| Rivista Italiana di Paleontologia e Stratigrafia | volume 117 | no. 1 | pp. 3-13 | April 2011 |
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# A NEW SPECIES OF *CYRTOSPIRIFER* (BRACHIOPODA) FROM THE MIDDLE DEVONIAN OF THE WESTERN SAHARA (NORTHWESTERN AFRICA)

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*Received: December 10, 2010; accepted: February 23, 2011*

*Key words*: *Cyrtospirifer*, Brachiopoda, phylogeny, palaeobiogeography, Givetian, Devonian, Western Sahara.

*Abstract*. A new species of *Cyrtospirifer* is described from the Middle to Upper Givetian of the Western Sahara (Northwest Africa). *Cyrtospirifer tindoufensis* n. sp. differs in its smaller number and coarser medial and flank plications and equibiconvex shell profile from the other Givetian species of *Cyrtospirifer* that all occur in Europe and to which the new species probably gives rise. The new implications of the proposed phylogeny of the earliest cyrtospiriferids and their origin from the Western Sahara are discussed. The palaeogeographic distribution of the cyrtospiriferids during the Givetian and Frasnian is shown and its migration ways are described considering the global transgression and regression cycles.

*Riassunto*. In questo lavoro viene descritta una nuova specie appartenente al genere *Cyrtospirifer* proveniente dal Givetiano medio-superiore del Sahara occidentale (Africa nord-occidentale). *Cyrtospirifer tindoufensis* n. sp. differisce dalle specie europee del genere *Cyrtospirifer*, alle quali ha dato origine, per il profilo equi-biconvesso e per il numero minore di plicae mediane e sui fianchi, le quali risultano inoltre più robuste. Vengono inoltre discusse le implicazioni della filogenesi proposta per i cyrtospiriferidi più antichi e la loro possibile origine nel Sahara occidentale. Vengono infine descritti la distribuzione paleogeografica dei cyrtospiriferidi durante il Givetiano e il Frasniano e i possibili modelli di migrazione tenendo conto dei cicli trasgressivi e regressivi globali.

## Introduction

Taxa attributed to the genus *Cyrtospirifer* Nalivkin in Fredericks, 1924 have been studied since the 19th century (e.g, Murchison 1840; Quenstedt 1871; Gosselet 1894) and are used as important index fossils for the Upper Devonian due to their distinctive morphology and global pan-tropical distribution. As a result, almost every Upper Devonian spiriferid with fine medial plications historically has been assigned to *Cyrtospirifer*. However, the oldest species of *Cyrtospirifer* first evolved by the mid-to-late Givetian (upper Middle Devonian) (e.g., Paeckelmann 1942; Brice et al. 1976, 1979; Brice 1982, 1988, 2003). In recent studies focused on revisions to key cyrtospiriferids Ma & Day (1999, 2000, 2003, 2007) and Ma *et al.* (2003) revised *Cyrtospirifer.* In their 2003 revision of *Cyrtospirifer* they highlighted the fact that historically *Cyrtospirifer* has been used as a taxonomic garbage can for Upper Devonian *Cyrtospirifer*-like taxa resulting in assignment of what have been demonstrated to be distinct genera and species (see examples cited by Gratsianova et al. 1989; Ma & Day 2003). Ma & Day (2003: 270) proposed an evolutionary tree for the early cyrtospiriferids of the Givetian and Frasnian. However, the oldest species shown in their tree is probably younger than the new species from North Africa described in this work, according to brachiopod data (Schemm-Gregory & Jansen 2005). The primitive morphologic characters of *C. tindoufensis*, such as coarse and few plications, help to fill in the record on the earliest-oldest known genuine species of *Cyrtospirifer* in the *Tenticospirifer-Cyrtospirifer* evolutionary lineage proposed by Ma & Day (2000).

## Geological setting

During field sampling conducted as part of the German-Moroccan co-operation "Genesis of Devonian Reefs" new specimens of cyrtospiriferid brachiopods were collected from Givetian-age carbonate

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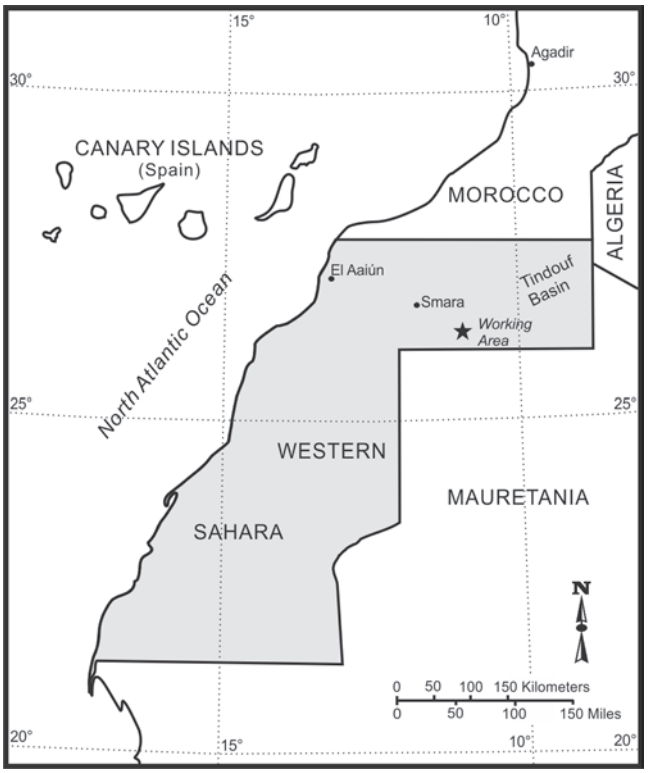


Fig. 1 - Map of the Western Sahara region of Northwest Africa showing location of the study area.

and clastic rocks on the southeastern flank of the Tindouf Syncline close to the military town of Smara in the Western Sahara (Northwest Africa) (Fig. 1). The Middle Devonian beds in the study area are dominated by sandstones, siltstones, and shales; thin beds of limestones and associated bioherms and biostromes occur at several levels. The homoclinal structure of this area, the lack of vegetation, and the removal of the surrounding shale created unique exposures revealing the structure of reefs and associated off-reef sedimentary successions. Between 1930 and 1950 Spanish and French geologists started to examine the Western Sahara for the purposes of petroleum exploration after the Second World War (for example Jacquet 1936; Hernández-Pacheco et al. 1949). Dumestre & Illing (1967) described the development of Middle Devonian reefs of this region and compared them with reefs of equivalent age in the Rainbow area of northwestern Alberta (Canada). The study area itself lacks a modern geological and paleontological study, thus the lithology is still undescribed and strata lack formation names. However, correlation with Western European and North African strata based on faunal content is possible and biostratigraphical assignment are done with different fossil groups. In the recent years, a few studies of the bryozoan and stromatoporid faunas have been started (Scholz et al. 2005; Königshof & Kershaw 2006). The brachiopod faunas recovered from the study area indicates correlation of the reefs to the Middle-Upper Givetian (upper Middle Devonian) and Lower Frasnian (lower Upper Devonian) (Schemm-Gregory & Jansen 2005). Conodont samples did not give sufficient data for stratigraphic assignment (P. Königshof, pers. comm. 2010). Recent palaeobiogeographic studies on the genus *Paracrothyris* (Wu in Wang et al. 1974) discuss the global faunal exchange between Nevada (western USA), South China, and the Western Sahara during this time interval (Schemm-Gregory & Jansen 2008).

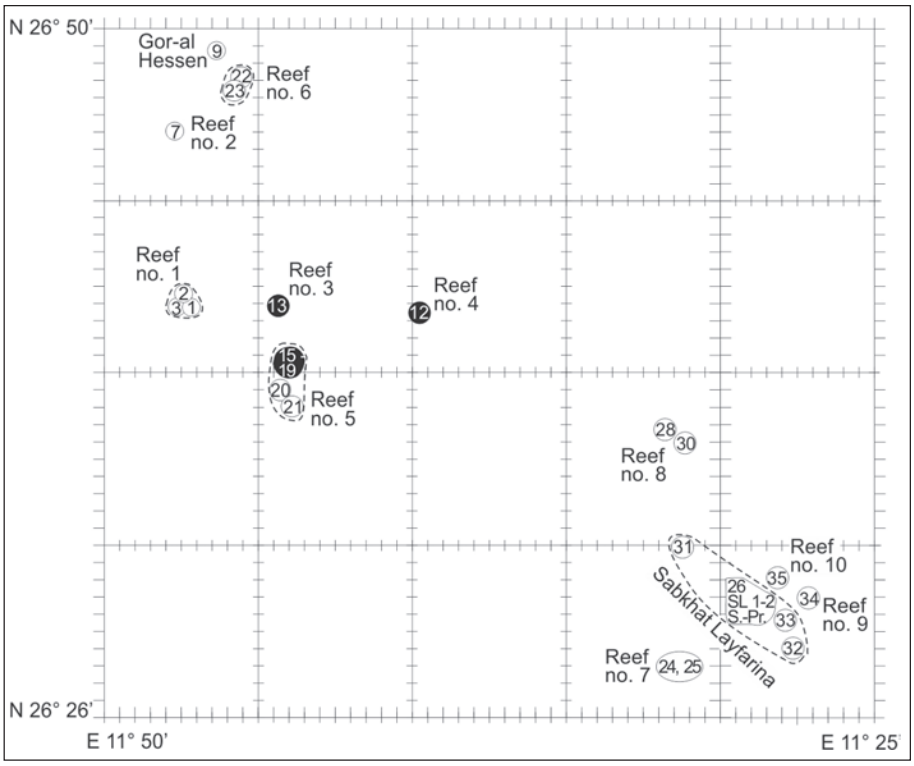


Fig. 2 - Geographical grit showing locations of fossil localities plotted.

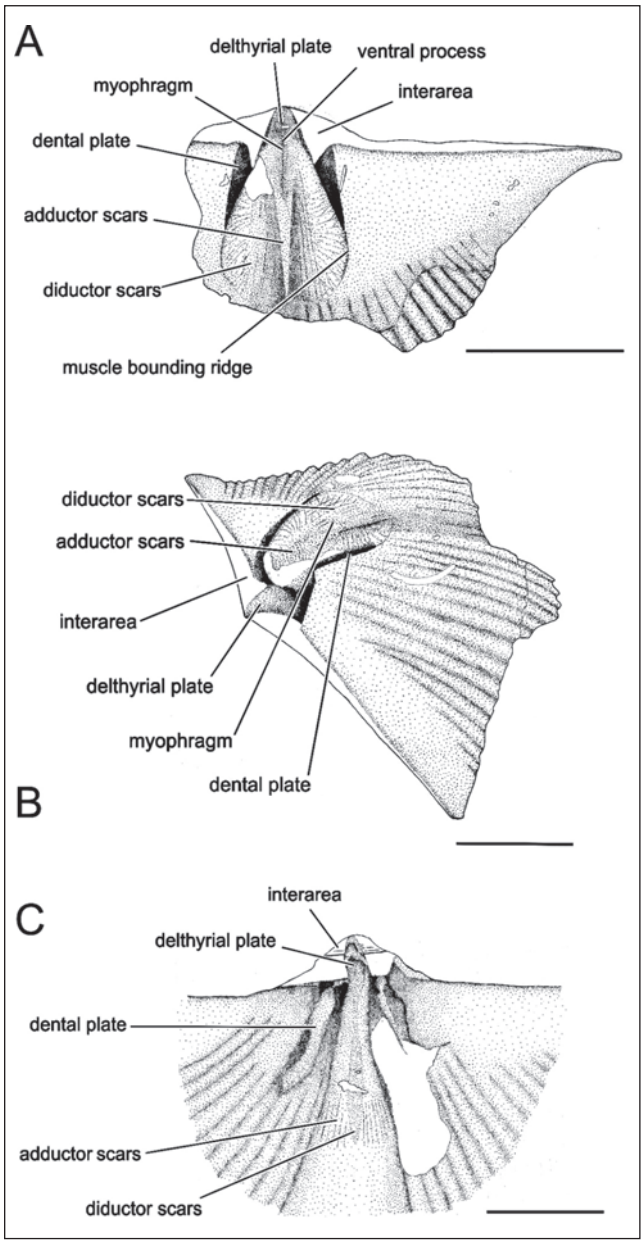


Fig. 3 - Morphological terms of internal ventral mould of *Cyrtospirifer tindoufensis*; A: SMF 66595b, ventral view. B: SMF 66081a, posterolateral view. C: SMF 66081c, holotype, plan view on latex cast. Scale bar =10 mm.

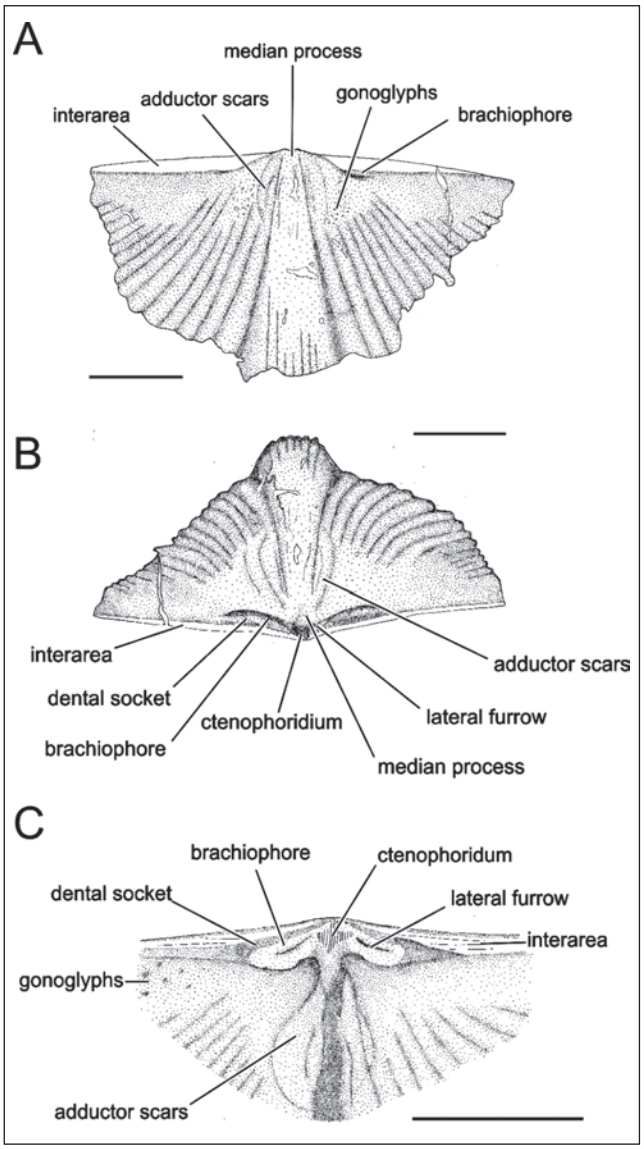


Fig. 4 - Morphological terms of internal dorsal mould of *Cyrtospirifer tindoufensis*, SMF 66081b; A: dorsal view. B: oblique posterior view. C: plan view of latex cast. Scale bar= 10 mm.

The studied outcrops form a belt in a northwest-southeast direction consisting of bioherms of different sizes. In previous works, the largest of the studied reefs was named "Sabkhat Lafayrina" situated in the SE, a smaller one "Gor-al Hessen" is located in the NW of the study area (Königshof et al. 2003). The other reefs are numbered 1 to 10 (Fig. 2). *Cyrtospirifer tindoufensis* was found in proximal off-reef strata near the reefs and, in rare cases, within reefs themselves.

## Material and methods

Specimens of *Cyrtospirifer* described herein are usually preserved as disarticulated internal and external moulds (Figs. 3A, B, 4 A, B). Articulated shells and rare isolated shells were also recovered. Because of weathering the shell material is poorly preserved and not well suited for taxonomic studies. Latex casts of internal and external moulds were made to study the internal features of the new taxon (Figs. 3C, 4C) as well as the micro-ornamentation (Fig. 5). Due to the extraordinary preservation of internal molds, serial sections of articulated specimens were omitted. Measurements were taken with a digital caliper and rounded to 0.1 mm. Drawings were made with the help of a camera lucida. Specimens were coated with magnesium oxide prior to being photographed.

**Institutional abbreviations**

SMF: Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany.

## Systematic palaeontology

Order **Spiriferida** Waagen, 1883

Suborder **Spiriferidina** Waagen, 1883

## Superfamily Cyrtospiriferoidea Termier & Termier, 1949

## Family Cyrtospiriferidae Termier & Termier, 1949

## Subfamily Cyrtospiriferinae Termier & Termier, 1949

## *Cyrtospirifer* Nalivkin in Fredericks, 1924

Type species: *Spirifer verneuili* Murchison, 1840: 252, pl. 2, figs. 3a-e.

**Diagnosis:** Medium to large-sized cyrtospiriferids with well developed delthyrial plate, plate thickened to various degrees, ventral interarea low-concave to high-straight; delthyrium wide, sometimes with pseudodeltidium in the upper third of the delthyrium; with micro-ornamentation (where preserved) of minute pustules in grooves and on plications: 8 to 30 sinal plications differentiated into a medial and two lateral regions; dental plates well developed. [After Ma & Day (2003)].

**Discussion.** This study shows that the diagnosis of *Cyrtospirifer* has to be emended to include shell features observed in the new material enhanced by the number of sinal plications, it decreases in *C. tindoufensis* n. sp. and increases in *C. syringothyriformis*. The ventral interarea may also be catacline and flat. However, a revision of *Cyrtospirifer* is far beyond the scope of this work.

**Stratigraphic distribution.** Middle Givetian to Lower Famennian (upper Middle Devonian to lower Upper Devonian).

**Geographic distribution.** Cosmopolitan.

### **Cyrtospirifer tindoufensis** n. sp.

Figs 3-7, Tab. 1

**Holotype:** Internal mould of ventral valve, stored in the Senckenberg Forschungsinstitut und Naturmuseum under the inventory number SMF 66081c (Figs. 6.1A-C, 9). Length 23.5 mm and width 41.5 mm.

**Derivation of name:** After the Tindouf syncline on which SE flank the type locality is situated.

**Type locality:** Reef No. 4 (N 26° 41,636, W 11° 39,904‘), Western Sahara (Northwest Africa).

**Type horizon:** Beds of upper Givetian (upper Middle Devonian).

**Stratigraphical distribution:** Middle Givetian to ?Lower Frasnian (upper Middle Devonian to ?lower Lower Devonian).

**Geographic distribution:** Tindouf Syncline, Western Sahara (Northwest Africa).

**Material:** *Reef No. 4:* Loc. 12 (N 26° 41.636‘, W 11° 39.904): 4 ventral internal moulds (SMF 66081a, c holotype, d, e); 1 dorsal internal mould (SMF 66081b); few single dorsal and ventral internal moulds (un-numbered). Loc. 13 (N 26° 41.646‘, W 11° 44.120‘): 2 ventral external moulds (SMF 666595a, b); 5 ventral internal moulds (SMF 66603, 66605a-c); 1 dorsal exfoliated shell (SMF 66604); 1 dorsal external mould (SMF 66607); few single dorsal and ventral internal moulds. *Reef No. 5:* Loc. 15 (N 26° 40.397‘, W 11° 44.028‘): numerous single dorsal and ventral external moulds. Loc. 16 (N 26° 40.229‘, W 11° 44.027‘): 2 ventral external moulds (SMF 66083, 66598); 4 ventral internal moulds (SMF 66594, 66596b, 66600, 66601); 1 dorsal external mould (SMF 66597); 1 dorsal internal mould (SMF 66596a); 1 articulated internal mould (SMF 66606); numerous single dorsal and ventral external moulds (un-numbered). Loc. 17 (N 26° 40.221‘, W 11° 44.090‘): numerous single dorsal and ventral external moulds (un-numbered). Loc. 18 (N 26° 40.216‘, W 11° 44.104‘): 1 exfoliated dorsal shell (SMF 66602); numerous single dorsal and ventral external valves (un-numbered).

**Remarks:** The locality numbers refer to the expedition locality numbers. Further details may be obtained by the curator of the brachiopod collection of the Senckenberg Forschungsinstitut und Naturmuseum.

**Diagnosis:** *Cyrtospirifer* with medium-sized shell and an equibiconvex to ventribiconvex profile. Megathyrid, in rare cases brachythyrid outline. Dental plates extrasinal, 8 to 12 plications in the sulcus.

| | ***C. tindoufensis*** n. sp. | ***C. verneuili*** (Murchisoni, 1840) | ***C. verneuiliformis*** (Paeckelmann, 1942) | ***C. syringothyriformis*** (Paeckelmann, 1942) |
|---|---|---|---|---|
| **Size** | medium to large | medium to large | medium to large | large |
| **Outline** | megathyrid to brachythyrid | megathyrid | megathyrid | strongly megathyrid |
| **Curvature in longitudinal section** | equibiconvex to ventribiconvex | ventribiconvex | ventribiconvex | dorsibiconvex |
| **Ventral interarea** | moderately high apsacline to catacline curved | moderately high apsacline to catacline curved | high catacline sometimes curved | high catacline straight |
| **Dental plates** | extrasinal | extrasinal | extrasinal | intrasinal |
| **Sulcus and fold in cross section** | flattened to rounded | flattened | rounded | rounded posterior, flattened anterior |
| **Number of plications in sulcus** | 8-12 | 14-20 | 15-20 | 20-30 |
| **Cardinal extremities** | convex | convex | ? | convex and laterally flat |
| **Bifurcation of plications on flanks** | - | - | + | - |
| **Fold** | strongly elevated | strongly elevated | hardly elevated | moderately elevated |
| **Crural plates** | + | + | ? | - |
| **Stratigraphic distribution** | Upper Givetian | Upper Givetian | Upper Givetian to Frasnian | Upper Givetian to Frasnian |

Tab. 1 - Comparison of species of *Cyrtospirifer* Nalivkin in Fredericks, 1924 occurring in the Givetian of Western Europe and North Africa.

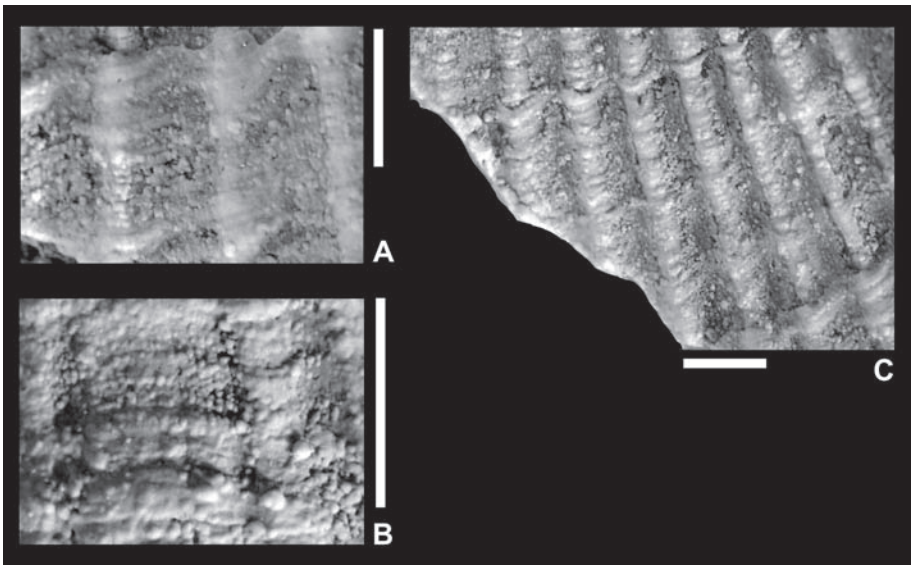


Fig. 5 - Latex cast of external ventral mould showing the micro-ornamentation of *Cyrtospirifer tindoufensis*, SMF 66083; A: dorsal view. B: oblique posterior view. C: plan view of latex cast. Scale bar 10 mm.

**Description of the holotype (SMF 66081c)**

*Form and size*

The ventral internal mould is transverse, semielliptic in outline, and megathyrid with small mucronations. The specimen is convex in longitudinal section.

*Exterior of ventral valve*

The ventral umbo extends to posterior over the hinge line. The ventral interarea is high, apsacline, and curved. The delthyrium is open. Deltidial lamellae very fine.

*Interior of ventral valve*

Ventral muscle field extends to posterior over the hinge line. Lateral apical cavities reaching almost to the posterior end of the muscle field. Hardly any shell material developed in apical region. A small and narrow delthyrial plate is posterior to the ventral muscle field from which it is separated by a noticeable constriction on the internal mould. Ventral process small and broad leaving a distinct groove on the internal mould at the posterior end of the muscle field. The myophragm is very thin, almost not recognisable leaving a very fine furrow through the whole ventral muscle field on the internal mould. The muscle field is elongated, pyriform in outline, and not impressed into floor of valve. Diductor scars are impressed as subradial striae in the centre and as longitudinal striae in the anterior part of the muscle field on the internal mould. Adductor scars elongated, thin, situated admedially to the myophragm, and enclosed completely by the diductor field; posterior and anterior pair of adductors gently impressed into shell. Free portions of dental plates short, leaving small slits on either side of the posterior half of the ventral muscle field on the internal mould. Gonoglyphs are not preserved. Sulcus deep, with steep flanks, and rounded in cross section. Impressions of 10 simple and fine plications are countable in the sulcus. Impressions of 18 plications on each flank are preserved, their expression diminishes towards the lateral margins. Plications are separated by narrower furrows; furrows and plications are rounded in cross section. Impressions of growth lamellae faintly preserved in the anterior half of the internal mould.

**Description of paratypes**

*Form and size*

Shells medium-sized and wider than long. Ventribiconvex profile and semicircular to semielliptic in outline. Megathyrid, in rare cases brachythyrid, with small, thin, and convex mucronations that are rarely preserved with their lateral terminations on the internal moulds. Maximum width 51.6 mm, maximum length 25.0 mm.

*Exterior of ventral valve*

Ventral interarea apsacline to catacline, in the upper part curved with transverse growth lamellae. Delthyrium open, restricted by a pair of fine deltidial lamellae. Sulcus conspicuous, moderately broad, with steep flanks, and weakly rounded to flat at the bottom.

*Exterior of dorsal valve*

Interarea lower than ventral one and anacline to orthocline. Notothyrium open. Fold strongly elevated, conspicuous, with steep flanks, and weakly rounded to flat on top.

*Macro-ornamentation*

Flanks, sulcus, and fold are covered by fine plications that are rounded in cross section and separated by narrower furrows. Plications in the sulcus and on fold bifurcate close to the anterior margin. Eight medial plications present in the sulcus, 7 on the fold before bifurcation on the external mould, increasing through bifurcation towards the anterior margin to 12 plications in the sulcus and 11 on the fold; up to 26 flank plications on the largest paratype; on the external dorsal mould are 2 plications less.

*Micro-ornamentation*

Micro-ornamentation fimbriate, with a single row of pustules at the edge of each growth lamellae (Fig. 5).

*Interior of ventral valve*

Fillings of the umbo and the lateral apical cavities extend posterior over the hinge line. Lateral cavities open. A distinct delthyrial plate is developed that is separated by a profound indentation from the ventral muscle field (Figs. 3A, B; 6.3, 4A-D). Ventral muscle field longer than wide, pyriform to subrhombic in outline and not, in some specimens weakly, embedded into shell material (Figs. 3B; 6.1A, 3, 4A, C). A small ventral process leaves a short groove on the internal

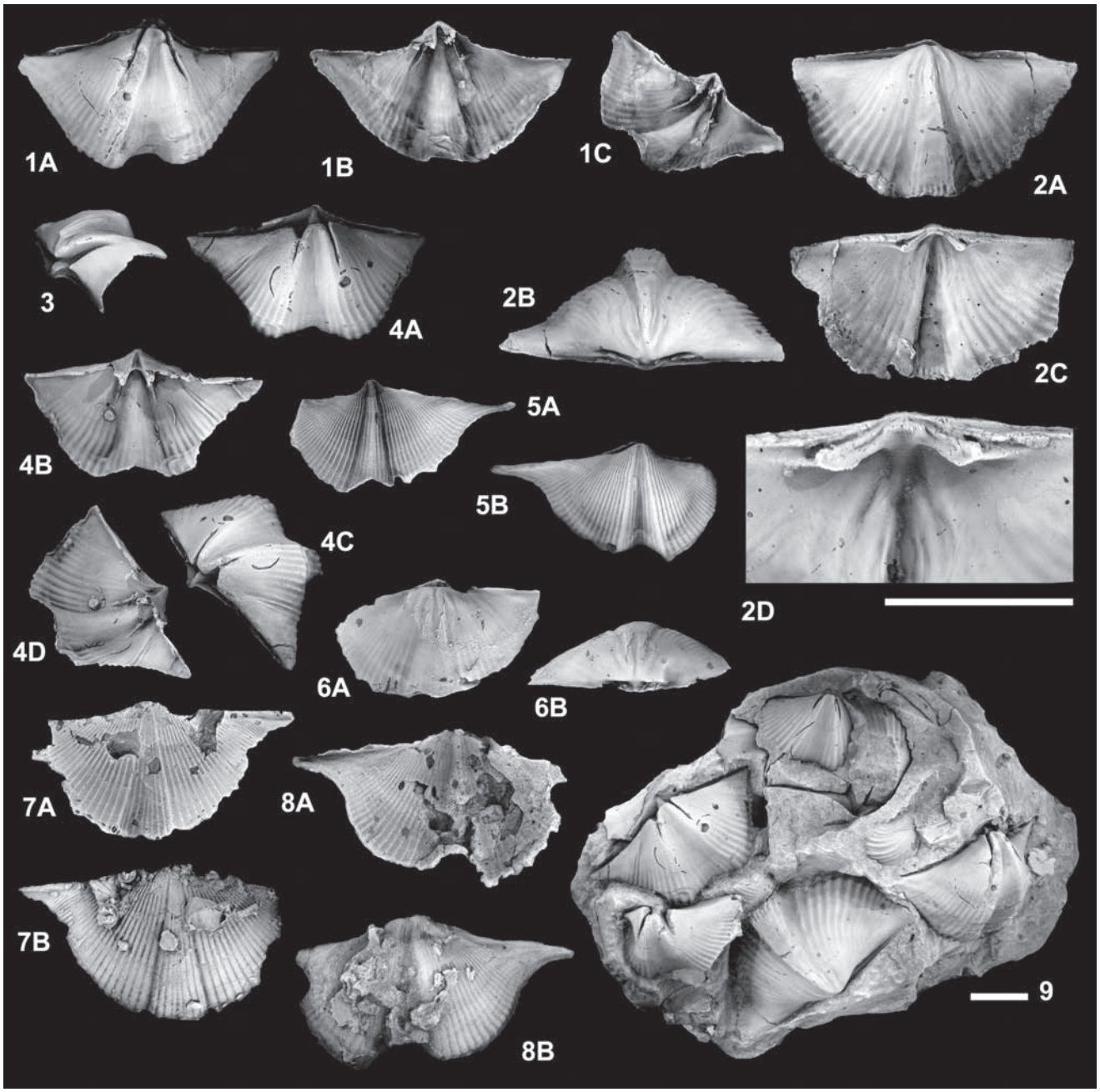


Fig. 6 - 1-9 - *Cyrtospirifer tindoufensis* sp. nov. All figures x 1.0, if no other indication. Stratum: Upper Givetian (upper Middle Devonian). Leg. U. Jansen 2002.

1 - SMF 66081c, holotype. Locality: 12. Ventral view of internal mould (A). Latex cast of ventral internal mould, upper (B) and oblique posterior (C) views of ventral interior. 2 - SMF 66081b. Locality: 12. Dorsal internal mould, dorsal (A) and oblique posterior (B) views. Latex cast of dorsal internal mould, upper view of dorsal interior (C) and cardinalia (D). Scale bar 10 mm. 3 - SMF 66594. Locality: 16. Ventral internal mould, oblique posterolateral view. 4 - SMF 66081a. Collecting locality: Loc. 12. Ventral internal mould, ventral (A) and oblique posterolateral (C) views. Latex cast of ventral internal mould, upper (B) and oblique posterolateral (D) views of ventral interior. 5 - SMF 66595a. Locality: 15. Upper view of ventral external mould (A) and latex cast (B). 6 - SMF 66596a. Locality: 16. Upper (A) and posterior (B) views on dorsal internal mould. 7 - SMF 66597. Locality: 16. Upper views on dorsal external mould (A) and latex cast (B). 8 - SMF 66598. Locality: 16. Upper views of ventral external mould (A) and latex cast (B). 9 - SMF 66081. Slab with holotype. Scale bar 10 mm.

mould. The ventral process gives rise to a low and thin myophragm, extending anterior of the muscle field expressed as a fine furrow on the internal mould. Flanking the myophragm are the thin and elongated adductor scars that are weakly embedded into the shell. The diductor scars enclose the adductors and are preserved as radial striae in the centre of the muscle field and as longitudinal striae at the anterior margin of the muscle field (Fig. 6.1A, B). Anterior margin of the muscle field inconspicuous, except in rare cases when a fine muscle bounding ridge leaves a very thin furrow on the internal mould. Dental plates extrasinal or positioned at sinal border, short to moderately long and thin, in adult specimens sometimes wedge-like. They enclose or bound the first half to two thirds of the lateral border of the ventral muscle field. External macro-ornamentation weakly impressed on the internal mould anterior of the ventral muscle field. Bifurcation of plications in sulcus or in fold normally not visible on floor of valve. Internal expression of plications diminishes towards the lateral margins. Weak impressions of growth lamellae at the anterior margin.

*Interior of dorsal valve*

Dorsal umbo extends slightly posterior of the hinge line. Ctenophoridium pointed at posterior widens anteriorly, situated perpendicular to the commissural plane beneath the dorsal muscle field, up to 24 lamellae are visible, the number of lamellae varies with the state of preservation. Notothyrial shelf usually lacking, sometimes indicated. Ctenophoridium bordered laterally by two very thin furrows expressed as a short ridge on either side on the internal mould (Figs. 4; 6.2A). Dental sockets short, cone-shaped, rounded in cross section, and pointing in apical direction. Brachiophores relatively thick and curved over the dental sockets (Fig. 6.2B-D). Crural bases (*sensu* Ma & Day 2003: 273, referring to rudimentary crural plate and crural base) are preserved as small indentions above the ctenophoridium. Dorsal muscle field elongate, lentiform in outline, and indented at its posterior margin by a small dorsal median process, giving rise to a thin myophragm bisecting the adductor field. Adductor scars extend laterally and are slightly impressed on the shell floor of the flanks. The posterior half is bordered by a low ridge expressed as a small furrow on the internal mould that diminishes anteriorly (Fig. 6.2A, B). Lateral of the muscle field a few widely spaced gonoglyphs are preserved as low-elongate bulges on the internal mould oriented almost parallel to hinge line. Fold moderately broad, strongly elevated, and rounded in cross section with steep flanks and flattened on top. Impressions of plications are preserved anterior of the dorsal muscle field. Medial plications of fold finer than flank plications. Bifurcating plications on fold not visible on the internal mould. Impressions of growth lamellae at the anterior margin.

**Discussion.** *Cyrtospirifer tindoufensis* differs from other Givetian *Cyrtospirifer* species by its shell outline, curvature of its interarea, and number of plications in the sulcus. Table 1 shows the morphologic features of *C. tindoufensis* and other closely related Givetian cyrtospiriferid species. *Cyrtospirifer tindoufensis* has the lowest number sinal plications (ranging from 8 to 12), whereas *C. verneuili* (Murchison, 1840), (figured by Brice 1988: pl. 44, figs. 1-10; and Ma & Day 2003: figs. 6.1-14) has 14 to 20. *Cyrtospirifer verneuiliformis* (Paeckelmann, 1942, pl. 2, fig. 3) is similar to the latter species with 15 to 20 sinal plications and *C. syringothyriformis* (Packelmann, 1942) with 20 to 30 as illustrated in Brice (1988: pl. 44, figs. 11-13). Shell profiles of *C. tindoufensis* are equibiconvex to ventribiconvex, whereas most shells of *C. verneuili* and *C. verneuiliformis* are ventribiconvex in longitudinal section. *Cyrtospirifer syringothyriformis* is the only species with a dorsibiconvex shell profile in the middle-late Givetian. The new species and *C. syringothyriformis* both have intrasinal dental plates, in contrast to the other two species that have extrasinal dental plates. *Cyrtospirifer tindoufensis* and *C. verneuiliformis* are both characterised by convex cardinal extremities and a moderately high, catacline to apsacline, and concave ventral interareas. The ventral interareas of both *C. verneuiliformis* and *C. syringothyriformis* are high and catacline, and rarely concave. Only *C. syringothyriformis* shows concave cardinal extremities. The fold and sulcus of *C. syringothyriformis* and *C. verneuiliformis* are rounded in cross section, whereas in *C. verneuili* and *C. tindoufensis* they are flattened and rarely rounded. *Cyrtospirifer verneuiliformis* is the only taxon with bifurcating flank plications which are also the finest of the four species compared here. In the other three species, shell plications are only observed to bifurcate in the sulcus and on the fold. *Cyrtospirifer tindoufensis* has the coarsest plications. *Cyrtospirifer syringothyriformis* is the only species lacking crural plates, in the others, crural plates are distinctly developed. *Cyrtospirifer verneuili* and *C. syringothyriformis* both range into the Frasnian, whereas *C. tindoufensis* and *C. verneuiliformis* became extinct in the Givetian.

## Stratigraphic interpretation

The new faunas collected from the Western Sahara range in age from Middle Givetian in the SE to Early Frasnian in the NW (Schemm-Gregory & Jansen 2005). Correlations of the brachiopod fauna found with the Blacourt Formation in Ferques (Boulonnais, northern France), the Portilla Formation (Cantabrian Mountains, northern Spain), and the Hamilton Group (eastern USA) show that the *C. tindoufensis*-yielding

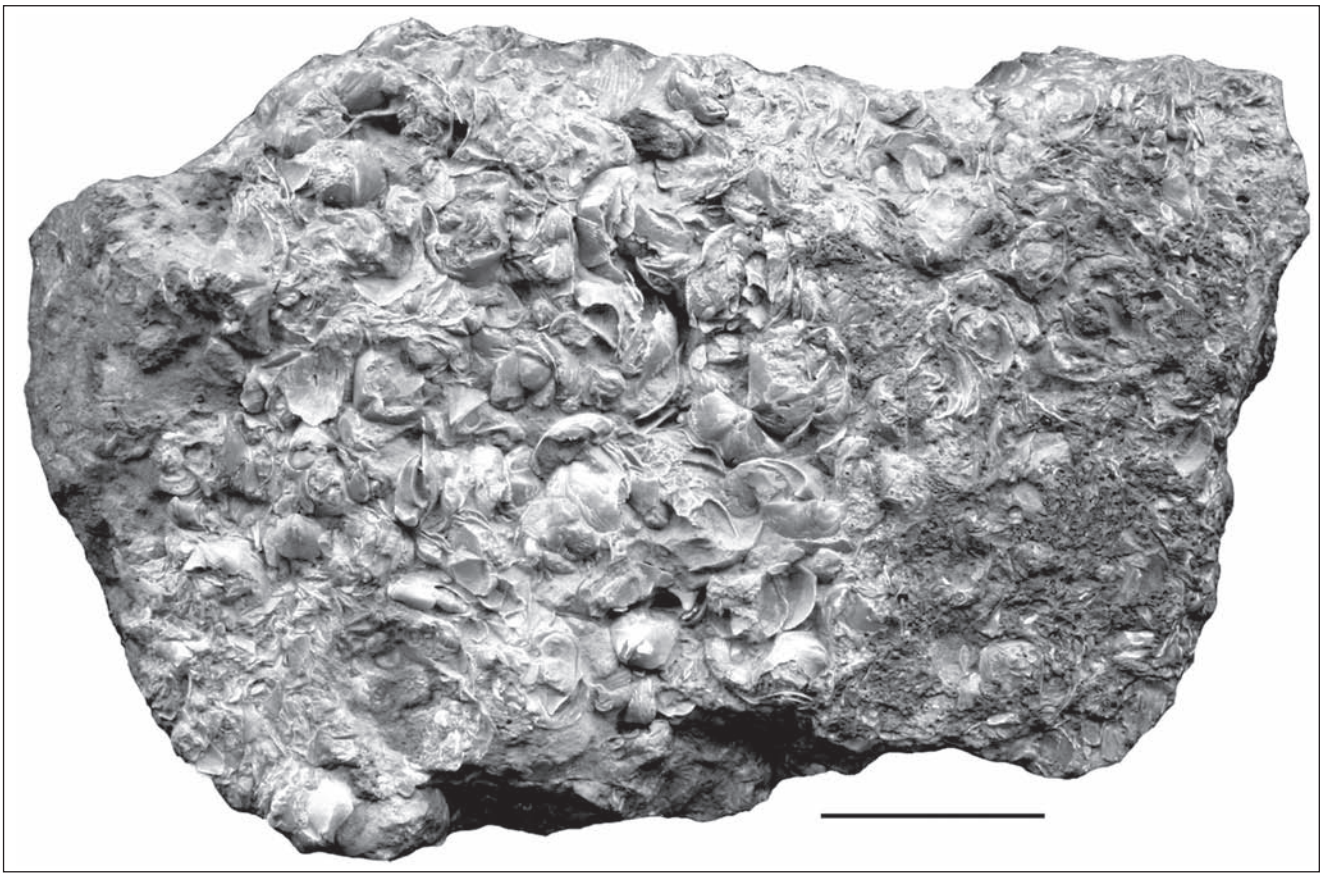

Fig. 7 - SMF 66599. Rock slab of *Cyrtospirifer tindoufensis* coquina. Scale bar=50 mm.

beds have a middle to late Givetian age but may reach to the lowermost Frasnian (unpublished data).

Low diversity coquina assemblages with *Cyrtospirifer tindoufensis* occur in either sandstones or limestones consisting almost entirely of shells of *C. tindoufensis* (Fig. 7). Other species found associated with *Cyrtospirifer* in the coquina shell beds include: *Meristina* sp., *Arcuaminetes* cf. *scitulites sensu* Racheboeuf (1981), *Xystostrophia* cf. *umbraculum* (von Schlotheim, 1820), ?*Adolfia* sp., *Schizophoria* sp., and *Desquamatia* sp. The occurrence of *Arcuaminetes* cf. *scitulites* and *Xystostrophia* cf. *umbraculum* suggest a Middle Givetian age. Other known deposits with *Arcuaminetes* cf. *scitulites sensu* Racheboeuf (1981) include the "calcareous limestones" in the Cantabrian Mountains (Spain) and the Kerbelec and the Lanvoy formations in the Armorican Massif (France) which are correlated with the *varcus* conodont zone (Middle Givetian) (Racheboeuf 1981). This form also resembles to *Arcuaminetes scitulites* (Cooper, 1945) from the North American Hamilton Group, however, this form is not suitable for refined correlation because of its long stratigraphic range. In North America it is reported from the late Eifelian of the Iowa and Michigan basins by Day & Koch (1994) and Koch & Day (1996) and the entire Givetian in the Appalachian Basin of eastern North America (Bizzarro 1995). The genera *Xystostrophia* Havlíček, 1965 and *Meristina* Hall, 1867 are restricted to the Givetian, but are not reported from the Frasnian. *Cyrtospirifer tindoufensis* occurs together with *Nalivkinaria issoumourensis* Drot, 1971 which is assigned to the Upper Givetian (P. Sartenaer, pers. com. 2004). In the northwest part of the study area *C. tindoufensis* was found close to beds of Early Frasnian age defined by the occurrence of *Douvillina dutertrei* (Murchison, 1840), however, the exact stratigraphic position of the *C. tindoufensis* in comparison to *D. dutertrei* is not clear so that the ongoing of *C. tindoufensis* into the Early Frasnian remains speculative.

### Early phylogeny of *Cyrtospirifer*

The new species contributes to the knowledge of the stratigraphic range and palaeogeographic occurrence of one of the oldest known (Middle Devonian) species of *Cyrtospirifer* to the early part of the phylogenetic tree of *Cyrtospirifer* proposed by Ma & Day (2003: fig. 2), however, the authors of that paper recommend a careful restudy of the Eurasian species attributed to *Cyrtospirifer* in the older literature. *Cyrtospirifer tindoufensis* new species displays primitive characters including its medium-sized equibiconvex shell, the small number of lateral and medial plica-

tions, the low apsacline ventral interarea, and flattened ventral sulcus and dorsal fold. Later in the phylogeny, shells of *Cyrtospirifer* become larger and the maximum width shifts to anterior to a megathyrid state. The shell profile tends to be either ventribiconvex or dorsibiconvex, and fold and sulcus are rounded in lateral cross section. Another trend is the increase in height of the ventral interarea and in the variation in its degree of curvature from apsacline and curved to catacline and straight. The majority of Frasnian *Cyrtospirifer* species known in Eurasia and western North America are alate, whereas the European and North African forms are still compact but record a trend towards enlargement of mucronate cardinal extremities.

Discussion of the origins of *Cyrtospirifer* from an older Middle Devonian species of *Tenticospirifer* Tien, 1938 (as revised by Ma & Day, 2000) requires the study of larger material of both genera but this is far beyond the scope of this work.

### Givetian-Frasnian palaeogeographic distribution of *Cyrtospirifer*

The occurrence of *C. tindoufensis* suggests that the initial endemic centre from which *Cyrtospirifer* dispersed from may have been the Middle Givetian shelf area of northern Gondwana (Northwest Africa) instead of Western Europe (France, Germany) as proposed by Ma & Day (2003). Because of their close palaeogeographic proximity, dispersal of *Cyrtospirifer* from northern Gondwana to Western Europe could have been easily accomplished (Jansen 2001; Schemm-Gregory 2008a, 2008b), supported by widespread occurrences of Frasnian species of *Cyrtospirifer* in France and other areas of western Eurasia. Descendants of *C. tindoufensis* such as *C. verneuili*, and *C. syringothyriformis* became widespread in the Early Frasnian in Eurasia and by the Middle Frasnian in western North America (Fig. 8). The known distribution of the oldest North American species of *Cyrtospirifer* indicates that the initial migration of members of two different species groups (see Ma and Day 2003) into western (Northwest Territories, Canada) and eastern North American (Appalachian Foreland Basin, New York) shelf areas took place during the initial major marine transgression of the Middle Frasnian Transgressive-Regressive (T-R) Cycle IIc of Johnson et al. (1985) during the *punctata* Zone. A second major North American migration into continental margin and epeiric carbonate platform habitats occurred during the Late Frasnian marine sea level rise of Devonian T-R cycle IId (Montagne Noire Zone 11 of Klapper, 1989). The late Frasnian migration from western Canada into most North American carbonate platforms is evidenced by occurrence of widespread species of *Cyrtospirifer* in the Great Basin (Idaho, Nevada, Utah), the southern Laurussian Ouchita continental margin (New Mexico), and epeiric carbonate platforms (Arizona, Iowa).

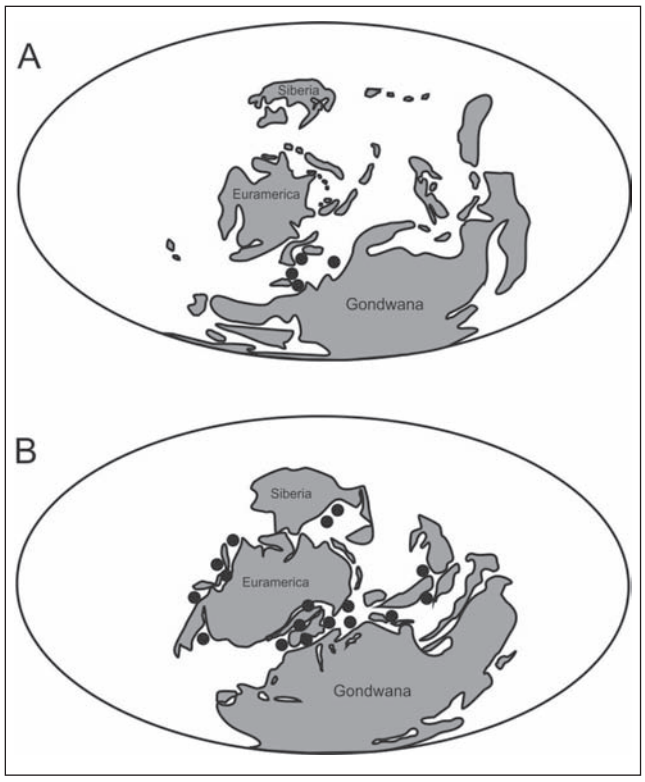


Fig. 8 - Palaeomaps showing the distribution of *Cyrtospirifer* plotted. A: Palaeogeography during the Givetian (Middle Devonian). B: Palaeogeography during the Frasnian (Late Devonian).

The faunal exchange between South China and Europe/North Africa began during the Late Emsian (late Early Devonian) as it is seen in delthyridoid spiriferids (Schemm-Gregory 2009). Evidence of later migrations includes the common occurrence of the terebratulid genus *Paracrothyris* in South China and the Western Sahara indicates a faunal connection between these two regions during Givetian time (Schemm-Gregory & Jansen 2008).

*Acknowledgements.* Special thanks go to Gerhard Plodowski for initiating this project, organising the expedition to the Western Sahara, and for fruitful discussions of the cyrtospiriferids. I am grateful to Ulrich Jansen for giving me access to the brachiopod collection. Many thanks are due to Juliane Eberhardt and Erika Schellerwagner for technical help, especially for preparing the latex casts. Peter Königshof, Eberhard Schindler, and Achim Wehrmann (all Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany) gave information on the studied reefs and their facies. I also thank Mike Reich for access to the brachiopod collection and Frank Langenstrassen (both Geowissenschaftliches Zentrum der Universität Göttingen, Museum, Germany) for discussing Middle Devonian brachiopods from Ferques, (Boulonnais, France). Jed Day (Illinois State University, Normal, USA) kindly improved the English of the manuscript and gave fruitful critics to an earlier version of the manuscript.

Lucia Angiolini (Università degli Studi di Milano, Italy) provided the Italian translation of the abstract.

The present study is part of the German-Moroccan co-operation programme "Genesis of Devonian Reefs" conducted by the following institutions: Senckenberg Forschungsinstitut und Naturmusem, Frankfurt am Main (Germany), Ministère de l'Energie et des Mines, Rabat (Morocco), Institut Scientifique, Département de Géologie, Rabat-Agdal (Morocco), and Centre Régional de la Géologie de Laayoune (Morocco). The expedition to the Western Sahara (2002) was funded by the Paul Ungerer Foundation, Senckenberg Forschungsinstitut und Naturmuseum.

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