirifer* Helmbrecht et Wedekind, 1923. In order to prepare a revised diagnosis for the genus, materials of the type species *A. primaevus* (Steininger, 1853) from its regio typica (Rheinisches Schiefergebirge, Germany) are redescribed. Well-preserved specimens display a fimbriate micro-ornamentation, with minute spines along the margins of concentric growth lamellae. This observation contradicts the diagnosis of the genus published by Gourvennec (1989) and the diagnosis of the family Acrospiriferidae Termier et Termier, 1949 published by Carter et al. (1994); both diagnoses include as a main character a capillate micro-ornamentation lacking minute spines.

Due to the new observations, the diagnosis of the genus *Acrospirifer* is revised. The taxonomic position of different species up to now assigned to the genus is discussed. According to the present knowledge, *Acrospirifer* is restricted to its type species probably only occurring in the Ardenno-Rhenish Mountains (? southern England, ? Czech Republic).

In the Lower Devonian of West Europe and North Africa purely capillate forms are abundant which have hitherto been determined as *Acrospirifer*; Gourvennec's diagnosis was also based on these forms. They do not belong to *Acrospirifer* but to the genus *Filispirifer* Jansen, 2001 comprising the group of "*Spirifer*" *fallax* Giebel, 1858. This group also occurs in the Lower Emsian Erbsloch-Grauwacke and in Hercynian Limestones (Kellerwald and Harz Mountains, Germany).

It is concluded that previous determinations of *Acrospirifer* or even *A. primaevus* in West Europe and North Africa should be reconsidered, and also stratigraphical alignments based on these determinations. At last, the family Acrospiriferidae can hardly be maintained in its present definition.

Key words: Brachiopoda, Spiriferida, Palaeozoic, Lower Devonian, stratigraphy, Rheinisches Schiefergebirge, Germany

Introduction

In the Lower Devonian of the Rheinisches Schiefergebirge (= Rhenish Slate Mountains, Germany), brachiopods represent a very abundant and diverse group of macrofossils. The biostratigraphical subdivision of the Rhenish Lower Devonian has mainly been based on articulate brachiopods (see e.g. Mittmeyer 1982). In spite of their high biostratigraphical potential, not many detailed systematic descriptions have been published up to now. This paper is the first one of an intended series dealing with Rhenish Lower Devonian brachiopods. In this work, the genus *Acrospirifer* is considered, starting from a re-study of its type species *A. primaevus* (Steininger, 1853) which is a classical index fossil for the Middle to Upper Siegenian in the Rheinisches Schiefergebirge.

The genus *Acrospirifer* has been erected by Helmbrecht – Wedekind (1923) who did not give a diagnosis but only mentioned the group of the species "*Spirifer*" *primaevus* Steininger, 1853 and named it *Acrospirifer*. The authors included "*Spirifer*" *primaevus* and "*S.*" *decheni* Kayser, 1878 (= *fallax* Giebel, 1858) in the genus, and a new species which they named *septalis*.

Wedekind (1926, p. 202) designated "*Spirifer*" *primaevus* as the type species of the genus. Maillieux (1931, p. 36) classified *Acrospirifer* as a subgenus of *Spirifer* and included species in the subgenus which share following features: simple and generally strong plications, fold without plications, sinus generally lacking plications but in some species with faint median costa; ventral muscle field impressed; dental plates thickened, more or less embedded in secondary shell thickenings. Maillieux regarded *Euryspirifer* Wedekind, 1926 (= *paradoxus*-group) and *Paraspirifer* Wedekind, 1926 (= *cultrijugatus*-group) as junior synonyms of *Acrospirifer*. From the present viewpoint, the range of the taxon was certainly too wide. As we know today, plicate spiriferids with smooth sulcus and fold and with impressed ventral muscle field rather represent a certain ecological morphotype adapted to turbid waters and sandy sedimentation, but they are not a natural phylogenetic unit. In a later publication, Maillieux (1941) distinguished between *Acrospirifer* and *Paraspirifer* and regarded them as subgenera of *Hysterolites* von Schlotheim, 1820.

In general, many coarsely costellate or plicate species occurring worldwide in Lower to Middle Devonian strata have been determined as *Acrospirifer* since the 1930's.

In an atlas of North American index fossils, Cooper (in Shimer – Shrock 1949) published a diagnosis resembling that of Maillieux: "subsemicircular to transversely semielliptical, costate and lamellose spiriferoids; fold and sulcus noncostate, dental plates strong, muscular field large, elongate-oval; dorsal interior with thick socket plates".

In his monograph on the *arduennensis-intermedius*-group, Solle (1953) maintained a rather wide concept of

Acrospirifer which he regarded as a subgenus of *Hysterolites*. Characters of his preliminary diagnosis were details of the shell form, impressed ventral muscle field, reduced dental plates, and a micro-ornamentation containing micro-spines (= "papillae"; however, it is not sure whether Solle considered material of the type species). Solle included the whole *arduennensis-intermedius*-group in *Hysterolites (Acrospirifer)*.

Havlíček (1959) also included the *arduennensis-intermedius*-group and the *paradoxus*-group in *Acrospirifer*. His diagnosis was quite differentiated containing apical characters and details of the micro-ornamentation, which he described as fimbriate.

Vandercammen (1963) revised the Devonian spiriferids of Belgium including the genus *Acrospirifer*. The type of micro-ornamentation and apical characters were used to distinguish between genera. Vandercammen investigated *Acrospirifer primaevus* and observed the presence of capillae ("microcostules") terminating as a fringe of minute spine bases over the anterior margin of each growth lamella, so that the micro-ornamentation of the species was considered to be essentially fimbriate. However, Vandercammen also included the purely capillate species "*Spirifer*" *beaujeani* Béclard, 1887 and "*S.*" *solitarius* Krantz, 1857 (today the type species of *Multispirifer* Kaplun, 1961) in *Acrospirifer*. Vandercammen recognized the differences in micro-ornamentation but obviously he did not consider them as very substantial. Apparently, he was also misled by a capillate specimen from the Armorican Massif (Vandercammen 1963, Pl. 2, Fig. 11) which he determined as *A. primaevus*. Further diagnostic characters were an excavated ventral muscle field and lacking crural plates. A similar diagnosis of *Acrospirifer* was published by Pitrat (1965) in the brachiopod volume of the "Treatise on invertebrate Paleontology". *Euryspirifer* and *Paraspirifer* were definitely accepted as separate genera.

In several publications (e.g. Amsden – Ventress 1963, Johnson 1970, Boucot 1973), North American species like e.g. "*Spirifer*" *murchisoni* Castelnau, 1843, "*S.*" *atlanticus* Clarke, 1907, and "*S.*" *kobehana* Merriam, 1940 were assigned to *Acrospirifer*.

"*Spirifer*" *fallax* Giebel, 1858 from Lower Emsian Hercynian Limestones and the Erbsloch-Grauwacke (Kellerwald and Harz Mountains, Germany) has for a long time been regarded as a species of *Acrospirifer* being very closely related to *A. primaevus* (see e.g. Mittmeyer 1973b, p. 20). Jahnke (1971) described *fallax* as a species of *Acrospirifer* supposing that *primaevus* was the phylogenetic forerunner of *fallax.* The author observed that *primaevus* – in contrast to *fallax* – is characterized by the presence of strongly developed plications bounding the sulcus, a thick dorsal median process ("myophragma" in Jahnke), and a well-developed notothyrial platform ("Kardinalplateau"). In *fallax*, he described a purely capillate micro-ornamentation. Jahnke recognized a fimbriate micro-ornamentation in "*Spirifer*" *arduennensis* and concluded that this group had to be separated from *Acrospirifer*. Therefore, he classified the *arduennensis*-group as a new subgenus of *Hysterolites* but did not give it a name.

Mittmeyer (1972) erected for the *arduennensis-intermedius*-group the new subgenus *Acrospirifer* (*Arduspirifer*) and later (1973b) elevated it to a separate genus. According to Mittmeyer (1973a), *Acrospirifer* (including *Arduspirifer*) shows a micro-ornamentation consisting of rows of long micro-spines ("Mikro-Dornen"). He assumed that capillae ("Mikro-Rippen") in *Acrospirifer primaevus* were probably a result of abrasion. Mittmeyer (1973b) united species with purely capillate and with fimbriate micro-ornamentation in *Acrospirifer*.

Considering only specimens from the Armorican Massif, Gourvennec (1989, p. 60–61) published a revised diagnosis of *Acrospirifer* including a purely capillate micro-ornamentation and lacking notothyrial platform as the most important characters. Gourvennec believed that the minute spines in *A. primaevus* described by Vandercammen (1963) were just a fallacious impression caused by "perturbations" of the capillae at the passage from one growth lamella to the next one.

Subsequently, Carter et al. (1994), preparing the spiriferid part of the new brachiopod volume of the "Treatise on invertebrate Paleontology", revised the diagnosis of the family Acrospiriferidae Termier et Termier, 1949. The family diagnosis included as a main character a capillate micro-ornamentation without micro-spines. *Acrospirifer* was put in a subfamily Acrospiriferinae, together with the purely capillate genera *Mauispirifer* and *Xerospirifer*. A capillate family Acrospiriferidae was maintained by Bizzarro – Lespérance (1999) in a cladistic analysis but, in addition, the Mucrospiriferinae have been included in the family. These workers even presented the capillate micro-ornamentation as the only diagnostic character of the family.

Johnson (1995) erected the genus *Patriaspirifer* including the North American species *Patriaspirifer kobehana* (Merriam, 1940) and *P. murchisoni* (Castelnau, 1843) which had been regarded as species of *Acrospirifer* before. The main character Johnson used to distinguish the North American genus from *Acrospirifer* was the presence of a fimbriate micro-ornamentation.

My investigation of *Acrospirifer primaevus* (Steininger, 1853) from the type region (northern Rheinisches Schiefergebirge) has largely confirmed Vandercammen's (1963) observations. This has taxonomic consequences described below. Further, the new results are important with respect to stratigraphical and palaeobiogeographical considerations. The main facts have already been presented on the "Millenium Brachiopod Congress" in London (Jansen 2000) and in a monograph (Jansen 2001). In the following systematic part, the genus *Acrospirifer* and its type species are briefly described. The type-species contains different morphotypes which may be distinguished as different subspecies in the future. A more detailed descrip-

tion also containing information on intraspecific variation and palaeobiology is planned by the author.

In this work, the classical subdivision of the Lower Devonian into the stages Gedinnian – Siegenian – Emsian is used, as it has been defined in Germany. This subdivision retains value in the Rheinisches Schiefergebirge because the international subdivision defined by GSSPs still cannot be exactly reproduced here.

Systematic paleontology

Order Spiriferida Waagen, 1883
Suborder Delthyridina Ivanova, 1972
Superfamily Delthyridoidea Phillips, 1841
Family Hysterolitidae Termier et Termier, 1949
Subfamily Hysterolitinae Termier et Termier, 1949

Genus *Acrospirifer* Helmbrecht et Wedekind, 1923

Type species: *Spirifera primaeva* Steininger, 1853

*pt 1923 *Acrospirifer* Helmbrecht et Wedekind, p. 952.
pt 1931 Sous-genre *Acrospirifer*. – Maillieux, p. 47.
pt 1935 *Acrospirifer*. – Allan, p. 18.
pt 1941 Sous-genre *Acrospirifer*. – Maillieux, p. 51.
pt 1949 *Acrospirifer*. – Cooper, in Shimer – Shrock, p. 323.
pt 1953 Untergattung *Acrospirifer*. – Solle, p. 29.
pt 1959 *Hysterolites (Acrospirifer).* – Havlíček, p. 98–99, 237.
pt 1963 *Acrospirifer*. – Vandercammen, p. 5–6.
pt 1964 *Acrospirifer*. – Drot, p. 45.
pt 1965 *Acrospirifer*. – Pitrat in Moore (Ed.), p. H 681–682.
pt 1973 *Acrospirifer*. – Mittmeyer, p. 38. – [1973a].
pt 1973 *Acrospirifer*. – Mittmeyer, p. 88–89. – [1973b].
non 1989 *Acrospirifer*. – Gourvennec, p. 60–61. – [=*Filispirifer*].
2001 *Acrospirifer.* – Jansen, p. 285.

Stratigraphical distribution: According to the present knowledge, the genus is confined to the Middle to Upper Siegenian (? lower Lower Emsian).

Geographical distribution: At present, *Acrospirifer* is restricted to its type species occurring in the Ardenno-Rhenish Mountains and probably in southern England and the Hrubý Jeseník Mountains (Czech Republic). Reports of occurrences in other regions have already proved to be incorrect, or they are at least doubted (see below, under "discussion").

Revised diagnosis: (from Jansen 2001) large and strongly biconvex, pauciplicate hysterolitines. Shells semicircular to somewhat transversely semielliptical in outline, with simple, very strong and angular plications; number of these generally ranging from 8 to 12 on each flank. Plications bounding the sulcus are strong, generally not weakened and not situated on a lower level with respect to the adjacent plications; only in rare cases they are weakened and included in the sulcus. Sulcus with median costa. Micro-ornamentation of the fimbriate type, with a fringe of rod-like micro-spines over each growth lamella; microspines are of subequal size. Deltidial lamellae poorly developed. Secondary shell in the apical regions of both valves very thick. Subdelthyrial plate absent. Ventral muscle field deeply impressed. Dental plates largely embedded in apical shell thickenings in adult stages. Notothyrial platform present, in general moderately to strongly developed, in rare cases poorly developed. Dorsal adductor field impressed, commonly divided by a strong median process in its posterior part. Free crural bases hardly pronounced. Free crural plates and outer hinge plates absent.
Species assigned: At present, only the type species *A. primaevus* is assigned to the genus with certainty (see below).
Discussion: In the last three decades, mainly following species have been assigned to *Acrospirifer*: *A. primaevus* (Steininger, 1853), "*A.*" *fallax* (Giebel, 1858), "*A.*" *beaujeani* (Béclard, 1887), "*A.*" *kobehana* (Merriam, 1940), and "*A.*" *murchisoni* (Castelnau, 1843). The latter two species from North America have already been excluded from the genus by Johnson (1995) who erected the new genus *Patriaspirifer* for them.

The diagnosis of the genus *Acrospirifer* published by Gourvennec (1989) included as main characters a capillate micro-ornamentation and a lacking notothyrial platform. However, Gourvennec exclusively referred to material from the Armorican Massif (western France). He described the species *primaevus* Steininger, 1853 and *fallax* Giebel, 1858. Subsequently, Johnson (1995) and Bizzarro – Lespérance (1999) also assumed a capillate micro-ornamentation in *Acrospirifer* and draw further systematic conclusions.

From my own observations and from literature I am sure, that many well-preserved specimens from the Kellerwald Mountains (eastern Rheinisches Schiefergebirge, see Jahnke 1971), the Anti-Atlas Mountains (southern Morocco, see Jansen 2001), the Celtiberian Chains (northeastern Spain, collection Carls), and the Armorican Massif (see Gourvennec 1989) which have hitherto been determined as *Acrospirifer* are in full accordance with Gourvennec's diagnosis. The typical capillate micro-ornamentation is figured by Jahnke (1971, Pl. 6, Fig. 10) and Gourvennec (1989, Pl. 3, Fig. 13).

However, the re-investigation of the type-species *Acrospirifer primaevus* (Steininger, 1853) from the type region in the Rheinisches Schiefergebirge has shown that this species is characterized by a fimbriate micro-ornamentation and a well-developed notothyrial platform (see below). According to my own experiences in delthyridoid brachiopods, I feel that the type of micro-ornamentation is an important generic character because it remains rather stable within a genus. Therefore, it was necessary to erect again a new diagnosis for the genus *Acrospirifer*.

In some of the *Acrospirifer*-like specimens with capillate micro-ornamentation from the Kellerwald and the Anti-Atlas Mountains which I have studied small nodules are visible where the concentric growth lines resp. lamellae cross the capillae. These nodules could be interpreted as reduced spines. However, the nodules are different from the spines in *A. primaevus* because they are never really free projections over the growth lamellae. Even in very well-preserved specimens, I have not seen real spines like in *A. primaevus*. This is the same

condition Gourvennec (1989, p. 64–65) observed in "*Acrospirifer primaevus*" from the Armorican Massif.

The *Acrospirifer*-like but capillate shells without micro-spines from West Europe and North Africa (commonly determined as *fallax* or *primaevus*) certainly do not belong to *Acrospirifer* but to the genus *Filispirifer* Jansen, 2001. This genus encompasses the group of "*Spirifer*" *fallax* Giebel, 1858 mainly distributed in the Mauro-Ibero-Armorican region. This region is regarded as a part of former North Gondwana, whereas the Ardenno-Rhenish region is considered to belong to the Old Red Continent (e.g. Robardet et al. 1990). The presence of "*Spirifer*" *fallax* in the Erbsloch-Grauwacke and in Hercynian Limestones (Kellerwald and Harz Mountains, Germany) is probably due to tectonic transport of these rocks from Gondwana to the North. Other faunal elements in the Erbsloch-Grauwacke (Lower Emsian, Kellerwald Mountains) support close palaeobiogeographical relationships to North Gondwana, e.g. the tabulate corals (Plusquellec – Jahnke 1999). I have investigated specimens of "*Spirifer*" *fallax* from the Erbsloch-Grauwacke, and these clearly exhibit a purely capillate micro-ornamentation. However, it cannot be excluded that the special facies conditions being of mixed Rhenish-Hercynian type are the reason for the presence of this species.

In contrast to previous opinions (e.g. Vandercammen 1963; Carls, in Brice et al. 2000), "*Spirifer*" *beaujeani* Béclard, 1887 from Siegenian strata of Belgium is not an *Acrospirifer* either. I have investigated the holotype that exhibits very clearly a capillate micro-ornamentation. The ventral muscle field of another specimen is hardly inpressed. The generic assignment of this rare species remains uncertain; perhaps it belongs to *Filispirifer* Jansen, 2001 or it is a member of another (? new) genus. If it actually belongs to *Filispirifer*, it would mean that this genus sporadically occurs in the Ardennes.

Occurrences of "*Acrospirifer*" have been reported from following North Gondwanan regions: Armorican Massif (Renaud 1942, Gourvennec 1989), Pyrenees (Laverdière 1930), Cantabrian Mountains (Jahnke et al. 1983, García-Alcalde et al. 1990), Celtiberian Chains (Carls 1987, 1999, Carls – Valenzuela-Ríos 1998; Carls, in Brice et al. 2000), Anti-Atlas Mountains (Drot 1964), northwestern Sahara (Le Maître 1952a), and Ougarta Chains (Le Maître 1952b; Gourvennec, in Boumendjel et al. 1997). These materials should be re-evaluated, and special attention must be paid to the micro-ornamentation. I have a strong suspicion that many or even all these specimens will turn out to be purely capillate.

One could argue that it is not a very big evolutionary step from the one type of micro-ornamentation to the other type. In the course of phylogenetic development, micro-spines were probably reduced to small nodules or, the other way round, nodules were extended to micro-spines. Perhaps, even environmental factors had a minor influence on this. In any case, the difference between capillate and fimbriate condition is present and certainly of taxonomic relevance.

In contrast to *Acrospirifer primaevus*, specimens of the capillate genus *Filispirifer* (= the *fallax*-group) I have seen are characterized by a lacking or poorly developed notothyrial platform, as also observed by Gourvennec (1989) in his Armorican specimens. Only in rare cases, the platform can be almost as strong as in *A. primaevus*. In addition, the plications bounding the sulcus are generally weaker than the adjacent second plications and included in the sulcus. In *A. primaevus*, the plications bounding the sulcus are mostly as strong as the adjacent plications. Concerning the other morphological characters, there are close similarities.

I am not sure about the taxonomic importance of the observed differences. In spite of these, close phylogenetic relationships appear to be possible. At present, the differences are regarded as relevant on the generic level only. On the other hand, the "*Acrospirifer* morphotype" could have developed in completely separate phylogenetic lineages and may represent a special ecological morphotype. Further research may elucidate the true phylogenetic relationships between the forms under consideration.

Acrospirifer primaevus is a classic index fossil for the Middle to Upper Siegenian in the Ardenno-Rhenish Mountains, "*Acrospirifer*" *fallax* (Giebel, 1858) an index fossil for the lower Lower Emsian (see e.g. Carls et al. 1982, Fuchs 1982, Mittmeyer 1982). Specimens assigned to *Acrospirifer* have been used for stratigraphical alignments in West Europe and North Africa as well. If these forms do not belong to *Acrospirifer*, what seems to be at least frequently the case, the drawn stratigraphical conclusions are problematic, of course. Moreover, the forms determined as "*Acrospirifer fallax*" from the lowest Emsian (Ulmen Group) of the Eifel region (Mittmeyer 1982, Fuchs 1989) are probably descendants of *Acrospirifer primaevus* and may have nothing to do with *fallax*.

Further, the results of this work have also consequences on palaeobiogeographical considerations: *Acrospirifer* is not available any further as a reliable witness for very close affinities between Ardenno-Rhenish and Mauro-Ibero-Armorican faunas. The observed differences rather support the assumption that there was an oceanic barrier between Gondwana and Euramerica in middle and late Early Devonian times, restricting the faunal migration between the shelf regions of the continents.

In the context of the revision of *Acrospirifer*, the North American genus *Patriaspirifer* Johnson, 1995 must be considered as well. The genus contains the two species *kobehana* Merriam, 1940 and *murchisoni* Castelnau, 1843 which had been included in *Acrospirifer* before Johnson's publication in 1995. After Johnson (1995), *Patriaspirifer* is distinguished from *Acrospirifer* by the presence of a fimbriate micro-ornamentation. Bizzarro – Lespérance (1999, p. 1062) accordingly stated: "The most significant difference between *Patriaspirifer* and *Acrospirifer* lies in the micro-ornament. *Spirifer primaevus* Steininger, 1853, the type species of *Acrospirifer*, has a spine-less micro-ornament consisting of capillae, while North American forms possess a fimbriate micro-ornament…".

Johnson, Bizzarro, and Lespérance are wrong in this point. Because *Acrospirifer primaevus* has a fimbriate micro-ornamentation, this difference does not exist. However, shells determined as species of *Patriaspirifer* possess considerable free lamellae along the inner socket ridges in the apical region of the dorsal valve (e.g. Johnson 1970, Pl. 56, Fig. 9, Pl. 58, Fig. 17; Amsden – Ventress 1963, Pl. 6, Fig. 2) which may be called outer hinge plates. Such lamellae are absent in *Acrospirifer primaevus*. In this species, there are only very little pronounced crural bases representing the free parts of the crura which are included in the articulation apparatus. Therefore, it seemingly still makes sense to maintain the North American genus *Patriaspirifer*.

The North American species "*Spirifer*" *atlanticus* Clarke, 1907 was assigned to *Acrospirifer* by Boucot (1973). Because the species is characterized by more transverse shells and more numerous and weaker plications than *Acrospirifer* I prefer to assign it to the genus *Euryspirifer*.

Benedetto (1984) determined *Acrospirifer* in the Lower Devonian of Venezuela. The specimens determined as "*Acrospirifer macrothyris* (Hall, 1867)" do not belong to *Acrospirifer*. They have much weaker plications and a different micro-ornamentation (cf. Benedetto 1984, Pl. 19, Fig. 10). The specimens assigned to "*Acrospirifer* cf. *murchisoni* (Castelnau, 1843)" do not belong to *Acrospirifer* either because of their smaller size and different micro-ornamentation.

Recently, Chen – Yao (1999) described a Chinese fauna and erected the species *shipengensis* which they determined as *Acrospirifer*. However, the description does not give enough information to be sure to which genus the species belongs. In general, I would hesitate to determine Ardenno-Rhenish brachiopod genera in China.

According to the present knowledge, the genus *Acrospirifer* should be restricted to its type species *A. primaevus* that probably occurs exclusively in the Ardenno-Rhenish region and possibly in southern England and the Czech Republic. Previous assignments of other species to this genus are regarded as doubtful and should be carefully reconsidered. Reports of *Acrospirifer* outside the Ardenno-Rhenish Mountains are doubted.

At last, *Acrospirifer* is the type genus of the family Acrospiriferidae Termier et Termier, 1949. Carter et al. (1994) published a revised family diagnosis which shall also be published in the forthcoming spiriferid part of the "Treatise on Invertebrate Paleontology". The main diagnostic character of the family is the presence of a capillate micro-ornamentation. However, a family diagnosis must harmonize with the morphology of its type genus. Due to the new observations, the family Acrospiriferidae can hardly be maintained in its present version.

C o m p a r i s o n : *Acrospirifer* is more or less closely related to several other Lower Devonian hysterolitines with coarsely ribbed or plicate shells bearing a fimbriate micro-ornamentation. Some of these were assigned to *Acrospirifer* in earlier times. Within the whole group, *Acrospirifer* is characterized by the strongest and most angular plications.

Euryspirifer Wedekind, 1926 is regarded as being closely related to *Acrospirifer*. However, the shells are alate in outline and multiplicate, the plications being weaker. On the other hand, the genus shares some of the diagnostic features with *Acrospirifer*: profile strongly biconvex, median costa in the sulcus present, similar micro-ornamentation, dental plates largely embedded in apical shell thickenings, ventral muscle field deeply impressed, notothyrial platform present, median process present, bisecting the impressed dorsal adductor field. Therefore, a close phylogenetic relationship between the two genera is assumed.

Hysterolites von Schlotheim, 1820 has smaller shells and a different micro-ornamentation; median costa in the sulcus absent; ventral muscle field not impressed; free dental plates are long and thin; free crural bases are more developed. *Brachyspirifer* Wedekind, 1926 is characterized by more ribs, not impressed ventral muscle field, longer free dental plates, and crural bases embedded to a lower degree in shell thickenings. *Paraspirifer* Wedekind, 1926 has more ribs which are finer and tend to bifurcate. *Arduspirifer* Mittmeyer, 1972 is discriminated from *Acrospirifer* by smaller shells and a slightly different micro-ornamentation with micro-spines being more variable in size within the concentric rows. A median costa in the sulcus is generally absent (except for *A. mosellanus* where a faint median costa may be present).

Dixonella Gourvennec, 1989 is smaller and has no median process separating the dorsal adductor field. The plications bounding the sulcus are weakened and situated on a lower level than the adjacent second plications. Apart from that, this genus is very similar to *Acrospirifer*. Occurring in the Lower Siegenian of West Europe and North Africa, *Dixonella* is older than *Acrospirifer* and could be the phylogenetic forerunner.

Torosospirifer Gourvennec, 1989 from the Siegenian of Spain and France, erected as a subgenus of *Brachyspirifer*, is regarded as a separate genus here. It is discriminated from *Acrospirifer* by more and finer ribs and considerable free crural bases ("lamelles apicales dorsales" sensu Gourvennec; ? outer hinge plates) along the inner socket ridges; such free lamellae are absent in *Acrospirifer*; free dental plates are generally longer in *Torosospirifer* (cf. Gourvennec 1989).

The similar genus *Australospirifer* Caster, 1939 from the Malvinocaffric Realm (South Africa, southern and eastern South America, Antarctica) is characterized by the presence of a subdelthyrial plate (Boucot et al. 1965, Pl. 7, Fig. 11, Pl. 8, Figs 7–8) which is absent in *Acrospirifer*.

For comparison with *Patriaspirifer* see above, under "discussion".

Rostrospirifer Grabau, 1931 and *Otospirifer* Hou et Xian, 1975 from China have more transversely elongated shells and more plications, so that they rather resemble *Euryspirifer*.

The forms bearing an exclusively capillate micro-ornamentation from the Lower Devonian (Siegenian – Emsian) of West Europe and North Africa which have been assigned to *Acrospirifer* up to now do not belong to this genus (see above, in the discussion). They belong to the genus *Filispirifer* comprising the group of "*Spirifer*" *fallax* Giebel, 1858 which is probably closely related to the capillate genus *Mauispirifer* Allan, 1947.

Multispirifer Kaplun, 1961 (type-species *Spirifer solitarius* Krantz, 1857) from the Middle Siegenian of the Rheinisches Schiefergebirge is characterized by a capillate micro-ornamentation as well; further, it has bifurcating costae.

Acrospirifer primaevus (Steininger, 1853)

Pl. I, Figs 1–14; Pl. II, Figs 1–12; Pl. III, Figs 1–7

v * 1853 *Spirifera primaeva* Steininger, p. 72, Pl. 6, Fig. 1.
1857 *Spirifer socialis* Krantz, p. 151–152, Pl. 8, Figs 3a, c, d (non Fig. 3b = *Vandercammenina bischofi* (Giebel, 1858)).
? 1864 *Spirifera cultrijugata* ? F. Roemer. – Davidson, p. 35–36, Pl. 8, Figs 1–3.
1885 *Spir. paradoxus* Schl. – Quenstedt, p. 727–728, Pl. 56, Fig. 20. – [non von Schlotheim 1813].
v 1886 *Spirifer prohystericus* Maurer, p. 19. – [semi-adult specimens of *A. primaevus*].
1897 *Spirifer primaevus*. – Frech, p. 139–141, 143–144, Pl. 23a, Fig. 6.
1900 *Spirifer primaevus*. – Scupin, p. 16, 35, 84, 89, 92, 121, 123, 128–130, 132, Pl. 8, Fig. 9.
1900 *Spirifer subhystericus* nov. nom. Scupin, p. 15–16, Pl. 8, Figs 9–10. – [semi-adult specimens of *A. primaevus*].
1904 *Spirifer primaevus*. – Drevermann, p. 246–249, Pl. 29, Figs 1–7.
1910 *Spirifer primaevus*. – Assmann, p. 140, Pl. 6, Figs 1–4.
1913 *Spirifer primaevus*. – Asselbergs, p. 102.
1913 *Spirifer primaevus*. – Kegel, p. 108–110, 145, 149, 151, 156, 162, Pl. 6, Figs 3–4.
1923 *Spirifer primaevus*. – Helmbrecht – Wedekind, p. 949, 951–953.
? 1923 *Spirifer septalis*. – Helmbrecht – Wedekind, p. 952–953.
1923 *Spirifer primaevus*. – Quiring, p. 91, 94, 98–100, 102–111.
1931 *Spirifer primaevus*. – Dahmer, p. 87, Pl. 7, Fig. 3.
1931 *Spirifer (Acrospirifer) primaevus*. – Maillieux, p. 44–47, Pl. 2, Figs 1, 1a, 2, 2a.
1932 *Spirifer primaevus*. – Dahmer, p. 373.
1934 *Spirifer primaevus*. – Dahmer: mentioned many times.
v 1934 *Spirifer prohystericus* Maurer, 1886. – Dahmer, p. 71–72, Pl. 8, Fig. 1.
1935 *Spirifer primaevus*. – Dahmer, p. 133–138. – [1935a].
1935 *Spirifer primaevus*. – Dahmer, p. 140. – [1935b].
v 1936 *Spirifer primaevus*. – Rose, p. 52, 57.
1936 *Spirifer primaevus*. – Dahmer, p. 25–27, Pl. 6, Figs 1–2, Text-fig. 2. – [1936a].
1936 *Spirifer primaevus*. – Dahmer, p. 641, 645. – [1936b].
1937 *Spirifer primaevus*. – Kutscher: mentioned many times.
1937 *Spirifer primaevus*. – Dahmer, p. 446–450, 452–453, 455–456, 458.
v 1940 *Spirifer primaevus*. – Simpson, p. 59, Tab. 4, Pl. 6, Fig. 5.
v 1940 *Spirifer primaevus*. – Dahmer, p. 81.
1940 *Spirifer primaevus*. – Kutscher, p. 107, 110–115, Pl. 1, Fig. 1.
1950 *Spirifer primaevus*. – Solle: mentioned many times.
1952 *Spirifer primaevus*. – Kutscher, p. 87, 89.
1957 *Hysterolites (Acrospirifer) primaevus*. – Jentsch – Röder, p. 124.
? 1957 *Hysterolites (Acrospirifer) fallax* (Giebel). – Jentsch – Röder, p. 124, 127, Pl. 6, Fig. 2.
? 1957 *Hysterolites (Acrospirifer)* sp. aff. *fallax* (Giebel). – Jentsch – Röder, p. 124, 127, Pl. 6, Fig. 3.
v 1960 *Acrospirifer primaevus*. – Paproth, Tab. 1, Pl. 1, Fig. 8, Pl. 3, Figs 6–7.
1960 *Hysterolites (Acrospirifer) primaevus*. – Jentsch, p. 193–194, Pl. 19, Figs 4–5, 7.
non 1961 *Acrospirifer primaevus kasachstanica* Kaplun, p. 101–105, Pl. 17, Figs 5–9. – [completely different micro-ornamentation].
v 1963 *Acrospirifer primaevus*. – Vandercammen, p. 12–19, Pl. 1 Figs 13–20, Pl. 2, Figs 1–10, 12–13 (non Fig. 11), Text-figs 4–9.
v 1963 *Spirifer primaevus*. – Martin, Pl. 7, Fig. 4.
1965 *Acrospirifer primaevus*. – Pitrat, H 682, Fig. 553.
v 1971 *Acrospirifer primaevus*. – Jahnke, p. 37, Pl. 11, Figs 25a–b. – [designation and re-figuration of lectotype].
1973 *Spirifer primaevus*. – Waterlot et al., Pl. 2, Fig. 5.
? 1973 *Acrospirifer primaevus*. – Mittmeyer, p. 89–90, Pl. 2, Figs 21–31. – [1973b].
v 1974 *Acrospirifer primaevus*. – Langsdorf, p. 379–380, Fig. 2.
? 1981 *Acrospirifer primaevus*. – Evans, p. 521, Pl. 1, Figs a–b.
1982 *Acrospirifer primaevus*. – Carls et al., p. 182–183, 185, 189, 190–191, Fig. 3.
1982 *Acrospirifer primaevus*. – Fuchs, p. 231, 233–234, 252, Fig. 10.
1982 *Acrospirifer primaevus*. – Mittmeyer, p. 259–262, chart 1.
1987 *Acrospirifer primaevus*. – Carls, p. 82–84, 99, Fig. 3.
non 1989 *Acrospirifer primaevus*. – Gourvennec, p. 61–67, Text-figs 32–35, Pl. 3, Figs 1–13. – [= a species of *Filispirifer*].
? 1989 *Acrospirifer primaevus*. – Chlupáč, p. 373, 378–379, 388, Fig. 5: 8–9.
1994 *Acrospirifer primaevus*. – Godefroid et al., Figs 2, 11.
v 2001 *Acrospirifer primaevus*. – Jansen, p. 286–287, Pl. 33, Figs 1–8.

Lectotype: designated by Jahnke (1971, p. 37); ventral valve external mould figured by Steininger (1853, Pl. 6, Fig. 1); internal mould belonging to the external mould is also present. Gypsoplasts and a latex cast are re-figured herein on Pl. I, Figs 1–3. The original material is housed in the Palaeontological Museum of the Humboldt University, Berlin.

Dimensions: ventral valve external mould: length > 50 mm, width > 68 mm; number of plications on each flank (referred to the former shell): 11. – ventral valve internal mould: length > 42 mm, width = ca. 65 mm; length of muscle field = ca. 27 mm, width = ca. 19.5 mm; there are 8 (+ 1) plications on each flank of the internal mould. The ventral interarea is 10 mm high.

Type horizon: (? Upper) Siegen Formation, (? Upper) Siegenian.

Type locality: Herdorf, Siegerland area, northern Rheinisches Schiefergebirge, Germany.

Stratigraphical range: The species is a classical index fossil for the Middle to Upper Siegenian (high Pragian in its original sense); ? lowest Emsian (Ulmen Group).

Distribution: Rheinisches Schiefergebirge, Germany; Ardennes, Belgium; ? S-England; ? Czech Republic. – Localities in Germany, formations of Middle to Late Siegenian age: Siegerland area, Siegen Formation: for localities see Paproth (1960), Quiring (1923); Westerwald area, Seifen Formation: see Dahmer (1934); Middle Rhine area near Bonn, Siegen Formation: see Dahmer (1931, 1936b); southern Rheinisches Schiefergebirge, Taunusquarzit Formation: see Kutscher (1937, 1952), Jentsch – Röder (1957); western Rheinisches Schiefergebirge, Eifel Hills: see Dahmer (1937, 1940), Simpson (1940), Fuchs (1982). – Uncertain: central Rheinisches Schiefergebirge, Middle Rhine area, Ulmen Group, lower Lower Emsian: see Mittmeyer (1973b). – Localities in Belgium, Ardennes, formations of Siegenian age: see Asselbergs (1913), Maillieux (1931, 1936), Vandercammen (1963), Godefroid et al. (1994). – Uncertain: southern England, Siegenian: see Davidson (1864), Evans (1981). – Uncertain: Czech Republic, Hrubý Jeseník Mountains, Siegenian: see Chlupáč (1989).

Studied materials: The investigated specimens are stored in the Senckenberg-Museum, Frankfurt am Main/Germany (collection

numbers: SMF...). The specimens are preserved as internal and external moulds. Latex casts have been made in order to be better able to describe the internal morphology of the valves and to make visible the external micro-ornamentation. The best-preserved specimens exhibiting details of the micro-ornamentation come from the localities "Seifen" (Westerwald area) and "Etzbach" (Siegerland area). – Following type specimens have been investigated: lectotype, ventral valve internal and external moulds (gypsoplasts); SMF 19236a–b. – List of investigated materials from different localities in the Rheinisches Schiefergebirge; all strata are of Middle to Late Siegenian age [abbreviations: DVI = dorsal valve internal mould(s), VVI = ventral valve internal mould(s), DVE = dorsal valve external mould(s), VVE = ventral valve external mould(s), DVI/VVI = internal mould of both valves in conjoined condition, TM25 = topographic mapsheet 1:25000]:
Etzbach/Sieg, Siegerland area (TM25 No. 5212 Wissen): 17 VVI, 14 DVKI, 1 DVI/VVI, 4 VVE; SMF 59870, 59877–59879, 59887, 65089–65091, 65093, 65095, 65097–65098, 65101, 65318, 65368, 65878. – Augustenthal near Neuwied (TM25 Neuwied/Rhein, No. 5510); Augustenthal Formation, Middle Siegenian: 1 DVI, 2 VVI, 1 VVE; SMF XVII 989a. – Seifen, Westerwald area (TM25 Altenkirchen, No. 5311); Seifen Formation, Middle Siegenian: 7 VVI, 5 DVI, 5 VVE, 4 DVE; SMF 59873–59874, 59882–59883, 59916, 65053, 65088, 65092, 65094, 65096, 65099–65100, 65868, 65872, 65879–65880, 65882–65886. – Ascheid, Westerwald area (TM25 Altenkirchen, No. 5311); Seifen Formation, Middle Siegenian: 1 DVE; SMF 59876. – Niederähren, Westerwald area, quarry near the road from Puderbach to Seifen (TM25 Altenkirchen, No. 5311); Seifen Formation, Middle Siegenian: 11 DVI, 13 VVI, 2 VVE; SMF 65891. – Mühlmerich quarry near Eichen/Westerwald area (TM25 Altenkirchen, No. 5311); Seifen Formation, Middle Siegenian: 5 DVI, 10 VVI, 1 DVI/VVI, 1 DVE, 2 VVE; SMF XV 1676 d, XVII 398a, XVII 398x, XVII 932d, 65890. – Weiersbach mill (Lieser valley), road cut behind the mill, Eifel Hills (TM25 Daun, No. 5806); Saxler Formation, Upper Siegenian: 1 DVI, 1 VVI (original specimens of Simpson 1940); SMF XVII 398m, XVII 398p. – Saxler, road to Ellscheid, Eifel Hills (TM25 Gillenfeld, No. 5807); Saxler Formation, Upper Siegenian: 3 DVI (original specimens of Simpson 1940); SMF 398f. – Ollenbachtal, Auderath mill, small quarry, Eifel Hills (TM25 Gillenfeld, No. 5807); Saxler Formation, Upper Siegenian: 1 DVI (original specimen of Simpson 1940); SMF XVII 398r. – Berenbach, Eifel Hills (TM25 Kelberg, No. 5707); Saxler Formation, Upper Siegenian: 1 DVI, 1 VVI (original specimens of Simpson 1940); SMF 398g. – Road cut SW Schönbach, Eifel Hills (TM25 Kelberg, No. 5707); Saxler Formation, Upper Siegenian: 1 VVI (original specimen of Simpson 1940); SMF XVII 398h. – Road from Bürresheim to Kirchesch (TM25 Virneburg, No. 5608); Middle Siegen Formation, Middle Siegenian: 1 DVI, 1VVI, 1 DVI/VVI, 1 DVE (original specimens of Dahmer 1940); SMF 398w. – Quarry W Köpfchen near Wald-Erbach, Hunsrück Hills (TM25 Stromberg, No. 6012); Upper Taunusquarzit Formation: 1 VVI, 1 VVE; SMF 65881. – Homburg, Kirbach mill, Taunus Hills (TM25 Bad Homburg v. d. Höhe, No. 5717); Taunusquarzit Formation: 1 VVE; SMF XVII 3110. – 100 m W Rheinstein castle (TM25 Bingen, No. 6013); Taunusquarzit Formation: 1 VVI, 1 VVE; SMF 65887. – Leingipfel near Rüdesheim/Rhine, Taunus Hills (TM25 Bingen, Nr. 6013); Upper Taunusquarzit Formation: 1 DVI, 31 VVI, 2 VVE; SMF 65870–65877. – Hartberg, W Bingen (TM25 Bingen, Nr. 6013); Upper Taunusquarzit Formation: 4 DVI, 7 VVI, 1 DVE; SMF 65888. – Allerbach, W Bingerbrück (TM25 Bingen, Nr. 6013); Taunusquarzit Formation: 4 DVI, 16 VVI, 1 DVE; SMF 65889. – Waldesch near Mayen, Eifel Hills, Siegen Formation: 1 DVI; SMF 65869.

Diagnosis: as for the genus.

Description of the species (based on materials cited above): Exterior. – Shells large, strongly biconvex, semicircular to somewhat transversely semielliptical in outline, equithyrid to megathyrid, with sulcus and fold flanked by plicate lateral areas. The shells reach some 70 mm width and 50 mm length. Short mucronate cardinal extremities are often present. Dorsal valve with high fold, ventral valve with corresponding deep sulcus. Sulcus angular in cross section, moderately wide, with faint median costa. Fold moderately wide, angular in cross section, without plications or costae. Plications of the flanks very strong, non-bifurcating, angular in cross section. The number of plications generally ranges from 8 to 12 on each flank. Plications bounding the sulcus are mostly not weakened and not situated at a lower level with respect to the adjacent second plications. Only in rare cases, they are weaker than the second plications and included in the sulcus.

The micro-ornamentation consists of short segments of fine pseudoradial striae ("capillae") terminating as a fringe of micro-spines situated at the anterior margin of each growth lamella. Concentric growth lamellae more or less strongly developed and imbricating, typically showing a somewhat irregular course; distances between the succeeding lamellae are different; the lamellae are crowded in the periphery of adult shells. "Capillae" in *A. primaevus* are generally not developed as continuous (pseudo-)radial ridges which are typical of the real capillate condition. In well-preserved specimens, there are no capillae in the proper meaning; these are frequently interrupted and rather occur as subordinate spine bases. The micro-spines are the dominant sculpture element. Therefore, the micro-ornamentation as a whole is clearly of the fimbriate type. The spines are rod-like and circular in cross-section. They are about 0.05 mm in diameter. There are 8 to 12 spines in 1 mm along a concentric growth lamella. The spines are regularly arranged in concentric rows and subequal in size.

Depending on the degree of abrasion of the shell, the micro-ornamentation exhibits different stages of preservation. If the shell is not well enough preserved (what is frequently the case), the spines are broken off and the micro-ornamentation may show a "pseudo-capillate" condition.

Ventral interarea high (reaching > 10 mm), apsacline, concave in longitudinal section, surface largely smooth, with very fine growth lines running parallel to the hinge line. Delthyrium large, open, triangular, bordered by a pair of thin deltidial lamellae. Dorsal interarea low, approximately orthocline. Notothyrium open.

Shells of both valves very thick, especially in the umbonal regions, probably to help the living animal in maintaining a beak-down orientation in its life position, and assisting the pedicle.

Ventral valve interior. – Apical cavity subdivided by dental plates into a central cavity and two lateral cavities. In juvenile and semi-adult ontogenetic stages ("*prohystericus*"-stage), short to moderately long free dental plates are present which leave, on the ventral internal mould, corresponding incisions lateral to the muscle field. Due to extensive deposition of secondary material, the free parts of the dental plates almost disappear in large specimens. The dental plates are subdivided into dental flange and ventral adminiculum. Dental flanges

support prominent hinge teeth. On the internal mould, the incisions left by the dental plates are situated lateral to the sulcus, in the backward prolongation of the second to third plications of the flanks. The dental plates are followed by very faint muscle bounding ridges enclosing the muscle field. Deltidial furrows present, situated just below the delthyrial margins.

Depending on the extent of umbonal shell thickenings, the lateral apical cavities are more or less clearly pronounced. They can leave sharp or rounded projections on the internal mould. There is a small median process bisecting the ventral muscle field in its posterior part. On the internal mould, this process leaves a clear median incision. The process grades anteriorly into a thin myophragm which reaches about the midlength of the muscle field.

The ventral muscle field reaches about the half length of the valve; it is suboval to rhomboid in outline, longer than wide, deeply impressed; diductor and adductor scars are arranged in pairs. Adductor scars long and narrow, situated in the sulcus area. Diductor scars lie lateral to the adductor scars and bear fine striations which bifurcate. The muscle field leaves a kind of cone on the internal mould (in German: "Muskel-Zapfen"). One to three pairs of plications run through this cone so that it gets an angular appearance. The muscle field is delimited anteriorly by a change in curvature and by the muscle bounding ridges.

The surface of the internal mould lateral to the muscle field is flattened and forms a kind of platform. In adult specimens, this area bears fine tubercles (small pits on the interior shell surface) which may have been left by the gonads. In this area, the plications are still weak or lacking.

In the peripheral regions of the internal mould, the plications are almost as strong as on the shell surface. The number of plications normally reaches 7 to 8 on each flank, in rare cases 9. The sulcus of the internal mould is rounded to subangular in cross section.

Dorsal valve interior. – Apical cavity delimited laterally by thick inner socket ridges. Notothyrial platform present, generally strong. In few specimens, the platform is only moderately or even poorly developed. Ctenophoridium (= dorsal diductor field) clearly developed, consisting of many and very thin lamellae, elevated on the notothyrial platform. Dental sockets begin thin apically and become suddenly voluminous distally. They are supported by thick callosities dorsally. Dorsal adductor field deeply impressed in most specimens, adductor scars arranged in pairs, irregularly striated. Adductor field commonly bisected by a strong median process in its posterior part, process grading into a fine and very long myophragm. The median process is variable in size; in few specimens it is almost lacking, and there is only a faint myophragm instead. The internal mould of the dorsal adductor field overhangs the hinge line posteriorly; it is more or less raised above the surrounding floor of the internal mould. Free crural bases are little pronounced. Free crural plates (= dorsal adminicula) and outer hinge plates are absent.

Lateral to the dorsal adductor field, the surface shows a peculiar pattern of irregular impressions probably left by the gonads; only visible in well-preserved specimens.

On the dorsal valve internal mould, generally 6 to 7 strong plications have been counted on each flank, rarely 8 or 9. The first two or three pairs of plications begin within the adductor field, the others lateral to it. The fold of the internal mould is subangular in cross section.

Summary

The type species of *Acrospirifer*, *A. primaevus* (Steininger, 1853), has been redescribed. Well-preserved specimens from the type region of the species (Rheinisches Schiefergebirge, Germany) exhibit a fimbriate micro-ornamentation with rows of micro-spines along each concentric growth lamella. Moreover, a strongly developed notothyrial platform in the dorsal valve is present in most specimens. Because these observations contradict the last published diagnosis of the genus based on Armorican material (Gourvennec 1989), a new diagnosis is erected. In North Gondwanan regions, similar but purely capillate forms occur which have hitherto been assigned to *Acrospirifer*. These forms, belonging to the group around "*Spirifer*" *fallax* Giebel, 1858, are now assigned to the genus *Filispirifer* Jansen, 2001. Apart from the different micro-ornamentation, they are further discriminated from *Acrospirifer* by the absence of a strongly developed notothyrial platform and by the presence of sulcus bounding plications which are commonly weakened and included in the sulcus. The taxonomic status of the rare capillate species "*Spirifer*" *beaujeani* Béclard, 1887 from the Siegenian of Belgium remains uncertain; perhaps it belongs to *Filispirifer* as well.

The North American genus *Patriaspirifer* Johnson, 1995, which has mainly been discriminated from *Acrospirifer* by the presence of a fimbriate micro-ornamentation, is to be re-evaluated, because this difference is not present. It appears, that there are minor differences concerning the cardinalia so that it seems to be justified to maintain this genus.

According to the present knowledge, *Acrospirifer* is restricted to its type species probably only occurring in the Ardenno-Rhenish Mountains (uncertain occurrences in southern England and in the Czech Republic). It is re-commended to re-evaluate all determinations of *Acrospirifer* in the Mauro-Ibero-Armorican region. Stratigraphical and palaeobiogeographical conclusions drawn on the base of the supposed occurrences should be reconsidered as well.

The family Acrospiriferidae in the sense of Carter et al. (1994) can hardly be maintained any further because it has been defined as capillate.

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O rodu *Acrospirifer* Helmbrecht et Wedekind, 1923 (Brachiopoda, spodní devon)

Četné devonské druhy spiriferidních brachiopodů se silně plikátními miskami, které byly rozšířeny téměr po celém světě byly přiřazovány k rodu *Acrospirifer* Helmbrecht et Wedekind, 1923. V průběhu připravované revize rodu byl materiál typového druhu *A. primaevus* (Steininger, 1853) z typické oblasti (Rýnské břidličné pohoří) znovu revidován. Na dobře zachovalých jedincích je zřetelná fimbriátní mikroornamentace, s malými trny podél okrajů koncentrických růstových lamel. Toto zjištění je v rozporu s diagnózou rodu publikovanou Gourvennecem (1989) a diagnózou čeledi Acrospiriferidae Termier et Termier, 1949, publikovanou Carterem et al. (1994); v obou diagnózách je uveden jako hlavní znak kapilátní mikroornamentace bez drobných trnů na lamelách.

Na základě nových zjištění je revidováno určení rodu *Acrospirifer* a je diskutováno taxonomické postavení druhů doposud tomuto rodu řazených. Na základě současných znalostí je rod *Acrospirifer* ve skutečnosti omezen pouze na typový druh, který se vyskytuje v Ardenách a Porýní, a s pochybnostmi i v jižní Anglii a České republice.Ve spodním devonu západní Evropy a severní Afriky jsou hojné výlučně typy s kapilátní mikroornamentací, které byly dosud určovány jako rod *Acrospirifer*; rovněž diagnóza uvedené Gourvennecem je založena na těchto taxonech. Ty však nenáleží k rodu *Acrospirifer,* ale k *Filispirifer* Jansen, 2001 spadajícímu do okruhu druhu "*Spirifer*" *fallax* Giebel, 1858. Tato skupina druhů se rovněž vyskytuje ve spodnoemských jednotkách Erbsloch-Grauwacke a v Hercynských vápencích v Kellervaldu a pohoží Harz v Německu.

Výskyty rodu *Acrospirifer* či dokonce druhu *A. primaevus* v západní Evropě a severní Africe je nutno přehodnotit a rovněž tak i stratigrafické závěry vycházející z těchto údajných výskytů. Rovněž je zřejmé, že koncept čeledi Acrospiriferidae je těžko udržitelný na základě její současné definice.

Explanation of plates

Plate I

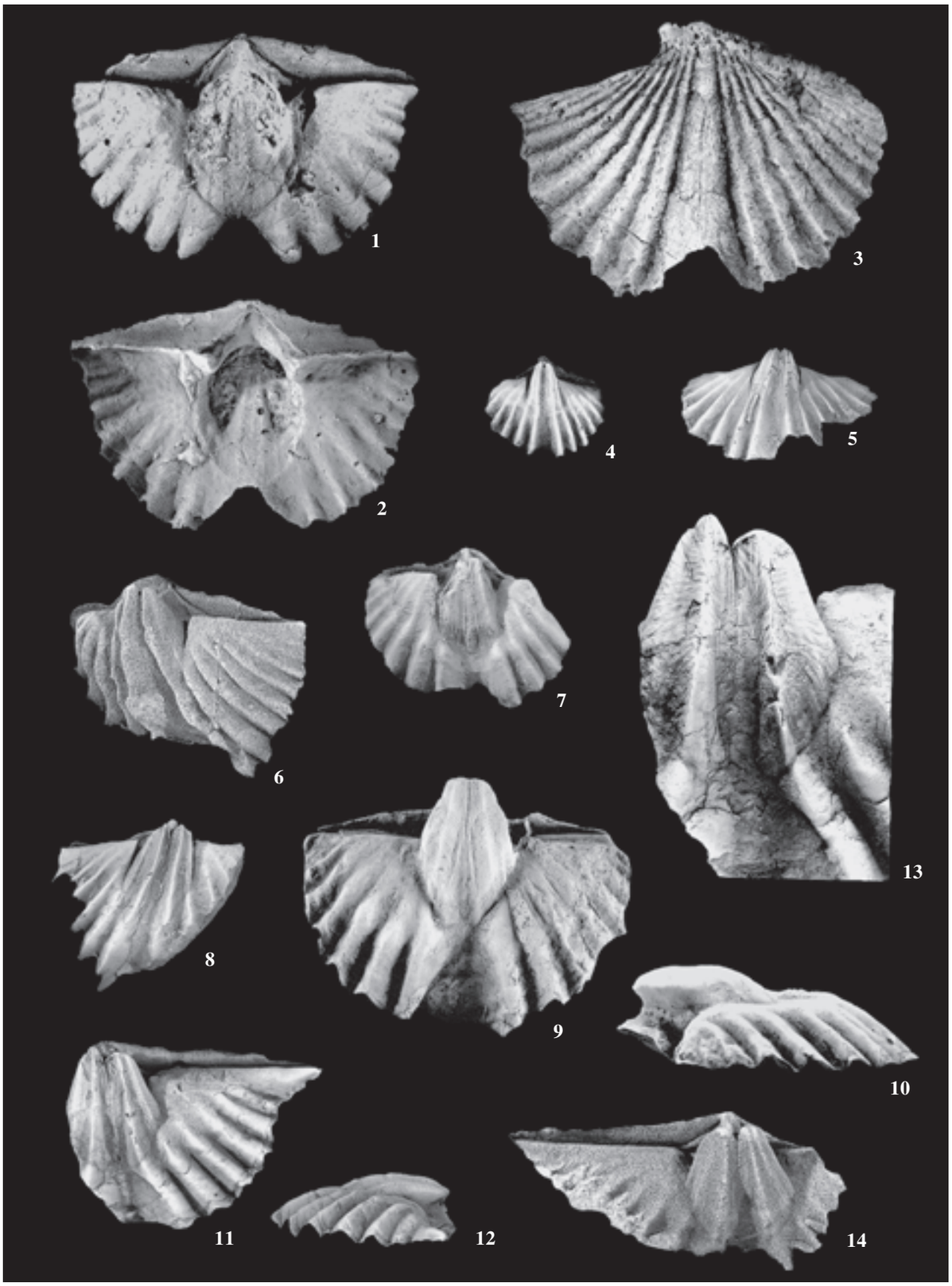
1–3 – *Acrospirifer primaevus* (Steininger, 1853). Lectotype, ventral valve internal and external moulds, latex cast of internal mould, specimen SMF 19236a–b. Locality: Herdorf, Siegerland area, Rheinisches Schiefergebirge. (? Upper) Siegen Formation, (? Upper Siegenian):
1 – ventral valve internal mould, gypsoplast of the original specimen, x1.
2 – latex cast of ventral valve internal mould, x1.
3 – ventral valve external mould, gypsoplast, x1.
4 – Ventral valve internal mould, juvenile specimen SMF 65890. Locality: Seifen, Westerwald area, Rheinisches Schiefergebirge. Seifen Formation, Middle Siegenian; x1.
5 – Ventral valve internal mould, specimen SMF XV1676d. Locality: Mühlmerich near Eichen, Westerwald area. Seifen Formation, Middle Siegenian; x1.
6 – Ventral valve internal mould, specimen SMF 65876. Locality: Leingipfel, Taunus Hills, southern Rheinisches Schiefergebirge. Upper Taunusquarzit Formation, Middle or Upper Siegenian; x1.
7 – Ventral valve internal mould, specimen SMF XVII 398m. Locality: Weiersbach mill, Eifel Hills. Saxler Formation, Upper Siegenian; x1.
8 – Ventral valve internal mould, specimen SMF 65096a. Locality: Seifen, Westerwald area. Seifen Formation, Middle Siegenian; x1.
9–10 – Ventral valve internal mould, specimen SMF 65368. Locality: Etzbach/Sieg. Middle or Upper Siegen Formation, Middle or Upper Siegenian:
9 – ventral view, x1.
10 – lateral view, x1.
11–13 – Ventral valve internal mould, specimen SMF 59870. Locality: Etzbach/Sieg. Middle or Upper Siegen Formation, Middle or Upper Siegenian:
11 – ventral view, x1.
12 – lateral view, x1.
13 – muscle field with fine striations, x2.1.
14 – Ventral valve internal mould, specimen SMF 65875. Locality: Leingipfel, Taunus Hills, southern Rheinisches Schiefergebirge. Upper Taunusquarzit Formation, Middle or Upper Siegenian; x1.

Plate II

Acrospirifer primaevus (Steininger, 1853)
1–8 – Dorsal valve internal mould and latex cast of it, specimen SMF 65868. Locality: Seifen, Westerwald area. Seifen Formation, Middle Siegenian:
1 – dorsal view of internal mould, x1.
2 – anterior view of internal mould, x1.
3 – posterior view of internal mould, x1.
4 – latex cast, x1.
5 – lateral view of internal mould, x1; 6. oblique view of internal mould, note median process and strongly developed notothyrial platform, x2;
7 – posterior view of internal mould, note median process, ctenophoridium, and dental sockets, x3.1.
8 – oblique view of latex cast showing cardinalia, note inner socket ridges and notothyrial platform, x2.6.
9 – Dorsal valve internal mould, specimen SMF 59874b. Locality: Seifen, Westerwald area. Seifen Formation, Middle Siegenian; x1.
10–12 – Dorsal valve internal mould, specimen SMF XVII 398a. Locality: Mühlmerich, Westerwald area. Seifen Formation, Middle Siegenian:
10 – lateral view, x1.
11 – anterior view, x1.
12 – dorsal view, x1.

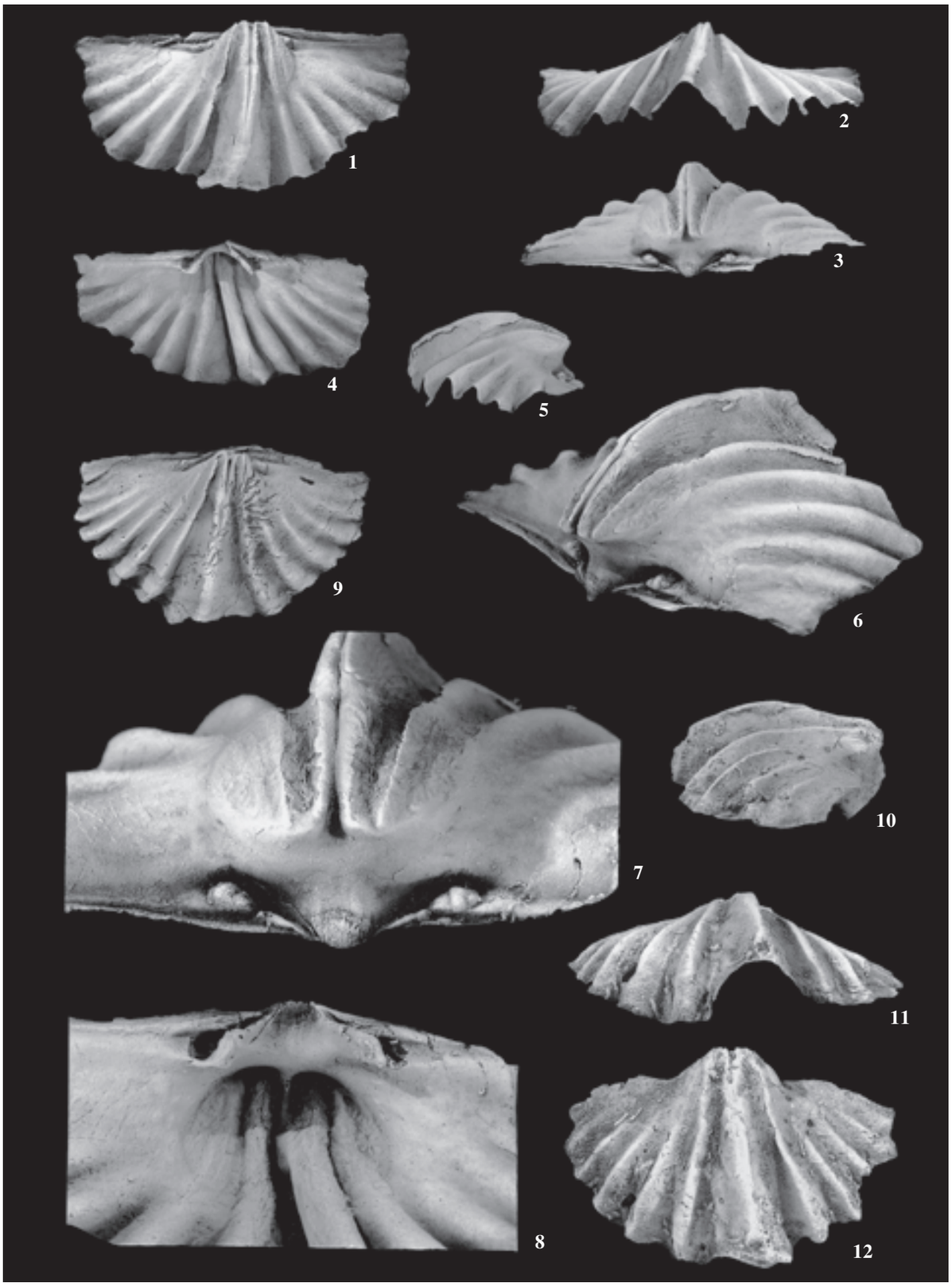
Plate III

Acrospirifer primaevus (Steininger, 1853)
1–7 – Dorsal valve external mould and latex cast of it, specimen SMF 59874a. The external mould belongs to the internal mould figured on Pl. 2, Fig. 9. Locality: Seifen, Westerwald area. Seifen Formation, Middle Siegenian:
1 – external mould, overview, x2.5.
2 – external mould, detailed view showing minute holes left by micro-spines, x19.
3 – latex cast showing rows of micro-spines, anterior region of fold, x12.
4 – latex cast, anterior region of fold, x5.4.
5 – latex cast, detailed view of fourth plication clearly exhibiting rows of micro-spines, x25.
6 – latex cast, detailed view of interspace between third and fourth plication, several projecting micro-spines, some of them are broken off, x44.
7 – latex cast, overview, x5.1.



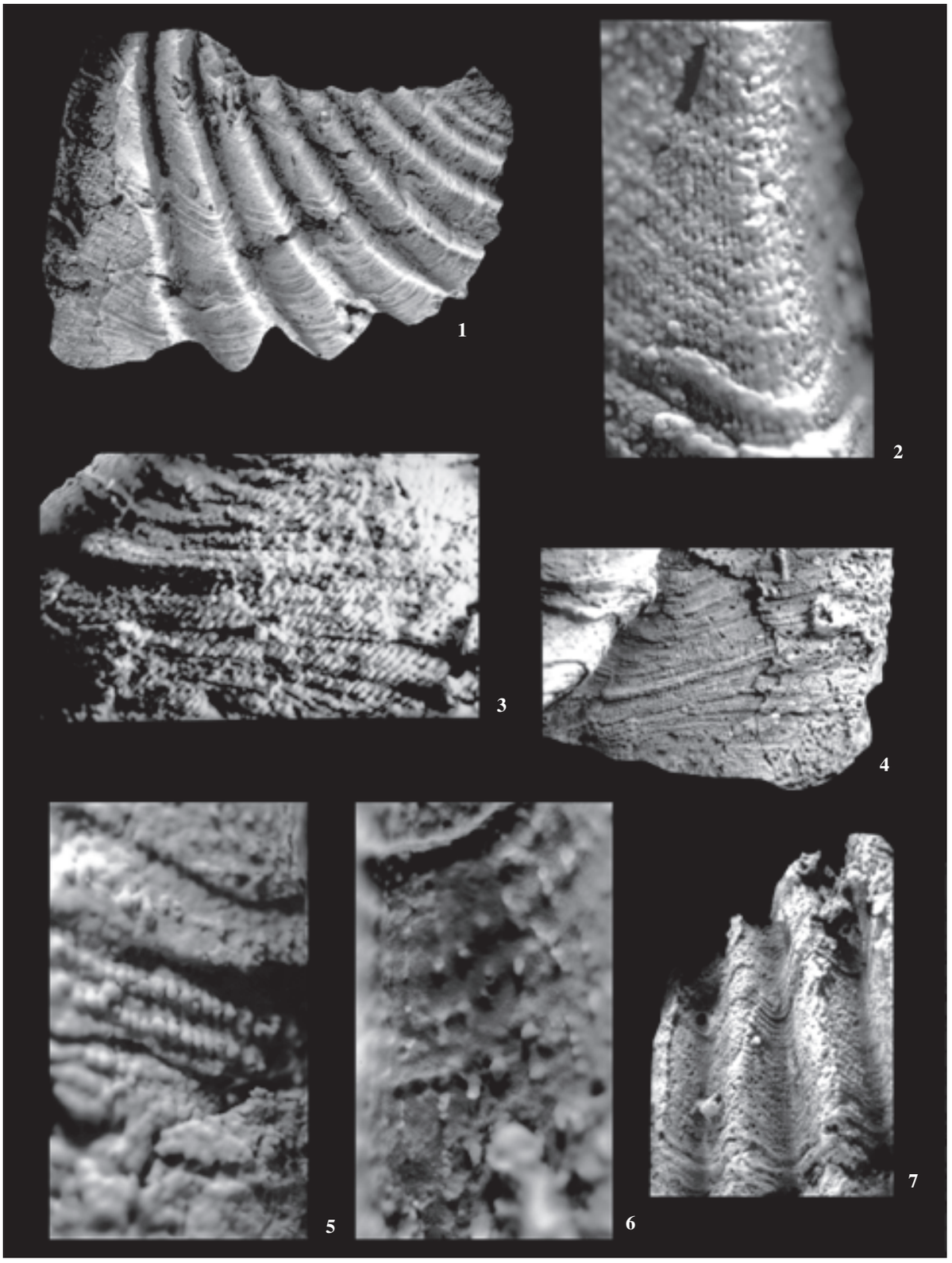
For explanation see p. 141

U. Jansen: On the genus *Acrospirifer* Helmbrecht et Wedekind, 1923 (Brachiopoda, Lower Devonian) (Pl. II)



For explanation see p. 141

U. Jansen: On the genus *Acrospirifer* Helmbrecht et Wedekind, 1923 (Brachiopoda, Lower Devonian) (Pl. III)



For explanation see p. 141