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MIDDLE DEVONIAN BRACHIOPODS FROM THE SOUTHERN MAÏDER (EASTERN ANTI-ATLAS, MOROCCO)

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Abstract: Sixty-two Middle Devonian brachiopod species are described on the basis of >1300 specimens from the Taboumakhloûf Formation (and subordinately probably also from the top of the El Otfal Formation) at Madène el Mrakib (middle to late Eifelian or early Givetian?), Aferdou el Mrakib (late Eifelian to middle Givetian), and Guelb el Maharch (early Givetian) on the southern edge of the Maïder Syncline (eastern Anti-Atlas, Morocco). Representatives of Craniida (2 taxa), Strophomenida (5), Productida (2), Orthotetida (2), Orthida (5), Pentamerida (5), Rhynchonellida (9), Atrypida (14), Athyridida (7), Spiriferida (9), and Spiriferinida (2) are present. The fauna is dominated quantitatively by the Atrypida (24% of taxa, about the half of specimens, and the commonest species *Atryparia dispersa* making up about 13% of the material); the Rhynchonellida (16% of taxa, about one-sixth of specimens) are the second largest order. A new genus of the family Pugnacidae (order Rhynchonellida), *Paulinaerhynchia*, is proposed with the type species *P. paulinae* gen. et sp. nov. from Maharch; it is closest to *Pugnax*, from which it differs in distinct costation, lack of a dorsal septum and septalium, and rudimentary dental plates. *Desquamatia* (*D.*) *deserti* sp. nov., a large and finely costate representative of the genus, is described also from Maharch. *Antirhynchonella* and *Glosshypothyridina* are reported for the first time or confirmed to be present in the Givetian. Forty (possibly up to 46) species (71 or possibly up to 82% of the taxa identified at the species level) are present also in either Eifel (Germany) or the Holy Cross Mountains (Poland). Such a high ratio of species in common attests to unconstrained faunal exchanges among benthic faunas between the northern and southern shores of the Variscan Sea during the Middle Devonian. This favours the palaeogeographic hypothesis of a narrow Variscan Sea.

Key words: systematics, Brachiopoda, Morocco, Devonian, Eifelian, Givetian, Variscan Sea, palaeobiogeography.

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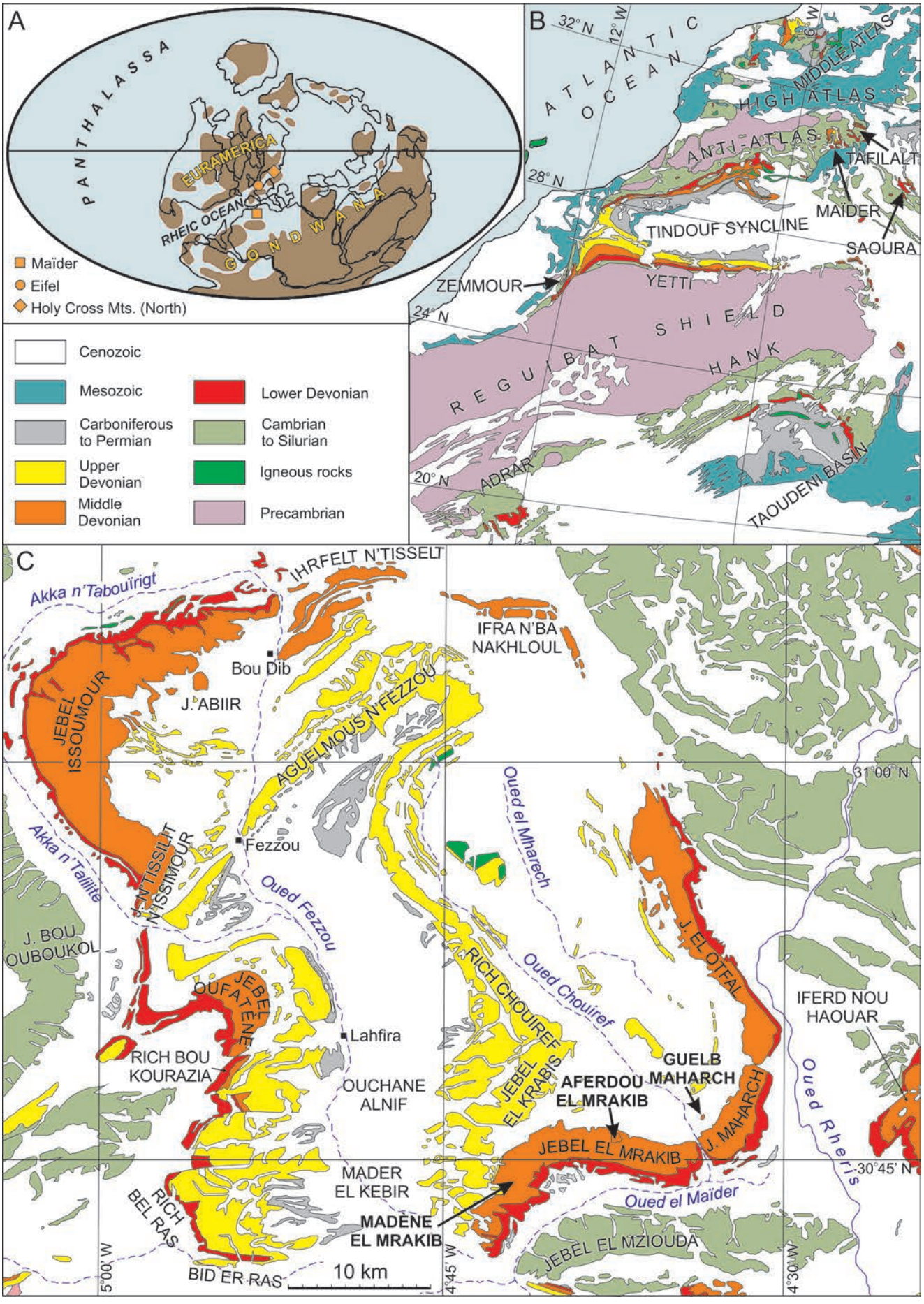
INTRODUCTION

The richness of Palaeozoic faunas in the Moroccan Anti-Atlas is famed. Devonian brachiopods, the major faunal component in several geological units, are especially numerous and diversified. However, despite several studies by previous authors, Middle Devonian brachiopods still are relatively poorly known, owing to, among other factors, collections having been assembled in large part for purposes of geological mapping. The aim of the present paper is (i) to present a detailed systematic account of a middle Eifelian to middle Givetian brachiopod fauna from three nearby localities in the southern Maïder; (ii) to define its palaeobiogeographic affinities, which lie, as will be shown, within the Rhenish subprovince; (iii) last, to discuss the impact of the new data upon questions of the width of the Variscan Sea and of the separation between Rhenish- and American-type brachiopod faunas in the Middle Devonian of northwestern Africa.

History of research

Geological studies in the eastern Anti-Atlas began only in the 1930s. As far as it was possible to establish, the first palaeontologist to describe Devonian brachiopods from Maïder was Dorothée Le Maître. On the basis of Georges Choubert's collections, she reported a small faunule from "Merakib" in the Maïder Syncline (Le Maître, 1939). Although the bulk of the fauna is Early Devonian in age, a part of it might belong to the Middle Devonian. The detailed study of this fauna, announced in the above-mentioned paper, has never appeared.

The systematic study of Devonian brachiopods from Maïder is mainly the work of geologist Henri Hollard, who collected extensively in Morocco for over twenty years (Hollard, 1962, 1963, 1974, 1985) and of palaeontologist Jeannine Drot. In a series of papers dealing with Silurian and Devonian brachiopods of the pre-Saharan Morocco (Anti-Atlas and northern flank of the Tindouf Syncline),


A
PANTHALASSA
EURAMERICA
RHEIC OCEAN
GONDWANA
Maïder
Eifel
Holy Cross Mts. (North)
B
ATLANTIC OCEAN
32° N
12° W
8° W
MIDDLE ATLAS
HIGH ATLAS
ANTI-ATLAS
TAFILALT
MAÏDER
SAOURA
TINDOUF SYNCLINE
ZEMMOUR
YETTI
28° N
24° N
REGUIBAT SHIELD
HANK
20° N
ADRAR
TAOUDENI BASIN
Cenozoic
Mesozoic
Carboniferous to Permian
Upper Devonian
Middle Devonian
Lower Devonian
Cambrian to Silurian
Igneous rocks
Precambrian
C
Akka n'Tabouïrigt
IHRFELT N'TISSELT
IFRA N'BA NAKHLOUL
Bou Dib
J. ABIIR
JEBEL ISSOUMOUR
AGUELMOUS N'FEZZOU
31° 00' N
Oued el Mharech
Fezzou
Akka n'Talilite
J. N'TISSILIT N'ISSIMOUR
Oued Fezzou
J. BOU OUBOUKOL
JEBEL OUFATENE
RICH CHOUIREF
Oued Chouiref
J. EL OTFAL
IFERD NOU HAOUAR
Lahfira
RICH BOU KOURAZIA
OUCHANE ALNIF
JEBEL EL KRABIS
AFERDOU EL MRAKIB
GUELB MAHARCH
J. MAHARCH
JEBEL EL MRAKIB
Oued Rheris
30°45' N
MADER EL KEBIR
RICH BEL RAS
MADÈNE EL MRAKIB
Oued el Maïder
JEBEL EL MZIOUDA
BID ER RAS
10 km
5°00' W
4°45' W
4°30' W

Drot (1964, 1966, 1971) described several taxa of Middle Devonian rhynchonellides and spiriferides from the Maïder (including Aferdou el Mrakib). Middle Devonian strophomenides, productides, orthotetides, orthides, pentamerides, athyrididés, and atrypides have not been under detailed research.

Struve (1995) illustrated and briefly commented upon several Middle Devonian pentamerides, atrypides, and spiriferides from the northern Maïder (Jebel Issomour). He also listed several other taxa (identified at genus level) and concluded that the affiliation of the fauna was referable to the Rhenish subprovince. Single Givetian brachiopod species from Maïder were described by Godefroid (2000), Schemm-Gregory (2009), and Franchi *et al.* (2012).

Last but not least, it is appropriate to note some major results regarding the geology of the study area. The age of the coral limestone (*calcaire coralligène*), now corresponding to a part of the Taboumakhloûf Formation (Hollard, 1974), was established as Givetian by Hollard (1962; considered as Eifelian by Delépine, 1951). The stratigraphic description of the Maïder was presented by Hollard, first in brief (Hollard, 1963) and then in detail (Hollard, 1981). A sedimentological study of the three sites, from which the fauna described in the present paper comes, was done by Kaufmann (1998). Conodont-based stratigraphy of the Eifelian of the eastern Anti-Atlas was presented by Belka *et al.* (1997). The Devonian palaeogeography of the Anti-Atlas was dealt with by Wendt (1985, 1988, 1993), by Belka *et al.* (1997), and by Döring and Kazmierczak (2001).

GEOLOGIC SETTING

The Maïder (spelt also Ma'der, Mader, Maader, and Maïdère) is a Variscan syncline, situated in the eastern part of the broadly named Anti-Atlas (i.e., including Jebel Sarhro and Jebel Ougnate; Joly *et al.*, 1949, p. 30; Choubert and Marçais, 1956; Joly, 1962; Michard, 1976, p. 41; Piqué, 1994, p. 26), itself a transitional zone between the stable domain of the West African craton in the south and the Variscan chain in the north (Piqué *et al.*, 1993; see also Ennih and Liégeois, 2008; Soulaimani and Burkhardt, 2008). The Arabic noun *maïder* denotes a fine-grained alluvial plain (Dresch *et al.*, 1952, p. 171; Joly, 1962, p. 546) and in this case describes the eroded Carboniferous core of the syncline, covered by Quaternary sediments (Daya el Maïder, Joly, 1962, p. 416, 537; corresponding to Mader el Kebir in Fig. 1C). This plain is bordered all round by low mountain ranges that are predominantly Devonian, listed clockwise, beginning from the northwest: Jebel Issomour (variant transcriptions: Jebel Issoumour, Jbel Issimour; including the solitary hill called Jebel Abiir), Jebel (el) Otfal, Jebel Maharch, Jebel (el) Mrakib, and Jebel Oufatène (Fig. 1C). The present paper is based on the material from three outcrops, situated in the southern part of these ranges (geologic map sheet Todrha-Ma'der, du Dresnay *et al.*, 1988), namely Madène el Mrakib, Aferdou el Mrakib and Guelb (el) Maharch.

In the Middle Devonian (Fig. 1A), the present Anti-Atlas region formed a part of the passive north-western margin of Gondwana (Piqué *et al.*, 1993) at a palaeolatitude of about 30–40° S (Scotese and McKerrow, 1990; Matte, 2001; Golonka *et al.*, 2006; Torsvik and Cocks, 2011; Stampfli *et al.*, 2013). In general, the eastern part of the Anti-Atlas is characterised during the entire Devonian by sediments with relatively low content of clastic and terrigenous components (as compared to the western part; Piqué and Michard, 1989). The subdivision of the eastern Anti-Atlas into four depositional realms (from west to east, the Maïder Platform, the Maïder Basin, the Tafilalt Platform, the Tafilalt Basin) resulted from bathymetric differentiation of the basin, due to early Variscan block faulting in the late Emsian (Wendt, 1985, 1988; Belka *et al.*, 1997). Aferdou el Mrakib and Guelb el Maharch are the two largest bioconstructions, several of which developed in a wide neritic facies belt, surrounding the central basinal part of the Maïder Basin (Wendt, 1993; Kaufmann, 1995). It may be noted that similar early Givetian reefs and mud mounds developed on both sides of the Variscan Ocean: on the northern borders of Gondwana further west (present-day Western Sahara: Dumestre and Illing, 1967; Wendt and Kaufmann, 2004) and east (Wendt *et al.*, 1997), as well as on the southern borders of Euramerica (present-day Sauerland: Krebs, 1967; May, 2003; present-day Eifel: Schmid *et al.*, 2001; present-day New York: Heckel, 1972; see also Krause, 2004).

The middle part of the Middle Devonian in the southern Maïder (Fig. 2) was divided into two major units (formations) by Hollard (1974). The ages given below, modified according to the results of Kaufmann (1998) in respect to Hollard (1974), are as follows:

1. upper Eifelian (*australis* Zone) shallow-water crinoidal grainstones (top of the El Otfal Formation) cropping out on the eastern flank of Aferdou;

2. upper Eifelian to lower Givetian (*kockelianus* to Lower *varcus* zones) mound debris and off-mound strata cropping out on western, northern, and partly eastern flanks of Aferdou (Taboumakhloûf Formation; about 45 m in thickness); this is the TM 554 locality of Drot (1971) and Hollard (1974, 1981, p. 28). This formation includes the lower Givetian *Ivdelinia pulchra* lumachelle (thickness about 3 m;

Fig. 1. Geological setting of fauna studied. **A.** Situation of study area and selected other important brachiopod faunas on a palaeogeographic reconstruction for the Middle Devonian [modified after Scotese and McKerrow (1990), Golonka *et al.* (2006), and Murphy *et al.* (2011)]. **B.** Schematic geologic map of northwestern Africa (much simplified after Choubert and Faure-Muret, 1988), showing areas mentioned in the text. (Due to map scale in some cases "Middle Devonian" stands for both Middle and Upper Devonian, and "Lower Devonian" for all three Devonian series.). **C.** Geologic map of the Maïder [modified and simplified after du Dresnay *et al.* (1988), Hollard (1974, 1985), and Destombes and Hollard (1986)]. Names of the three sites studied in the present paper are in capital boldface. Geological structures, mountain ranges, and other topographic features in capitals. Waters (seas in A and B, wadis in C) in italics. Towns and villages in Roman typeface

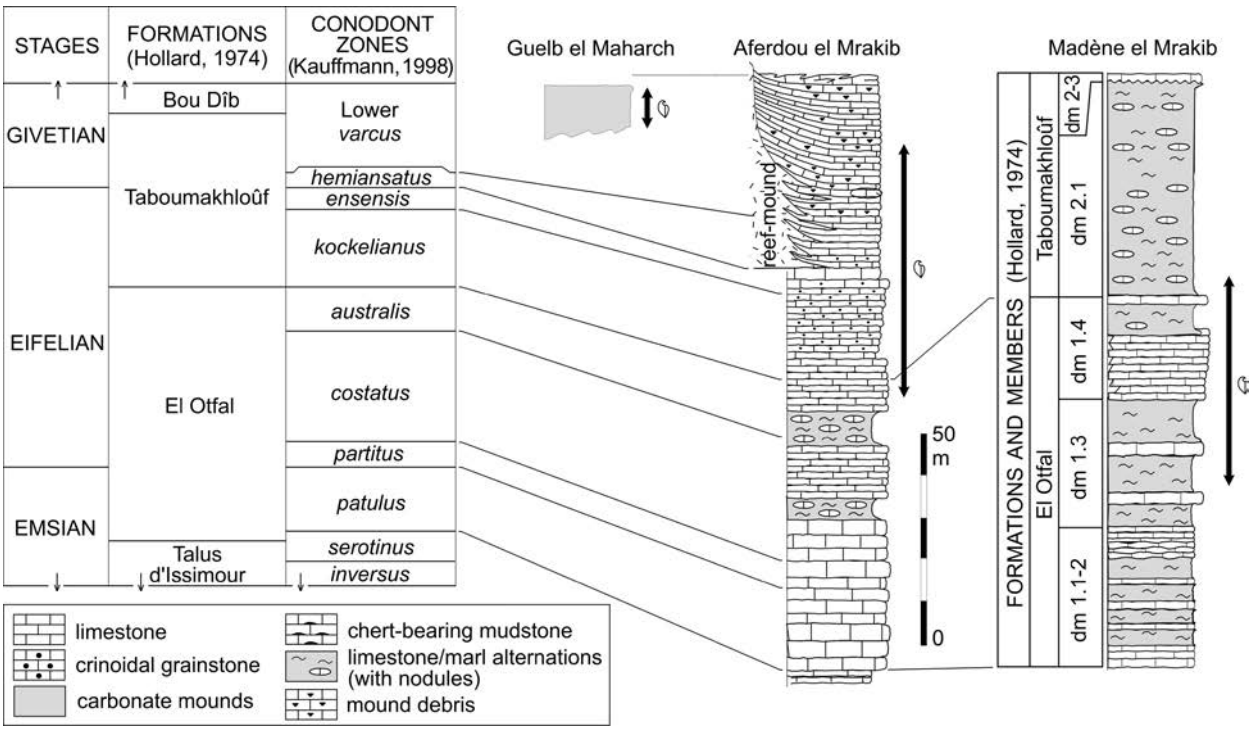


Fig. 2. Stratigraphic sections of upper Emsian to lower Givetian strata at the three localities of the Maïder Syncline (eastern Anti-Atlas) studied, showing the approximate position of the horizons, from which brachiopod fauna has been collected (black vertical arrowed lines). Stratigraphic and lithologic data after Hollard (1974) and Kaufmann (1998)

Tessitore *et al.*, 2013) cropping out in some points of the eastern flank.

The fauna studied comes from three localities, situated within 20 km of each other. A description of them is given in the next chapter.

MATERIAL AND METHODS

Description of localities and general characteristics of their fauna

Madène el Mrakib denotes a continuous section of (at least) Lower to Middle Devonian strata situated at approximately 30°44'N 4°41'W (ca. 2 km NE from the copper mine). The authors used rich collections (>200 specimens) made by U. Jansen (SMF) in 1998 from the *Drotops* beds (Fig. 2; Eifelian, according to Struve, 1990; a *Drotops* horizon is lower Givetian in age at Aferdou, according to Kaufmann, 1998; however, most probably there is more than one *Drotops* horizon in the Middle Devonian) characterised by common occurrence of the above-mentioned phacopid trilobite. Another collection (172 specimens) from the same section was made in February and March 2000 from an excavation at 30°44'57"N 4°41'42"W ("kegelförmiger Berg, Drotopsschurf") by the late Volker Ebbighausen. It has been donated to the Natural History Museum in Berlin and could be studied by the present authors, although only at a very advanced stage of preparation of the manuscript. Better outcrops of the same level were described from the northern Maïder by Struve (1995). These strata are characterised by the frequent occurrence of the pentameride *Glyptogypa multiplicata* (>120 specimens). *Atrypa* (*Planatrypa*?) *confusa* is also common (>30 specimens).

Aferdou el Mrakib (variant transcription: Aferdou n' Merakib; in the systematic part abridged as Aferdou) is a flat-topped mountain, about 900 m in diameter and up to 130 m high (Kaufmann, 1998, pls 1, 2), situated on the northern flank of the Jebel Mrakib at about 30°46'N 4°37'W. The general geology was presented by Hollard (1974, p. 24–28, 48–49) and a detailed sedimentological account of this and the following outcrop was given by Kaufmann (1998) and is followed here. Colonial rugose corals and stromatoporoids are dominant builders of this largest reef of the eastern Anti-Atlas. Rich brachiopod collections (833 specimens in total) were assembled, mostly from the Taboumakhloûf Formation (Fig. 2). The most frequent brachiopods are atrypides, which constitute the dominant order with 12 taxa and over 400 specimens, in particular, the commonest species *Atryparia dispersa* represented by 125 specimens, *Atrypa* (*Planatrypa*?) *confusa* with >90 specimens, and *Kerpina vineta* with 77 specimens. The rhynchonellide *Kransia parallelepipeda* (91 specimens) and the lumachelle-forming pentameride *Ivdelinia pulchra* (123 specimens) are also frequent. It should be noted that brachiopods were collected mostly as weathered specimens from the scree on the flanks of Aferdou el Mrakib. Accordingly, in most cases, the detailed stratigraphic position of single taxa cannot be given. Except for pentamerides, collected from the lower Givetian lumachelle (Tessitore *et al.*, 2013), it was impossible to make any distinction between specimens, eroded from the Eifelian and Givetian parts of the Taboumakhloûf Formation. The latter might be more numerous, but it should be stressed that the

sample from Aferdou does contain taxa, reported up to now as being both solely from the Eifelian (e.g., *Plectospira ferita* and *Phragmophora schnuri*) and solely from the Givetian (e.g., *Kransia subcordiformis* and *Spinatrypa trigonella*).

Guelb el Maharch (variant transcription: Guelb Mharch; in the systematic part abridged as Maharch) is a solitary dome-like hill, about 45 m high (Kaufmann, 1998, pl. 4: 1) and situated on the plain (about 30°47'N 4°33'W) near Foum el Maïder, which is the gorge of Oued Chouiref, constituting the border between Jebel Maharch in the east and Jebel Mrakib in the west. It consists solely of massive limestone of early Givetian (Fig. 2; *hemiansatus* to Lower *varcus* zones; Kaufmann, 1998) age. Tabulates and crinoids are quite common, while colonial rugosans are absent (Kaufmann, 1998). Characteristic (i.e., most frequent and occurring only at this locality) brachiopods of Guelb el Maharch (106 specimens at the authors' disposal) include *Paulinaerhynchia paulinae* gen. et sp. nov. (21 specimens) and *Desquamatia* (*D.*) *deserti* sp. nov. (40 specimens). Given the geologic setting described above, all the material collected at this locality comes from the upper part of the Taboumakhloûf Formation and is undoubtedly early Givetian in age (Kaufmann, 1998).

Out of the twenty species found at Madène el Mrakib, eight (40%) have not been found at the other two sites. However, the general aspect of brachiopod faunas at Madène el Mrakib and at Aferdou is not very different, the common species being in part the same (*Xystostrophia umbraculum*, *Atrypa confusa*). Taxa common at Madène and very rare or absent at Aferdou include *Glyptogypa multiplicata* and *Quiringites arensentiae*; their presence is probably due to older strata cropping out at the former locality. Out of eleven species found at Maharch, five (45%) are known only from this site. The numerical ratio is quite the same as in the previous case, yet the general aspect of the Maharch fauna is very different from that at Aferdou. At Maharch, the fauna is dominated by *Paulinaerhynchia paulinae* and *Desquamatia deserti*, both of which do occur at Aferdou, but are represented only by single specimens. This dissimilarity corresponds to different bathymetric situations: moderate water depths (but below the photic zone) in the mid-ramp zone for Aferdou (and probably Madène) and a deeper outer ramp setting for Maharch (Kaufmann, 1998). As in the case of cnidarians and sponges (Kaufmann, 1998), the brachiopod fauna at Aferdou is much richer (49 taxa, compared to 11 in Maharch). One should, however, bear in mind that in the former section, brachiopods have been collected from a much longer stratigraphic interval and from a larger outcrop.

The collection and preparation of brachiopods from Aferdou was relatively easy, owing to their abundance in the scree. Only in some cases, a small amount of mechanical preparation was required. The preservation of this material is quite variable: many specimens are cracked and their external surfaces are abraded, owing to aeolian corrasion; nonetheless, a lot of very good specimens have been collected as well, in some cases even with microornamentation (Figs 6B, 12L, 34L, 35R, S). Internal structures are relatively well preserved. On the other hand, the limestone at Maharch is very hard, making mechanical preparation difficult. Shell microornamentation is never preserved, while the interiors are always broken and/or recrystallised. For example, interpreting the internal structures of *Paulinaerhynchia paulinae* gen. et sp. nov. required the sectioning of five specimens. The preservation of brachiopods coming from Madène el Mrakib is quite similar to those from Aferdou, at least so far as the exteriors are concerned (serial sections were not made on specimens from this locality). Material from the excavations, made by the late V. Ebbighausen, is particularly well preserved.

Repositories

The described material (>1300 specimens) is kept in the Institute of Paleobiology of the Polish Academy of Sciences (Warsaw, Poland) under the collection number ZPAL Bp 68 (68/1, Aferdou and 68/2, Maharch; the authors' and Błażej Berkowski's collections), in the Senckenbergische Naturforschende Gesellschaft in Frankfurt am Main (Madène el Mrakib; Ulrich Jansen's collection; institutional abbreviation SMF), and in the Museum für Naturkunde in Berlin (Madène el Mrakib, Volker Ebbighausen's collection; institutional abbreviation MB). Additional material from the institutions listed below also was used: BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin-Spandau, Germany; GFCL, Faculté libre des Sciences et Technologies, Lille, France; HLMD, Hessisches Landes-Museum, Darmstadt, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Mass., USA; MGUWr, Muzeum Geologiczne Uniwersytetu Wrocławskiego, Wrocław, Poland; and MNHN, Muséum national d'Histoire naturelle, Paris, France.

Specimens of described species from other sections in north-western Africa, representing the species described here, have been reported, if relevant, under "Additional material" (Figs 3A, H, I–K, 5J–M, 7DD, EE, 19I–M, 25M–Q). However, the material from the northern Maïder is quoted only seldom, as it will be the object of a separate study. In exceptional cases, specimens from outside NW Africa have been figured or discussed (Figs 4T–V, 14A–E, P–T, 16V–Z, 19Y–DD, 33B); they are listed under the heading "Other material examined". However, descriptions, unless otherwise stated, are based solely on specimens from the three localities investigated.

Special taxonomic questions

Since a monograph of Middle Devonian brachiopod faunas from central Europe, including the systematic revision of taxa on the basis of type and topotypic collections, is now in progress (Halamski, 2004a, 2009), several problems are discussed only briefly in the present account, with reference to the above. Given that on the one hand it seemed advisable to the authors to publish the present description as soon as possible and on the other there was a delay in publishing subsequent parts of the Holy Cross Mountains brachiopod monograph (first part by Halamski, 2009), the result is that some taxonomic decisions out of necessity were anticipated, in particular those concerning the representatives of *Kransia*.

Whenever possible, synonymies are limited to the original publication and a single (exceptionally more) reference to papers, in which a given species was most thoroughly discussed and where a full list of references is to be found. This rule suffers three exceptions: papers dealing with North African material always have been cited fully; taxa not dealt with in the above-mentioned monograph (Halamski, 2009) have been given complete synonymies; and additions to the already published first part of the monograph also have been taken into account. Formalised signs in synonymic lists follow Halamski (2009; further references therein).

In the authors' opinion, the value of the present description of a Rhenish-type fauna from Africa is largely in an extensive photographic documentation of the material, testifying that the use of European taxa names is not the fancy of a lumping-style taxonomy, but the only solution that could be taken after a meticulous study of the brachiopods. In some cases, this has required photographing material of otherwise poorly illustrated taxa originating from Europe. Images were taken mostly using a Fujifilm Finepix S2 pro camera with a Nikon micro 60 mm lens; in some cases a Canon 350D camera with a Canon EF 100 mm macro lens was used. Enlargements were photographed under a Nikon SMZ 1500 binocular microscope, equipped with a Nikon D800 digital camera. Specimens were coated with ammonium chloride before being photographed. Some photographs were assembled from a series of up to five frames, using the Helicon Focus programme. Internal structures were examined, if needed, through the standard method of serial sections and acetate peels; drawings were prepared with a camera lucida.

Descriptions

Phylum Brachiopoda Duméril, 1805
Subphylum Craniiformea Popov *et al.*, 1993
Class Craniata Williams *et al.*, 1996
Order Craniida Waagen, 1885
Family Craniidae Menke, 1828

Genus *Deliella* Halamski, 2004 [2004b]
Type species: *Deliella deliae* Halamski, 2004 [2004b]; Skały, northern region of the Holy Cross Mountains; lower part of the Skały beds, upper Eifelian

Remarks: The material of *Deliella* from northern Africa is scarce (five individuals), nonetheless it may be quite easily divided into two groups, differing in character and the density of ornamentation. The first group is characterised by thick (i.e., thicker than furrows between them) and relatively scarce radial ribs, whereas the second one has fine (i.e., narrower than furrows between them) and numerous ribs. If a numerical character is needed, the quotient of the total rib numer and the maximal shell diameter may be taken; its values are between 6.5 and 11.3 in the first group and between 16.6 and 26.3 in the second one. The two groups are described below as separate taxa, but their variability should be checked on a larger sample.

Deliella deliae Halamski, 2004 [2004b]
Fig. 3Q2, R2, S2

v* 2004b *Deliella deliae* n. gen. et sp. – Halamski: pp. 184–188, figs 1A–F, 2C–D, 3B–D.
v**.** 2009 *Deliella deliae* Halamski, 2004 – Halamski, p. 49, pl. 1, figs 9, 13 [*ubi syn.*].

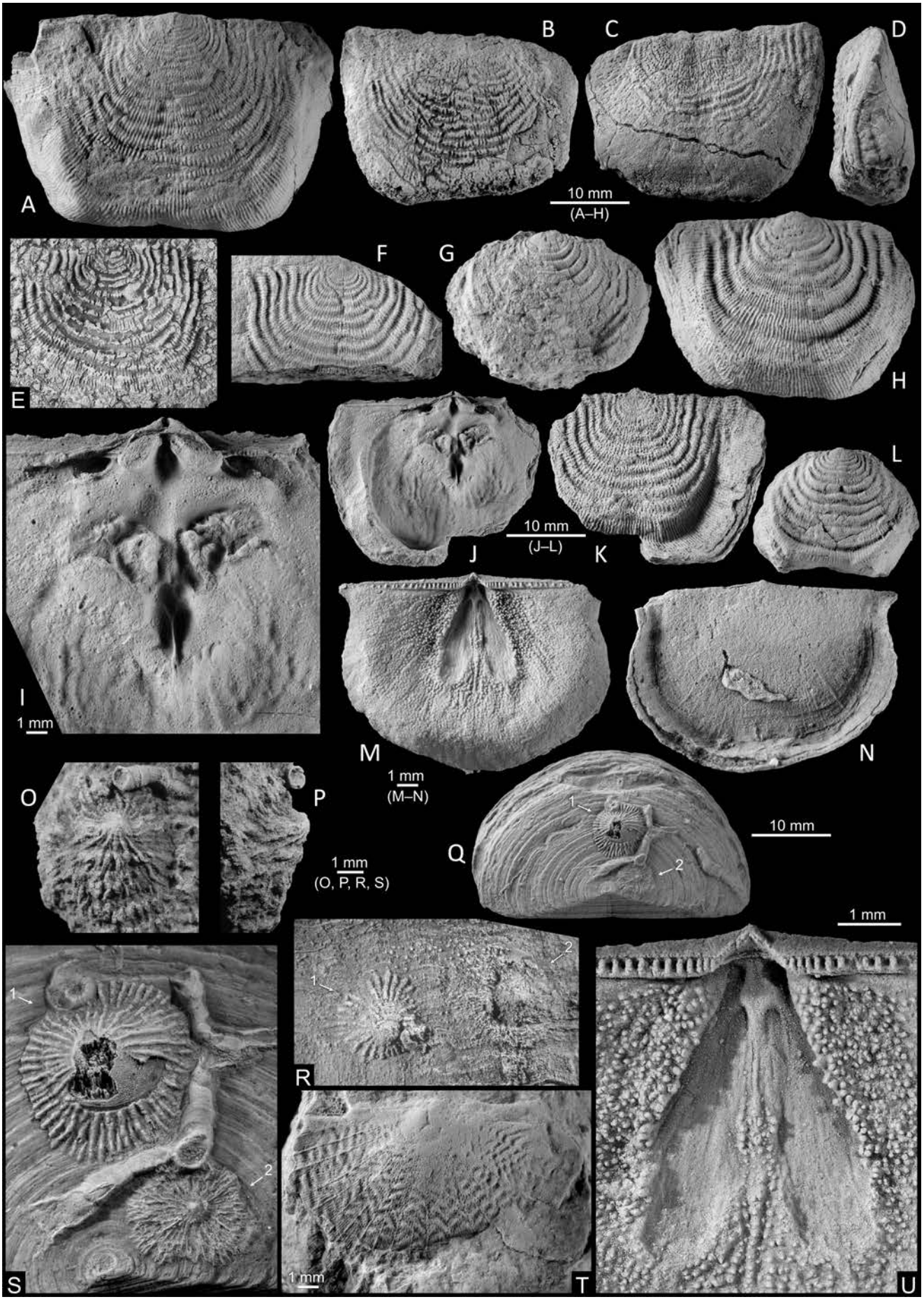
Material: MB.B.9384b attached to the ventral valve of *Spinocyrtia* cf. *elburzensis* (MB.B.9384c), from Madène el Mrakib (coll. V. Ebbighausen).
Additional material: MNHN.F.A48107c attached to the operculum of *Calceola* sp. (MNHN.F.A48107a), locality 348A *sensu* Sougy (1964; Zemmour Noir, Mauritania).
Description: Dorsal valve conical, elliptic in outline, 4.1 mm long. Apex excentric, situated 1.4 mm from the posterior margin (34% of the maximal diameter). Radial ornamentation of ca. 108 straight, fine ribs (total numer of ribs estimated on the basis of count on the preserved fourth of the shell).
Remarks: The finely ribbed representative of *Deliella* from northern Africa shows no significative differences from *D. deliae* from the Holy Cross Mountains.
Distribution: Holy Cross Mountains, Maïder, and Mauritania; upper Eifelian to lower Givetian.

Deliella aff. *rhenana* (Dahmer, 1930)
Fig. 3O, P, Q1, R1, S1

aff. 1930 *Philhedra rhenana* n. sp. – Dahmer: pp. 92–93, pl. 6, fig. 2.
v 2009 *Deliella* sp. – Halamski, p. 49, pl. 9, fig. 8.
aff. 2012 *Deliella rhenana* (Dahmer, 1930) – Franke, p. 135, pl. 1, figs 1–3 [*ubi syn.*].

Material: Two individuals, MB.B.9382a attached to the dorsal valve of *Xystostrophia umbraculum* (MB.B.9832b) and MB.B. 9384a attached to the ventral valve of *Spinocyrtia* cf. *elburzensis* (MB.B.9384c), both from Madène el Mrakib (coll. V. Ebbighausen).

Fig. 3. Middle Devonian Craniida and Strophomenida from northwestern Africa. **A–L.** *Leptagonia analogaeformis* Biernat, 1966. A. Articulated shell MNHN.F.A48100 in ventral view. Maïder, locality TM 810/1, coll. H. Hollard. B–D. Articulated shell ZPAL Bp 68/1/8/1 from Aferdou in ventral, dorsal, and lateral views. E. Dorsal valve ZPAL Bp 68/1/8/3 from Aferdou. F. Specimen ZPAL Bp 68/1/8/2 from Aferdou in dorsal view. G. Specimen ZPAL Bp 68/1/8/4 from Aferdou in ventral view. H. Specimen MNHN.F.A48106 from locality 346N *sensu* Sougy (1964) (Zemmour Noir, Mauritania). I–K. Dorsal valve SMF 94838 from Jebel Abiir, close-up of cardinalia, internal and external views. L. Specimen ZPAL Bp 68/1/8/5 from Aferdou in ventral view. **M–N, U.** *Parastrophonella anaglypha* (Kayser, 1871). Ventral valve SMF 94853 from Madène el Mrakib. External (N) and internal (M) views, and muscle area (U). **O–S**. *Deliella* aff. *rhenana* (Dahmer, 1930). All specimens from Madène el Mrakib. O, P. Shell MB.B.9382a attached onto the dorsal valve of *Xystostrophia umbraculum* (von Schlotheim, 1820) MB.B.9832b in ventral (O) and lateral (P) views. Q, S. Shell MNHN. F.A48107b attached onto an operculum of *Calceola* sp. MNHN.F.A48107a in general (Q1) and enlarged (S1) views. R. Shell MB.B. 9384a (R1) attached on the ventral valve of *Spinocyrtia* cf. *elburzensis* MB.B.9384c (see also Fig. 34E). **Q–S**. *Deliella deliae* Halamski, 2004. All specimens from Madène el Mrakib. Q, S. Shell MNHN.F.A48107c attached onto an operculum of *Calceola* sp. MNHN.F. A48107a in general (Q2) and enlarged (S2) views. R. Shell MB.B.9384b (R2) attached on the ventral valve of *Spinocyrtia* cf. *elburzensis* MB.B.9384c (see also Pl. 34E). **T.** Protodouvillininae gen. et sp. indet. Fragmentary ventral valve ZPAL Bp 68/1/12/1 from Aferdou


A
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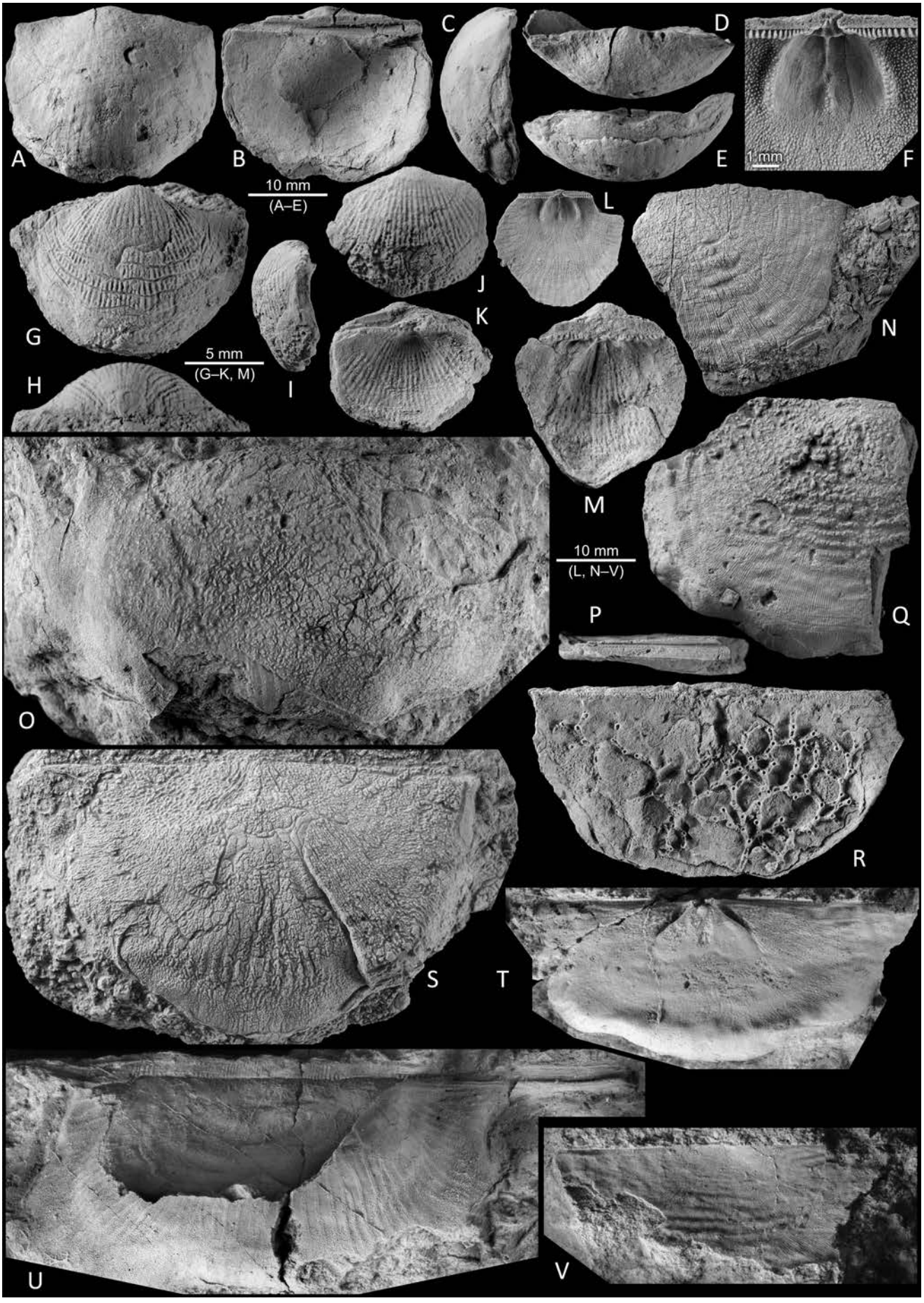
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1 mm
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(G–K, M)
10 mm
(L, N–V)
O
P
Q
R
S
T
U
V

Additional material: One individual MNHN.F.A48107b attached to the operculum of *Calceola* sp. (MNHN.F.A48107a), locality 348A *sensu* Sougy (1964; Zemmour Noir, Mauritania).
Other material examined: SMF 66200 attached to *Protodouvillina interstrialis*, Eifel, Middle Devonian, illustrated by Halamski (2009, p. 1, fig. 8).
Description: Dorsal valve conical, elliptic in outline, up to 7.1 mm long and 6.1 mm wide. Apex excentric, its distance from the posterior margin being 29–35% (N = 3) of the maximal diameter. Radial ornamentation of thick, straight costae, bifurcating rather rarely, 35–55 in number.
Remarks: As observed already by Halamski (2009), the Eifel representative of *Deliella* has coarser ornamentation than those from the Holy Cross Mountains. The analysis of the material from Africa confirms this separation. The coarsely ornamented Middle Devonian species is most similar to late Emsian *Deliella rhenana* from which it differs in its smaller size (the diameter of the holotype of *D. rhenana* is 18 mm; Franke, 2012). It may represent a new species, but the material is insufficient to provide a basis for a formal description.
Distribution: Eifel, Maïder, and Mauritania, Middle Devonian.

Subphylum Rhynchonelliformea Williams *et al.*, 1996
Class Strophomenata Williams *et al.*, 1996
Order Strophomenida Öpik, 1934
Family Rafinesquinidae Schuchert, 1893

Genus *Leptagonia* M'Coy, 1844
Type species: *Producta analoga* Phillips, 1836; probably Bolland, Yorkshire; lower Visean

Leptagonia analogaeformis (Biernat, 1966)
Fig. 3A–L

1934 *Leptaena rhomboidalis* (Wilckens) – Torley, p. 128, pl. 9, fig. 82.
v 1964 *Leptaena rhomboidalis* (Wilckens) – Sougy, pl. 44, figs 10–11.
v* 1966 *Leptagonia analogaeformis* n. sp. – Biernat, pp. 38–42, text-figs 6, 7, pl. 3, figs 1– 16, pl. 4, figs 1–13.
v. 2009 *Leptagonia analogaeformis* (Biernat 1966) – Halamski, pp. 50–52, text-figs 2, 3, pl. 1, figs 16–19, 21–23, 25, pl. 2, figs 1–12, 14, 15, 17, pl. 16, figs 19–22, 29 [*ubi syn.*].

Material: Five subcomplete to fragmentary specimens from Aferdou, ZPAL Bp 68/1/8/1; nine articulated shells SMF 85681 and MB (unnumbered; V. Ebbighausen's collection) from Madène el Mrakib.
Additional material: Articulated shell MNHN.F.R10276 from Aguelt Tighirt figured by Sougy (1964, pl. 44, p. 10); articulated shell MNHN.F.R10277 from Amgala marls figured by Sougy (1964, pl. 44, p. 11); articulated shell MNHN.F.A48106 from the locality 346N; two ventral valves MNHN.F.A48105 from the locality 2428; all the above from the Zemmour Noir, Mauritania, coll. J. Sougy; isolated dorsal valve SMF 94838, Jebel Abiir, northern Maïder, coll. U. Jansen; articulated shell MNHN.F.A 48100 from the locality TM 810/1, Maïder?, coll. H. Hollard.
Description: Shell up to ca. 30 mm in width, transverse (width-to-length ratio ca. 1.5), subrectangular to subtrapezoidal in outline, geniculate. Hinge line and anterior commissure straight, parallel. Ventral valve with weakly convex (sometimes flattened laterally) disk and dorsally directed trail; interarea rectangular, apsacline. Dorsal valve concave (flat disk and geniculation); interarea low, hypercline. Pseudodeltidium and chilidium not preserved. Ornamentation of concentric rugae, (6–)8–10 per cm, and radial costae and costellae, ca. 7–8 per 5 mm at anterior margin.

Interior (description based on the specimen SMF 94838 from Jebel Abiir). Dorsal valve: cardinal process consisting of two massive lobes; muscle area rhomboidal, bisected by a median septum that continues anteriorly for a short length; vascular imprints in anterior region of the valve. Ventral valve unknown.
Remarks: The material described here agrees in both external and (dorsal) internal characters with *Leptagonia analogaeformis* (Biernat, 1966) from the Middle Devonian of the Holy Cross Mountains and the Eifel (Halamski, 2009). The density of concentric rugae is apparently a variable character with individuals from the Holy Cross Mountains and from Mauritania, having sometimes as few as 4 rugae per cm; nonetheless, this is not a sufficient reason to subdivide this long-lasting member of a bradytelic lineage.
Distribution: Middle Devonian of the Holy Cross Mountains, Eifel, Sauerland, Maïder, and Mauritania; possibly also Inner Mongolia and Japan (Chen and Tazawa, 2003).

Family Douvillinidae Caster, 1939

Genus *Protodouvillina* Harper and Boucot, 1978
Type species: *Strophomena inaequistriata* Conrad, 1842; New York; Hamilton (Middle Devonian)

Protodouvillina interstrialis (Phillips, 1841)
Fig. 4A–F, L

* 1841 *Orthis interstrialis*, *Leptaena interstrialis* – Phillips: pp. 61–62, pl. 25, fig. 103 a–e.
v. 1885 *Strophomena interstrialis* Phillips – Maurer, pp. 144–145, pl. 5, fig. 17.
v. 1964 *Douvillina* sp. e. g. *interstrialis* (Phillips, 1841) – Sougy, p. 451.
v. 2009 *Protodouvillina interstrialis* (Phillips 1841) – Halamski, pp. 53–54, text-fig. 4, pl. 3, figs 1–6, 8–17, 19–20, 30–32 [*ubi syn.*].

Material: A single subcomplete, but decorticated articulated shell

Fig. 4. Middle Devonian Strophomenida and Productida from northwestern Africa and Europe. **A–F, L.** *Protodouvillina interstrialis* (Phillips, 1841). A–E. Articulated shell ZPAL Bp 68/1/52/1 from Aferdou in anterior, posterior, ventral, dorsal, and lateral views. F, L. Interior of the ventral valve MB.B.9383 from Madène el Mrakib in general (L) and enlarged (F) views. **G–K, M.** *Devonaria* sp. All specimens from Aferdou. G, H. Ventral valve 68/1/11/3 embedded in limestone in ventral and posterior views. I–K. Subcomplete articulated shell 68/1/11/1 in lateral, ventral, and dorsal views. M. Incomplete articulated shell 68/1/11/2 in dorsal view. **N–V.** *Radiomena irregularis* (Roemer, 1844). N. Incomplete ventral valve 68/1/7/3 from Aferdou embedded in limestone. O. Incomplete articulated shell ZPAL Bp 68/1/6/1 from Aferdou in ventral view. P. Incomplete articulated shell 68/1/7/4 from Aferdou in posterior views. Q. Incomplete articulated shell 68/1/7/2 from Aferdou in ventral view. R. Articulated shell 68/1/7/1 from Aferdou overgrown by bryozoans. S. Incomplete ventral valve 68/1/7/5 from Aferdou embedded in limestone. T, V. Internal (T) and external (V) mould of a ventral valve (part and counterpart); holotype HLMD-Mr 8845, 8847 of *Strophomena porrigata* Maurer, 1885 from Grube Hainau at Waldgirmes. U. Incomplete ventral valve HLMD-Mr 8842 from Grube Hainau at Waldgirmes embedded in limestone

from Aferdou, ZPAL Bp 68/1/52/1 and a single ventral valve MB. B.9383 from Madène el Mrakib (V. Ebbighausen's collection).
Additional material: Two articulated shells MNHN.F.A48117, 48118 from the locality 402M, 1.5 km ENE from Agouelt Oudiate el Khyan, Zemmour Noir, Mauritania; "basis of the *Calceola* marls, lower Givetian"; coll. J. Sougy.
Other material examined: Fragmentary specimen HLMD-Mr 11605, 11606 from Grube Rothe Erde at Waldgirmes (Lahn Syncline) figured by Maurer (1885, pl. 5, p. 17).
Description: The single available shell is concavo-convex, ca. 27 mm wide, ca. 22.5 mm long, and ca. 12 mm thick. Hinge line straight. Interareas low, longitudinally striate. Anterior commissure rectimarginate.

Ornamentation parvicostellate, poorly preserved; 1(–2) cost-(ell)ae per mm at anterior margin and 3–4 striae between each pair of cost(ell)ae. Shell substance punctate.

Ventral interior: muscle area as long as one fourth of the valve length, bilobed, bordered laterally by low rounded ridges, posteriorly bisected by a short median septum; valve floor pustulose. Dorsal interior unknown.
Distribution: This species was reported from several Early to Late Devonian localities in Europe and Asia (Brice, 1971) and indeed it seems a cosmopolitan taxon, even if part of these data requires confirmation (Halamski, 2009).

Genus *Radiomena* Havlíček, 1962
Type species: *Orthis irregularis* Roemer, 1844, Gerolstein, Eifel; Middle Devonian

Radiomena irregularis (Roemer, 1844)
Fig. 4N–V

v* 1844 *Orthis irregularis mihi* – Roemer: p. 75, pl. 4, fig. 1 a–c.
v. 1885 *Strophomena irregularis* Roemer – Maurer, pp. 145–146, pl. 5, figs 18–20.
v. 1885 *Strophomena porrigata* n. s. – Maurer, pp. 148–149, pl. 6, fig. 1.
v. 2009 *Radiomena irregularis* (Roemer 1844) – Halamski, p. 56, pl. 7, figs 12, 16, 19, 22, 23, pl. 16, figs 2, 25–28 [*ubi syn.*].
v. 2009 *Zophostrophia*? *aaatos* sp. n. – Halamski, pp. 59–60, pl. 2, figs 13, 23, pl. 4, figs 1–10, pl. 16, fig. 1 [*ubi syn.*].

Material: One subcomplete, three incomplete specimens, one exfoliated and showing traces of dorsal internal structures, one poorly preserved ventral interior, four fragments, all from Aferdou, ZPAL Bp 68/1/6/1, 68/1/7/1–7.
Other material examined: Ventral valve embedded in limestone HLMD-Mr 8842, Grube Hainau at Waldgirmes (Lahn Syncline), figured by Maurer (1885, pl. 5: 20); holotype of *Strophomena porrigata* HLMD-Mr 8845, 8847 from Grube Hainau at Waldgirmes (internal mould and external cast of the same specimen, see Fig. 4T, V; HLMD-Mr 8846 is the original gutta-percha cast by F. Maurer).
Description: Shell subrectangular to subtrapezoidal in outline, geniculate, up to 71 mm wide, width-to-length ratio 1.65–2.09, dorsally geniculate. Posterior margin straight. Ventral valve convex in umbonal region, flat in lateral flanks, irregularly undulating; sometimes, however, nearly flat. On the trail, traces of poorly preserved parvicostellate ornamentation with 3–4 costellae per mm. Ventral interarea anacline, higher than the apsacline dorsal one. Ornamentation of faint rugae, 3–4 per 5 mm, and slightly wavy radial costae and costellae, 4–6 (–7) per mm at disk margin. Ventral interior: muscle field bordered by fine ridges divergent at 70°; a fine and low median septum on low elongated callus in the posterior third of the valve; teeth not preserved; floor pustulose laterally from the muscle field; radial mantle canals impressions preserved anteriorly. Dorsal interior: traces of a very poorly preserved muscle field and mantle canals.
Remarks: Maurer (1885) and Halamski (2009) were misled in interpreting flat-valved and more weakly ornamented individuals of *R. irregularis* as separate species, *Strophomena porrigata* and *Zophostrophia*? *aaatos*, respectively. They are better considered as end members of variation series of the former.
Distribution: *R. irregularis* is known from the Eifelian to Givetian of the Eifel, the Ardennes (Godefroid, 1975, p. 76), the Lahn Syncline, the Holy Cross Mountains, Devonshire, Moravia, and Burma (Harper *et al.*, 1967; Halamski, 2009).

Genus *Parastrophonella* Bubličenko, 1956
Type species: *Strophomena anaglypha* Kayser, 1871; Eifel, Prüm Syncline; Crinoiden-Schicht, Middle Devonian (middle Eifelian?)

Parastrophonella anaglypha (Kayser, 1871)
Fig. 3M, N, U

v* 1871 *Strophomena anaglypha* – Kayser: pp. 628–629, pl. 14, fig. 3 a–f.
v. 1885 *Strophomena anaglypha* Kayser – Maurer, p. 148, pl. 5, fig. 26.
v. 1961b ? *Parastrophonella anaglypha* (Kayser 1871) – Drot, pp. 257–258, pl. 3, figs 1, 2–4.
v. 2009 *Parastrophonella anaglypha* (Kayser 1871) – Halamski, pp. 60–62, text-fig. 7, pl. 5, figs 1–5, 9–13, 16–20, 23–27, 30–47 [*ubi syn.*].

Material: Two ventral valves SMF 94853 and MB unnumbered (V. Ebbighausen's collection) from the *Drotops* beds at Madène el Mrakib.
Other material examined: HLMD-Mr 8837 from Grube Hainau at Waldgirmes (Lahn Syncline), figured by Maurer (1885, pl. 5: 26).
Description: The single available ventral valve is ca. 13 mm wide and 8.9 mm long, mucronate, and ventrally geniculate with a trail ca. 3 mm high; interarea anacline, triangular, low, pseudodeltidium preserved only in the apical part; hinge line denticulate. Traces of poorly preserved, multicostellate ornamentation. Diductor scars deep, extending to about 1/2 of the valve length, slightly flabellate, their external borders forming an angle of ca. 30°. Adductor scars narrow, elongate, separated by a low, rounded median ridge. Valve floor strongly pustulose outside the muscle scars, pustules having even in some cases the appearance of high rows or rounded spines.
Distribution: This Eifelian to Givetian species is known from the Eifel, the Lahn Syncline, the Ardennes, the Holy Cross Mountains, the Pyrenees, the Montagne Noire, Morocco, and Mauritania (Harper and Boucot, 1978; Halamski, 2009, and references therein).

Protodouvillininae gen. et sp. indet.
Fig. 3T

Material: A single fragmentary specimen embedded in limestone (fragment of the ventral valve visible) from Aferdou, ZPAL Bp 68/1/12/1.
Description: The fragmentary ventral valve is >14.4 mm wide and >7 mm long, weakly convex, and subtriangular in anterior view. The umbo is rather fine, weakly incurved, and the posterior margin is straight. The ornamentation consists of radial and subconcentric elements: costae, costellae, and striae form a parvicostellate pattern with ca. 2 cost(ell)ae per mm at 5 mm from the umbo and 5–7 striae between each pair of cost(ell)ae, whereas numerous transverse wrinkles are aligned along presumed growth lines, 3–4 lines of them per mm.

Remarks: This fragmentary specimen is included within the subfamily Protodouvillininae Caster, 1939 on account of characteristic ornamentation. However, choosing between several genera in which it is present, such as, e.g. *Cymostrophia* Caster, 1939 or *Moravostrophia* Havlíček, 1962, is impossible.

Order Productida Sarytcheva and Sokolskaya, 1959
Suborder Chonetidina Muir-Wood, 1959
Family Anopliidae Muir-Wood, 1962

Genus *Devonaria* Biernat, 1966
Type species: *Chonetes zeuschneri* Sobolew, 1909; Skały, Holy Cross Mountains, Skały beds, upper Eifelian

Devonaria sp.
Fig. 4G–K, M

Material: Four incomplete specimens from Aferdou, ZPAL Bp 68/1/11/1–4.
Description: Shell up to ca. 12 mm in length, transverse. Posterior margin straight. Ventral valve moderately to strongly convex with orthocline interarea; dorsal valve concave, interarea not preserved. Anterior commissure rectimarginate. Ornamentation of straight costae and costellae, 3(–4) per mm, the latter appearing by bifurcation.
Remarks: The available material shows some variation in valve convexity and ornamentation density; this is interpreted as intraspecific variation. *Devonaria zeuschneri* (Sobolew, 1909) from the late Eifelian to early Givetian of the Holy Cross Mountains and *D. minuta* (von Buch, 1837) from the Eifelian of the Eifel [reported also from the Zemmour Noir by Sougy, 1964; "*Devonaria* sp., *minuta*? (Buch, 1837)" from Smara by Schemm-Gregory and Jansen (2005)] have coarser ornamentation with, respectively 2 and 1.6 ± 0.2 cost(ell)ae per mm (and not 5–6 as erroneously stated for the former by Halamski, 2009, p. 62; data for *D. minuta* after Struve, 1981b). *D. minutissima* Struve, 1981 [1981b] has a similarly fine ornamentation (3.8 ± 0.45 costellae per mm) but is significantly smaller, its maximal width being about 6 mm (Struve, 1981b).

Suborder Productidina Waagen, 1883
Family Monticuliferidae Muir-Wood and Cooper, 1960

Genus *Poloniproductus* Biernat and Lazarev, 1988
Type species: *Productella varians* Biernat, 1966; Skały, Holy Cross Mountains; Skały beds, upper Eifelian

Poloniproductus varians (Biernat, 1966)
Fig. 5A–U

vp 1964 *Productella subaculeata* (Murchison, 1840) – Sougy, p. 446, pl. 44, fig. 9.
v* 1966 *Productella varians* n. sp. – Biernat: pp. 66–73, text-figs 19–21, pl. 11, figs 1–23, pl. 12, figs 1–16, pl. 13, figs 1–10.
v 1988 *Poloniproductus varians* (Biernat, 1966) – Biernat and Lazarev, pp. 67–68, text-fig. 2, pl. 17, figs 1–5, pl. 18, figs 1–4, pl. 19, figs 1–3, pl. 20, figs 1–2.

Material: Four subcomplete articulated shells, one fragmentary specimen, two ventral valves embedded in limestone, all from Aferdou, ZPAL 68/1/10/1–7; six articulated shells (MB unnumbered; V. Ebbighausen's collection) and a single poorly preserved dorsal interior SMF 94850 from Madène el Mrakib.
Additional material: Sixty specimens, MNHN.F.A48110, 48113, 50411, 50412, mostly fragmentary but including some subcomplete articulated shells and single valves from locality 2118 *sensu* Sougy (1964); two fragmentary specimens, MNHN.F.A48114, west from a small escarpment 2 km NE from Aguelt Oudiate el Khyam; all from Zemmour Noir, Mauritania.
Description: Shell concavo-convex, wider than long, auriculate, up to 27.2 mm in width. Ventral valve strongly convex, umbo very thick, beak strongly incurved. Interareas linear. Radial ornament lacking. Irregular rugae present on both valves. Ventral spines arranged in a row along the hinge line, 2 per mm (spine bases poorly preserved in two specimens), otherwise irregularly distributed on the ventral valve; no dorsal spines. Dorsal interior (Fig. 5C, M, N): cardinal process bifid, the dorsal surface of the lobes with two longitudinal ridges, separated by a median furrow; dental sockets shallow, wide; median septum high, but short. Ventral interior unknown.
Remarks: The described sample is included in *Poloniproductus* on account of irregular rugae on the dorsal valve and absence of ribs. In *Productella* Hall, 1867 the ventral valve is smoother. *Spinulicosta* Nalivkin, 1937 and *Helaspis* Imbrie, 1959 have anterior ribbing. *Devonoproductus* Stainbrook, 1943 has regular rugae and ventral ribbing. The maximal size of the Maïder specimens is slightly greater than that of the Holy Cross ones (27 mm vs. 22 mm; data for the latter after Biernat, 1966), but in view of significant variability of this species expressed even in its name it is judged insignificant.

The examined material of *Productella subaculeata sensu* Sougy (1964, p. 446, pl. 44: 9) is conspecific with *Poloniproductus varians*, as above. However, other Middle Devonian productides may also be present in the Zemmour (*Productella navicella sensu* Sougy, 1964; MNHN.F.A48109, 48111, 48112 from Tighirt, locality 526; Sougy, 1964, p. 388). *Productella subaculeata* reported by Brousmiche (1975) from the Famennian of the Drâa valley is unrelated to the samples described here.
Distribution: Holy Cross Mountains (Eifelian and Givetian; Halamski, 2009 and references therein) and Maïder.

Order Orthotetida Waagen, 1884
Family Chilidiopsidae Boucot, 1959

Genus *Xystostrophia* Havlíček, 1965
Type species: *Terebratulites umbraculum* von Schlotheim, 1820; Gerolstein (Eifel); Middle Devonian (most probably Eifelian)

Xystrostrophia umbraculum (von Schlotheim, 1820)
Fig. 6B, E–K

* 1820 *Terebratulites umbraculum* – von Schlotheim: p. 256.
? 1940 *Streptorhynchus umbraculum* Schloth. – Cottreau, p. 196.
non 1950 *Schellwienella umbracula* Schlotheim – Termier and Termier, pl. 88, figs 24, 25.
? 1950 Indeterminé – Termier and Termier, pl. 89, figs 17–21.
? 1950 *Orthotetes Chouberti* nov. sp. – Termier and Termier, pl. 91, figs 13–18.
v. 1952b *Schellwienella umbracula* (Schlotheim) – Le Maître, pp. 326–327, pl. 2, figs 21–22.
1960 *Schellwienella umbracula* Schlotheim – Gevin, p. 162.
v. 1964 *Schuchertella* sp. e. g. *umbracula* (Schlotheim) – Sougy, pl. 49, fig. 13.
2005 *Xystostrophia* cf. *umbraculum* (von Schlotheim, 1820) – Schemm-Gregory and Jansen, p. 27.
v. 2009 *Xystrostrophia umbraculum* (von Schlotheim 1820) – Halamski, pp. 69–71, pl. 5, figs 6–8, 14, 15, 21, 22, 28, 29, pl. 9, figs 1–31, pl. 16, figs 3, 4, 8, 9, 13, 17, 18 [*ubi syn.*].

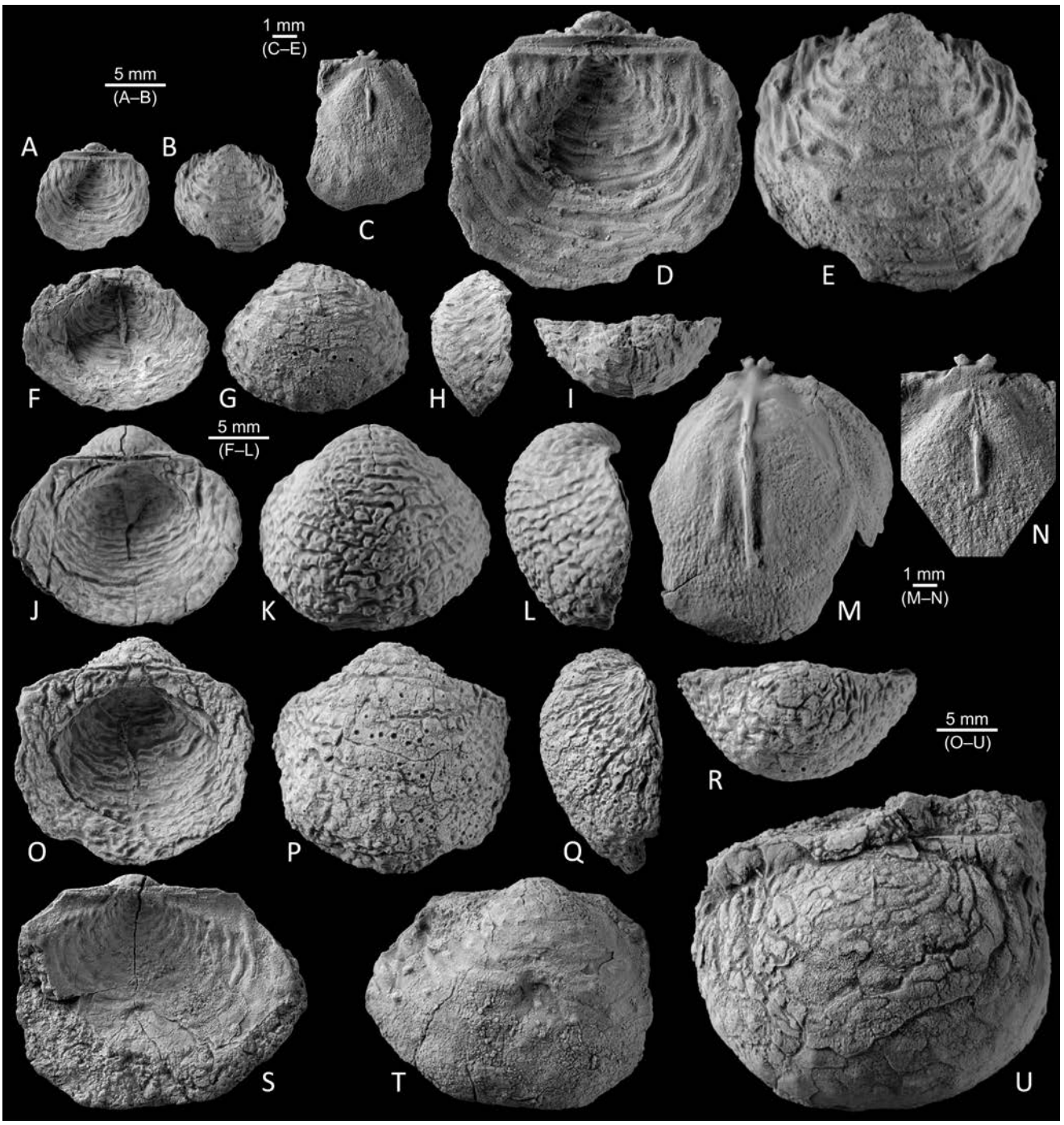


Fig. 5. *Poloniproductus varians* (Biernat, 1966). Aferdou. **A, B, D, E**. Articulated shell ZPAL Bp 68/1/10/1 in dorsal (A, D) and ventral (B, E) views. **C, N**. Incomplete dorsal interior SMF 94850 from Madène el Mrakib. **F–I**. Articulated shell ZPAL Bp 68/1/10/2 in dorsal, ventral, lateral, and posterior views. **J–L**. Articulated shell MNHN.F.A50411 from the locality S2118B *sensu* Sougy (1964) (Zemmour Noir, Mauritania) in dorsal, ventral, and lateral views. **M**. Dorsal interior MNHN.F.A50412 from locality S2118B *sensu* Sougy (1964) (Zemmour Noir, Mauritania). **O–R**. Articulated shell ZPAL Bp 68/1/10/3 in dorsal, ventral, lateral, and posterior views. **S–T**. Articulated shell ZPAL Bp 68/1/10/2 in dorsal and ventral views. **U.** Ventral interior ZPAL Bp 68/1/10/7

Material: Three subcomplete to incomplete articulated shells from Aferdou, ZPAL Bp 68/1/41/1-3; one articulated shell MB.B. 9382b, two isolated dorsal valves SMF 94851 and MB unnumbered (V. Ebbighausen's collection), and a single ventral valve SMF 94852 from the *Drotops* beds at Madène el Mrakib.

Additional material: Articulated shell MNHN.F.R10286 from the "Givetian" of Amgli Zguilma (Mauritania) figured by Sougy (1964); articulated shells MNHN.F.A48119, 48122, 48123, 48124 from the localities 2103T, 346I, 401A, 508G, Zemmour Noir, Mauritania, coll. J. Sougy; two articulated shells MNHN.F.A 48121 from the locality Tf 82, Morocco, coll. H. Hollard; articulated shell GFCL 2623 collected south from Hassi el Motleh (Adrar, Mauritania) figured by Le Maître (1952b, pl. 2: 21–22); articulated shell MB.B.1933 from Jebel Issomour, northern Maïder, coll. V. Ebbighausen, figured by Halamski (2009, pl. 16: 3, 4, 8, 9, 13, 17, 18).

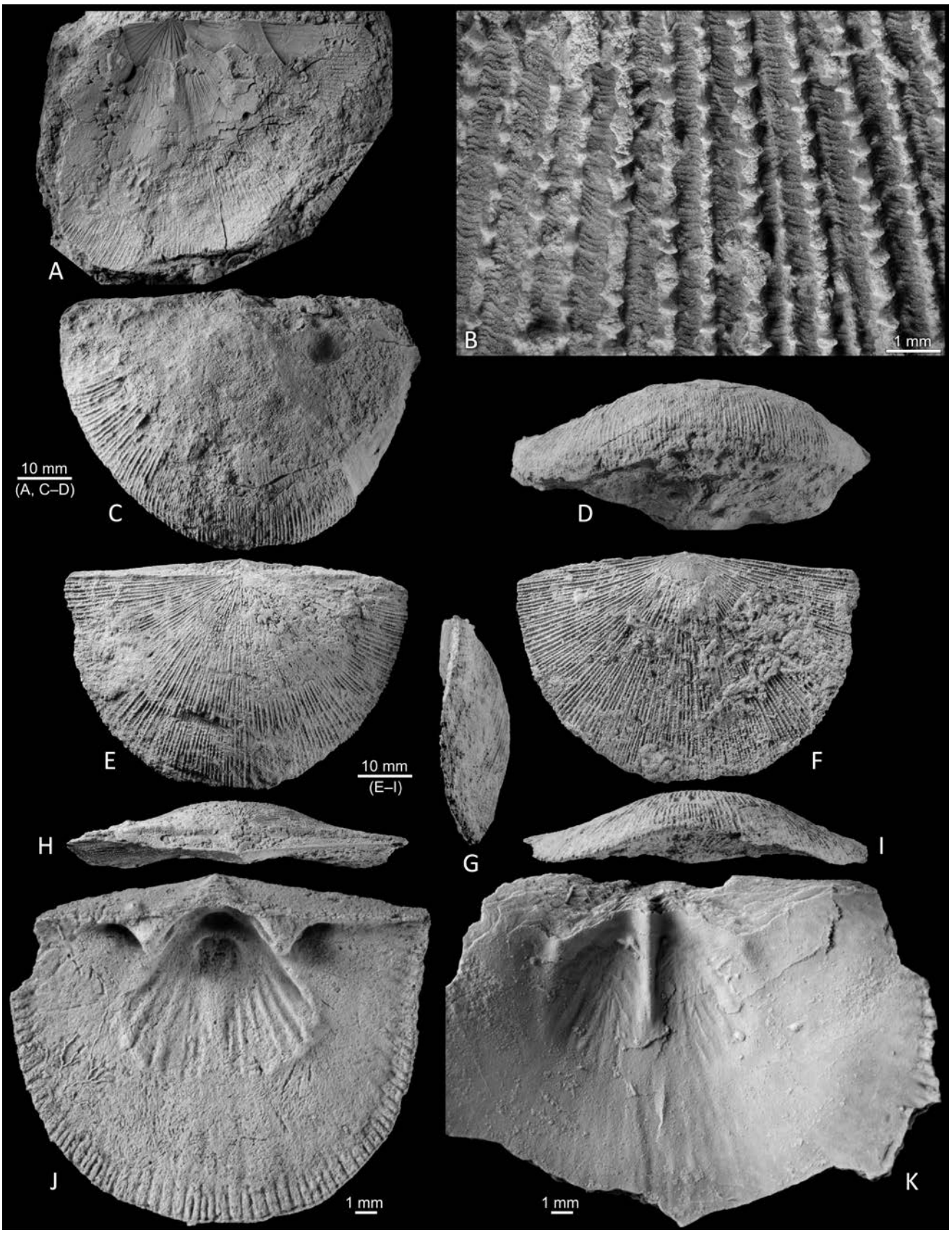
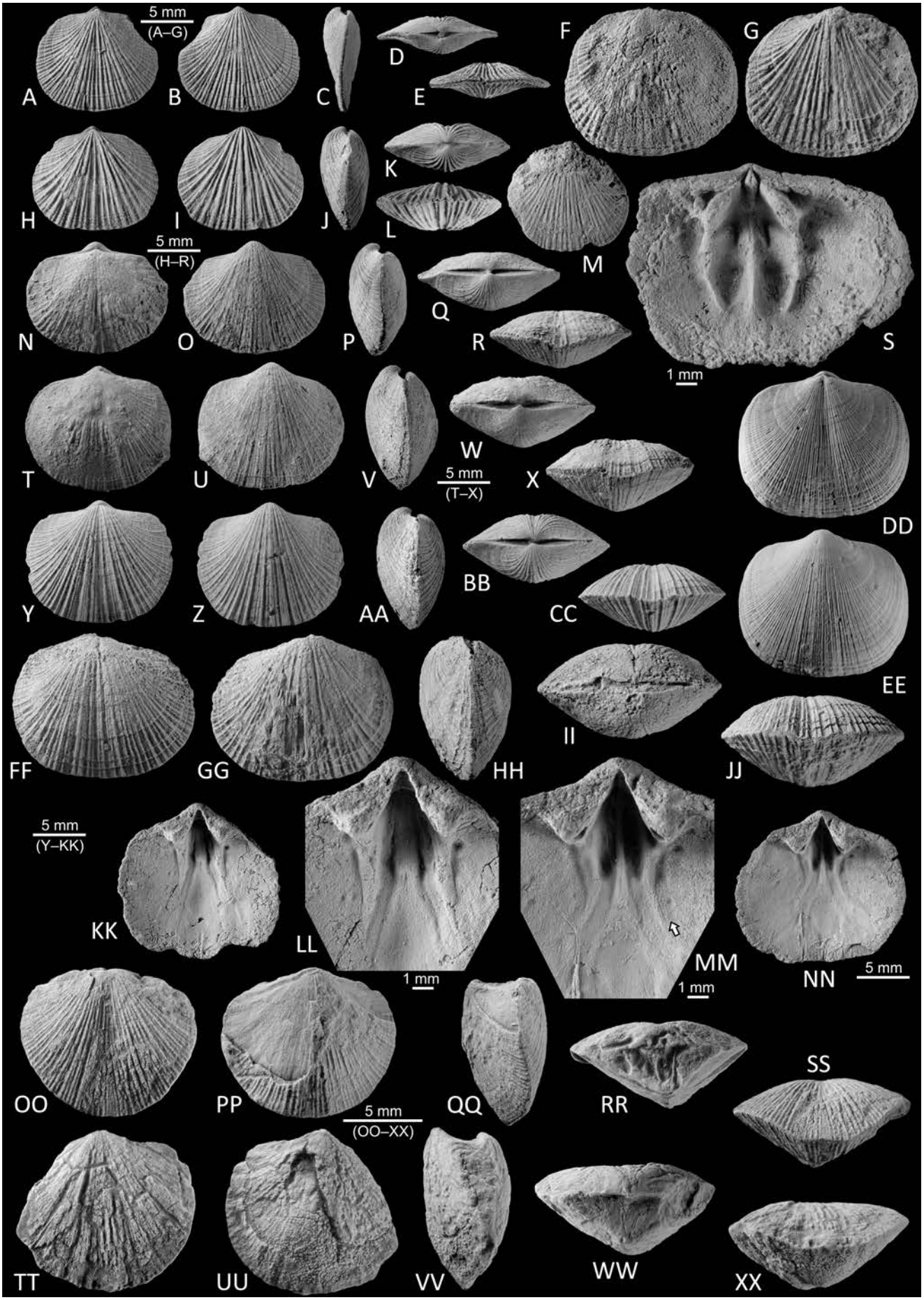


Fig. 6. Middle Devonian Orthotetida from southern Maïder. **A, C–D.** *Iridistrophia* cf. *undifera* (Schnur, 1854 in 1853–54) from Aferdou. A. Fragmentary shell showing traces of dorsal interior. C, D. Incomplete articulated shell in ventral and anterior views. **B, E–K.** *Xystostrophia umbraculum* (von Schlotheim, 1820). B. Microornamentation of the articulated shell ZPAL Bp 68/1/41/2 from Aferdou. E–I. Articulated shell ZPAL Bp 68/1/41/1 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. J. Ventral interior SMF 94852 from Madène el Mrakib. K. Dorsal interior SMF 94851 from Madène el Mrakib


5 mm
(A–G)
A
B
C
D
E
F
G
H
I
J
K
L
M
5 mm
(H–R)
N
O
P
Q
R
S
1 mm
T
U
V
W
5 mm
(T–X)
X
DD
Y
Z
AA
BB
CC
EE
FF
GG
HH
II
JJ
5 mm
(Y–KK)
KK
LL
1 mm
MM
1 mm
NN
5 mm
OO
PP
5 mm
(OO–XX)
QQ
RR
SS
TT
UU
VV
WW
XX

Description: Shell up to 63.3 mm in width, moderately to markedly transverse (width-to-length ratio 1.21 to 1.50), slightly resupinate. Ventral interarea apsacline, high, pseudodeltidium well developed; dorsal interarea anacline, linear. Ornamentation (Fig. 6B) of crenulated costae and costellae, 1–2 per mm.

Ventral interior: teeth stout; dental plates prolonging as ridges bordering muscle scars; diductor scars large, radially striate, bisected by a low median septal ridge; adductor scar situated medially, rounded; valve floor elevated posteriorly to the adductor scar. Dorsal interior: cardinal process bifid with two ventrally directed lobes, posteriorly with four ridges visible in the pedicle opening; muscle scars strongly sculptured, subdivided by a low median ridge.

Remarks: It may be useful to note that the presumed Givetian age of a specimen of *X. umbraculum* from Jebel Issomour in the northern Maïder (Halamski, 2009, pl. 16) was based on a preliminary investigation of that section; moreover, the specimen itself was collected from rubble (†V. Ebbighausen, pers. comm., 2008). In any case, any specimens of this species, for which an accurate age determination can be given, are from the Eifelian (see Halamski, 2009 for details). The Givetian age given for the Zemmour material by Sougy (1964) might also perhaps result from a misidentification of an *Anarcestes* as a *Wernerоceras* (Dumestre and Illing, 1967), giving a too young age for an important correlation horizon (see also Basse, 2012, p. 30). Contrary to the opinion of Racheboeuf *et al.* (2001, p. 146), *Schellwienella umbracula sensu* Le Maître (1952b) from the Mauritanian Adrar represents *X. umbraculum* and not a representative of *Iridistrophia*.

Distribution: Eifel, Holy Cross Mountains, Maïder, Zemmour Noir, Adrar, Turkestan, Burma (Halamski, 2009, supplemented); Middle Devonian.

Genus *Iridistrophia* Havlíček, 1967
Type species: *Orthis umbella* Barrande, 1848, Barrandien, Bohemia; upper Lochkovian

Iridistrophia cf. *undifera* (Schnur, 1854 in 1853–54)
Fig. 6A, C–D

cf. 1854 *Orth*[*is*] *undifera* n. sp. – Schnur: p. 217, pl. 45, fig. 1a–d.
v**.** 2009 *Iridistrophia* cf. *undifera* (Schnur, 1854 *in* 1853–54) – Halamski, p. 71–72, pl. 8, figs 1–11, pl. 16, figs 5–7, 11, 12, 16 [*ubi syn.*].

Material: Four incomplete articulated shells, three fragments, three poorly preserved interiors, one ventral and two dorsal, all from Aferdou, ZPAL Bp 68/1/9/1–9.

Additional material: fragmentary ventral valve MNHN.F.A48127 from the locality TM 809, Maïder?, Morocco, coll. H. Hollard.

Description: Shell up to ca. 80 mm in width, semielliptic in outline, transverse (width-to-length ratio 1.38–1.63), dorsibiconvex. Posterior margin straight. Dorsal valve strongly convex. Ventral valve weakly convex, interarea high. Ornamentation of smooth costae and costellae, 1–2 per mm at anterior margin; in marginal region fila, not continuous through the costellae. Dorsal interior: a short median septum occupies up to 1/4 of the valve length. Ventral interior: traces of adductors wide, distally flabellate; their exterior borders diverging at ca. 80°.

Remarks: This characteristic brachiopod is very similar (and, in consequence, considered conspecific) to *Iridistrophia* cf. *undifera* from the Middle Devonian of the Eifel and of the Holy Cross Mountains (Halamski, 2009). The type material of *I. undifera* from the Eifel is lost, wherefore the use of open nomenclature is justified.

Distribution: Eifel, Holy Cross Mountains, Maïder; Middle Devonian.

Class Rhynchonellata Williams *et al.*, 1996
Order Orthida Schuchert and Cooper, 1932
Family Rhipidomellidae Schuchert, 1913

Genus *Aulacella* Schuchert and Cooper, 1931
Type species: "*Orthis eifeliensis* Schnur, 1853" (misspelling for *eifliensis*; = *Orthis prisca* Schnur, 1851); Eifel, Middle Devonian

Aulacella prisca (Schnur, 1851)
Fig. 7A–M

v* 1851 *O*[*rthis*] *prisca* nob. – Schnur: p. 13.
1950 *Aulacella interlineata* Sowerby – Termier and Termier, pl. 81, figs 19–26.
v**.** 1959 *Aulacella eifeliensis* (de Verneuil) – Biernat, pp. 26–35, text-figs 9, 10, text-pl. 3, pl. 1, figs 10–15, pl. 2, figs 1–15, pl. 3, figs 9, 10, pl. 12, figs 1, 2.
v**.** 1964 *Aulacella interlineata* – Sougy, p. 437, pl. 42, figs 18–19.
v**.** 2009 *Aulacella prisca* (Schnur, 1851) – Halamski, pp. 74–77, pl. 11, figs 1–36, pl. 14, figs 3–10, 13–16, 21–27, 29, 30, text-fig. 11 [*ubi syn.*].

Material: Thirty-one for the most part complete specimens from Aferdou, ZPAL Bp 68/1/13/1–31; one poorly preserved from Maharch, ZPAL Bp 68/2/13/1; a single juvenile from Madène el Mrakib, MB unnumbered (V. Ebbighausen's collection).

Additional material: Articulated shell MNHN.F.R10268 and internal mould MNHN.F.R10269, both from the "Givetian" of Bir Aïdiate (Zemmour Noir, Mauritania), figured by Sougy (1964, pl. 42: 18–19); over twenty five articulated shells MNHN.F.A48143 from a small escarpment 2 km ENE from Aguelt Oudiate el Khyam (section D-13, levels 7–8), Zemmour Noir, Mauritania,

Fig. 7. Middle Devonian Orthida from northwestern Africa. **A–M.** *Aulacella prisca* (Schnur, 1851). A–E. Articulated shell ZPAL Bp 68/1/13/1 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. F, G. Large articulated shell ZPAL Bp 68/1/13/3 from Aferdou in dorsal and ventral views. H–L. Articulated shell ZPAL Bp 68/1/13/2 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. M. Incomplete articulated shell ZPAL Bp 68/2/13/1 from Maharch in ventral view. **N–NN.** *Tyersella canalicula* (Schnur, 1851). N–R. Articulated shell ZPAL Bp 68/1/14/1 in dorsal, ventral, lateral, posterior, and anterior views. S. Dorsal valve ZPAL Bp 68/1/14/5. T–X. Articulated shell ZPAL Bp 68/1/14/2 in dorsal, ventral, lateral, posterior, and anterior views. Y–CC. Articulated shell ZPAL Bp 68/1/14/3 in dorsal, ventral, lateral, posterior, and anterior views. DD, EE. Articulated shell MNHN.F.A50413 from a small escarpment 2 km ENE from Aguelt Oudiate el Khyam; section D13, bed 7–8, level 80 *sensu* Sougy (1964) (Zemmour Noir, Mauritania). FF–JJ. Articulated shell ZPAL Bp 68/1/14/4 in dorsal, ventral, lateral, posterior, and anterior views. KK, LL. Ventral valve SMF 94848, interior (KK) and enlargement (LL) of the muscle area. MM, NN. Ventral valve SMF 94849, interior (NN) and enlargement (MM) of the muscle area (vasculum myare arrowed). **OO–XX.** *Phragmophora schnuri* Cooper, 1955. Articulated shells from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. OO–SS. Specimen ZPAL Bp 68/1/16/1. TT–XX. Specimen ZPAL Bp 68/1/16/2

"upper Couvinian", bed 80, coll. J. Sougy; two articulated shells, one ventral and two dorsal valves, and some fragments MNHN.F. A48099 from the locality Zl 16 (H 683), Morocco, coll. H. Hollard.

Description: Shell subelliptic in outline, transverse, up to 16.3 mm in width, ventribiconvex or more seldom aequibiconvex. Maximal width anteriorly to midlength. Anterior commissure straight to broadly and very shallowly unisulcate. Dorsal valve with a shallow sulcus, slit-like posteriorly, flat-bottomed medially, and disappearing anteriorly. Dorsal interarea orthocline, linear; ventral one triangular, apsacline, umbo weakly incurved. Ornamentation of radial costae and costellae, (1–)2(–3) per mm at anterior margin. Interior not studied.

Remarks: Variability of this widespread Middle Devonian species was discussed in detail by Biernat (1959) and Halamski (2009). *Aulacella interlineata* (Sowerby, 1840) is a Famennian species present in Tafilalt (Halamski, unpublished data), but the report from the Middle Devonian of Zemmour Noir in Mauritania (Sougy, 1964; most probably also that of Termier and Termier, 1950 from the same region) concerns *A. prisca* (Halamski and Baliński, 2009).

Distribution: Eifel, Holy Cross Mountains, Maïder, Mauritania, Burma (Halamski, 2009, supplemented; reported also from Belgium, Spain, and Iran); Eifelian and Givetian.

Family Dalmanellidae Schuchert and Cooper, 1931

Genus *Tyersella* Philip, 1962

Type species: *Tyersella typica* Philip, 1962; Victoria, Australia; Siluro-Devonian boundary beds

Tyersella canalicula (Schnur, 1851)

Fig. 7N–NN

v* 1851	*O*[*rthis*] *canalicula*, n. sp. – Schnur: p. 13
vp 1885	*Strophomena* conf. *pecten* Linné sp. – Maurer, pp. 150–151, *non* pl. 6, fig. 3.
? 1964	*Isorthis* sp. e. g. *tetragona* (Roemer, 1844) – Sougy, p. 437, *non* pl. 36, fig. 7.
v. 2009	*Tyersella canalicula* (Schnur 1851) – Halamski, pp. 77–79, text-fig. 12, pl. 12 figs 1–8, 28, 29, 31–34, pl. 13, figs 1–25 [*ubi syn.*].

Material: Twenty-four complete or subcomplete articulated shells, a single incomplete dorsal valve from Aferdou, ZPAL Bp 68/1/14/1–22; one articulated shell, one dorsal valve (MB unnumbered, V. Ebbighausen's collection), and two subcomplete ventral valves SMF 94848, 94849 from Madène el Mrakib.

Other material examined: Ventral valve HLMD-Mr 8835, embedded in limestone from Grube Hainau at Waldgirmes (Lahn Syncline).

Description: Shell subrectangular in outline, transverse, aequibiconvex to moderately ventribiconvex, up to 21.1 mm in width. Margins rounded, antero-lateral more so than the postero-lateral. Dorsal valve with a flat-bottomed, U-, V-, or slit-shaped median sulcus. Ventral valve triangular to semielliptic in anterior view; interarea apsacline to anacline, rather high; umbo thick, incurved. Anterior commissure weakly unisulcate; tongue subtrapezoidal to V-shaped, low, narrow to moderately broad. Ornamentation uniformly to unequally costellate, costae and costellae 1–3 per mm at anterior margin.

Ventral interior: teeth stout, sometimes with cavities on the anterior part of the admedial surface; dental plates prolonging as thick subparallel or slightly anteriorly converging ridges bordering the diductor scars; the latter narrow, bisected by a low to distinct median ridge, first undivided, then with a median furrow, anteriorly bifurcating. Vascula media situated anteriorly to the muscle field; a pair of elongate scars (one of them arrowed in Fig. 7MM) situated antero-laterally to the muscle field might represent vascula myaria. Dorsal interior: cardinal process small; brachiophores strong, flattened, divergent at ca. 80–100°; dental sockets very deep. Muscle area 4.6 mm long in a specimen 11.7 mm long, bordered by two strong C-shaped ridges and subdivided by a strong median septum; posterior diductor scars narrow, anterior ones broad, separated by an indistinct ridge.

Remarks: The material from the "upper Couvinian" of the Zemmour Noir (over fifteen articulated shells and isolated dorsal and ventral valves MNHN.F.A48142, 50413 from a small escarpment 2 km ENE from Aguelt Oudiate el Khyam; section D-13, levels 7–8; bed 80, coll. J. Sougy) is identical in shape to *T. canalicula*, but has finer ornamentation (Fig. 7DD, EE). It is tentatively considered conspecific to the above-mentioned species.

Distribution: This species is known from the Holy Cross Mountains, Eifel, and from Maïder; most probably its stratigraphic range includes only the Eifelian (see Halamski, 2009 for details). Walmsley and Boucot (1975, p. 61) report an isolated occurrence of this taxon (neither description nor figure) from the Emsian of Bathurst Island (Arctic Canada); this report is considered doubtful.

Genus *Phragmophora* Cooper, 1955

Type species: *Phragmophora schnuri* Cooper, 1955; Gerolstein, Eifel; crinoid beds (Eifelian)

Phragmophora schnuri Cooper, 1955

Fig. 7OO–XX

v* 1955	*Phragmophora schnuri* Cooper, n. sp. – Cooper: p. 52, pl. 12b, figs 12–26, pl. 14a, figs 1–7 [*ubi syn.*].
v. 2009	*Phragmophora schnuri* Cooper, 1955 – Halamski, pp. 81–83, text-fig. 15, pl. 10, figs 39–48, pl.13, figs 26–48 [*ubi syn.*].

Material: Two subcomplete articulated shells from Aferdou, ZPAL Bp 68/1/16/1–2.

Description: Shell up to 11 mm in width, wider than long, ventribiconvex. Posterior margin straight, anterior commissure broadly and shallowly unisulcate. Dorsal valve moderately convex, with a median sulcus, slit-like posteriorly, broad, shallow, and U-shaped anteriorly. Ventral valve subpyramidal, interarea apsacline, high. Ornamentation of radial costae and costellae, 3–5 per mm at anterior margin.

Remarks: The species was described in detail, including its intraspecific and ontogenetic variability, by Biernat (1959) and Halamski (2009).

Distribution: This species is known from the Eifelian of the Holy Cross Mountains, Eifel, and Maïder (Halamski, 2009).

Family Schizophoriidae Schuchert and LeVene, 1929

Genus *Schizophoria* King, 1850

Type species: *Conchyliolithes Anomites resupinatus* Martin, 1809; Derbyshire; Lower Carboniferous

Schizophoria schnuri Struve, 1965 [1965a]

Fig. 8A–E, H–L

* 1965a	*Schizophoria schnuri* n. sp. – Struve: pp. 202–208, pl. 19, fig. 4; pl. 20, pl. 21.
? 1995	*Schizophoria* sp. – Struve, fig. 27.
v. 2012	*Schizophoria* (*Schizophoria*) *schnuri* Struve, 1965 – Halamski, pp. 352–359, figs 3P–II, 4A–G, I, M, Q–EE, 5–7.

Material: A single complete articulated shell and four fragmentary ones, one subcomplete ventral valve, ZPAL Bp 68/1/15/1–6,

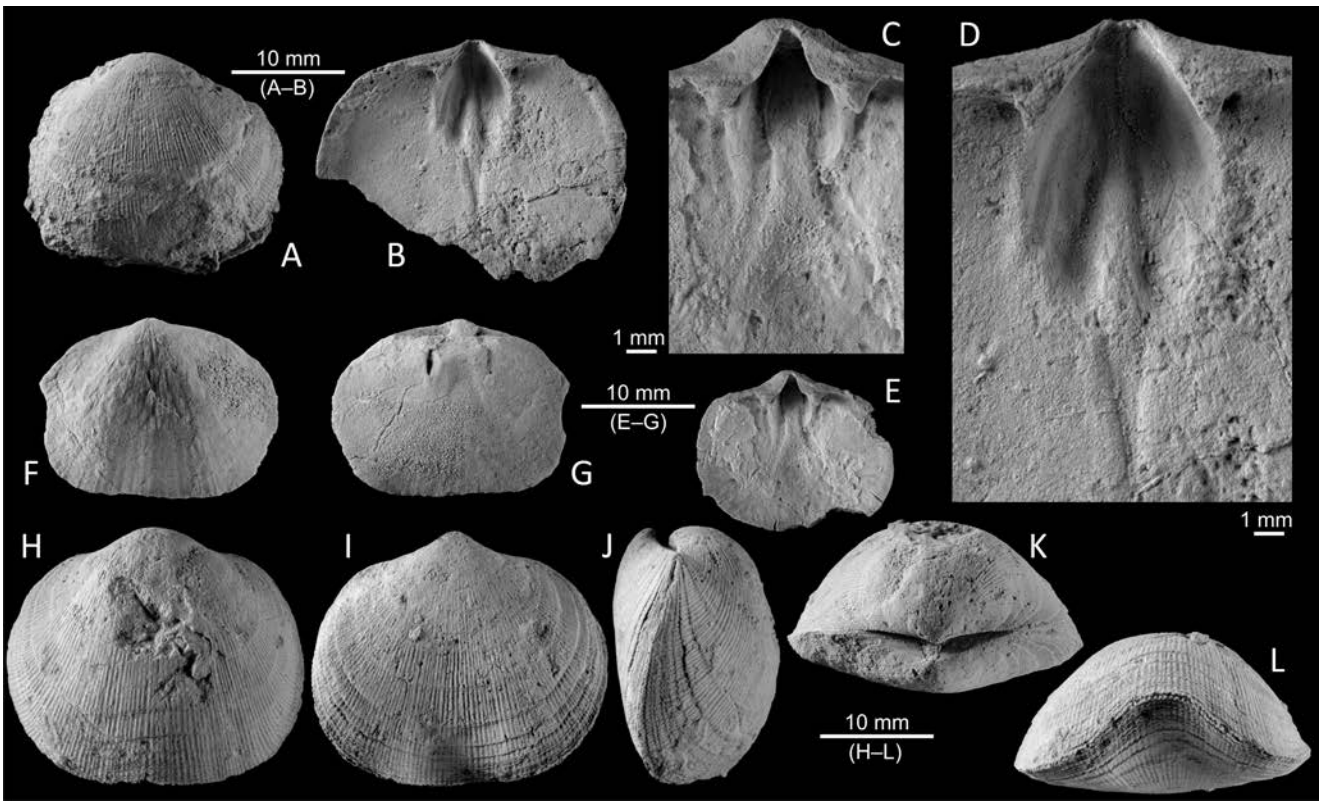


Fig. 8. Middle Devonian Orthida from southern Maïder. **A–E, H–L.** *Schizophoria schnuri*. A. Dorsal valve ZPAL Bp 68/1/15/1 from Aferdou in dorsal view. B, D. Ventral interior SMF 94860 from Madène el Mrakib. C, E. Ventral interior SMF 94860. H–L. Articulated shell SMF 94862 from Madène el Mrakib in dorsal, ventral, lateral, posterior, and anterior views. **F–G.** *Schizophoria*? sp. Incomplete internal mould ZPAL Bp 68/2/42/1 from Maharch in dorsal and ventral views

two complete articulated shells and a ventral valve from Madène el Mrakib, SMF 94860, 94862, 94863. Forty articulated shells and a single ventral valve from Madène el Mrakib, SMF 94899 and MB unnumbered (V. Ebbighausen's collection).

Description: Shell subelliptic in outline, transverse, dorsibiconvex, up to 38.2 mm in width. Maximal width at mid-length or slightly anteriorly. Dorsal interarea apsacline, ventral one anacline. Anterior commissure broadly uniplicate. Ornamentation of radial costae and costellae, 2–3 per mm at anterior margin. Ventral interior: teeth moderately strong to stout; muscle field elongate, attaining one third to two fifth of the valve length, bordered by a ridge, slightly medially incised and subdivided either anteriorly or throught its entire length by a low median ridge. Dorsal interior unknown.

Remarks: *Schizophoria schnuri* is a long-lasting species, subdivided into a series of chronosubspecies (Struve, 1965a; Halamski, 2012). The material from Aferdou is not identifiable at the subspecies level. The material from Madène el Mrakib shows intergrading of morphotypes, referable to more than one subspecies, as delimited by Struve (1965a), a situation similar to that at Skały in the Holy Cross Mountains (Halamski, 2012).

Distribution: Eifel, Ardennes, Holy Cross Mountains, Moravia, Maïder, Burma (Halamski, 2012).

Schizophoria? sp.
Fig. 8F, G

Material: A single incomplete specimen from Maharch, ZPAL Bp 68/2/42/1.

Description: The single available specimen is elliptic in outline, ca. 23 mm wide, >16 mm long, and >8 mm thick, weakly dorsibi- convex. Dorsal valve with a very shallow V-shaped sulcus. On the dorsal valve and in the anterior region of the ventral valve poorly preserved costellate ornamentation with ca. 1–2 costellae per 2 mm at anterior margin. Traces of subparallel dental plates.

Remarks: *Schizophoria*? sp. differs from *Schizophoria schnuri* from Aferdou in the presence of a dorsal sulcus and ornamentation density.

Order Pentamerida Schuchert and Cooper, 1931
Family Gypidulidae Schuchert and Le Vene, 1929

Genus *Gypidula* Hall, 1863

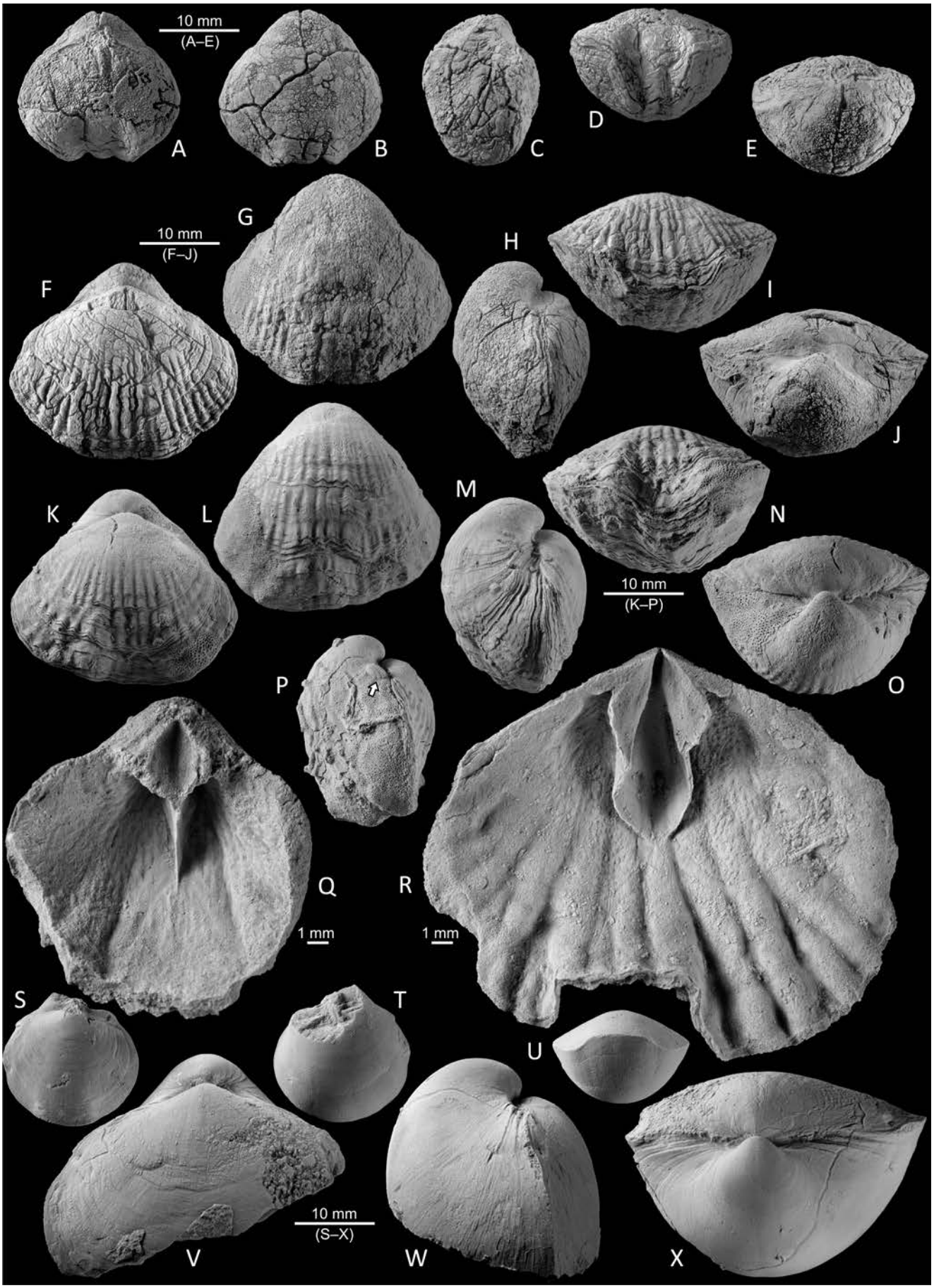
Type species: *Gypidula typicalis* Amsden, 1953 (= *Pentamerus occidentalis* Hall, 1858 *non* Hall, 1852); Independence, Iowa; Hamilton Group (Middle Devonian)

Gypidula biplicata (Schnur, 1851)
Fig. 9A–E

v* 1851 *P*[*entamerus*] *biplicatus*, n. sp. – Schnur: p. 8
v. 1966 *Gypidula* (*Gypidula*) cf. *biplicata* – Biernat, pp. 29–30 pl. 1, fig. 11.

Material: A single complete, slightly decorticated shell from Aferdou, ZPAL Bp 68/1/2/1.

Description: The single available shell is subpentagonal in outline, strongly ventribiconvex, 20.4 mm wide, 19.0 mm long, and 14.9 mm thick; maximal width at anterior third of the shell length. Dorsal valve moderately convex, subtriangular in anterior view, with a flat-bottomed sulcus in the anterior third; a broad median plica present in the immediate proximity of the anterior margin. Ventral valve strongly convex; umbo thick, beak strongly incur-


10 mm
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ved; two low plicae, separated by a shallow furrow, present in the immediate proximity of the anterior margin. Anterior commissure plicosulcate, tongue subtrapezoidal, 9.3 mm wide at the base and 4.0 mm at the top, 6.7 mm high. Shell smooth. Interior not studied.
Distribution: Eifel, Holy Cross Mountains, Maïder, possibly Armenia (Abramân, 1974); Middle Devonian.

Genus *Glyptogypa* Struve, 1992
Type species: *Pentamerus galeatus* var. *multiplicata* Roemer, 1856, Schwiersheim near Prüm, Eifel; Middle Devonian (probably Eifelian)

Glyptogypa multiplicata (Roemer, 1856)
Fig. 9F–R

* 1856 *Pentamerus galeatus* var. *multiplicata* – Roemer: p. 352, pl. 2, fig. 9a-c.
vp 1964 *Gypidula* sp. – Sougy, p. 455, pl. 44, fig. 4a–c; *non* p. 358, pl. 33, fig. 12.
v**.** 1966 *Gypidula* (*Ivdelinia*) sp. cf. G. (*Ivdelinia*) *multiplicata* – Biernat, pp. 33–34, pl. 2, figs 2–4.
v**.** 1995 *Glyptogypa* sp., Gr. *multiplicata* (C. F. Roemer 1844) – Struve, p. 100, fig. 31.
v**.** 1995 *Gypidula* sp. cf. *chouberti* Termier and Termier 1950 – Struve, p. 100, fig. 30.
1995 *Glyptogypa* cf. *multiplicata* (Roemer, 1856) – Godefroid, pp. 83–85, fig. 6a–e.

Material: One hundred and thirty-one complete or subcomplete (often deformed) articulated shells SMF 94864–94868 and MB unnumbered (V. Ebbighausen's collection), three ventral, SMF 94854–94855, 94870, and six dorsal valves, SMF 94856–94859, 94869, 94871, and over thirty fragments from the *Drotops* beds at Madène el Mrakib; a single articulated shell ZPAL Bp 68/1/1/1 from Aferdou.
Additional material: Articulated shells SMF 54779, 54781 from the Eifelian of Jebel Issomour (Fp. 2999, northern Maïder), figured by Struve (1995); one subcomplete articulated shell and one fragment MNHN.F.R10274 from the "Givetian" of Aguelt Oudiate (Zemmour, Mauritania), coll. J. Sougy.
Description: Shell up to 31.7 mm in length, nearly as wide as long (width-to-length ratio 0.84 to 1.19, mean 1.02; N = 21), moderately ventribiconvex, sometimes slightly asymmetric; maximal width in the anterior third. Dorsal valve broadly triangular, with a flat-bottomed sulcus in the anterior half; interarea obscured by overhanging umbo. Ventral valve parabolic in anterior profile, with a thick umbo and a strongly incurved beak; no fold; palintrope high, concave, with well marked beak ridges, apsacline near the hinge margin. Anterior commissure unisulcate; tongue subtrapezoidal, in a single case subtriangular, its width 0.29 to 0.46 (mean 0.35; N = 20) of that of the shell, its height 0.17 to 0.55 (mean 0.35; N = 19) of the shell thickness. Ornamentation of irregular costae and costellae, the latter arising by both bifurcation and intercalation, 13–24 (mean 18; N = 18) on the dorsal valve, 17–30 (mean 21; N = 19) on the ventral valve. Costellae sometimes disappear before reaching the anterior margin.

Ventral interior (Fig. 9Q): spondylium supported by a median septum, the latter thick posteriorly, high and blade-like anteriorly. Dorsal interior (Fig. 9R): muscle area extending at most to the one third of the valve length, inner hinge plates converging on the valve floor, coalescent with crural bases, outer hinge plates flattened, rather wide, separated by a rounded indentation from wide, flattened outer socket ridges. Gonoglyphs on dorsal and ventral valve floors adjacent to muscle fields.
Remarks: Halamski (unpublished) distinguished *G. multiplicata* (Roemer, 1856) from central Europe (Eifel, Holy Cross Mountains) and *G. chouberti* (Termier and Termier, 1950) from Northern Africa (Morocco, Mauritania), on the basis of ornamentation density: in the samples investigated, the quotient of ventral costae number and the shell width varied between 0.81 and 1.26 for the former presumed species and between 1.30 and 1.59 for the latter. The value for the investigated specimen (0.64 to 1.26, mean 0.82; N = 20) falls clearly within the variation range of the European sample. Given the uncertainty on exact stratigraphic position of these brachiopods, it is unclear, whether the two morphotypes represent separate members of an evolutionary lineage, co-occurring species, or only end members of a continuous variation series.

Glyptogypa multiplicata is probably the species, which is the most encrusted by epizoans (bryozoans, microconchids, favositid tabulates) in the material studied (Fig. 9K–P). This is arguably related to its large size and strong ornamentation, as shown by Zapalski (2005) for coeval deposits of the Holy Cross Mountains.
Distribution: Rhenish Slate Mountains, Ardennes (Godefroid, 1995), Holy Cross Mountains, Maïder, and Mauritania; Middle Devonian.

Genus *Ivdelinia* Andronov, 1961
Type species: *Gypidula ivdelensis* Khodalevich, 1951, Ivdel, Eastern Urals; Emsian–Eifelian

Ivdelinia (*Ivdelinia*) *pulchra* Franchi, Schemm-Gregory and Klug, 2012
Figs 10A–P, 11

v**.** 1995 *Ivdelinia* sp., cf. *formosa* (Schnur, 1851) – Struve, p. 100, figs 28, 29.
v**.** 1998 *Ivdelinia* sp. – Kaufmann, p. 59, pl. 13, fig. 11.
* 2012 *Ivdelinia pulchra* sp. nov. – Franchi *et al.*: pp. 5–6, fig. 3.
. 2013 *Ivdelinia pulchra* – Tessitore *et al.*, p. 25, text-figs 2 [*p.p.*], 3, 5, 11.

Material: Over one hundred articulated shells from Aferdou, mostly from the *Ivdelinia* bed, a large part of them complete and well preserved; collection number ZPAL Bp 68/1/3.
Additional material: articulated shells SMF 54776, 54777 from Jebel Issomour (northern Maïder), figured by Struve (1995).
Description: Shell up to 47.5 mm in width, slightly transverse through aequidimensional to slightly elongate, strongly ventribiconvex. Ventral valve strongly convex, umbo swollen, beak strongly incurved, nearly touching the dorsal valve; a low and flat fold in the anterior half. Ventral palintrope smooth, as wide as the

Fig. 9. Middle Devonian Pentamerida from southern Maïder. **A–E.** *Gypidula biplicata* (Schnur, 1851), Aferdou. Articulated shell ZPAL Bp 68/1/2/1 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. **F–R.** *Glyptogypa multiplicata* (Roemer, 1856). F–J. Articulated shell ZPAL Bp 68/1/1/1 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. K–O. Articulated shell SMF 94867 from Madène el Mrakib in dorsal, ventral, lateral, posterior, and anterior views. P. Articulated shell SMF 94871 from Madène el Mrakib in lateral view. Q. Ventral interior SMF 94855 from Madène el Mrakib. R. Dorsal interior SMF 94857 from Madène el Mrakib. **S–X.** *Antirhynchonella sublinguifera* (Maurer, 1885). S–U. Fragmentary shell ZPAL Bp 68/2/18/1 from Maharch in dorsal, ventral, and anterior views. V–X. Fragmentary shell ZPAL Bp 68/1/18/1 from Aferdou in dorsal, lateral, and posterior views

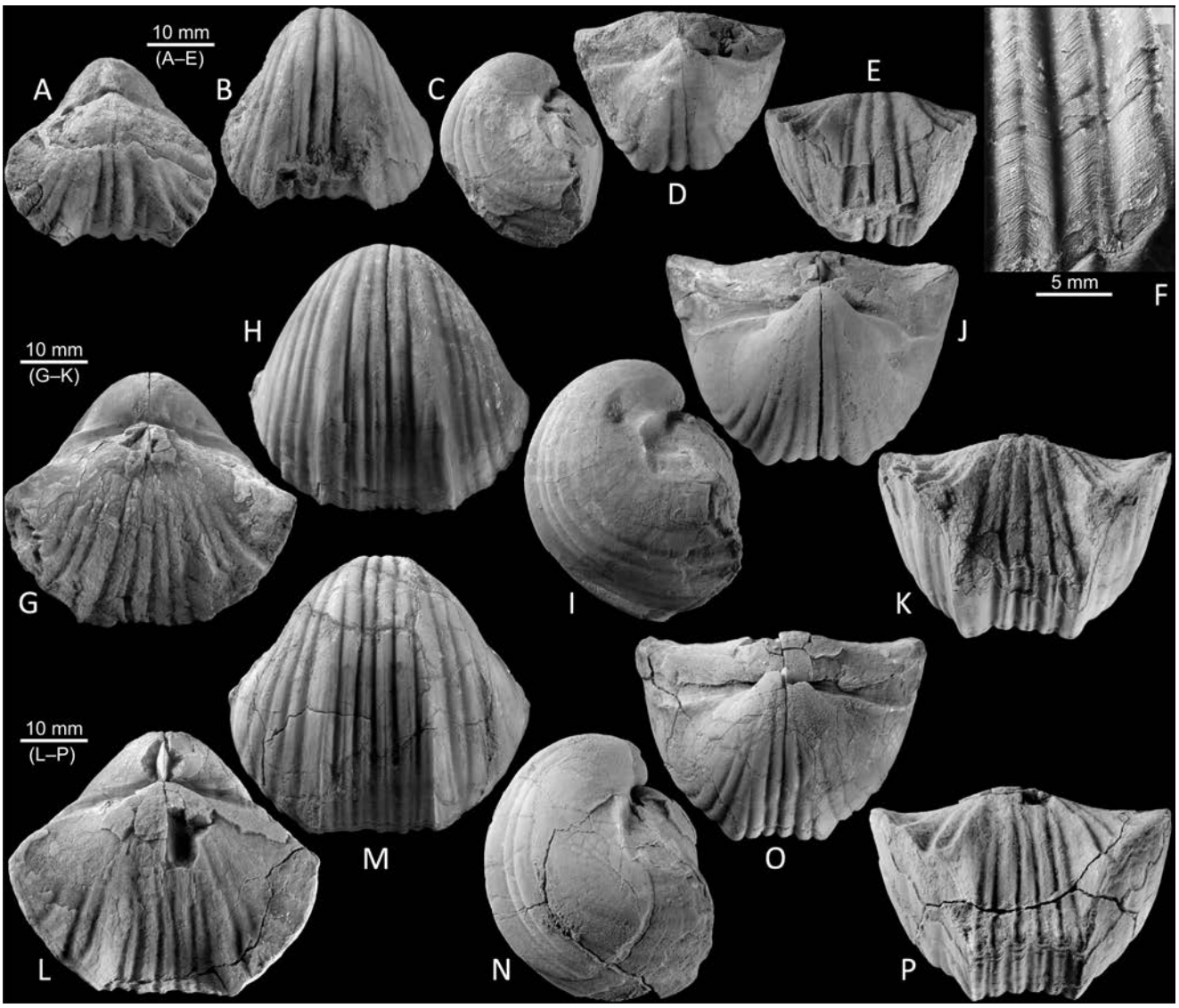


Fig. 10. *Ivdelinia* (*Ivdelinia*) *pulchra* Franchi, Schemm-Gregory and Klug, 2012. **A–E**. A middle-sized articulated shell ZPAL Bp 68/1/3/1 from marls overlying the lumachelle in Aferdou in dorsal, ventral, lateral, posterior, and anterior views. **F–J, K–O**. Two large articulated shells ZPAL Bp 68/1/3/2,3 from the lumachelle in Aferdou in dorsal, ventral, lateral, posterior, and anterior views. **P**. Magnification of the growth lines observed in the anterior region of a ventral valve of the specimen ZPAL Bp 68/1/3/4 from the lumachelle

valve, medially lower, higher in marginal regions, separated from the rest of the valve by an acute ridge. Dorsal valve moderately convex postero-medially, with elevated flanks; sulcus flat and shallow, visible in the anterior half. Dorsal palintrope absent. Anterior commissure unisulcate, deflection rectangular to trapezoidal, rather low to moderately high, occupying a half to two-third of the shell width.

Ornamentation of thick, rounded costae and costellae, observable on both valves from about 1 cm from the umbones, separated by narrower furrows. Costae and costellae bisected by shallow furrows, in some cases a cost(ell)a passes in this way into a pair of costellae; up to two bifurcations of a primary costa have been observed. Costae bordering the ventral fold are stronger than the other ones. Costae and costellae 3–4 on the fold, 4–5 in the sulcus, up to 5 on each lateral flank. Concentric growth lines were observed at anterior margin, 3–4 per mm (Fig. 10F).

Ventral interior: shell substance thick; median septum well developed, supporting the spondylium posteriorly, then disappearing. Dorsal interior: hinge plates very long, extending about 11 mm anteriorly in the sectioned shell; outer hinge plates converging on the valve floor and forming cruralium; anterior tips of the inner hinge plates unsupported give rise to the crescentic in cross section crura (Fig. 11).

Remarks: *Ivdelinia pulchra* is included within the subgenus *I.* (*Ivdelinia*) on account of the presence of a well developed ventral septum, despite its external similarity to *I.* (*Ivdelinella*) *ellesmerensis* Brice, 1982 from the Emsian–Eifelian of Canada (Brice, 1982), the type species of the subgenus *Ivdelinella* Brice, 1982 [flattened costae, as opposed to strongly raised costae or plicae in *I.* (*Ivdelinia*); Blodgett *et al.*, 2002]. This species was identified in the Holy Cross Mountains, where it occurs as a rare component in the Eifelian–Givetian boundary beds (Halamski, 2004a). The valid name was introduced by Franchi *et al.* (2012), on the basis of the external morphology of thirteen specimens. Detailed description of external and internal morphology and synonymy limited to North African occurrences of the species are presented herein. The palaeoecology of the *Ivdelinia* brachiopod bed was dealt with by Tessitore *et al.* (2013).

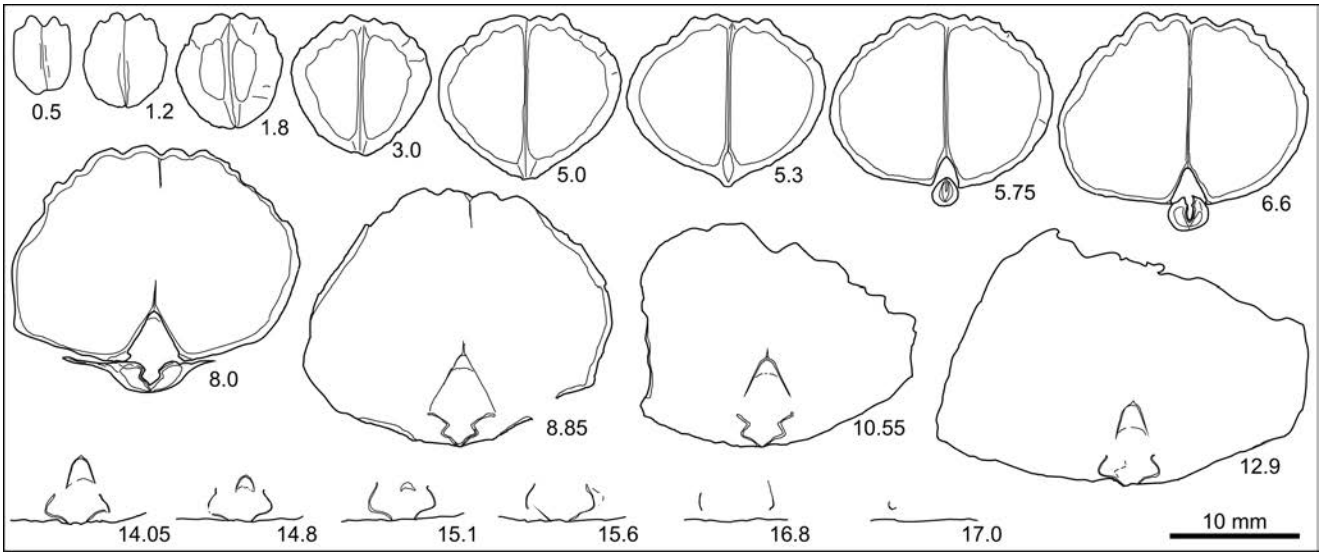


Fig. 11. Transverse serial sections of *Ivdelinia* (*Ivdelinia*) *pulchra* Franchi, Schemm-Gregory and Klug, 2012 through the shell ZPAL Bp 68/1/3/5. Distances measured in millimetres from the tip of the ventral umbo

Distribution: Middle Devonian of Eifel, Holy Cross Mountains, and Maïder (Halamski, 2004a).

Genus *Devonogypa* Havlíček, 1951
Type species: *Gypidula* (*Devonogypa*) *spinulosa* Havlíček, 1951; Čelechovice na Hané (Moravia); Middle Devonian

Devonogypa spinulosa (Havlíček, 1951)
Fig. 12A–M

* 1951 *Gypidula* (*Devonogypa*) *spinulosa* nov. nom. – Havlíček: pp. 5–7, pl. 2, figs 2, 3, 5.
v**.** 1966 *Gypidula* (*Devonogypa*) *spinulosa* Havlíček, 1951 – Biernat, pp. 28–29, pl. 1, figs 1–5, pl. 2, fig. 10.
. 2013 *Devonogypa* sp. – Tessitore *et al.*, p. 25; text-figs 2 [*p.p.*], 4, 10b, 12.

Material: Twenty-four specimens from Aferdou, one complete, three subcomplete, the other fragmentary, ZPAL Bp 68/1/17/1–24; two specimens from Madène el Mrakib (MB unnumbered, V. Ebbighausen's collection).
Additional material: Incomplete articulated shell MNHN.F.A 48135 (microornamentation not preserved) from the locality 2389, Zemmour Noir, Mauritania, coll. J. Sougy.
Description: Shell rounded in outline, most often longer than wide, rarely wider than long, strongly ventribiconvex, up to ca. 67 mm in length. Dorsal valve weakly convex, broadly triangular in anterior view. Ventral valve strongly convex with steep flanks and moderately convex to flattened median region; umbo very large (one fifth to a quarter of the total shell length), beak strongly incurved. Ventral palintrope concave, delthyrium occupying ca. one third of its width. Anterior commissure rectimarginate. Ornamentation (seldom preserved; Fig. 12L) of microscopic spines, ca. 0.1–0.2 mm in diameter; otherwise shell smooth. Ventral interior (Fig. 12A): spondylium; dorsal interior: weakly divergent inner hinge plates extending up to ca. one third of the valve length; otherwise not studied.
Distribution: Holy Cross Mountains, Moravia, Maïder, and Mauritania; Middle Devonian.

Family Clorindidae Rzhonsnitskaya, 1956

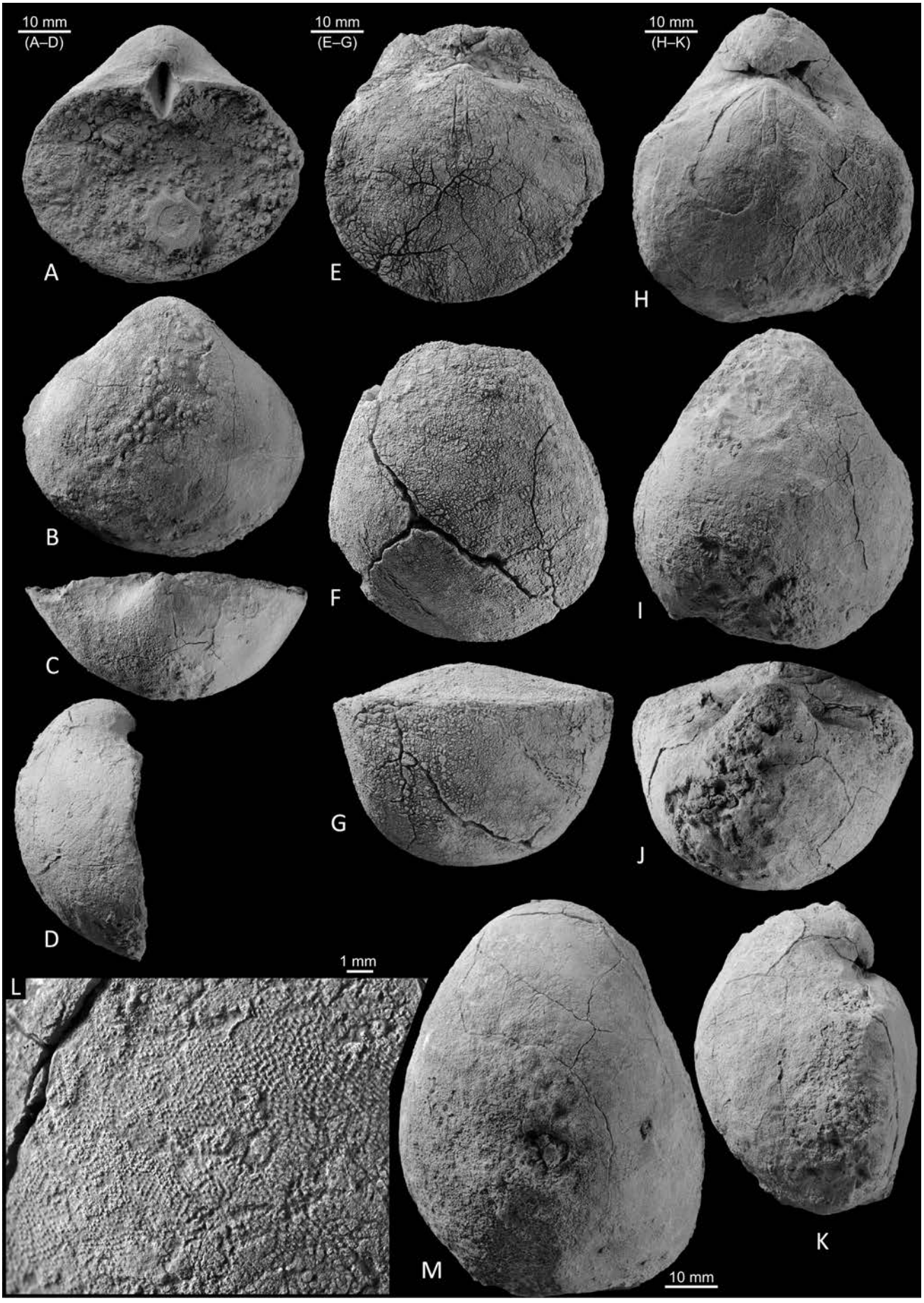
Genus *Antirhynchonella* Œhlert in Fischer, 1887
Type species: *Atrypa linguifera* Sowerby, 1839; Stumps Wood, Malvern hills, western England; Wenlock Limestone, Silurian

Range: Eifelian to early Givetian. Up to now the last known occurrence of the genus (Boucot *et al.*, 2002) was in the Miłoszów Limestone of the Holy Cross Mountains of unclear stratigraphic position, containing both Eifelian and Givetian species (Halamski, 2009) and therefore equivocal. The presence of *Antirhynchonella* in the lower Givetian is confirmed herein.

Antirhynchonella sublinguifera (Maurer, 1885)
Fig. 9S–X

v* 1885 *Pentamerus sublinguifer* n. s. – Maurer: pp. 218–221, pl. 9, figs 9, 10.
vp 1964 *Dicamara prunulum* Schnur – Sougy, p. 451, pl. 12, fig. 13a–c; *non* pl. 42, fig. 1a–b.
v**.** 1966 *Antirhynchonella linguiformis* n. sp. – Biernat, pp. 35–36, text-fig. 5, pl. 2, figs 2–5.

Material: Six incomplete articulated shells, one from Aferdou, ZPAL Bp 68/1/18/1, and three from Maharch, ZPAL Bp 68/2/18/1–2.
Additional material: Articulated shell MNHN.F.R10264 from the "Givetian", 800 m SSE from Aguelt Nebka, Zemmour Noir, Mauritania, coll. J. Sougy; figured by Sougy (1964, pl. 12: 13).
Description: Shell longitudinally elliptic in outline; dorsal valve transverse (width-to-length ratio 1.08–1.28), strongly ventribiconvex, up to ca. 40 mm in width. Dorsal valve in anterior view resembling a Gauss curve. Ventral palintrope weakly concave. Anterior commissure unisulcate in smaller individuals, parasulcate in larger ones, tongue broad and low, rounded to subtrapezoidal. Shell entirely smooth except for growth lines.
Remarks: The Maharch sample contains both uniplicate and paraplicate individuals. This is an example of intraspecific variability and an argument for taking the species discussed broadly (see synonymy). Similar intraspecific variability was described by Koz-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1 mm
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łowski (1929) and Baliński (2012) in closely related Silurian to Middle Devonian genus *Clorinda*.
Distribution: Rhenish Slate Mountains, Holy Cross Mountains, Maïder, and Mauritania; Middle Devonian.

Order Rhynchonellida Kuhn, 1949
Family Hebetoechiidae Havlíček, 1960

Genus *Kransia* Westbroek, 1967
Type species: *Terebratula parallelepipeda* Bronn, 1837 *sensu* Westbroek, 1967, Gerolstein Syncline, Eifel; Eifelian

Kransia parallelepipeda (Bronn, 1834 in 1834–38 ["1835–37"])
Fig. 13K–II

v*p 1834 *Terebratula Wilsoni* [*parallelepipeda*] – Bronn: p. 73.
1960 *Uncinulus parallelepipedus* Bronn – Gevin, p. 162.
v. 1964 *Uncinulus parallelepipedus* (Bronn, 1837) – Sougy, p. 445, pl. 42, fig. 7.
v. 1966 *Uncinulus parallelepipedus* (Bronn, 1837) – Biernat, pp. 90–91, text-fig. 30, pl. 17, figs 8–11.
v. 2005 "*Kransia parallelepipeda*" (Bronn, 1837) – Schemm-Gregory and Jansen, p. 27.

Material: One hundred articulated shells from Aferdou, several of them complete and well preserved, ZPAL Bp 68/1/19/1–91.
Additional material: Six articulated shells (mostly complete; partly mislabelled as "*Uncinulus primipilaris*") MNHN.F.A 48128, 48129 from the locality 2073F, Zemmour Noir, Mauritania, coll. J. Sougy.
Description: Shell in shape of a rounded heptagon, usually slightly transverse (width-to-length ratio 0.90 to 1.23, mean 1.08; N = 20), moderately to markedly dorsibiconvex, up to 15.8 mm in width but typically about 11–12 mm wide. Dorsal valve with a flat fold in the anterior half. Ventral valve with a wide and shallow, nearly flat-bottomed sulcus, most often bordered by two slight elevations of the dorsal valve perceptible only in the immediate proximity of the anterior margin. Beak weakly incurved; foramen permesothyrid, up to ca. 1 mm in diameter; umbo relatively fine. Anterior commissure uniplicate to paraplicate; tongue high, rounded, in some cases lateral slopes subvertical, subparallel to each other. Ornamentation of low, rounded costae and costellae, separated by sublinear furrows, (3–)5–7 on the fold, 1–2 on the flanks of the fold, 9–10 on each lateral flank.
Remarks: This species was treated in a broad sense, owing to the insufficiently precise first description (Bronn, 1835–37). The choice of a lectotype/neotype from the Eifelian of the Eifel (MCZ collections; Halamski unpublished) will allow to subdivide the widely understood *K. parallelepipeda* s.l. and distinguish between *K. parallelepipeda* s.s. (incl. *Terebratula angulosa* Schnur, 1851; basal Eifelian to lower or middle Givetian) and its probable evolutionary descendant (as yet unnamed) in the late Givetian (e.g., Brice and Morzadec, 1983).
Distribution: Eifel, Holy Cross Mountains, Maïder, and southern limb of the Tindouf Syncline (Schmidt, 1941a; Biernat, 1966; Halamski, 2004a; Schemm-Gregory and Jansen, 2005); Middle Devonian (Eifelian and lower to middle Givetian).

Kransia subcordiformis (Schnur, 1853)
Fig. 13JJ–NN

v* 1853 *Terebratula subcordiformis* n. sp. – Schnur: p. 186, pl. 25, fig. 6a–k.
v. 1941a *Uncinulus subcordiformis* (Schnur) – Schmidt, pp. 19–20, pl. 2, fig. 20, pl. 4, fig. 71 [*ubi syn.*].

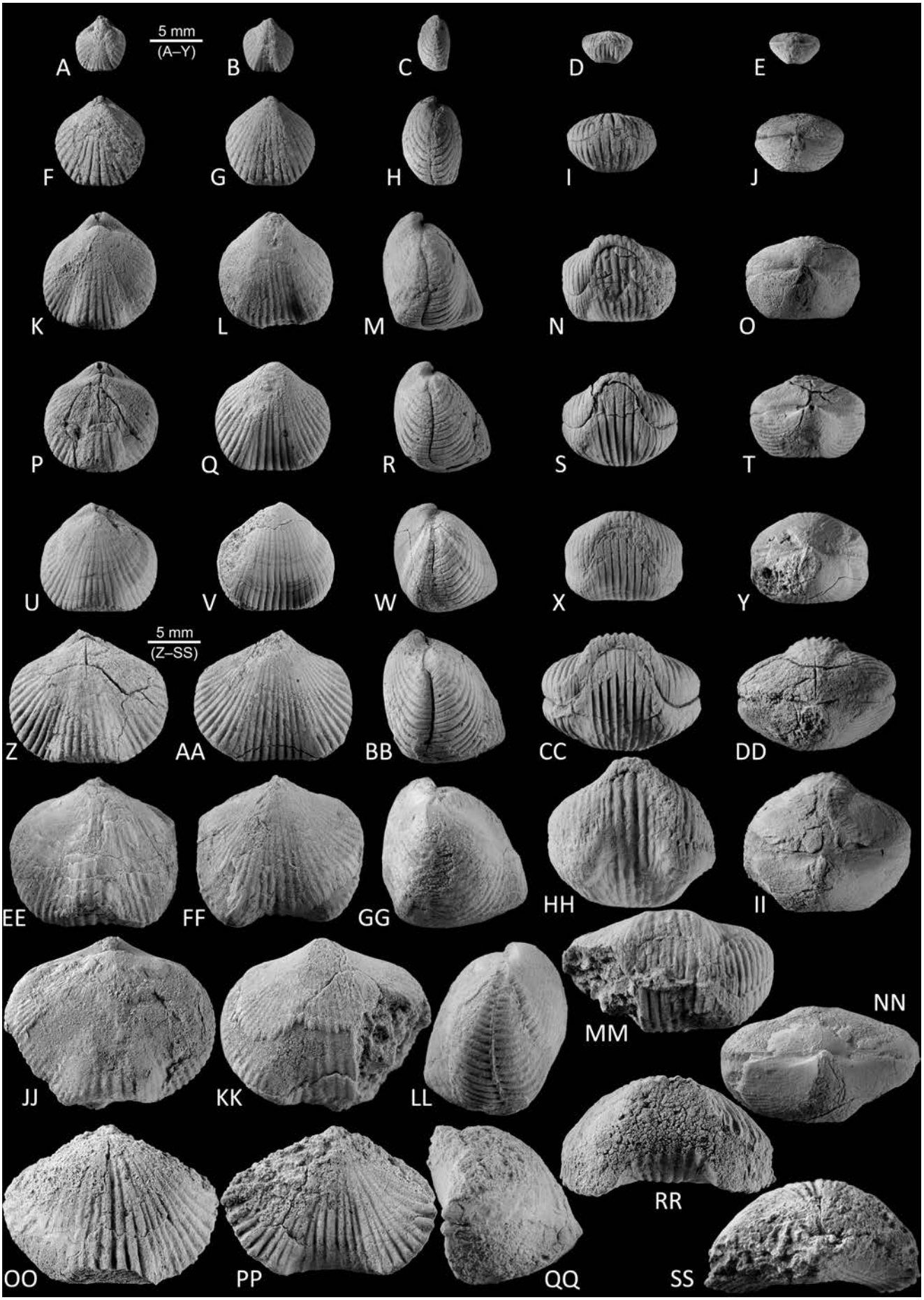
Material: A single slightly incomplete and decorticated specimen from Aferdou, ZPAL Bp 68/1/4/1.
Description: The single available shell is 20.1 mm wide, 15.7 mm long, and 11.5 mm thick, dorsibiconvex; the outline is roundly subrectangular. Ventral valve with a rather shallow flat-bottomed sulcus, visible in the anterior half; umbo strong, beak incurved. Dorsal valve with a flat fold developed in the anterior half, separated from lateral flanks of the shell by steep slopes. Anterior commissure uniplicate, tongue semicircular, evenly convex, ca. 10 mm wide. Ornamentation of flat costae and costellae, 7 on the top of the fold, 2 on its slopes, ca. 17 on lateral flanks.
Remarks: *Kransia subcordiformis* differs from *K. parallelepipeda* in larger size, usually greater width to length ratio, and a slightly weaker fold.
Distribution: Eifel, Holy Cross Mountains, Cantabrian Mountains (Mohanti, 1972), Maïder; Middle Devonian (Givetian only?).

Kransia? *coronata* (Kayser, 1871)
Fig. 13OO–SS

v* 1871 *Rhynchonella coronata* n. sp. – Kayser: pp. 512–513, pl. 9, fig. 5.
v. 1941a *Uncinulus coronatus* (Kayser) – Schmidt, p. 24, pl. 2, fig. 24, pl. 4, fig. 73, pl. 6, fig. 18.
? 1971 "*Uncinulus*" *coronatus* (Kayser) – Drot, pp. 71–72, text-pl. 1, pl. 3, fig. 1.

Material: Eighteen articulated shells (three complete, three sub-c omplete, and five incomplete) from the *Drotops* beds at Madène el Mrakib, SMF 98178 and MB unnumbered (V. Ebbighausen's collection); a single articulated shell ZPAL Bp 68/1/5/1 from Aferdou.
Description: Shell up to 20.9 mm wide, transverse (width-to-length ratio 1.15 to 1.41, mean 1.24; N = 4), strongly dorsibiconvex. Dorsal valve with a low flattened fold developed in the anterior third. Ventral valve weakly convex in posterior third, with a shallow flat-bottomed sulcus in the anterior two-thirds; lateral flanks concave; umbo rather slender but poorly preserved. Anterior commissure uniplicate, tongue subtrapezoidal, its bottom width 0.44–0.56, top width 0.33–0.48 of that of the shell, its height 0.55–0.72 of the shell thickness. Ornamentation of strong, acute costae and costellae, the latter appearing by bifurcation, 7–8 on the fold, 5–7 in the sulcus, 8–10 on lateral flanks. Interior not studied.
Remarks: This species is distinguished from remaining representatives of *Kransia* by the form of the dorsal valve and stronger, acute costae, whence the quotation mark afer the genus name.
Distribution: Eifel (Schmidt, 1941a), Holy Cross Mountains (Biernat, 1966), Maïder; Middle Devonian (Eifelian only?).

Fig. 12. *Devonogypa spinulosa* (Havlíček, 1951) from Aferdou. **A–D**. Ventral valve in dorsal, ventral, posterior, and lateral views. **E–G**. Incomplete articulated shell in dorsal, ventral, and anterior views. **H–K**. Subcomplete articulated shell in dorsal, ventral, posterior, and lateral views. **L–M**. Ventral valve in ventral view; general view (M) and microornamentation (L)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Genus *Beckmannia* Mohanti, 1972
Type species: *Uncinulus minor beckmanni* Schmidt, 1951; Letmathe, Rhenish Slate Mountains; Middle Devonian (lower Givetian?)

Beckmannia beckmanni (Schmidt, 1951)
Fig. 13A–J

* 1951 *Uncinulus minor beckmanni* n. ssp. – Schmidt: pp. 89–90, pl. 1, figs 1–3.
1985 *Beckmannia minor beckmanni* (Schmidt 1951) – Brice, pp. 135–136, text-fig. 3, pl. 1, figs 10–13 [*ubi syn.*].

Material: ten articulated shells from Aferdou, ZPAL Bp 68/1/20/1–10.
Description: Shell in outline of a rounded pentagon, as wide as long, moderately ventribiconvex. Maximal width about midlength. Dorsal valve moderately convex; a very low flat fold sometimes visible in the anterior fourth. Ventral valve convex, with a nearly imperceptible sulcus in anterior half; umbo fine, elongate, beak incurved. Anterior commissure uniplicate; tongue low, rounded, occupying ca. 0.6–0.8 of the shell width. Ornamentation of low, rounded costae separated by very narrow interspaces, 3–4 on fold, 0–1 on its flanks, ca. 6 on each lateral flank. Interior not studied.
Remarks: As far as the exteriors are concerned, the specimens studied are indistinguishable from the type collection of *Beckmannia beckmanni* (Schmidt, 1951) from the Middle Devonian of the Rhenish Slate Mountains.
Distribution: Eifel, Holy Cross Mountains, Maïder, Cantabrian Mountains (Mohanti, 1972), Montagne Noire (Massif Central, France; Brice, 1985); Middle Devonian (Givetian, mostly about Middle *varcus* Zone).

Family Hypothyridinidae Rzhonsnitskaya, 1956

Genus *Glosshypothyridina* Rzhonsnitskaya, 1978
Type species: *Rhynchonella procuboides* Kayser, 1871; Eifel, Germany; Eifelian.

Range: Eifelian to early Givetian, emended herein (Eifelian only according to Savage *in* Savage *et al.*, 2002) on account of presence of *G. procuboides* at Maharch.

Glosshypothyridina procuboides (Kayser, 1871)
Fig. 14F–Y

v* 1871 *Rhynchonella procuboides* n. sp. – Kayser: pp. 513–514, pl. 9, fig. 3.
vp 1941a *Camarotoechia triloba fornicata* (Schnur 1853) – Schmidt, pp. 12–13, pl. 5, fig. 9, *non* pl. 4, fig. 59.
1964 *Hypothyridina procuboides* (Kayser) – Sougy, p. 450, pl. 42, fig. 8.
v**.** 1966 *Hypothyridina* cf. *procuboides* (Kayser) – Biernat, pp. 105–106, pl. 21, fig. 2.

Material: Three articulated shells from Aferdou (two complete), ZPAL Bp 68/1/21/1–3; seven individuals from Maharch (one subcomplete articulated shell), ZPAL Bp 68/2/21/1–6, 68/2/43/1.
Description: Shell approximately isometric to transverse, very strongly dorsibiconvex, up to 25.9 mm in width (incomplete specimens suggest a maximal width up to 30 mm). Maximal width about shell midlength, seldom about the anterior fifth of the shell length. Dorsal valve very strongly convex, with a slightly flattened fold in anterior two-fifths. Ventral valve moderately to strongly convex in umbonal region, flat on flanks, with a wide flat-bottomed to W-shaped sulcus anteriorly; umbo low, beak incurved. Anterior commissure uniplicate, tongue very broad, occupying 0.6–0.7 of the shell width, bordered by vertical deflexions of the commissure. Ornamentation of low, flattened, grooved costae, separated by very narrow furrows, 9–13(–19) on the tongue, 8–12 on the fold, 12–16 on flanks. Interior not studied.
Remarks: This is a very variable species; the specimen ZPAL Bp 68/2/43/1 from Maharch (Fig. 14F–J) is slightly outside of the usual extent of intraspecific variability in its exceedingly fine costation (19 costae on the tongue compared to 9–13 in the remaining material) and in the position of the maximal width of the shell (half vs. four-fifths of the shell length). It is quite similar to the individual SMF XVII 749a from the Eifel (Fig. 14P–T), misidentified by Schmidt (1941a, pl. 5: 9) as *Ladogifornix fornicatus* (Schnur, 1851). The holotype of the latter species is illustrated for comparison in Fig. 14A–E.
Distribution: Eifel, Holy Cross Mountains, Maïder; Middle Devonian.

Family Septalariidae Havlíček, 1960

Genus *Septalaria* Leidhold, 1928
Type species: *Terebratula ascendens* Steininger, 1853; Eifel; Middle Devonian

Septalaria gracilis (Gürich, 1896)
Figs 15, 16K–O, Q–OO

v* 1896 *Camarophoria gracilis* n. sp. – Gürich: pp. 278–279, pl. 7, fig. 3a–g.
. 1909 *Liorhynchus gracilis* Gürich – Sobolew, p. 503, pl. 6, figs 8–12, 16.
vp 1934 *Septalaria ascendens* (Steininger) – Torley, p. 78, text-fig. Gr. A, figs 11–12, pl. 2, figs 49–53, 58–57, *non* pl. 2, figs 54–57.
v**.** 1966 *Septalaria* cf. *gracilis* (Gürich, 1896) – Biernat, pp. 97–98, pl. 7, fig. 6.
1971 «*Pugnax*» *pugnoides latus* Herta Schmidt, 1941 – Drot, pp. 89–90, pl. 3, fig. 4.
v**.** 1975 *Septalaria descendens* n. sp. – Schmidt, pp. 93–96, text-figs 2, 6, pl. 3, figs 15–16, pl. 4, figs 17–18 [*ubi syn.*].
1985 *Septalaria* aff. *descendens* Schmidt 1975 – Brice, pp. 138–139, text-fig. 5, pl. 2, figs 1–3.

Material: Twenty-two articulated shells (most of them complete)

Fig. 13. Middle Devonian Rhynchonellida from southern Maïder. **A–J.** *Beckmannia beckmanni* (Schmidt, 1951). A–E. Specimen ZPAL Bp 68/1/20/1. F–J. Specimen ZPAL Bp 68/1/20/2. **K–II.** *Kransia parallelepipeda* (Bronn, 1834 in 1834–38 [‘1835–37’]). K–O. Specimen ZPAL Bp 68/1/19/1. P–T. Specimen ZPAL Bp 68/1/19/2. U–Y. Specimen ZPAL Bp 68/1/19/3. Z–DD. Specimen ZPAL Bp 68/1/19/4. EE–II. Specimen ZPAL Bp 68/1/19/5. **JJ–NN.** *Kransia subcordiformis* (Schnur, 1853). Specimen ZPAL Bp 68/1/4/1. **OO–SS.** *Kransia*? *coronata* (Kayser, 1871). Specimen ZPAL Bp 68/1/5/1. All photographs are of articulated shells from Aferdou in dorsal, ventral, lateral, posterior, and anterior views

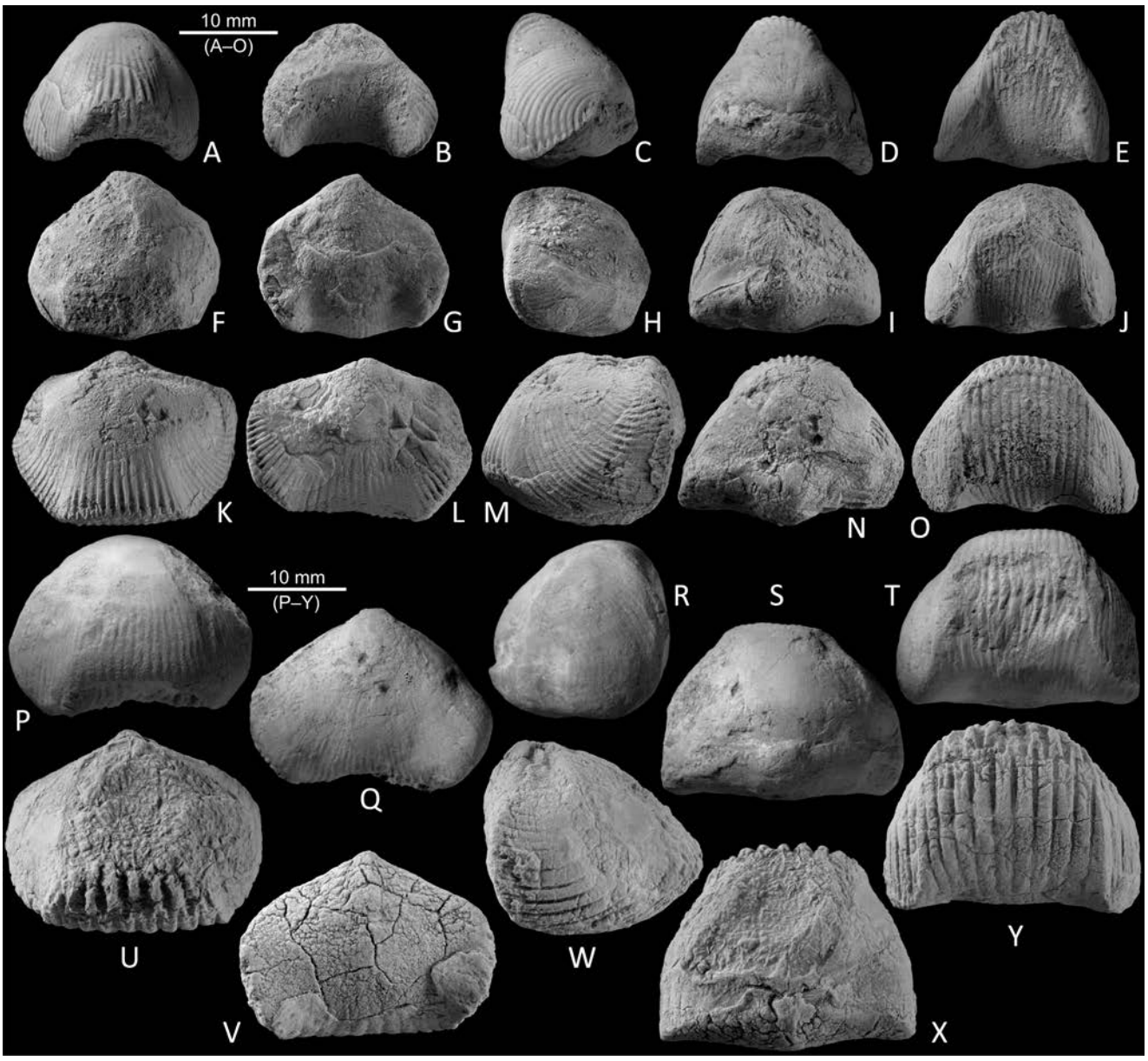


Fig. 14. Middle Devonian Rhynchonellida from southern Maïder and Europe. **A–E.** *Ladogifornix fornicatus* (Schnur, 1851). Holotype from Schnur's collection (Bonn University; unnumbered) from the Middle Devonian of the Eifel. **F–Y.** *Glosshypothyridina procuboides* (Kayser, 1871). F–J. Specimen ZPAL Bp 68/2/43/1 from Maharch. K–O. Specimen ZPAL Bp 68/1/21/1 from Aferdou. P–T. Specimen SMF XVII 749a from Uxheim (Eifel), Eifelian. U–Y. Specimen ZPAL Bp 68/2/21/1 from Maharch. All photographs are of articulated shells in dorsal, ventral, lateral, posterior, and anterior views

from Aferdou, ZPAL Bp 68/1/22/1–22, and two (one complete) from Maharch, ZPAL Bp 68/2/22/1–2.

Other material examined: one complete and three fragmentary articulated shells MGUWr 1966s from Śniadka (Łysogóry Region, Holy Cross Mountains), syntypes of *Camarophoria gracilis* Gürich, 1896; two articulated shells SMF 29599/1–2 from Bilveringsen (Sauerland), coll. K. Torley (sub *Septalaria ascendens*).

Description: Shell subpentagonal in outline, in some cases asymmetric, most often transverse, seldom as wide as long, strongly dorsibiconvex, up to 27.4 mm in width. Dorsal valve with a flattened fold appearing slightly anteriorly to midlength, flanks steep. Ventral valve convex in umbonal region, flattened on flanks, with a wide and shallow flat-bottomed sulcus anteriorly; umbo fine, beak moderately incurved. Anterior commissure uniplicate, tongue broad, occupying (0.5–)0.58–0.69 of the shell width, high, trapezoidal. Ornamentation of rather low, rounded costae, appearing at ca. 5 mm from the umbo, separated by narrower furrows, 6–11 on tongue, 8–18 on flanks.

The interior of the single partly recrystallised sectioned specimen (Fig. 15) does not reveal the presence of dental plates. Dorsal interior with well developed septalium; median septum high and fairly long; posterior region of the septalium lined with thickened cardinal process; outer hinge plates subhorizontal with slightly dorsally curved inner margins; crura short, slightly laterally divergent and with ventrally bent distal ends.

Remarks: Selected metric characters of three populations of *Septalaria gracilis* are compared in Table 1.

Table 1

Comparison of selected biometric characteristics of *Septalaria gracilis* from the Holy Cross Mountains, Sauerland, and Maïder. Data for the Holy Cross Mountains, either after Gürich (1896) or calculated after photographs in Sobolew (1909); those for Sauerland and Maïder after present authors

Taxon	*Septalaria gracilis*		
Character	Holy Cross Mts.	Sauerland	Maïder
Width [mm]	14.4 (11–19)	19.5 (17.4–20.7)	24.3 (19.8–27.3)
Width to length ratio	1.15 (1.04–1.36)	1.25 (1.13–1.38)	1.34 (1.21–1.43)
Costae on tongue	3.6 [(2–)4]	4.9 (2–7)	8.2 (7–11)
Costae/shell width	0.27 (0.18–0.31)	0.25 (0.11–0.34)	0.34 (0.26–0.40)
Costae/tongue width	0.48 (0.33–0.51)	0.52 (0.42–0.65)	0.65 (0.55–0.82)
Number of specimens	5/8	8	8

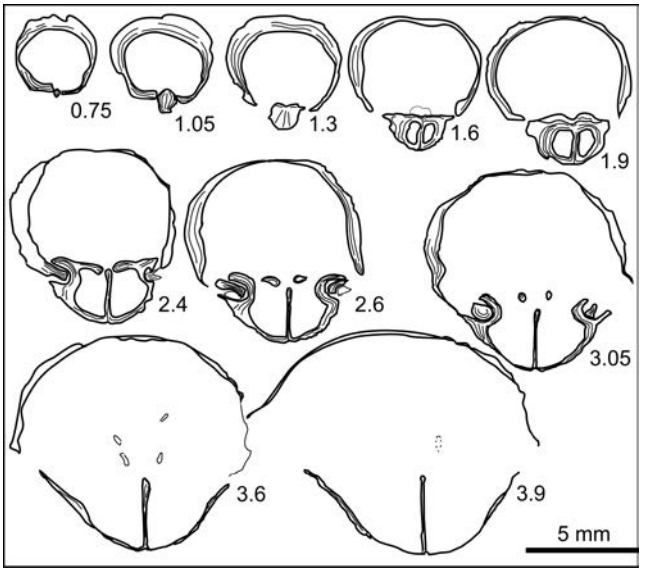


Fig. 15. Transverse serial sections of *Septalaria gracilis* (Gürich, 1896) through the shell ZPAL Bp 68/1/22/6 from Aferdou. Distances measured in millimetres from the tip of the ventral umbo

Each sample has its own biometric characteristicts, but all three are considered conspecific, on the basis of overall similarity of shape and intergrading values of biometric characters. In view of such marked variability, *Septalaria* aff. *descendens sensu* Brice (1985) from La Serre in the Montagne Noire (Massif Central, France) should probably be considered as representing the species discussed, as well. Unfortunately, the Moroccan material of *Septalaria*, described by Drot (1964), could not be traced at the MNHN.
Distribution: Eifel, Holy Cross Mountains (North), and Maïder, probably also Montagne Noire; Middle Devonian.

Family Pugnacidae Rzhonsnitskaya, 1956

Genus *Parapugnax* Schmidt, 1964

Type species: *Pugnax pugnus brecciae* Schmidt, 1941 [1941b]; Langenaubach near Haiger, Lahn Syncline, Germany; Iberg Limestone, Frasnian

Parapugnax? cf. *skalensis* (Biernat, 1966)
Fig. 16A–J, P

cf. 1966 ?*Nemesa skalensis* n. sp. – Biernat: pp. 100–101, pl. 22, figs 14–17.

Material: Four specimens (two subcomplete) from Aferdou, ZPAL Bp 68/1/23/1–4.
Description: Shell irregularly pentagonal (nearly triangular) in outline, transverse (width-to-length ratio ca. 1.3–1.5), strongly dorsibiconvex, up to ca. 20 mm in width. Maximal width at 1/2 to 1 of the shell length. Ventral valve moderately convex in umbonal region, flattened to slightly concave on flanks, with a wide U-shaped sulcus anteriorly. Dorsal valve very deep (the thickness of the shell is roughly equal to its length), approximately semicircular in posterior view. Ventral beak poorly preserved. Anterior commissure uniplicate, tongue broad, high, subtrapezoidal. Ornamentation of high, strong, acute costae developed in the anterior half of the valves, separated by V-shaped furrows of approximately the same width as the costae, 4 on fold, 3 on flanks.
Remarks: *Parapugnax skalensis* (Biernat, 1966) from the upper Eifelian of Skały in the Holy Cross Mountains has a regularly convex dorsal valve (Biernat, 1966). *P. brecciae* from the Frasnian of Langenaubach has two costae on each flank, is larger, and has also a regularly convex dorsal valve.

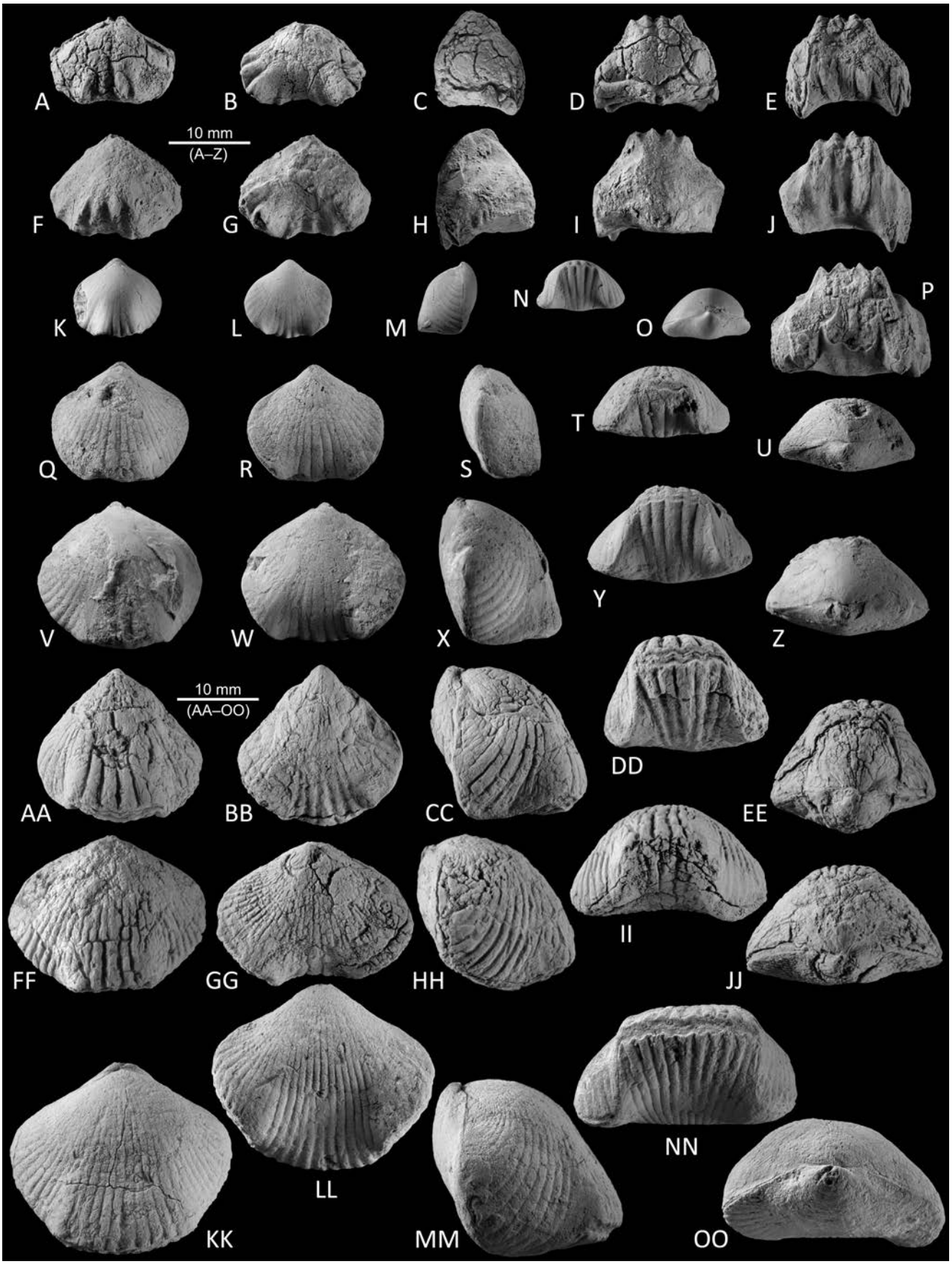
Paulinaerhynchia new genus

Type species: *Paulinaerhynchia paulinae* gen. et sp. nov., as below

Derivatio nominis: As for the type species.
Diagnosis: Large-sized, strongly costate Pugnacidae; dorsal septum and septalium absent; dental plates close to lateral walls and not reaching the ventral valve floor.
Remarks: This genus is quite close to *Pugnax* in external form and anatomy; it differs in having numerous costae (few in *Pugnax*) and in its raduliform crura (laterally flattened and subparallel in *Pugnax*; Savage *et al.*, 2002, p. 1164). *Pugnax* is in need of revision, as testified by its improbable alleged stratigraphic range (Middle Devonian to Upper Permian, Savage *et al.*, 2002; see also Sartenaer, 1968).

Paulinaerhynchia paulinae new genus and species
Figs 17, 18

Type material: Holotype (a complete articulated shell) ZPAL Bp 68/2/24/1 and twenty paratypes, incl. four complete articulated shells; four paratypes serially sectioned) from Maharch, ZPAL Bp 68/2/24/2–21; three dubious fragmentary specimens from Aferdou, ZPAL Bp 68/1/24/1–3.
Etymology: In honour of Paulina Halamska, senior author's spouse.
Diagnosis: As for the genus.
Description: Shell subpentagonal in outline, transverse with width to length ratio 1.3–1.7 (N = 5), strongly dorsibiconvex, up to 41.2 mm in width (dimensions given in Table 2). Maximal width about mid-length or slightly anteriorly. Dorsal valve strongly convex (shell thickness equalling 0.8–1.3 its length), with a rounded, relatively high fold and steep flanks. Ventral valve weakly convex in umbonal region, flattened on flanks, with a U-shaped deeply excavated sulcus anteriorly. Both umbones thick, ventral beak incurved. Anterior commissure uniplicate, tongue very broad, occupying 0.67–0.86 of the shell width, and high, with subvertical lateral slopes and semicircular top. Ornamentation of distinct, rounded


A
B
C
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10 mm
(A–Z)
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W
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Y
Z
10 mm
(AA–OO)
AA
BB
CC
DD
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FF
GG
HH
II
JJ
KK
LL
MM
NN
OO

Table 2

Biometric characteristics of *Paulinaerhynchia paulinae* gen. et sp. nov.; measurements in millimetres

Specimen	W	L	T	w	W/L	T/L	w/W	Nc	Nl	Nc/W
24/1	49.0	29.0	30.7	32.7	1.69	1.06	0.67	11	7	0.34
24/4	38.5	28.5	27.3	33.0	1.35	0.96	0.86	14	?	0.42
24/2	34.0	25.7	24.2	26.9	1.32	0.94	0.79	8	4?	0.30
24/3	28.0	28.7	32.0	28.0	1.32	0.80	0.74	8	6?	0.29
24/5	40.0	23.9	30.3	30.9	1.67	1.27	0.77	9	?	0.29

W – width; L – length; T – thickness; w – width of the tongue; Nc – number of costae and costellae on the tongue; Nl – number of costae and costellae per a dorsal lateral flank

costae, separated by narrower furrows, 7–14 on tongue, (4–)6–8 less strong ones on flanks, but ornamentation only seen in the anterior half of large shells.

Ventral interior with very short, rudimentary, ventrally divergent dental plates situated close to the lateral valve walls (resulting in narrow dental cavities) and not reaching the floor of the valve; teeth slender and short. In the dorsal valve septalium and median septum absent but a high myophragm revealed in one of the sectioned specimens; hinge plates divided; outer hinge plates flat, nearly horizontal, with well marked crural bases forming sharp ridges along inner margins of outer hinge plates; crura curving ventrally, triangular in section, raduliform. A low, triangular in cross-section median ridge developed at some distance from the hinge margin in a single specimen (Fig. 18D) can be interpreted as a myophragm dividing muscle attachment area.

Remarks: The specimens shown in Fig. 17 illustrate the variability of the external morphology, expressed mainly in the shell thickness (compare the shell illustrated in Fig. 17A–E with the remaining three), as well as the width and the shape of the bottom of the ventral sulcus; the latter is usually slightly concave to (seldom) very weakly convex.

Comparisons of *Paulinaerhynchia paulinae* gen. et sp. nov. with similar rhynchonellides are hindered, because in several cases, the interior features are unknown. Homoeomorphic taxa do exist, as exemplified by representatives of *Amissopecten* Havlíček, 1960 (Camarotoechiidae; Havlíček, 1961, Havlíček and Kukal, 1990) or *Ladogioides* McLaren, 1961 (Yunnanellidae; McLaren, 1962).

"*Rhynchonella acuminata* var. *platiloba* Sowerby" *sensu* Maurer (1885, p. 207, pl. 8: 35) from the approximately coeval strata of Grube Hainau at Waldgirmes (material examined: HLMD-Mr. 10770, 10771) and Brilon (material examined: BGR, Koch'sche Sammlung, ZGI, no number) is very similar in shape to *Paulinaerhynchia paulinae* gen. et sp. nov., but is smaller and lacks costae on lateral flanks. The tongue is striate (4–5 per mm), but this feature might have been lost in the material of the present study. The interior is unknown.

Atrypa triloba (Sowerby, 1840) "a handsome shell" (Sowerby, 1840, [717], pl. 56: 14) from the (Middle?) Devonian of Plymouth (possibly present also in the Boulonnais; Devos, 1962) is similar in outline and about the same size as *Paulinaerhynchia paulinae* gen. et sp. nov., but its fold is higher and appears closer to the umbonal region; the costation is stronger. It is not certain, whether *Camarotoechia triloba sensu* Schmidt (1941a) be conspecific with the above-mentioned English taxon.

All Middle Devonian Pugnacidae from Germany (Schmidt, 1941a, b) are smaller and have fewer costae. *Pugnax proboscidea* Nalivkin, 1930 from the Upper Devonian of East Ferghana is similarly large-sized, but the costae are fewer in number (Nalivkin, 1930, p. 89–90, 186–187, pl. 6: 14, 31); the interior is unknown.

Dumestre and Illing (1967) reported a few brachiopod taxa from a Givetian reef in the Uein Terguet region (near the town of Semara, Western Sahara, Morocco; western part of the Tindouf Syncline) and among them a "large rhynchonellid superficially resembling *Hypothyridina* or *Uncinulus* but which proved on sectioning to have totally different internal structure and to be nearest to *Ladogioides*" (written communication of H.M. Muir-Wood in Dumestre and Illing, 1967). One may wonder, if this does not refer to the same genus as here. *Ladogioides* has similarly oriented dental plates, but possesses a dorsal septum and a septalium. Unfortunately, this material could not be traced in the Natural History Museum, in London (S. Long, personal communication, 6th Nov., 2012).

Halamski (2004a) reported a single fragmentary shell of a similar rhynchonellide from the Eifelian to Givetian boundary beds at Sitka in the Holy Cross Mountains and referred to it as "Hypothyridinidae? gen. et sp. nov.".

Type locality: Guelb el Maharch.
Type level: Guelb el Maharch mud mound, Taboumakhloûf Formation; lower Givetian.
Stratigraphic distribution: lower Givetian.
Deposition of types: ZPAL.
Distribution: The new taxon remains unconfirmed, outside the type locality and stratum.

Rhynchonellida fam., gen. et sp. indet.
Fig. 30A–E

Material: Two articulated shells (one subcomplete, one fragmentary) from Aferdou, ZPAL Bp 68/1/50/1.
Description: The single measurable shell is subpentagonal in outline, with greatest width at about two-thirds of the shell length, dorsibiconvex, ca. 10 mm wide, 9.4 mm long, and 6.5 mm thick. Anterior commissure uniplicate, ca. 8 mm broad, high, rounded. Beak incurved. Shell macroscopically smooth. Interior unknown.
Remarks: This brachiopod is identified as a member of the Rhynchonellida, on account of its astrophic shell, hidden interareas, and absence of pedicle foramen. It is certainly different from all the forms identified above, but the possibility of any identification is precluded by the scarcity of material. It is illustrated here to call attention to the presence of smooth rhynchonellides in the fauna studied.

Fig. 16. Middle Devonian Rhynchonellida from the southern Maïder and Europe. **A–J, P.** *Parapugnax*? cf. *skalensis* (Biernat, 1966). All specimens from Aferdou. A–E. Articulated shell ZPAL Bp 68/1/23/1 in dorsal, ventral, lateral, posterior, and anterior views. F–J. Articulated shell ZPAL Bp 68/1/23/2 in dorsal, ventral, lateral, posterior, and anterior views. P. Fragmentary specimen ZPAL Bp 68/1/23/3 in anterior view. **K–O, Q–OO.** *Septalaria gracilis* (Gürich, 1896). Articulated shells in dorsal, ventral, lateral, posterior, and anterior views. K–O. Specimen ZPAL Bp 68/1/22/5 from Aferdou. Q–U. Specimen ZPAL Bp 68/1/22/3 from Aferdou. V–Z. Specimen SMF 29599.1 from Bilveringsen (Sauerland). AA–EE. Specimen ZPAL Bp 68/1/22/2 from Aferdou. FF–JJ. Specimen ZPAL Bp 68/1/22/1 from Aferdou. KK–OO. Specimen ZPAL Bp 68/1/22/4 from Aferdou

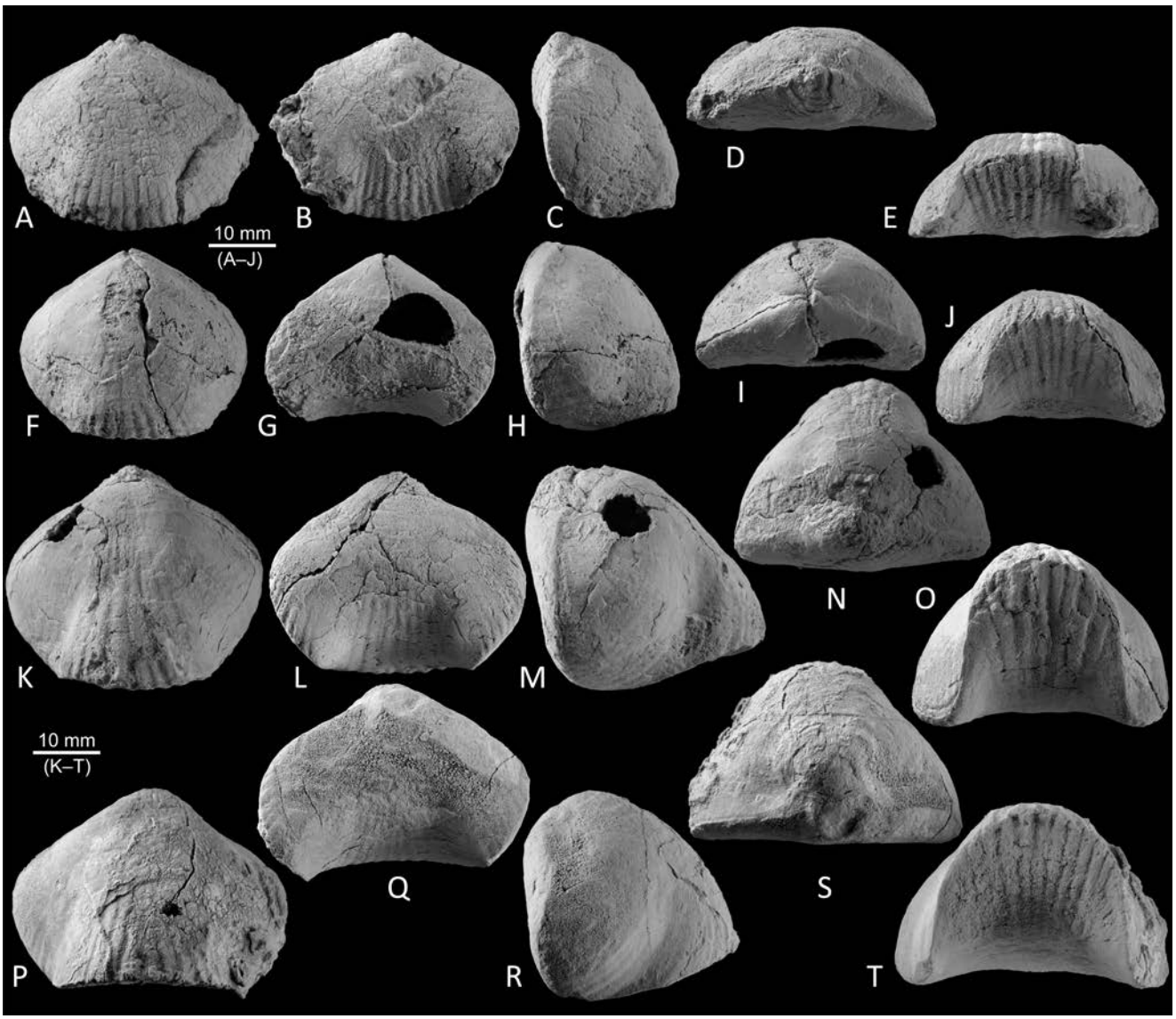


Fig. 17. *Paulinaerhynchia paulinae* gen. et sp. nov. Articulated shells in dorsal, ventral, lateral, posterior, and anterior views. **A–E.** Paratype ZPAL Bp 68/2/24/10 from Maharch. **F–J.** Paratype ZPAL Bp 68/2/24/3 from Maharch. **K–O.** Paratype ZPAL Bp 68/2/24/2 from Maharch. **P–T.** Holotype ZPAL Bp 68/2/24/1 from Maharch

Order Atrypida Rzhonsnitskaya, 1960
Family Atrypidae Gill, 1871

Genus *Atrypa* Dalman, 1828
Type species: *Anomia reticularis* Linnaeus, 1758; Gotland; lower Hemse Beds, Ludlow, Silurian

Atrypa (*Planatrypa*?) *confusa* (Struve, 1992)
Figs 19G–JJ, 20

vp 1964 *Atrypa reticularis* – Sougy, p. 383.
v* 1992 *Planatrypa confusa* n. sp. – Struve: pp. 552–554.
. 1995 *Atrypa* (*Planatrypa*) *confusa* (Struve, 1992) – Godefroid, pp. 87–89, text-fig. 8,; pl. 2, figs 6–8.
v. 2001 *Planatrypa confusa* Struve 1992 – Thormann and Weddige, pl. 2, fig. 15.

Material: Over ninety specimens (mainly complete or subcomplete, articulated shells) from Aferdou, ZPAL Bp 68/1/48; about sixty articulated shells from the *Drotops* beds at Madène el Mrakib, SMF 94845–94847, 98179 and MB unnumbered (V. Ebbighausen's collection).

Additional material: three articulated shells MNHN.F.A48101, 50414 from locality 363o, Zemmour Noir, Mauritania, coll. J. Sougy.

Other material examined: Paratypes SMF 94878, collected near Ahütte railway station (St. 190; both this and the following locality number refer to an unpublished register of Struve's collecting localities kept at the SMF), and SMF 97879 from the quarry Müllertchen at Ahütte (Fp. 2162); both Hillesheim Syncline, Eifel; Ahbach Formation, middle Eifelian.

Description: Shell heptagonal, rounded, or shield-shaped in outline, strongly dorsibiconvex to planoconvex, usually longer than wide, typically 21 to 26 mm wide, more seldom up to 36 mm wide. Shoulder angle 130°–150°(–160°). Dorsal valve regularly arched. Ventral valve weakly to distinctly convex in umbonal region, flanks weakly convex to concave, in the latter case redressed at margins; beak suberect to incurved; foramen obscured by pedicle

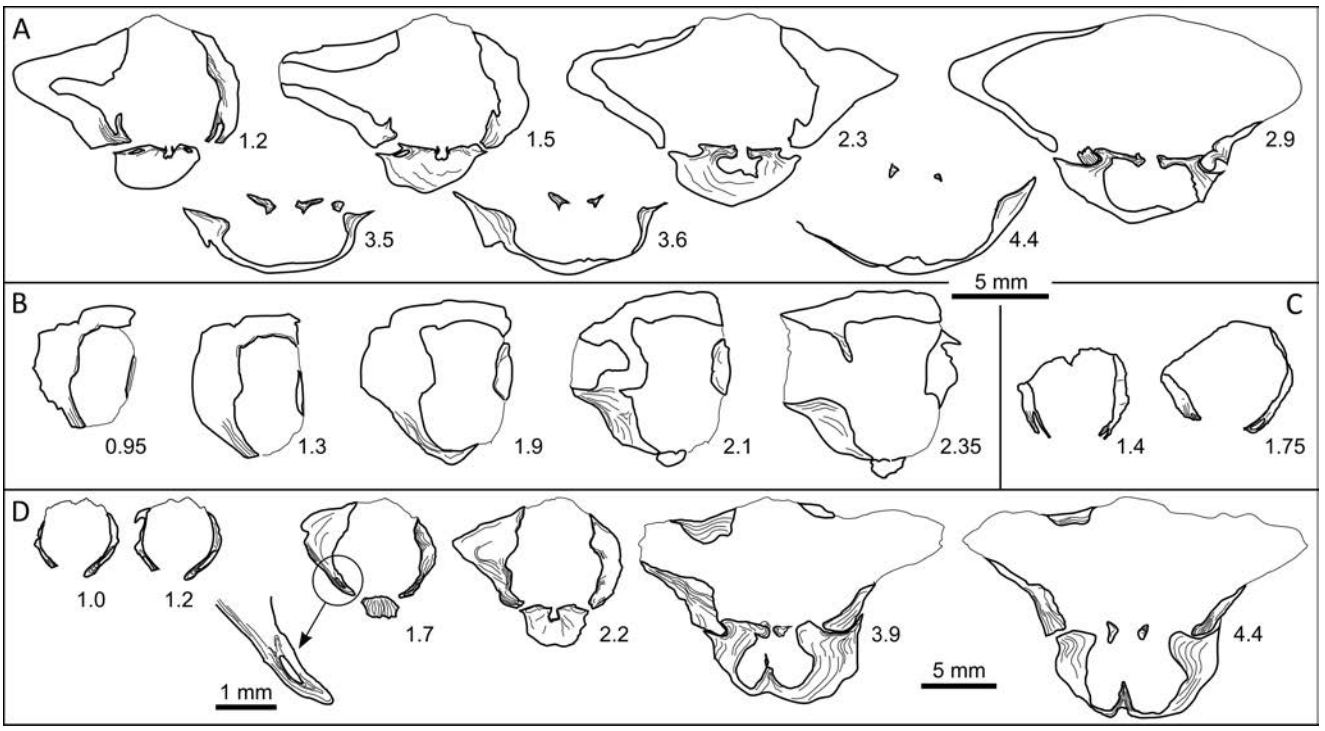


Fig. 18. Transverse serial sections of *Paulinaerhynchia paulinae* gen. et sp. nov. through shells ZPAL Bp 68/2/24/6 (A), 68/2/24/7 (B), 68/2/24/8 (C), and 68/2/24/9 (D) from Maharch. Distances measured in millimetres from the tip of the ventral umbo

callist. Anterior commissure nearly straight to uniplicate; tongue usually rather narrow and low. Ornamentation of fine ribs, (5–) 6–9 per 5 mm, interrupted by frequent growth lines. Frills uncommonly preserved, up to 5 mm long.

Ventral interior with pedicle callist and pedicle collar (Fig. 20B: 1.4 and 1.65); teeth large, long, and strong, nearly vertical, with poorly developed lateral lobes; dental nuclei distinct (Fig. 20B: 1.2, 1.4, and 1.65). Dorsal valve with massive hinge plates; cardinal pit deep with distinct attachments of diductor muscles (cardinal process) lining also inner socket ridges posteriorly; the median ridge dividing adductor muscle distinct and fairly long.

Remarks: The discussed brachiopod was included within the genus *Planatrypa* by Struve (1992) [subgenus *Atrypa* (*Planatrypa*) Struve, 1966 herein]. However, it differs from *Atrypa* (*Planatrypa*) in possessing frills and dental nuclei; the latter character distinguishes it also from *Kyrtatrypa* Struve, 1966, which has solid teeth (Copper, 2002). It resembles respresentatives of *Atrypa* (*Atrypa*) Dalman, 1828, a subgenus to this time known up to the Emsian (Copper, 2002), in having convexoplane to dorsibiconvex shell, uniplicate commissure, obscured foramen, and multiple frills (diagnostic characters after Copper, 2002). The frills being an uncertain diagnostic character, because of preservational bias (P. Copper, personal communication April 2013), the subgeneric appurtenance of the brachiopod discussed is considered here as unresolved; it is reported under the conservative heading "*Atrypa* (*Planatrypa*?) *confusa*". It is worth noting that Copper (1967c) reported the presence of deflected growth lamellae and minute dental nuclei in some species of *Atrypa* (*Planatrypa*) from the Eifelian of Germany.

Reinvestigation of the type material of "*Planatrypa confusa* Struve, 1992" from the Eifel permitted the discovery of frills (Fig. 19Z) and a plate covering the delthyrium, characters excluding assignment to *Atrypa* (*Planatrypa*) and concordant with the present material. These internal characters are also evident in the material from the Ardennes (Godefroid, 1995, fig. 8, especially 0.4). The original material of Struve (1992) (five specimens only) did not allow the author to account for the variability of this species, which is illustrated more fully herein. A specimen from the Zemmour Noir (Mauritania) is illustrated (Fig. 19I–M) to document the presence of *A. confusa* in that region.

Distribution: Eifel, Ardennes, Maïder, and Zemmour Noir; Middle Devonian.

Genus *Atryparia* Copper, 1966

Type species: *Atryparia instita* Copper, 1966; Mühlenberg near Niederehe, Hillesheim Syncline, Eifel; Ahbach Beds, upper Eifelian (Copper, 1966b)

Remarks: A potentially misleading report of "a specimen, possibly related to *Atryparia*, from the Devonian near the Algeria-Morocco border" (Copper, 1966b, p. 983), therefore in close proximity to the area studied in the present paper, is corrected here: as a matter of fact, the brachiopod originated in the Mouydir Basin, some 800 km further south-east (Flamand, 1911).

Atryparia dispersa (Struve, 1966)
Figs 21F–O, 22, 28L

* 1966 *Atrypa (Hyponeatrypa) dispersa* n. sp. – Struve: pp. 142–143, text-fig. 11, pl. 16, fig. 10.

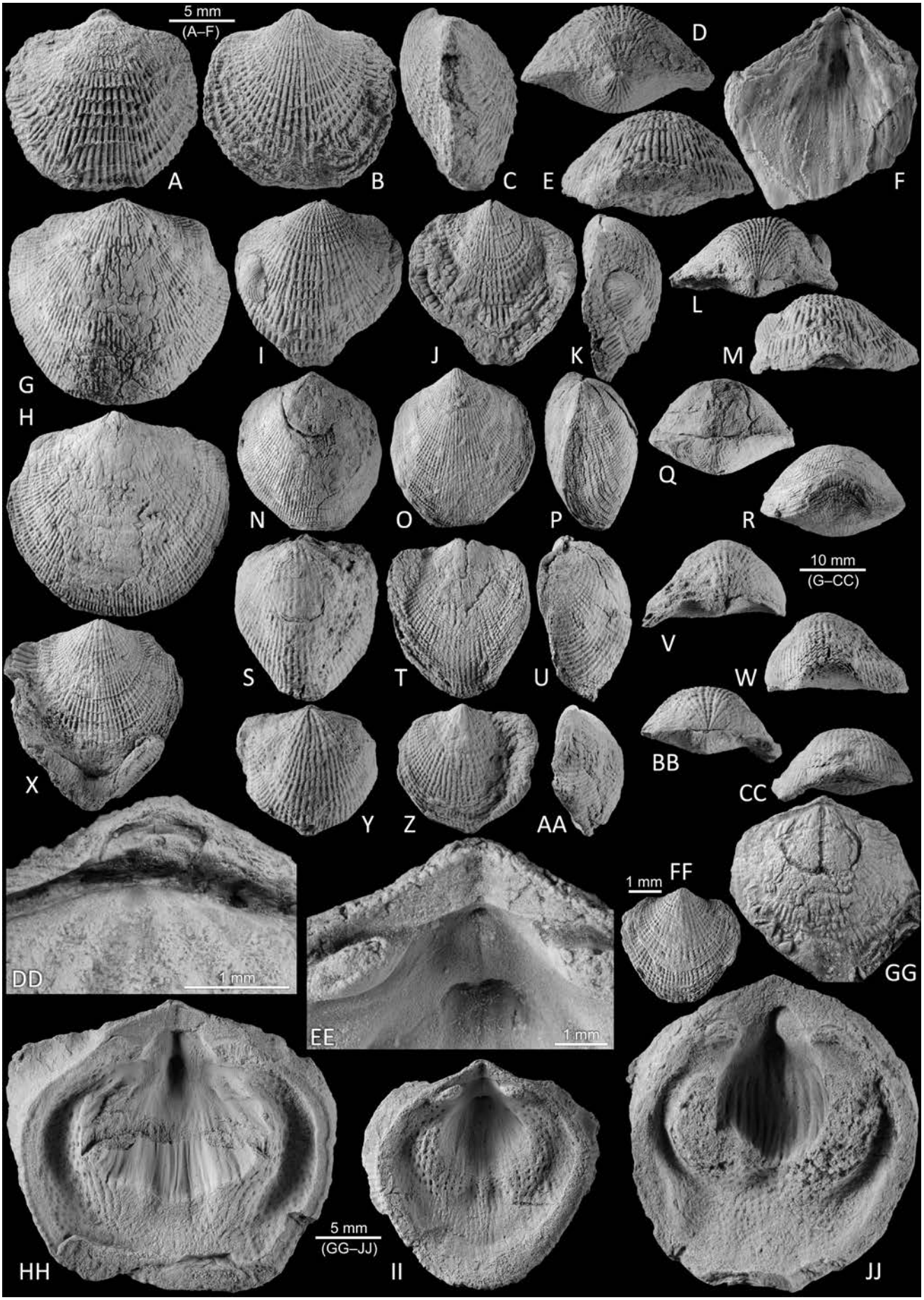
non 1970 *Atryparia dispersa* (Struve, 1966) – Godefroid, pp. 97–98, text-fig. 5, pl. 1, fig. 2, pl. 2, figs 1–2 [*A. instita*; *fide* Godefroid, 1995].

1987 *Atryparia* (*Atryparia*) *dispersa* (Struve, 1966) – Komarov, pp. 106–109, text-fig. 33, pl. 2, figs 4, 5.

. 1995 *Atryparia dispersa* (Struve 1966) – Struve, p. 100, figs 33–34.

1995 *Atryparia* sp., aff. *dispersa* (Struve 1966) – Struve, p. 100, figs 35–36.

non 2007 Atryparia dispersa (Struve 1966) – Hubert *et al.*, p. 260 [*A. instita*].


5 mm
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A
B
C
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L
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1 mm
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(GG–JJ)
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II
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Fig. 19. Middle Devonian Atrypida from southern Maïder and Europe. **A–F.** *Desquamatia* (*D.*) *microzonata* Struve, 1966. All specimens from Madène el Mrakib. A–E. Articulated shell SMF 94842 in dorsal, ventral, lateral, posterior, and anterior views. F. Ventral interior SMF 94840. **G–JJ.** *Atrypa* (*Planatrypa*?) *confusa* Struve, 1992. G, H. Articulated shell ZPAL Bp 68/1/48/1 from Aferdou in dorsal and ventral views. I–M. Articulated shell MNHN.F.A50414 from locality 346o *sensu* Sougy (1964) in the Zemmour Noir (Mauritania). N–R. Articulated shell ZPAL Bp 68/1/48/2 from Aferdou. S–W. Articulated shell ZPAL Bp 68/1/48/3 from Aferdou. X. Articulated shell ZPAL Bp 68/1/48/4 from Aferdou in ventral view, showing frills. Y–DD. Articulated shell SMF 94879 from the Ahbach beds (upper Eifelian) of the quarry "Müllertchen", 470 m S from the Ahütte railway station, Eifel (Fp. 2162 *sensu* Struve unpublished) in dorsal, ventral, lateral, posterior, and anterior views. EE, FF, II. Ventral valve SMF 94847 shown in external (FF) and internal (II) views; enlargement of the umbo (EE). GG. Articulated shell ZPAL Bp 68/1/48/7 from Aferdou, showing traces of the dorsal interior. HH, JJ. Two ventral interiors SMF 94846, 94845 from Madène el Mrakib

Material: Over one hundred and twenty articulated shells (several of them complete and well preserved) from Aferdou, ZPAL Bp 68/1/28/1.

Description: Shell usually over 30 mm in width, up to ca. 38 mm, longer than wide, seldom wider than long. Ventral valve subcircular to shield-shaped in outline with greatest width, respectively, about midlength or posteriorly (up to posterior fifth of the valve), moderately convex in umbonal region, somewhat flattened on flanks; beak poorly preserved, possibly incurved. Dorsal valve convex to strongly convex. Anterior commissure nearly straight to strongly uniplicate, usually with a distinct but poorly delimitated plica.

Ornamentation of strong, flattened ribs, some of them bifurcating up to three times on the ventral valve, more seldom on the dorsal one, (2.5–)3–4 per 5 mm at anterior margin, interrupted by strong growth lines. Frills (Fig. 28L) preserved up to 9 mm in length, with ribs either similar to those on the shell or much finer (ca. 10 per 5 mm).

Ventral interior with thick, well developed pedicle callist, on the sectioned specimen funnelled into collar; teeth strong, with lateral lobes and small dental nuclei. Dorsal valve with a large cardinal pit, moderately strong hinge plates and widely triangular in transverse section myophragm; sockets with large inner socket ridges and a distinct median ridge.

Remarks: In the material from the northern Maïder (7 specimens), Struve (1995) separated *A. dispersa* and *A.* aff. *dispersa*, on the basis of the greatest width of the shell, either at mid-length or more posteriorly. In the much more abundant material, studied by the present authors, these morphotypes intergrade, wherefore they are considered conspecific.

Distribution: In the type area, this species is known from the Junkerberg to Ahbach formations (middle to upper Eifelian; Struve, 1966). This species was also reported from Transcaucasia (Komarov, 1997) and erroneously from the Ardennes (Godefroid, 1970; the error was corrected by Godefroid, 1995, but was repeated by Hubert *et al.*, 2007).

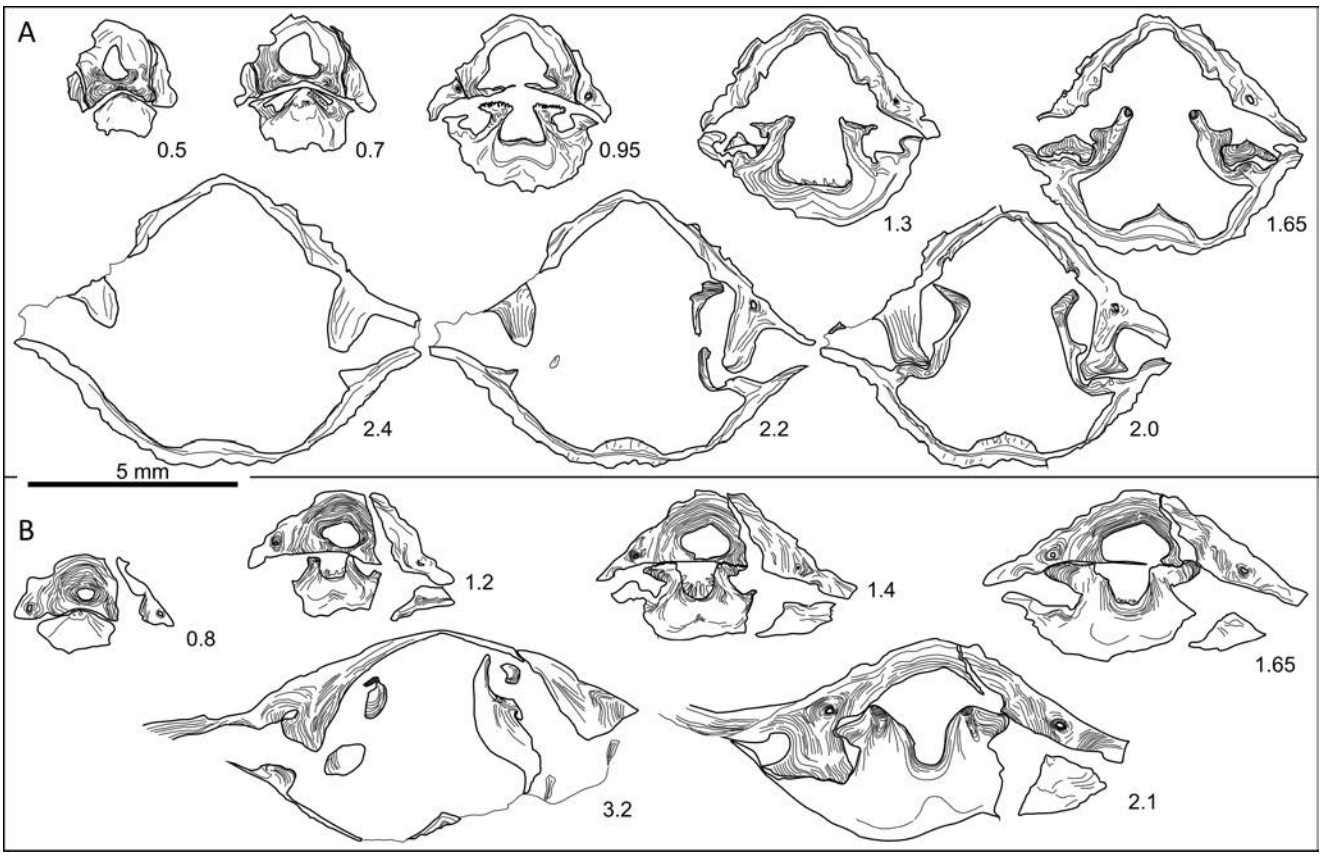


Fig. 20. Transverse serial sections of *Atrypa* (*Planatrypa*?) *confusa* through shells ZPAL Bp ZPAL Bp 68/1/48/5 (A) and 68/1/48/6 (B) from Aferdou. Distances measured in millimetres from the tip of the ventral umbo

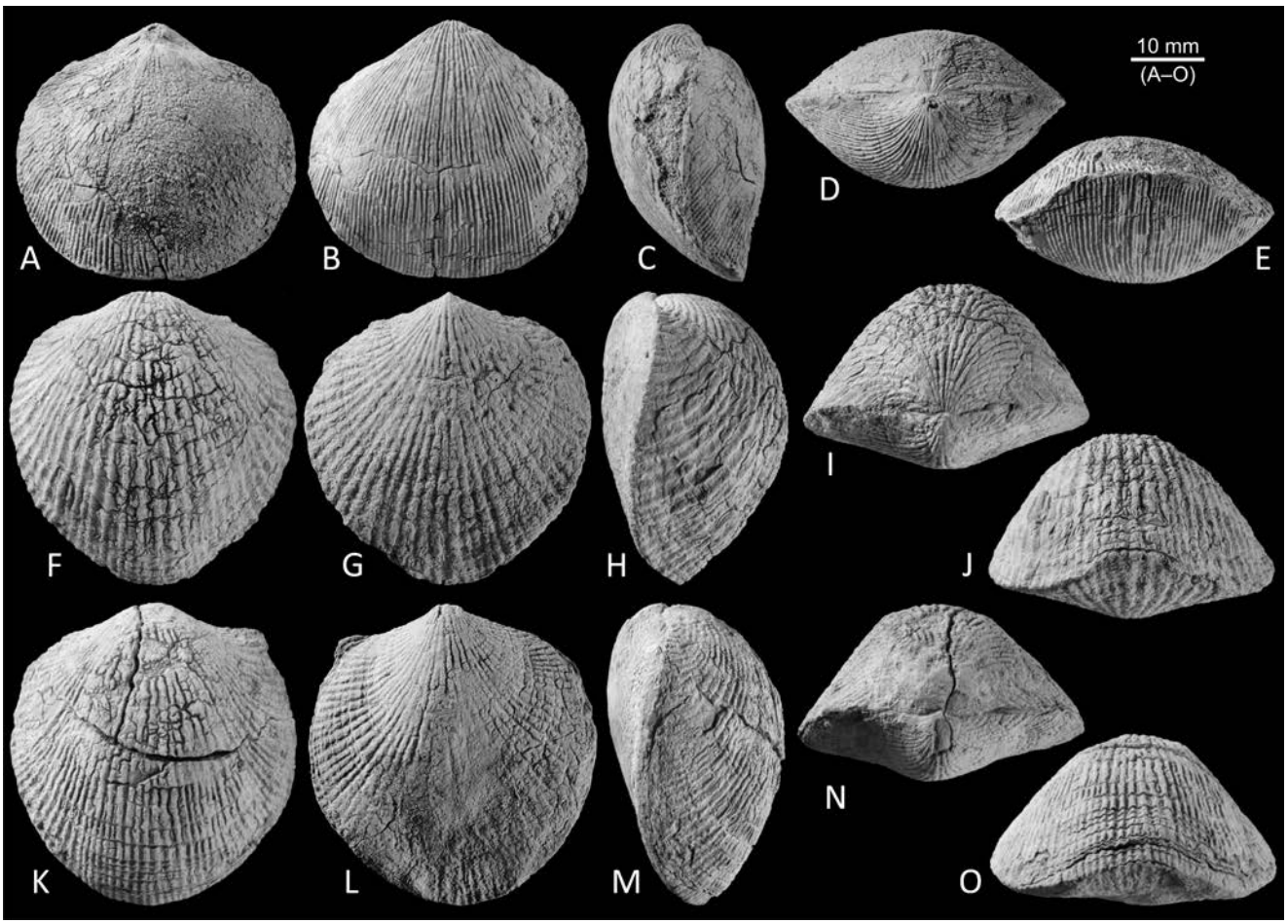


Fig. 21. Middle Devonian Atrypida from southern Maïder. **A–E.** *Gruenewaldtia latilinguis* (Schnur, 1851). Specimen ZPAL Bp 68/1/30/1. **F–O.** *Atryparia dispersa* (Struve, 1966). F–J. Specimen 68/1/28/1. K–O. Specimen 68/1/28/2. All specimens are articulated shells from Aferdou in dorsal, ventral, lateral, posterior, and anterior views

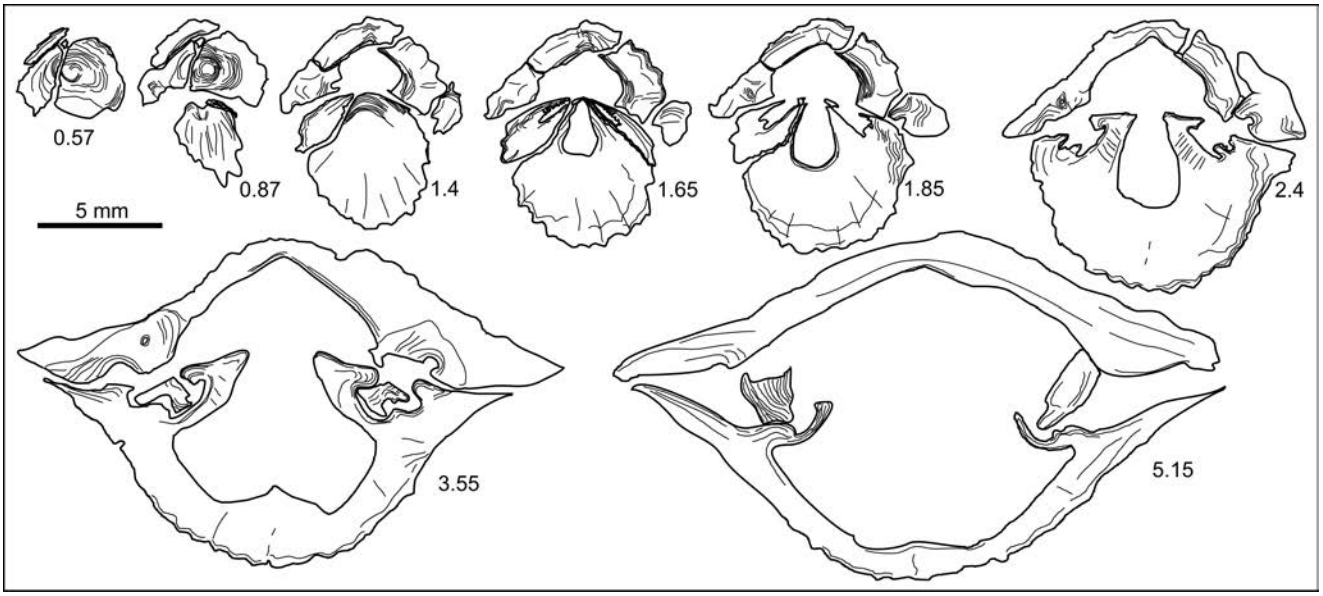


Fig. 22. Transverse serial sections of *Atryparia dispersa* (Struve, 1966) through shell ZPAL Bp 68/1/28/3 from Aferdou. Distances measured in millimetres from the tip of the ventral umbo

Genus *Invertina* Copper and Chen, 1995
Type species: *Atrypa aspera* var. *sinensis* Kayser, 1883; Yunnan; Givetian?

Invertina cf. *struvei* Godefroid, 2000
Fig. 23A–E

cf. 2000 *Invertina struvei* n. sp. – Godefroid: pp. 269–271, text-figs 2–6, pl. 1, figs 1–8.

Material: A single specimen from Aferdou, ZPAL Bp 68/1/45/1.
Description: The single available shell is elliptic in outline, elongate, venribiconvex, 10.3 mm wide, 11.8 mm long, and 4.9 mm thick. Dorsal valve weakly convex in umbonal region, with a median sulcus in the posterior fourth, nearly flat in lateral and anterior regions. Ventral valve triangular in anterior view; umbo very fine, strongly incurved. Anterior commissure nearly straight. Ornamentation of rounded ribs, 6–7 per 5 mm.
Remarks: The specimen described is of small size and nearly planoconvex; it is probably a juvenile, like that of *Invertina sinensis* illustrated by Copper and Chen (1995, fig. 2: 11–15) from the middle Givetian of Sichuan. The comparison with the slightly younger (Upper *varcus* Zone) *Invertina struvei* from the northern Maïder (Godefroid, 2000) is therefore difficult; open nomenclature has been used for this reason. As for other Middle Devonian ventribiconvex atrypides, *Kerpina* is usually asymmetric (Struve, 1961; Copper, 1967b) and *Invertina fasciplicata* is nearly aequibiconvex (Copper, 1967a).

Genus *Kerpina* Struve, 1961
Type species: *Kerpina vineta* Struve, 1961; Eifel, Eifelian

Kerpina vineta Struve, 1961
Figs 23F–T, 24

v* 1961 *Kerpina vineta* n. g., n. sp. – Struve: p. 333, pl. 1, figs 3, 4.

Material: Seventy-seven specimens from Aferdou El-Mrakib, some of them well preserved, a large part slightly deformed, some incomplete, ZPAL Bp 68/1/27/1–77.
Description: Shell circular to elliptic in outline, slightly longer than wide to slightly wider than long, moderately ventribiconvex to moderately dorsibiconvex, up to 28.0 mm in width. Dorsal valve uniformly convex. Ventral valve moderately inflated or with flattened attachment area in umbonal region, sometimes slightly geniculated in the lateral profile, with a steep marginal region; beak straight to moderately incurved, with an apical foramen; ventral interarea very high, transversely striate, weakly curved to nearly flat, usually apsacline, seldom weakly anacline. Anterior commissure uniplicate, tongue occupying about two-thirds of the shell width.
Ornamentation of strong costae and costellae, 6–8 per 5 mm, crossing with strong growth lines.
Internally, shell wall thick, especially posteriorly; thick pedicle callist and massively thickened deltidial plates form wide, irregular pedicle collar (Fig. 24); teeth solid, without dental nuclei, thick. Dorsal interior with low and thick hinge plates; median myophragm wide, well developed.
Remarks: This species is easily distinguished from co-occurring atrypides by its exceptionally high ventral interarea, asymmetry, and a steep marginal region of the ventral valve. The type collection of *Kerpina vineta* Struve, 1961 from the late Eifelian Freilingen Formation of the Eifel contains individuals that are smaller (usually ca. 15 mm wide, maximum width 20.2 mm; Copper, 1967b, and the present authors), have approximately the same ornamentation density and flat to weakly convex dorsal valve. The differences of size and convexity, although clear and constant, are interpreted to reflect infraspecific and/or ontogenetic variability. *Kerpina atrypoides* Struve, 1961 is a poorly known taxon from the same strata of the Eifel (Struve, 1961), of similarly smaller size than the material described here. This is the first report of *Kerpina* from Africa.
Distribution: *Kerpina vineta* was described originally from the late Eifelian of the Eifel area in Germany, where it is confined to the "Rasenriff" or thicket reef biotope (Copper, 1967b).

Genus *Spinatrypa* Stainbrook, 1951
Type species: "*Atrypa hystrix* var. *occidentalis* Hall" (errore pro *Atrypa aspera* var. *occidentalis* Hall, 1858) *sensu* Stainbrook, 1945; Iowa, USA; Cedar Valley Formation, Frasnian

Spinatrypa (*Spinatrypa*) cf. *trigonella* (Davidson, 1882)
Fig. 25K–HH

cf. 1882 *Atrypa*? *trigonella*, Dav. – Davidson, p. 40, pl. 1, figs 19, 19a, 19b.
vp 1964 *Atrypa aspera* (Schlotheim, 1813) – Sougy, pp. 445–446, pl. 50, fig. 7.
cf. 1965 *Spinatrypa trigonella* (Davidson) – Copper, p. 360.

Material: Forty-eight articulated shells, several of them complete and well preserved, from Aferdou, ZPAL Bp 68/1/29/1–48.
Additional material: Articulated shell MNHN.F.R10288 from Oudeï Askaf (Zemmour, Mauritania) figured by Sougy (1964, pl. 50: 7); fourteen mostly complete articulated shells MNHN.F.A 48102, 50415 from the locality 2108A, det. P. Copper; articulated shell MNHN.F.A48104 from the locality 2428; three articulated shells MNHN.F.A48103 from the locality 346c; all the above from the Zemmour Noir, Mauritania, coll. J. Sougy.
Description: Shell approximately as wide as long, more rarely transverse, ventribiconvex, usually about 17 to 23 mm in width, seldom up to ca. 28 mm. Ornamentation of undulating ribs, 14–16 (–22) in total, 3(–4.5) per 5 mm; tubular spines present.
Remarks: This species is included into *Spinatrypa*, on account of wave-like ribs and the presence of spines; it is referred to the inadequately known species *Spinatrypa trigonella* (Davidson, 1882), described from the Middle Devonian (Givetian; Elliott, 1961 as "Upper Givetian", but probably lower if the Bilveringsen fauna is an equivalent; Copper, 1965) of Lummaton near Torquay (Devonshire; Davidson, 1882) on account of similar shape and ornamentation. The type material has not been restudied recently, wherefore open nomenclature is used as a precaution. *Spinatrypa trigonella* probably occurs also in the Rhenish Massif (Büchel in the Bergisches Land; Copper, 1965, p. 360). *Spinatrypa* cf. *trigonella* from Aferdou resembles early Eifelian *Spinatrypa variaspina* Copper, 1967 [1967a] from the Eifel, which has, however, finer ornamentation. Two other species from the Eifel show some more distant resemblance to the material studied: the early Givetian *Spinatrypa curvirostra* Copper, 1967 [1967a] has coarser ornamentation, while the middle Givetian *Spinatypa orthoclina* Copper, 1967 [1967a] is flatter (Copper, 1967a).
Distribution: This species is known from the Middle Devonian of Maïder and of Zemmour Noir (Mauritania); most probably also of Devonshire and the Rhenish Massif.

Spinatrypa (*Spinatrypa*) *globulina* Copper, 1967 [1967a]
Fig. 25A–J

* 1967a *Spinatrypa globulina* n. sp. – Copper: pp. 506–507, pl. 78, figs 11–24.

Material: Two articulated shells (one subcomplete, one incomplete) from Aferdou, ZPAL Bp 68/1/47/1–2.

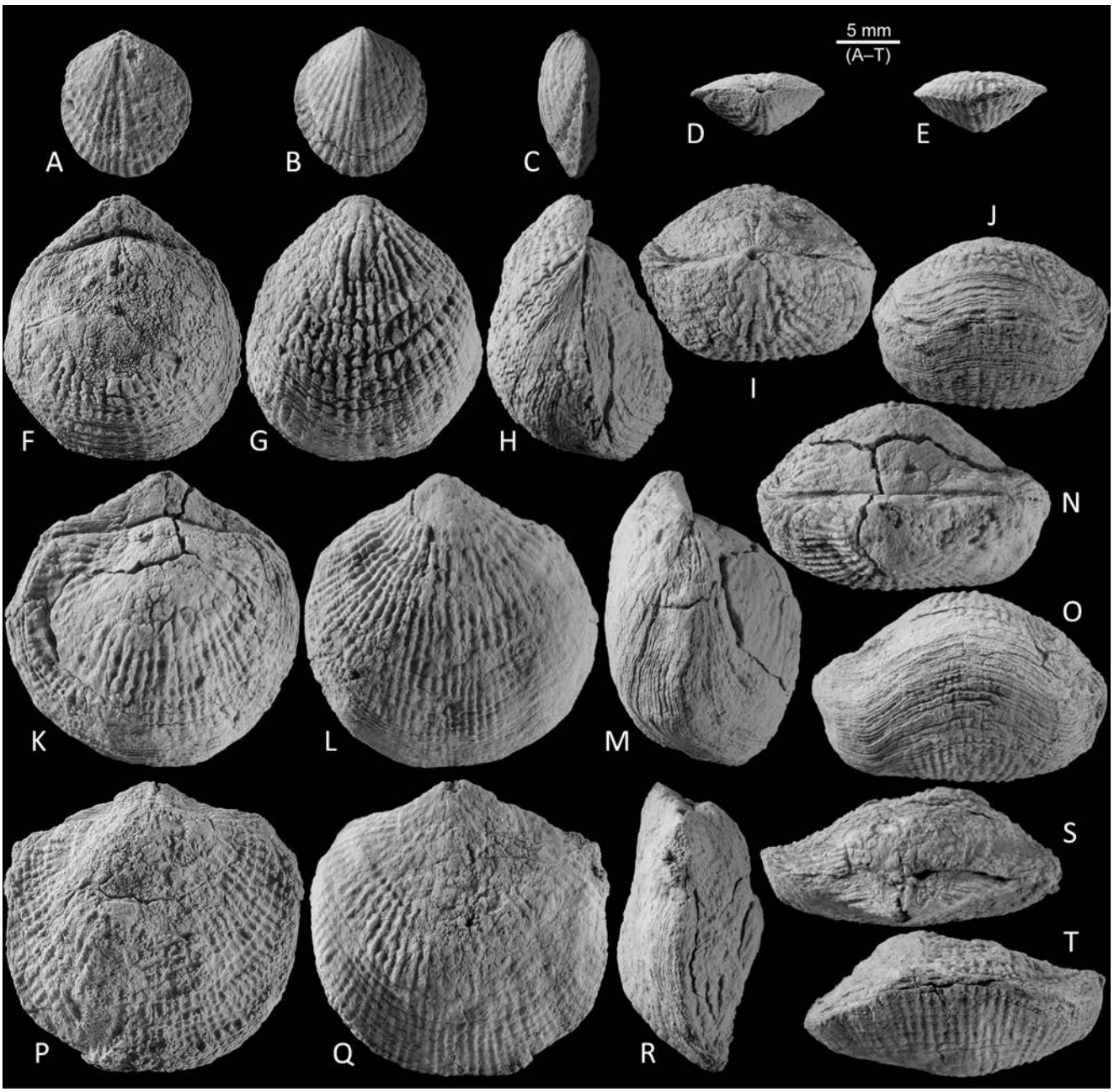


Fig. 23. Middle Devonian Atrypida from southern Maïder. **A–E.** *Invertina* cf. *struvei* Godefroid, 2000. Articulated shell ZPAL Bp 68/1/45/1 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. **F–T.** *Kerpina vineta* Struve, 1961. Articulated shells from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. F–J. Specimen ZPAL Bp 68/1/27/1. K–O. Specimen ZPAL Bp 68/1/27/2. P–T. Specimen ZPAL Bp 68/1/27/3

Description: Shell approximately circular in outline, weakly to moderately dorsibiconvex, up to ca. 20 mm in width. Anterior commissure uniplicate, tongue broad and low. Ornamentation of rounded, undulose, broad ribs, 1–2 per 5 mm at anterior margin. The ventral midrib pair is stronger than the other ribs.

Remarks: This species is distinguished from the co-occurring *Spinatrypa* cf. *trigonella* by its coarser ribs and the presence of a stronger ventral midrib pair.

Distribution: In the type area, *S. globulina* is found in the Loogh Formation (lowermost Givetian, Eifel, Germany; Copper, 1967a).

Genus *Desquamatia* Alekseeva, 1960

Subgenus *Desquamatia* (*Desquamatia*) Alekseeva, 1960

Type species: *Atrypa* (*Desquamatia*) *khavae* Alekseeva, 1960; Urals, Russia; lower Eifelian

Desquamatia (*Desquamatia*) *microzonata* Struve, 1966

Fig. 19A–F

vp 1964 *Atrypa reticularis* – Sougy, p. 448.

v* 1966 *Desquamatia (Synatrypa) microzonata* n. sp. – Struve: pp. 151–153, pl. 16, fig. 12.

1970 *Desquamatia* (*Synatrypa*) *microzonata* Struve, 1966

– Godefroid, p. 117–119, fig. 21, pl. 1, fig. 3.

1995 *Desquamatia (Synatrypa) microzonata* Struve, 1966 – Godefroid, p. 94, pl. 3, fig. 5.

Material: Five articulated shells SMF 94839–94842 and MB unnumbered (V. Ebbighausen's collection) from the *Drotops* beds at Madène el Mrakib.

Additional material: Three articulated shells MNHN.F.A48116 from the "basal Givetian" of Aguelt Oudiate el Khyam (locality 401), Zemmour Noir, Mauritania, coll. J. Sougy, det. P. Copper [as "*Desquamatia* (*Synatrypa*) cf. *microzonata*"].

Description: Shell subcircular in outline, up to 16.9 mm wide, moderately to markedly dorsibiconvex. Ornamentation of ribs, 8–9 per 5 mm at anterior margin. Interior not studied.

Remarks: As far as the exteriors are concerned, the material studied is indistinguishable from the type collection from the Eifel.

Distribution: *Desquamatia microzonata* is known from the middle Eifelian of the Eifel (Struve, 1966) and of the Ardennes (Godefroid, 1970, 1995), as well as from the Middle Devonian of Maïder and of the Zemmour Noir. *Desquamatia* cf. *microzonata* was reported from the Middle Devonian of Padaupkin in Burma (Anderson *et al.*, 1969). The subgenus *Desquamatia* (*Synatrypa*) is a synonym of *D.* (*Desquamatia*) (Copper, 2002).

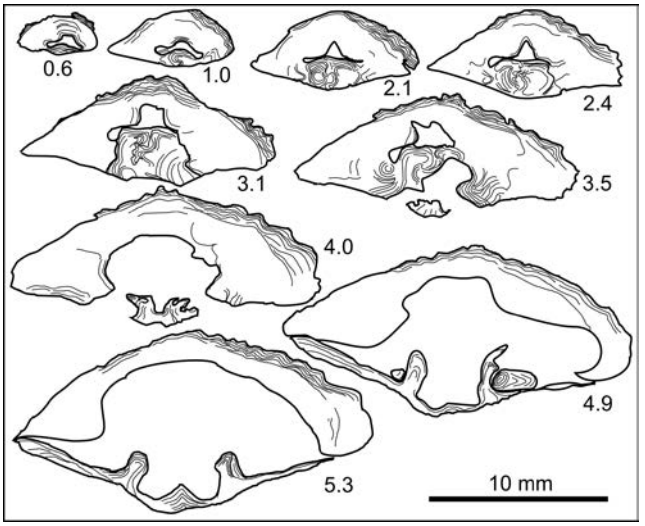


Fig. 24. Transverse serial sections of *Kerpina vineta* Struve, 1961 through shell ZPAL Bp 68/1/27/4 (A) from Aferdou. Distances measured in millimetres from the tip of the ventral umbo

Desquamatia (*Desquamatia*) *deserti* new species
Figs 26A–O, 27

Type material: Holotype, complete articulated shell ZPAL Bp 68/2/26/1 and thirty nine paratypes, ZPAL Bp 68/2/26/2–40, (among them some complete articulated shells), all from Maharch.

Etymology: *Desertum*, Latin for desert.

Dimensions: See Table 3.

Diagnosis: *Desquamatia* (*Desquamatia*) with nearly flat ventral valve and fine ornamentation, 7–9(–13) ribs per 5 mm at anterior margin.

Description: Shell more frequently longer than wide, usually over 35 mm in width, up to ca. 40 mm. Shoulder angle ca. 140–150°. Dorsal valve high. Ventral valve subtriangular in anterior view, convex in umbonal region, otherwise flattened. Anterior commissure broadly uniplicate. Ornamentation of fine ribs, 7–9(–13) per 5 mm at anterior margin.

Ventral valve with pedicle callist with tendency to develop into a short collar; teeth long, strong with a lateral lobe and small dental cavities. Dorsal valve with a rather small cardinal pit and a triangular myophragm; hinge plates with comblike cardinal process developed posteriorly; crural bases well visible, expanding into sharply deflected laterally and feathered crura (Fig. 27).

Remarks: *Desquamatia* (*D.*) *deserti* sp. nov. may be compared to some fine-ribbed and large-sized atrypides, although none of them is closely similar. *Desquamatia* (*D.*) *ovata* Copper, 1966 from the Eifelian of the Eifel (Nohn Formation) is quite similar in outline (Copper, 1966a); it differs in its more convex ventral valve. The finely ribbed *Atrypa desquamata* var. *alticola* Frech, 1891 from the Givetian of the Carnic Alps (Frech, 1891) probably does not represent the genus *Desquamatia* (see Baliński, 1979, 1998). The new species shows some external similarity to the finely ribbed *Desquamatia* (*D.*) *alticoliformis* Rzhonsnitskaya, 1975, reported from the late Frasnian of Russia (Rzhonsnitskaya, 1975; Rzhonsnitskaya *et al.*, 1998), Eifel (Godefroid and Hauser, 2003), Ardennes (Godefroid and Helsen, 1998; Mottequin, 2008a), and Poland (Racki and Baliński, 1998). Besides having a different stratigraphic range, the species from Aferdou differs also in having a not as wide, rather shield-shaped outline of the shell, with a narrowly elongated anterior region. The late Givetian *Desquamatia* (*D.*?) *globosa* (Gürich, 1896) has a more convex ventral valve (Racki and Baliński, 1981).

The single specimen ZPAL Bp 68/1/26/1 from Aferdou (Fig. 26A–E) is tentatively referred to the discussed species.

Type locality: Guelb el Maharch.

Type level: Guelb el Maharch mud mound, Taboumakhloûf Formation; lower Givetian.

Stratigraphic distribution: lower Givetian.

Deposition of types: ZPAL.

Distribution: Except for the single dubious specimen from Aferdou, the new taxon is unknown outside the type locality and stratum.

Subgenus *Desquamatia* (*Independatrypa*) Copper, 1973
Type species: *Atrypa independensis* Webster, 1921, Iowa, USA; middle Givetian

Desquamatia (*Independatrypa*) *circulareformis* Biernat, 1964
Fig. 26U–DD

v* 1966 *Desquamatia circulareformis* n. sp. – Biernat: pp. 326–327, pl. 8, fig. 8, pl. 12, figs 2–3.

Material: Four specimens (three subcomplete artciulated shells) from Aferdou, ZPAL Bp 68/1/25/1–4.

Description: Shell weakly transverse (width to length ratio 1.13–1.17), strongly dorsibiconvex, up to 43 mm in width. Dorsal valve moderately convex (thickness to width ratio 0.53–0.58). Ventral valve rounded, moderately convex, triangular in anterior view; beak elongate, incurved. Anterior commissure uniplicate, tongue subtrapezoidal to rounded, wide, moderately high. Ornamentation of ribs,

Table 3

Biometric characteristics of *Desquamatia* (*D.*) *deserti* sp. nov.; measurements in millimetres

Specimen	W	L	T	R-10	Ra
2/26/1	35.1	36.6	21.6	8-10	8–9
2/26/2	37.5	36.3	24.2	15	11–13
2/26/5	36.1	42.1	25.5	11-12	9

W – width; L – length; T – thickness; R-10 – number of ribs per 5 mm counted at 10 mm from the beak; Ra – numer of ribs per 5 mm at anterior margin

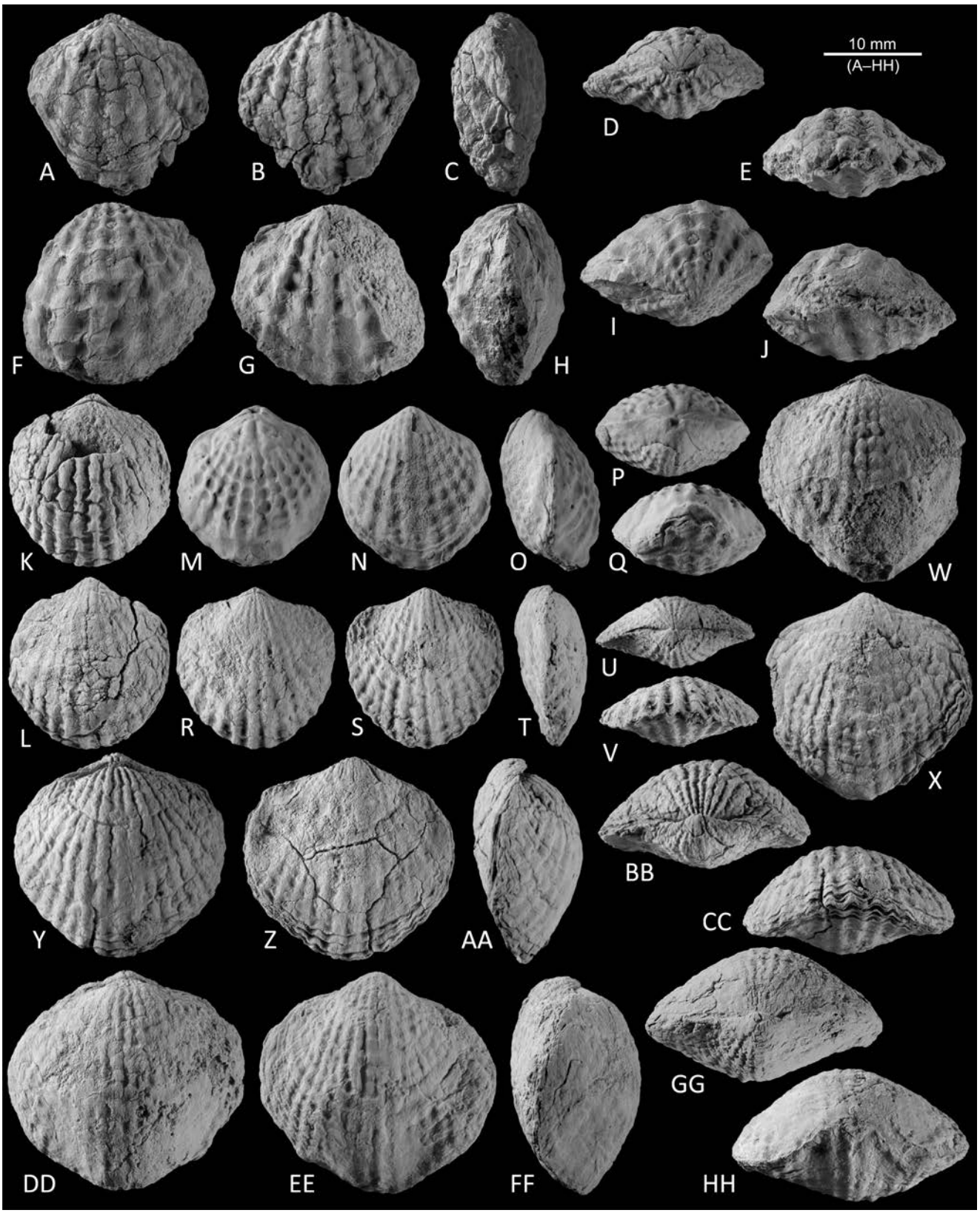


Fig. 25. Middle Devonian Atrypida from northwestern Africa. **A–J.** *Spinatrypa globulina* Copper, 1967. Incomplete articulated shells from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. A–E. Specimen ZPAL Bp 68/1/47/1. F–J. Specimen ZPAL Bp 68/1/47/2. **K–HH.** *Spinatrypa* cf. *trigonella* (Davidson, 1882). K, L. Articulated shell ZPAL Bp 68/1/29/1 from Aferdou in dorsal and ventral views. M–Q. Articulated shell MNHN.F.A50415 from the locality 2108A *sensu* Sougy (1964) (Zemmour Noir, Mauritania) in dorsal, ventral, lateral, posterior, and anterior views. W, X. Articulated shell ZPAL Bp 68/1/29/2 from Aferdou in dorsal and ventral views. Y–CC. Articulated shell ZPAL Bp 68/1/29/3 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. DD–HH. Articulated shell ZPAL Bp 68/1/29/4 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views

4–6 per 5 mm at anterior margin; growth lines sparse, lamellose.
Remarks: The above-mentioned material is considered conspecific with *D. circulareformis*, a poorly known, approximately coeval species from Miłoszów, in the Holy Cross Mountains (Biernat, 1964).

Three poorly preserved very large shells from Aferdou (ZPAL Bp 68/1/25B/1–3) are similar to *D.* (*I.*) *circulareformis*, as above, but differing in their larger size (up to 51 mm), nearly flat dorsal valves and very high tongues, with subparallel lateral slopes; they are tentatively referred to as *D.* (*I.*) cf. *circulareformis*.
Distribution: Holy Cross Mountains and Maïder, upper Eifelian to lower–middle Givetian.

Desquamatia? sp. 1
Fig. 26P–T

Material: Four specimens (two complete articulated shells) from Aferdou, ZPAL Bp 68/1/25A/1.
Description: Shell approximately as wide as long (width-to-length ratio 0.99–1.02), markedly dorsibiconvex, up to 41 mm in width. Shoulder line composed of two concave segments. Dorsal valve markedly convex (thickness to width ratio 0.65–0.69). Ventral valve shield-shaped, convex in umbonal region, lateral flanks flattened to concave; beak small. Anterior commissure uniplicate, tongue subtriangular, wide, high. Ornamentation of ribs, 4–5(–6) per 5 mm at anterior margin; growth lines dense, lamellose.
Remarks: The large size of this rare form would support appurtenance to *Desquamatia* (*Independatrypa*), yet the dense ornamentation indicates *D.* (*Desquamatia*). It is difficult to find any comparable species.

Family Davidsoniidae King, 1850

Genus *Prodavidsonia* Havlíček, 1956
Type species: *Prodavidsonia dalejensis* Havlíček, 1956; Bohemia; Choteč Formation, Eifelian

Prodavidsonia sp.
Fig. 28A–E

Material: A single subcomplete specimen from Aferdou El-Mrakib, ZPAL Bp 68/1/32/1.
Description: Shell 12.6 mm wide, >8.3 mm long, and 1.7 mm thick, its outline being best described as an ellipse cut by the straight line of the posterior margin. Dorsal valve flat, with a very narrow (ca. 1 mm) median sulcus beginning <1.5 mm from the umbo and continuing to the anterior margin. Ventral valve very low, but acutely triangular in anterior view, with barely perceptible low median carina; interarea very broad, nearly flat, catacline. Anterior commissure rectimarginate. Shell smooth except for fine growth lines. Interior unknown.
Remarks: This specimen cannot be matched with any representative of *Prodavidsonia* (incl. *Quasidavidsonia* Havlíček, 1987, following Copper, 2002), described up to now. *P. tenuissima* (Barrande, 1879) and *P. mediocarinata* Havlíček, 1967, both from the Eifelian of Bohemia, have similar width-to-length ratios, but their ventral valves are concave anteriorly (Barrande, 1879; Havlíček, 1967). *P. dalejensis* Havlíček, 1956 from the Eifelian of Bohemia has a similar weakly convex ventral valve and flat dorsal one, but its shape is more transverse (Havlíček, 1956). In *P. vicina* Havlíček, 1967 from the Eifelian of Moravia the carina and the sulcus are less distinct (Havlíček, 1967). The same can be said about the Givetian *P. havliceki* García-Alcalde, 2010 from the Asturias, which is, moreover, smaller. The late Eifelian to early Givetian *P. scalensis* (Sobolew, 1904) from the Holy Cross Mountains has a concave dorsal valve (Halamski, 2004a). ?*Prodavidsonia* sp., reported by Drot (1961a) from the upper Givetian of Drâa valley in Morocco, is also concavo-convex.

Family Carinatinidae Rzhonsnitskaya, 1960

Genus *Carinatina* Nalivkin, 1930
Type species: *Orthis arimaspus* Eichwald in von Buch, 1840; Bogoslowsk, Russia; Middle Devonian

Carinatina arimaspus (Eichwald in von Buch, 1840)
Fig. 28F–K

* 1840 *Orthis Arimaspus* Eichw. – von Buch: pp. 108, 112.
1978 *C*[*arinatina*] *arimaspus* (Eichwald, *in* Buch 1840) – Copper, p. 310, pl. 7, figs 1–6.

Material: Fourteen specimens (three subcomplete) from Aferdou, ZPAL Bp 68/1/31/1–14.
Description: Shell transverse (width-to-length ratio 1.3–1.4), up to ca. 28 mm in width, very low (up to 7 mm thick). Posterior margin straight. Dorsal valve with a deep U-shaped median sulcus. Ventral valve with a median carina, lateral flanks posteriorly flat, anteriorly convex; interarea apsacline. Anterior commissure rectimarginate. Ornamentation (Fig. 28K) of high, acute, frequently bifurcating ribs, 3–7 per 5 mm at anterior margin (higher or lower numbers depend on presence or absence of bifurcation in close proximity to the anterior margin, respectively). Growth lines regular, dense.
Distribution: Bohemia, Lower Devonian (Suchomasty Limestone, Emsian; Havlíček and Kukal, 1990); Holy Cross Mountains and Maïder, Middle Devonian.

Family Paraferellidae Spriesterbach, 1942

Genus *Gruenewaldtia* Tschernyschew, 1855
Type species: *Terebratula latilinguis* Schnur, 1851; Germany; Eifelian

Gruenewaldtia latilinguis (Schnur, 1851)
Figs 21A–E, 29

* 1851 *Terebratula latilinguis*, n. sp. – Schnur: p. 7.
1955 *Grünewaldtia latilinguis latilinguis* (Schnur 1851) – Struve, pp. 228–229, text-fig. 8a.
v. 1964 *Gruenewaldtia latilinguis latilinguis* (Schnur, 1851) – Biernat, pp. 332–334, text-fig. 20, pl. 14, figs 1–6, 8–9.
1965 *Gruenewaldtia latilinguis* (Schnur) – Copper, pp. 369–371, text-fig. 8, pl. 47, figs 1–3.
1970 *Gruenewaldtia latilinguis* (Schnur, 1851) – Godefroid, pp. 123–125, text-fig. 23.

Material: Five articulated shells from Aferdou, ZPAL Bp 68/1/30/1–5.
Description: Shell rounded, slightly wider than long or longer than wide, weakly ventribiconvex to moderately dorsibiconvex, ca. 30 to 40 mm in width. Dorsal valve slightly flattened medially. Ventral valve regularly convex; tongue present but sulcus imperceptible; umbo very massive, beak incurved; deltidial plates fused. Anterior commissure unisulcate, tongue very broad, rounded. Ornamentation of uninterrupted subacute ribs, 5–8 per 5 mm at anterior margin.

Ventral interior with massive muscle platform supported anteriorly by two thick and coarse crystalline septa and extending anteriorly for about one fourth of the valve length; pedicle collar not observed in the single sectioned specimen, but distinct internal projections of deltidial plates are present (Fig. 29, distances 3.0 and 3.2 mm). In the dorsal valve the inner socket ridges thick; distinctive striated cardinal process lining posteriorly inner socket ridges and cardinal pit; muscle platform thick, well developed and rised somewhat anteriorly from the umbo, supported by two coarse crystalline lateral septa and a poorly differentiated median septum

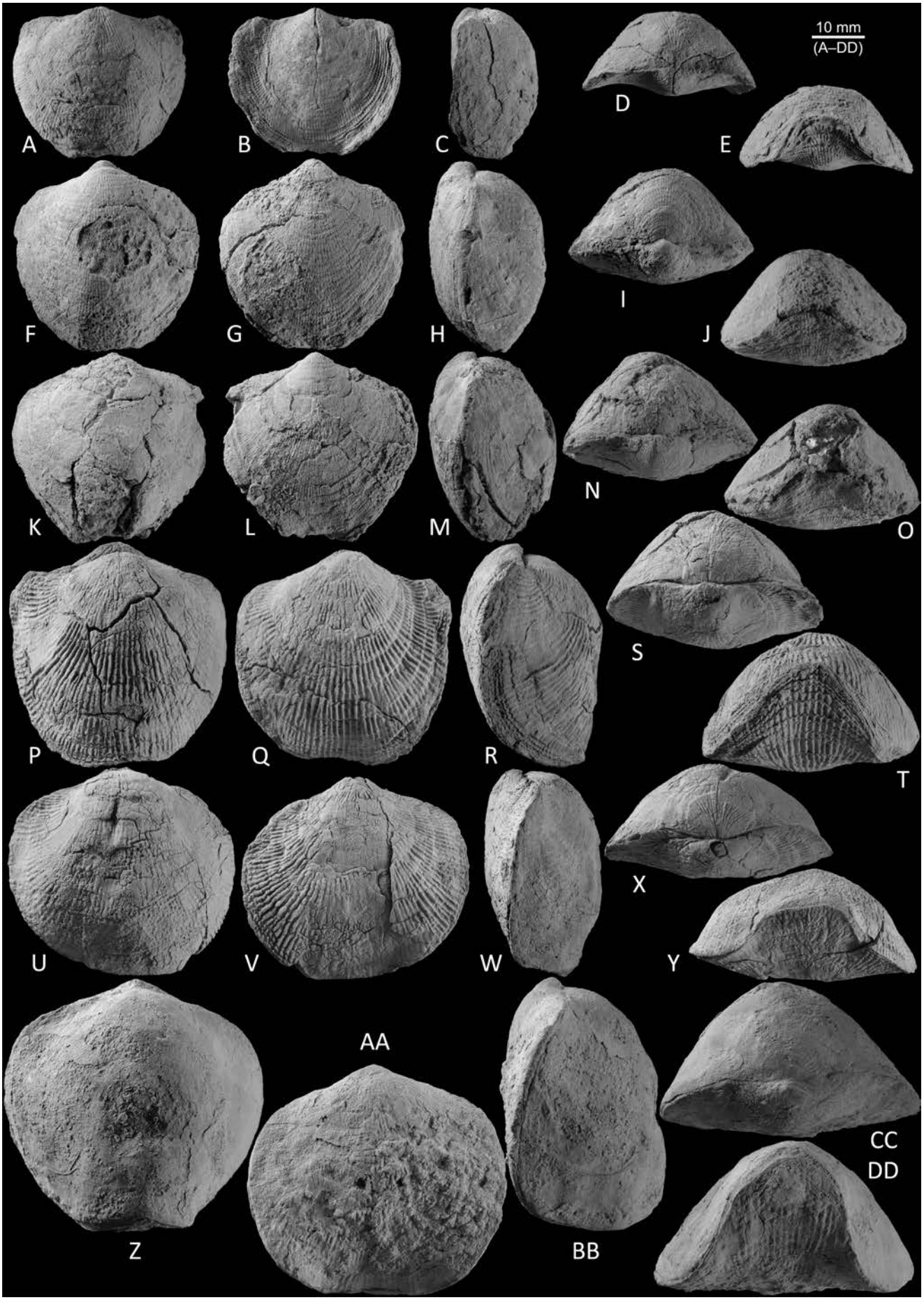

10 mm
(A–DD)
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y
Z
AA
BB
CC
DD

Fig. 26. Middle Devonian Atrypida from southern Maïder. **A–O.** *Desquamatia* (*D.*) *deserti* sp. nov. A–E. Specimen ZPAL Bp 68/1/26/1 from Aferdou tentatively referred to the species. F–J. Holotype ZPAL Bp 68/2/26/1 from Maharch. K–O. Paratype ZPAL Bp 68/2/26/2 from Maharch. **P–T.** *Desquamatia*? sp. 1 from Aferdou. Articulated shell ZPAL Bp 68/1/25A/1 in dorsal, ventral, lateral, anterior, and posterior views. **U–DD.** *Desquamatia* (*Independatrypa*) *circulareformis* Biernat, 1964 from Aferdou. U–Y. Specimen ZPAL Bp 68/1/25/1. Z–DD. Specimen ZPAL Bp 68/1/25/2. All photographs are of articulated shells in dorsal, ventral, lateral, posterior, and anterior views

(Fig. 29, distances 12.5 and 13.1 mm); thick median ridge with rounded top, anteriorly medially grooved, appears at about 8 mm anteriorly from the umbo, running on the upper surface of the muscle platform.

Remarks: Differences in the internal structures of the *Gruenewaldtia* taxa, occurring in the Eifel area, are best interpreted as representing specific distinctions, whereas external morphology is a poor taxonomic character (Copper, 1965 and P. Copper, pers. comm., April 2013). The material described here is similar to *G. latilinguis* (Struve, 1955, fig. 8a) in having the ventral platform supported by two lateral septa without a median septum, in contrast to *G. matutina* Struve, 1955 with several ventral septa (Struve, 1955, fig. 8b–i).

Distribution: Eifel (Eifelian), Ardennes (Couvin, Co2c), Holy Cross Mountains (Skały beds), England (Chercombe Bridge shales), Nakhichevan Republic (Djahannamdarasi valley, upper Eifelian), Maïder; Middle Devonian (Struve, 1955; Biernat, 1964; Copper, 1965; Godefroid, 1970; Mamedov, 1974).

Family Lissatrypidae Twenhofel, 1914

Genus *Peratos* Copper, 1986

Type species: *Peratos arrectus* Copper, 1986; Germany; upper Eifelian

Peratos arrectus Copper, 1986
Figs 31A–J, 32

* 1986 *Peratos arrectus* n. sp. – Copper: pp. 859–860, text-figs 16–17, pl. 74, figs 32–36, pl. 75, fig. 1.

Material: Over seventy specimens (mostly complete articulated shells) from Aferdou, ZPAL Bp 68/1/40 and over fifteen specimens (usually complete articulated shells) from Maharch, ZPAL Bp 68/2/40.

Additional material: Five partly decorticated articulated shells MNHN.F.A48141 from a small escarpment 2 km ENE from Aguelt Oudiate el Khyam (section D-13, levels 5–6); "upper Couvinian" (bed 80), Zemmour Noir, Mauritania, coll. J. Sougy.

Description: Shell circular to teardrop-shaped in outline, aequibiconvex to moderately ventribiconvex, up to ca. 15 mm in width. Ventral umbo elongate, fine, beak strongly incurved. Anterior commissure straight to very weakly uniplicate. Growth lines usually well visible, but rare, becoming conspicouous and crowded in marginal region.

Internally, thick shelled, especially posteriorly; dental plates thin, subparallel to slightly divergent ventrally; dental cavities large and wide; small deltidial plates developed. In the dorsal valve cardinal pit wide and shallow; hinge plates low, inner socket ridges nearly horizontal, wide.

Distribution: This species was described from upper Eifelian Freilingen Formation of the Eifel (Copper, 1986). This is the first report of this genus in Africa (Maïder and Zemmour Noir).

Order Athyridida Boucot, Johnson and Staton, 1964
Family Athyrididae Davidson, 1881

Genus *Athyris* M'Coy, 1844

Type species: *Terebratula concentrica* von Buch, 1834; Eifel, Germany; Eifelian

Athyris ex gr. *concentrica* (von Buch, 1834)
Fig. 30F–O

ex gr. 1996 *Athyris (Athyris) concentrica* (von Buch 1834) –

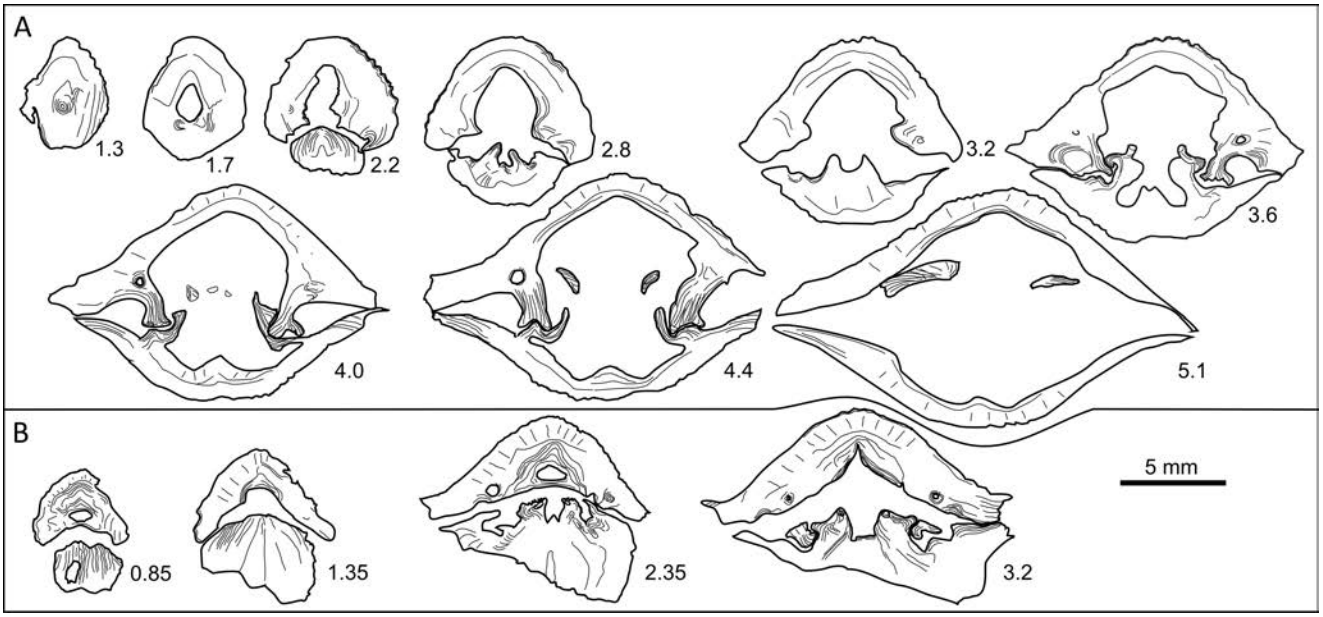


Fig. 27. Transverse serial sections of *Desquamatia* (*D.*) *deserti* sp. nov. through shells ZPAL Bp 68/2/26/3 (A) and 68/2/26/4 (B) from Maharch. Distances measured in millimetres from the tip of the ventral umbo

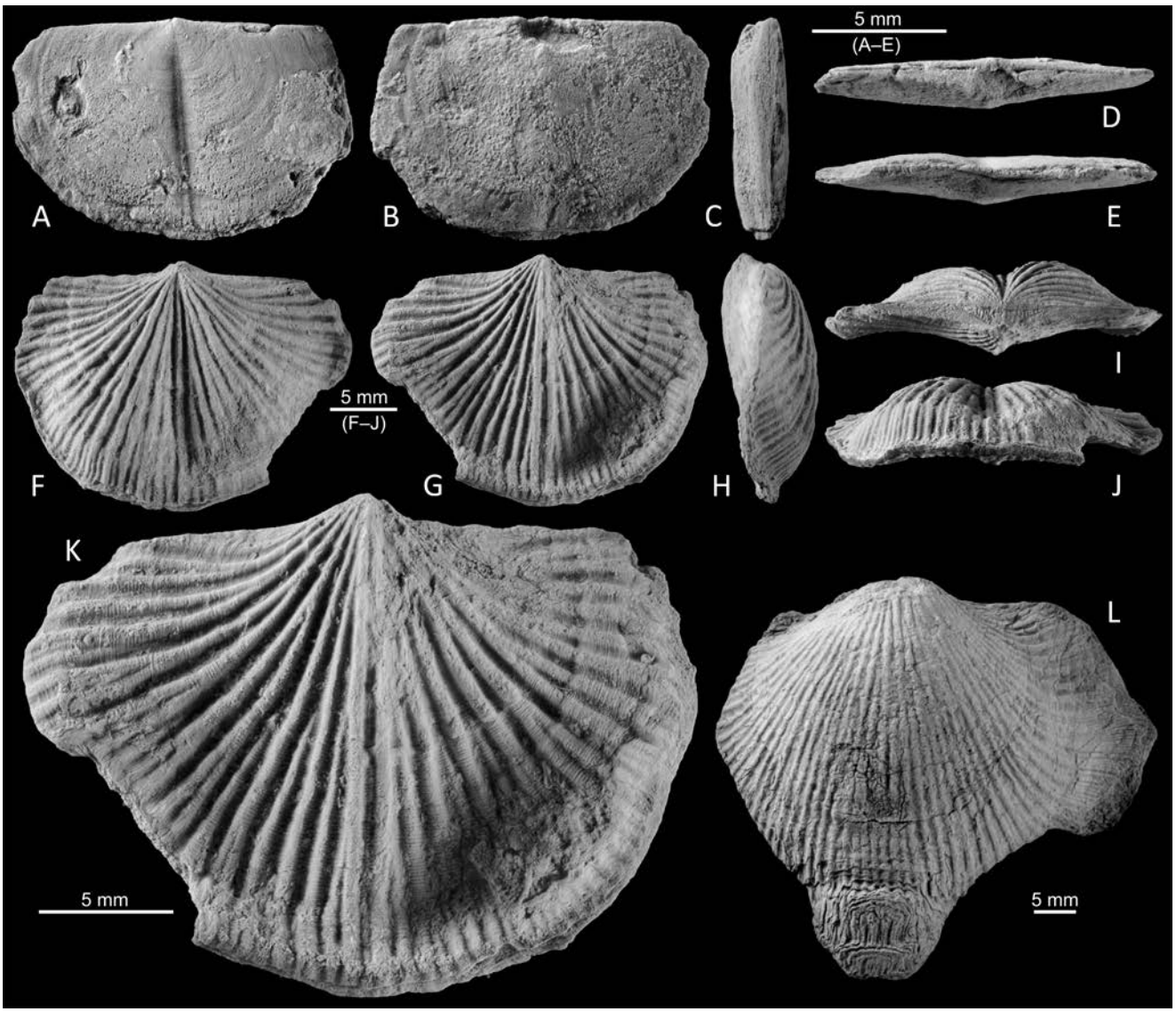


Fig. 28. Middle Devonian Atrypida from southern Maïder. **A–E.** *Prodavidsonia* sp. Articulated shell ZPAL Bp 68/1/32/1 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. **F–K.** *Carinatina arimaspus* (Eichwald in von Buch, 1840). Articulated shell ZPAL Bp 68/1/31/1 from Aferdou in dorsal, ventral (G, K), lateral, posterior, and anterior views. **L.** *Atryparia dispersa* (Struve, 1966). Articulated shell ZPAL Bp 68/1/28/4 from Aferdou in dorsal view showing frills

Alvarez *et al.*, pp. 78–82, text-figs 12, 14, pl. 1, figs 1–6.

Material: Four articulated shells (two subcomplete) from Aferdou, ZPAL Bp 68/1/34/1–4.

Description: Shell rounded to roundedly pentagonal in outline, weakly transverse (width to length ratio 1.16–1.18), aequibiconvex to weakly dorsibiconvex, up to 14.9 mm in width. Dorsal valve subtriangular to rounded in anterior view; an indistinct rounded fold appearing in anterior sixth. Ventral valve with a shallow U-shaped sulcus appearing slightly posteriorly to midlength, narrow posteriorly, somewhat broadening anteriorly. Ventral beak short, fine, strongly incurved; foramen medium-sized, circular, palintrope small. Anterior commissure uniplicate; tongue moderately narrow to moderately broad (0.3–0.5 of the shell width), rounded to triangular, very low (Fig. 30J) to moderately high (Fig. 30O). Growth lines prominent. Interior not studied.

Remarks: *Athyris concentrica* (von Buch, 1834) has been interpreted both narrowly (Alvarez *et al.*, 1996) and widely (Grunt and Weyer, 2002). The studied material does not allow participation in this discussion (Alvarez and Brunton, 2005); a cautious approach and open nomenclature are preferred.

Athyris? aff. *curvata* (von Schlotheim, 1820)
Fig. 30P–T

aff. 1996 *Athyris (Triathyris?) curvata* (Schlotheim 1820) – Alvarez *et al.*, pl. 8, figs 46–47.

Material: One poorly preserved articulated shell from Aferdou, ZPAL Bp 68/1/46/1.

Description: The single available shell is irregularly pentagonal (nearly triangular) in outline, strongly dorsibiconvex, 18.5 mm wide, >13.9 mm long, and 11.8 mm thick. Maximal width at about three-fifths of the shell length. Shoulder angle ca. 120°. Dorsal valve strongly convex, subtrapezoidal in anterior view because of steep flanks and narrow flattened fold in the anterior third; umbo massive, beak incurved. Ventral valve moderately convex in umbonal region, with a wide, shallow, U-shaped (nearly flat-bottomed) sulcus, beginning at valve mid-length. Anterior commis-

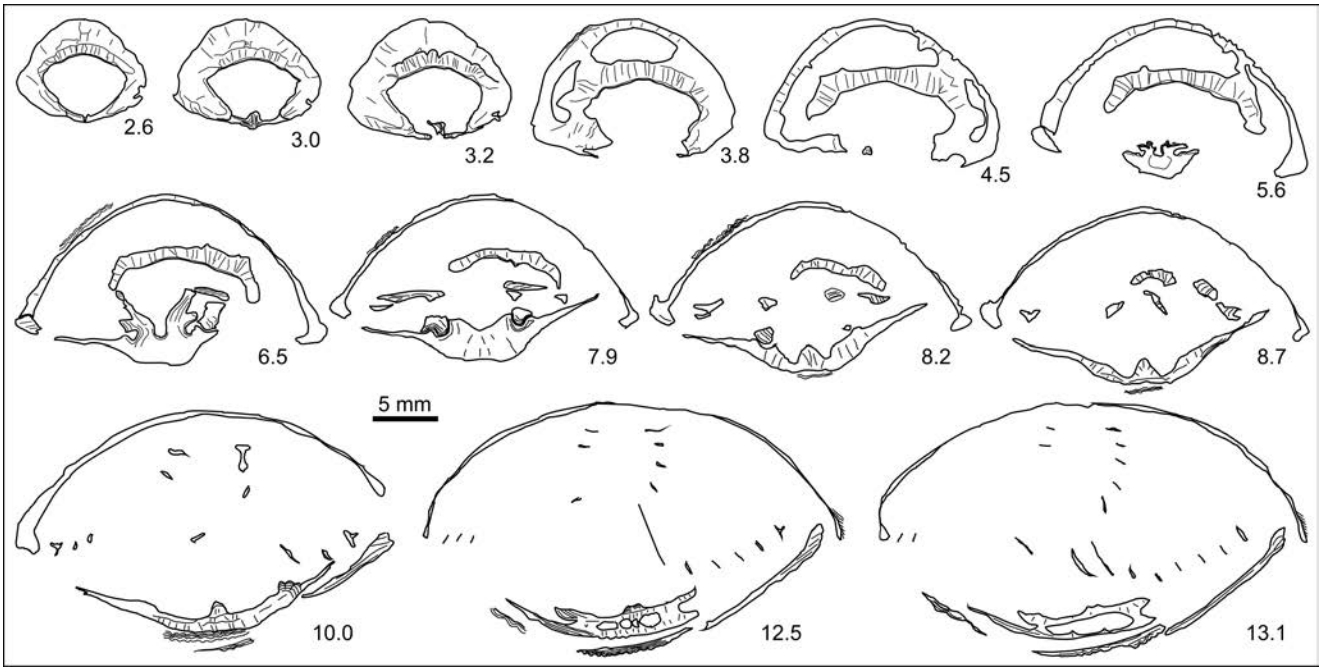


Fig. 29. Transverse serial sections of *Gruenewaldtia latilinguis* through shell ZPAL Bp 68/1/30/2 from Aferdou. Distances measured in millimetres from the tip of the ventral umbo

sure uniplicate, tongue 9.5 mm wide, rounded, high. Traces of strong growth lines, otherwise shell smooth. Interior unknown.
Remarks: This single specimen is tentatively compared, on account of similarity in shape, to the poorly known early to middle Eifelian *Athyris curvata* (von Schlotheim, 1820) illustrated, but not described, by Alvarez *et al.* (1996). *Cleiothyridina blacourti* Brice, Mottequin and Loones, 2008 from the Givetian (Middle to Upper *varcus* zones) of the Boulonnais is similar in shape, but the microornamentation is different (Brice *et al.*, 2008).

Family Meristidae Hall and Clarke, 1893

Genus *Camarium* Hall, 1859

Type species: *Camarium typum* Hall, 1859; Cumberland, Maryland, USA; Lower Helderberg Group, Lochkovian (after Alvarez and Brime, 2000; Alvarez and Rong, 2002)

Remarks: *Camarium* Hall, 1859 is reported to differ from *Dicamara* Hall and Clarke, 1893 in the lack of mystrochial plates (Alvarez and Rong, 2002, p. 1572). This tiny structure can be observed solely through serial sections, but would not appear on internal moulds. Hall and Clarke (1894, p. 772) selected *Atrypa plebeia* Sowerby, 1840 as the type species of *Dicamara*, but their interpretation is based on internal moulds and isolated valves of a presumed *Dicamara scalprum* Roemer, 1844 (Hall and Clarke, 1894, pl. 33: 16–19; figs 18, 19 are those of a Late Devonian brachiopod from the Harz, probably not the same species as *D. scalprum* from the Eifel represented in figs 16, 17). Siehl (1962, pl. 32: 1) figured serial sections of a "*Dicamara plebeja*" from Gerolstein in the Eifel, but without representing the exterior. Alvarez and Rong (2002, p. 1572, fig. 1069.4) admitted the synonymy between *D. plebeia* from Mount Wise near Plymouth, England and *D. scalprum* from Germany. Struve (1964, p. 516) argued for separating both species. It follows that no specimen of the type species of *Dicamara* from the type area in England has ever been serially sectioned. This is especially unfortunate in a group full of homoeomorphic species (e.g., "*Dicamara plebeia*" *sensu* Torley, 1934 is a *Camarium*; see below, Fig. 33B). Characters of *Dicamara* should be considered as uncertain.

Camarium sp.
Figs 31K–Z, 33

v**.** 1934 *Dicamara plebeja* (Sowerby) – Torley, p. 116–117, text-fig. D, figs 51–54.

Material: Seven (mostly subcomplete) articulated shells from Maharch, ZPAL Bp 68/2/50.
Other material examined: SMF XVII 278h from Bilveringsen (Sauerland), coll. K. Torley (Fig. 33B).
Description: Shell subpentagonal in outline, weakly to markedly ventribiconvex, up to 17.4 mm in length. Dorsal umbo thick, beak very short, strongly incurved. Ventral umbo thick, rather long, beak incurved. Anterior commissure uniplicate with broad, low trapezoidal tongue. Shell smooth.

Ventral interior with long, thin, subparallell dental plates, supported by a long shoe-lifter process; mystrochial plates not revealed. In the dorsal valve septalium short, narrow, supported by a high and long median septum; laterally directed spiralia of at least seven whorls (Fig. 31K).
Remarks: At Maharch, this species co-occurs with the externally similar *Peratos arrectus*. The latter has straight anterior comissure, is more rounded, and has more distinct growth lines.
Distribution: Sauerland, Maïder; Givetian.

Family Meristellidae Waagen, 1893

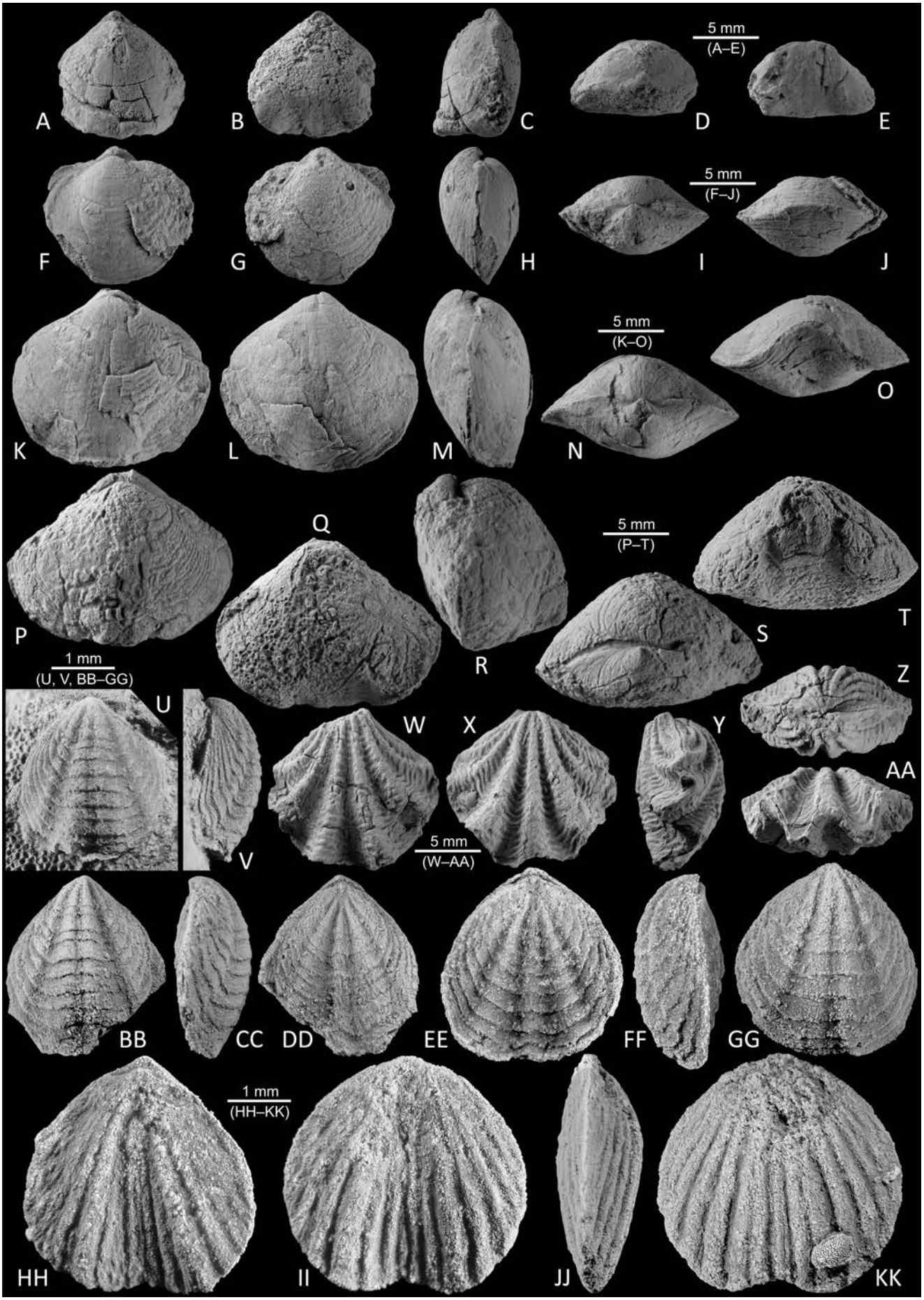
Genus *Meristella* Hall, 1859

Type species: *Atrypa laevis* Vanuxem, 1842; Albany County, New York, USA; Lower Heidelberg Froup, Lower Devonian (see Alvarez and Brime, 2000 for a detailed discussion)

Meristella cf. *iconensis* Struve, 1964
Fig. 31AA–EE

v cf. 1964 *Meristella iconensis* n. sp. – Struve: p. 510–513, figs 2–5.

Material: Two articulated shells (one decorticated) from Aferdou, ZPAL Bp 68/1/51/1–2.


5 mm
(A–E)
A
B
C
D
E
5 mm
(F–J)
F
G
H
I
J
5 mm
(K–O)
K
L
M
N
O
5 mm
(P–T)
P
Q
R
S
T
1 mm
(U, V, BB–GG)
U
V
W
X
Y
Z
AA
5 mm
(W–AA)
BB
CC
DD
EE
FF
GG
1 mm
(HH–KK)
HH
II
JJ
KK

Description: Shell pentagonal, elongate (width to length ratio 0.80–0.82), moderately to markedly ventribiconvex, up to 22.4 mm long. Ventral umbo elongate, beak incurved. Anterior commissure uniplicate, tongue subtrapezoidal, moderately high. Ventral interior: very long traces of the shoe-lifter can be observed nearly up to valve midlength.
Remarks: These two specimens differ from *Camarium* sp., occurring in Maharch, because of its elongate shape. They are identical in external characters with *Meristella iconensis* Struve, 1964 (Meristellidae; see Struve, 1964). Approximately coeval *Dicamara prunulum* (Schnur, 1851) (Meristidae) usually has a narrower tongue. In the absence of serial sections of the Maharch material, open nomenclature has been used as a precaution.

Family Neoretziidae Dagys, 1972

Genus *Plectospira* Cooper, 1942
Type species: *Terebratula ferita* von Buch, 1834; Eifel; Eifelian

Plectospira ferita (von Buch, 1834)
Fig. 30W–AA

v* 1834 *Terebratula ferita* n. – von Buch: p. 76, pl. 17, fig. 4.
1982 *Plectospira ferita* (v. Buch) – Biernat and Baliński, pp. 857–866, text-fig. 1, pl. 92, figs 1–6, pl. 93, figs 1–7, pl. 94, figs 1–7, pl. 95, figs 1–6.

Material: A single subcomplete (ventral umbo lacking) articulated shell from Aferdou El-Mrakib, ZPAL Bp 68/1/33/1.
Description: The single available shell is subpentagonal in outline, 13.0 mm wide, >12.2 mm long, and 6.7 mm thick, weakly dorsibiconvex. Dorsal beak fine, strongly incurved. Anterior commissure zigzagging. Ornamentation of stout plicae, nine dorsal and eight ventral ones, separated by wide U-shaped furrows, in which strong growth lines are visible. Interior not studied.
Distribution: *Plectospira ferita* is known from the Middle Devonian (Eifelian, possibly also Givetian) of the Eifel, the Holy Cross Mountains, Moravia (Ficner and Havlíček, 1978), Burma (Anderson *et al.*, 1969), and Turkey (Gourvennec and Hoşgör, 2012).

Family Anoplothecidae Schuchert, 1894

Genus *Bifida* Davidson, 1882
Type species: *Terebratula lepida* d'Archiac and de Verneuil, 1842; Eifel; Eifelian

Bifida lepida (d'Archiac and de Verneuil, 1842)
Fig. 30U–V, BB–GG

* 1842 *Terebratula lepida* Goldfuss, Bonn Mus. – d'Archiac and de Verneuil, p. 368, pl. 35, figs 2, 2a–c.
1973 *Bifida lepida* (Archiac and Verneuil 1842) – Copper, pp. 123–128, text-figs 1, 2[a], 3, pl. 4, figs 5–8, pl. 5, figs 3–4, pl. 6, figs 1–4, pl. 7, figs 23–24.

Material: Four articulated shells SMF 94896–94898 from Madène el Mrakib, including one attached to a bryozoan covering a part of a shell of *Glyptogypa multiplicata*, SMF 94871 (Figs 9P, 29U, V).
Description: Shell rounded in outline, up to 2.9 mm in width, longer than wide, planoconvex to strongly ventribiconvex, with incurved ventral umbo and apparently absent foramen. The ventral ornamentation consists of a median pair of thick, subparallel costae, separated by a narrow median furrow, and an external pair of lower and thinner costae; the dorsal ornamentation of a median costa, a strong pair of costae situated laterally from the former, and an external pair of faint costae; the growth lines are sublamellose.
Remarks: The material described is included in the Eifelian species *Bifida lepida*. The Givetian *B. nitida* (Schmidt, 1951) is larger and has a more convex dorsal valve (Schmidt, 1951; Copper, 1973; Halamski, unpublished). The shell SMF 94871b may be interpreted as preserved in the *in vivo* position (Figs 9P, 29U, V), being attached during life by a short pedicle, although a preservational artefact (two shells cemented *post mortem*) cannot be excluded.
Distribution: This species is known from the Eifelian of the Eifel, Ardennes (Maillieux, 1938 and B. Mottequin, pers. comm. June 2013), of the Holy Cross Mountains, and Maïder (Copper, 1973, supplemented).

Family Kayseriidae Boucot, Johnson and Staton, 1964

Genus *Kayseria* Davidson, 1882
Type species: *Orthis lens* Phillips, 1841; England; Middle Devonian

Kayseria alvea Copper, 1973
Fig. 30HH–KK

* 1973 *Kayseria alvea* sp. nov. – Copper: pp. 134–136, text-fig. 6, pl. 7, figs 12–22.

Material: Two articulated shells (one complete), SMF 98180, 98181, from Madène el Mrakib.
Description: Shell subcircular in outline, up to 3.9 mm wide, slightly longer than wide, weakly dorsibiconvex. Anterior margin medially indented. Both valves with median sulci. Ornamentation of radial ribs, beginning in umbonal region. On the dorsal valve (Fig. 30 HH, II), a strong pair of ribs bordering the sulcus with fine and dense ribs inside and medium-sized ribs on lateral flanks; on the ventral valve (Fig. 30 KK), ribs of approximately the same size.
Remarks: *Kayseria alvea* is distinguished from the slightly older *Kayseria lens* (Phillips, 1841) and *K. dividua* (Schnur, 1851) (externally indistinguishable and of the same age, therefore probably

Fig. 30. Middle Devonian Rhynchonellida and Athyridida from southern Maïder. **A–E.** Rhynchonellida fam., gen. et sp. indet. Articulated shell ZPAL Bp 68/1/50/1 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. **F–O.** *Athyris* ex gr. *concentrica* (von Buch, 1834), Aferdou. F–J, K–O. Articulated shells ZPAL Bp 68/1/34/1, 2 in dorsal, ventral, lateral, posterior, and anterior views. **P–T.** *Athyris*? aff. *curvata* (von Schlotheim, 1820). Articulated shell ZPAL Bp 68/1/46/1 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. **U–V, BB–GG.** *Bifida lepida* (d'Archiac and de Verneuil, 1842). Specimens from Madène el Mrakib. BB–DD. Articulated shell SMF 94896 in ventral, lateral, and dorsal views. EE–GG. Articulated shell SMF 94897 in dorsal, lateral, and ventral views. U, V. Articulated shell SMF 94871b in probable *in vivo* position [see discussion in the text] on the ventral valve of *Glyptogypa multiplicata* (cf. Fig. 9P) in ventral and lateral views. **W–AA.** *Plectospira ferita* (von Buch, 1834). Articulated shell ZPAL Bp 68/1/33/1 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. **HH–KK.** *Kayseria alvea* Copper, 1973. Articulated shells from Madène el Mrakib. HH. Specimen SMF 98180 in dorsal view. II–KK. Specimen SMF 98181 in dorsal, lateral, and ventral (with an attached palaeocopide ostracod, possibly a representative of Primitiopsidae; det. E. Olempska-Roniewicz) views

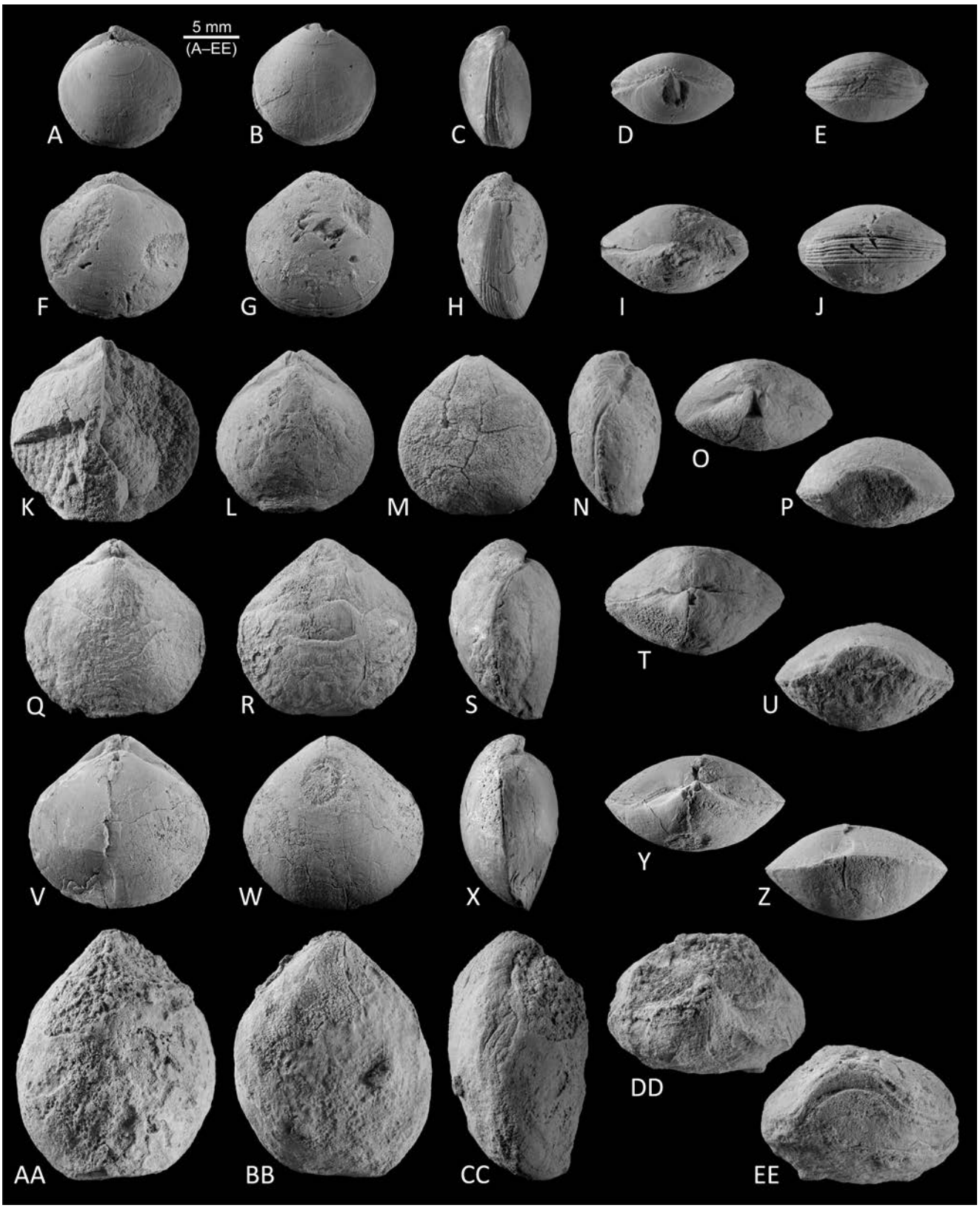


Fig. 31. Middle Devonian Atrypida and Athyridida from southern Maïder. **A–J.** *Peratos arrectus* Copper, 1986. Articulated shells in dorsal, central, lateral, posterior, and anterior views. A–E. Specimen ZPAL Bp 68/2/40/3 from Maharch. F–J. Specimen ZPAL Bp 68/1/40/2 from Aferdou. **K–Z.** *Camarium* sp. from Maharch. K. Partly broken articulated ZPAL Bp 68/2/50/4 shell showing spiralium; dorsal view. L–P. Articulated shell ZPAL Bp 68/2/50/1 dorsal, ventral, lateral, posterior, and anterior views. Q–U. Articulated shell ZPAL Bp 68/2/50/2 in dorsal, ventral, lateral, posterior, and anterior views. V–Z. Articulated shell ZPAL Bp 68/2/50/3 in dorsal, ventral, lateral, posterior, and anterior views. **AA–EE.** *Meristella* cf. *iconensis* Struve, 1964. Articulated shell ZPAL Bp 68/1/51/1 from Aferdou in dorsal, central, lateral, posterior, and anterior views

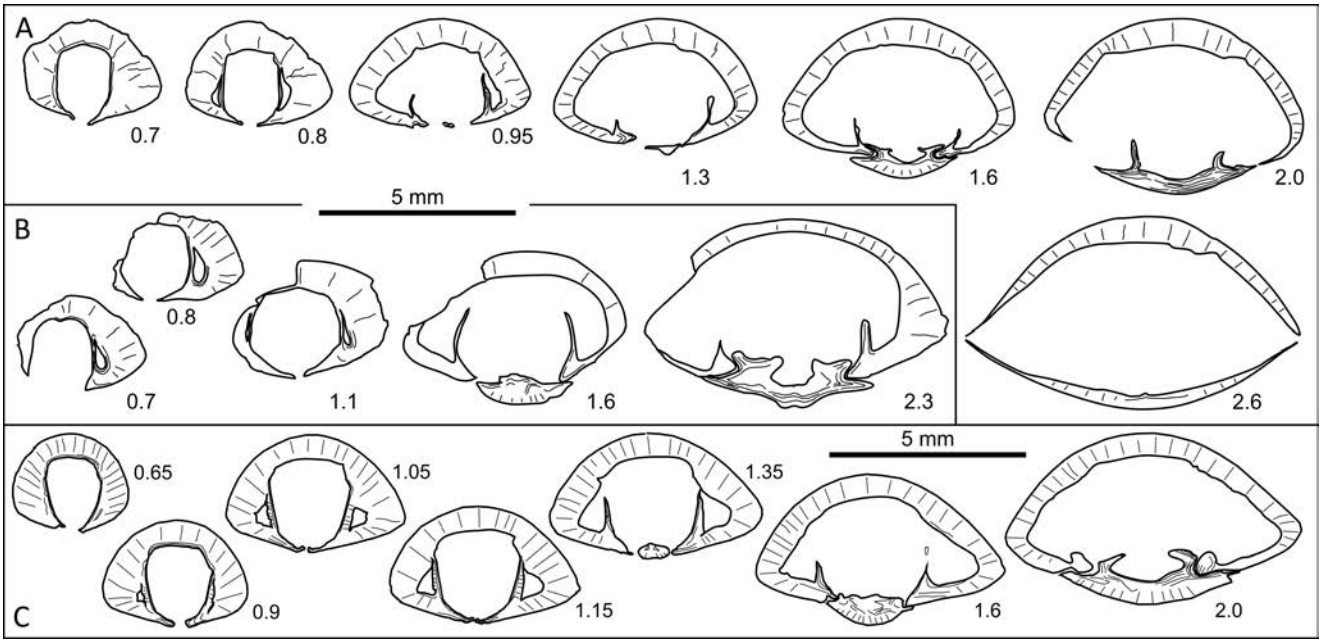


Fig. 32. Transverse serial sections of *Peratos arrectus* through shells ZPAL Bp 68/2/40/1 from Maharch (A), 68/1/40/1 from Aferdou (B), and 68/2/40/2 (C) from Maharch. Distances measured in millimetres from the tip of the ventral umbo

synonymous; Davidson, 1882, p. 24) in possessing a stronger rib pair, bordering the sulcus (absent in the latter).

Distribution: Eifel, uppermost Eifelian in the traditional sense (Ahbach Beds, mostly Müllert horizon; Copper, 1973), therefore mostly lowermost Givetian according to the modern definition (Walliser *et al.*, 1995; Bultynck and Hollevoet, 1999); Maïder, Middle Devonian (Eifelian?).

Order Spiriferida Waagen, 1883
Family Spinocyrtiidae Ivanova, 1959

Genus *Spinocyrtia* Fredericks, 1919

Type species: *Delthyris granulosa* Conrad, 1839; New York, USA; Givetian

Spinocyrtia cf. *elburzensis* Brice, 1973
Fig. 34A–H, L

cf. 1973 *Spinocyrtia elburzensis* nov. sp. – Brice *in* Brice *et al.*: pp. 203–206, text-fig. 14, pl. 22, figs 9–10, pl. 23, figs 1, 5, pl. 24, figs 2–3.

1995 *Spinocyrtia* (*Spinocyrtia*) *elburzensis elburzensis* Brice – Struve, p. 100, figs 38–41.

Material: Forty-six specimens SMF 94880–94892, MB.B.9384c, and MB unnumbered (V. Ebbighausen's collection) from the *Drotops* level at Madène el Mrakib.

Description: Shell up up to 56.4 mm in width, transverse (width-to-length ratio 1.32–1.84; mean 1.50; N = 7), more frequently dorsibiconvex (among measurable specimens fourteen were dorsibiconvex and five were ventribiconvex, the latter being usually smaller); hinge line nearly straight. Ventral valve convex, with a deep V-shaped sulcus originating at beak, the latter incurved; interarea concave, subrectangular, apsacline, delthyrial cover not preserved. Dorsal valve convex with a rounded fold (ca. 12 mm wide and 5 mm high in an individual ca. 45 mm wide) beginning at beak; the fold with a median groove, the width of which is from one-third to a half of that of the fold. Ornamentation of straight plications, 14–20 per flank (Nc/w 0.28 to 0.44; mean 0.36; N = 6). Microornamentation (Fig. 34L) of granules arranged on microfila, the latter 2–3 per mm.

Remarks: This species is included into *Spinocyrtia*, on account of macro- and microornamentation and relatively low ventral interarea (Johnson, 2006a). It is quite similar to *S. elburzensis* from the Middle Devonian of Elburz (Iran) which is, however, always ventribiconvex (Brice, 1973). Probably conspecific representatives of this genus were described by Struve (1995) from coeval deposits of the northern Maïder.

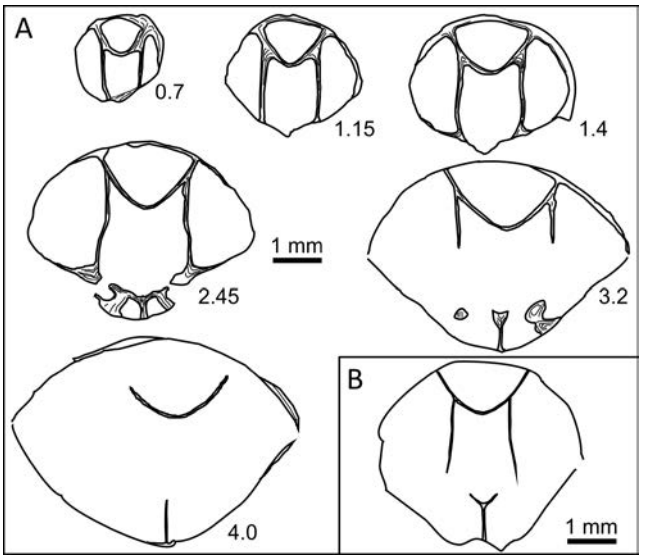


Fig. 33. Transverse serial sections of *Camarium* sp. through shells ZPAL Bp 68/2/50/5 from Maharch (A) and SMF XVII 278h from Bilveringsen (B). Distances measured in millimetres from the tip of the ventral umbo

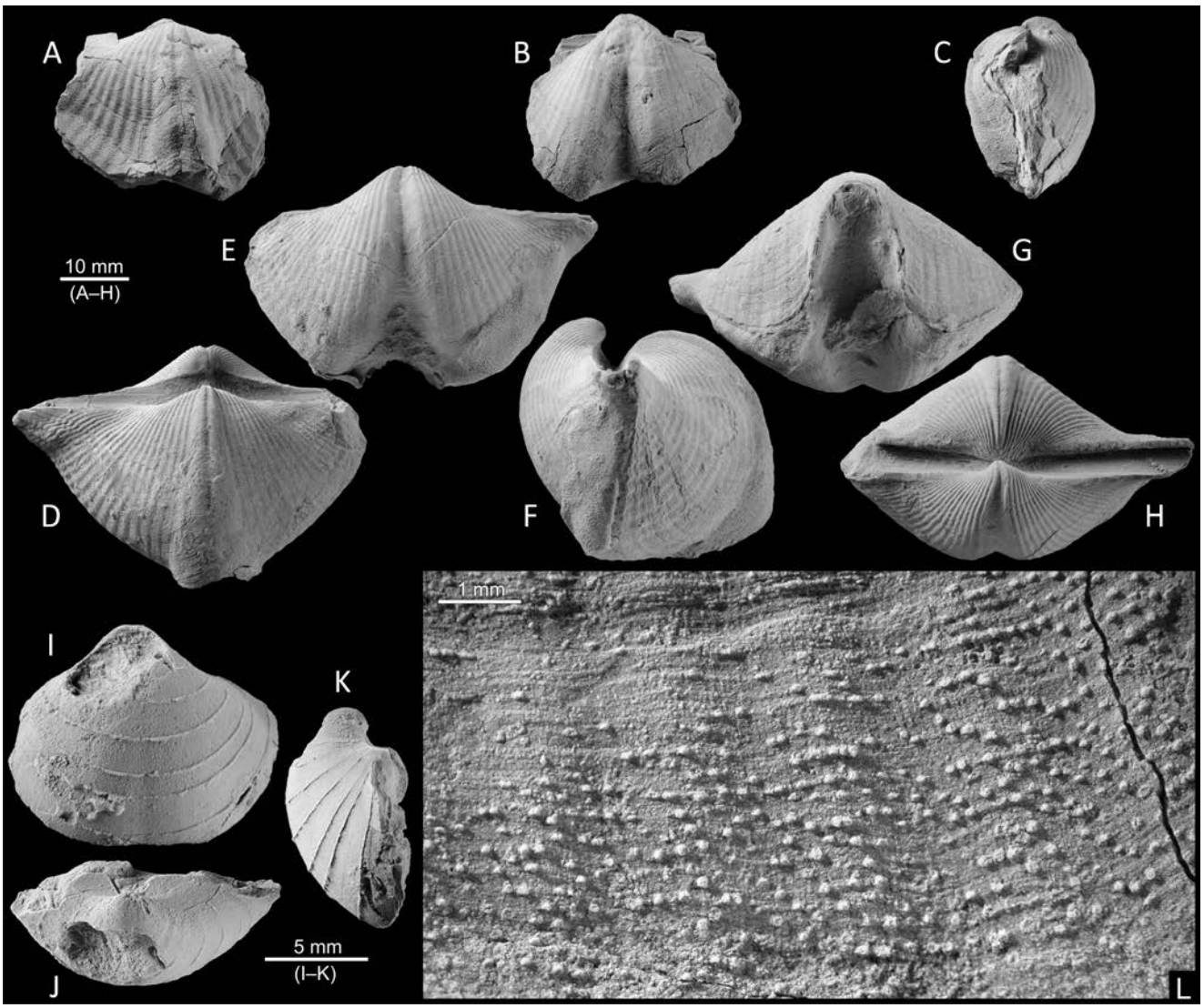


Fig. 34. Middle Devonian Spiriferida from southern Maïder. **A–H, L.** *Spinocyrtia* cf. *elburzensis* Brice, 1973. Both specimens from Madène el Mrakib. A–C, L. Incomplete articulated shell SMF 94880 in dorsal, ventral, and lateral views; enlargement of microornamentation. D–H. Articulated shell MB.B. 9384c in dorsal, ventral, lateral, anterior, and posterior views. **I–K.** Reticularioidea fam., gen. et sp. indet. Ventral valve ZPAL Bp 68/1/53/1 from Aferdou in ventral, posterior, and lateral views

Family Delthyrididae Phillips, 1841

Genus *Ivanothyris* Havlíček, 1957
Type species: *Spirifer gibbosus* Barrande, 1879; Bohemia; Lochkovian

Ivanothyris aculeata (Schnur, 1851)
Fig. 35A–E

* 1851 *Sp[irifer] aculeatus* nob. – Schnur: pp. 10–11.
. 1853 *Sp[irifer] aculeatus* m. – Schnur, p. 203, pl. 34, fig. 2a–f.
1963 *Delthyris aculeata* – Vandercammen, pp. 112–116, pl. 11, figs 1–8.
1997b *"Spirifer aculeatus"* Schnur 1853 – Gourvennec in Boumendjel *et al.*, p. 109–110.

Material: Single subcomplete articulated shells, one from Aferdou, ZPAL Bp 68/1/35/1, and one from Madène el Mrakib, MB unnumbered (V. Ebbighausen's collection).
Description: The single available shell is rhombic in outline, aequibiconvex, 20.8 mm wide, 14.8 mm long, and 12.0 mm thick. Dorsal valve widest near the hinge line, with three pairs of thick lateral plications and a high median fold; lateral plications low and acute, beginning in umbonal region, the most lateral pair nearly imperceptible; median fold beginning at umbo. Dorsal umbo thick, beak short, strongly incurved. Ventral valve widest about its midlength, with a median V-shaped sulcus beginning at umbo and three pair of thick plications, diminishing in size towards lateral flanks. Ventral interarea occupying less than half of the shell width, apsacline; umbo elongate, rather thick, beak incurved. Growth lines strong, 3–4 per mm.
Distribution: This species is known from the Eifelian of the Eifel (Schnur, 1853), of the Ardennes (Jemelle Formation; Vandercammen, 1963), of the Holy Cross Mountains (Halamski, unpublished), and of the Maïder; it is equally rare in all four regions. It has been reported from the lower part of the Chefar el Amhar Formation (uppermost Emsian or Eifelian) of the Saoura valley (Gourvennec in Boumendjel *et al.*, 1997b).

Genus *Quiringites* Struve, 1992
Type species: *Spirifera elegans* Steininger, 1853; Gerolstein, Eifel; Nohn Formation, lower Eifelian

Quiringites arensentiae Schemm-Gregory, 2009
Fig. 35F–P, R

v* 2009 *Quiringites arensentiae* sp. nov. – Schemm-Gregory: pp. 11–13, figs 6B, 7–9.

Material: Twenty-five complete or subcomplete articulated shells and several more fragmentary ones, SMF 94872, 94873, 94893–94895, and MB unnumbered (V. Ebbighausen's collection); four dorsal and three ventral valves SMF 94843, 94844 and MB unnumbered (V. Ebbighausen's collection); all from Madène el Mrakib.
Description: Shell transverse, mucronate, up to 24.9 mm in width, ventribiconvex. Dorsal valve with a rounded fold originating at beak. Ventral valve with wide, shallow, U-shaped sulcus originating at beak; the latter strongly incurved; interarea low, apsacline, subrectangular, and strongly concave. Ornamentation of strong, rounded plications, (4–)5–6(–10) per flank of the dorsal valve. Microornamentation (Fig. 35R) of irregularly placed swollen spine bases.

Ventral interior (Fig. 35O): teeth not preserved; dental plates embedded in a strongly developed callus; muscle scars not visible; muscle area prolonged anteriorly by a short and low myophragm; gonoglyphs present abmedially from dental plates. Dorsal interior (Fig. 35P): ctenophoridium with ca. 11 lamellae; dental sockets deep; a pair of strong plates is formed by inner socket ridges coalescent with crural bases (these are "brachiophores" *sensu* Schemm-Gregory, 2009; the terminology of Brunton *et al.*, 1996 and of Baliński and Sun, 2010: fig. 5 is followed) poorly preserved, divergent; a thin, low, rounded median myophragm extends up to ca. two third of the valve length.
Remarks: Characters separating *Q. arensentiae* and *Q. elegans* given by Schemm-Gregory (2009, p. 11) are largely of low taxonomic value. In particular, development of the callus does not seem to be a good discriminator at species level. Moreover, as shown by the present study, *Q. arensentiae* has (although seldom) up to ten costae per flank (Fig. 35K); this character cannot therefore be used for distinguishing the taxa discussed [Schemm-Gregory (2009) suggested that *Q. arensentiae* has up to 7 plications, whereas *Q. elegans* has up to 10 plications]. However, *Q. arensentiae* and *Q. elegans* are judged to be separate species, on account of the incurvation of the ventral umbo (Fig. 35I, L, M), constantly much greater in the former taxon.
Distribution: Maïder (north and south), middle Eifelian to middle Givetian (Schemm-Gregory, 2009, supplemented). *Q.* cf. *arensentiae* was reported from the Drâa valley (Schemm-Gregory, 2009).

Family Cyrtinopsidae Wedekind, 1926

Genus *Cyrtinopsis* Scupin, 1896
Type species: *Spirifer undosus* Schnur, 1853; Gerolstein Syncline, Eifel; Middle Devonian

Cyrtinopsis cf. *brachyptera* (Maillieux, 1914)
Fig. 35Q, S

cf. 1914 *Cyrtina undosa* Schnur sp. var. *brachyptera* nov. var. – Maillieux: pp. 4–6, figs 3–4.
p cf. 1963 *Cyrtinopsis undosa* (J. Schnur, 1851) Vandercammen, pp. 101–104, pl. 10, figs 3–8.
cf. 1964 *Cyrtinopsis undosa maiderensis* ssp. n. – Drot, pp. 69–70, pl. 6, figs 1–8.
cf. 1965b *Cyrtinopsis brachyptera* (Maillieux 1914) – Struve, pp. 13–22, pl. 1, figs 2–4, pl. 2, figs 1–2, 4, pl. 3, fig. 4.

Material: A single fragmentary ventral valve from Aferdou, ZPAL Bp 68/1/48/1.
Description: The available specimen is an incomplete half of a ventral valve, length ca. 17 mm, total width estimated at ca. 28 mm. Outline subtrapezoidal in anterior view with steep flanks and a ca. 5 mm wide (estimated) deep median sulcus. Beak elongated, incurved. Interarea triangular, apsacline, ca. 3 mm high. Ornamentation consisting of both radial and concentric elements: seven rounded plications, diminishing in size towards the lateral flank, separated by U-shaped interspaces; strong, undulating, sublamellose growth lines, 7–8 per 5 mm, covered by radial striae (Fig. 35S; capillae *sensu* Krans, 1971). Median septum high.
Remarks: This fragmentary specimen may be included confidently in *Cyrtinopsis*, on account of the characteristic ornamentation and the ventral median septum. Specific identification is more problematic; a rounded and moderately transverse outline indicates affinities with *C. brachyptera*, the only species present in Northern Africa, according to Struve (1965b). Comparison with the single chronosubspecies, in particular with *C. brachyptera maiderensis* Drot, 1964 is not possible, given the scarcity of the material.
Distribution: The type material of *C. brachyptera* comes from the Eifelian Jemelle Formation (B. Mottequin, pers. comm., 2013). The stratigraphic distribution of this species is reported to be confined to the middle part of the Eifelian (Struve, 1965b), whereas the specimen discussed belongs probably to the late Eifelian, although its collection from the rubble precludes any definitive conclusions.

Family Reticulariidae Waagen, 1883

Genus *Rhenothyris* Struve, 1970
Type species: *Rhenothyris rhenana* Struve, 1970; Eifel; middle Eifelian

Rhenothyris sinuata (Gürich, 1896)
Fig. 36M–Q

* 1896 *Reticularia sinuata* nov. nom. – Gürich: pp. 259–260, pl. 9, fig. 10.
v. 1966 *Eoreticularia eifeliensis* (Frech in Scupin) – Biernat, pp. 126–128, text-figs 43–44, pl. 30, figs 13–19 [*non Reticulariopsis eifliensis* (Scupin, 1900)].

Material: Two subcomplete articulated shells from Aferdou, ZPAL Bp 68/1/36/1–2.
Description: Shell subrectangular to transversely elliptic in outline (hinge line and median part of the anterior commissure subparallel) with broadly rounded postero-lateral margins, transverse (width-to-length ratio 1.53–1.56), strongly ventribiconvex, up to 24 mm in width. Maximal width at midlength of the dorsal valve. Dorsal valve with a low, rounded fold appearing in posterior fourth; interarea low, approximately orthocline. Ventral valve with a shallow U-shaped sulcus bordered by a pair of thick ribs; the sulcus and the ribs appearing in umbonal region; interarea high, apsacline, gently curved; umbo thick, beak incurved. Anterior commissure uniplicate; tongue as broad as ca. one-third of the shell, high, rounded. Shell macroscopically smooth; microornamentation of concentric growth lamellae bearing bands of marginal spine bases, 3–4 per mm. Interior unknown.
Remarks: The material described is very similar to the late Eifelian to early Givetian taxon, described by Gürich (1896) from the Holy Cross Mountains and reported by Biernat (1966) under erroneous generic and specific names (Halamski, 2004a). This is the youngest known member of *Rhenothyris* (Struve, 1970; Halamski, 2004a).
Distribution: Eifel, Holy Cross Mountains, Maïder; Middle Devonian.

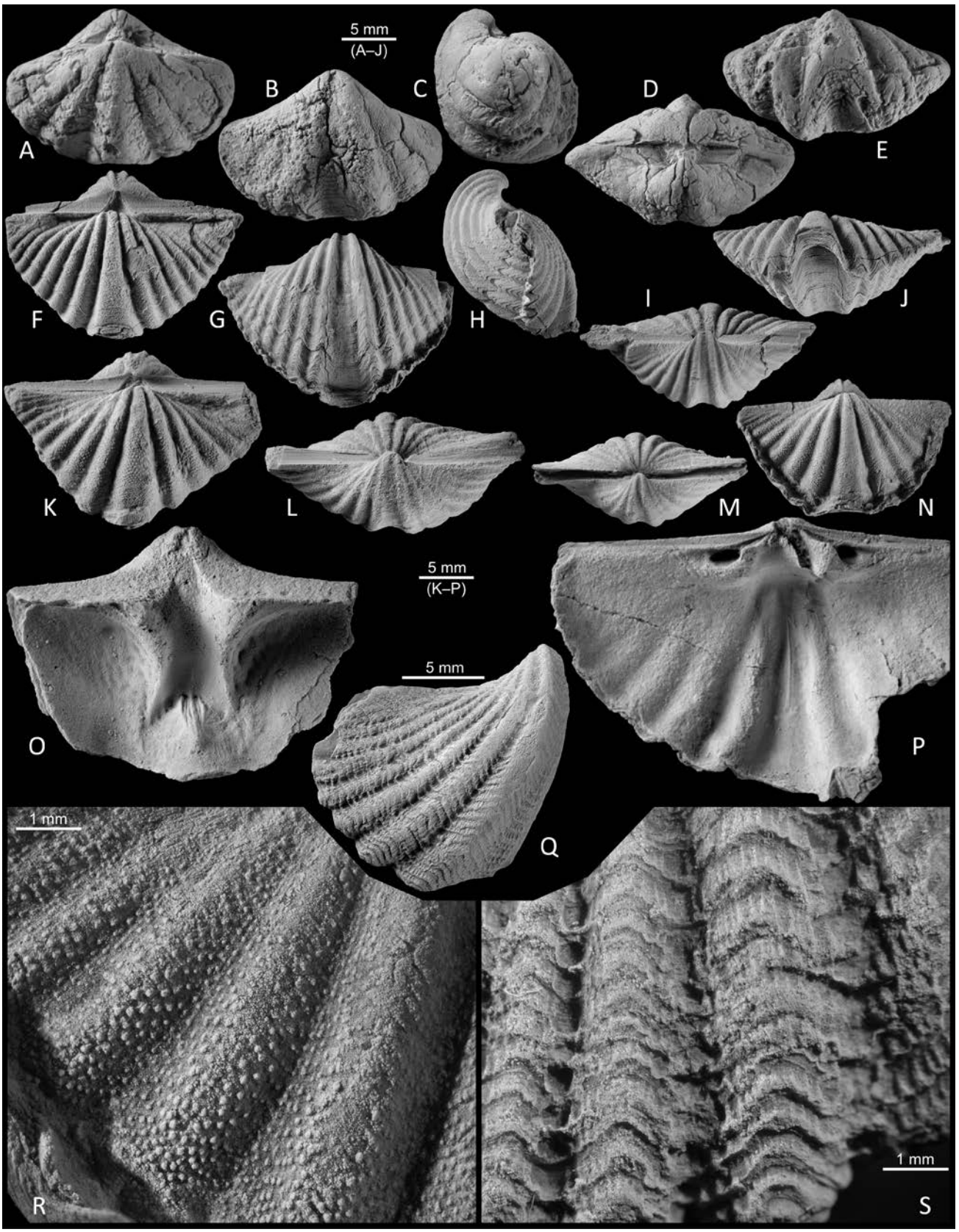


Fig. 35. Middle Devonian Spiriferida from southern Maïder. **A–E.** *Ivanothyris aculeata* (Schnur, 1851). Articulated shell ZPAL Bp 68/1/35/1 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. **F–P, R.** *Quiringites arensentiae* Schemm-Gregory, 2009 from Madène el Mrakib. F–J. Articulated shell SMF 94872 in dorsal, ventral, lateral, posterior, and anterior views. K, L. Articulated shell SMF 94893 in dorsal and posterior views. M, N, R. Articulated shell SMF 94894 in dorsal and posterior views, and microornamentation (R). O. Ventral interior SMF 94843. P. Dorsal interior SMF 94844. **Q, S.** *Cyrtinopsis* cf. *brachyptera* (Maillieux, 1914). Fragmentary ventral valve ZPAL Bp 68/1/48/1 from Aferdou (Q) and microornamentation (S)

Genus *Deltospirifer* Wang and Rong, 1986
Type species: *Elytha transversa* Wang, 1956; Guangxi, southern China; Emsian

Deltospirifer? new species
Fig. 36R–V

Material: A single subcomplete articulated shell from Aferdou, ZPAL Bp 68/1/51/1.
Description: Shell widely, irregularly pentagonal in outline, with gently rounded antero-lateral margins and cardinal extremities, transverse (width to length ratio 1.64), moderately ventribiconvex, 26 mm in width. Maximal width posteriorly to midlength of the dorsal valve. Dorsal valve with a low, flat fold appearing in umbonal region, bordered by a pair of distinct furrows; interarea low, apsacline. Ventral valve with a shallow sulcus, posteriorly V-shaped, anteriorly approximately flat-bottomed, bordered by a pair of thick ribs; the sulcus and the ribs appearing in umbonal region; interarea high, apsacline, incurved; umbo not preserved. Anterior commissure paraplicate; tongue as broad as ca. one-third of the shell, low, subtrapezoidal. A single pair of low, rounded, ca. 1.8 mm wide costae adjacent to the furrows bordering the dorsal fold, otherwise shell smooth; microornamentation of spine bases arranged in dense concentric lines, 8–9 per mm. Interior unknown.
Remarks: This shell differs from *Rhenothyris sinuata* co-occurring in the same outcrop, in microornamentation density, shell outline (more transverse, position of the greatest width), inclination of the dorsal interarea, smaller ventribiconvexity, incipient costation, and form of the tongue. It is tentatively included in *Deltospirifer*, on account of its overall similarity to the Emsian *D. transversus* (Wang, 1955) (Wang and Rong, 1986, pl. 71: 1–18). Differences include higher interarea and less developed costation in the Aferdou specimen; it represents a new species, which is not named, because the material is too scarce.

Genus *Undispirifer* Havlíček, 1957
Type species: *Spirifer undiferus* Roemer, 1844; Rhenish Slate Mountains and Eifel [Roemer (1844, p. 73) indicates three localities for his new species; this problem has not been resolved in the revision made by Vandercammen (1967, p. 6)]; Middle Devonian

Undispirifer aff. *rzhonsnitzkajae* Mamedov, 1961
Fig. 36W–AA

aff. 1961 *Undispirifer rzhonsnitzkajae* Mamedov, sp. nov. – Mamedov: pp. 53–55, pl. 5, fig. 2.
aff. 1974 *Undispirifer rzhonsnickajae* Mamedov, 1961 – Abramân, pp. 62–63, pl. 16, fig. 1.

Material: Seven mostly fragmentary specimens from Maharch, ZPAL Bp 68/2/37/1–7.
Description: Shell subrectangular to rounded in outline (width-to-length ratio 1.02–1.25), weakly to strongly ventribiconvex, up to at least 28 mm in width. Dorsal valve with a flat fold appearing at posterior fourth; the fold has a narrow median furrow; maximal width of the dorsal valve about its midlength; interarea very low, anacline. Ventral valve with a narrow and rather low, apsacline interarea and a shallow but relatively wide sulcus appearing at posterior fourth. Anterior commissure uniplicate; tongue subtrapezoidal, rather low, its width 0.40–0.55 of that of the shell. Ornamentation of rounded costae, weak or very weak (to evanescent?) except the pair bordering the ventral sulcus, which are somewhat higher and thicker, 3–5 (?) per flank; a single case of bifurcation observed. Microornamentation not preserved. Interior: long dental plates in the ventral valve; otherwise unknown.
Remarks: The scarce material, described here, is most similar to *U. rzhonsnitskajae* Mamedov, 1961 from the Middle Devonian of Danzik in the Nakhitchevan Republic (Caucasus), which has, however, only one or two costae per flank (Mamedov, 1961). This taxon was included in *Nakazatothyris* Minato and Kato, 1977, proposed as a subgenus of *Undispirifer* to accommodate three Lower to Middle Devonian species with obsolescent costation (Minato and Kato, 1977). However, Gracianova *et al.* (1990) reclassified *U. rzhonsnitzkajae* within *Deltospirifer* Wang and Rong, 1986; Chen and Tazawa (2003) reclassified *U.* (*N.*) *vandercammeni* Minato and Kato, 1977, the type species of *Nakazatothyris*, within *Kymatothyris* Struve, 1970. Carter and Gourvennec (2006) considered *Nakazatothyris* as a junior subjective synonym of *Undispirifer*. The material described does not allow participation in this discussion.

Representatives of *Undispirifer* from Zemmour (Sougy, 1964), Boulonnais (*U. rigauxi* Brice and Loones, 2002), and the Lahn Syncline (Halamski unpublished; SMF collections) are strongly costate. Geographically and stratigraphically restricted samples of *Undispirifer* usually show rather restricted variation (e.g., Brice and Loones, 2002); this is against the wide interpretation of the taxa (e.g., Schnur, 1853; Davidson, 1864, p. 36–37; Cottreau, 1940, p. 198), as observed already by Sandberger and Sandberger (1850–56, p. 314) and more recently by Struve (1970, 1981a).

Family Thomasariidae Cooper and Dutro, 1982

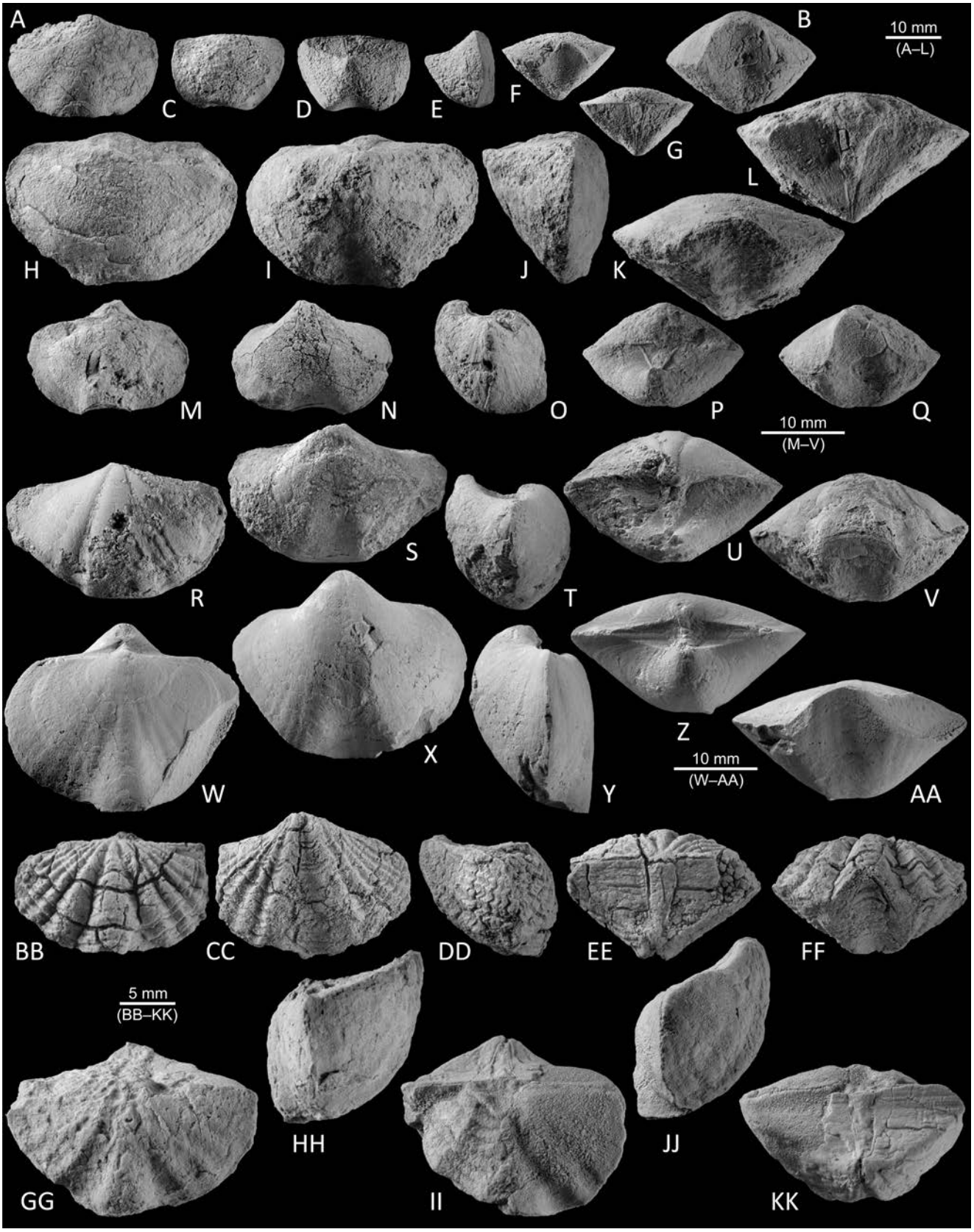
Genus *Thomasaria* Stainbrook, 1945
Type species: *Thomasaria altumbona* Stainbrook, 1945; Iowa; Independence Shale, Frasnian

Remarks: *Pyramidalia* Nalivkin, 1947 (type species *Spirifera simplex* Phillips, 1841) has been considered (Johnson, 2006b: 1882) as a junior subjective synonym of *Squamulariina* Fredericks, 1916 (type species *Cyrtina parva* Gürich, 1896; Cyrtinidae, Spiriferidina). This view is provisionally rejected here, on account of the impunctate shell of the Moroccan material of *Thomasaria*? *simplex* (Phillips, 1841) investigated; this however, should be confirmed on the type material of that species from south Devon (Phillips, 1841). Following Baliński (1979), *Pyramidalia* is provisionally considered to be a junior subjective synonym of *Thomasaria* Stainbrook, 1945 although spines diagnostic for the latter genus could not be found in the material studied, owing to aeolian corrasion and notwithstanding the fact that Frasnian *T. simplex sensu* Baliński (1979) is probably not conspecific with the Middle Devonian *Spirifera simplex* Phillips, 1841 (Halamski, 2004a).

Thomasaria? *simplex* (Phillips, 1841)
Fig. 36A–L

* 1841 *Spirifera simplex* – Phillips: p. 71, pl. 29, fig. 124α; pl. 60, fig. 124α.
v. 1966 *Pyramidalia* cf. *simplex* (Phillips, 1841) – Biernat, p. 136, pl. 27, fig. 1.
? 1985 *Thomasaria*? *serrensis* n. sp. – Brice, pp. 144–146, text-fig. 12, pl. 3, figs 3–5.

Material: Six specimens (including four subcomplete articulated shells) from Aferdou, ZPAL Bp 68/1/39/1, and two subcomplete articulated shells from Maharch, ZPAL Bp 68/2/39/1.
Description: Shell pyramidal (thickness to width ratio 0.55–0.6), transverse (width-to-length ratio ca. 1.4–1.5), strongly ventribiconvex, up to ca. 40 mm in width. Hinge line straight. Maximal width between the hinge line and midlength of the dorsal valve. Dorsal valve weakly to strongly convex; a flat fold in the anterior third, relatively low, but distinct to imperceptible; interarea linear, more or less orthocline. Ventral valve pyramidal with a shallow, U-shaped sulcus, beginning in umbonal region and triangularly


A
B
C
D
E
F
G
H
I
J
K
L
10 mm
(A–L)
M
N
O
P
Q
10 mm
(M–V)
R
S
T
U
V
W
X
Y
Z
AA
10 mm
(W–AA)
BB
CC
DD
EE
FF
5 mm
(BB–KK)
GG
HH
II
JJ
KK

widening anteriorly; interarea very high, slightly procline, more seldom catacline, flat, more rarely weakly concave, as wide as the hinge line length; delthyrium narrow (0.2–0.3 of the interarea width), with apical angle attaining about 20°, covered in the upper third or fourth by an apical plate. Anterior commissure uniplicate; tongue rounded to subtrapezoidal, moderately high to high, occupying 0.35–0.5 of the shell width. Shell smooth. Interior not studied.

Remarks: The material studied allows an appreciation of the ontogenetic and intraspecific variation of the species discussed. Smaller individuals have the maximal shell width near the hinge line (like shells figured by Phillips, 1841), while in larger ones it is situated near the mid-length of the dorsal valve. The ventral interarea can be flat or concave; the latter variant was distinguished (Sobolew, 1909) as *Spirifer simplex* var. *subsimplex* Sobolew, 1909, but this character does not seem to be taxonomically significant. *Thomasaria*? *serrensis* Brice, 1985 from the Givetian (Middle *varcus* Zone) of the Montagne Noire is externally indistinguishable from the small specimens of *T.*? *simplex* from Aferdou (Fig. 36C–G): synonymy of the two species therefore is tentatively proposed; however, it should be remembered that the type material of this species is in need of revision (see above, remarks on the genus). *Spirifer pyramidalis* Schnur, 1853 and *S. nudus* Schnur, 1853 (both from the Eifel) are also quite close to *T. simplex* (Mottequin, 2008b, p. 516).

Distribution: Eifel, Holy Cross Mountains, Maïder, Montagne Noire?; Middle Devonian.

Family unknown

Reticularioidea fam., gen., et sp. indet.
Fig. 34I–K

Material: One incomplete ventral valve ZPAL Bp 68/1/53/1 from Aferdou.

Description: The single available ventral valve is subelliptic in outline, 13.1 mm wide (incomplete; estimated wisth ca. 14 mm) and 10.5 mm long. A faint sulcus is present anteriorly. Beak thick; interarea apsacline, weakly concave; delthyrium open, its apical angle ca. 80°. Shell macroscopically smooth except rare prominent, sublamellose growth limes; microornamentation not preserved. Poorly preserved dental plates present; otherwise, interior unknown.

Remarks: This poorly preserved specimen differs from *Rhenothyris sinuata* co-occurring in the same outcrop, in ornamentation; it is included in the superfamily Reticularioidea Waagen, 1883, on account of an open delthyrium, a macroscopically smooth shell, and sublamellose growth lines. The overall similarity to *Yeothyris* Struve, 1992 is noted, yet the lack of microornamentation and internal structures precludes the possibility of identification.

Order Spiriferinida Ivanova, 1972
Family Cyrtinidae Fredericks, 1911

Genus *Cyrtina* Davidson, 1858
Type species: *Cyrtina heteroclita* Defrance, 1828; Néhou, Normandy; Pragian (or lower Emsian?)

Remarks: The species-level taxonomy of *Cyrtina* is difficult to elaborate. Although usually there is relatively small variation within a sample, different samples show a lack of similarity. It is unclear whether morphological characters, such as the number of costae, valve form, or interarea position, are under genetic or environmental control. This may result in either all-lumping or all-splitting taxonomies.

Late Eifelian to early Givetian populations of *Cyrtina* from the Holy Cross Mountains and the Eifel have been shown to represent *C. sauvagei* Rigaux, 1908 (Halamski unpublished) and not its evolutionary Pragian (to early Emsian?) predecessor *C. intermedia* Œhlert, 1887 (for this species, see Gourvennec, 1989), the main difference being in the shape of the dorsal valve (moderately transverse in the former and strongly transverse in the latter; see Table 4). The meagre material from Maïder is difficult to interpret. Samples from Aferdou and Maharch show biometric characteristics of *C. sauvagei* and *C. intermedia*, respectively (Table 4); the specimens from the latter locality are similar to those from the late Emsian to early Eifelian strata of Saoura (Le Maître, 1952a; see also Boumendjel *et al.*, 1997b). Given the ecological separation between the two localities, the two samples are described separately; one of them in open nomenclature. Co-occurrence of several species of *Cyrtina* in strata of the same age has already been reported (Keyes and Pitrat, 1978). For example, two species of *Cyrtina* are present in the Givetian of La Serre (Montagne Noire; Brice, 1985); one (*Cyrtina* sp. 1 *sensu* Brice, 1985) is quite similar to *C. sauvagei*, whereas the other (*Cyrtina* sp. 2 *sensu* Brice, 1985) might be compared to *C.* ex gr. *intermedia*. *Cyrtina hamiltonensis* (Hall, 1857) is an approximately coeval species from the eastern United States: it is very similar to *C. sauvagei*; differences include slightly more transverse shape and slightly larger number of costae. It is not excluded these taxa are conspecific but this cannot be decided at present. Reports of *C. hamiltonensis* from Africa (Gevin, 1964; Schemm-Gregory and Jansen, 2005) may possibly refer to *C. sauvagei*.

Cyrtina sauvagei Rigaux, 1908
Fig. 36BB–FF

* 1908 *Cyrtina Sauvagei* – Rigaux: p. 6, 20; pl. 1: 8.
? 1940 *Cyrtina heteroclita* Defr. – Cottreau, p. 198, pl. 7, figs 13, 13a.

Fig. 36. Middle Devonian Spiriferida and Spiriferinida from southern Maïder. **A–L.** *Thomasaria*? *simplex* (Philips, 1841). A, B. Incomplete articulated shell ZPAL Bp 68/2/39/1 from Maharch in dorsal and anterior views. C–G. Articulated shell ZPAL Bp 68/1/39/2 from Aferdou in dorsal, ventral, lateral, anterior, and posterior views. H–L. Articulated shell ZPAL Bp 68/1/39/1 from Aferdou in dorsal, ventral, lateral, anterior, and posterior views. **M–Q.** *Rhenothyris sinuata* (Gürich, 1896). Articulated shell ZPAL Bp 68/1/36/1 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. **R–V.** *Deltospirifer*? sp. nov. Articulated shell ZPAL Bp 68/1/51/1 in dorsal, ventral, lateral, posterior, and anterior views. **W–AA.** *Undispirifer* aff. *rzhonsnitzkajae* Mamedov, 1961. Articulated shell ZPAL Bp 68/2/37/1 from Maharch in dorsal, ventral, lateral, posterior, and anterior views. **BB–FF.** *Cyrtina sauvagei* Rigaux, 1908. Articulated shell ZPAL Bp 68/1/38/1 from Aferdou in dorsal, ventral, lateral, posterior, and anterior views. **GG–KK.** *Cyrtina* ex gr. intermedia Œhlert, 1887. GG, HH. Articulated shell ZPAL Bp 68/2/38/2 from Maharch in dorsal and lateral views. II–KK. Articulated shell ZPAL Bp 68/2/38/2 from Maharch in dorsal, lateral, and posterior views

Table 4

Comparison of selected biometric characteristics of selected Lower and Middle Devonian representatives of *Cyrtina*

Character / Taxon and sample	Age	Number of costae	Width to length ratio				Source
			minimal value	average	maximal value	N	
C. intermedia topotypic (Brittany)	Pragian	3–6	1.44	1.94	2.72	22	Gourvennec, 1989
C. intermedia Saoura	late Emsian to early Eifelian	(2–)3	1.56	1.84	2.29	12	this work (original material of Le Maître)
C. hamiltonensis Traverse Group, Mi.	Middle Devonian	5–8	1.40	1.65	1.98	24	Keyes and Pitrat, 1978
C. hamiltonensis Onondaga Fm., N.Y.	Eifelian	5–8	1.19	1.56	1.75	9	Feldman, 1994
C. sauvagei Holy Cross Mts.	late Eifelian to early Givetian	(3–)4–6(–7)	1.34	1.50	1.74	22	Halamski, unpublished
C. sauvagei topotypic (Boulonnais)	early Givetian	5-7	1.30	1.46	1.62	9	Brice, 1988
C. sauvagei Aferdou	late Eifelian to early Givetian	4–5	1.49	1.62	1.76	3	this work
C. ex gr. *intermedia* Maharch	early Givetian	3–4	1.79	1.89	2.00	2	

? 1964 *Cyrtina Hamiltonensis* Hall – Sougy, p. 161.
v. 1966 *Cyrtina heteroclita intermedia* – Biernat, p. 133–135, text-fig. 47, pl. 23, figs 9–27, pl. 32, fig. 14.
? 1985 *Cyrtina* sp. 1 – Brice, p. 147, pl. 3, figs 15–16.
1988 *Cyrtina sauvagei* Rigaux 1908 – Brice, pp. 359–360, pl. 43, figs 11–12.
? 2005 *Cyrtina* cf. *hamiltonensis* (Hall, 1857) – Schemm-Gregory and Jansen, p. 27.

Material: Three specimens (two articulated shells) from Aferdou, ZPAL Bp 68/1/38/1–3.
Description: Shell up to 18.0 mm in width, wider than long (average width-to-length ratio 1.62, N = 3), very strongly ventribiconvex. Maximal width and thickness at hinge line. Ventral valve high, pyramidal; interarea moderately apsacline, high, transversely striate, flat or somewhat concave. Delthyrium narrow, occupying less than one-seventh of the shell width, closed by a strongly convex deltidium. Pedicle foramen in the middle of the deltidium or closer to the apex. Dorsal valve slightly convex to nearly flat.

Ornamentation of rounded costae, 4–5 on each flank. Strong median dorsal fold with flattened top, exceptionally with a faint median groove on it. Ventral sulcus flat-bottomed. Interior not studied.
Remarks: For a comparison with *Cyrtina* ex gr. *intermedia*, see Remarks on the genus.
Distribution: Boulonnais, Holy Cross Mountains, Maïder, Eifel?; Middle Devonian.

Cyrtina ex gr. *intermedia* Œhlert, 1887
Fig. 36GG–KK

ex gr. 1887 *Cyrtina heteroclita*, var. *intermedia* Œhl. – Œhlert: p. 42, pl. 3, figs 29–35.
ex gr. 1952a *Cyrtina heteroclyta* var. *intermedia* Oehlert – Le Maître, p. 132.
ex gr. 1989 *Cyrtina intermedia* (Oehlert) – Gourvennec, pp. 56–59, text-figs 28, 30–31, pl. 2, figs 20–36 [*ubi syn.*]

Material: Two subcomplete shells from Maharch, ZPAL Bp 68/2/38/1–2.
Description: Like the previous, except: shell strongly transverse (average width-to-length ratio 1.89, N = 2); interarea weakly apsacline; costae 3–4 per flank; ventral sulcus V-shaped.
Remarks: For a comparison with *Cyrtina sauvagei*, see Remarks on the genus. A moderately transverse (width to length ratio 1.5) *Cyrtina* with five costae per flank was described from the presumed upper Givetian of the Zap river valley in south-eastern Turkey under the name of *C. intermedia* (Gourvennec and Hoşgör, 2012); it is different from the material dealt with here.

PALAEOBIOGEOGRAPHY

Middle Devonian brachiopod faunas from north-western Africa

The brachiopod fauna of the Tindouf Syncline (Fig. 1B) is especially important for comparisons with the brachiopods, dealt with in the present paper. Middle Devonian brachiopods, first briefly reported by Menchikoff (1935), Jacquet (1936), and Menchikoff and Monod (1936), were first illustrated by Cottreau (1940) on the basis of collections, made by Odette du Puigaudeau et Marion Sénones. The best documented fauna was described by Sougy (1964; see also Drot, 1961b) from the Zemmour Noir (area at the NW edge of the Reguibat Shield, probably a northern extension of the Mauritanides fold belt, mostly in Mauritania; Lécorché *et al.*, 1991). Proximity of brachiopod faunas from the southern Maïder and the Zemmour Noir may be exemplified by co-occurrence of *Atrypa confusa* and *Spinatrypa* cf. *trigonella*, two otherwise rare species, at Aferdou and at the locality 346 of Sougy (1964, p. 382–383) in the Zemmour. Species lists without either descriptions or figures were given from the southern flank of the Tindouf Syncline (the northern border of the Reguibat Shield, mostly in Algeria, partly also in Mauritania) by Gevin (1960). The western part of the Tindouf Syncline is more poorly known (Königshof *et al.*, 2003); a few taxa from this area (Western Sahara, southern Morocco) were reported by Dumestre and Illing (1967; identifications H. Muir-Wood) and by Schemm-Gregory and Jansen (2005, 2008).

The Devonian of the Ougarta chain, cropping out in the Oued Saoura valley (western Algeria; Saoura in Fig. 1B; for regional details see Alimen *et al.*, 1952; Boumendjel *et al.*, 1997a), yielded a rich brachiopod fauna, described by Le Maître (1952a) and restudied by Boumendjel *et al.* (1997b)

and Brice *et al.* (2011). Most of this fauna is Early Devonian in age; a part belongs to the Middle Devonian.

There follows an enumeration of other Middle Devonian brachiopod faunas from northern and north-western Africa. Termier and Termier (1950) described several Devonian taxa from a large number of localities, scattered from northern Morocco to Mauritania (but apparently not a single Middle Devonian brachiopod from Maïder among them). A few Eifelian to Givetian taxa from the Drâa (Dra) valley were described by Becker *et al.* (2004) and by Ebbighausen *et al.* (2007). Givetian brachiopods have also been described from the Adrar (Racheboeuf *et al.*, 2001) and from the Taoudeni Basin (Racheboeuf *et al.*, 2004). Eifelian and/or Givetian brachiopods were described from the Tamesna Basin (South Ahaggar Massif) by Mergl and Massa (2004). Givetian brachiopods from Libya and Niger were described by Boucot *et al.* (1983).

Analysis of the fauna studied

The palaeobiogeographic analysis was conducted on the basis of the distribution of 56 out of the 62 species reported in the present paper, including 13 taxa described in open nomenclature, the remaining 6 being identified only at the genus or family level, and therefore not suitable for this purpose (see Halamski, 2008 for details of methodology; for the Otsuka coefficient, see Cheetham and Hazel, 1969). This middle Eifelian to early Givetian fauna was analysed as a single unit [i.e., not separating the Eifelian and Givetian parts; see Halamski (2008) for arguments for this approach].

First of all, it must be observed that no common species were found with the following coeval faunas from northwestern Africa: from the Tamesna Basin (Mergl and Massa, 2004) and from Libya (Boucot *et al.*, 1983; Mergl and Massa, 1992).

The distribution of the species investigated in selected other regions is summarised in the Table 5. "Tindouf South" includes faunas from the Zemmour (Sougy, 1964), those from the southern flank of the Tindouf Syncline proper (Gevin, 1960), as well as those from the Western Sahara (Dumestre and Illing, 1967; Schemm-Gregory and Jansen, 2005, 2008). The Rhenish Massif includes the Eifel (left or western side of the Rhine, according to the traditional German terminology) and the Sauerland, Bergisches Land, Siegerland, and Westerwald (right or eastern side of the Rhine) (Schnur, 1853; Kayser, 1871; Torley, 1934; Schmidt, 1941a, b, and especially numerous papers by Struve, listed in Weddige and Ziegler, 2000). The "Holy Cross Mountains North" refers to the Middle Devonian faunas of the Bodzentyn Syncline in the Łysogóry region of the Holy Cross Mountains (Poland), described by Gürich (1896), Sobolew (1904, 1909), Siemiradzki (1909), Biernat (1959, 1964, 1966), and revised by Halamski (2004a, 2009; see also Halamski, 2005; Halamski and Racki, 2005).

The main conclusion of this enumeration is the remarkable similarity between brachiopod faunas of the northern (Euramerican) and southern (Gondwanan) shores of the Variscan Sea. Out of the 62 species present in the Maïder, at least forty are present also either in the Eifel or in the Holy Cross Mountains. This supports the idea of a relatively narrow oceanic zone (McKerrow *et al.*, 2000), against the opposite conclusion (a wide Rheic Ocean: Ziegler, 1990; Plusquellec *et al.*, 1997; Tait *et al.*, 2000; Torsvik and Cocks, 2011; see also the summary of this contention in Bełka and Narkiewicz, 2008, p. 383–384). Secondly, not a single American-type species is present in the southern Maïder (unless *Cyrtina sauvagei* be conspecific with *C. hamiltoni* and thus a widely distributed species), not even an Appallachian-type genus (*sensu* Boucot *et al.*, 1969).

The same conclusion was made by Brice (*in* Boumendjel *et al.*, 1997b) for the Lower to Midle Devonian brachiopod faunas from the Saoura. It may be noted too that the analysis of latest Emsian brachiopods from the Cantabrian Zone showed also great similarity of faunas from northern Gondwana and from Euramerica, and therefore minor significance of the Variscan Sea as a barrier to faunistic exchanges (García-Alcalde, 1995, 2001). This is not astonishing, insofar as palaeocurrents are reconstructed as having circulated along the margins of the ocean (Oczlon, 1990; Dopieralska, 2009), thus forming a system that allowed the easy dispersion of benthic faunas.

Middle Devonian brachiopod faunas from the Tindouf Syncline have not been under detailed research. However, generally speaking, they are composed partly of the same species as in the southern Maïder (14 or 19 common species, Table 3). American affinities of these faunas have been invoked, on account of the presence of *Tropidoleptus* (Gevin, 1960; Schemm-Gregory and Jansen, 2005) and *Amphigenia* (Gevin, 1960). As a matter of fact, the former genus is cosmopolitan (Harper, 2007) and the latter widely distributed (Lee *et al.*, 2006, p. 1996). Three taxa "similar to forms from eastern North America" have been reported from Western Sahara (Schemm-Gregory and Jansen, 2005, p. 27): *Cyrtina* cf. *hamiltonensis* (Hall, 1857), *Devonochonetes* cf. *scitulites* (Cooper, 1945), and *Rhipidomella* cf. *vanuxemi* (Hall, 1857). All three are identified under open nomenclature, wherefore the actual extent of presumed American influences cannot be estimated before the systematic revision of this material.

Racheboeuf (1991) and Racheboeuf *et al.* (2001, p. 153) divided the Devonian of West Africa into two major regions: the Taoudeni Basin (south of the emerged area of the Reguibat Shield; Golonka *et al.*, 2006, fig. 20) with faunas showing "close faunal relationships with the Northeastern American Realm" (an observation already made by Le Maître, 1952b) and the Zemmour and Tindouf Basins with European-type faunas. This broad subdivision was established mainly on the basis of chonetoid brachiopod distributions. It remains to see to what extent these conclusions pertain to the entire brachiopod faunas.

The available incomplete data on Middle Devonian non-chonetoid brachiopods from the Taoudeni Basin do not support the strong separation with more northern faunas, advocated by Racheboeuf *et al.* (2001). Affinities with the Appallachian region were postulated on the basis of taxa, reported under open nomenclature. On the contrary, taxa identified at the species level are mainly European forms: *Xystostrophia umbraculum*, *Schizophoria schnuri* (see above), *Atrypa Planatrypa*) *collega*, *A.* (*P.*) "*squamifera*", and *Kyrtatrypa culminigera* (Copper in Racheboeuf *et al.*, 2001). Similarly,

Table 5

Synopsis of occurrences of taxa present in the studied material in selected coeval faunas.

Taxon / Region		Gondwana				Euramerica (Laurussia)		
		Maïder			Tindouf (S)	Rhenish Massif	Holy Cross Mts. (N)	Other
		Madène	Aferdou	Maharch				
Craniida	*Deliella deliae*	+					+	
	Deliella aff. *rhenana*	+				+		
Strophomenida	*Leptagonia analogaeformis*	+	+		+	+	+	
	Protodouvillina interstrialis	+	+		+	+	+	+
	Radiomena irregularis		+			+	+	+
	Parastrophonella anaglypha	+			+	+	+	+
	Protodouvillininae indet.		+					
Productida	*Devonaria* sp.		+					
	Poloniproductus varians	+	+		+		+	
Orthotetida	*Xystostrophia umbraculum*	+	+		+	+	+	+
	Iridistrophia cf. *undifera*		+		+	+	+	
Orthida	*Aulacella prisca*		+	+	+	+	+	+
	Tyersella canalicula	+	+		?	+	+	
	Phragmophora schnuri	+	+			+	+	
	Schizophoria schnuri	+	+			+	+	+
	Schizophoria? sp.			+				
Pentamerida	*Gypidula biplicata*		+			+	+	?
	Glyptogypa multiplicata	+	+		+	+	+	
	Ivdelinia pulchra		+			+	+	
	Devonogypa spinulosa	+	+		?	+	+	+
	Antirhynchonella sublinguifera		+	+	+	+	+	
Rhynchonellida	*Kransia parallelepipeda*		+		+	+	+	
	Kransia subcordiformis		+			+	+	+
	Kransia? *coronata*	+	+			+	+	
	Beckmannia beckmanni		+			+	?	+
	Glosshypothyridina procuboides		+	+		+	+	
	Parapugnax? cf. *skalensis*		+				cf.	
	Septalaria gracilis		+			+	+	?
	Paulinaerhynchia paulinae		+	+	?			
	Rhynchonellida indet.		+					
Atrypida	*Atrypa* (*Planatr.*?) *confusa*	+	+		+	+		+
	Atryparia dispersa		+			+		+
	Invertina cf. *struvei*		+					
	Spinatrypa cf. *trigonella*		+		+	cf.		cf.
	Spinatrypa globulina		+			+		
	Desquamatia deserti			+				
	Desquamatia microzonata	+			+	+		
	Desquamatia circulareformis		+				+	
	Desquamatia sp. 1		+					
	Kerpina vineta		+			+		
	Prodavidsonia sp.		+					
	Carinatina arimaspus		+			+	+	+
	Gruenewaldtia latilinguis		+			+	+	+
	Peratos arrectus		+	+	+	+		
Athyridida	*Plectospira ferita*		+			+	+	+
	Athyris ex gr. *concentrica*		+		?	?		
	Athyris? aff. *curvata*		+					

Table 5 continued

Taxon	Region	Gondwana				Euramerica (Laurussia)		
		Maïder			Tindouf (S)	Rhenish Massif	Holy Cross Mts. (N)	Other
		Madène	Aferdou	Maharch				
Athyridida	*Camarium* sp.			+		+		
	Meristella cf. *iconensis*		+			cf.		
	Bifida lepida	+				+	+	
	Kayseria alvea	+				+		
Spiriferida	*Spinocyrtia* cf. *elburzensis*	+						cf.
	Ivanothyris aculeata	+	+			+	+	
	Quiringites arensentiae	+						
	Cyrtinopsis cf. *brachyptera*		+			cf.		
	Rhenothyris sinuata		+			+	+	
	Deltospirifer? sp. nov.		+					
	Undispirifer aff. *rzhonsnitzkajae*			+				aff.
	Thomasaria? *simplex*		+	+		+	+	?
	Reticularioidea indet.		+					
Spiriferinida	*Cyrtina sauvagei*		+		?	?	+	?
	Cyrtina ex gr. *intermedia*			+				?
BRACHIOPODA	TOTAL (absolute number of taxa in the Maïder and of species in common with other regions)	20	49	11	14 (19)	38 (42)	31 (33)	–
		62				40 (46)		
	Total, for palaeobiogeography and percentages of species in common between Maïder and a given region	56			26 (35) %	66 (75) %	55 (59) %	–
						71 (82) %		
	Total, species (in parentheses: fit for palaeobiogeographic analysis)	62			≈70	300	120 (75)	–
						348 (329)		
	Total, genera (in parentheses: fit for palaeobiogeographic analysis)	52 (49)			–	106	84 (69)	–
						133 (118)		
	Total, genera in common between the Maïder and a given region	49			–	42	37 (39)	–
						44 (45)		
	Otsuka coefficient, species (%)	100			–	29 (32)	47 (51)	–
						29 (34)		
	Otsuka coefficient, genera (%)	100			–	58	66 (70)	–
						58 (59)		

Biogeographic data, unless other reference is given, after Halamski (2008). Greyed cells denote taxa unfit for palaeobiogeographic analysis. See text for further explanation

"close affinities with the NEA Realm" were postulated for brachiopods coming from the Hodh (southern Mauritania) on account of presence of "?*Arcuaminetes*, *Longispina*, *Eleutherokomma*, and *Cupularostrum*" (Racheboeuf *et al.*, 2004, p. 100); as a matter of fact, the oldest *Eleutherokomma* is known from the Holy Cross Mountains (Halamski, 2004a) and *Cupularostrum* is cosmopolitan (Savage *et al.*, 2002, p. 1056). It seems probable that faunal exchanges with territories, situated in the present North America, were more intense south of the Reguibat Shield, owing to the latter and the Acadian Highlands acting as barriers (see fig. 1 in Stigall Rode and Lieberman, 2005 and references therein). However, the extent of Old and New World faunal influences north and south of the Reguibat Shield may only be estimated after systematic revision of these faunas will have been completed.

A preliminary observation, concerning links of northwestern African Middle Devonian brachiopod faunas with South China, as exemplified by the genera *Deltospirifer* (present only in those two regions; Carter and Gourvennec, 2006 and data presented herein; however, it should be borne in mind that the identification of the single specimen at the disposal of the authors is tentative), *Invertina* (only those two also; Godefroid, 2000; Copper, 2002) and *Paracrothyris* (present in Western Sahara, South China, and Nevada; Schemm-Gregory and Jansen, 2008), may be made, as well.

A detailed palaeobiogeographic analysis of early Givetian rugosan corals from Jebel Driss in the southwestern

Maïder was conducted by Pedder (1999), who concluded that there were strong similarities between the north and south shores of the Variscan Sea and very weak links with the Appallachian Region (Eastern Americas Realm). Similarly, May (2008) deduced that there were close biogeographic relationships between the Givetian tabulates of Morocco and of central Europe, without any special influence of the Eastern Americas Realm. A detailed analysis of brachiopods, crinoids, trilobites, corals, and chitinozoans from the Lower to Middle Devonian of Saoura (Boumendjel *et al.*, 1997b) showed that the presumed North American affinities of this fauna (Le Maître, 1952a) as a matter of fact, were weak at best. These conclusions are fully concordant with those, made on the basis of brachiopods from the southern Maïder, studied by the present authors.

CONCLUSIONS

1. A diverse Middle Devonian (middle? Eifelian to middle Givetian; mainly Taboumakhloûf Formation, subordinately probably also the El Otfal Formation) brachiopod fauna is present at Madène el Mrakib, Aferdou el Mrakib, and Guelb el Maharch in the southern Maïder (eastern Anti-Atlas, Morocco). Sixty-two taxa (2 representatives of Craniida, 5 of Strophomenida, 2 of Productida, 2 of Orthotetida, 5 of Orthida, 5 of Pentamerida, 9 of Rhynchonellida, 14 of Atrypida, 7 of Athyridida, 9 of Spiriferida, and 2 of Spiriferinida) are described, on the basis of >1,300 specimens. The fauna is dominated by representatives of the order Atrypida (14 taxa, about half of the material).

2. *Strophomena porrecta* Maurer, 1885 and *Zophostrophia*? *aaatos* Halamski, 2009 are junior subjective synonyms of *Radiomena irregularis* (Roemer, 1844). *Septalaria descendens* Schmidt, 1975 is a junior subjective synonym of *S. gracilis* (Gürich, 1896).

3. *Paulinaerhynchia* is proposed as a new genus of Pugnacidae (Rhynchonellida) with type species *P. paulinae* gen. et sp. nov. from Maharch. It is closest to *Pugnax*, from which it differs in its strong costation, lack of septum and septalium, and rudimentary dental plates.

4. *Glosshypothyridina* Rzhonsnitskaya, 1978, known up to now from the Eifelian, is reported in the lower Givetian. A questionable occurrence of *Antirhynchonella* in the lower Givetian is confirmed.

5. *Desquamatia* (*D.*) *deserti* sp. nov. from Maharch is a new large-sized and finely costate representative of the genus. It is closest to *Desquamatia* (*D.*) *ovata* Copper, 1966 [1966a] from the Eifelian of the Eifel, from which it differs in a more convex ventral valve.

6. The Middle Devonian brachiopod fauna from the southern Maïder is surprisingly similar to coeval faunas from central Europe: out of 56 taxa fit for palaeobiogeographic analysis (those described in open nomenclature are mostly excluded), 66% (possibly up to 75%) of species are common with the Eifel and 55% (59%?) of species with the northern region of the Holy Cross Mountains; if both the latter faunas are treated as a single unit, the ratio of species in common is as high as 71 (82)%. Brachiopod faunas of the northern and southern shores of the Variscan Ocean were thus very similar in a biological sense (same species, not only same genera). In contrast, no Appallachian (Eastern North American realm) brachiopod species or genera were noted in the study area.

7. Palaeobiogeographic proximity of the northern Gondwana and southern Laurussia shores favours palaeogeographic reconstructions with a narrow Variscan Ocean, like that of McKerrow *et al.* (2000).

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REFERENCES

Abramân, M. S., 1974. Devonskaâ sistema, brahiopody. In: Akopân, V. T. (ed.), Atlas iskopaemoj fauny Armânskoj SSR. Editions of the Armenian SRR Academy of Sciences, Erevan, 48–64. [In Russian].

Alekseeva, R. E., 1960. O novom podrode *Atrypa* (*Desquamatia*) subgen. nov. iz sem. Atrypidae Gill (Brahiopody). *Doklady Akademii Nauk SSSR*, 131: 421–424.

Alimen, H., Le Maître, D., Menchikoff, N., Petter, G. & Poueyto, A., 1952. *Les chaînes d'Ougarta et la Saoura.* XIX^{ème} Congrès géologique international, Monographies régionales,1ère Série : Algérie – n° 15. Alger, 114 pp.

Alvarez, F. & Brime, C., 2000. Type specimens of athyridid brachiopods from the James Hall collection. *The University of Kansas, Paleontological Contributions, New Series,* 12: 1– 15.

Alvarez, F. & Brunton, C. H. C., 2005. On the name-bearing type of *Athyris concentrica* (von Buch, 1834). *Lethaia*, 38: 86–87.

Alvarez, F., Brunton. C. H. C. & Struve, W., 1996. On *Athyris* (Brachiopoda) and its type species '*Terebratula*' *concentrica* von Buch. *Senckenbergiana lethaea*, 76: 65–105.

Alvarez, F. & Rong Jia-yu, 2002. Athyridida. In: Kaesler, R. L. (ed.), *Treatise on Invertebrate Paleontology. Part H, Bra-*

chiopoda, Revised, Volume 4: Rhynchonelliformea. The Geological Society of America, Inc. and The University of Kansas. Boulder, Colorado and Lawrence, Kansas, pp. 1475– 1614.

Amsden, T. W., 1953. Some notes on the Pentameracea, including a description of one new genus and one new subfamily. *Journal of the Washington Academy of Sciences,* 43: 137–147.

Anderson, M. M., Boucot, A. J. & Johnson, J. G., 1969. Eifelian brachiopods from Padaupkin, Northern Shan States, Burma. *Bulletin of the British Museum (Natural History), Geology*, 18: 105–163.

d'Archiac, E. J. A. D. & de Verneuil, E. P. P., 1842. On the fossils of the older deposits in the Rhenish provinces; preceded by a general survey of the fauna of the Palaeozoic rocks, and followed by a tabular list of the organic remains of the Devonian System in Europe. *Transactions of the Geological Society of London*, 6: 304–408.

Baliński, A., 1979. Brachiopods and Conodonts from the Frasnian of the Dębnik Anticline, Southern Poland. *Palaeontologia Polonica*, 39: 3–95.

Baliński, A., 2012. The brachiopod succession through the Silurian–Devonian boundary beds at Dnistrove, Podolia, Ukraine. *Acta Palaeontologica Polonica*, 57: 897–924.

Baliński, A. & Sun, Y., 2010. New paeckelmannelloidean spiriferids (Brachiopoda) from the Early Mississippian of southern China. *Special Papers in Palaeontology*, 84: 91–98.

Barrande, J., 1848. Über die Brachiopoden der silurischen Schichten von Böhmen. *Naturwisseschaftliche Abhandlungen*, 2: 155–256.

Barrande, J., 1879. Système Silurien du centre de la Bohême. I^{ère} partie: Recherches paléontologiques. Vol. 5 : Classe des Mollusques, Ordre des Brachiopodes. Chez l'auteur. Prague – Paris, pp. 1–226.

Basse, M., 2012. *Fossilium Catalogus. I: Animalia. Pars 150: Trilobites Africae: Catalogus Typorum*. Backhuys Publishers, Markgraf publishers, Weikersheim, 311 pp.

Becker, T. R., Bockwinkel, J., Ebbighausen, V., Aboussalam, S. Z., El Hassani, A. & Nübel, H., 2004. Lower and Middle Devonian stratigraphy and faunas at Bou Tserfine near Assa (Dra Valley, SW Morocco). *Documents de l'Institut Scientifique, Rabat*, 19: 90–100.

Bełka, Z. & Narkiewicz, M., 2008. Devonian. In: McCann, T. (ed.), *The Geology of Central Europe. Volume 1: Precambrian and Palaeozoic.* The Geological Society, London, pp. 383–410.

Bełka, Z., Kaufmann, B. & Bultynck, P., 1997. Conodont-based quantitative biostratigraphy for the Eifelian of the eastern Anti-Atlas, Morocco. *Geological Society of America, Bulletin*, 109: 643–651.

Biernat, G., 1959. Middle Devonian Orthoidea of the Holy Cross Mountains and Their Ontogeny. *Palaeontologia Polonica*, 10: 1–78.

Biernat, G., 1964. Middle Devonian Atrypacea (Brachiopoda) from the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica*, 9: 277–340.

Biernat, G., 1966. Middle Devonian Brachiopods from the Bodzentyn Syncline (Holy Cross Mountains, Poland). *Palaeontologia Polonica*, 17: 1–162.

Biernat, G. & Baliński, A., 1982. Shell structure of the Devonian brachiopod *Plectospira ferita*. *Palaeontology*, 25: 857–867.

Biernat, G. & Lazarev, S. S., 1988. Genus *Poloniproductus* nov. (Brachiopoda, Devonian). *Acta Palaeontologica Polonica*, 33: 59–71.

Blodgett, R. B., Boucot, A. J. & Rong Jia-yu, 2002. Gypiduloidea. In: Kaesler, R. L. (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda (Revised), Vol. 4: Rhynchonelliformea.* Geological Society of America and University of Kansas Press, pp. 1005–1020. Boulder, Colorado and Lawrence, Kansas.

Boucot, A. J., Johnson, J. G. & Talent, J. A., 1969. Early Devonian brachiopod zoogeography. *Geological Society of America, Special Papers*, 119: 1–113.

Boucot, A. J., Massa, D. & Perry, D. G., 1983. Stratigraphy, biogeography, and taxonomy of some Lower and Middle Devonian brachiopod-bearing beds of Libya and northern Niger. *Palaeontographica, Abteilung A*, 180: 91–125.

Boucot, A. J., Rong, Jia-yu & Blodgett, R. B., 2002. Pentameridina. In: Kaesler, R. L. (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda, Revised. Volume 4: Rhynchonelliformea*. Geological Society of America and University of Kansas Press. Boulder, Colorado and Lawrence, Kansas, pp. 960–1026.

Boumendjel, K., Morzadec, P., Paris, F. & Plusquellec, Y., 1997a. Le Dévonien de l'Ougarta (Sahara occidental, Algérie). *Annales de la Société géologique du Nord*, 2ème *série*, 5: 73–87.

Boumendjel, K., Brice, D., Copper, P., Gourvennec, R., Jahnke, H., Lardeux, H., Le Menn, J., Melou, M., Morzadec, P., Paris, F., Plusquellec, Y. & Racheboeuf, P., 1997b. Les faunes du Dévonien de l'Ougarta (Sahara occidental, Algérie). *Annales de la Société géologique du Nord*, 2ème *série*, 5: 89–116.

Brice, D., 1971. Étude paléontologique et stratigraphique du Dévonien de l'Afghanistan. *Notes et Mémoires sur le Moyen-Orient*, 11: 1–364.

Brice, D., 1982. Brachiopodes du Dévonien inférieur et moyen des formations de Blue Fiord et Bird Fiord des Îles Arctiques canadiennes. *Geological Survey of Canada, Bulletin*, 326: 1–175.

Brice, D., 1985. Les brachiopodes de La Serre (Sud de Cabrières – Montagne Noire) près de la limite Dévonien moyen – Dévonien supérieur). *Hercynica*, 1: 131–154.

Brice, D., 1988. Brachiopodes du Dévonien de Ferques (Boulonnais – France). In: Brice, D. (ed.), Le Dévonien de Ferques, Bas-Boulonnais (N. France). *Biostratigraphie du Paléozoïque*, 7: 323–389.

Brice, D. & Loones, C., 2002. Nouvelles données sur des brachiopodes Cyrtospiriferidae, Reticulariidae, Uncitidae et Stringocephalidae du Dévonien de Ferques (Boulonnais – France). *Annales de la Société géologique du Nord*, 2^{e} *série*, 9: 91–109.

Brice, D. & Morzadec, P., 1983. Rhynchonellida (Brachiopodes) du Dévonien moyen et supérieur de la Rade de Brest (Massif Armoricain). *Géobios*, 16: 549–581.

Brice, D., Lafuste, J., de Lapparent, A. F., Pillet, J. & Yassini, I., 1973. Etude de deux gisements paléozoïques (Silurien et Dévonien) de l'Elbourz oriental (Iran). *Annales de la Société géologique du Nord*, 43: 177–218.

Brice, D., Mottequin, B. & Loones, C., 2008. Découverte de nouveaux brachiopodes dans le Givétien (Dévonien) du Boulonnais (N. France). *Annales de la Société géologique du Nord*, 2ème *série*, 15: 1–14.

Brice, D., Boumendjel, K., Racheboeuf, P. R. & Mottequin, B., 2011. Lower Devonian rhynchonellid brachiopods from the Ougarta area (western Sahara, Algeria). *Bulletin of Geosciences*, 86: 71–90.

Bronn, H. G., 1835–37 [published 1834–38 (39?)]. *Lethaea geognostica, oder Abbildungen und Beschreibungen der für die Gebirgs-Formationen bezeichnendsten Versteinerungen. Zweite Auflage. Erster Band, das Übergangs- bis Oolithen-Gebirge enthaltend. Atlas, XLVII Tafeln mit Abbildungen zur Lethäa geognostica*. E. Schweitzerbart's Verlagshandlung, Stuttgart, 544 pp.

Brousmiche, C., 1975. Etude de quelques *Productida (Brachio-*

poda) du Maroc présaharien. *Annales de Paléontologie*, 61: 119–163.

Brunton, C. H. C., Alvarez, F. & MacKinnon, D., 1996. Morphological terms used to describe the cardinalia of articulate brachiopods: homologies and recommendations. *Historical Biology*, 11: 9–41.

Buch, L. von, 1834. *Über Terebrateln, mit einem Versuch, sie zu classificiren und zu beschreiben. Eine in der Königliche Akademie der Wissenschaften gelesene Abhandlung*, 124 pp., pls I–III. Berlin, Druckerei der Königl. Akademie der Wissenschaften.

Buch, L. von, 1837. Über *Delthyris* oder *Spirifer* und *Orthis*. *Abhandlungen der königlichen Akademie der Wissenschaften*, 1836: 1–79, pls 1–2.

Buch, L. von, 1840. Beiträge zur Bestimmung der Gebirgsformationen in Russland. *Archiv für Mineralogie, Geognosie, Bergbau und Huttenkünde*, 15: 3–128.

Bultynck, P. & Hollevoet, C., 1999. The Eifelian–Givetian boundary and Struve's Middle Devonian Great Gap in the Couvin area (Ardennes, southern Belgium). *Senckenbergiana lethaea*, 79: 3–11.

Carter, J. L. & Gourvennec, R., 2006. Reticularioidea. In: Kaesler, R. L. (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda, Revised. Volume 5: Rhynchonelliformea*. Geological Society of America and University of Kansas Press. Boulder, Colorado and Lawrence, Kansas, pp. 1848–1870.

Cheetham, A. H. & Hazel, J. H., 1969. Binary (presence-absence) similarity coefficients. *Journal of Paleontology*, 43: 1130–1136.

Chen, X.-Q. & Tazawa, J.-I., 2003. Middle Devonian (Eifelian) Brachiopods from the southern Kitakami Mountains, northeast Japan. *Journal of Paleontology*, 77: 1040–1052.

Choubert, G. & Marçais, J., 1956. Les grands traits de la géologie du Maroc. *Notes et Mémoires du Service géologique du Maroc*, 134: 1–38.

Choubert, G. & Faure-Muret, A. (coord.), 1988. *Carte géologique internationale de l'Afrique 1/5 000 000*. Feuille 1. Commission de la Carte géologique du monde.

Conrad, T. A. 1839. Descriptions of new species of organic remains. Second Annual Report on the Palaeontological Department of the Survey. *New York State Geological Survey*, *Annual Report*, 3: 57–66.

Conrad, T. A., 1842. Observations on the Silurian and Devonian systems of the United States with descriptions of new organic remains. *Journal of the Academy of Natural Sciences of Philadelphia*, 8: 228–280.

Cooper, G. A., 1945. New species of brachiopods from the Devonian of Illinois and Missouri. *Journal of Paleontology*, 19: 479–489.

Cooper, G. A., 1955. New genera of Middle Paleozoic brachiopods. *Journal of Paleontology*, 29: 45–63.

Copper, P., 1965. Unusual structures in Devonian Atrypidae from England. *Palaeontology*, 8: 358–373.

Copper, P., 1966a. The *Atrypa zonata* brachiopod group in the Eifel, Germany. *Senckenbergiana lethaea*, 47: 1–55.

Copper, P., 1966b. European mid-Devonian correlations. *Nature*, 209 (5027): 982–984.

Copper, P., 1967a. *Spinatrypa* and *Spinatrypina* (Devonian Brachiopoda). *Palaeontology*, 10: 489–523.

Copper, P., 1967b. Morphology and distribution of *Kerpina* Struve (Devonian Atrypida). *Paläontologische Zeitschrift*, 41: 73–85.

Copper, P., 1967c. *Atrypa (Planatrypa)*, a new Devonian brachiopod-species group. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 128: 229–243.

Copper, P., 1973. *Bifida* and *Kayseria* (Brachiopoda) and their affinity. *Palaeontology*, 16: 117–138.

Copper, P., 1978. Devonian atrypoids from western and northern Canada. In: Stelck, C. R. & Chatterton, B. D. E. (eds), *Western and Arctic Canadian Biostratigraphy. Geological Association of Canada, Special Paper*, 18: 289–331.

Copper, P., 1986. Evolution of the earliest smooth spire-bearing atrypoids (Brachiopoda: Lissatrypidae, Ordovician–Silurian). *Palaeontology*, 29: 827–866.

Copper, P., 2002. Atrypida. In: Kaesler, R. L. (ed.), *Treatise on Invertebrate Paleontology. Part H, Brachiopoda, Revised, Volume 4: Rhynchonelliformea*. The Geological Society of America, Inc. and The University of Kansas. Boulder, Colorado and Lawrence, Kansas, pp. 1377–1474.

Copper, P. & Chen, Yuanren, 1995. *Invertina*, a new Middle Devonian atrypid brachiopod genus from South China. *Journal of Paleontology*, 69: 251–256.

Cottreau, J., 1940. Coralliaires, brachiopodes et crinoïdes mésodévoniens du Sahara mauritanien et occidental. *Bulletin de la Société géologique de France*, 5ème *série*, 10: 187–200.

Dahmer, G., 1930. Mandelner Schichten (Zweischalerfauna des obersten Unterdevons) an der Mosel. *Jahrbuch der preußischen geologischen Landesanstalt*, 51: 88–94.

Davidson, T., 1864. A monograph of British Devonian Brachiopoda. Part VI, first portion. *Palaeontographical Society Monographs*, 16 (68): 1–56.

Davidson, T., 1882. A monograph of the British fossil Brachiopoda. Vol. 5, part 1: Devonian and Silurian Supplements. *Palaeontographical Society Monographs*, 36 (172): 1–134.

Defrance, J. L. M., 1828. Calcéole. Calceola. 306. In: Cuvier, F. (ed.), *Dictionnaire des Sciences naturelles, dans lequel on traite méthodiquement des différens êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement à l'utilité qu'en peuvent retirer la médecine, l'agriculture, le commerce et les arts.* Tome XXXII (Mollus–Morf). 567 pp. F. G. Levrault, Strasbourg–Paris & Le Normant, Paris.

Delépine, G., 1951. Studies of the Devonian and Carboniferous of Western Europe and North Africa. *Proceedings of the Geologists' Association*, 62: 140–166.

Destombes, J. & Hollard, H. (eds), 1986. Carte géologique du Maroc au 1: 200 000. Feuille Tafilalt–Taouz. *Notes et Mémoires du Service géologique du Maroc*, 244.

Devos, I., 1962. *Contribution à l'étude du Givétien et du Frasnien du Boulonnais.* Unpublished D.E.S. thesis. Université de Lille, Faculté des Sciences, 162 pp.

Dopieralska, J., 2009. Reconstructing seawater circulation on the Moroccan shelf of Gondwana during the Late Devonian: Evidence from Nd isotope composition of conodonts. *Geochemistry, Geophysics, Geosystems*, 10 (3) [Q03015, doi:10.1029/2008GC002247].

Döring, S. & Kazmierczak, M., 2001. Stratigraphy, geometry, and facies of a Middle Devonian ramp-to-basin transect (Eastern Anti-Atlas, SE Morocco). *Facies*, 44: 137–150.

Dresch, J., Gigout, M., Joly, F., Le Coz, J. & Raynal, R., 1952. *Aspects de la géomorphologie du Maroc.* XIX^{e} Congrès géologique international, Monographies régionales. 3^{e} série: Maroc, n^{o} 3. Rabat, 182 pp.

Dresnay, R., du, Hindermeyer, J., Emberger, A., Caia, J., Destombes, J. & Hollard, H., 1988. Carte géologique du Maroc: Todrha – Ma'der (Anti-Atlas oriental, zones axiale et périphérique Nord et Sud) – Echelle : 1/200 000. *Notes et Mémoires du Service géologique du Maroc*, 243.

Drot, J., 1961a. Quelques formes de Brachiopodes givétiens du Drâa (Maroc présaharien) peu communes en Afrique du Nord. *Notes du Service géologique du Maroc*, 20: 59–68.

Drot, J., 1961b. Remarques préliminaires sur la faune de brachiopodes du Zemmour (Mauritanie). *Bulletin de la Société géologique de France*, *7e série*, 3: 257–265.

Drot, J., 1964. Rhynchonelloidea et Spiriferoidea siluro-dévoniens du Maroc pré-saharien. *Notes et Mémoires du Service géologique du Maroc*, 178: 1–240.

Drot, J., 1966. Nouvelles observations sur les brachiopodes dévoniens du Maroc présaharien. *Bulletin de la Société géologique de France*, *7e série*, 8: 877–883.

Drot, J., 1971. Rhynchonellida siluriens et dévoniens du Maroc présaharien. Nouvelles observations. *Notes du Service géologique du Maroc*, 31 (237) : 65–108.

Dumestre, A. & Illing, L. V., 1967. Middle Devonian reefs in Spanish Sahara. In: Oswald, D. H. (ed.), *International Symposium on the Devonian System, Vol. 2.* Alberta Society of Petroleum Geologists, Calgary, pp. 333–350.

Ebbighausen, V., Becker, R. T., Bockwinkel, J. & Aboussalam, Z. S., 2007. Givetian (Middle Devonian) brachiopod–goniatite–correlation in the Dra Valley (Anti-Atlas, Morocco) and Bergisch Gladbach–Paffrath Syncline (Rhenish Massif, Germany). In: Becker, R. T. & Kirchgasser, W. T. (eds), *Devonian Events and Correlations*. *Geological Society, London, Special Publication*, 278: 157–172.

Elliott, G. F., 1961. A new British Devonian alga, *Palaeoporella lummatonensis*, and the brachiopod evidence of the age of the Lummaton Shell-Bed. *Proceedings of the Geologists' Association*, 72: 251–260.

Ennih, N. & Liégeois, J.-P., 2008. The boundaries of the West African craton, with special reference to the basement of the Moroccan metacratonic Anti-Atlas belt. In: Ennih, N. & Liégeois, J.-P. (eds), *The boundaries of the West African craton. Geological Society, London, Special Publications*, 297: 1–17.

Feldman, H. R., 1994. Brachiopods of the Onondaga Formation, Moorehouse Member (Devonian, Eifelian), in the Genesee Valley, Western New York. *Bulletins of American Paleontology*, 107: 3–56.

Ficner, F. & Havlíček, V., 1978. Middle Devonian brachiopods from Čelechovice, Moravia. *Sbornik geologických věd* (*Journal of Geological Sciences*), *Paleontologie*, 21: 49–106.

Flamand, G.-B.-M., 1911. *Recherches géologiques et géographiques sur le haut-pays de l'Oranie et sur le Sahara (Algérie et Territoires du Sud).* Lyon. A. Rey, 1001 pp.

Franchi, F., Schemm-Gregory, M. & Klug, C., 2012. A new species of *Ivdelinia* Andronov, 1961 from the Moroccan Givetian and its palaeoecological and palaeobiogeographical implications. *Bulletin of Geosciences*, 87: 1–11.

Franke, C., 2012. Marine Fauna der Wiltz-Schichten (Ober-Emsium,Unter-Devon) der Mulde von Wiltz und der Daleider Mulden-Gruppe (Luxemburg, Deutschland). Teil 3: Craniida. *Ferrantia*, 68: 133–147.

Frech, F., 1891. Ueber das Devon der Ostalpen, II. *Zeitschrift der deutschen geologischen Gesellschaft*, 43: 672–687.

García-Alcalde, J. L., 1995. L'évolution paléogéographique prévarisque de la Zone Cantabrique septentrionale (Espagne). *Revista Española de Paleontología*, 10: 9–29.

García-Alcalde, J. L., 2001. Paleobiogeographical relationships between North Gondwana and South Baltica: The *Ivanothyris havliceki* fauna (Cantabrian Zone, latest Emsian). *Journal of the Czech Geological Society*, 46: 121–130.

García-Alcalde, J. L., 2010. Givetian Brachiopod faunas of the Palentian Domain (N Spain). *Revista Española de Paleontología* 25: 43–69.

Gevin, P., 1960. Études et reconnaissances géologiques sur l'axe cristallin Yetti-Eglab et ses bordures sédimentaires. Première partie : Bordures sédimentaires. *Publications du Service de la Carte géologique de l'Algérie (nouvelle série), Bulletin*, 23: 1–328.

Godefroid, J., 1970. Caractéristiques de quelques Atrypida du Dévonien belge. *Annales de la Société géologique de Belgique*, 93: 87–126.

Godefroid, J., 1995. Les brachiopodes (Pentamerida, Atrypida et Spiriferida) de la fin de l'Eifelien et du début du Givétien à Pondrôme (Belgique, bord sud du Synclinorium de Dinant). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 65: 69–116.

Godefroid, J., 2000. *Invertina struvei*, a new atrypid brachiopod from the Givetian of Morocco. *Senckenbergiana lethaea*, 79: 267–273.

Godefroid, J. & Hauser, J., 2003. The Frasnian Pentamerida and Atrypida (Brachiopoda) from the Reichle quarry (Eifel, Germany). *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, 73: 53–68.

Godefroid, J. & Helsen, S., 1998. The last Frasnian Atrypida (Brachiopoda) in southern Belgium. *Acta Palaeontologica Polonica*, 43: 241–272.

Golonka, J., Krobicki, M., Pająk, J., Van Giang, N. & Zuchiewicz, W., 2006. *Global Plate Tectonics and Paleogeography of Southern Asia.* AGH University of Science and Technology, Kraków, 128 pp.

Gourvennec, R., 1989. Brachiopodes Spiriferida du Dévonien inférieur du Massif Armoricain. Systématique, paléobiologie, évolution, biostratigraphie. *Biostratigraphie du Paléozoïque*, 9: 1–281.

Gourvennec, R. & Hoşgör, I., 2012. New record of a Middle Devonian brachiopod fauna from the Northern Arabian Plate, Zap Anticline, Çukurca-Hakkari, Southeastern Turkey. *Bulletin of Geosciences*, 87: 347–358.

Gracianova, R. T., Šiškina, G. R. & Talent, J. A., 1990. Gomeomorfnye rody devonskih retikulâriid (Brahiopody). *AN SSSR, Sibirskoe Otdelenie, Trudy Instituta Geologii i Geofiziki*, 770: 75–93. [In Russian].

Grunt, T. & Weyer, D., 2002. On the name-bearing type of *Athyris concentrica*. *Paleontological Journal*, 36: 356–367.

Gürich, G., 1896. Das Palaeozoicum im polnischen Mittelgebirge. *Verhandlungen der Russisch-Kaiserlichen mineralogischen Gesellschaft zu Sankt-Petersburg*, (2), 32: 1–539.

Halamski, A. T., 2004a. *Analyse faunistique des Brachiopodes mésodévoniens de la partie septentrionale des Monts Sainte-Croix (Pologne).* Unpublished Ph.D. thesis, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, and Université Claude-Bernard Lyon 1, Warszawa–Lyon, 354 pp.

Halamski, A. T., 2004b. *Deliella*, a new Devonian craniid brachiopod. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 2004: 181–192.

Halamski, A. T., 2005. Annotations to the Devonian Correlation Table, R220dm05: Poland; Holy Cross Mts; Łysogóry Region. *Senckenbergiana lethaea*, 85: 185–187.

Halamski, A. T., 2008. Palaeobiogeographical signature of the Middle Devonian Łysogóry region brachiopod fauna. *Fossils and Strata*, 54: 87–98.

Halamski, A. T., 2009. Middle Devonian brachiopods from the northern Part of the Holy Cross Mountains, Poland in relation to selected coeval faunas. Part I: Introduction, Lingulida, Craniida, Strophomenida, Productida, Protorthida, Orthida. *Palaeontographica, Abt. A*, 287: 41–98.

Halamski, A. T., 2012. Diversity of the *Schizophoria* lineage (Brachiopoda: Orthida) in the Lower and Middle Devonian of Poland and adjacent areas. *Paläontologische Zeitschrift*, 86: 347–365.

Halamski, A. T. & Baliński, A., 2009. Latest Famennian brachio-

pods from Kowala, Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica*, 54: 289–306.

Halamski, A. T. & Racki, G., 2005. Devonian Correlation Table. Supplements 2005. *Senckenbergiana lethaea*, 85: 191–200.

Hall, J., 1857. Descriptions of Palaeozoic Fossils. In: Lansing, G. Y. (ed.), *Tenth Annual Report of the Regents of the University of the State of New York, on the Condition of the State Cabinet of Natural History and the historical and antiquarian collection annexed thereto*, 39–186

Hall, J., 1859. Contributions to the Palaeontology of New York; being some of the results of investigations made during the years 1855, '56, '57 and '58. *New York State Cabinet of Natural History Annual Report*, 12: 7–110.

Hall, J. & Clarke, J. M., 1894. *An Introduction to the Study of the Brachiopoda, Intended as a Hand Book for the Use of Students. Part II.* James B. Lyon, State printer, Albany, pp. 751–943.

Harper, C. W., Jr. & Boucot, A. J., 1978. The Stropheodontacea. Part I: Leptostrophiidae, Eostropheodontidae and Strophonellidae. *Palaeontographica, Abt. A*, 161: 55–118.

Harper, C. W., Jr., Johnson, J. G. & Boucot, A. J., 1967. The Pholidostrophiinae (Brachiopoda; Ordovician, Silurian, Devonian). *Senckenbergiana lethaea*, 48: 403-461.

Harper, D. A. T., 2007. Uncertain. In: Selden, P. A. (ed.), *Treatise on Invertebrate Paleontology. Part H, Brachiopoda, Revised, Volume 6: Supplement.* The Geological Society of America, Inc. and The University of Kansas. Boulder, Colorado and Lawrence, Kansas, pp. 2820–2821.

Havlíček, V., 1951. Paleontologická studie z čelehovického devonu (Brachiopoda, Pentameracea, Rhynchonellacea, Spiriferacea). *Sborník Ústředního ústavu geologického*, 18: 1–20.

Havlíček, V., 1956. Ramenonožci vápenců branických a hlubočepských z nejbližšího pražského okolí. *Sborník Ústředního ústavu geologického*, 22: 535–665.

Havlíček, V., 1961. Rhynchonelloidea des böhmischen älteren Paläozoikums (Brachiopoda). *Rozpravy Ústředního ústavu geologického*, 27: 1–211.

Havlíček, V., 1967. Brachiopoda of the Suborder Strophomenidina in Czechoslovakia. *Rozpravy Ústředniho ústavu geologickégo*, 33: 1–235.

Havlíček, V. & Kukal, Z., 1990. Sedimentology, benthic communities, and brachiopods in the Suchomasty (Dalejan) and Acanthopyge (Eifelian) limestones of the Koněprusy area (Czechoslovakia). *Sbornik geologických věd, Paleontologie*, 31: 105–205.

Heckel, P. H., 1972. Possible inorganic origin for stromatactis in calcilutite mounds in the Tully Limestone, Devonian of New York. *Journal of Sedimentary Research*, 42: 7–18.

Hollard, H., 1962. Attribution au Givétien des calcaires coralligènes du Maïder (Maroc présaharien). *Comptes-rendus sommaires de la Société géologique de France*, 6: 175–176.

Hollard, H., 1963. Un tableau stratigraphique du Dévonien du Sud de l'Anti-Atlas. *Notes du Service géologique du Maroc*, 23 (172): 105–109.

Hollard, H., 1974. Recherches sur la stratigraphie des formations du Dévonien moyen, de l'Emsien supérieur au Frasnien, dans le Sud du Tafilalt et dans le Ma'der (Anti-Atlas oriental). *Notes du Service géologique du Maroc*, 36 (264): 7–68.

Hollard, H., 1981. Tableaux de corrélations du Silurien et du Dévonien de l'Anti-Atlas. *Notes et Mémoires du Service géologique du Maroc*, 42: 23.

Hollard, H. (coord.), 1985. Carte géologique du Maroc [feuille Nord]. Echelle 1/1000000. *Notes et Mémoires du Service géologique du Maroc*, 260.

Hubert, B. L. M., Zapalski, M. K., Nicollin, J.-P., Mistiaen, B., 2007. Selected benthic faunas from the Devonian of the Ardennes: an estimation of palaeobiodiversity. *Acta Geologica Polonica*, 57: 223–262.

Jacquet, F., 1936. Le flanc méridional du synclinal de Tindouf dans les confins de la Mauritanie septentrionale. *Comptes-rendus de l'Académie des Sciences*, 203: 1171.

Johnson, J. G., 2006a. Cyrtospiriferoidea. In: Kaesler, R. L. (ed.), *Treatise on Invertebrate Paleontology. Part H, Brachiopoda, Revised, Volume 5: Rhynchonelliformea*. The Geological Society of America, Inc. and The University of Kansas. Boulder, Colorado and Lawrence, Kansas, pp. 1722–1732.

Johnson, J. G., 2006b. Cyrtinoidea. In: Kaesler, R. L. (ed.), *Treatise on Invertebrate Paleontology. Part H, Brachiopoda, Revised, Volume 5: Rhynchonelliformea (part).* The Geological Society of America, Inc. and The University of Kansas. Boulder, Colorado and Lawrence, Kansas, pp. 1881–1883.

Joly, F., 1962. Études sur le relief du Sud-Est marocain. *Travaux de l'Institut scientifique chérifien, Série Géologie et Géographie physique*, 10: 1–563.

Joly, F., Ayache, A., Fardel, J. & Suech, L., 1949. *Géographie du Maroc.* Delagrave, Paris, 168 pp.

Kaufmann, B., 1995. Part IX: Middle Devonian mud mounds of the Ma'der Basin in the eastern Anti-Atlas, Morocco. In: Reitner, J. & Neuweiler, F. (coord.), *Mud Mounds: A Polygenetic Spectrum of Fine-grained Carbonate Buildups. Facies*, 32: 49–57.

Kaufmann, B., 1998. Facies, stratigraphy and diagenesis of Middle Devonian reef- and mud-mounds in the Mader (eastern Anti-Atlas, Morocco). *Acta Geologica Polonica*, 48: 43–106.

Kayser, E., 1871. Die Brachiopoden des Mittel- und Ober-Devon der Eifel. *Zeitschrift der deutschen geologischen Gesellschaft*, 23: 491–647.

Kayser, E., 1883. Devonische Versteinerungen aus südwestlichen China. 75–105. In: Richthofen, F. von, *China, Ergebnisse eigener Reisen und darauf gegründeter Studien*, 4. D. Reimer, Berlin.

Keyes, S. W. & Pitrat, C. W., 1978. Spiriferid brachiopods from the Traverse Group of Michigan: Cyrtinacea. *Journal of Paleontology*, 52: 221–233.

Khodalevich, A. N. [Hodalevič, A. N.], 1951. Nižnedevonskie i èjfel'skie brahiopody Sverdlovskoj oblasti. *Sverdlovskij Gornyj Institut, Trudy*, 18: 1–169.

Komarov, V. N., 1987. *Devonian Atrypids of Transcaucasus.* Nauka, Moskva, 198 pp.

Königshof, P., Wehrmann, A., Schindler, E., Jansen, U. & Plodowski, G., 2003. Geologische Expedition in die westliche Sahara. *Natur und Museum*, 133: 302–310.

Kozłowski, R., 1929. Les Brachiopodes gothlandiens de la Podolie polonaise. *Palaeontologia Polonica*, 1: 1–254.

Krans, T. F., 1971. The relation between the genera *Cyrtinopsis* Scupin, 1896 and *Kozlowskiellina* Boucot, 1957. *Leidse geologische Mededelingen*, 47: 99–113.

Krause, F. F., 2004. Paleozoic mud-mound database. [ftp://rock.geosociety.org/pub/reposit/2004/2004031.pdf] Accessed 7th Nov, 2013.

Krebs, W., 1967. Reef development in the Devonian of the eastern Rhenish Slate Mountains, Germany. In: Oswald, D. H. (ed.), *International Symposium on the Devonian System; Calgary, 1967. Volume II*. Alberta Society of Petroleum Geologists, Calgary, Alberta, pp. 295–306.

Le Maître, D., 1939. Observations sur la faune de gisements dévoniens du Tafilalet (Maroc). *Bulletin de la Société géologique de France, 5ème série*, 9: 201–206.

Le Maître, D., 1952a. La faune du Dévonien inférieur et moyen de la Saoura et des abords de l'Erg el Djemel (Sud-Oranais). *Matériaux pour la Carte géologique de l'Algérie, 1ère série*,

Paléontologie, 12 : 1–171.

Le Maître, D., 1952b. Contribution à l'étude des faunes paléozoïques de l'Adrar mauritanien (Sahara occidental). *Bulletin de la Direction des mines de l'Afrique Occidentale Française*, 15: 297–352.

Lécorché, J. P., Bronner, G., Dallmeyer, R. D., Rocci, G., Roussel, J., 1991. The Mauritanide Orogen and Its Northern Extensions (Western Sahara and Zemmour), West Africa. In: Dallmeyer, R. D. & Lécorché, J. P. (eds), *The West African Orogens and Circum-Atlantic Correlatives*. Springer-Verlag, pp. 187–227. Berlin, Heidelberg, New York, London, Paris, Tokyo, Hong Kong, Barcelona, and Budapest.

Lee, D. E., Dagys, A. S., Smirnova, T. N., Sun Dong-li & Jin Yiu-gan, 2006. Terebratulidina. In: Kaesler, R. L. (ed.), *Treatise on Invertebrate Paleontology. Part H, Brachiopoda, Revised, Volume 5: Rhynchonelliformea.* The Geological Society of America, Inc. and The University of Kansas. Boulder, Colorado and Lawrence, Kansas, pp. 1994–2028.

Linnaeus, C., 1758. *Systema Naturæ, per regna tria Naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.* (Editio decima, reformata.) 824 pp. Impensis Direct. Laurentii Salvii, Holmiæ.

Maillieux, E., 1914. Observations sur *Cyrtina undosa* Schnur sp. et description d'une variété nouvelle. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, 28, Procès verbaux: 2–6.

Maillieux, E., 1938. Le Couvinien de l'Ardenne et ses faunes. *Mémoires du Musée royal d'Histoire naturelle de Belgique*, 83: 1–57.

Mamedov, A. V., 1961. Novye devonskie vidy brahiopod iz Nahičevanskoj ASSR. *Paleontologičeskij Žurnal*, 1961 (3): 51–56. [In Russian].

Mamedov, A. V., 1974. Pervaâ nahodka tipogo vida roda *Gruenewaldtia* v SSSR. *Paleontologičeskij Žurnal*, 1974 (1): 140–143. [In Russian].

Matte, P., 2001. The Variscan collage and orogeny (480–290 Ma) and the tectonic definition of the Armorica microplate: a review. *Terra Nova*, 13: 122–128.

Maurer, F., 1885. Die Fauna der Kalke von Waldgirmes bei Giessen. *Abhandlungen der grossherzoglich hessischen geologischen Landesanstalt zu Darmstadt*, 1: 63–340.

May, A., 2003. Die Fossilführung des Mitteldevons im Raum Attendorn-Olpe (West-Sauerland; Rechtsrheinisches Schiefergebirge). *Geologie und Paläontologie in Westfalen*, 60: 47–79.

May, A., 2008. Corals (Anthozoa, Tabulata and Rugosa) and chaetetids (Porifera) from the Devonian of the Semara area (Morocco) at the Museo Geominero (Madrid, Spain), and their biogeographic significance. *Bulletin de l'Institut scientifique, Rabat, Section Sciences de la Terre*, 30: 1–12.

McKerrow, W. S., Mac Niocaill, C., Ahlberg, P. E., Clayton, G., Cleal, C. J. & Eagar, R. M. C., 2000. The Late Palaeozoic relations between Gondwana and Laurussia. *Geological Society, London, Special Publications*, 179: 9–20.

McLaren, D. J., 1962. Middle and early Upper Devonian rhynchonelloid brachiopods from western Canada. *Geological Survey of Canada, Bulletin*, 86: 1–122.

Menchikoff, N., 1935. Le Dévonien des confins du Rio-de-Oro. *Comptes-rendus sommaires de la Société géologique de France*, 1935: 38–39.

Menchikoff, N. & Monod, T., 1936. Coupe géologique du Hank à Taoudeni. *Comptes-rendus de l'Académie des Sciences*, 203: 230–232.

Mergl, M. & Massa, D., 1992. Devonian and Lower Carboniferous brachiopods and bivalves from central Libya. *Biostratigraphie du Paléozoïque*, 12: 1–115.

Mergl, M. & Massa, D., 2004. Devonian brachiopods of the Tamesna Basin (Central Sahara; Algeria and North Niger). Part 1. *Acta Musei Nationalis Pragae, Series B, Historia Naturalis*, 60: 61–112.

Michard, A., 1976. Eléments de géologie marocaine. *Royaume du Maroc, Notes et mémoires du Service géologique*, 252: 1–408.

Minato, M. & Kato, M., 1977. A reticulate spiriferid from the Devonian Nakazato Formation of the Kitakami Mountains, Japan. *Journal of the Faculty of Sciences, Hokkaido University, series IV*, 17: 619–627.

Mohanti, M., 1972. The Portilla Formation (Middle Devonian) of the Alba Syncline, Cantabrian Mountains, Prov. Leon, northwestern Spain: carbonate facies and rhynchonellid palaeontology. *Leidse Geologische Mededelingen*, 48: 135–205.

Mottequin, B., 2008a. Late Middle to Late Frasnian Atrypida, Pentamerida, and Terebratulida (Brachiopoda) from the Namur-Dinant Basin (Belgium). *Geobios*, 41: 493–513.

Mottequin, B., 2008b. New observations on Upper Devonian brachiopods from the Namur–Dinant Basin (Belgium). *Geodiversitas*, 30: 455–537.

Murphy, J. B., van Staal, C. R. & Collins, W. J., 2011. A comparison of the evolution of arc complexes in Paleozoic interior and peripheral orogens: Speculations on geodynamic correlations. *Gondwana Research*, 19: 812–827.

Nalivkin, D., 1930. Brachiopods from the Upper and Middle Devonian of the Turkestan. *Mémoires du Comité géologique, Nouvelle Série*, 180: 1–221.

Oczlon, M. S., 1990. Ocean currents and unconformities: The North Gondwana Middle Devonian. *Geology*, 18: 509–512.

Œhlert, D. P., 1887. Étude sur quelques fossiles dévoniens de l'Ouest de la France. *Annales des Sciences géologiques*, 19: 1–80.

Pedder, A. E. H., 1999. Paleogeographic implications of a Devonian (Givetian, Lower Varcus Subzone) rugose coral fauna from the Ma'der Basin (Morocco). *Abhandlungen der geologischen Bundesanstalt*, 54: 385–434.

Philip, G. M., 1962. The palaeontology and stratigraphy of Silurо-Devonian sediments of the Tyres area, Gippsland, Victoria. *Proceedings of the Royal Society of Victoria*, 75: 123–246.

Phillips, J., 1836. *Illustrations of the Geology of Yorkshire; or a Description of the Strata and organic Remains: accompanied by a geological map, sections, and diagrams, and figures of the fossils. Part II. The Mountain Limestone District.* 253 pp., pls I – XXIV. John Murray, London.

Phillips, J., 1841. *Figures and Descriptions of the Palæozoic Fossils of Cornwall, Devon and West Somerset; Observed in the Course of the Ordnance Geological Survey of That District.*, Longman, Brown, Green & Longmans, London, 231 pp.

Piqué, A., 1994. *Géologie du Maroc. Les domaines régionaux et leur évolution structurale.* Pumag, Rabat, 284 pp.

Piqué, A. & Michard, A., 1989. Moroccan Hercynides: a synopsis. The Palaeozoic sedimentary and tectonic evolution at the northern margin of West Africa. *American Journal of Science*, 289: 286–330.

Piqué, A., Bossière, G., Bouillin, J.-P., Chalouan, A. & Hoepffner, Ch., 1993. Southern margin of the Variscan belt: the northwestern Gondwana mobile zone (eastern Morocco and Northern Algeria). *Geologische Rundschau*, 82: 432–439.

Plusquellec Y., Boumendjel K., Morzadec P. & Paris F., 1997. Les faunes dévoniennes d'Ougarta dans la paléogéographie des régions Maghrébo-Européennes. *Annales de la Société géologique du Nord*, *2ème série*, 5: 123–128.

Racheboeuf, P. R., 1991. Silurian to Middle Devonian chone-

tacean brachiopods from the northwestern Gondwanaland margin: A review in space and time. In: MacKinnon, D. I., Lee, D. E. & Campbell, J. D. (eds.), *Brachiopods through time*. *Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 5–9 February 1990*. A. A. Balkema, Rotterdam–Brookefield, pp. 319–325

Racheboeuf, P. R., Girard, C., Lethiers, F., Derycke, C., Herrera, Z. A. & Trompette, R., 2001. Evidence for Givetian stage in the Mauritanian Adrar (West Africa): biostratigraphical data and palaeogeographic implications. *Newsletters on Stratigraphy*, 38: 141–162.

Racheboeuf, P. R., Gourvennec, R., Deynoux, M. & Brice, D., 2004. The Devonian of the Hodh area (Islamic Republic of Mauritania): paleontology and stratigraphy. *Journal of Paleontology*, 78: 98–110.

Racki, G. & Baliński, A., 1981. Environmental interpretation of the atrypid shell beds from the Middle to Upper Devonian boundary of the Holy Cross Mts and Cracow Upland. *Acta Geologica Polonica*, 31: 177–211.

Racki, G. & Baliński, A., 1998. Late Frasnian Atrypida (Brachiopoda) from Poland and the Frasnian–Famennian biotic crisis. *Acta Palaeontologica Polonica*, 43: 273–304.

Rigaux, E., 1908. *Le Dévonien de Ferques et ses Brachiopodes*. Boulogne-sur-Mer, Chez Mlle Deligny, 33 pp.

Roemer, C. F., 1844. *Das Rheinische Uebergangsgebirge. Eine palaeontologisch-geognostische Darstellung. Mit sechs lithographirten Tafeln.* Hahn'sche Buchhandlung, Hannover, 96 pp.

Roemer, F., 1856. Palaeo-Lethaea: II. Theil: Kohlen-Periode (Silur-, Devon-, Kohlen-und Zechstein-Formation). In: Bronn, H. G. & Roemer, F., *Lethaea geognostica oder Abbildung und Beschreibung der für die Gebirgs-Formationen bezeichnendsten Versteinerungen.* Dritte, Stark vermehrte Auflage. Schweizerbart, Stuttgart, 788 pp.

Rzhonsnitskaya, M. A., 1975. Biostratigrafiâ devona okrain Kuzneckogo bassejna. Tom 2: Opisanie brahiopod; Čast' 1: Pentamerida i Atrypida. *Geologičeskij Institut, Trudy*, 244: 3–231.

Rzhonsnitskaya, M. A., Markovskii, B. P., Yudina, Y. A. & Sokiran E. V., 1998. Late Frasnian Atrypida (Brachiopoda) from the south Urals, South Timan and Kuznetsk Basin (Russia). *Acta Palaeontologica Polonica*, 43: 305–344.

Sandberger, G. & Sandberger, F., 1850–1856. *Die Versteinerungen des rheinischen Schichtensystems in Nassau, mit einer kurzgefassten Geognosie dieses Gebietes und mit steter Berücksichtigung analoger Schichten anderer Länder.* Kreidel & Niedner, Verlagshandlung. Wiesbaden, 564 pp., Atlas: Taf. I–XLI.

Sartenaer, P., 1968. *Eurycolporhynchus*, nouveau genre de Brachiopode Rhynchonellide du Givétien supérieur. *Senckenbergiana lethaea*, 49: 565–574.

Savage, N., Manceñido, M. O. & Owen, E. F., 2002. Rhynchonellida. In: Kaesler, R. L. (ed.), *Treatise on Invertebrate Paleontology. Part H, Brachiopoda, Revised, Volume 4: Rhynchonelliformea*. The Geological Society of America, Inc. and The University of Kansas. Boulder, Colorado and Lawrence, Kansas, pp. 1027–1376.

Schemm-Gregory, M., 2009. On the genus *Quiringites* Struve, 1992 (Brachiopoda, Middle Devonian). *Bulletin of the Peabody Museum of Natural History*, 50: 3–20.

Schemm-Gregory, M. & Jansen, U., 2005. Middle and Upper Devonian Brachiopods from the Western Sahara (Morocco). 27. In: Harper, D. A. T., Long, S. L. & McCorry, M. (eds), *Fifth International Brachiopod Congress: Copenhagen 2005. Abstracts.* Geological Survey of Denmark and Greenland, 54 pp.

Schemm-Gregory, M. & Jansen, U., 2008. First report of the stringocephalid genus *Paracrothyris* (Brachiopoda, Middle Devonian) from North Africa. *Bulletin of Geosciences*, 83: 169–173.

Schlotheim, E. F. von, 1820. *Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert.* Becker'sche Buchhandlung, Gotha, LXII + 437 pp.

Schmid, D. U., Leinfelder, R. U. & Nose, M., 2001. Growth dynamics and ecology of Upper Jurassic mounds, with comparisons to Mid-Palaeozoic mounds. *Sedimentary Geology*, 145: 343–376.

Schmidt, H., 1941a. Die mitteldevonischen Rhynchonelliden der Eifel. *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft*, 459: 1–79.

Schmidt, H., 1941b. Rhynchonellidae aus rechtsrheinischem Devon. *Senckenbergiana*, 23: 277–290.

Schmidt, H., 1951. Zur Brachiopodenfauna des mitteldevonischen Flinzkalks von Iserlohn-Letmathe. *Senckenbergiana*, 32: 87–94.

Schmidt, H., 1975. Septalariinae (Brachiopoda, Rhynchonellida) im Devon westlich und östlich des Rheins. *Senckenbergiana lethaea*, 56: 85–121.

Schnur, J., 1851. Die Brachiopoden aus dem Uebergangsgebirge der Eifel. In: Viehoff, H. (ed.), *Programm der vereinigten höhern Bürger- und Provinzial-Gewerberschule zu Trier für das Schuljahr 1850–1851 womit zu den am 29. und 30. August stattfindenden öffentlichen Prüfungen und der Schlußfeier ergebenst einladet.* Trier: Fr. Lintz, pp. 1–16.

Schnur, J., 1853–1854 [pp. 169–216 published 1853, pp. 217–248 and plates published 1854]. Zusamenstellung und Beschreibung sämmtlicher im Uebergangsgebirge der Eifel vorkommenden Brachiopoden, nebst Abbildungen derselben. *Palaeontographica*, 3: 169–253.

Scotese, C. R. & McKerrow, W. S., 1990. Revised world maps and introduction, In: McKerrow, W. S. & Scotese, C. R. (eds), Palaeozoic palaeogeography and biogeography: *London, Geological Society Memoir*, 12: 1–21.

Siehl, A., 1962. Der Greifensteiner Kalk (Eiflium, Rheinisches Schiefergebirge) und seine Brachiopodenfauna. I. Geologie; Atrypacea und Rostrospiracea. *Palaeontographica, Abteilung A*, 119: 173–221.

Siemiradzki, J., 1909. Sur la faune dévonienne des environs de Kielce d'après les collections originales de feu le professeur L. Zejszner. *Bulletin international de l'Académie des Sciences de Cracovie, Classe des Sciences mathématiques et naturelles*, 1909 (5): 765–770.

Sobolew, D., 1904. Devonskiâ otloženiâ profilá Gržegorževice-Skaly-Vlohi. *Izvěstíâ Varšavskago Politexničeskago Instituta*, 1904: 1–107. Varšava. [In Russian].

Sobolew, D., 1909. Devon Kělecko-Sandomirskago krâža. *Materìaly po geologìi Rossìi*, 24: 43–536. [In Russian].

Sougy, J., 1964. *Les formations paléozoïques du Zemmour noir (Mauritanie septentrionale). Étude stratigraphique, pétrographique et paléontologique*. Dakar, 695 pp.

Soulaimani, A. & Burkhardt, M., 2008. The Anti-Atlas chain (Morocco): the southern margin of the Variscan belt along the edge of the West African craton. In: Ennih, N. & Liégeois, J.-P. (eds), *The Boundaries of the West African Craton. Geological Society, London, Special Publications*, 297: 433–452.

Sowerby, J. de Carle, 1839. Organic remains. In: Murchison, R. I. (ed.), *The Silurian System.* John Murray, London, pp. 579–712, 26 pls.

Sowerby, J. de Carle, 1840. [Explanation of the plates and wood-

cuts.] Organic remains engraved and described. In: Sedgwick, A. & Murchison, R. I., *On the Physical Structure of Devonshire, and on the Subdivisions and Geological Relations of its Older Stratified Deposits &c.* London, pp. unnumbered, pls LII–LVII.

Stainbrook, M. A., 1945. Brachiopoda of the Independence Shale of Iowa. *Geological Society of America, Memoirs*, 14: 1–74.

Stampfli, G. M., Hochard, C., Vérard, C., Wilhem, C. & von Raumer, J., 2013. The formation of Pangea. *Tectonophysics*, 593: 1–19.

Steininger, J., 1853. *Geognostische Beschreibung der Eifel.* Fr. Lintz'sche Buchandlung, Trier, 144 pp., pls I–IX.

Stigall Rode, A. L. & Lieberman, B. S., 2005. Paleobiogeographic patterns in the Middle and Later Devonian emphasizing Laurentia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 222: 272–284.

Struve, W., 1955. *Grünewaldtia* aus dem Schönecker Richtschnitt (Brachiopoda, Mittel-Devon der Eifel). *Senckenbergiana lethaea*, 36: 205–234.

Struve, W., 1961. Zur Stratigraphie der südlichen Eifler Kalkmulden (Devon: Emsium, Eifelium, Givetium). *Senckenbergiana lethaea*, 42: 291–345.

Struve, W., 1964. Über einige homöomorphe Brachiopoden-Arten (Meristellidae). *Senckenbergiana lethaea*, 45: 507–521.

Struve, W., 1965a. *Schizophoria striatula* und *Schizophoria excisa* in ihrer ursprünglichen Bedeutung. *Senckenbergiana lethaea*, 46: 193–215.

Struve, W., 1965b. Zur Morphologie, Biochronologie und Phylogenie der mitteleuropäisch-nordafrikanischen *Cyrtinopsis*-Arten (Spiriferacea). *Fortschritte in der Geologie von Rheinland und Westfalen*, 9: 7–50.

Struve, W., 1966. Einige Atrypinae aus dem Silurium und Devon. *Senckenbergiana lethaea*, 47: 123–163.

Struve, W., 1970. "Curvate Spiriferen" der Gattung *Rhenothyris* und einige andere Reticulariidae aus dem Rheinischen Devon. *Senckenbergiana lethaea*, 51: 449–577.

Struve, W., 1981a. Das untergivetische Leit-Fossil *Undispirifer givefex* (Spiriferida/Reticulariidae). *Senckenbergiana lethaea*, 61: 437–443.

Struve, W., 1981b. Über einige Arten von *Subtransmena* und *Devonaria* (Strophomenida). *Senckenbergiana lethaea*, 62: 227–249.

Struve, W., 1990. Paläozoologie III (1986–1990). *Courier Forschungsinstitut Senckenberg*, 127: 251–279.

Struve, W., 1992. Neues zur Stratigraphie und Fauna des rhenotypen Mittel-Devon. *Senckenbergiana lethaea*, 71: 503–624.

Struve, W., 1995. Die Riesen-Phacopiden aus dem Maïder, SE-marokkanische Prä-Sahara. *Senckenbergiana lethaea*, 75: 77–129.

Tait, J., Schätz, M., Bachtadse, V. & Soffel, H., 2000. Palaeomagnetism and Palaeozoic palaeogeography of Gondwana and European terranes. *Geological Society, London, Special Publications*, 179: 21–34.

Termier, G. & Termier, H., 1950. Paléontologie marocaine. II: Invertébrés de l'ère primaire. Fascicule II: Bryozoaires et Brachiopodes. *Notes et Mémoires du Service géologique du Maroc*, 77: 1–253.

Tessitore, L., Schemm-Gregory, M., Korn, D., Wild, F. R. W. P., Naglik, C. & Klug, C., 2013. Taphonomy and palaeoecology of the green Devonian gypidulid brachiopods from the Aferdou El Mrakib, eastern Anti-Atlas, Morocco. *Swiss Journal of Palaeontology*, 132: 23–44.

Thormann, F. & Weddige, K., 2001. Addendum zu Struve, W. (1992), Neues zur Stratigraphie und Fauna des rhenotypen Mittel-Devon: Abbildungen der Holotypen. *Senckenbergiana lethaea*, 81: 307–327.

Torley, K., 1934. Die Brachiopoden des Massenkalkes der oberen Givet-Stufe von Bilveringsen bei Iserlohn. *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft*, 43: 67–148.

Torsvik, T. H. & Cocks, L. R. M., 2011. The Palaeozoic palaeogeography of central Gondwana. In: Van Hinsbergen, D. J. J., Butter, S. J. H., Torsvik, T. H., Gaina, C. & Webb, S. J. (eds), *The formation and evolution of Africa: a synopsis of 3.8 Ga of Earth history. Geological Society, London, Special Publications*, 357: 137–166.

Vandercammen, A., 1963. Spiriferidae du Dévonien de la Belgique. *Mémoires de l'Institut royal des Sciences naturelles de Belgique*, 150: 1–179.

Vandercammen, A., 1967. Révision de quelques Spiriferida conserves à l'Université de Bonn. *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, 43 (14): 1–10.

Vanuxem, L., 1842. Geology of New York. Part 3, comprising the survey of the third geological district. *Natural History of New York*, 4 (3). D. Appleton & Co., New York, 306 pp.

Walliser, O. H., Bultynck, P., Weddige, K., Becker, R. T. & House, M.R., 1995. Definition of the Eifelian–Givetian stage boundary. *Episodes*, 18: 107–115.

Walmsley, V. G. & Boucot, A. J., 1975. The phylogeny, taxonomy and biogeography of Silurian and Early to Mid Devonian Isorthinae (Brachiopoda). *Palaeontographica, Abt. A*, 148: 34–108.

Wang Yu., 1956. Some new brachiopods from the Yukiang Formation of southern Kwangsi Province [in Chinese]. *Acta Palaeontologica Sinica*, 4: 137–162. [Also published in English in 1957: *Scientia Sinica*, 5: 373–388.]

Wang, Yu & Rong, Jiayu, 1986. Yukiangian (early Emsian, Devonian) brachiopods of the Nanning-Liujing district, central Guangxi, southern China. *Palaeontologia Sinica*, *new series, B*, 22 [172]: 1–282.

Webster, C.L., 1921. Notes on the genus *Atrypa*, with description of new species. *American Midland Naturalist*, 7: 13–20.

Weddige, K. & Ziegler, W., 2000. Das bibliographische Lebenswerk von Dr. Wolfgang Struve. *Senckenbergiana lethaea*, 79: 603–636.

Wendt, J., 1985. Disintegration of the continental margin of northwestern Gondwana: Late Devonian of the eastern Anti-Atlas (Morocco). *Geology*, 13: 815–818.

Wendt, J., 1988. Facies pattern and paleogeography of the Middle and Late Devonian in the eastern Anti-Atlas (Morocco). In: McMillan, N. J., Embry, A. F. & Glass, D. J. (eds), *Devonian of the World, vol. 1. Canadian Society of Petroleum Geologists, Memoir*, 14: 467–480.

Wendt, J., 1993. Steep-sided carbonate mud mounds in the Middle Devonian of the eastern Anti-Atlas, Morocco. *Geological Magazine*, 130: 69–83.

Wendt, J. & Kaufmann, B., 2006. Middle Devonian (Givetian) coral-stromatoporoid reefs in West Sahara (Morocco). *Journal of African Earth Sciences*, 44: 339–350.

Wendt, J., Belka, Z., Kaufmann, B., Kostrewa, R. & Hayer, J., 1997. The world's most spectacular carbonate mud mounds (Middle Devonian, Algerian Sahara). *Journal of Sedimenatry Research*, 67: 424–436.

Zapalski, M. K., 2005. Palaeoecology of Auloporida: an example from the Devonian of the Holy Cross Mts., Poland. *Geobios*, 38: 677–683.

Ziegler, P. A., 1990. *Geological Atlas of Western and Central Europe. Second and completely revised edition.* Shell Internationale Petroleum Maatschappij B.V., 241 pp.