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

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Abstract: Sixty brachiopod species are reported from the Taboumakhlouf Formation (upper Eifelian) and the Bou Dib Formation (upper Eifelian to Givetian) of Jbel Issoumour, northern Maïder, Anti-Atlas, Morocco, on the basis of collections made by Volker Ebbighausen. The stratigraphy is based on reports of co-occurring trilobite assemblages. The relatively diversified fauna pre-dates the Taghanic event and is dominated in terms of diversity by atrypides and rhynchonellides (11 species each); other frequent species include *Poloniproductus varians, Aulacella prisca, Tyersella tetragona, Schizophoria schnuri, Athyris* ex gr. *concentrica, Yeothyris? sinuata*, and *Thomasaria simplex. Spinatrypa ennigaldinannae* Halamski and Baliński sp. nov. from the upper Eifelian is characterised by a transverse shell, typically 16–18 mm wide with 19–22 ribs. *Prodavidsonia ebbigahuseni* Halamski and Baliński sp. nov. differs from other representatives of the genus in having nearly flat shells. *Eressella coronata* Halamski and Baliński, nom. nov. is proposed as a replacement name for the permanently invalid *Rhynchonella coronata* Kayser, 1871 (non *R. coronata* Moore, 1861). *Thomasaria simplex* is documented as being a particularly variable species (costation, tongue, interarea position), so its broad taxonomic treatment is favoured. The brachiopod fauna shows distinct Rhenish affinities (numerous species in common with the Eifel and the Holy Cross Mountains) like the coeval fauna from southern Maïder, described previously. The Middle Devonian brachiopod fauna from the whole Maïder (north, described here and south, described previously) totals 87 species.

Key words: Systematics, Brachiopoda, Morocco, Devonian, Eifelian, Givetian.

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INTRODUCTION (BY ATH & AB)

During the Palaeozoic, brachiopods were the most important group of filter-feeding benthic organisms and Devonian outcrops of north-western Africa are among the best places in the world to study the faunas of this period. As shown by the number of papers dealing with Devonian brachiopods from this area published during the last fifteen years (Schemm-Gregory and Jansen, 2008; Schemm-Gregory, 2009, 2014; Brice *et al.*, 2011; Halamski and Baliński, 2013, 2018a, b; Mottequin *et al.*, 2015; Mergl, 2018; Gourvennec, 2019; Halamski *et al.*, 2020; García-Alcalde and El Hassani, 2020), their diversity is still far from being satisfactorily sampled, not to mention palaeoecological, palaeobiogeographic, or evolutionary questions.

The present study is a continuation of the work on Middle Devonian brachiopods from the southern part of the Maïder region in Moroccan Anti-Atlas by the same authors (Halamski and Baliński, 2013). Sixty-two species were reported from three localities, Aferdou el Mrakib, Guelb el Maharch, and Madène el Mrakib, situated in Jbel El Mrakib and Jbel Maharch, mountain ranges forming the south-eastern border of the Maïder plain.

Herein, the authors investigate the Middle Devonian brachiopods of the Jbel Issoumour area which forms the north-western border of the Maïder plateau. Sixty species are reported, of which two are new. A significant part of the brachiopod fauna from northern Maïder studied here (25 species, 42%) had not been recorded from the previously described, approximately coeval palaeofauna of southern Maïder (Halamski and Baliński, 2013).

For history of research and general geology of the study area, the reader is referred to the previous paper (Halamski and Baliński, 2013; see also Wendt, 2021). Questions related to the detailed geological setting of the studied fauna are dealt with below (Material, Geologic setting). Authors' contributions: The main part of the present paper (brachiopod systematics; Figs 3–45) is authored by Adam T. Halamski and Andrzej Baliński. The stratigraphic interpretation of the brachiopod-bearing beds has been elaborated mostly on the basis of trilobite co-occurrence data by Jens Koppka, who is the first author of the corresponding chapter. The Figures 1–2 are by ATH, AB & JK.

MATERIAL (BY ATH & AB)

Origin of the studied collection

The material described in the present paper is a part of a bequest of the late Volker Ebbighausen, received by the Museum für Naturkunde in Berlin after his death. This large collection continues to serve as a basis of palaeontological studies (e.g., Korn *et al.*, 2020); a brief account of its origin is given here.

Volker Ebbighausen (10.2.1941–3.6.2011) was a chemist, who had a keen interest in palaeontology (for a biographical note see Becker, 2012), having started to collect fossils already as a pupil. He co-authored 32 papers, focussing mainly on Devonian and Carboniferous ammonoids (e.g., Becker *et al.*, 2000; Ebbighausen *et al.*, 2002; Bockwinkel and Ebbighausen, 2006; a full list is given by Becker, 2012). Volker Ebbighausen collected fossils from the Devonian and Cretaceous rocks of Germany (Bergisch Gladbach area, Eifel, Münsterland) and from the Devonian, Cretaceous, and Cenozoic rocks of Morocco. His collection (several thousand specimens) was bequeathed to the Museum für Naturkunde in Berlin and is conserved there.

Even before this formal gift, Volker Ebbighausen's collection was available for palaeontologists; a list of 20 papers based in part on his material is given by Becker (2012). In the description of Middle Devonian brachiopods from southern Maïder, Halamski and Baliński (2013) also used specimens collected by Volker Ebbighasusen at Madène el Mrakib. This is another argument – if any more evidence were still needed – that amateur and citizen scientists (see Cooper *et al.*, 2021 for terminology problems) are a paramount part of the palaeontological community and that private fossil collecting is generally beneficial for research on fossil biota (Haug *et al.*, 2020).

Strong and weak points of the studied material

The collection, serving as the basis of the present paper, consists of over 1,200 brachiopod specimens, representing 60 species (poorly preserved unidentified specimens not counted). The state of preservation is mostly good to excellent and several specimens show exquisite details of microornamentation (e.g., Figs 15P, Q; 41D, E) and diversified epizoan communities (e.g., Figs 7C, 29F). The latter will be the subject of a separate work (in progress). Such a situation is relatively rare in brachiopods collected in deserts, insofar as aeolian erosion (corrasion) quickly destroys both surficial shell features and smaller epibionts. Excellent preservation of some specimens collected by Volker Ebbighausen is due to their origin from purposefully dug excavations.

In contrast, the data concerning the collection localities (see below) are less precise than what at present is considered standard. This is due both to the collecting activity occurring mostly in the pre-GPS epoch (between 1994 and 1996 for those specimens that are dated) and to Volker Ebbighausen's sudden death, resulting in some parts of the card index with locality details being lost (see e.g., Halamski and Baliński, 2018a, p. 30). A tentative stratigraphic scheme was erected mainly on the basis of the trilobites, reported as co-occurring with the brachiopods on the original labels made by the collector (V. Ebbighausen). The present authors had at their disposal a very large collection of well-preserved brachiopods, the elements of which nevertheless can be localised and dated, although less precisely than one might desire. In an ideal world, the solution would be another field season, aimed at identifying and re-sampling the fossil localities, but at present it is unrealistic to suppose that this could be achieved in a reasonable time. It should also be noted that in some cases well-preserved specimens are preferable, even if their original locations are not known with accuracy (Rudwick, 1965, p. 136).

In brief, the available collection is described herein, with the above limitations in mind.

GEOLOGIC SETTING (BY JK, ATH & AB)

Localities and stratigraphy

The brachiopod fauna studied comes from a series of localities, situated in the Jbel Issoumour (also spelt Issomour or Issimour), a hill range in the northwestern part of the Maïder (Ma'der, Mader). The first five are localities 89, 93, 151, 152, and 153 (see below for a detailed description with transcripts of the original labels). They are situated from 3 to 8 km west or south-west of Taboumakhlouf (Fig. 1C). A few samples are described only as coming from Jbel Issoumour, without further topographic details. A single sample is labelled with geographical coordinates (31°31.974' N 5°18.067' W 976 m), which are manifestly false, as they fall in the Jbel Saghro, an area devoid of Devonian rocks. This sample (Parapugnax denticulatus) is interpreted tentatively as coming from the Jbel Issoumour, owing to its position among the other brachiopods originating from this area and is described together with the rest of the Jbel Issoumour brachiopods.

The entire collection can be dated to the middle part of the Middle Devonian, that is, from the middle Eifelian to the middle Givetian and is thus approximately coeval with faunas, studied in the southern Maïder (Halamski and Baliński, 2013). According to the stratigraphic scheme accepted here, the oldest brachiopod-bearing strata analysed in the present paper belong to the lower part of the Taboumakhlouf Formation (dm2.1) and are late Eifelian in age, whereas the youngest investigated brachiopod-bearing strata are in the overlying Bou Dib Formation (dm3) and are Givetian in age (see below).



Fig. 1. Geographic, palaeogeographic, and geologic context of the studied fauna (partly based on Halamski and Baliński, 2013 and references therein). **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. (Owing 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 region [modified and simplified after du Dresnay *et al.* (1988), Hollard (1974, 1985), and Destombes and Hollard (1986)]. Geological localities in boldface: those studied in the present paper (black triangles) numbered, those from southern Maïder denoted by abbreviations (Af, Aferdou el Mrakib; Md, Madène el Mrakib; Mh, Maharch). Geological structures, mountain ranges, and other topographic features in capitals. Waters (seas in A and B, wadis in C) in italics. Towns, villages, and localities in Roman typeface.

Stratigraphic position of outcrops

As explained above, the numbers of localities (89, 93, 151–153) correspond to those in a handwritten catalogue by the late Volker Ebbighausen. This catalogue is incomplete and detailed data on the five localities are not available. Original labels are fully transcribed and translated into English below and inventory numbers of brachiopod samples are given. In some cases, labels corresponding to a single, numbered locality are slightly or even markedly different (e.g., 151 includes material from both "lower" and "upper" trilobite levels); these have been distinguished by means of letters (e.g., 151A, 151B) by the present authors. The locality VEsn1 [the present authors' abbreviation for Volker Ebbighausen sine numero, i.e., Latin for "without a number"] corresponds to the material labelled as "Jebel Issimour untere Trilobitenlage?" without an original number. The locality VEsn2 corresponds to the material labelled with clearly false coordinates (see the text for a full explanation), also without an original number.

Despite these limitations, some labels (e.g., 151A–C) provide a clear reference to two distinct and characteristic trilobite horizons in the Taboumakhlouf area. The *Drotops* layers, which have been mined by local

workers in deep trenches since about 1984 (Struve, 1995; see map in Jobbins et al., 2021) for the well-known, large phacopids Drotops megalomanicus (Struve, 1990) and Drotops armatus (Struve, 1995). These horizons are good index layers and the brachiopod material can be determined precisely as belonging to the dm2.1 lithostratigraphic unit (sensu Hollard, 1974, pp. 17–18) and thus the lower part of the Taboumakhlouf Formation. According to Kaufmann (1998, fig. 31), this level corresponds to the basal kockelianus Zone of the late Eifelian (see Fig. 2). This correlation can be deduced from the geological map of the Issoumour area (Dresnay et al., 1988), and lithological and faunistic information provided by Hollard (1974, 1981), together with the conodont data of Kaufmann (1998), and insights given by Struve (1995) based on conodonts, brachiopods, and trilobites. The Drotops layers can be traced over several kilometres in an area, known to the locals as Talghoumte (coordinates 31°2'3.85"N, 5°0'47.34"W), meaning "she-camel" in the Berber language (pers. comm. A. Oumouhou 2021). The trilobites occur together with abundant brachiopods in two separate layers with D. megalomanicus at the bottom and D. armatus 10 m above (Struve, 1995; Campbell et al., 2002, fig. 1), along steep marl slopes in several valleys, which cut deeply into the Taboumakhlouf



Fig. 2. Stratigraphic sections of uppermost Lower to lowermost Upper Devonian strata in Jbel Issoumour (Taboumakhloûf), Jbel el Mrakib, and Madène el Mrakib. Stratigraphic and lithologic data after Hollard (1974) and Kaufmann (1998); compare Halamski and Baliński (2013, fig. 2). Presumed stratigraphic positions of the brachiopod-bearing localities denoted by black, vertical, arrowed lines.

Formation. Pictures of the Talghoumte outcrop, provided by V. Ebbinghausen to W. Struve (1995, figs 25–26), show the type locality of the two *Drotops* species and most likely are where V. Ebbinghausen collected some of his brachiopod material. According to Struve (1995), brachiopods from the *Drotops armatus* layer collected by Ebbinghausen in 1992 (locality SMF-Fp. 3599), are stored in the collection of the Senckenberg Museum. The small-sized fauna was reported to consist of *Aulacella, Phragmophora, Hypsomyonia, Mystrophora, Devonaria, Parastrophonella, Productella, Beckmannia, Athyris, Ambothyris*, and *Cyrtina*.

It has to be noted that some authors, like Campbell et al. (2002) and McKellar and Chatterton (2009), have dated the Drotops layers to the Givetian as part of the Bou Dib Formation. This conclusion was based on very few conodont data (see Campbell et al., 2002). However, the Drotops layers appear to be poor in conodonts, with surprisingly few specimens found in promising looking pieces cut from the Drotops-bearing limestones by Struve (1995). According to him, the conodonts recovered (determined by K. Weddige) belong to Polygnathus linguiformis linguiformis, Polygnathus pseudofoliatus, and Icriodus struvei, giving a range between the kockelianus Zone and the ensensis Zone and allow at least confirmation of a "middle to late Eifelian" age. This requires two comments. First, a tripartite subdivision of the Eifelian was based on the lithostratigraphy of the Eifel area (middle = Ahrdorf + Junkerberg; upper = Freilingen + Ahbach). In modern use, the Eifelian is subdivided into two parts, defined on the basis of conodont occurrences (Becker et al., 2016, 2020). Secondly, the two cited, polygnathid species have relatively long vertical ranges (Bultynck and Hollard, 1980; Klapper and Johnson, 1980; Aboussalam and Becker, 2007; Narkiewicz and Bultynck, 2007; Hogancamp and Over, 2013; Bahrami et al., 2015), whereas Icriodus struvei, known from the costatus Zone (Weddige, 1977) to the lowermost part of the *hemiansatus* Zone (Bultynck, 2003; Liao and Valenzuela-Rios, 2021), so that the upper part of the range is thus already in the lowermost Givetian.

So far as the giant Maïder phacopids are concerned, with Drotops as an endemic element, restricted so far as is known to Morocco, only Hypsipariops vagabundus Struve, 1990 affords some stratigraphic utility. According to Struve (1995), the species is morphologically intermediate between the late Eifelian Hypsipariops eurycaulus (Struve, 1970) and Hypsipariops lahrensis (Struve, 1982) from the basal Givetian of the Eifel mountains in Germany. Hypsipariops vagabundus occurs in the Taboumakhlouf area at 31°1'57.00"N, 4°59'24.00"W (pers. comm., the late Dieter Holland), in a region mapped by Hollard (1974) as uppermost dm2.1, very close to dm.2.2. The species is associated with the dechenellid trilobite Cyberella lemkei Basse (in Basse and Müller, 2004) and a long-spined subspecies of Drotops armatus (according to the material acquired by JK from that site). The Phacops site (locality 89 sensu V. Ebbinghausen) might correspond to this area. Hypsipariops vagabundus is called "Phacops noir" (black Phacops) by local workers. The Eifelian/Givetian boundary is difficult to determine in the area; according to the conodonts, studied by Kaufmann (1998) at various outcrops in the Maïder Basin, the boundary is correlated with the limit of units dm2.2 and dm3 of Hollard (1974).

In the following list, a double dagger ‡ before an inventory number or series of numbers indicates that the origin of this sample (these samples) is not entirely certain.

- 89. Maider (Marokko) (89) Jbel Issoumour Lesefunde Berghänge "Phacopsstelle", Devon/Eifel. [Surface samples from the slope of the "*Phacops* site", Devonian/Eifelian]. Estimated stratigraphic and geographic position: Taboumakhlouf Formation, dm2.1 or dm2.2; late Eifelian; between 31°1′57″N, 4°59′24″W (*Hypsipariops vagabundus* horizon) and 31°1′57″N, 5°1′2″W (*Drotops* horizons of Talghoumte). MB.B.9410, ±9411, 9453–9458.
- 93A. Maider (Marokko) (93) Lesefunde Mergelhänge Jbel Issoumour, 11 km SW Bou-Dib, Mittel-Devon. [Surface samples from the marl slopes of Jbel Issoumour, 11 km southwest of Bou Dib, Middle Devonian.]
 Estimated stratigraphic and geographic position: upper Taboumakhlouf Formation to Bou Dib Formation, dm2.2–dm3; late Eifelian or early Givetian; approximately at 31°1′5″N, 4°59′5″W. MB.B. 9385, ‡9386, 9390–9393, 9395, 9403, ‡9404, 9408, 9409, 9424–9427, ‡9428, 9444, 9445, 9471–9479.
- 93B. Maider (Marokko) (93) Lesefunde E Seite Jbel Issoumour Taboumakhlouf, leg. Lahcem, Ait Ou Amar, Marokkoreise November 1996, Mittel-Devon. [Surface samples from the east side of Jbel Issoumour, Taboumakhlouf; leg. Lahcem, Ait Ou Amar, Morocco journey November 1996, Middle Devonian.]
 Estimated stratigraphic and geographic position:

upper Taboumakhlouf Formation to lower Bou Dib Formation, dm2.2-dm3; late Eifelian or early Givetian; centre of Taboumakhlouf area; 31°1′57″N, 4°58′51″W.

MB.B. 9416, \$9417-9419.

93C. Maider (Marokko) (93) Lesefunde O Seite Jbel Issoumour Taboumakhlouf von einem Hirten gesammelt, Mittel-Devon. [Surface samples from the east side of Jbel Issoumour, Taboumakhlouf, collected by a herder, Middle Devonian.]. Estimated stratigraphic and geographic position: upper Taboumakhlouf to lower Bou Dib Formations, dm2.3–dm3; late Eifelian or early Givetian; southwest of Taboumakhlouf area, 31°1′20″N, 4°58′20″W.

MB.B. 9445–9450, \$9451.

151A. Jbel Issimour (C) (151) W Taboumakhlouf (5–6 km) ca. 10 m im Liegenden des unteren Trilobitenschurfs Marokkoreise November 1995, Mittel-Devon. [Jbel Issoumour (C) (151), 5 to 6 km west of Taboumakhlouf, ca. 10 m below the lower trilobite horizon (with *Drotops megalomanicus*). Morocco journey November 1995, Middle Devonian.] Estimated stratigraphic and geographic position: basal Taboumakhlouf Formation, dm2.1; late Eifelian;

31°1′53″N, 5°2′2″W (estimated coordinate corresponds with the lower *Radiaspis* horizon, a brachiopod-rich level, found some metres below the *D. megalomanicus* layer, pers. comm. M. Koumali 2020). MB.B.9437.

151B. Jebel Issoumour (151) Plateau auf dem Gipfel Bergrücken ca. 8 km W Taboumakhlouf, obere Drotopslage, Marokkoreise März 1994, Mittel-Devon. [Jebel Issimour (151), plateau on top of the ridge, ca. 8 km west of Taboumakhlouf, upper *Drotops* layer (= *D. armatus*), Morocco journey March 1994, Middle Devonian.].

Estimated stratigraphic and geographic position: lower Taboumakhlouf Formation, dm2.1; late Eifelian; 31°1′46″N, 5°2′35″W, coordinates refer to a ridge with the *D. megalomanicus* horizon visible at its northern flank, ca. 6.2 km W of Taboumakhlouf. MB.B. 9394, 9396, \$9397–9401, 9402, 9412, \$9413–9415, 9422–9423, 9429, \$9430–9436, 9486–9491, \$9492–9498, 9500.

151C. Plateau (Verebnungsfläche) ca. 5 km W Taboumakhlouf, ca. 2 km vor der Abbruchkante; etwa obere Trilobitenlage; Marokkoreise Dezember 1995, Mittel-Devon. [Plateau (denudation surface), ca. 5 km west of Taboumakhlouf and 2 km from the edge of the cliff; ca. upper trilobite layer (*Drotops armatus* level), Morocco journey December 1995, Middle Devonian.]

> Estimated stratigraphic and geographic position: lower Taboumakhlouf Formation, dm2.1; late Eifelian. Best fit is a little hill situated at $31^{\circ}2'17''N$, $5^{\circ}1'33''W$. Some ruins exist on top of a plane denudation surface and the *D. megalomanicus* horizon is from a deep excavation on the marly flanks of the hill. The site is called by the local Berber Ab'aire (meaning camel foal, pers. comm. A. Oumouhou 2021).

> MB.B. 9387, \$9388, 9406, 9407, 9440–9441, \$9442–9443, 9446, 9459, 9466–9470, 9480–9485.

152A. Jebel Issimour (152) Taleinschnitt am Übergang des Gebirgzuges in die Ebene ca. 3 km SW Taboumakhlouf, Marokkoreise März 1994, Mittel-Devon. [Jbel Issoumour (152), valley cut at the transition between hill zone and plain, ca. 3 km southwest of Taboumakhlouf, Morocco journey 1994, Middle Devonian.]

> Estimated stratigraphic and geographic position: Bou Dib Formation, dm3; Givetian. The coordinate refers to a valley, about 3 km SW of Taboumakhlouf at $31^{\circ}0'23''N$, $4^{\circ}59'45''W$, as the probable source of the material.

MB.B.9389.

152B. Jebel Issimour (152) Taleinschnitt am Übergang des Gebirgzuges in die Ebene ca. 3 km SW Taboumakhlouf, ca. 2 km W Bou Terga Marokkoreise November 1995, Mittel-Devon. [Jbel Issoumour (152), valley cut at the transition between hill zone and plain, ca. 3 km Southwest of Taboumakhlouf, ca. 2 km West of Bou Terga, Morocco journey 1995, Middle Devonian.] Estimated stratigraphic and geographic position: Bou Dib Formation, dm3; Givetian. Same location as 152A (alternative coordinate for a similar but more southwards situated valley would be 30°59'35"N, 4°59'58"W). MB.B.9438.

153. Jbel Issimour (153) Höhenrücken ca. 6 km W Taboumakhlouf, unterer Trilobitenschurf, Marokkoreise März 1994, Mittel-Devon. [Jbel Issoumour (153), ridge ca. 6 km west of Taboumakhlouf, lower trilobite horizon, Morocco journey March 1994, Middle Devonian.]
Estimated stratigraphic and geographic position: *D. megalomanicus* horizon, lower Taboumakhlouf Formation, dm2.1; late Eifelian. The coordinate 31°1′55″N, 5°2′15″W marks the *D. megalomanicus* horizon, exposed over 1.5 km on the northern flank of a mountain ridge at the given distance from

MB.B.9420, **\$**9421, 9499.

Taboumakhlouf.

- VEsn1.Jebel Issimour untere Trilobitenlage? [Jbel Issoumour, lower trilobite horizon?]
 Estimated stratigraphic and geographic position: The lower trilobite horizon probably refers to the D. *megalomanicus* horizon, lower Taboumakhlouf Formation, dm2.1; late Eifelian. Without more geographic information, the place is impossible to pinpoint but is likely to be close to the above-mentioned sites of these strata.
 MB.B.9460–9465.
- VEsn2.Material labelled with clearly false coordinates (see text) "31°31'974 N5°18'067 W 976 m". Possibly originating from Jbel Issoumour. MB.B.9439.

METHODS (BY ATH & AB)

Repository

The collection studied is in the Museum für Naturkunde in Berlin, Germany (institutional abbreviation MB) under the collection numbers MB.B.9385 to MB.B.9500. Under a single inventory number, there may be from one to 250 specimens. The numbering was made before the detailed taxonomic study, so in a few cases a single inventory number corresponds to more than one species (for example, MB.B.9429.1–23: *Yeothyris? sinuata*; MB.B.9429.24–25: *Athyris* ex gr. *concentrica*; MB.B.9429.26: *Echinocoelia dorsoplana*).

Special taxonomic questions

Both the study of brachiopods from southern Maïder (Halamski and Baliński, 2013) and the present paper evidence strong affinities between Middle Devonian faunas from Europe (Rhenish Slate Mountains, including the Eifel region; the Holy Cross Mountains) and from Africa (Maïder in the Anti-Atlas). As a consequence, for a few taxa it seemed advisable to defer a detailed study, so that it could be made on the European and African material together, as was done for *Eressella* (Halamski and Baliński, 2018a) as well as *Kransia* (*Fatimaerhynchia*) and *Lebanzuella* (Halamski *et al.*, 2020). This concerns the representatives of the family Hebetoechiidae (Rhynchonellida) as well as representatives of the genera *Bifida*, *Echinocoelia*, and *Yeothyris*. Such taxa are either only named without being described in the present paper or described without a detailed revision, the latter being deferred to a further study.

Images were taken using a Fujifilm Finepix S2 pro camera with a Nikon micro 60 mm lens. 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 Helicon Focus software.

Internal features of the brachiopods were investigated, using the standard technique of serial sections and acetate peels. The peels were mounted between microscope slides and photographed under a binocular microscope. The photographs were imported to CorelDRAW and internal details were drawn using a digital drawing tablet.

Calculations were mostly made with PAST (Hammer *et al.*, 2001) and Microsoft Excel software. Measurements of the material studied are given as follows: (a-)b-c(-d) [N], with a – minimum value; b – first quartile; c – third quartile; d – maximum value; N – number of observations.

Synonymies, although an essential part of the taxonomic work, are kept as short as possible, so for species considered in the southern Maïder paper (Halamski and Baliński, 2013) the reader is referred to them with the abbreviation *ubi syn. (ubi synonymia*, Latin: where synonymy [is to be found]). Synonymies are commented upon by means of the signs proposed by Richter (1948) and Matthews (1973), as used by Halamski (2009, p. 46–47).

Following the taxonomic tradition, diagnoses of new species are deliberately kept as short as possible (Linnaeus, 1737, p. 212). Given that no high-level revision is intended, super- and subfamily names are omitted for the sake of conciseness.

SYSTEMATIC PALAEONTOLOGY (BY ATH & AB)

Phylum Brachiopoda Duméril, 1806 Subphylum Craniiformea Popov *et al.*, 1993 Class Craniata Williams *et al.*, 1996 Order Craniida Waagen, 1885 Family Craniidae Menke, 1828 Genus *Petrocrania* Raymond, 1911

Type species: *Craniella meduanensis* Œhlert, 1888; Mayenne, western France, Lower Devonian. **Synonym:** *Craniella* Œhlert, 1888 non Schmidt, 1870.

> Petrocrania sp. Fig. 3CC

Material: Two shells attached onto the dorsal valve of *Xystostrophia umbraculum* (von Schlotheim, 1820) MB.B.9386, probably from locality 93A.

Description: Dorsal valve elliptic in shape (ratio of greater to smaller diameter about 1.1), very flat, maximum size 9.7–11.7 mm. Apex eccentric; shell substance in apical region thicker, forming a callosity ca. 3–4 mm in diameter. Ornamentation mimicking that of the host; growth lines visible outside the apical region, irregular.

Remarks: These two specimens are classified as *Petrocrania* on account of weakly convex shells, mimicking the ornamentation of the host and lacking spines or ribs. As the internal features remain unknown, a more detailed identification is not possible (see Holmer *et al.*, 2013). Middle Devonian representatives of *Petrocrania* were described from several localities in the USA, Europe, and China. The genus has a cosmopolitan distribution, occurring from the Lower Ordovician to the Lower Carboniferous (Bassett, 2000; see also Mottequin, 2021, p. 40).

Distribution: Probably the upper part of the Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian.

Genus Deliella Halamski, 2004 [2004b]

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

Deliella aff. rhenana (Dahmer, 1930) Fig. 3DD

- aff. 1930 *Philhedra rhenana* n. sp. Dahmer, pp. 92–93, pl. 6, fig. 2.
- v 2013 Deliella aff. rhenana (Dahmer, 1930) Halamski and Baliński, pp. 248–251, fig. 3O, P, Q1, R1, S1.

Material: Shell fragment attached onto a dorsal valve of *Devonogypa spinulosa* (Havlíček, 1951) MB.B.9412 from locality 151B.

Description: The material consists of less than half of a conical, dorsal valve (preserved length ca. 4 mm, estimated total length ca. 6 mm). Ornamentation of relatively coarse, radial ribs.

Remarks: This single fragmentary specimen from Jbel Issoumour is similar to approximately coeval, coarsely ornamented shells from Madène el Mrakib, described by Halamski and Baliński (2013), under open nomenclature as *Deliella* aff. *rhenana*, as opposed to finely ornamented *Deliella deliae* (see detailed discussion therein).

Distribution: The lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian.

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. 3V–BB

- v* 1966 *Leptaena analogaeformis* n. sp. Biernat, pp. 38–42, text-figs 6, 7, pl. 3, figs 1–16, pl. 4, figs 1–13.
- v. 2013 Leptagonia analogaeformis (Biernat, 1966)
 Halamski and Baliński, p. 251, fig. 3A–L [ubi syn.].

Material: Four articulated shells MB.B.9428.1–4, probably from locality 93A; isolated dorsal valve SMF 94838, Jebel Abiir, northern Maïder, coll. U. Jansen.

Description: Shell large, preserved width up to 31.8 mm, estimated total width of a fragmentary specimen ca. 50 mm; moderately to markedly transverse (width to length ratio 1.25-1.81), subrectangular in outline, dorsally geniculate. Hinge line wide, equals the maximal shell width; anterior commissure straight. Ornamentation of concentric rugae, (4–)6–8 per cm, and radial costae and costellae, ca. 7–8 per 5 mm at anterior margin.

Ventral interior: see Halamski and Baliński (2013, p. 251). **Remarks:** Reliable identification of *Leptagonia* species requires a knowledge of internal morphology (Bassett and Bryant, 2006; Ghobadi Pour et al., 2013; Mottequin and Simon, 2017). The material from Jbel Issoumour consists solely of articulated shells. However, the single ventral interior from Jbel Abiir (Halamski and Baliński, 2013, fig. 3I–J) agrees with Leptagonia analogaeformis (Biernat, 1966) from the Middle Devonian of the Holy Cross Mountains and the Eifel (Halamski, 2009). The material described here has been considered broadly, including three moderately transverse shells (width-to-length ratios 1.25-1.58) with coarser ornamentation having (4-)5-6 rugae per cm (Fig. 3V-Z) and a single, more transverse shell (width-tolength ratio 1.81) with finer ornamentation, 7-8 rugae per cm (Fig. 3AA-BB).

Distribution: Probably the upper part of the Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian. General distribution includes the Middle Devonian of the Holy Cross Mts., Eifel, Sauerland, Maïder, and Mauritania (Halamski and Baliński, 2013 and references therein); possibly also Eastern Asia (Chen and Tazawa, 2003). Family Douvillinidae Caster, 1939 Genus *Gibbodouvillina* Jansen, 2014

Type species: *Strophomena taeniolata* Sandberger and Sandberger, 1856; Rhenish Slate Mountains, upper Emsian (see Jansen, 2014, p. 128 for details).

cf. *Gibbodouvillina interstrialis* (Phillips, 1841) Fig. 3A–E

- cf. 1841 Orthis interstrialis, Leptaena interstrialis Phillips, pp. 61–62, pl. 25, fig. 103 a–e.
- cf. 2013 *Protodouvillina interstrialis* (Phillips, 1841) Halamski and Baliński, pp. 251–252, fig. 4A–F, L.
- cf. 2019 *Protodouvillina* cf. *interstrialis* (Phillips, 1841) – Mergl and Budil, pp. 95–96, pl. 1, figs 1–3.
- 2020 Gibbodouvillina cf. interstrialis (Phillips, 1841) García-Alcalde and El Hassani, p. 18, fig. 7.2–7.6.

Material: Fragmentary articulated shell MB.B.9468.1 from locality 151C.

Description: The only available shell lacks lateral regions and the anterior commissure; it is concavo-convex, probably semi-elliptic in outline, with a straight hinge, distinct ears (inferred from the growth lines) and most probably a straight anterior commissure. Preserved width 11.8 mm, estimated total width ca. 18 mm, preserved length 10.0 mm. Both interareas of comparable height, striate; chilidium convex, pseudodeltidium poorly preserved. Ornamentation parvicostellate, ventral valve with 13 costae in the umbonal region and ca. 25 at anterior commissure; usually 4–6 costellae between the latter. Interior not studied.

Remarks: This shell is strongly reminiscent of the widely reported Devonian species *Gibbodouvillina interstrialis* (Phillips, 1841), but in the absence of interiors, identification is reported under open nomenclature. Intraspecific variation in convexity within this species is notable (compare Halamski, 2009, pl. 3, figs 3 and 10); the present specimen is relatively flat.

Poorly preserved material from the lower to middle Givetian of the ODE section in the Jbel Ou Driss was tentatively referred to this species by García-Alcalde and El Hassani (2020).

Distribution: Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. This species is reported from the Early, Middle, and even Late Devonian (Brice, 1970; Halamski, 2009 and references therein) of several regions, but lacks a comprehensive revision.

Fig. 3. Middle Devonian Craniida and Strophomenida from northern Maïder. **A–E.** cf. *Gibbodouvillina interstrialis* (Phillips, 1841). Incomplete articulated shell MB.B.9468 in dorsal, ventral, lateral, posterior, and anterior views. Locality 151C. **F–L.** *Parastrophonella anaglypha* (Kayser, 1871). F, L. Ventral valve MB.B.9463.2, internal view (L) and enlargement of the muscle field (F). G–K. Articulated shell MB.B.9463.1 in dorsal, ventral, lateral, posterior, and anterior views. Locality VEsn1. **M–U.** *Leptodontella lanthanomena* Halamski, 2009. M. Incomplete articulated shell MB.B.9406.2 in ventral view. O–P. Articulated shell MB.B.9406.1 in anterior and ventral views. N, Q–U. Articulated shell MB.B.9407 in dorsal, ventral, lateral, posterior, and anterior views (Q–U) and enlargement of the posterior region of the partly decorticated ventral valve showing traces of the muscle field (N). Locality 151C. **V–BB.** *Leptagonia analogaeformis* (Biernat, 1966). V–Z. Articulated shell MB.B.9428.1 in dorsal, ventral, lateral, posterior, and anterior views. AA–BB. Articulated shell MB.B.9428.2 in dorsal and ventral views. Locality 93A. **CC.** *Petrocrania* sp. Two shells attached onto a dorsal valve of *Xystostrophia umbraculum* (von Schlotheim, 1820) MB.B.9386 [compare Fig. 7C]. Locality 93A. **DD.** *Deliella* aff. *rhenana* (Dahmer, 1930). Fragmentary specimen attached onto a dorsal valve of *Devonogypa spinulosa* (Havlíček, 1951) MB.B.9412 [compare Fig. 15H]. Locality 151B.

Genus Leptodontella Khalfin, 1948

Type species: *Leptaena caudata* Schnur, 1854 in 1853–54; Eifel, Eifelian.

Leptodontella lanthanomena Halamski, 2009 Fig. 3M–U

v* 2009 Leptodontella lanthanomena sp. n. – Halamski, pp. 56–59, text-figs 5, 6D, pl. 3, fig. 18, pl. 4, figs 11–20, 22–23, 26 [ubi syn.].

Material: Three articulated shells MB.B.9406.1–2, 9407, two of them decorticated, from locality 151C.

Description: Shell transverse, rounded, subtrapezoidal in outline, ventrally geniculate, up to ca. 33 mm in width, width-to-length ratio about 1.5–1.6. Posterior margin straight; postero-lateral extremities not preserved. Tongue high, subtrapezoidal to nearly parallel-sided, occupying about one third of the shell width. Dorsal valve flat except for the geniculation; interarea linear, chilidium poorly preserved. Ventral valve nearly flat, except for the geniculation; intererea striate, pseudodeltidium convex; disc in two specimens eroded in posterior half, allowing one to see the major part of diductor scars that are narrowly trapezoidal in outline (Fig. 3N).

Remarks: Two specimens from Jbel Issoumour are slightly eroded and allow examination of the form of the diductor scars, which usually is not the case for articulated shells. Halamski (2009) separated L. lanthanomena from the Holy Cross Mts. (Halamski, 2009, pl. 3, fig. 18; pl. 4, fig. 26) from L. caudata Schnur, 1854 from the Eifel (Halamski, 2009, pl. 4, fig. 25) on the basis of the form of the diductor scars, narrowly trapezoidal (width in the anterior part about the same as in the posterior part, margins subparallel) in the former and flabellate (width in the anterior part at least twice that in the posterior part, margins diverging anteriorly) in the latter. The narrowly trapezoidal shape of the ventral muscle field of the specimens described here is intermediate between the two species, but apparently closer to L. lanthanomena than to L. caudata. The two species cannot be distinguished on the basis of external morphology alone and variability of internal characters is poorly known because isolated or decorticated valves are infrequent in the fossil material.

Distribution: Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. This species is also known from the upper Eifelian part of the Skały beds in the Łysogóry region of the Holy Cross Mts. (Halamski, 2009).

Genus Parastrophonella Bubličenko, 1956

Type species: *Strophomena anaglypha* Kayser, 1871; Eifel, Prüm Syncline, Crinoiden-Schicht, Middle Devonian.

Parastrophonella anaglypha (Kayser, 1871) Fig. 3F–L

v* 1871 Strophomena anaglypha – Kayser, pp. 628–629, pl. 14, fig. 3a–f. v. 2013 Parastrophonella anaglypha (Kayser, 1871) – Halamski and Baliński, p. 252, fig. 3M, N, U.

Material: Articulated shell MB.B.9451, probably from locality 93C; ventral valve MB.B.9463 from locality VEsn1. Description: Shell subrectangular-semielliptic in outline, transverse, ventrally geniculate, 12.6-13.4 mm wide, widthto-length ratio ca. 1.4-1.6. Hinge margin straight, denticulate; postero-lateral extremities mucronate. Anterior commissure straight. Both valves nearly flat, dorsal and ventral interareas of comparable height. Ornamentation parvicostellate. Ventral interior: diductor scars extending to about half length of the valve, weakly flabellate; adductor scars confluent with those of the diductors; valve floor pustulose. Remarks: Detailed descriptions of this widely distributed species were given by Harper and Boucot (1978) and Halamski (2009). Halamski and Baliński (2013, p. 252) inadvertently described the ornamentation of the disc of the ventral valve as multicostellate; it is parvicostellate. Distribution: Probably Taboumakhlouf Formation to lower part of the Bou Dib Formation, dm2.1-dm3, upper Eifelian to Givetian. Otherwise, Eifel, Lahn Syncline, Ardennes, Holy Cross Mountains, Pyrenees, Montagne Noire, Morocco, and Mauritania; Eifelian to Givetian (Harper and Boucot, 1978;

Order Productida Sarytcheva and Sokolskaya, 1959 Suborder Chonetidae Muir-Wood, 1962 Family Anopliidae Muir-Wood, 1962 Genus *Devonaria* Biernat, 1966

Halamski, 2009 and references therein).

Type species: *Chonetes zeuschneri* Sobolew, 1909; Skały, Holy Cross Mts.; Skały beds, upper Eifelian.

Synonym: *Plicodevonaria* Boucot and Harper, 1968 (type species: *Orthis minuta* Goldfuss *in* von Buch, 1837); see Racheboeuf (1998, p. 58; 2000, p. 387). The type species of *Devonaria* and *Plicodevonaria* are different; the two genus names are subjective synonyms, not objective synonyms, as indicated erroneously by Racheboeuf (1998, 2000).

Species assigned: *Devonaria zeuschneri* (Sobolew, 1909); Holy Cross Mts., northern region; Skały beds, upper Eifelian to lower Givetian (see Halamski, 2009);

Devonaria minuta (Goldfuss *in* von Buch, 1837); Blankenheim, Eifel; Eifelian (probably Freilingen Formation, upper Eifelian; Struve, 1981);

Devonaria minutissima Struve, 1981; Hillesheim; Junkerberg Fm., Eifelian;

Devonaria cf. minutissima sensu Halamski, 2009; Świętomarz, Holy Cross Mts.; lower Givetian;

Devonaria obtusa Afanasjeva, 1978; Nakhichevan; Givetian;

Devonaria gevini Racheboeuf, 1990 (= *Devonaria* sp. nov. E *sensu* Racheboeuf, 1991); Northern Saharan Region; lower Givetian.

Species doubtful: Chonetes productoides Paeckelmann, 1925 non Stuckenberg, 1898 (*Plicodevonaria* after Boucot and Harper, 1968, p. 162; probably *Loreleiella* after Racheboeuf, 1990, p. 311; *Devonaria* after Racheboeuf, 1998, p. 58); Bosphorus, Turkey; Emsian?; other species **Species excluded:** *Devonaria* sp. *sensu* Drot (1961b); Zemmour Noir; Givetian [= *Longispina* sp. nov. D. *sensu* Racheboeuf, 1991]

Remarks: There have been contradictory opinions on the presence or absence of spines in *Devonaria*. According to Racheboeuf (1981, p. 81), spines never have been observed in *Devonaria* and the diagnosis given in the revised *Treatise* states "no spines developed but canal apertures alternating on each side of umbo" (Racheboeuf 2000, p. 387). However, *Devonaria* is listed among "genera with dissymmetrical spines" by Racheboeuf and Garcia (1996, p. 325). On the material examined here, evident spine bases at the hinge line are visible (see description below).

Devonaria minuta (Goldfuss in von Buch, 1837) Figs 4F-T, 5

- * 1837 Orthis minuta Goldf. von Buch, p. 68.
- 1962 *Retichonetes minutus* (Von Buch) Muir-Wood, p. 64, pl. 4, figs 7–11.
- p 1964 Chonetes minutus (Goldfuss) Sougy, p. 446, pl. 49, fig. 9.
 - 1968 *Plicodevonaria minuta* (Von Buch, 1836) – Boucot and Harper, pp. 164–165, pl. 28, figs 2–10 [*ubi syn*.].
 - 1981 *Devonaria minuta* (Buch 1837) Struve, pp. 233–235.

Material: Thirteen articulated shells MB.B.9432.2–3, 9492.1–11, probably from locality 151B.

Description: Shell concavo-convex, semi-elliptic in outline, weakly to moderately transverse, seldom weakly elongate, up to 9.7 mm in width, auriculate; maximum width at hinge line. Ventral interarea concave, approximately orthocline; dorsal interarea hypercline. Ventral spines present near the hinge line, 1–2 on both sides of the umbo, probably obliquely inserted (only bases preserved, ca. 0.3–0.5 mm in diameter and up to 0.2 mm in preserved length), distance between two successive spine bases 1.3–1.8 mm. Ornamentation costellate with a total number of (18-) 20–23(–24) costae and costellae.

Interior not studied.

Remarks: In comparison with *D. minuta* from the Eifel, the sample from Jbel Issoumour contains slightly smaller shells, typically 8–9 mm wide, compared to 10–12 mm in the Eifel (Halamski and Jansen, unpublished data). The shape and the ornamentation are similar in both samples, the mean width-to-length ratio being 1.13 (N= 11) in Maïder and 1.10 (N = 10) in the Eifel, but the Moroccan sample is clearly more variable (range 0.94–1.39 compared to 1.03–1.17 in the Eifel). The same observation may be made about the ornamentation with the mean ratio of the number of ventral costellae to width being 2.50 in Jbel Issoumour and 2.47 in the Eifel, but extreme values ranging 2.08–3.16 in the former and 2.11–2.92 in the latter.

The type species *D. zeuschneri* is larger (up to ca. 18 mm) and has more numerous ribs (30–40 in shells 15–18 mm wide; Halamski, 2009, p. 63). Struve (1981, p. 234)

concluded that this difference should be interpreted as being of taxonomic value and not caused by ecological factors. *Devonaria gevini* Racheboeuf, 1990 has still denser ornamentation, with 34–37 ventral costellae in shells 12– 16 mm wide (Racheboeuf, 1990, p. 311). *Devonaria obtusa* Afanasjeva, 1978 has up to 50 ribs (Alekseeva *et al.*, 2018, p. 139). *Devonaria minutissima* Struve, 1981 and *Devonaria* cf. *minutissima sensu* Halamski, 2009 have small (up to 7 mm in width) and finely ribbed shells (Halamski, 2009, p. 64).

Distribution: Probably the lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise, Eifel, Eifelian and possibly also upper Emsian to Givetian (Struve, 1981; see also localities given by Boucot and Harper, 1968); Belgium, England, Morocco, and Burma, possibly Brittany (France): Eifelian (Boucot and Harper, 1968 and references therein).

According to the present state of knowledge, *Devonaria minuta* is thus the only representative of its genus in England and Belgium. In Germany, it co-occurs with *D. minutissima* and in northwestern Africa (Maïder, Zemmour Noir) with *D. gevini*. It has not been found either in Poland or in the Caucasus, where it is replaced by possibly vicariant species *D. zeuschneri* and *D. obtusa*, respectively, but apparently it reappears further east (Padaupkin, Burma: Anderson *et al.*, 1969).

Devonaria gevini Racheboeuf, 1990 Fig. 4U–W

- * 1990 *Devonaria gevini* n.sp. Racheboeuf, pp. 310–312, pl. 1, figs 6–15 [*ubi syn.*].
- v. 2013 Devonaria sp. Halamski and Baliński, p. 253, fig. 4G–K, M.

Material: A single shell, embedded in limestone, MB.B.9432.1 probably from locality 151B.

Description: Shell interpreted as concavo-convex (ventral valve convex, dorsal valve concealed by matrix), semielliptic in outline, 11.4 mm long, ca. 15 mm wide, and ca. 3.8 mm thick. Ventral umbo relatively thick, interarea concave, approximately orthocline; dorsal interarea hypercline. Hinge line wide, equals the maximal shell width; anterior commissure straight. Ornamentation of poorly preserved, straight costae and costellae, about 40 in total, ca. 3–4 per mm.

Remarks: *Devonaria* sp. *sensu* Halamski and Baliński (2013), from Aferdou el-Mrakib in southern Maïder, has distinctly finer ornamentation than *D. minuta* (>30 costellae in a specimen 10.1 mm wide; Halamski and Baliński, 2013, fig. 4G–K) and should be referred to *D. gevini* Racheboeuf, 1990, already reported from Maïder on the basis of specimens collected by H. Hollard in Jbel Zireg (TM 306; Racheboeuf, 1990). Two species of *Devonaria* co-occur thus in the Maïder.

It may be mentioned that the paper containing the original description of *D. gevini* is dated "1990" both on the first page and on the cover, but the official record of the legal deposit is given on the inside of the cover as "4^e Trimestre 1992", so 1992 should be assumed as the year of printing.



Fig. 4. Middle Devonian Productida (Chonetidina and Strophalosiidina) from northern Maïder. **A–E.** Anopliidae gen. et sp. indet. Articulated shell MB.B.9458.13 dorsal, ventral, lateral, posterior, and anterior views. Locality 89. **F–T.** *Devonaria minuta* (Goldfuss *in* von Buch, 1837). F–J, K–O, P–T. Articulated shells MB.B.9492.1, 9492.2, 9492.3 in dorsal, ventral, lateral, posterior, and anterior views. Locality 151B. **U–W.** *Devonaria gevini* Racheboeuf, 1992. Ventral valve MB.B.9432.1 partly embedded in limestone in lateral, ventral, and posterior views. Locality 151B. **X.** *Devonalosia*? sp. Fragmentarily preserved shell attached onto the dorsal valve of *Eressella coronata* Halamski and Baliński, nom. nov. MB.B.9422.3 (compare Halamski and Baliński, 2018, fig. 2E). Locality 151B.



◊D. minuta, Issoumour ■D. minuta, Eifel ▲D. gevini, Issoumour

Fig. 5. Devonaria minuta (Goldfuss in von Buch, 1837 and Devonaria gevini Racheboeuf, 1992. Scatter diagrams of shell width to shell length (**A**) and of number of ventral costae to shell width (**B**). In both cases, two samples for the former species are given, one studied herein and another from the type area (Eifel).

Distribution: Probably the lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise Tindouf Basin, south flank near Mabbès and Oued Thala (Gevin, 1960; Racheboeuf, 1990); Maïder: Aferdou el Mrakib (Halamski and Baliński, 2013), Jbel Zireg (Racheboeuf, 1990); Zemmour Noir: Aguelt Oudiate el Khyam (Sougy, 1964). If confirmed, this would be the first report of this species from the Eifelian, in all cases where sufficient stratigraphic precision is available, its stratigraphic position being lower Givetian (Racheboeuf, 1990).

Material: One articulated shell MB.B.9458.13 from locality 89.

Description: The single articulated shell is rounded subtriangular in outline, strongly concavo-convex, 4.3 mm long, 6.2 mm wide, and 2.3 mm thick. Ventral interarea concave, approximately orthocline; dorsal interarea linear, hypercline. A single hinge spine base situated ca. 1 mm from the umbo observed. Ornamentation capillate with about seventy capillae in total, ca. 10 per mm in median region, ca. 8 per mm near postero-lateral extremities.

Remarks: This brachiopod is included in the family Anopliidae on account of its minute size, concavo-convex shell, and capillate ornamentation. Scarcity of material precludes a more detailed taxonomic evaluation. **Distribution:** Probably Taboumakhlouf Formation, dm2.1 or dm2.2, upper Eifelian.

Suborder Productidina Waagen, 1883 Family Sentosiidae McKellar, 1970 Genus *Caucasiproductus* Lazarev, 1987

Type species: *Caucasiproductus gretschischnikovae* Lazarev, 1987; Transcaucasia, Givetian.

Other species: see Lazarev (1987, p. 50); moreover: *Caucasiproductus dissimilis* Oleneva, 1998, Mongolian Altai, Frasnian; *Caucasiproductus sardarensis* Legrand-Blain, 1999, eastern Iran, Frasnian; *?Caucasiproductus* sp. sensu Mottequin (2008), Ardennes, Frasnian.

Caucasiproductus? sp. Fig. 6P–II

Material: Nine articulated shells, MB.B.9395.1–8 from locality 93A, 9448 from locality 93C.

Description: Shell up to 26.5 mm in width, concavo-convex, transverse, semi-oval to rounded subrectangular in outline, width-to-length ratio usually about 1.2, but in the largest specimen about 1.4. Hinge line attains ca. three-quarters of the shell width; anterior commissure straight; ginglymus in both valves (Fig. 6P, U); cicatrix none. Ventral valve most strongly curved in umbonal region. Ornamentation of low, subcontinuous rugae and densely and evenly arranged spines on both valves, distance between a pair of adjacent spines about 1 mm; indistinct ribbing present on the dorsal valve in the immediate proximity of the anterior commissure. Interior not studied.

Remarks: These shells are assigned to *Caucasiproductus* on account on their concavo-convex shape and the dense spinosity of both valves (compare Lazarev, 1990, pl. 1, fig. 8; pl. 24, fig. 8). Diagnostic, internal characters are not available in the material studied, so open nomenclature is used.

The original description of *C. gretschischnikovae* is laconic. The measurements are not provided, the shells are described as "isometric" (Lazarev, 1987, p. 50). Oleneva (1998) stated that *C. dissimilis* (width-to-length ratio 1.1–1.2) has wider shells than those of the type species. However, the figured specimens of *C. gretschischnikovae* (Lazarev, 1987, pl. 5, figs 11, 12) are clearly transverse. Given the inadequate descriptions, the present authors are unable to identify the described material at the species level. **Distribution:** Probably the upper part of the Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian.

Family Monticuliferidae Muir-Wood and Cooper, 1960 Genus *Poloniproductus* Biernat and Lazarev, 1988

Type species: *Productella varians* Biernat, 1966; Skały, Holy Cross Mts., upper Eifelian.



Fig. 6. Middle Devonian Productidina from northern Maïder. A–E. *Devonoproductus* cf. *minimus* Crickmay, 1963. Specimen MB.B.9472. Locality 93A. F–O. *Poloniproductus varians* (Biernat, 1966). F–J, K–O. Specimens 9387.1, 9387.2. Locality 151C. P–II. *Caucasiproductus*? sp. P–T, U–Y, Z–DD, EE–II. Specimens 9395.1, 9395.2, 93953, 9448. Locality 93A. All specimens are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.

- 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. 2013 *Poloniproductus varians* (Biernat, 1966) Halamski and Baliński, p. 253, fig. 5 [*ubi syn.*].
 - 2019 *Poloniproductus varians* (Biernat 1966) Mergl and Budil, pp. 96–97, pl. 1, figs 6–11.

Material: MB.B.9387.1–25 from locality 151C, 9420.1–12 from locality 153.

Description: see Halamski and Baliński (2013).

Remarks: The material described is included in *Poloniproductus* on account of the irregular dorsal rugae and the absence of ribs (see detailed comparison in Halamski and Baliński, 2013, p. 253). In some individuals, ventral spines are less densely distributed than in *P. varians* from the Holy Cross Mts. and the southern Maïder; given the variability, this is estimated to be of no taxonomic significance. In comparison with conspecific sample from southern Maïder, the shells described herein are slightly smaller (maximum recorded width 21.1 mm, as opposed to 27.2 mm).

Spinulicosta spinulicosta sensu Brousmiche (1975) from the Givetian–Frasnian of the eastern Anti-Atlas (Hollard's locality TM584) has distinct, concentric lamellae on the ventral valve.

Distribution: Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise, Holy Cross Mts., Maïder, Middle Devonian, possibly Koněprusy area, Eifelian– Givetian boundary (juvenile shells, Mergl and Budil, 2019).

Genus Devonoproductus Stainbrook, 1943

Type species: *Productella walcotti* Fenton and Fenton, 1924; Iowa, Frasnian (see Muir-Wood and Cooper, 1960, pp. 177–179).

Devonoproductus cf. minimus Crickmay, 1963 Fig. 6A–E

cf. 1963 Devonoproductus minimus sp. n. – Crickmay, pp. 25–26, pl. 5, figs 17–20, pl. 14, figs 6–9, 21–22.

Material: Two articulated shells MB.B.9471, 9472 probably from locality 93A.

Description: Shell concavo-convex, weakly auriculate, weakly transverse, 10.0–11.4 mm long, 11.0–12.4 mm wide, and 5.3–5.9 mm thick, widest at hinge line; anterior commissure rectimarginate. Dorsal valve semi-elliptic in outline. Umbo of the ventral valve very thick, overhanging the interarea.

Ornamentation on both valves different. Dorsal valve entirely covered by fine, dense, regular, continuous, sublamellose growth lines, about 3 per mm. Ventral valve entirely covered by fine radial costae and costellae, usually about (3–)4–5 per mm; spine bases not visible due to wear of the shell surface.

Interior not studied.

Remarks: The two specimens from Jbel Issoumour are similar to *D. minimus* from the Givetian Presqu'ile Formation

of southern shore of Great Slave Lake, Canada, in shape and ornamentation of the ventral valve. The ornamentation of the dorsal valve is coarser in *D. minimus* (1–2 per mm). Given the limited material of both samples available for comparison, open nomenclature is used.

Distribution: Probably upper part of the Taboumakhlouf Formation to lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian.

Suborder Strophalosiidina Schuchert, 1913a Family Araksalosiidae Lazarev, 1989 Genus *Devonalosia* Muir-Wood and Cooper, 1960

Type species: *Devonalosia wrightorum* Muir-Wood and Cooper, 1960; Ontario, Canada, Arkona Shale, Givetian.

Devonalosia? sp. Fig. 4X

Material: Two fragmentarily preserved ventral valves, attached onto the dorsal valve of *Eressella coronata* Halamski and Baliński, nom. nov. MB.B.9422.3 (compare Halamski and Baliński, 2018a, fig. 2E) from outcrop 151B and onto the dorsal valve of *Septalaria gracilis* (Gürich, 1896) MB.B.9425.1 from outcrop 93A. (illustrated on Fig. 17U–Y)

Description: The better (illustrated) specimen is a ventral valve, of which only the external contour is preserved in the form of a rim; the outline is hexagonal and the valve is about 1.5 mm wide and long; four spines and two further spine bases are preserved, spines are straight and the longest one is about 1.5 mm long.

Remarks: This fragmentary specimen is tentatively included in *Devonalosia* on account of the valve being attached and possessing relatively thick spines. A similar brachiopod from the Devonian of the Holy Cross Mountains was described and illustrated by Halamski (2009, pl. 7, fig. 21). A single specimen of *Devonalosia*? sp. *A* was described by García-Alcalde (2012) from the middle Givetian of the Cantabrian Mountains (N Spain).

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. 7A–G

- * 1820 Terebratulites umbraculum von Schlotheim, p. 256
- 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 1–30, pl. 16, figs 3, 4, 8, 9, 13, 17, 18 [*ubi syn.*].
- v. 2013 *Xystrostrophia umbraculum* (von Schlotheim, 1820) Halamski and Baliński, pp. 253–257, fig. 6B, E–K.

Material: Articulated shells MB.B.193B3 [loc. ?], 9454 [locality 89], 9386 [loc. 93A?]; ventral valves MB.B.9416 [loc. 93], 9462 [loc. VEsn1]; dorsal valve MB.B.9430 [loc. 151?]. **Description:** See Halamski and Baliński (2013).

Remarks: Shells from northern Maïder may reach even slightly larger sizes than those from southern Maïder (maximum recorded width in Jbel Issoumour is 65 mm, compared to 63 mm in Halamski and Baliński, 2013). The width-to-length ratios of the small sample described herein range from 1.11 to 1.33, as compared to 1.21–1.50 in southern Maïder (Halamski and Baliński, 2013, p. 257), 1.08–1.44 in the Holy Cross Moutains, and 1.16–1.59 in the Eifel (Halamski, 2009, p. 70).

Distribution: Probably the Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.1–dm3, upper Eifelian to Givetian. Otherwise, Eifel, Holy Cross Mts., Maïder, Zemmour Noir, Adrar, Turkestan, Burma (Halamski and Baliński 2013 and references therein); Middle Devonian. Most reports of *X. umbraculum* are from the Eifelian stage. Halamski (2009, p. 70) and Halamski and Baliński (2013, p. 257) discussed the reports from the Givetian stage. In view of the report from the Gerolstein Syncline in the Eifel by Winter (1965, p. 295), the presence of *X. umbraculum* in the Givetian should be considered as undoubted.

Class Rhynchonellata Williams *et al.*, 1996 Order Protorthida Schuchert and Cooper, 1931 Family Skenidiidae Kozłowski, 1929

Genus *Skenidioides* Schuchert and Cooper, 1931 **Type species:** *Skenidioides billingsi* Schuchert and Cooper, 1931; near the Ottawa River, Québec, Canada; Black River Formation, Sandbian, upper Ordovician.

Species assigned: see Boucot *et al.* (1966, pp. 364–365), Havlíček (1977, p. 101), Halamski (2009, p. 72), and Baliński *et al.* (2016, p. 138).

Skenidioides polonicus (Gürich, 1896) Figs 8, 9

- 1896 *Skenidium polonicum* Gürich, pp. 237–238, pl. 10, figs 3, 14.
 - 1961a *Skenidium* aff. *polonicum* Drot, pp. 61–63, pl. 1, fig. 6.
 - 1975 Skenidioides aff. polonicum (Guerich, 1896) Drot, p. 50, pl. 1, fig. 24.
- ? 1985 Skenidium polonicum Gürich Zhang, p. 247, pl. 1, fig. 3.

С



Fig. *1. Xystostrophia umbraculum* (von Schlotheim, 1820). **A, B.** Ventral valve MB.B.9430.1 in external and internal views. Locality 151B. **C, D.** Incomplete ventral valve MB.B.9430.2: general view and enlargement of the muscle area. Locality 151B. **E.** Articulated shell MB.B.9386 overgrown by epizoans in dorsal view [compare Fig. 3CC]. Locality 93A. **F–I.** Ventral valve MB.B.9462: general views (ventral, I; ventrolateral, G) and enlargements of the muscle area (ventral view, H; ventrolateral view, F). Locality VEsn1.

- v. 2009 *Skenidioides polonicus* (Gürich 1896) Halamski, pp. 72–74, text-fig. 10, pl. 10, figs 1–38, pl. 12, fig. 30 [*ubi syn*.].
- ? 2010 Skenidium cf. polonicum Gürich, 1896 García-Alcalde, pp. 50–51, fig. 6.

Material: Sixteen articulated shells, two dorsal and one ventral valve, MB.B.9458.1–12 from locality 89, 9477.2 from locality 93A, 9481.1–5 from locality 151C.

Description: Shell markedly ventribiconvex, nearly hemipyramidal [thickness-to-length ratio (0.51-)0.54-0.59(-0.68); N = 11], transverse [width-to-length ratio (1.08-)1.14-1.22(-1.54); N = 11] (Fig. 9A), up to 6.9 mm in width, typically about 5–6 mm wide, 3.5–5 mm long, and 2–3 mm thick [see Appendix 1 for measurements]. Hinge line slightly less than or equal to the maximal shell width, postero-lateral extremities mucronate, anterior commissure ventrally deflected. Dorsal valve weakly convex, medially shallowly grooved; interarea relatively low, anacline. Ventral valve rounded triangular in anterior view; interarea high, apsacline, in a single case catacline [dorsal valve length-to-total length ratio (0.78-)0.85-0.91(-1.00)]; delthyrium occupying about one sixth to one fifth of the interarea width.

Ornamentation of rounded costae and costellae, the latter appearing by both bifurcation and intercalation. Total number of costae and costellae on each valve (18-)19-23(-26) [N = 12]; the median pair of dorsal costellae lower than the adjacent ones, appearing at about ¹/₄ of the valve length. Ratio of the number of dorsal ribs to width (3.2-)3.6-4.1(-5.2) [N = 12] (Fig. 9B).

Dorsal valve: Cardinal process continuous with the median septum. Sockets rather short and shallow. Brachiophores diverging at 70° – 100° . Septalium shorter than half the valve length, supported by the median septum equalling about 0.75–0.85 of the valve length. Shallow anterior adductor scars antero-laterally adjacent to the septalium. Ventral interior not studied.

Remarks: The single specimen described by Drot (1961a, 1975) from Foum Medfa, south of Assa in the Drâa valley as *Skenidium* aff. *polonicum* falls within the variability of *S. polonicus*.

The material from the Asturias, identified by García-Alcalde (2010) as Skenidium cf. polonicum, consists of two samples, a single shell from the middle Givetian and three specimens, along with a few fragments, from the Frasnian. All the figured material is from the Frasnian. The shell DPO 127849 (García-Alcalde, 2010, fig. 6c) has about 25 dorsal costae and costellae, a width-to-length ratio of about 1.3 but is less than 3 mm wide. Adult shells of Skenidioides polonicus from the type region have a similar shape but are about 5.5-6 mm wide (Halamski, 2009, pl. 10, figs 24-38), whereas juvenile shells, about 3 mm wide, have width-to-length ratios about 1.6-2.0 (Halamski, 2009, pl. 10, figs 2-6, 8-12, 14–18). It is thus likely that the shells DPO 127849–127850 represent another species, the adults of which are much smaller than those of S. polonicus. The internal mould DPO 127851 is difficult to interpret; its stratigraphic position might indicate the lower Frasnian species Skenidioides cretus Halamski in Baliński et al. (2016).

Zhang (1985) described *Skenidium polonicum* from the Eifelian of Inner Mongolia (Zhusilenghaierhan Region), but these shells are 5–7 mm long and have 14–18 costae and costellae on the dorsal valve, which is out of the variability of *S. polonicus* from the type region. Langestrassen (2008, p. 429) reported *Skenidioides* cf. *polonicus* from the Ohle Formation (middle Eifelian) of the Sauerland.

Distribution: The Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.1–dm3, upper Eifelian to Givetian. Otherwise, Holy Cross Mts., upper Eifelian to lower–middle Givetian (Halamski, 2009); Drâa valley, upper Givetian (Drot, 1961a).

Order Orthida Schuchert and Cooper, 1932 Family Rhipidomellidae Schuchert, 1913b 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. 10

v* 1851 O[rthis] prisca nob. – Schnur, p. 13

v. 2013 Aulacella prisca (Schnur, 1851) – Halamski and Baliński, pp. 257–258, fig. 7A–M [ubi syn.].

Material: Thirty-eight articulated shells, MB.B.9421 probably from locality 153, 9443.1–37 probably from locality 151C.

Description: See Halamski and Baliński (2013).

Remarks: The material studied consists mostly of small shells (usually about 10 mm wide) and of a single shell 21.4 mm wide; in view of the intraspecific variability (Biernat, 1959; Halamski, 2009), they are interpreted as conspecific.

Distribution: Probably the lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise, Eifel, Holy Cross Mts., Maïder, Zemmour Noir, Burma (Sougy, 1964; Halamski, 2009; Halamski and Baliński, 2013); Eifelian and Givetian.

Family Dalmanellidae Schuchert and Cooper, 1931 Genus *Costisorthis* Havlíček, 1974

Type species: Orthis occlusa Barrande, 1848; Bohemia, Pragian.

Costisorthis canalicula (Schnur, 1851) Fig. 11A–J, 12D–F

- v* 1851 O[rthis] canalicula, n. sp. Schnur, p. 13
- 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.*].
- vp 2013 *Tyersella canalicula* (Schnur, 1851) Halamski and Baliński, p. 258, fig. 7N–CC, FF–NN, non fig. 7DD–EE [= *T. tetragona* (Roemer, 1844)].





Fig. 9. *Skenidioides polonicus* (Gürich, 1896). Scatter diagrams of shell width to shell length for the sample studied and a sample from the type area near Świętomarz in the Holy Cross Mts. (A) and of number of dorsal ribs to shell width for the studied sample (B).



Fig. 10. *Aulacella prisca* (Schnur, 1851). A–E, F–J. Articulated shells MB.B.9443.1, 9443.2 in dorsal, ventral, lateral, posterior, and anterior views. Locality 151C. K–O. Exceptionally large-sized, articulated shell MB.B.9421 in dorsal, posterior, lateral, anterior, and ventral views. Locality 153.

Fig. 8. Middle Devonian Protorthida from northern Maïder. A–W. *Skenidioides polonicus* (Gürich, 1896). A–E, F–J, K–O, P–T. Articulated shells MB.B.9458.1–4 in dorsal, ventral, lateral, posterior, and anterior views. U, X. Dorsal interior MB.B.9458.5 in ventral (U) and oblique ventrolateral (X) views. V, W, Z. Dorsal interior MB.B.9458.6 in ventral (V), oblique ventrolateral (Z) and anteroventral (W) views. Y. The widest articulated shell MB.B.9458.7 in dorsal view. Locality 89.

Material: Twelve articulated shells MB.B.9394.1–10 from locality 151B, 9443.38 probably from locality 151C, 9499.1 from locality 153, two dorsal valves MB.B.9499.2–3 from locality 153 and one ventral valve, MB.B.9465 from locality VEsn1.

Description: Shell subrectangular to subtrapezoidal in outline, up to ca. 23 mm in width [see Appendix 1 for measurements], but in the material studied mostly 13–15 mm wide, transverse [width-to-length ratio (1.04-)1.10-1.14(-1.18), N = 11], moderately thick [thickness-to-length ratio (0.50-) 0.54–0.61(–0.64), N = 10]. Maximum width slightly anteriorly to midlength. Dorsal valve with a median sulcus; interarea moderately high, apsacline. Anterior commissure rectimarginate to weakly unisulcate. Ornamentation multicostellate, costae and costellae 1–3 per mm at anterior margin.

Ventral interior (Fig. 12F): Teeth stout; didutor scars deep, narrow, diverging at about 20°, their length less than $\frac{1}{3}$ of that of the valve; adductor scars in admedial regions of diductor scars, their length approximately equalling $\frac{1}{4}$ of the valve length; muscle scars divided by wide, well-developed median myophragm, especially well marked anteriorly.

Dorsal interior (Fig. 12D, E): Cardinal process relatively thick, bilobed, partly filling the notothyrium. Sockets deep. Brachiophores stout, diverging at about 90°. Muscle area length equalling half of the valve length, quadripartite, divided by a thick and high median ridge narrowing anteriorly. Anterior adductors longer than the posterior ones.

Remarks: Orthis canalicula Schnur, 1851 was included into *Isorthis* by Biernat (1959), into *Tyersella* by Walmsley and Boucot (1975) and Halamski (2009), and into *Costisorthis* by Havlíček (1977) under the misspelt name "Orthis canaliculata Schnur, 1853" (see also García-Alcalde, 2018). Orthis canaliculata Lindström, 1861 is a Silurian species, belonging to *Levenea* Schuchert and Cooper, 1931 (Schuchert and Cooper, 1931, 1932; Walmsley and Boucot, 1975; Rubel, 2011).

Tyersella canalicula sensu Halamski and Baliński (2013) corresponds partly to the genuine *C. canalicula* (material from Aferdou and Madène el Mrakib in southern Maïder) and partly to *T. tetragona* (Sougy's material from Aguelt Oudiate el Khyam in the Zemmour Noir).

Distribution: Most of the material is certainly from the lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian, and the remaining specimens are probably from the same level. Otherwise, Holy Cross Mts., Rhenish Slate Mts. (incl. Eifel), Maïder; Middle Devonian, probably Eifelian (see Halamski, 2009 for details).

Genus Tyersella Philip, 1962

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

Tyersella tetragona (Roemer, 1844) Figs 11K–DD, 12A–C

 * 1844 Orthis testudinaria Dalm. var. tetragona m. – Roemer, p. 76, pl. 5, fig. 6.

- v. 1964 Isorthis sp. e. g. tetragona (Roemer, 1844) Sougy, p. 437, pl. 36, fig. 7.
 - 1975 Isorthis (Tyersella) tetragona (Roemer, 1844) – Walmsley and Boucot, pp. 61–62, 101, pl. 2, figs 1–4 [ubi syn.].
 - 1981 Isorthis (Tyersella) tetragona (Roemer, 1844) Mélou, pp. 76–77, pl. 4, figs 1–10.
- vp 2013 Tyersella canalicula (Schnur, 1851) Halamski and Baliński, p. 258, fig. 7DD–EE, non fig. 7N– CC, FF–NN [= Costisorthis canalicula (Schnur, 1851)].

Material: Eighty-two articulated shells 9403.1-82 and three dorsal valves MB.B.9403.83-85 from locality 93A. A single, articulated shell MB.B.9394.16 from locality 151B. Description: Shell rounded subrectangular in outline, up to 24.1 mm in width, but usually about 16-20 mm wide [see Appendix 1 for measurements], transverse [width-to-length ratio (1.06-)1.13-1.19(-1.32), N = 30], relatively weakly convex [thickness-to-length ratio (0.40–)0.44–0.50(–0.56), N = 30]. Hinge line width 0.57–0.74 of the maximum width, the latter about shell midlength. Dorsal valve with a flat-bottomed, U-shaped, or rounded V-shaped sulcus, its width at anterior commissure being 0.19-0.26 of that of the valve; interarea sublinear, orthocline to weakly apsacline. Ventral valve (broadly) triangular in anterior view; umbo fine; interarea rather low, apsacline. Anterior commissure unisulcate to incipiently paraplicate. Ornamentation multicostellate, costae and costellae 2-4 per mm at anterior margin.

Dorsal interior: Cardinal process blade-like with two lateral lobes triangular in outline, partly filling the notothyrium. Sockets deep. Brachiophores stout, diverging at about 110°. Length of muscle area equalling half of the valve length, quadripartite, divided by a broad median ridge, bearing sometimes a sharp, low keel on its top. Septum sometimes extending anteriorly further than the muscle area and accompanied by closely situated traces of vascula media (Fig. 12B, C). Anterior adductors shorter than the posterior ones. Ventral interior unknown.

Remarks: *Tyersella tetragona* may be distinguished from *Costisorthis canalicula* co-occurring in the study area (but mostly not in the same outcrops) by being less thick (median of the thickness-to-length ratio 0.47, compared to 0.58 in the latter), having a smaller ventral umbonal region and the maximum width about shell midlength, as well as in finer ornamentation. *Levenea polonica* (Sobolew, 1909) from the lower–middle Givetian of the Holy Cross Mts. has a very similar ornamentation but differs in its larger size and more rounded outline (Halamski, 2009).

Distribution: Most of the material is from the upper part of the Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian, thus apparently younger than *Costisorthis canalicula*. A single specimen of *T. tetragona* was found in the same strata as *C. canalicula*, namely the lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Other occurrences are from the Rhenish Slate Mts., upper Eifelian (May, 1984); Pyrenees, basal Eifelian (Valenzuela Ríos and Carls, 1994); Asturias, Emsian SPR (Soto and García Alcalde, 1976, p. 91; García-Alcalde, 1995, p. 21); Central Iberian Zone, Emsian



Fig. 11. Middle Devonian dalmanellid orthides from northern Maïder, exterior views. **A–J.** *Costisorthis canalicula* (Schnur, 1851). A–E, F–J. Specimens MB.B.9394.1 from locality 151B and 9499.1. from locality 153. **K–DD.** *Tyersella tetragona* (Roemer, 1844). K–O, P–T, U–Y, Z–DD. Specimens MB.B.9403.1, 9403.2, 9403.3, 9403.4. Locality 93A. All specimens are articulated shells in dorsal, ventral, later-al, posterior, and anterior views.



Fig. 12. Middle Devonian dalmanellid orthides from northern Maïder, interior views. **A–C.** *Tyersella tetragona* (Roemer, 1844). A, B, C. Dorsal valves MB.B.9403.31–33. Locality 151B. **D–F.** *Costisorthis canalicula* (Schnur, 1851). D, E. Dorsal valves MB.B.9443.3 from locality 151C and 9499.2 from locality 153. F. Ventral valve MB.B.9465. Locality VEsn1.

(Pardo Alonso and García-Alcalde, 1996); Maïder, Middle Devonian; Drâa valley, Emsian (Jansen *et al.*, 2004); Zemmour Noir, Emsian and Eifelian? (Sougy, 1964); Brittany (Reun ar C'Hrank, Gahard): upper Emsian (Mélou, 1981). Reported from Ashton, Harberton parish (Devon, England; Davidson, 1882: 51; pl. 3, fig. 17).

Genus Phragmophora Cooper, 1955

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

Phragmophora schnuri Cooper, 1955 Fig. 13A–O

- 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 26–47 [ubi syn.].
- v. 2013 *Phragmophora schnuri* Cooper, 1955 Halamski and Baliński, p. 258, fig. 700–XX.
- ? 2020 *Phragmophora* cf. *schnuri* Cooper, 1955–García-Alcalde and El Hassani, p. 20–21, fig. 9.1–9.8.

Material: Seventeen articulated shells MB.B.9433.1–5 probably from locality 151B, 9440.1–12 from locality 151C.

Description: See Cooper (1955), Halamski (2009), and Halamski and Baliński (2013).

Remarks: Representatives of *Phragmophora schnuri* from northern Maïder are larger (maximum recorded width 16.3 mm) than those from southern Maïder (maximum recorded width 11 mm; Halamski and Baliński, 2013), so the costae and costellae are coarser in the former sample (typically 2–3 per mm at anterior margin, 3–5 per mm in the latter), but the identity of both samples of this relatively little variable species cannot be doubted. Shells reported from the lower to middle Givetian of the ODE section in the Jbel Ou Driss by García-Alcalde and Hassani (2020) as *Phragmophora* cf. *schnuri* have maximum width situated more posteriorly and it is uncertain whether thay represent the same species as the sample described here.

Shells of this species in the material studied are in general rather well preserved, but all bear a tiny hole (about 1 mm long and 0.5 mm wide) in the ventral umbonal region (Fig. 13B, G, M), most often not directly on the beak, but at a small distance from it. The consistent position of this hole in all shells studied indicates correspondence to some constructional weakness, resulting in similar fractures appearing probably *post mortem* (during transportation?). It might be hypothesised that the holes, closely adjacent to the pedicle foramen situated in the apical region of the delthyrium, result from breaking down of a more fragile part of the shell, when it is no longer supported by the pedicle after the latter has rotted. Interpreting such holes as predation traces seems less plausible.

Distribution: Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise, Holy Cross Mts., Eifel, and southern Maïder; Middle Devonian, in all cases, where sufficient precision is available, Eifelian (Cooper, 1955; Halamski, 2009; Halamski and Baliński, 2013).

Family Mystrophoridae Schuchert and Cooper, 1931 Genus *Biernatium* Havlíček, 1975

Type species: *Skenidium fallax* Gürich, 1896; Śniadka, bed 10 sensu Gürich (1896) [Sierżawskie Doły between Świętomarz and Sierżawy = Szerzawy], northern region of the Holy Cross Mountains, Poland; Sierżawy beds sensu Gürich (1896) [middle or upper part of the Skały beds], middle? Givetian, Middle Devonian.

Remarks: The literature on Biernatium contains several successive misunderstandings. The type material of Skenidium fallax, the type species of Biernatium, is from the (middle?) Givetian of the Świętomarz-Śniadka section (Gürich, 1896; Halamski, 2009). On the basis of cruralium features, Havlíček (1977) correctly interpreted the material from the upper Eifelian of Skały, described by Biernat (1959) under Kayserella lepida, as Biernatium. García-Alcalde (2018) was right in pointing out that the Świętomarz and Skały samples subsumed by Havlíček (1977) and Halamski (2009) under Biernatium fallax represent different species, but wrong in assuming that B. fallax from Moravia (Havlíček, 1977) is conspecific with the genuine *B. fallax* from Swietomarz as illustrated by Gürich (1896) and Halamski (2009). As shown by Baliński (in Baliński et al., 2016, p. 142), the Moravian form differs from *B. fallax* in a much longer cruralium. The taxonomy of the Middle Devonian Kayserellidae and Mystrophoridae from the Holy Cross Mountains and Moravia is summarised in Table 1 which supplements and corrects a similar table given by Halamski (2009, tab. 5). The conclusion about the absence of the Eifel species Kayserella lepida in the Holy Cross Mountains (Halamski, 2009, p. 86) remains valid.

Biernatium sucoi García-Alcalde, 2018 Fig. 13P–DD

* 2018 Biernatium sucoi nov. sp. – García-Alcalde, pp. 71–77, figs 12–15.

Material: Thirteen articulated shells MB.B.9468.2, 9470.1–4, both samples from locality 151C, 9495.1–3 probably from locality 151B, 9489.1–3 from locality 151B.

Description: Shell shield-shaped, markedly ventribiconvex, up to 12.2 mm in width, typically ca. 10–11 mm wide, weakly transverse [width-to-length ratio (1.03-)1.08-1.15(-1.22)], weakly convex (thickness-to-length ratio 0.44-0.57). Hinge line wide, attaining ca. 77–81% of the shell width; postero-lateral extremities obtuse; maximum width about midlength or slightly posteriorly. Dorsal valve weakly convex in umbonal and lateral regions, either flat or with a broad sulcus medially; width of the sulcus, if present, at anterior commissure about $\frac{1}{3}-\frac{1}{2}$ of that of the shell. Dorsal umbo fine, beak suberect to incurved, interarea anacline to orthocline. Ventral valve broadly triangular in anterior view; beak straight to suberect, interarea apsacline, rather high, delthyrium rather narrow, with an apical plate. Anterior commissure broadly unisulcate, tongue rounded (Fig. 13T, Y) to subtrapezoidal (Fig. 13DD). Ornamentation costellate. Interior not studied.

Remarks: *Biernatium sucoi*, described from the Givetian Portilla Formation of the Asturias, is characterised by weakly transverse shells with a moderately high ventral interarea, similar to the material of the present authors. The shells described here are, however, larger (maximum reported width of *B. sucoi* is 8.15 mm). *Biernatium fallax* (Gürich, 1896) from the lower Givetian of the Świętomarz-Śniadka section in the Holy Cross Mts. (see the lectotype illustrated by Halamski 2009, pl. 15, fig. 32; incorrectly termed holotype) has a larger, ventral umbo and the ventral beak is erect to incurved (Halamski 2009, pl. 15, figs 18, 24, 29). Lower Frasnian *B. minus* Baliński in Baliński *et al.* (2016) is smaller and more transverse.

Distribution: Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian; otherwise Portilla Formation, Givetian, Asturias, Spain (García-Alcalde, 2018).

Family Schizophoriidae Schuchert and LeVene, 1929 Genus Schizophoria King, 1850

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

Remarks: Recent revisions of *Schizophoria* (Pocock, 1966; Jansen, 2001; Stigall, 2005; Halamski, 2009) are based largely on anatomical characters studied on internal moulds and isolated valves, so it is difficult to use the results for material consisting solely of articulated shells, like that described herein.

Schizophoria schnuri Struve, 1965 Fig. 14A–J

- * 1965 *Schizophoria schnuri* n. sp. Struve, pp. 202–208, pl. 19, fig. 4, pl. 20, pl. 21.
- v. 2013 Schizophoria schnuri Struve, 1965 Halamski and Baliński, pp. 258–259, fig. 8A–E, H–L.

Material: Forty-one articulated shells, MB.B.9399.1–3 probably from locality 151B, 9402.1–38 from locality 151B.

Description: Shell rounded rectangular in outline, transverse, dorsibiconvex, up to 37.2 mm in width, width-to-length ratio (1.00-)1.15-1.18(-1.26). Maximum width at midlength or slightly anteriorly. Anterior commissure uniplicate, tongue usually occupying about one third of the shell width. Ornamentation multicostellate, costae and costellae 10-11(-14) per 5 mm at anterior margin. Interior not studied.

Remarks: The sample MB.B.9402 is composed of smaller individuals (usually 20–25 mm wide) mostly similar to the (chrono?)subspecies *S. schnuri biscissa* Struve, 1965 (width-to-length ratio mostly 1.1–1.2). Shells from the sample MB.B.9399 are larger (over 30 mm wide) and more diverse in shape (width-to-length ratio 1.00–1.26),

Locality	Gürich (1896)	Sobolew (1904, 1909)	Biernat (1959)	Havlíček (1977)	Halamski (2009)	García- Alcalde (2018)	This work
Skały	Kayserella lepidiformis	Kayserella lepidiformis	Phragmophora schnuri	_	Phragmophora schnuri	_	Phragmophora schnuri
Skały and Śniadka	Kayserella lepidiformis	Kayserella lepidiformis	_	_	partly Phr. schnuri, partly Aulacella prisca	_	as in Halamski (2009)
Śniadka	Skenidium fallax	Skenidium fallax	_	Biernatium fallax	Biernatium fallax	Biernatium fallax	Biernatium fallax
Moravia	_	_	_	Biernatium fallax	Biernatium fallax	Biernatium fallax	<i>Biernatium</i> ? sp. nov. B
Skały	_	Skenidium fallax	Kayserella lepida	Biernatium fallax	Biernatium fallax	<i>Biernatium</i> sp.	<i>Biernatium</i> sp. nov. A

Comparison of taxonomic treatments of *Biernatium*, *Kayserella*, and *Phragmophora* by Gürich (1896), Sobolew (1094, 1909), Biernat (1959), Havlíček (1977), Halamski (2009), García-Alcalde (2018), and the present authors.

some similar to *S. schnuri biscissa* (Fig. 14A–E) and some to *S. schnuri blankenheimensis* Struve, 1965 (Fig. 14F–J). Similar intergrading of morphotypes was described by Halamski (2012). Given the limited control on stratigraphic position of samples, a more detailed subdivision of *S. schnuri* is not attempted here.

Distribution: Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise, Eifel, Ardennes, Holy Cross Mts., Moravia, Maïder, Burma (Halamski, 2012).

Schizophoria sp. 1 Fig. 14K–R

Material: Six mostly poorly preserved articulated shells, MB.B.9385.1 from locality 93A, MB.B.9398.1–5 probably from locality 151B.

Description: Shell rounded rectangular to subcircular in outline, approximately as long as wide to distinctly transverse (width-to-length ratio about 1.0-1.3), dorsibiconvex, up to ca. 50 mm in width (estimated; maximum recorded width 42.2 mm). Maximum width about midlength. Anterior commissure uniplicate, tongue usually occupying about more than half of the shell width. Ornamentation of radial costae and costellae, some of them distinctly stronger than others, 8-14 per 5 mm at anterior margin. Interior not studied.

Remarks: The samples MB.B.9385 and MB.B.9398 are more heterogenous and less well preserved than MB.B.9399 and MB.B.9402, described above as *S. schnuri*. The former contains both shells differing from *S. schnuri*

in being less transverse, having a wider tongue, and unequal ribs (MB.B.9385.1, MB.B.9398.1–5) and shells more similar to *S. schnuri* (MB.B.9385.2–12, MB.B.9398.6–8). Given the limited stratigraphic control on these samples, the specimens of different morphology are described here separately as *Schizophoria* sp. 1, but no further analysis is attempted.

Ornamentation consisting of unequal costellae was noted in the Emsian *S. interstrialis* Biernat, 1954 (Halamski, 2009, p. 352, fig. 2U), but this character is not constant. The shells sampled together with *Schizophoria* sp. 1, but more similar to *S. schnuri*, thus also could belong to the former taxon; here they are referred to as *Schizophoria* sp. **Distribution:** Probably Taboumakhlouf Formation to lower part of the Bou Dib Formation, dm2.1–dm3, upper Eifelian to Givetian.

Order Pentamerida Schuchert and Cooper, 1931 Family Gypidulidae Schuchert and LeVene, 1929 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. 15A–E

 * 1856 Pentamerus galeatus var. multiplicata – Roemer, p. 352, pl. 2, fig. 9.



Fig. 13. Middle Devonian orthides *Phragmophora* and *Biernatium* from northern Maïder. **A–O.** *Phragmophora schnuri* Cooper, 1955. A–E, F–J, K–O. Specimens MB.B.9440.3, 9440.2, 9440.1. Locality 151C. **P–DD.** *Biernatium sucoi* García-Alcalde, 2018. P–T, U–Y, Z–DD. Specimens MB.B.9495.1–2 from locality 151C and MB.B.9468.2 from locality 151B. All specimens are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.



Fig. 14. Middle Devonian orthide *Schizophoria* from northern Maïder. **A–J.** *Schizophoria schnuri* Struve, 1965. A–E. F–J. Articulated shells MB.B.9402.1, 9399.1 in dorsal, ventral, lateral, anterior, and posterior views. Locality 151B. **K–R.** *Schizophoria* sp. 1. K–O. Articulated shell MB.B.9385.1 in dorsal, ventral, lateral, posterior, and anterior views. Locality 93A. P–R. Incomplete shell MB.B.9398.1 in dorsal, lateral, and posterior views. Locality 151B.

v. 2013 *Glyptogypa multiplicata* (Roemer, 1856) – Halamski and Baliński, p. 261, fig. 9F–R [*ubi syn*.].

Material: A single articulated shell MB.B.9397, probably from locality 151B.

Description: See Halamski and Baliński (2013)

Remarks: The single available shell is 29.3 mm wide and 30.2 mm long, slightly asymmetric. It falls within the variability limits of *G. multiplicata* described from southern Maïder (Halamski and Baliński, 2013).

Distribution: Probably lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise, Rhenish Slate Mts. (type locality: Schirzheim near Prüm, Eifel; Eifelian), Holy Cross Mts., Maïder; Middle Devonian.

Genus Devonogypa Havlíček, 1951

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

Devonogypa spinulosa (Havlíček, 1951) Fig. 15F–Q

- * 1951 Gypidula (Devonogypa) spinulosa nov. nom. Havlíček, pp. 5–7, pl. 2, figs 2, 3, 5.
- v. 2013 *Devonogypa spinulosa* (Havlíček, 1951) Halamski and Baliński, p. 263, fig. 12 A–M.

Material: Five articulated shells MB.B.9412 from locality 151B, 9413 probably from locality 151B, 9442.1–3 probably from locality 151C.

Description: Macromorphology and interior, see Halamski and Baliński (2013).

Ornamentation consisting of microscopic spines, subcylindrical in shape, rounded at the extremity. Ca. 5 mm from the umbo, spines are up to 0.03 mm in diameter; ca. 15 mm from the umbo they reach ca. 0.1 mm in diameter; this corresponds to the definitive spine size observed up to the anterior commissure. The spines are distributed irregularly, although sometimes short alignments parallel to growth lines may be observed (Fig. 15P, Q). About the centre of the ventral valve, there are ca. 10-12 spines per mm². Remarks: Representatives of D. spinulosa from northern Maïder are smaller (length up to 28 mm) than those described from southern Maïder (length up to 67 mm; Halamski and Baliński, 2013). Othwerwise, the shape and the ornamentation are very similar. Marked size differences between single samples of this species are not unusual; for example, the sample from Błonia Sierżawskie, near Świetomarz in the Holy Cross Mts. (Halamski, 2004a), is intermediate in size between those fom southern and northern Maïder.

Size differences between representatives of the same brachiopod species from different populations or samples are generally ascribed to ecological conditions. Pakhnevich (2009, p. 1461) listed several, possible reasons for dwarfism in brachiopods: hard substrate deficit, heightened hydrodynamics, roiling of water, sedimentation, abundance of phytoplankton, activity of hydrothermal springs, and settlements of barnacles (Curry, 1982; Zezina, 1985, 2002; Pakhnevich, 2000). Zezina (2008) used the general term "marginal conditions". Peck and Harper (2010, p. 2211) noted that size is probably dictated by competition, predation, and resource availability. Barnacles are rather unlikely, as they are unknown before the Carboniferous (Newman et al., 1969; Chan et al., 2021), but otherwise even a hypothetical reason why the representatives of Devonogypa spinulosa from Jbel Issoumour are small-sized cannot be given as information on the palaeoenvironment is lacking, the sample having not been collected bed-by-bed.

The particularly well-preserved ornamentation of the specimen MB.B.9442.1 allowed a more detailed description. **Distribution:** Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise, Holy Cross Mts., Moravia, Maïder, Zemmour Noir; Middle Devonian (Havlíček, 1951; Halamski and Baliński, 2013).

Order Rhynchonellida Kuhn, 1949 Family Hebetoechiidae Havlíček, 1960 Genus *Kransia* Westbroek, 1967

Type species: *Terebratula parallelepipeda* Bronn, 1837 sensu Westbroek, 1967; Eifel, Middle Devonian.

Remarks: Halamski *et al.* (2020) subdivided *Kransia* Westbroek, 1967 into *K.* (*Kransia*) and *K.* (*Fatimaerhynchia*) according to the absence or presence of a septalium, respectively.

Kransia (K.) parallelepipeda (Bronn, 1834 in 1835–37) Fig. 16F–J

- v*p 1834 Terebratula Wilsoni [parallelepipeda] Bronn, p. 73.
- v. 2013 Kransia parallelepipeda (Bronn, 1834 in 1834– 38 ["1835–37"]) – Halamski and Baliński, p. 265, fig. 13K–II.

Material: Seventy-two articulated shells, MB.B.9390.1–71 from locality 93A, 9490 from locality 151B.

Remarks: The description of this material will be given separately in a common treatment of the European and African Hebetoechiidae.

Distribution: Taboumakhlouf Formation, certainly lower part, dm2.1, upper Eifelian; probably also upper part thereof and lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian.

> Kransia (K.) subcordiformis (Schnur, 1853) Fig. 16K–O

- 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.].
- v. 2013 *Kransia subcordiformis* (Schnur, 1853) -Halamski and Baliński, p. 265, fig. 13JJ–NN.

Material: Forty-six articulated shells, MB.B.9389.1–44 from locality 152A, 9449.1, 9450, both from locality 93C. **Remarks:** The description of this material will be given separately in a common treatment of the European and African Hebetoechiidae.

Distribution: Probably the upper part of the Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian.

Kransia (Fatimaerhynchia) signata (Schnur, 1851)

- v* 1851 *T*[*erebratula*] *Wahlenbergii* Gldf., Var. *signata* nob. Schnur, pp. 5–6.
- v. 2020 Kransia (Fatimaerhynchia) signata (Schnur, 1851)
 Halamski et al., pp. 61–65, figs 7, 8C, 9, 10.

Material: Fifty-six articulated shells MB.B.9392.1–55 from locality 93A, 9447.1 from locality 93C.

Description and discussion: See Halamski *et al.* (2020). **Distribution:**Probably the upper part of the Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian. Otherwise, Eifel, Holy Cross Mts.; Middle Devonian (see Halamski *et al.*, 2020, p. 65 for details).

Genus Beckmannia Mohanti, 1972

Type species: *Uncinulus minor beckmanni* Schmidt, 1951; Letmathe, Rhenish Slate Mountains; Middle Devonian (lower Givetian?).

Beckmannia beckmanni (Schmidt, 1951) Fig. 16A–E



Fig. 15. Middle Devonian Pentamerida from northern Maïder. **A–E.** *Glyptogypa multiplicata* (Roemer, 1856). Articulated shell MB.B.9397 in dorsal, ventral, lateral, posterior, and anterior views. Locality 151B. **F–Q.** *Devonogypa spinulosa* (Havliček, 1951). F–J. Articulated shell MB.B.9412 in dorsal, ventral, lateral, posterior, and anterior views. Locality 151B. K–Q. Articulated shell MB.B.9442.1 in dorsal, ventral, lateral, posterior views with enlargements of dorsal (P) and ventral (Q) microornamentations. Locality 151C.



Fig. 16. Middle Devonian Rhynchonellida from northern Maïder. A–E. *Beckmannia beckmanni* (Schmidt, 1951). Specimen MB.B.9444.1. Locality 93A. F–J. *Kransia parallelepipeda*, Specimen MB.B.9390.1. Locality 93A. K–O. *Kransia subcordiformis*. Specimen MB.B.9450. Locality 93C. P–T. *Glosshypothyridina procuboides*. Specimens MB.B.9487.1. Locality 151B. All specimens are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.

- * 1951 Uncinulus minor beckmanni n. ssp. Schmidt, pp. 89–90, pl. 1, figs 1–3.
- v 2013 *Beckmannia beckmanni* (Schmidt, 1951) Halamski and Baliński, p. 267, fig. 13A–J.

Material: Forty-nine articulated shells MB.B.9444.1–49 from locality 89.

Remarks: This small-sized brachiopod has a poorly defined sulcus and fold, features of *Beckmannia* Mohanti, 1972 (Mohanti, 1972, p. 167), but possesses a thick dorsal median

septum, a feature of *Kransia* Westbroek, 1967. Its treatment is reported to a further study, together with remaining species of the family Hebetoechiidae.

Genus Lebanzuella García-Alcalde, 1999

Type species: *Uncinulus lebanzus* Binnekamp, 1965; Lebanza, Cantabrian Mountains, Spain; Lebanza Fm., lower Siegenian (Pragian), Lower Devonian. Lebanzuella? issoumourensis issoumourensis (Drot, 1971)

- * 1971 Kransia (?) issoumourensis n. sp. Drot, pp. 72– 76, text-pl. 2, pl. 1, figs 4, 5.
- v. 2020 Lebanzuella? issoumourensis issoumourensis (Drot, 1971) — Halamski et al., pp. 55–58, figs 2A–T, 3, 5.

Material: MB.B. 9393.1–250 from locality 93A.

Description and discussion: See Halamski *et al.* (2020). **Distribution:** The material of *Lebanzuella? issoumourensis issoumourensis* comes probably from the upper part of the Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian (Jbel Issoumour). *Lebanzuella? issoumourensis smarensis* Halamski, Baliński and Jansen, 2020 was described from the Givetian of Western Sahara.

> Family Uncinulidae Rzhonsnitskaya, 1956 Genus *Eressella* Halamski and Baliński, 2018a

Type species: *Eressella coronata* Halamski and Baliński, nomen novum pro *Rhynchonella coronata* Kayser, 1871 non *Rhynchonella coronata* Moore, 1861; Eifel Mts., Prüm Syncline; Eifelian, probably middle or upper Eifelian in the traditional sense, thus approximately *australis* to *ensensis* zones (Ziegler and Klapper, 1985, fig. 5).

Eressella coronata Halamski and Baliński, nom. nov.

- v* 1871 Rhynchonella coronata n. sp. Kayser, pp. 512–513, pl. 9: 5.
- v. 2013 *Kransia? coronata* (Kayser, 1871) Halamski and Baliński, p. 265, fig. 1300–SS.
- v. 2018a *Eressella coronata* (Kayser, 1871) Halamski and Baliński, pp. 25–29, figs 2–5 [*ubi syn.*].
- non 2020 *Eressella*? aff. *coronata* (Kayser, 1871) García-Alcalde and El Hassani, pp. 22–23, fig. 10.1–10.8.

Material: Eleven articulated shells, MB.B.9422.1–4 and 9422.6–12 from locality 151B.

Description: See Halamski and Baliński (2018a, p. 25–29, figs 2–5).

Remarks: Halamski and Baliński (2018a, p. 21) commented on the homonymy of *Rhynchonella coronata* Kayser, 1871 and *R. coronata* Moore, 1861 and concluded that "the stability of nomenclature is best served by continuing the use of Kayser's specific name". However, as pointed out by Professor R.T. Becker (pers. comm., 2018), the name *R. coronata* Kayser, 1871 is invalid (a permanently invalid name; Art. 57 of the ICZN) and requires replacement. As a substitute name, the present authors propose *Eressella coronata* Halamski and Baliński, nom. nov. (type material, locality, and stratum as for *R. coronata* Kayser, 1871).

Brachiopods reported from the upper part of the Taboumakhlouf Formation (ODE 2–3) in the Jbel Ou Driss (lower to middle Givetian) by García-Alcalde and El Hassani (2020) as *Eressella*? aff. *coronata* either belong to or are closely related to *Parapugnax*? *anisodonta* (Phillips, 1841) (see below). It is thus probable that the provisional

identification of *Uncinulus coronatus* sensu Godefroid *in* Bultynck (1989) is a misidentification (see García-Alcalde and El Hassani 2020, p. 23). As a consequence, the discussion of the stratigraphic distribution of *Eressella coronata* should be modified: there is no confirmed Givetian record of this species (Jbel Ou Driss: material probably misidentified), although its presence in this stage cannot be excluded either (uncertain stratigraphy of the Aferdou material). The occurrence in Jbel Issoumour is dated here to the Eifelian. **Distribution:** Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise southern Maïder, Eifel, Holy Cross Mts.; Middle Devonian, probably mostly Eifelian (see above and Halamski and Baliński, 2018a, pp. 29–31).

Family Hypothyridinidae Rzhonsnitskaya, 1956 Genus *Glosshypothyridina* Rzhonsnitskaya, 1978

Type species: *Rhynchonella procuboides* Kayser, 1871; Eifel, Eifelian.

Glosshypothyridina procuboides (Kayser, 1871) Fig. 16P–T

- v* 1871 Rhynchonella procuboides n. sp. Kayser, pp. 513–514, pl. 9, fig. 3.
- v. 2013 Glosshypothyridina procuboides (Kayser, 1871) – Halamski and Baliński, p. 267, fig. 14F–Y [ubi syn.].

Material: One articulated shell MB.B.9487 from locality 151B.

Description: See Halamski and Baliński (2013).

Remarks: The single available shell is 16.7 mm wide, 13.0 mm long, 12.9 mm thick, and with eight costae on the tongue; it is thus smaller than all the specimens described from southern Maïder by Halamski and Baliński (2013).

Distribution: Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise, Eifel, Holy Cross Mts., southern Maïder; Middle Devonian.

> Family Septalariidae Havlíček, 1960 Genus Septalaria Leidhold, 1928

Type species: *Terebratula ascendens* Steininger, 1853; Eifel; Middle Devonian.

Septalaria gracilis (Gürich, 1896) Fig. 17K–Y, 18

- v* 1896 *Camarophoria gracilis* n. sp. Gürich, pp. 278–279; pl. 7, fig. 3a–g.
- 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.].
- v. 2013 Septalaria gracilis (Gürich, 1896) Halamski and Baliński, pp. 267–269, figs 15, 16K–O, Q–OO [ubi syn.].

Material: Nine articulated shells, MB.B.9425.1–4, 9426.1–5 from locality 93A.

Description: Shell irregularly subpentagonal in outline, transverse (width-to-length ratio 1.06–1.31, mean 1.17, N = 9), maximum width typically slightly anteriorly to midlength, strongly dorsibiconvex, up to 13.9 mm in width, typically about 10–12 mm wide [see Appendix 1 for measurements]. Dorsal valve with a flattened fold appearing at about the mid-length, fold flanks steep. Ventral valve convex in umbonal region, flattened on flanks, with a wide and shallow, flat-bottomed sulcus anteriorly; umbo suberect. Anterior commissure uniplicate, tongue broad, occupying 0.62–0.83 (mean 0.74, N = 9) of the shell width, high, rectangular to weakly trapezoidal.

Ornamentation of rather low, rounded costae, appearing in the posterior half of the shell (the exact location is difficult to discern, owing to aeolian corrasion), separated by narrower furrows, 6-11 (most often 8) on fold, 6-10 (most often 8) on tongue, (6-)8-10(-12) per flank. Interior not studied.

Remarks: The sample from Jbel Issoumour is similar in shape to representatives of *Septalaria*, described as *S. gracilis* (Gürich, 1896), *S. descendens* Schmidt, 1975, and *S. struvei* Schmidt, 1975. It is assigned to the broadly understood *S. gracilis* (see Halamski and Baliński, 2013), although the much smaller size of the shells results in the costation being much finer. The reason why the sample from Jbel Issoumour consists of particularly small-sized shells cannot be proposed even as a hypothesis, as the sample has not been collected bed-by-bed (see above, *Devonogypa spinulosa*, for a more extensive discussion of a similar case). In any case, mere size difference is not considered to be a valid taxonomic discriminator at the species level.

The Eifelian species *S. struvei* seems to differ in realtively coarser costation at the smaller size (see Tab. 2; detailed measurements not available), although this should be checked on a larger amount of material.

Distribution: Probably the upper part of the Taboumakhlouf Formation to lower part of the Bou Dib Formation,

dm2.2–dm3, upper Eifelian to Givetian. Otherwise, Eifel, Holy Cross Mts. (North), and southern Maïder; Middle Devonian.

Family Pugnacidae Rzhonsnitskaya, 1956 Genus Parapugnax Schmidt, 1964

Type species: *Pugnax pugnus brecciae* Schmidt, 1941b; Langenaubach near Haiger; Iberg limestone, Frasnian.

Remarks: There has been some hesitation among researchers about the gender of the genus names *Pugnax* and *Parapugnax*. *Pugnax* is masculine, as stated clearly in the first description (Hall and Clarke 1893, p. 81/829), although it has been sometimes erroneously treated as feminine (e.g., "*Pugnax acuminata*", Maillieux, 1940, p. 12; "*Pugnax anisodonta*", Hodalevič and Brejvel', 1972, p. 119). *Parapugnax* did not receive detailed treatment and usage was inconsistent (masculine: Mizens, 2009; feminine: Rozman, 1960; Wang, 1985). It is proposed here to fix the gender as masculine, like that of *Pugnax*.

> Parapugnax denticulatus (Maurer, 1885) Figs 17Z–II, 19

- * 1885 *Rhynchonella anisodonta* Phill. var. *denticulata* n. – Maurer, pp. 205–206, pl. 8, fig. 32.
 - 1966 Pugnax cf. anisodonta (Phillips, 1841) Biernat,
 p. 109, pl. 17, fig. 13, pl. 19, fig. 30.

Material: Eight articulated shells, some of which incomplete, MB.B.9439.1–8 from locality VEsn2.

Description: Shell irregularly pentagonal in outline, with maximum width situated anteriorly, at about $\frac{2}{3}$ of the length, transverse (width to length ratio 1.35–1.55, N = 5), strongly dorsibiconvex, up to 21.9 mm in width, typically about 20 mm wide. Ventral valve moderately convex in umbonal region, flattened to slightly concave on flanks, with a wide

Table 2

Comparison of selected biometric characteristics of *Septalaria gracilis* from the Holy Cross Mts., Sauerland, and Maïder north and south and of *S. struvei* from the Eifel. Data for the Holy Cross Mts. either after Gürich (1896) or calculated after photographs in Sobolew (1909); for Sauerland and Maïder south after Halamski and Baliński (2013); for Eifel after Schmidt (1975).

Taxon		S. struvei			
Character	Holy Cross Mts.	Sauerland	Maïder south	Maïder north	Eifel
Width [mm]	14.4 (11–19)	19.5 (17.4–20.7)	24.3 (19.8–27.3)	11.4 (9.4–13.9)	12.3 (10–14.5)
Width-to-length ratio	1.15 (1.04–1.36)	1.25 (1.13–1.38)	1.34 (1.21–1.43)	1.17 1.06–1.31	1.06
Costae on tongue	3.6 [(2–)4]	4.9 (2–7)	8.2 (7–11)	8.3 (6–10)	3–6
Costae / shell width	0.27 (0.18–0.31)	0.25 (0.11–0.34)	0.34 (0.26–0.40)	0.74 (0.65–0.96)	?
Costae / tongue width	0.48 (0.33–0.51)	0.52 (0.42–0.65)	0.65 (0.55–0.82)	1.00 (0.63–1.37)	?
Number of specimens	5/8	8	8	9	?





Fig. 18. Septalaria gracilis (Gürich, 1896). Scatter diagrams of shell width to shell length (**A**), of number of dorsal costae to shell width (**B**), and of number of dorsal costae to tongue width (**C**). Four samples are shown, that studied here (Issoumour), as well as those from southern Maïder (Aferdou), Holy Cross Mts., and Rhenish Slate Mts. Data for the three latter samples after Halamski and Baliński (2013).

U-shaped sulcus anteriorly. Dorsal valve strongly convex (thickness-to-length ratio 0.72–1.17). Anterior commissure uniplicate; tongue high, subtrapezoidal, broad, occupying 0.64–0.75 of the shell width. Ornamentation of high, strong, acute costae; those on the fold and in the sulcus appearing quite closely to the umbonal region, always less than 5 mm from the beak; those on flanks slightly later, but always in the posterior half of the shell; costae 5–6 on the fold, 4–5 in the sulcus, 3–5 per flank; separated by V-shaped furrows of approximately the same width as the costae.



Fig. 19. Transverse serial sections of *Parapugnax denticulatus* (Maurer, 1885) through the shell MB.B.9439.3 from locality VEsn2. Distances measured in millimetres from the tip of the ventral umbo.

Ventral interior: Dental plates strong and distinct, slightly divergent ventrally in the most posterior region, becoming progressively convergent anteriorly, situated close to the posterolateral walls of the valve; dental cavities small; teeth massive.

Dorsal interior: Hinge plates subhorizontal, massive, posteriorly buried in thick shell deposits, divided, not supported by median septum; sockets deep; low, widely triangular median ridge (myophragm) present; crura triangular in cross-section, gently curved ventrally.

Remarks: These brachiopods are classified within the genus *Parapugnax* on account of their pugnacoid shell form, strong dental plates, divided hinge plates, and absence of septalium. They are tentatively identified as a poorly known Givetian species *P. denticulatus* (Maurer, 1885), described from Waldgirmes (Hessen), on account of similarly strong ornamentation (costae developed on entire shell) and similar shape (width-to-length ratio 1.29–1.45; thickness-to-length ratio 0.79–0.82; Maurer, 1885).

Pugnax anisodontus (Phillips, 1841) from the Middle Devonian of England has costae developed only in the anterior half of the shell (Phillips, 1841, pl. 34, fig. 154; Davidson, 1865, pl. 12, fig. 12). The mutual relationships of *P. denticulatus* and *P. anisodontus* are unclear. One might wonder whether these two taxa, differing solely in costation strength, do not represent morphotypes of a single variable species; their co-occurrence at Waldgirmes could be an argument in favour of lumping them, as suggested by Höflinger and Jung (2020). Solving this problem does not appear feasible at present, as stratigraphic details or the variability of the type samples of either taxon are unknown. *P. denticulatus* and *P. anisodontus* provisorily were distinguished thus, although their inclusion within a single biological species is probable.

Fig. 17. Middle Devonian Rhynchonellida from northern Maïder. A–E. *Isopoma*? sp. Specimen MB.B.9478. Locality 93A. F–J. Rhynchonellida fam., gen. et sp. indet. Specimen MB.B.9424. Locality 93A. K–Y. *Septalaria gracilis* (Gürich, 1896). Specimens MB.B.9425.2, 9426.1, 9425.1. Locality 93A. Z–II. *Parapugnax denticulatus* (Maurer, 1885). Specimens MB.B.9439.1, 9439.2. Locality VEsn2. All specimens are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.

Pugnax cf. anisodonta sensu Biernat (1966) from the upper Eifelian of Skały has costae covering the entire shell, so, if the above-mentioned convention is to be followed, it is described better as Parapugnax denticulatus. Shells of Pugnax denticulatus, reported from the upper Eifelian? (Ahbach Fm.) of the Eifel and from the Givetian of Sauerland by Höflinger and Jung (2020, p. 146), have costae developed only in the anterior region of the shell, so, with the same reservations as given above, they might be described better as Parapugnax anisodontus. The same applies to Parapugnax? cf. skalensis sensu Halamski and Baliński (2013) from the Middle Devonian of southern Maïder (the epithet skalensis was applied erroneously on the basis of mislabelled material from the Holy Cross Mts.; Nemesa skalensis Biernat, 1966 is a camarotoechioid). P. anisodontus was also reported from the Givetian of the western slope of northern Urals (Hodalevič and Brejvel', 1972, pp. 119-120).

Distribution: The locality VEsn2 is the only one, for which the present authors cannot provide any satisfactory stratigraphic assignment, insofar as it is described solely with reference to clearly false geographic coordinates (see above, Geologic Setting). Otherwise *Pugnax denticulatus* is known from the Givetian of Hessen and from the upper Eifelian of the Holy Cross Mountains (see above).

Family Aseptirhynchiidae Savage, 1996 Genus *Isopoma* Torley, 1934

Type species: *Isopoma brachyptyctum* (Schnur, 1853); Eifel, Eifelian.

Remarks: It should be noted that the original diagnosis of the genus *Isopoma*, given by Torley (1934), is based on Givetian specimens from Sauerland, whereas the type species was described from the Eifelian of the Eifel. The Sauerland material was interpreted as belonging to *I. brachyptyctum* by Torley (1934) and by Mohanti and Brunton (1998) and as representing a different (unnamed) species by Sartenaer and Ebbighausen (2007).

Isopoma was assigned to the family Aseptirhynchiidae Savage, 1996 within the superfamily Pugnacoidea Rzhonsnitskaya, 1956 by Savage*etal*. (2002, p. 1189) and to the separate family Isopomidae Sartenaer and Ebbighausen, 2007, unplaced in any superfamily by Sartenaer and Ebbighausen (2007, p. 43); the former classification is followed here. If the latter family is accepted in the future, its correct name should be Isopomatidae (Greek *poma*, Gen. *pomatos*, lid).

Isopoma? sp. Fig. 17A–E

Material: One articulated shell MB.B.9478 from locality 93A.

Description: The single articulated shell is teardrop-shaped, weakly dorsibiconvex, 7.0 mm long, 7.6 mm wide, and 4.5 mm thick. Ventral umbo rather fine, beak suberect. Dorsal fold and ventral flat-bottomed sulcus weakly developed. Anterior commissure uniplicate, tongue trapezoidal, about 4.5 mm wide. Ornamentation of rounded costae

developed only in immediate proximity to the anterior margin, two on the fold, one in the sulcus, and 2–3 per flank. Interior not studied.

Remarks: This single specimen is tentatively assigned to Isopoma on account of similarity of the form to I. brachyptyctum (see Schmidt, 1941a). It differs from the above-mentioned species in its smaller size (typically 10-11 mm in I. brachyptyctum; Sartenaer and Ebbighausen, 2007) and in having fewer costae [3(-5)] in the fold in *I. brachyptyctum*; Sartenaer and Ebbighausen, 2007]. Isopoma lummatoniense (Davidson, 1865), from the Givetian of Devonshire, is similarly small and has a single costa in the sulcus; the tongue, however, is higher (Mohanti and Brunton, 1998, figs 9-10) and there is a dorsal median furrow, the latter being among reasons for rejecting it from Isopoma (without better assignment) by Sartenaer and Ebbighausen (2007, p. 46-47). Isopoma gryps Schmidt, 1965 from the Eifelian of Greifenstein has a sharply delimited ventral sulcus, beginning at the umbo.

Distribution: probably upper part of the Taboumakhlouf Formation to lower part of the Bou Dib Formation, dm2.2– dm3, upper Eifelian to Givetian.

> Family unknown Rhynchonellida fam., gen. et sp. indet. Fig. 17F–J

Material: A single incomplete articulated shell MB.B.9424 from locality 93A.

Description: The single available shell is rounded irregularly pentagonal in outline, strongly dorsibiconvex, and transverse (length 19.7 mm, preserved width 25.6 mm, estimated total width ca. 27 mm, thickness 15.1 mm); maximum width at about $\frac{2}{3}$ of the shell length. Dorsal valve strongly convex; ventral valve convex in umbonal region, nearly flat on flanks, with a wide, U-shaped sulcus anteriorly. Anterior commissure uniplicate, tongue high, round, ca. 15 mm wide. Shell smooth. Interior unknown.

Remarks: This shell can be identified as that of a rhynchonellide on account of the astrophic shell, hidden interareas, and absence of pedicle foramen. Rhynchonellida fam., gen. et sp. indet. from Aferdou el Mrakib (Halamski and Baliński, 2013, p. 271; fig. 30A–E) might represent juvenile shells of the same species.

Distribution: Probably the upper part of the Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian.

Order Atrypida Rzhonsnitskaya, 1960 Family Atrypidae Gill, 1871 Genus *Atrypa* Dalman, 1828

Type species: *Anomia reticularis* Linnaeus, 1758; Hammarudden, Östergarn parish, Gotland; lower Hemse beds, early Ludlow, Silurian (see Copper, 2004).

Subgenus Atrypa (Planatrypa) Struve, 1966

Type species: *Atrypa* (*Planatrypa*) *collega* Struve, 1966; Eifel; Junkerberg beds, middle Eifelian.

Remarks: According to Copper (2002, p. 1391; 2004, p. 35), in *A.* (*Planatrypa*) frills are "not known to be present" or even "any sign" of them is lacking. However, it should be noted that frills in *A.* (*P.*) collega were reported by Komarov (1997) and in *A.* (*P.*?) confusa by Halamski and Baliński (2013).

Atrypa (Planatrypa?) confusa (Struve, 1992) Figs 20A-P, 21

- v* 1992 Planatrypa confusa n. sp. Struve, pp. 552-554.
- v. 2013 Atrypa (Planatrypa?) confusa (Struve, 1992) Halamski and Baliński, pp. 272–273, figs 19G–JJ, 20 [ubi syn.].

Material: MB.B.9410.1-25 from locality 89.

Description: Shell rounded to shield-shaped in outline, middle-sized for the genus (typically 20–24 mm wide, maximum recorded width 26.6 mm), about as wide as long [width-to-length ratio (0.88–)0.98–1.03(–1.09), N = 15], convexoplane to very strongly dorsibiconvex. Ventral valve weakly convex in umbonal region, otherwise flat; dorsal valve highly arched; thickness-to-length ratio (0.56–)0.60–0.67(–0.92) [N = 15]. Anterior commissure uniplicate, tongue low to high, rounded to subtriangular. Ornamentation of rounded bifurcating ribs, middle-sized (4–6 per 5 mm) in the median region of the valve, much finer in the anterior region (6–8 per 5 mm). Frills sometimes preserved (Fig. 20M).

Ventral interior: Delthyrial area adpressed to the dorsal umbo, without deltidial plates; pedicle callist thick, developed into collar anteriorly; teeth strong with small accessory lobes, tiny dental nuclei observed in posteriormost region of umbo only. Dorsal interior: Hinge plates fairly massive, subhorizontal, posteriorly closely set; cardinal process observed on hinge plates and in narrow cardinal pit; sockets rather shallow; myophragm wide; crural bases small distally expanding into fibrous crura.

Remarks: This species was described on the basis of a limited collection by Struve (1992) and more fully by Halamski and Baliński (2013). For comparison with *Kyrtatrypa*? sp., see below.

Distribution: Probably the Taboumakhlouf Formation, dm2.1 or dm2.2, upper Eifelian. Otherwise, Eifel, southern Maïder, and Zemmour Noir; Middle Devonian (Halamski and Baliński, 2013).

Genus Atryparia Copper, 1966

Type species: *Atrypa (Hyponeatrypa) aureolata* Struve, 1966; Eifel; middle Eifelian.

Atryparia dispersa (Struve, 1966) Figs 24L–U

- * 1966 Atrypa (Hyponeatrypa) dispersa n. sp. Struve, pp. 142–143, text-fig. 11, pl. 16, fig. 10.
- v. 2013 Atryparia dispersa (Struve, 1966) Halamski and Baliński, pp. 273–275, figs 21F–O, 22, 28L [ubi syn.].

Material: Two articulated shells MB.B.9414.1–2 probably from locality 151B.

Description: See Halamski and Baliński (2013).

Remarks: The shells described here are 25–26 mm wide, so rather small for the species.

Distribution: Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise, Eifel, Transcaucasia, southern Maïder; Middle Devonian (Struve, 1966; Komarov, 1997). Erroneously reported from the Ardennes by Godefroid (1970; identification corrected to *A. instita* by Godefroid, 1995; earlier identification inadvertently repeated by Hubert *et al.*, 2007).

Genus Kyrtatrypa Struve, 1966

Type species: *Atrypa* (*Kyrtatrypa*) *culminigera* Struve, 1966; Eifel, Eifelian.

Kyrtatrypa? sp. Figs 20Q, 22, 23, 24V–Z, BB

Material: MB.B.9400.1–3 probably from locality 151B, 9404.1–13 probably from locality 93A.

Description: Shell shield-shaped in outline, relatively largesized (typically 26–30 mm wide, maximum recorded width 34.1 mm), weakly but invariably transverse [width-to-length ratio (1.02–)1.03–1.11(–1.15); N = 14], convexoplane or very strongly dorsibiconvex. Ventral valve usually convex in posterior region, flattened laterally and anteriorly; dorsal valve regularly and strongly convex; thickness-to-length ratio (0.51–)0.56–0.62(–0.67) [N = 14]. Anterior commissure uniplicate, tongue moderately low to moderately high, rounded, more seldom narrowly subtrapezoidal (Fig. 22O). Ornamentation of rounded bifurcating ribs, of similar size in median and anterior regions of the shell, (5–)6–7 per 5 mm at anterior margin, 6–8(–9) per 5 mm at 10 mm from the umbo (all rib counts made on the ventral valve). Frills frequently preserved (Fig. 20Q).

Ventral interior: Delthyrial area adpressed to the dorsal umbo, without deltidial plates; pedicle cavity filled with thick pedicle callist developed into collar; teeth strong with accessory lobes and minute dental nuclei. Dorsal interior: hinge plates fairly widely separated, sockets deep; crural bases high giving arise to feathered crura laterally adpressed to the lateral valve walls; low myophragm dividing adductor scars extends for about posterior one-sixth of the shell length.

Remarks: The assignment of these brachiopods into a genus is an intricate matter. According to Copper (2002), *Kyrtatrypa* differs from *Atrypa* (*Planatrypa*) in biconvex shells and the presence of frills. These shells are convexoplane and have frills.

Kyrtatrypa? sp. and *Atrypa confusa* can be distinguished by their ribbing: the ribs in *Kyrtatrypa*? sp. are finer but are of similar size in median and anterior regions of the valves (Fig. 20Q), whereas in *A.* (*P*?) *confusa* they are thicker in the median region of the valves and distinctly finer through bifurcation in the anterior region (Fig. 20P). Moreover, *Kyrtatrypa*? sp. has larger, but somewhat flatter shells [mean thickness-to-length ratio 0.60, compared to 0.67 in *A.* (*P*?) *confusa*]. *Atrypa* (*P.*) *gibbera* (Struve, 1992) from



Fig. 20. Middle Devonian Atrypida from northern Maïder. **A–Q.** *Atrypa confusa* (Struve, 1992). A–E, Q. Articulated shell MB.B.9410.3 in dorsal, ventral, lateral, posterior, and anterior views and enlargement of the ventral valve showing ornamentation (Q). Locality 89. F–J, K–O. Articulated shells MB.B.9410.2, 9410.1 in dorsal, ventral, lateral, posterior, and anterior views. P. Partial enlargement of the ventral valve of the articulated shell MB.B.9410.5 showing ornamentation and frills. Locality 89. **R.** *Kyrtatrypa*? sp. Enlargement of the ventral valve MB.B.9404.3 showing ornamentation and frills (compare Fig. 22V). Locality 93A.

→


Fig. 21. Transverse serial sections of *Atrypa (Planatrypa?) confusa* (Struve, 1992) through the shell MB.B.9410.4 from locality 89. Distances measured in millimetres from the tip of the ventral umbo.





Fig. 23. Transverse serial sections of *Kyrtatrypa*? sp. through the shell MB.B.9404.4 from locality 93A. Distances measured in millimetres from the tip of the ventral umbo.

the middle Eifelian of the Eifel has a more convex ventral valve (Thormann and Weddige, 2001, pl. 2, figs 12–14) and finer ribbing (5–8 ribs per 5 mm).

The specimen MB.B.9400.3 is almost complete, with estimated length about 37 mm, estimated width about 33.5 mm, and thickness 18.0 mm. It is rounded in outline, dorsibiconvex; the ventral beak is fine and incurved; there is no sulcus or fold, the anterior commissure is slightly uniplicate. Ribs 4–5 per 5 mm at anterior margin; growth lines strong, in anterior region with frills. It is interpreted as an extreme morphological variant and tentatively included in *Kyrtatrypa*? sp.

Distribution: Probably the Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.1–dm3, upper Eifelian to Givetian.

Genus Invertina Copper and Chen, 1995

Type species: *Atrypa aspera* var. *sinensis* Kayser, 1883; Yunnan, Givetian?.

Invertina cf. struvei Godefroid, 2000 Fig. 24A–F

- 2000 Invertina struvei n. sp. Godefroid, pp. 269–271, text-figs 2–6, pl. 1, figs 1–8.
- v. 2013 *Invertina* cf. *struvei* Godefroid, 2000 Halamski and Baliński, p. 277, fig. 23A–E.

Material: One flattened and incomplete, articulated shell MB.B.9417 probably from locality 93B.

Description: The single available shell is elliptic in outline, elongate, ventribiconvex, 11.2 mm long, 10.3 mm wide, presumably ca. 4 mm thick (preserved thickness 3.2 mm). Dorsal valve weakly convex in umbonal region, otherwise flattened. Ventral valve triangular in anterior view; umbo poorly preserved. Anterior commissure nearly straight. Ornamentation of rounded ribs, about 22 in total on the dorsal valve, 6–7 per 5 mm at anterior margin; growth lines distinct and dense.

Remarks: The described specimen, like that from southern Maïder described by Halamski and Baliński (2013), is of small size and probably a juvenile, but it seems more than likely that it represents *Invertina struvei*, described from the Givetian (Upper *varcus* Zone) of the northern Maïder (Godefroid, 2000).

Distribution: Probably upper part of the Taboumakhlouf Formation to lower part of the Bou Dib Formation, dm2.2– dm3, upper Eifelian to Givetian. The type locality in

Fig. 24. Middle Devonian Atrypida from northern Maïder. **A–F.** *Invertina* cf. *struvei* Godefroid, 2000. Articulated shell MB.B.9417 in dorsal, ventral, lateral, posterior and anterior views, and enlargement of the ventral ornamentation. Locality 93B. **G–K, AA.** *Desquamatia* cf. *subzonata* Biernat, 1964. Articulated shell MB.B.9438 in dorsal, ventral, lateral, posterior, and anterior views, and enlargement of the ventral ornamentation. Locality 152B. **L–U.** *Atryparia dispersa* (Struve, 1966) L–P, Q–U. Articulated shells MB.B.9414.2, 9414.1 in dorsal, ventral, lateral, posterior, and anterior views. Locality 151B. **V–Z, BB.** *Kyrtatrypa*? sp. Articulated shell MB.B.9400.3 in dorsal, ventral, lateral, posterior, and anterior views, and enlargement of the ventral ornamentation. Locality 151B.



the northern Maïder was dated to the Givetian (see above). The material from southern Maïder was dated to the middle part of the Middle Devonian. This species has not been reported from any other region.

Genus Spinatrypa Stainbrook, 1951

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

Spinatrypa ennigaldinannae Halamski and Baliński new species Figs 25A–T, 26, 27A

v. 2013 Spinatrypa (Spinatrypa) cf. trigonella (Davidson, 1882) – Halamski and Baliński, p. 277, fig. 25K–HH [non Atrypa? trigonella Davidson, 1882, p. 40; pl. 1, fig. 19, 19a, 19b].

Type material: Holotype, articulated shell MB.B.9396.1 (Fig. 25K–O) and thirty topotypic paratypes, articulated shells, MB.B.9396.2–31.

Etymology: In honour of En-Nigaldi-Nanna (6th century B.C.), Babylonian princess, curator of the oldest known museum in the world (see Woolley, 1954).

Dimensions: see Appendix 1.

Diagnosis: Transverse *Spinatrypa*, adult shells typically about 16–18 mm wide and with 19–22 ribs.

Description: Shell similar in outline to a rounded lozenge in adults, shield-shaped in small individuals, transverse [in adult shells invariably, in smaller shells mostly; width-tolength ratio (0.96-)1.05-1.10(-1.19), N = 20], relatively weakly convex, nearly aequibiconvex to markedly dorsibiconvex [thickness-to-length ratio (0.49–)0.56–0.68(–0.76), N = 20], up to 20.2 mm in width, typically about 16–18 mm wide. Ventral umbo fine, beak suberect to incurved; interarea low. Anterior commissure most often uniplicate with a moderately low, rounded or rounded triangular tongue occupying (0.45-)0.54-0.62(-0.77) of the shell width; in single cases tongue altogether absent or high and subtrapezoidal in shape. Dorsal ribs in shells over 15 mm wide (18–)19–22 in total, 3–4.75 (usually 4) per 5 mm at anterior margin, 4.5-6.5 per 5 mm at 5 mm from the umbo. Spines present, although seldom preserved (Fig. 26).

Ventral interior: Delthyrium closed by hollow and conjunct deltidial plates (Fig. 27A, sections at 0.5 and 0.7 mm; Fig. 27B, sections at 1.0 and 1.2 mm); teeth strong with small dental nuclei. Dorsal interior: hinge plates moderately thick, subhorizontal, sockets deeply excavated with well marked outer socket ridges; cardinal process weak, ridged, lining small cardinal pit; median myophragm low, with rather rounded top; crura curved and feathered.

Remarks: In the study of brachiopods from southern Maïder, the present authors described similar brachiopods as Spinatrypa cf. trigonella (Davidson, 1882) on the basis of the unpublished data of Paul Copper (mainly labels placed in various museum collections; see also Copper, 1965a, pp. 237-238; 1965b, p. 360). Atrypa? trigonella Davidson, 1882 was described on the basis of material from Lummaton (holotype: Sedgwick Museum, Cambridge, UK, specimen SM H 4293). Whidborne (1893, p. 118; pl. 13, figs 11–12) commented on the holotype being quite non-representative for the genus and provided a more detailed description. The African material described here cannot be placed under Davidson's species. The main differences are in the general form (the shell is flat in Atrypa? trigonella) and in the form of the umbo (elongate, with a high interarea in Atrypa? trigonella; see Whidborne, 1893). Specimens from the upper Givetian Büchel beds in the Paffrath Syncline illustrated by Copper (1965a, pl. 29, figs 2-4) as Spinatrypa cf. trigonella are more convex and have coarser costation.

The sample discussed is included in *Spinatrypa* on account of the presence of spines (Fig. 26) and internal characteristics. It ranges among the more finely ornamented representatives of the genus. The number of species of *Spinatrypa* is relatively high, so comparison is made here with Middle Devonian taxa, showing a likeness in some way to the sample discussed; evidently different Middle Devonian representatives of the genus are not mentioned, just as pre-Middle Devonian or Frasnian ones.

The most similar species is the lower Eifelian *S. variaspina* Copper, 1964 known from the Nohn beds of the Eifel, which has, however, more costae (22–28) and flatter shells. The lower Eifelian (possibly upper Emsian?) *S. dorsata* Biernat, 1964 from the Grzegorzowice beds of Wydryszów in the Holy Cross Mts. is smaller and longer than wide.

Another notably similar species is Spinatrypa tribulosa Norris in Norris et al., 1992 from the uppermost Williams Island Formation by the Abitibi River, Ontario, Canada (uppermost Givetian or lowermost Frasnian): the shape is similar, but dimensions are smaller (about 9-12 mm wide) and costation denser (about 21-23 ribs in total in figured specimens despite their smaller size; Norris et al., 1992). Spinatrypa hornensis McLaren in McLaren and Norris, 1964 from the upper Givetian Horn Plateau Formation of the District of Mackenzie, Canada, is similar in shape to the sample described here, but larger (maximum recorded width 31 mm) and flatter (thickness-to-length ratio 0.41-0.56; McLaren and Norris, 1964, p. 55). Spinatrypa sinuata (Cleland, 1911) from the Middle Devonian Lake Church Formation of Wisconsin has 20-24 ribs but is much wider and has a stronger fold (Griesemer, 1965). The lower Givetian Spinatrypa coriacea Crickmay, 1960 is larger (the specimen figured by Copper, 1978, pl. 3, figs 3-8 is ca. 29 mm wide). Spinatrypa undulata Copper, 1978 from the Givetian of northern Canada is more transverse and

Fig. 25. Middle Devonian Atrypida from northern Maïder. **A–T.** *Spinatrypa ennigaldinannae* sp. nov. A–E, F–J, K–O, P–T. Specimens MB.B.9396.2, 9396.3 (paratypes), 9396.1 (holotype), 9396.4 (paratype). Locality 151B. U–**NN.** *Spinatrypa globulina* Copper, 1967. U–Y, Z–DD, EE–II, JJ–NN. Specimens MB.B.9398.1, 9398.2, 9398.3, 9398.4. Locality 151B. All specimens are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.





Fig. 26. *Spinatrypa ennigaldinannae* sp. nov. Enlargement of the anterior region of the ventral valve MB.B.9396.6 showing a single preserved spine. Locality 151B.

has rarer and anteriorly obsolescent ribs. The Givetian species *S. andersonensis* (Warren, 1944) is longer than wide (Copper, 1978, pl. 2, figs 11–14; pl. 3, figs 1–2). The poorly known *S. lata* (Warren, 1944) from the Middle Devonian Hume Formation of the District of Mackenzie, Canada, has denser ribbing (McLaren *et al.*, 1962, pl. 8, figs 16–18). *Spinatrypa mosolovica* Ljaschenko, 1958 from the Givetian of the Russian Platform has a strong pair of median ribs (Ljaschenko, 1959, pl. 4, figs 1–7).

Among the dubious species of *Spinatrypa* listed by Copper (1967), *Atrypa squamosa* (Sowerby, 1840) from the Middle Devonian of Plymouth has fewer costae (Sowerby, 1840, pl. 57, fig. 1). *Terebratula insperata* Phillips, 1841 from Coddon Hill seems to have a median fold (Phillips, 1841, p. 83). *Atrypa reticularis* var. *sagittata* Maurer, 1885 from the Givetian of Waldgirmes is much longer than wide (Maurer, 1885, p. 184). *Atrypa aspera* var. *paffrathi* Wehrli, 1931 from the Givetian of Hand in Paffrath Syncline has coarser costae.

Isospinatrypa subspinosa (Lazutkin in Rzhonsnitskaya, 1955) from the Eifelian of Kuzbass has similar ribbing, but the shells are flatter, less dorsibiconvex, and more transverse (Rzhonsnitskaya, 1975, pp. 113–116, pl. 23, figs 1–9; Sapel'nikov and Mizens, 2000, pp. 82–83, pl. 29, figs 1–4; Komarov, 2006, pp. 83–84; pl. 12, figs 13–14). *Isospinatrypa? modica* Tâževa, 1962 from the Eifelian of Bashkiria is similar in size and ribbing pattern, but aequibiconvex (Tâževa, 1962, pp. 76–77; pl. 17, figs 7–9)

It follows that the sample discussed is best described as a new species.

Type locality: Jbel Issoumour, locality 151B (see above, Geologic Setting for details).

Type level: Most probably the lower part of the Taboumakhlouf Formation; Middle Devonian, probably upper Eifelian.

Stratigraphic distribution: Middle part of the Middle Devonian: probably upper Eifelian in Jbel Issoumour, stratigraphic data insufficiently detailed in the other areas.

Deposition of types: MB.

Distribution: Middle Devonian, northern and southern Maïder, Zemmour Noir (Halamski and Baliński, 2013).

Spinatrypa globulina Copper, 1967 Figs 25U–NN, 27B

- * 1967 Spinatrypa globulina n. sp. Copper, pp. 506– 507, pl. 78, figs 11–24.
- v. 2013 *Spinatrypa (Spinatrypa) globulina* Copper, 1967 – Halamski and Baliński, pp. 277–278, fig. 25A–J.

Material: MB.B.9388.1–22 probably from locality 151C.

Description: Shell rounded to weakly shield-shaped in outline, about as wide as long to weakly transverse [width-to-length ratio (0.93-)1.00-1.08(-1.17; N = 16], weakly dorsibiconvex [thickness-to-length ratio (0.52-)0.56-0.66(-0.82)], up to 26 mm in width, typically 20–24 mm wide [see Appendix 1 for measurements]. Ventral umbo fine, beak suberect to weakly incurved. Anterior commissure mostly uniplicate with a very low to low tongue (mostly up to

5 mm high), occupying (0.37-)0.52-0.66(-0.91) of the shell width; more seldom straight. Dorsal ribs usually 14–17 in total, 2(-3) per 5 mm at anterior margin, usually about 4 per 5 mm at 5 mm from the umbo; ventral midrib pair in some case stronger than the remaining ones.

Ventral interior: Delthyrium partly closed by minute hollow and separated deltidial plates; pedicle callist weak; teeth strong, with small accessory lobes and small dental nuclei. Dorsal interior: Hinge plates fairly massive, subhorizontal, partly buried in thick shell deposits; sockets deep; low, widely triangular median ridge or myophragm reaching about a quarter of the shell length, posteriorly dividing adductor scars; crura feathered, laterally oriented.

Remarks: This sample broadly agrees with *Spinatrypa globulina* Copper, 1967 known from the lower Givetian of the Eifel.

Distribution: Eifel, Loogh beds, lower Givetian (Copper, 1967); Jbel Issoumour, lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian.

Genus Desquamatia Alekseeva, 1960

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

Remarks: *Desquamatia subzonata* Biernat, 1964 is the type species of the subgenus *Desquamatia* (*Synatrypa*) Copper, 1966. According to Copper (2002), this subgenus is synonymous with *D*. (*Desquamatia*).

Desquamatia cf. subzonata Biernat, 1964 Fig. 24G–K, AA

cf. 1964 *Desquamatia subzonata* n. sp. – Biernat, pp. 319–322, text-figs 3(3), 8(3), 16, 17, pl. 7, fig. 10, pl. 8, figs 1–7, pl. 9, figs 1–8.

Material: One articulated shell MB.B.9438 from locality 152B.

Description: The single available shell is subcircular in outline, 22.6 mm long and wide, and 13.9 mm thick, dorsibiconvex; maximum width and thickness about shell midlength. Ventral beak suberect. Anterior commissure weakly uniplicate, sulcus rounded, about 11 mm wide and 2 mm



Fig. 27. Transverse serial sections of representatives of *Spinatrypa*. **A.** *Spinatrypa ennigaldinannae* sp. nov., shell MB.B.9396.5 from locality 151B. **B.** *Spinatrypa globulina* Copper, 1967, shell MB.B.9388.5 from locality 151B. Distances measured in millimetres from the tip of the ventral umbo. Greyed areas obscured by recrystallization.

high. Ornamentation of radial ribs, 6–8 per 5 mm at anterior margin; growth lines realtively weak, easily discernible only in the anterior half.

Remarks: This shell does not belong to either of the two species of *Desquamatia*, reported from southern Maïder. It is larger than *D. microzonata* Struve, 1966 (under 15 mm wide) and smaller than *D. deserti* Halamski and Baliński, 2013 (typically over 35 mm wide). It is suggestive of *D. subzonata* Biernat, 1964, described from the upper Eifelian of Skały (see Halamski and Zapalski, 2006), with which it shares a subcircular outline (width subequal to length), size, ornamentation density, and maximum thickness situated about shell mid-length. *D. globosa* (Gürich, 1896) from the Givetian–Frasnian boundary beds of Chęciny (Racki and Baliński, 1981) is larger and has a wider tongue. The scarce material allows tentative identification at best.

Distribution: The Bou Dib Formation, dm3, Givetian. In the type area (Holy Cross Mts.), *Desquamatia subzonata* is known from the upper Eifelian (Biernat, 1964; Halamski

and Zapalski, 2006) and from the lower Givetian (Halamski, 2004a).

Suborder Davidsoniidina Copper, 1996 Family Davidsoniidae King, 1850 Genus *Prodavidsonia* Havlíček, 1956

Type species: *Prodavidsonia dalejensis* Havlíček, 1956; Třebotov Limestone, Eifelian; Holyně, Bohemia. **Remarks:** The present authors follow Copper (2002, p. 1444) in considering *Quasidavidsonia* Havlíček, 1987 as a synonym of *Prodavidsonia* (see García-Alcalde, 2010, p. 53 for a contrary view).

> Prodavidsonia ebbighauseni Halamski and Baliński new species Fig. 28, 29F

2013 Prodavidsonia sp. – Halamski and Baliński, p. 281, fig. 28A–E. **Type material:** Holotype MB.B.9446.1 (Fig. 28K–O) and twenty-nine topotypic paratypes 9446.2–20 (loc. 151C); ten approximately stratotypic paratypes MB.B.9423.1–10 (loc. 151B); two non-stratotypic paratypes 9457.1–2 (loc. 89): in total thirty-two articulated shells, mostly complete.

Etymology: In honour of Volker Ebbighausen who collected the described material (see above, Material).

Dimensions: See Appendix 1.

Diagnosis: *Prodavidsonia* with a nearly flat (very weakly convex) dorsal valve and a convex ventral valve.

Description: Shell subrectangular through subtrapezoidal to semi-elliptic in outline, (10.7-)13.3-15.1(-17.4) mm wide [N = 23 here and for the following numerical data], (8.1–)9.8–11.0(–12.2) mm long, and (1.9–)2.6–3.1(–3.9) mm thick, transverse [width-to-length ratio (1.11-)1.31-1.44(-1.56); mean 1.36], low [thickness-to-length ratio (0.20-)0.25-0.28(-0.37)]. Maximum width usually posteriorly to mid-length of the shell, maximum thickness usually about mid-length of the shell. Dorsal valve approximately flat with a median sulcus; interarea sublinear, anacline. Ventral valve posteriorly weakly carinate, subtriangular in anterior view; interarea apscaline; delthyrium occupying one-seventh to one-sixth of the interarea width, nearly completely sealled by convex deltidial plates. Growth lines strong, otherwise, shell smooth. Cardinal process visible in the delthyrium when deltidial plates are damaged, otherwise interior not studied.

Remarks: This sample is different from all the species of Prodavidsonia (incl. Quasidavidsonia) previously described in having a nearly flat (very weakly convex) dorsal valve and a convex ventral valve. The type species P. dalejensis Havlíček, 1956 from the Eifelian of Bohemia has an almost flat ventral valve and is more transverse [width-to-length ratio 1.59-1.97; Havlíček, 1967, pl. 47, figs 13-17; Johnson and Boucot, 1972, pl. 1, figs 20-22]. Prodavidsonia tenuissima (Barrande, 1879) and P. mediocarinata Havlíček, 1967, both from the Eifelian of Bohemia, as well as P. vicina Havlíček, 1967 from the Eifelian of Moravia have more or less concave ventral valves (Havlíček, 1967, pl. 47, figs 9-11; pl. 49, figs 10-20; Johnson and Boucot, 1972, pl. 1, figs 15-19). Prodavidsonia scalensis (Sobolew, 1904) from the Eifelian and Givetian of the Holy Cross Mountains has a concave dorsal valve and a wider delthyrium (Sobolew, 1904, pl. 7, fig. 13; Halamski, 2004a). Prodavidsonia havliceki García-Alcalde, 2010 from the Givetian of the Palentian Domain has a weakly concave dorsal valve (García-Alcalde, 2010, fig. 8) and is smaller.

Type locality: Jbel Issoumour, locality 151C (see above, Geologic setting for details).

Type level: Most probably the lower part of the Taboumakhlouf Formation; Middle Devonian, probably upper Eifelian.

Stratigraphic distribution: Taboumakhlouf Formation, certainly dm2.1, probably also dm2.2, upper Eifelian. **Deposition of types:** MB.

Distribution: Taboumakhlouf Formation of the Jbel Issoumour.

Genus Davidsonia Bouchard-Chantereaux, 1849

Type species: *Davidsonia verneuillii* Bouchard-Chantereaux, 1849; Eifel, Germany; upper Eifelian, Middle Devonian.

Davidsonia verneuillii Bouchard-Chantereaux, 1849 Fig. 29G, H

- * 1849 *Davidsonia verneuillii* Bouchard-Chantereaux, pp. 92–93, pl. 1, figs 2, 2a.
 - 1996 *Davidsonia verneuillii* Bouchard-Chantereaux, 1849 Copper, pp. 594–596, figs 4, 5.

Material: A single complete shell (MB.B.9411, probably from locality 89) and two ventral valves (MB.B.9401, probably from locality 151B), all three attached to undersides of coralla of *Roseoporella* sp.

Description: Shell transverse, semi-elliptic to trapezoidal in shape, ca. 12–14 mm wide and ca. 7–10 mm long (width-to-length ratio ca. 1.4–1.7), smooth. Dorsal valve weakly convex. Ventral valve cemented to the substrate; interarea apsacline, ca. 3 mm high in a shell ca. 10 mm long, delthyrium completely covered by two deltidial plates contacting along a median seam. Ventral interior: Spiralial grooves deeply incised, three whorls observed; median septum relatively stout, extending for about posterior 2/3 of the shell length; gonadal pits strong. Dorsal interior unknown.

Remarks: The material described is assigned to *D. verneuillii* on account of shells rounded to rounded subquadrate in shape, with ventral median septum not extending for the entire shell length, and strong gonadal pits (see Copper, 1996). The late Givetian *D. septata* Copper, 1996 differs in constantly subquadrate shell and in always possessing a strong median septum. The distinction of these two species seems valid, despite variation stronger than noted by Copper (1996). Early Frasnian *Davidsonia enmerkaris* Halamski in Baliński *et al.*, 2016 and Middle Devonian (upper Eifelian to lower Givetian?) *Rugodavidsonia woodwardiana* (de Koninck, 1855) have costate shells.

Distribution: Probably Taboumakhlouf Formation, dm2.1– dm2.2, upper Eifelian. Otherwise, Eifel, middle Eifelian (Junkerberg Fm.) to early Givetian (Cürten Fm.; Copper, 1996, p. 596); southern Maïder, Middle Devonian; Holy Cross Mountains, Givetian (Baliński and Halamski, unpublished data). Possibly several other regions in Europe, Asia, and North America, Middle Devonian (see Copper, 1996, p. 594).

> 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. 29A–E

* 1840 Orthis Arimaspus Eichw. - von Buch, p. 108, 112.



Fig. 28. *Prodavidsonia ebbighauseni* sp. nov. A–E, F–J, K–O, P–T, U–Y. Articulated shells MB.B.9446.2, 9446.3 (paratypes), 9446.1 (holotype), 9446.4, and 9446.5 (paratypes) in dorsal, ventral, lateral, posterior, and anterior views. Locality 151C.

- v. 2013 *Carinatina arimaspus* (Eichwald in von Buch, 1840) Halamski and Baliński, p. 281, fig. 28F–K.
- ? 2019 Carinatina arimaspus (Eichwald in von Buch, 1840) – Mergl and Budil, p. 98, pl. 2, figs 8, 9, 14.

Material: MB.B.9479 from locality 93A, 9500 from locality 151B.

Description: See Halamski and Baliński (2013).

Remarks: The single available adult shell is 23.9 mm wide and 21.6 long, slightly larger than the maximum size in the sample from southern Maïder. **Distribution:** probably Taboumakhlouf Formation, dm2.1–dm2.2, upper Eifelian. Otherwise, Bohemia, Lower Devonian (Suchomasty Limestone, Emsian; Havlíček and Kukal, 1990) and possibly Eifelian–Givetian boundary (poorly preserved material; Mergl and Budil, 2019); Holy Cross Mts. and southern Maïder, Middle Devonian.

> Suborder Lissatrypidina Copper, 1996 Family Lissatrypidae Twenhofel, 1914 Genus *Peratos* Copper, 1986



Fig. 29. Middle Devonian davidsoniidine Atrypida from northern Maïder. A–E. *Carinatina arimaspus* (Eichwald in von Buch, 1840). Articulated shell MB.B.9500 in dorsal, ventral, lateral, posterior, and anterior views. Locality 151B. F. *Prodavidsonia ebbighauseni* sp. nov. Articulated shell MB.B.9446.6 in dorsal view, showing epibionts. Locality 151C. G, H. *Davidsonia verneuillii* Bouchard-Chantereaux, 1849. G. Articulated shell MB.B.9411 attached to a corallum of *Roseoporella* sp. Locality 89. H. Two ventral valves MB.B.9401 attached to a corallum of *Roseoporella*? sp. Locality 151B.

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

Peratos arrectus Copper, 1986 Figs 30, 31

- * 1986 *Peratos arrectus* n.sp. Copper, pp. 859– 860, text-figs 16, 17, pl. 74, fig. 32–36, pl. 75, fig. 1.
- v. 2013 *Peratos arrectus* Copper, 1986 Halamski and Baliński, p. 283, figs 31A–J, 32.

Material: MB.B. 9435.1–9 probably from locality 151B, 9474 from locality 93A, 9480 from locality 151C.

Description: Shell teardrop-shaped to rounded pentagonal in outline, most often aequibiconvex, in larger specimens weakly longer than wide but beak sometimes lacking in the material studied, typically 11.5–12.5 mm long (recorded maximum length 14.6 mm), 11–12 mm wide, and 5–6.5 mm thick. Ventral umbo elongate, fine; beak suberect. Delthyrium with medially coalescent deltidial plates and an apical foramen. Anterior commissure straight to very weakly uniplicate. Growth lines dense in marginal region.

Internally, shell thick-walled. Ventral valve: Dental plates thin, subparallel, dental cavities distinct. Dorsal valve: Hinge plates delicate, subhorizontal, rather widely separated, low.

Distribution: Taboumakhlouf Formation, dm2.1–dm2.2, upper Eifelian. Otherwise, Eifel, upper Eifelian (Copper, 1986); southern Maïder, Middle Devonian.

Order Athyridida Boucot, Johnson and Staton, 1964 Family Athyrididae Davidson, 1881 Genus *Athyris* M'Coy, 1844



Fig. 30. *Peratos arrectus* Copper, 1986. A–E. Articulated shell MB.B.9435.1 in dorsal, ventral, lateral, posterior, and anterior views. F. Articulated shell MB.B.9435.2 in dorsal view. G. Enlargement of the posterior region of the articulated shell MB.B.9435.3 in dorsal view showing the delthyrium. All from locality 151B.

Type species: *Terebratula concentrica* von Buch, 1834; Eifel, Middle Devonian.

Athyris ex gr. concentrica (von Buch, 1834) Figs 32K–Y, 33

- ex gr. 1834 Terebratula concentrica n. von Buch, pp. 103–104.
- ex gr. 2001 *Athyris concentrica* (Buch, 1834) Grunt, pp. 4–7, text-fig. 5, pl. 1, fig. 1.
- 2013 Athyris ex gr. concentrica (von Buch, 1834) – Halamski and Baliński, pp. 283– 284, fig. 30F–O.

Material: Fifty-nine articulated shells, MB.B.9409.1–35 from locality 93A, 9418.1–8, 9419.1–12, both collections probably from locality 93B, 9441.1–4 from locality 151C.

Description: Shell rounded to rounded pentagonal in outline, usually weakly transverse [width to length ratio (0.97-)1.08-1.21(-1.26); N = 15], aequibiconvex to markedly dorsibiconvex, most often weakly dorsiboconvex, usually 15–19 mm wide, up to 21.2 mm in width. Dorsal valve usually subtriangular in anterior view; sometimes there is an indistinct fold in anterior region, but more often it is hardly discernible. Ventral valve with a shallow sulcus appearing in umbonal region, sublinear posteriorly, broader and U-shaped anteriorly. Ventral beak fine, incurved;



Fig. 31. Transverse serial sections of *Peratos arrectus* Copper, 1986 through the shell MB.B.9435.4 from locality 151B. Distances measured in millimetres from the tip of the ventral umbo.

foramen permesothyrid. Anterior commissure always uniplicate; tongue moderately broad, occupying (0.41-)0.58-0.66(-0.77) of the shell width, rounded subtriangular through subtrapezoidal to subrectangular, rather variable in height, the ratio of the latter to shell thickness being (0.26-)0.36-0.53(-0.66). Growth lines prominent.

Ventral interior: Umbonally thickened with secondary shell material; dental plates short, strong, slightly convergent ventrally, dental cavities subrounded, small; teeth strong; ventral muscle field impressed.



Fig. 32. Devonian Athyridida from northern Maïder. **A–J.** Meristidae gen. et sp. indet. A–E, F–J. Specimens 9437.1, 9437.2. Locality 151A. **K–Y.** *Athyris* ex gr. *concentrica* (von Buch, 1834), K–O, P–T, U–Y. Specimens 9441.1 from locality 151C, 9409.1 from locality 93A, and 9418.1 from locality 93B. All specimens are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.

Dorsal interior: Cardinal plate thick, narrow, slightly convex ventrally, bordered laterally by high inner socket ridges, apically perforate; crural bases quite strong, elevated above cardinal plate; jugum U-shaped, high, jugal stem Y-shaped proximally in cross-section; spiral cones composed of eight laterally directed whorls in the sectioned specimen (Fig. 33, section at 7.6 mm); a low myophragm appears in umbonal cavity and continues to about twothirds of the shell length. **Remarks:** The samples discussed are included in *Athyris* M'Coy, 1844 on the basis of laterally directed spiralia, strong dental plates, and middle-sized, dorsibiconvex, approximately as wide as long to moderately transverse shells with moderately strong, concentric ornamentation and no radial ornamentation.

There is no consensus on the interpretation of *Terebratula concentrica* von Buch, 1834 (Alvarez *et al.*, 1996; Grunt, 2001; Grunt and Weyer, 2002, 2016; Alvarez and Brunton,



Fig. 33. Transverse serial sections of *Athyris* ex gr. *concentrica* (von Buch, 1834) through the shell MB.B.9409.2 from locality 93A. Distances measured in millimetres from the tip of the ventral umbo.

2005; see also Halamski and Baliński, 2019, p. 406). Moreover, the stratigraphic control for the sample discussed is poor, so open nomenclature is used.

The present collection corresponds to *Athyris concentrica* sensu Grunt (2001), insofar as both consist of weakly dorsibiconvex shells of similar size (11.9–21.2 mm wide here; 18.8–25.8 mm wide in Grunt's sample from Junkerberg beds in the Eifel) with the ventral sulcus beginning about the umbo. *Athyris concentrica* sensu Alvarez *et al.* (1996) and *A. ventrosa* sensu Grunt, 2001 also possess a ventral sulcus beginning at the umbo but are smaller (about or less than 15 mm; Alvarez *et al.*, 1996; Grunt, 2001). *Athyris concentrica ventrosa* sensu Alvarez *et al.* (1996) is barely distinguishable from their *A. concentrica* s.s.

Athyris africana Schemm-Gregory, 2014 from the upper Givetian of the southern flank of the Tindouf Basin is usually smaller but might fall within the variability of A. concentrica s.l. Athyris aquilonia Norris in McLaren and Norris, 1964 from the Givetian of northern Canada is more transverse. The Givetian-Frasnian A. howardi Alvarez, Modzalevskaya, and Brime, 2011 from Asturias is ventribiconvex. In Athyris murchisoni Brice, 1988 (Frasnian of the Boulonnais and perhaps of the Ardennes; Brice, 1988; Mottequin, 2008), A. davidsoni (Rigaux, 1872) (Givetian and Frasnian of the Boulonnais; Brice, 1988), and A. oehlerti Rigaux, 1908 (Frasnian of the Boulonnais and of the Ardennes; Brice, 1988; Mottequin, 2008) the sulcus begins at about the mid-length of the ventral valve. The Givetian Athyris kaisini Rigaux, 1908 and the Frasnian A. bayeti Rigaux, 1908, both from the Boulonnais, have two ribs bordering the sulcus. The Eifelian species Athyris krantzi Grunt, 2001 from the Eifel (Junkerberg Fm.) is smaller (maximum width 15.5 mm; Grunt, 2001).

Athyris ex gr. *concentrica* sensu Halamski and Baliński (2013) has a ventral sulcus appearing slightly posteriorly to midlength, but the species is here accepted broadly, pending further revision. *Athyris concentrica* sensu Termier and Termier (1950, p. 91) is clearly heterogeneous.

Distribution: Probably the Taboumakhlouf Formation to the lower part of the Bou Dib Formation dm2.1–dm3, upper Eifelian to Givetian. No consensus exists as to the stratigraphic distribution of *Athyris concentrica*.

Family Meristidae Hall and Clarke, 1893 Meristidae gen. et sp. indet. Fig. 32A–J

Material: Five articulated shells, of which two party decorticated, MB.B.9434.1–2 probably from locality 151B, 9437.1–2 from locality 151A, 9475 from locality 93A.

Description: Shell subpentagonal in outline, width subequal to length, maximum width anteriorly to midlength of the shell, weakly to markedly ventribiconvex, up to 17.5 mm in length. Ventral umbo thick, beak suberect to incurved. Anterior commissure uniplicate, trapezoidal, broad, low to high. Shell smooth with widely spaced growth lines.

Interior, as revealed in the decorticated specimens: well-developed shoe-lifter process present in both valves; dorsal shoe-lifter supported by a long median septum.

Remarks: *Camarium* sp., described by Halamski and Baliński (2013) from southern Maïder, has similar form, but the tongue is usually lower. The presence of a shoe-lifter process in both valves in the shells studied indicates that they may represent *Dicamara*. However, a reliable identification of meristid genera requires serial sections, which

were not done here, owing to the small size of the sample studied and given that most classical taxa in this group lack modern revisions (see more detailed comment by Halamski and Baliński 2013, p. 285), so identification under open nomenclature would be unavoidable, in any case.

Distribution: The Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian.

Family Neoretziidae Dagys, 1972 Genus *Plectospira* Cooper, 1942

Type species: *Terebratula ferita* von Buch, 1834; Eifel; Middle Devonian.

Plectospira ferita (von Buch, 1834) Fig. 34F–J

* 1834 Terebratula ferita von Buch, p. 76, pl. 17, fig. 4.

v. 2013 *Plectospira ferita* (von Buch, 1834) – Halamski and Baliński, p. 287, Fig. 30W–AA [*ubi syn.*].

Material: A single, complete, articulated shell MB.B.9431, probably from locality 151B.

Description: The single available shell is rounded in outline, 5.1 mm long, 4.8 mm wide, and 2.2 mm thick. Ventral beak suberect; foramen mesothyrid, ca. 0.2 mm wide; delthyrium covered by a pair of deltidial plates. Anterior commissure zigzagging. Ornamentation of stout plicae: on the dorsal valve four strong ones (two on each lateral flank), a lower, median one, and two weak postero-lateral ones, thus seven in total; on the ventral valve, four strong plicae, two weaker external ones, and two barely visible postero-lateral ones, thus six or eight in total. Interior not studied.

Remarks: García-Alcalde and El Hassani (2020, pp. 24-25) questioned the correspondence between subsequent reports of the discussed species and the original meaning of Terebratula ferita (von Buch, 1834, p. 76; pl. 2, fig. 37), and, as a consequence, the characteristics of the genus Plectospira. It may be noted here that in the original description, von Buch (1834) gives a detailed account of a shell with a median rib on the ventral valve and a median sinus on the dorsal valve, or, in other words, with an even number of dorsal ribs (10) and an odd number of ventral ribs (9), thus apparently the opposite of Retzia ferita Kayser, 1871 and subsequent authors. This is strengthened by the reference to Terebratula diodonta Dalman, 1828 (now Rhytidorhachis diodonta; Silurian of Gotland) which also has a ventral median rib and a dorsal median furrow (Jin and Caldwell, 1990, pl. 2, figs 1-10). The original figure (von Buch, 1834) shows a brachiopod with a high dorsal fold, bisected by a median furrow and relatively low lateral ribbing.

In the opinion of the present authors, this characterstic species was understood in general correctly by Sandberger and Sandberger (1850–1856) and Schnur (1853), that is, in accordance with von Buch's (1834) description, although sometimes too broadly [incorrectly including *Plectospira longirostris* (Kayser, 1871)]. The apparent discordance in the number of dorsal and ventral ribs between von Buch (1834) and subsequent authors can be easily explained as

resulting from differences in ontogenetic stage (older specimens develop a median ventral rib and a dorsal median furrow lacking in many shells). Presumed differences in microornamentation (García-Alcalde and Hassani, 2020, p. 24) should be checked on a larger sample of well-preserved specimens.

Distribution: Probably Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise *Plectospira ferita* is known from the Middle Devonian (Eifelian, possibly also Givetian) of the Eifel, the Holy Cross Mts., and Maïder. It has been reported from several other regions (see Halamski and Baliński, 2013); these data require confirmation.

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. 34A–E

- * 1842 Terebratula lepida Goldfuss, Bonn Mus. d'Archiac and de Verneuil, p. 368, pl. 35, fig. 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.
 - 2013 *Bifida lepida* (d'Archiac and de Verneuil, 1842) Halamski and Baliński, p. 287, fig. 30U–V, BB–GG.

Material: Four articulated shells, three of which complete, MB.B.9455.1–2 from locality 89, MB.B.9473 from locality 93A, MB.B.9483 from locality 151C.

Description: Shell teardrop-shaped, up to 5.4 mm in length, width-to-length ratio 0.85–1.05, planoconvex; anterior commissure weakly deflected ventrally. Dorsal valve with a wide, flat-bottomed sulcus bisected by a thin median rib and bordered by a stronger rib pair; another weaker rib on each lateral flank. Ventral valve with a poorly preserved (incurved?) beak and two rib pairs, the median ones thicker and stronger. Growth lines lamellose. Interior not studied.

Remarks: Exterior characters of these brachiopods allow unminstakable assignment to *Bifida* Davidson, 1882. Pending revision, small planoconvex shells are assigned to the Eifelian species *B. lepida*, as opposed to the Givetian ventribiconvex *B. nitida* Schmidt, 1951.

Distribution: The Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian. Otherwise Eifelian of the Eifel, Ardennes, Holy Cross Mts., and Maïder (Maillieux, 1938; Biernat, 1966; Copper, 1973; Halamski, 2004a; Halamski and Baliński, 2013; B. Mottequin, pers. comm., 2013).

Family Kayseriidae Boucot, Johnson and Staton, 1964 Genus Kayseria Davidson, 1882

Type species: *Orthis lens* Phillips, 1841; Hope's Nose near Torquay, Devon, England; Middle Devonian, probably (upper?) Eifelian (Copper, 1973).



Fig. 34. Middle Devonian small-sized Athyridida from northern Maïder. **A–E.** *Bifida lepida* (d'Archiac and de Verneuil, 1842). Specimen MB.B.9473. Locality 93A. **F–J.** *Plectospira ferita* (von Buch, 1834). Specimens MB.B.9431. Locality 151B. **K–T.** *Kayseria alvea* Copper, 1973, K–O, P–T. Specimens MB.B.9436.1, 9436.2. Locality 151B. All specimens are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.

Kayseria alvea Copper, 1973 Fig. 34K–T

- * 1973 *Kayseria alvea* sp. nov. Copper, pp. 134–136, text-fig. 6, pl. 7, fig. 12–22.
- v. 2013 *Kayseria alvea* Copper, 1973 Halamski and Baliński, pp. 287–289, fig. 30HH–KK.

Material: Thirteen mostly complete, articulated shells, MB.B.9436.1–6, probably from locality 151B,

MB.B.9482.1–6 from locality 151C, MB.B.9496.1 probably from locality 151B.

Description: Shell teardrop-shaped, anteriorly weakly medially indented, about 8 mm long, slightly longer than wide (width-to-length ratio 0.92–1.00), weakly biconvex, usually about 3 mm thick. Both valves with median sulci; the dorsal one usually about 2 mm wide at anterior commissure, the ventral one usually much narrower. Ornamentation of radial ribs; on the dorsal valve 4–6 usually, but not always, fine ones in the sulcus, two strong ones bordering the sulcus and 6–8 additional, moderately strong ones per flank; ribbing pattern on the ventral valve more variable, with 1–6 fine median rib(s) and the difference between ribs bordering the sulcus and lateral ones less strong.

Remarks: *Kayseria alvea* has a stronger rib pair bordering the sulcus, more so on the dorsal valve (compare Copper, 1973, pl. 7, figs 15 and 16). Such a rib pair is absent in *Kayseria lens* (Phillips, 1841) and *K. dividua* (Schnur, 1851) (the two probably synonymous; Davidson, 1882, p. 24). *Kayseria procera* Ficner and Havlíček, 1978 from the Givetian of Čelechovice (Moravia) is much longer than wide (width-to-length ratio 0.75–0.92).

Distribution: Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise, Eifel, uppermost Eifelian in the traditional sense (Ahbach beds, mostly Müllert horizon; Copper, 1973), so mostly lowermost Givetian as presently understood (Walliser *et al.*, 1995; Bultynck and Hollevoet, 1999); southern Maïder, Middle Devonian.

> Order Spiriferida Waagen, 1883 Family Spinocyrtiidae Ivanova, 1959 Genus *Spinocyrtia* Fredericks, 1916

Type species: *Delthyris granulosa* Conrad, 1839; New York, USA; Givetian (neotype from the Wanakah shale; Ehlers and Wright, 1955).

Spinocyrtia cf. ascendens (Spriesterbach, 1935) Fig. 35F-Q

- cf. * 1935 Spirifer (Spinocyrtia) ascendens Spriesterbach, p. 498, pl. 45, figs 1–2.
- cf. 1942 Sp. (Spinocyrtia) ascendens Spriesterbach Paeckelmann, pp. 16–18, text-fig. 14, pl. 1, fig. 4.
- cf. 1961b Spinocyrtia ascendens (Spriesterbach 1935) var. zemmourensis nov var. – Drot, pp. 261– 262, pl. 3, fig. 6.
- cf. 1963 Spinocyrtia ascendens (J. Spriesterbach, 1935) – Vandercammen, pp. 139–143, text-figs 95– 99, pl. 13, figs 1–29.
- cf. 1964 Spinocyrtia ascendens (Spriesterbach, 1935) Sougy, p. 465, pl. 49, fig. 4.
- cf. 1964 Spinocyrtia ascendens (Spriesterbach, 1935) var. zemmourensis Drot, 1961) – Sougy, p. 465, pl. 49, fig. 3 [k Drot, 1961].
- cf. 1964 Spinocyrtia ascendens (Spriesterbach) Webby, pp. 17–19, pl. 1, figs 1–7.

Material: Three subcomplete articulated shells MB.B.9453.1–3 from locality 89.

Description: Shell up to ca. 24 mm in length, transverse (width-to-length ratio 1.5–1.8; estimated width not exceeding ca. 40 mm), ventribiconvex; widest at or near the hinge line. Ventral valve convex, subtriangular in anterior view, with a deep V-shaped sulcus originating in umbonal region; interarea approximately catacline. Dorsal valve convex with a rounded fold (ca. 7.5 mm wide in a shell ca. 28.5 mm wide); the fold with a median groove, the width of which

is about one third of that of the fold. Radial ribs 12–14 per flank. Microornamentation of tear-shaped granules 0.2 0.3 mm long and 0.1–0.15 mm wide, placed on radial microfila. Interior unknown.

Remarks: This sample is included into *Spinocyrtia* on account of non-costate fold and sulcus and microornamentation (compare Fig. 35P–Q and Paeckelmann, 1942, pl. 1, fig. 4; Ehlers and Wright, 1955, pls 2, 3, 5, 7, 8, 11), and compared to *Spinocyrtia ascendens* described from the Givetian of Bergisches Land on account of markedly transverse, markedly ventribiconvex with 12–14 costae per flank (13–18 in *S. ascendens*; Webby, 1964). The isolated sample precludes a definitive taxonomic conclusion. *Spinocyrtia* cf. *elburzensis* Brice *in* Brice *et al.*, 1973 described from southern Maïder by Halamski and Baliński (2013) has more numerous (14–20) ribs, a lower ventral interarea (subrectangular; triangular here) and is dorsibiconvex.

Distribution: Probably the Taboumakhlouf Formation, dm2.1 or dm2.2, upper Eifelian. *Spinocyrtia ascendens* is present in the Givetian of Bergisches Land (Spriesterbach, 1935), Eifel (Paeckelmann, 1942), Ardennes (mainly southern flank of the Dinant Synclinorium; Vandercammen, 1963), West Somerset in England (Webby, 1964), and Zemmour Noir (Drot, 1961b; Sougy, 1964).

Family Ambocoeliidae George, 1931 Genus *Echinocoelia* Cooper and Williams, 1935

Type species: *Echinocoelia ambocoelioides* Cooper and Williams, 1935; New York state, USA; Tully Formation, Middle Devonian (late middle Givetian according to Baird *et al.*, 2011 and references therein). A detailed locality and type stratum were not selected by Cooper and Williams (1935), but all the figured specimens for which these data are provided are from the upper Laurens member [= Smyrna bed; Baird *et al.*, 2011] cropping out one mile northeast of Laurens.

Species assigned: *Echinocoelia similior* Vogel, Xu, and Langenstrassen, 1989; Guangxi; Tangxiang Fm., Emsian;

Echinocoelia denayensis Johnson, 1966; Roberts Mts., Nevada; *Leptathyris circula* Zone and lower part of the *Warrenella kirki* Zone [approximately middle part of the Eifelian; Johnson *et al.*, 1996];

Echinocoelia williamsi Johnson, 1974; Nevada, *Leiorhynchus castanea* Community, Eifelian–Givetian boundary Zone (Johnson and Klapper, 1990);

Echinocoelia incurva Cooper and Williams, 1935; New York; Mottville Member, Hamilton Group [Skaneateles Formation, approximately lower Givetian];

Martinia halli Branson, 1922; Iowa; upper part of the Solon Member, Little Cedar Fm.; lower part of the *varcus* Zone (Day, 1992);

Echinocoelia ambocoelioides, as above, upper middle Givetian;

Echinocoelia careocamera Johnson, 1978; Nevada; faunal intervals 20 to 26 [middle to upper Givetian; upper part of the middle *varcus* Zone to lower part of the *disparilis* Zone; Johnson and Klapper, 1990];

Echinocoelia pretiosa Cooper and Dutro, 1982; New Mexico; Oñate Formation, approximately upper Givetian;



Fig. 35. Middle Devonian ribbed Spiriferida from northern Maïder. **A–E.** Delthyrididae gen. et sp. indet. Articulated shell MB.B.9491.1 in dorsal, ventral, lateral, posterior, and anterior views. Locality 151B. **F–R.** *Spinocyrtia* cf. *ascendens* (Spriesterbach, 1935). F–J. Articulated shell MB.B.9453.1 in dorsal, ventral, lateral, posterior, and anterior views. Locality 89. K–O, Q. Articulated shell MB.B.9453.3 in dorsal, ventral, lateral, posterior and anterior views, and enlargement of the ventral microornamentation (Q). Locality 151B. P, R. Articulated shell MB.B.9453.2, ventral view (P) and enlargement of the ventral microornamentation (R). Locality 151B.

Echinocoelia parva Baliński in Baliński *et al.*, 2016; Józefka, Holy Cross Mts.; lower Frasnian;

Echinocoelia cf. *incurva* sensu Vandercammen (1956); Frasnes-lez-Couvin, Ardennes; middle Frasnian.

Other occurrences: Specifically unidentified representatives of *Echinocoelia* were reported from the middle to upper part of the upper Emsian of Hamar Laghdad in the Moroccan Anti-Atlas by Mergl (2018); from the Givetian (Hare Indian Fm., Pine Point Formation; approximately the *varcus* Zone) of the District of Mackenzie, Northwest Territories, Canada (Caldwell, 1967; Norris and Uyeno, 1998); from the Givetian Silica Shale of Michigan (Kesling and Chilman, 1975). A poorly preserved fragmentary specimen from the upper Eifelian Kennett Fm. of northern California was tentatively referred to this genus by Savage and Boucot (1978). **Species excluded:** *Echinocoelia septata* Johnson in Johnson *et al.*, 1980, *E. guangsiensis* Sun, 1992 (both belong to *Cyrtinoides* Yudina and Rzhonsnitskaya, 1985; see Baliński and Sun, 2016).

Echinocoelia cf. *williamsi* sensu Sennikov *et al.* (2018, pl. 1, fig. 5) from the upper Eifelian–lower Givetian of the Yuryung-Tumus Peninsula, eastern Siberia, has a weakly but distinctly paraplicate anterior commissure and a ventral sulcus. It does certainly not represent the Nevada species and most probably not the genus, either.

Remarks: *Pyramina* Ljaschenko, 1969 (type species: *P. oskolensis* Ljaschenko, 1969; known solely from a borehole in the Voronezh region; Givetian) was considered a synonym of *Echinocoelia* by Johnson *et al.* (2006, p. 1736). Oleneva (2006, pp. 422–424) listed differences in internal structures and microornamentation, on account of which *Pyramina* is better regarded as a separate genus.

Echinocoelia dorsoplana (Gürich, 1896) Fig. 36A–J, Q–R

- v*1896 *Reticularia dorsoplana* nov. nom. Gürich, p. 260, pl. 9, fig. 3.
- v. 1975 Proreticularia dorsoplana Gürich Baliński, p. 179, pl. 32, fig. 2, pl. 35, fig. 7.

Material: Eight articulated shells, MB.B.9464 from locality VEsn1, MB.B.9485.1–3 from locality 151C, 9486 from locality 151B, 9493.1–3 probably from locality 151B.

Description: Shell small (usually about 8 mm wide), weakly transverse (width-to-length ratio 1.06-1.23), strongly ventribiconvex (dimensions in mm of the largest shell: width 9.0, length 8.5, thickness 6.1, length of the dorsal valve 6.9). Maximum width about the midlength of the shell or anteriorly, so from about the posterior fifth to the midlength of the dorsal valve; anterior commissure rectimarginate. Dorsal valve transverse (width-to-length ratio about 1.3) with rounded postero-lateral extremities and semi-circular anterior margin, weakly convex, lowly triangular in anterior view; interarea low, orthocline to weakly anacline. Ventral valve strongly convex, parabolic in anterior view, umbo thick, beak usually incurved; interarea strongly apsacline (nearly catacline), in a single case weakly procline, transversely striated; delthyrium taking about one third of its width, incompletely closed. No fold, sulcus, or ribs; microornamentation of dense concentric lines, about 12 per mm on the dorsal valve, with concentric bands of closely spaced spine bases (Fig. 36Q).

Remarks: Halamski (2004a) investigated the internal structures of this species from the type area and assigned it to *Echinocoelia*. The interiors of the African material have not been studied, but the agreement of external characters is perfect. As far as it was possible to check, this is the first report of this species outside the type section.

Echinocoelia cf. *incurva* Cooper and Williams, 1935 reported by Drot (1964, pp. 85–86; pl. 8, fig. 2) from the "upper Givetian" locality TM 129 (northernmost Maïder) is longer than wide (width-to-length ratio about 0.96) and the ventral interarea is weakly apsacline (nearly orthocline). *Echinocoelia tikhiensis* Baranov and Alkhovik, 2006 from the Givetian (*varcus* Zone) of the Sette-Daban Mountains in eastern Siberia is much similar to *E. dorsoplana*; it seems to differ in having a higher ventral interarea, but the data at hand are insufficient for a detailed comparison.

Distribution: The lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. The stratigraphic position of the type level is in the lower to middle part of the Givetian (Halamski and Segit, 2006).

Family Delthyrididae Phillips, 1841 Delthyrididae gen. et sp. indet. Fig. 35A–E

Material: Two articulated shells MB.B.9491.1–2 from locality 151B.

Description: Shell up to 10.0 mm in width, rounded in outline, transverse (width-to-length ratio 1.25–1.30), weakly ventribiconvex. Maximum width at about shell midlength, so posteriorly to dorsal valve midlength; hinge line 0.73–0.80 of the maximum width. Ventral umbo thick, beak incurved; ventral interarea apsacline, delthyrium occupying about one fourth of the interarea width; dorsal interarea anacline. Ornamentation of relatively thick, rounded ribs beginning in umbonal region; 7–9 on the dorsal valve, 8 on the ventral valve; ventral median sulcus U-shaped. Microornamentation poorly preserved; growth lines not observed. Interior not studied.

Remarks: This sample is tentatively included in the Delthyrididae on account of the external similarity with representatives of *Howelella* Kozłowski, 1946, *Delthyris* Dalman, 1828, and *Ivanothyris* Havlíček, 1957. Emsian *Microttia* García-Alcalde, 2005 is somewhat similar, but has a slightly wider hinge line and flattened sulcus and fold (Gourvennec and Carter, 2007).

The microornamentation is not preserved satisfactorily. Two possible spine bases might have been arranged on a single capilla, but the observed radial structures correspond rather to paralelly arranged calcite crystals belonging to the primary layer.

Ivanothyris aculeata (Schnur, 1851) reported from southern Maïder is similar in form but differs in being aequibiconvex and in having acute ribs (Halamski and Baliński, 2013, fig. 35A–E).

Distribution: Lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian.

Family Reticulariidae Waagen, 1883 Genus *Yeothyris* Struve, 1992

Type species: *Tingella bicollina* Struve, 1992; Eifel, Germany; Junkerberg Formation, middle Eifelian.

Remarks: The description of the internal features of the type species (Struve, 1961, 1970, 1992) was prepared on the basis of "artificial moulds" (*künstliche Steinkerne*), so comparison with taxa investigated using the standard method of serial sections is not straightforward. In particular, it is unclear whether the short crural plates, mentioned in the original description (Struve, 1970, p. 510; fig. 10), are genuine crural plates (that is, plates buttressing the crura and resting on the ventral valve floor) or the imprint of the inner



Fig. 36. Middle Devonian smooth Spiriferida from northern Maïder. **A–J, Q–R.** *Echinocoelia dorsoplana* (Gürich, 1896). A–E, F–J. Articulated shells MB.B.9493.1–2 in dorsal, ventral, lateral, posterior, and anterior views. Locality 151B. Q, R. Enlargement of the microornamentation on dorsal valve and enlargement of the ventral interarea with deltidial and apical plates in slightly oblique view, MB.B.9485.1. Locality 151C. **K–P.** *Quadrithyris* cf. *macrorhyncha* (Schnur, 1853). Articulated shell MB.B.9456.1 in dorsal, ventral, lateral, posterior, and anterior views (K–O) and enlargement of the ventral microornamentation (P). Locality 89.

socket ridges. A more extensive discussion is given below in the remarks on the species *Yeothyris? sinuata*.

Yeothyris? sinuata (Gürich, 1896) Figs 37, 38

- * 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.
- ? 2013 *Rhenothyris sinuata* (Gürich, 1896) Halamski and Baliński, p. 291, fig. 36M–Q.

Material: MB.B.9429.1–23 from localty 151B, 9459.1–20 from locality 151C.

Description: Shell elliptic to subtrapezoidal in outline, transverse [width-to-length ratio (1.12-)1.25-1.38(-1.49), N = 30], up to 20 mm in width, usually 14–18 mm wide, moderately to strongly ventribiconvex [thickness-to-length ratio (0.78-)0.86-0.92(-0.99), N = 29]. Maximum width either at mid-length or in the posterior region of the dorsal valve, but never at hinge. Dorsal valve rounded subtriangular

in anterior view; low fold observable in the anterior half of the valve; interarea low, approximately orthocline. Ventral valve markedly convex, umbo thick, beak blunt, interarea mostly strongly apsacline (seldom first weakly procline, then apsacline), high, incurved. Anterior commissure weakly paraplicate; tongue occupying (0.32-)0.38-.46(-0.55) [N = 28] of the shell width. One or two obsolescent ribs are sometimes present on each lateral flank, in this case the anterior commissure is deflected by corresponding low undulations.

Ventral interior: Dental plates strong, divergent ventrally, umbonally conjunct by callus and thus forming an apical plate expanding below the surface of the interarea; teeth strong; ventral muscle field narrow, impressed. Dorsal interior: Ctenophoridium well developed; inner socket ridges strong, crural bases apically entombed in callus, anteriorly thin and slightly concave; crura forming two delicate, concave blades hanging quite low above the valve bottom; crural plates none; spiral cones composed of eight whorls in the sectioned specimen (Fig. 38, section at 5.65 mm); adductor scars impressed.

Microornamentation of concentric growth bands and densely packed marginal spines.

Remarks: These brachiopods are included in the superfamily Reticularioidea on the basis of biconvex shells and microornamentation of concentrically arranged spines bases and into the family Reticulariidae on account of the lack of a ventral median septum. The assignment to a reticulariid subfamily is less evident. The Obesariinae Gourvennec, 1994 and the Eoreticulariinae Gourvennec, 1994 are clearly excluded as they lack a ctenophoridium (Carter and Gourvennec, 2006). However, the presence or absence of crural plates might be a less clear-cut feature, if different methods of study are used (see above, Remarks on the genus). If the formal definition of crural plates is followed, the brachiopods described here have none. However, their likeness to Yeothyris bicollina (Struve, 1961), consisting in a similar external morphology and the presence of strong dental plates, seems to constitute a clear indication of close relationships. The brachiopods discussed are tentatively included in Yeothyris; this should be confirmed through sectioning of the type species Y. bicollina.

In comparison with *Yeothyris bicollina*, *Yeothyris? sinuata* is smaller (width about 30 mm in the former) and has undulations of the anterior commissure (none in the former). It is compared to a poorly known species, described from the Givetian of Śniadka in the Holy Cross Mountains as *Reticularia sinuata* Gürich, 1896 and afterwards from slightly older strata of Skały in the same region as *Eoreticularia eifeliensis* sensu Biernat (1966). *Spirifer robustus* var. *eifeliensis* Frech in Scupin, 1900 has crural plates and belongs to *Reticulariopsis* Fredericks, 1916 (Gourvennec, 1994).

Both reticulariids described from southern Maïder (Halamski and Baliński, 2013) differ in the form of the tongue and dorsal fold: it is higher in *Rhenothyris sinuata* sensu Halamski and Baliński (2013) [more transverse shells, so possibly a misidentification] and wider in *Deltospirifer*? sp. nov. *Reticulariopsis* Fredericks, 1916 is externally similar, but differs in having long crural plates (Gourvennec, 1994; Carter and Gourvennec, 2006), so in this case no confusion seems likely.

Distribution: The lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. In the Holy Cross Mountains, the position of the type level is in the lower to middle part of the Givetian, but the species is also present in the upper Eifelian (Biernat, 1966; Halamski and Zapalski, 2006).

Genus Quadrithyris Havlíček, 1957

Type species: *Spirifer robustus* Barrande, 1848; Koněprusy, Bohemia, Pragian.

Quadrithyris cf. macrorhyncha (Schnur, 1853) Fig. 36K–P

- cf. * 1853 *Sp[irifer] macrorhynchus* n. sp. Schnur, p. 209, pl. 36, fig. 4a, b, non c.
- cf. 1940 Spirifer macrorhynchus Schnur Cottreau, p. 198, pl. 7, fig. 10.
- cf. 1952 *Delthyris macrorhyncha* Schnur Le Maître, p. 119.
- cf. 1962 *Quadrithyris macrorhyncha* Schnur, 1853 Boucot, pp. 416–417, pl. 50, figs 8–10, pl. 51, fig. 11.
- cf. 1964 « *Delthyris* » macrorhynchus (Schnur, 1853) Sougy, p. 444, pl. 39, fig. 6.
- cf. 1964 *Quadrithyris macrorhyncha* (Schnur, 1853) Drot, p. 80, pl. 7, fig. 1.

Material: Two articulated shells, one complete, one incomplete, MB.B.9456 from locality 89, 9476 from locality 93A. **Description:** Shell elliptic in outline, 13.9–17.0 mm wide, transverse (width-to-length ratio 1.17–1.28), strongly ventribiconvex (the ventral valve accounting for more than two thirds of the total thickness of the shell). Maximum width about the mid-length of the dorsal valve. Dorsal valve with a flat fold; interarea orthocline or weakly apsacline. Ventral valve with a shallow sulcus arising in umbonal region; umbo very thick, beak suberect to incurved; ventral interarea relatively narrow and high, strongly apsacline to catacline. Anterior commissure paraplicate, tongue triangular in one specimen, not preserved in the other. Microornamentation of concentrically arranged microspines. Interior unknown.

Remarks: The identification is tentative because isolated sample has not allowed serial sectioning and variation of this species in the type area is insufficiently known. Figured specimens of this species have a subtrapezoidal tongue (Boucot, 1962, fig. 11b; Sougy, 1964).

Distibution: The Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.1–dm3, upper Eifelian to Givetian. The genuine *Quadrithyris macrorhyncha* is known in the Middle Devonian of the Eifel (Schnur, 1853; Junkerberg Formation, so middle Eifelian, according to Boucot, 1962), Zemmour Noir (Sougy, 1964), and southern Maïder (Drot, 1964). Reported also from the "lower Eifelian" of Erg El Djemel (Le Maître, 1952).

Family Thomasariidae Cooper and Dutro, 1982 Genus *Thomasaria* Stainbrook, 1945



Fig. 37. *Yeothyris? sinuata* (Gürich, 1896). **A–E, F–J, K–O, P–T, U–Y.** Articulated shells 9459.2 from locality 151C, 9429.3, 9429.2 from locality 151B, 9459.1 from locality 151C, and 9429.1 from locality 151B in dorsal, ventral, lateral, posterior, and anterior views. Z–AA, DD. Enlargements of microornamentation of shells 9459.1 (Z, dorsal) and MB.B.9459.3 (AA, DD, both ventral). Locality 151C. BB, CC. Enlargements of the posterior region of the articulate shell MB.B.9429.4 in oblique and dorsal views to show the delthyrium. Locality 151B.



Fig. 38. Transverse serial sections of *Yeothyris*? *sinuata* (Gürich, 1896). through shells MB.B.9429.5 from locality 151B (A) and MB.B.9459.4 from locality 151C (B). Distances measured in millimetres from the tip of the ventral umbo.

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

Synonym: *Pyramidalia* Nalivkin, 1947 (type species *Spirifera simplex* Phillips, 1841; south-western England; Givetian; see Halamski and Baliński, 2019).

Remarks: García-Alcalde and El Hassani (2020) proposed the new subgenus Thomasaria (Mzerrebiella) with T. (M.) bultyncki García-Alcalde and El Hassani, 2020 from the Givetian of Oued Mzerreb as the type species. Several diagnostic features of the subgenus T. (Mzerrebiella), given by García-Alcalde and El Hassani (2020), also can be observed in the specimens of T. simplex from its type area (southwestern England), this species being the type species of the genus Pyramidalia Nalivkin, 1947 (see Halamski and Baliński, 2019). Features, such as the subelliptical shell outline, rounded cardinal extremities, short hinge line, smooth shell with occasionally weak, obsolescent ribs, delthyrium cover and short dental plates, are common to both forms and thus cannot be helpful in distinguishing the new subgenus. Other features, mentioned by García-Alcalde and El Hassani (2020) as diagnostic for T. (Mzerrebiella), such as small shell size and weaker fold and sulcus, seem insufficient to clearly define the subgenus.

Thomasaria simplex (Phillips, 1841) Figs 39–42

- * 1841 *Spirifera simplex* Phillips, p. 71, pl. 29, fig 124αa–d, pl. 60, fig. 124α.
- v 2013 *Thomasaria*? *simplex* (Phillips, 1841) Halamski and Baliński, pp. 293–295, fig. 36A–L.
- v 2019 *Thomasaria simplex* (Phillips, 1841) Halamski and Baliński, pp. 404–406, figs 2A–F, 3A, B [*ubi syn.*].

Material: MB.B.9408.1–75 from locality 93A, 9498.5–6 probably from locality 151B.

Description: Shell medium-sized, (9.9–)15.4–19.8(–26.3) mm in width [see Appendix 1 for measurements], transverse, width-to-length ratio (1.05)-1.28-1.44(-1.57), hemipyramidal, strongly ventribiconvex, ventral valve ca. 1.7–3.3 times as thick as the dorsal one. Hinge line (and interareas) attain 0.59-0.88 (0.74 on average) of the total shell width, maximal width in posterior half of the dorsal valve length; cardinal extremities rounded, lateral margins weakly arched, anterior margin usually straight to indented, anterior commissure uniplicate. Dorsal valve subtrapezoidal to semioval in outline, parabolic in anterior view; fold low, appearing usually at midlength, poorly delineated from flanks; interarea low to almost linear, anacline to orthocline. Ventral valve hemipyramidal in specimens with more or less catacline interarea or convex in those with more apsacline interarea; interarea very variable, very high when catacline to procline, but much lower when apsacline, flat to weakly concave, rather well delimited laterally; delthyrium with delthyrial angle 13-21°, closed in its apical one to two thirds by a concave plate arising from converging umbonal thickenings (Figs 39I, S; 42A, sections at 1.8 and 2.6 mm; 41A, C); pseudodeltidium not observed.

Shell smooth, with a few (in a single case, up to nine) low, rounded, often hardly discernible ribs per flank. Microornamentation consisting of regularly spaced, concentric growth lines with densely packed spine bases (Fig. 41D, E).

Ventral interior: Dental plates strong, divergent ventrally, posteriorly partially buried in umbonal thickening, umbonally fused, forming an apical plate expanding below the surface of the interarea and partially occluding the delthyrium (Fig. 42A, sections at 1.8 and 2.6 mm); teeth rather strong.

Dorsal interior: Ctenophoridium (Fig. 41A–C) well developed; inner socket ridges strong, crural bases apically entombed in callus, anteriorly thin and slightly concave; crura form two delicate, concave blades hanging quite low above valve floor; crural plates absent; adductor scars impressed.

Remarks: A remarkable feature of the described sample is variability in the inclination of the ventral interarea. As shown in the diagram (Fig. 39), the inclination ranges from strongly procline, through catacline, to apsacline. Among the examined specimens as many as 79% have high, procline to catacline ventral interarea (with inclination 42–100°), which results in hemipyramidal shape of the shell (Fig. 39C, H, M, W). The remaining 21% specimens have less high and apsacline interarea with inclination of 108–131°. The latter shells are less hemipyramidal and less ventribiconvex (Fig. 39R).

It is worth noting that similar variability in the inclination of the ventral interarea within the *Thomasaria* species was noted, among others, by Crickmay (1967) in the Frasnian *T. rockymontana* (Warren, 1928) and by Cooper and Dutro (1982) in the Frasnian *T. demissa* Cooper and Dutro, 1982 and *T. warreni* Cooper and Dutro, 1982. This remarkable variability of the ventral interarea seems to be characteristic of at least some species of *Thomasaria* and provides the main argument for a wide taxonomic treatment of the species described here.

The specimens from Issoumour are characterized by having larger size of the shell in comparison with several species of the genus that rarely exceed 20 mm in shell width. On the contrary, shells of this species described from southern Maïder (Halamski and Baliński, 2013) and from south-western England (Halamski and Baliński, 2019) may attain larger size (up to about 40 mm in width) but are otherwise similar.

The specimens studied, especially those with procline to anacline interarea, show a great similarity in the shell shape and (partly) size as well as in the development of sulcation to *Thomasaria simplex* (Phillips, 1841) from the Givetian of south-western England, which was recently re-described by Halamski and Baliński (2019). However, it remains an important question as to whether a similar variation in the curvature of the ventral interarea also occurs in the sample from the type area. This issue has to remain unresolved for the time being, because only a few specimens of this species from the type region have been found so far (Halamski and Baliński, 2019).

Thomasaria bultyncki García-Alcalde and El Hassani, 2020 was described from the Givetian of Oued Mzerreb on the basis of a relatively limited sample (eight measured specimens). The shells are small (maximum width 11.7 mm),



Fig. 39. *Thomasaria simplex* (Phillips, 1841). **A–E, F–J, K–O, P–T, U–Y.** Articulated shells MB.B.9408.5, 9408.4, 9408.3, 9408.1, 9408.2 in dorsal, ventral, lateral, posterior, and anterior views. Locality 93A.



Fig. 40. *Thomasaria simplex* (Phillips, 1841). Scatter diagrams of shell width to dorsal valve length and ventral interarea length to dorsal valve length (**A**) and of ventral interarea inclination angle to dorsal valve length (**B**). All values for the studied sample.

but both width-to-length and hinge length-to-total length ratios fall within the values of the sample described here as *T. simplex* (hinge length-to-total length: 0.68–0.78 in *T. bultyncki*, 0.59–0.88 herein).

Distribution: The upper (and probably lower) part of the Taboumakhlouf Formation to the lower part of the Bou Dib Formation, (dm2.1–)dm2.2–dm3, upper Eifelian to Givetian. South-western England, Givetian (Halamski and Baliński, 2019); Eifel, Holy Cross Mts., Maïder, Middle Devonian.

Order Spiriferinida Ivanova, 1972 Family Cyrtinidae Fredericks, 1911 Genus *Cyrtina* Davidson, 1859

Type species: *Calceola heteroclita* Defrance in Blainville, 1824; Néhou, Normandy; Lower Devonian (Pragian or lower Emsian?).

Remarks: Halamski and Baliński (2013, p. 295) and Gourvennec (2019, p. 119) commented on difficulties in finding a biologically plausible taxonomic treatment of *Cyrtina*. Localised samples are separable from each other on the basis of subtle differences, but consistent recognition of them as species resulted in a genus containing over 100 species (Gourvennec, 2019), arguably an over-splitting.

However, given that such style of taxonomy is used consistently in treatments of the genus (Griesemer, 1965; Ehlers and Wright, 1975; Keyes and Pitrat, 1978; Gourvennec, 1989, 2019) and, on the other hand, a revision of *Cyrtina* is evidently beyond the scope of the present paper, a morphographic approach is followed here. Three morphotypes are thus distinguished, the first of which, described as *Cyrtina* cf. *multiplicata* (Davidson, 1864) is distinctly different from the remaining material of the genus. The two others, described here as *Cyrtina* cf. *sauvagei* Rigaux, 1908 and *Cyrtina* cf. *evanescens* Gourvennec, 2019, come from a single outcrop; the extreme terms of the variation are very different, but intermediate morphotypes do occur as well (see below).

Cyrtina cf. *multiplicata* (Davidson, 1864) Fig. 43A–R

- cf. * 1864 [*Cyrtina heteroclita*, Defrance (sp.)] Var. *multiplicata*, Dav.– Davidson, pp. 49–50, pl. 9, figs 11–14.
- cf. 1893 *Cyrtina heteroclita*, var. *multiplicata*, Davidson – Whidborne, p. 112, pl. 12, fig. 13.

Material: Nine articulated shells MB.B.9427.1–9 from locality 93A.

Description: Shell up to ca. 22 mm wide, transverse to strongly transverse (width-to-length ratio 1.5-2.5), strong-ly ventribiconvex, mucronate. Dorsal valve with a low rounded or flattened fold, sometimes with a narrow and shallow median depression, with (4-)5-6(-8) ribs per flank. Ventral valve with the rib pair bordering the sulcus noticeably stronger than the remaining ones; interarea distinctly procline.

Remarks: The characteristic features of this sample include a high, procline ventral interarea and transverse shape. It is compared to the insufficiently known taxon *Cyrtina multiplicata* (Davidson, 1864), described from the Middle Devonian of southwestern England (Barton and Lummaton). The number of ribs in the English species is slightly greater (six to ten per flank; Davidson, 1864) than in the sample of the present authors.

Cyrtina varia Clarke, 1900 from the Lower Devonian of North America (New York, Nevada) is similar in general form and in having the median pair of ventral ribs stronger than the other ones but has 4–5 ribs per flank and a catacline interarea (Clarke, 1900; Johnson, 1970). *Cyrtina* sp. nov. A sensu Baliński *et al.* (2016) from the lower Frasnian of Józefka, Holy Cross Mts. is similarly fusiform and has a procline area, but the ribbing is denser (14 ribs per flank). *Cyrtina* ex gr. *intermedia* sensu Halamski and Baliński, 2013 from southern Maïder is similarly strongly transverse, but the ribs are less numerous and the ventral interarea is apsacline.

Distribution: The upper part of the Taboumakhlouf Formation to the lower part of the Bou Dib Formation, dm2.2–dm3, upper Eifelian to Givetian.

Cyrtina cf. sauvagei Rigaux, 1908 Fig. 43CC-GG

cf. * 1908 *Cyrtina Sauvagei* – Rigaux, p. 6, 20, pl. 1, fig. 8.



Fig. 41. *Thomasaria simplex* (Phillips, 1841). **A–C.** Enlargements of the delthyrium MB.B.9408.8 showing the cardinal process (A, B, posterior views showing the entire delthyrium and a partial enlargement; C, oblique ventral views). **D.** Enlargement of the dorsal micro-ornamentation of the shell MB.B.9408.17. **E.** Enlargement of the dorsal microornamentation of the shell MB.B.9408.6. Locality 93A.

cf. 2013 *Cyrtina sauvagei* Rigaux, 1908 – Halamski and Baliński, pp. 295–296, fig. 36BB–FF.

Material: Four articulated shells MB.B.9415 probably from locality 151B, 9488.1–2 from locality 151B, 9497 probably from locality 151B.

Description: Shell typically about 15 mm wide, transverse (width-to-length ratio about 1.5), strongly ventribiconvex, maximum width anteriorly to hinge line. Dorsal valve with a flattened fold and 5–6 ribs per flank. Ventral valve pyramidal, sulcus mildly V-shaped, interarea catacline or weakly procline, nearly flat.

Remarks: The shell MB.B.9488.1 is much alike the European representatives of this species as revised by Brice (1988), with relatively strong costation. The shell MB.B.9415 is similar in shape and ornamentation but distinctly larger (over 25 mm wide); it is included tentatively here. The shell MB.B.9497 has a similar shape to both above-mentioned samples, but the ribs are low and blunt, the general ornamentation pattern seems thus intermediate in character between the former and those described below as *Cyrtina* cf. *evanescens*.

Distribution: The lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian.

Cyrtina cf. evanescens Gourvennec, 2019 Fig. 43S–BB

cf. * 2019 *Cyrtina evanescens* sp. nov. – Gourvennec, pp. 120–122, text-figs 13, 14, pl. 11, figs 34–54.

Material: Four articulated shells MB.B.9498.1–4 probably from locality 151B.

Description: Shell typically 16–17 mm wide in adults, transverse (width-to-length ratio about 1.6), strongly ventribiconvex, maximum width anteriorly to hinge line. Dorsal valve with a flattened fold and ornamentation, consisting of obsolescent ribs, about four per flank. Ventral valve with an apsacline interarea.

Remarks: This sample is identified as *C*. cf. *evanescens*, a species described from approximately coeval sediments of the Tindouf Syncline (Gourvennec, 2019) on account of obsolescent ribs and non-mucronate cardinal extremities. For comparison with *Cyrtina* cf. *sauvagei* see above, Remarks to the genus and to the species.

Distribution: The lower part of the Taboumakhlouf Formation, dm 2.1, upper Eifelian. Otherwise Bou Bernous section, Tindouf Syncline, upper Eifelian – lower Givetian (Gourvennec, 2019).



Fig. 42. Transverse serial sections of *Thomasaria simplex* (Phillips, 1841) through shells MB.B.9408.45–47 from locality 93A. Distances measured in millimetres from the tip of the ventral umbo. Greyed areas obscured by recrystallization.



Fig. 43. Middle Devonian Spiriferinida from northern Maïder. **A–R.** *Cyrtina* cf. *multiplicata* (Davidson, 1864). A–E, F–J, K–M, N–R. Specimens MB.B.9427.1, 9427.2, 9427.3, 9427.4. Locality 93A. **S–BB.** *Cyrtina* cf. *evanescens* Gourvennec, 2019. S–W, X–BB. Specimens MB.B.9498, 9497. Locality 151B. **CC–GG.** *Cyrtina* cf. *sauvagei* Rigaux, 1908. Specimen MB.B.9488.1. Locality 151B. All specimens are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.

GENERAL CHARACTERISTICS OF THE MAÏDER BRACHIOPOD FAUNA (BY ATH & AB)

Summary quantitative analysis

The quantitative overview of the brachiopod fauna from northern Maïder with data for southern Maïder and elements for a basic palaeobiogeographic analysis are given in Table 3.

The fauna studied is globally composed of 60 taxa, out of which 40 are identified with certainty at the species level, 10 at the species level with doubt (cf. or ex gr.), four at the genus level, and the remaining six at the family or order level. These taxa are described on the basis of 1,209 specimens and the numbers of invividuals per taxon range from 1 to 250. Among the 60 species, there are 12 singletons (one specimen in the material) and 7 doubletons.

Summing the above-mentioned 60 species with 62 ones reported from southern Maïder by Halamski and Baliński (2013), the number of Middle Devonian brachiopods from the whole Maïder amounts to 87. Among these 87 species, 34 [$34/87\approx39\%$] are common for both regions, 25 [$25/60\approx42\%$] are present solely in the north, and 27 [$27/62\approx44\%$] solely in the south (see Table 3). The brachiopod assemblages from northern and southern Maïder, as sampled, appear thus as relatively different from each other.

Diversity indices for single assemblages, both regions, and for the Maïder fauna are given in Table 4. Single assemblages are rather different from each other, as expressed by diversity indices 1-D and H. The Berger-Parker index values (Berger and Parker, 1970) are also relatively different from each other, ranging from 0.11 to 0.98, which is often simply explainable by the size of the samples.

The value 0.53 for the assemblage 89 is due to the presence of a single very abundant species (*Lebanzuella? issoumourensis*; see Halamski *et al.*, 2020). Regional values correspond to globally diverse faunas. The rarefaction curves for selected localities, the two assemblages (northern and southern Maïder) and for the total Middle Devonian fauna of the Maïder region are given in Fig. 44. The individual assemblages are clearly unsaturated (Fig. 44A, B), but even at regional scale no evident asymptotes can be observed (Fig. 44C).

The Simpson index $1-D\approx 0.96$ for the aggregated assemblage has a rather high value, so the Maïder brachiopod fauna may be described as relatively diversified, not unusual for assemblages pre-dating the Taghanic event (see e.g., Brett *et al.*, 2009). The absolute number of species N = 87 is nonetheless distinctly lower in comparison with values for coeval faunas from areas with longer traditions of research (Eifel: 300 species, Holy Cross Mountains: 122 species, Halamski, 2008; Asturias: >150 species, J. García-Alcalde, pers. comm. 30th June, 2020). This remains true, even allowing for a part of the fauna not being sampled (see Tab. 4, Chao1 asymptotic estimator of species richness; Chao, 2005; Chao et al., 2009). Two explanations are possible: either an actual alpha-diversity lower in the Anti-Atlas than in other regions, or incomplete sampling, accompanied by significantly underestimated total richness. From a palaeobiological point of view, the latter possibility seems more plausible. Apparently, in this case the Chao1 estimator performs poorly, which might be owing to the regional scale of the study. In such a case, effects due to spatial turnover between elementary faunules might become more important than sampling issues (Cam et al., 2002; Gotelli and Colwell, 2011).

Table 3

Summary of distribution and frequencies of Middle Devonian brachiopods from northern and southern Maïder (northern Maïder, this paper; southern Maïder, after Halamski and Baliński, 2013). Localities and regions: Af – Aferdou el Mrakib; HCM – Holy Cross Mountains; Md – Madène el Mrakib; Mh – Maharch; RSM – Rhenish Slate Mountains (incl. Eifel). Taxa not identified at least at genus level and thus unfit for quantitative palaeobiogeographic analysis marked by greyed cells in the last two columns. ? – species doubtfully present. Totals: species in Roman typeface, *specimens in italics*. Last two columns: the total number counted twice, first with doubtful presences counted as absences, secondly (in parentheses) as presences.

Taxa		Localities												
	Species	Africa											Europe	
der			northern Maïder southern Maïder											
O		TO- TAL	89	93	151	152	153	VE sn1	VE sn2	Af	Md	Mh	RSM	НСМ
_	Petrocrania sp.	2	-	2	-	-	-	-	-	-	-	-		
niida	Deliella deliae	-	-	-	-	-	-	-	-	-	1	-	+	+
Craı	Deliella aff. rhenana	1	-	-	1	-	-	-	-	-	2	_	+	
nida	Leptagonia analogaeformis	5	_	5	_	-	_	-	-	5	9	-	+	+
Strophomer	Gibbodouvillina interstrialis	1	-	-	1	-	-	-	-	1	1	-	+	+
	Radiomena irregularis	_	_	_	_	_	_	_	_	10	_	_	+	+

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Таха		Localities												
							Africa						Eu	rope
rder	Species	northern Maïder southern M									thern Ma	aïder	-	
O	1	TO- TAL	89	93	151	152	153	VE sn1	VE sn2	Af	Md	Mh	RSM	НСМ
nida	Leptodontella lanthanomena	3	-	-	3	-	-	-	_	-	-	-		+
phome	Parastrophonella anaglypha	2	_	1	_	-	_	1	_	-	2	-	+	+
Strol	Protodouvillininae indet.	_	-	_	_	-	_	_	_	1	_	-		
	Devonaria minuta	13	-	-	13	-	-	-	-	-	-	-	+	
	Devonaria gevini	1	-	-	1	-	-	-	-	4	-	-		
	Anopliidae indet.	1	1	-	-	-	-	-	-	-	-	-		
uctida	<i>Caucasiproduc-</i> <i>tus</i> ? sp.	9	-	9	_	-	-	_	-	-	-	-		
Prod	Poloniproductus varians	37	-	-	25	-	12	_	_	7	7	-		+
	<i>Devonoproductus</i> cf. <i>minimus</i>	2	-	2	_	-	-	_	_	-	-	-		
	Devonalosia? sp.	2	-	1	1	-	-	-	-	-	-	-		?
etida	Xystostrophia umbraculum	6	-	3	1	_	_	1	_	3	4	_	+	+
Orthote	Iridistrophia cf. undifera	_	-	_	-	-	_	_	-	10	_	_	cf.	cf.
	Skenidioides polonicus	19	12	1	5	-	_	_	_	_	_	_	+	+
	Aulacella prisca	38	-	-	37	-	1	_	-	31	1	1	+	+
	Costisorthis canalicula	15	-	-	11	-	3	1	_	25	4	_	+	+
ida	Tyersella tetragona	86	_	85	1	-	_	_	_	-	_	-	+	
Orth	Biernatium sucoi	13	-	-	13	-	-	-	-	-	-	-		
	Phragmophora schnuri	17	-	-	17	-	-	_	_	2	_	-	+	+
	Schizophoria schnuri	41	-	-	41	-	-	-	_	6	44	-	+	+
	Schizophoria sp.	6	-	1	5	-	-	-	-	-	-	-		
	Schizophoria? sp.	-	-	-	-	-	-	-	-	-	-	1		
	Gypidula biplicata	_	-	-	-	-	_	_	-	1	-	-	+	+
ida	Glyptogypa multiplicata	1	-	-	1	-	-	-	_	1	170	-	+	+
mer	Ivdelinia pulchra	-	-	-	-	-	-	-	-	100	-	-		+
Penta	Devonogypa spinulosa	5	-	-	5	-	_	_	-	24	2	-		+
	Antirhynchonella sublinguifera	_	_	_	_	_	_	_	_	1	2	_		+
а	Kransia (K.) parallelepipeda	72	_	71	1	_	_	_	_	100	_	_	+	+
onellida	Kransia (K.) subcordiformis	46	_	2	_	44	_	_	_	1	_	_	+	+
Shynch	Kransia (F.) signata	56	_	56	_	-	_	_	_	_	_	_	+	
R	Beckmannia beckmanni	49	_	49	_	_	_	_	_	10	_	-	*	*

MIDDLE DEVONIAN BRACHIOPODS FROM NORTHERN MAÏDER

Таха		Localities												
							Africa						Europe	
der	Species	northern Maïder southern Maïder									aïder			
0		TO- TAL	89	93	151	152	153	VE sn1	VE sn2	Af	Md	Mh	RSM	HCM
	Lebanzuella? issoumourensis	250	_	250	_	_	_	_	_	_	_	-		
	Eressella coronata	11	-	-	11	-	-	-	-	1	18	-	+	+
	Glosshypothyridi- na procuboides	1	_	-	1	_	_	_	_	3	-	7	+	+
ida	Septalaria gracilis	9	-	9	-	_	-	-	-	22	-	2	+	+
chonell	Parapugnax denticulatus	8	_	-	_	_	_	_	8	-	_	-		+
Rhyn	Parapugnax anisodontus	_	_	-	_	_	_	_	_	4	_	-	+	+
	Isopoma? sp.	1	-	1	-	_	_	-	_	-	_	-		
	Paulinaerhynchia paulinae	-	-	-	-	-	-	-	-	3?	-	21		
	Rhynchonellida indet.	1	_	1	_	_	_	_	_	2	_	_		
	Atrypa confusa	25	25	_	-	_	-	-	-	90	60	_	+	
	Atryparia dispersa	2	-	-	2	-	-	-	-	120	-	_	+	
	Kyrtatrypa sp.	16	-	13	3	_	_	_	_	_	_	_		?
	Invertina cf. struvei	1	-	1	_	_	_	-	_	1	_	-		
	Kerpina vineta	-	-	-	-	-	-	-	-	77	-	-	+	
	<i>Spinatrypa</i> ennigaldinannae sp. nov.	31	_	_	31	_	_	_	_	48	_	_		
	Spinatrypa globulina	22	_	-	22	-	_	_	_	2	_	_	+	
	Desquamatia microzonata	_	_	-	_	_	_	_	_	_	5	_	+	
oida	<i>Desquamatia</i> cf. <i>subzonata</i>	1	_	_	_	1	_	_	_	_	_	_		cf.
Atry	Desquamatia deserti	_	_	_	_	_	_	_	_	_	_	40		
	Desquamatia circulareformis	_	_	_	_	_	_	_	_	4	_	_		+
	<i>Desquamatia</i> ? sp. 1	-	_	-	_	-	_	_	_	4	_	_		
	Prodavidsonia ebbighasuseni sp. nov.	32	2	_	30	_	_	_	_	1	_	_		
	Davidsonia verneuillii	3	1	-	2	_	_	_	_	_	_	_	+	+
	Carinatina arimaspus	1	_	_	1	_	_	_	_	14	_	_		
	Gruenewaldtia latilinguis	_	_	_	_		_	_	_	5	_	_	+	+
	Peratos arrectus	11	1	-	10	-	_	_	_	70	_	15	+	
ridida	<i>Athyris</i> ex gr. <i>concentrica</i>	59	55	-	4	_	_	_	_	4	_	_	?	?
Athyı	Athyris? aff. curvata	_	_	_	_	_	_	_	_	1	_	_		

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Таха		Localities												
							Africa						Eu	rope
rder	Species			r	norther	n Maïdei	•	r	ſ	sou	thern Ma	nïder	RSM	
		TO- TAL	89	93	151	152	153	VE sn1	VE sn2	Af	Md	Mh		НСМ
	Camarium sp.	-	-	_	_	_	_	-	_	-	-	7		
yridida	<i>Meristella</i> cf. <i>iconensis</i>	_	_	_	_	_	_	_	_	2	_	_	cf.	
	Meristidae indet.	5	1	-	4	-	_	_	-	-	-	-		
Ath	Plectospira ferita	1	-	_	1	_	_	-	_	1	_	-	+	+
	Bifida lepida	4	2	1	1	-	-	-	_	-	4	-	+	+
	Kayseria alvea	13	-	-	13	-	-	-	-	-	2	-	+	
	Spinocyrtia cf. elburzensis	_	_	_	_	_	_	_	_	_	46	_		
	Spinocyrtia cf. ascendens	3	3	_	_	_		_	_	_	_	_	cf.	
	Ivanothyris aculeata	_	_	_	_	_	_	_	_	1	1	_	+	+
	Quiringites arensentiae	_	_	_	_	_	_	_	_	_	35	_		
	<i>Cyrtinopsis</i> cf. <i>brachyptera</i>	_	_	_	_	_	_	_	_	1	_	_		
ida	Echinocoelia dorsoplana	8	_	_	7	_	_	1	_	-	_	_		+
rifer	Yeothyris? sinuata	43	-	-	43	-	_	-	-	2	_	-		+
Spii	Delthyrididae indet.	2	_	-	2	_	_	_	-	-	-	_		
	Quadrithyris cf. macrorhyncha	2	1	1	_	_	_	_	_	_	_	_	cf.	
	<i>Deltospirifer</i> ? sp. nov.	_	_	-	_	_	_	-	_	1	_	_		
	Undispirifer aff. rzhonsnitzkajae	_	_	_	_	_	_	_	_	_	_	7		
	Reticularioidea indet.	_	-	-	_	_	_	_	_	1	_	_		
	Thomasaria simplex	77	_	75	2	_	_	_	_	6	_	2	?	+
	<i>Cyrtina</i> (cf.) <i>sauvagei</i>	4	_	_	4	_	_	_	_	3	-	_	?	+
erinida	<i>Cyrtina</i> cf. <i>multiplicata</i>	9	-	9	_	-	-	-	_	-	_	-		
Spirif	<i>Cyrtina</i> cf. <i>evanescens</i>	4	_	_	4	_	_	_	_	_	_	_		
	<i>Cyrtina</i> ex gr. <i>intermedia</i>	_	_	_	_	_	_	_	_	_	_	2		
			11 <i>104</i>	24 659	40 <i>381</i>	2 45	3 16	4 4	1 8	48 <i>837</i>	21 <i>420</i>	11 106	36	36
	TOTAL				120	60 09					62 1363		(43)	(41)
						25	87 572						(5	47 55)

The rank-abundance distributions (Whittaker plots; Magurran, 2004) for selected assemblages and for aggregated samples are given in Figure 45. Curves for single assemblages are of two kinds (Fig. 45A):

- assemblages characterised by smaller absolute numbers of taxa (N < 25) and low evenness (steep slope of the curve): localities 89, 93, and Md;
- assemblages characterised by greater absolute numbers of taxa (N > 35) and higher evenness (shallow gradient of the curve): localities 151 and Af.

This reflects diverse ecological settings of the faunules. At a regional scale the assemblages are closely comparable (Fig. 45B).

Stratigraphic distribution of the studied brachiopods

Most brachiopod species dealt with in the present paper are late Eifelian in age (localities 151, 153, most probably also localities 89 and VEsn1). Other brachiopods may be dated to an interval probably spanning the upper Eifelian and a part of the Givetian (locality 93), whereas only two are dated confidently solely to the Givetian (locality 152). Among the brachiopods, for which the age may be established with relative confidence, one may distinguish several different situations:

- species known solely from the Eifelian both in the study area and in Europe (Eifel, Holy Cross Mountains): Devonaria minuta, Phragmophora schnuri, Eressella coronata, Kayseria alvea, Bifida lepida;
- species known from the Eifelian and the Givetian, both in the study area and in Europe: Leptagonia analogaeformis, Skenidioides polonicus and Kransia parallelepipeda;
- species known from the Eifelian in the study area, but from the Givetian in other regions: *Devonaria* gevini (Givetian of Northern Sahara; Racheboeuf, 1990), *Biernatium sucoi* (Givetian of Spain, García-Alcalde, 2018), *Echinocoelia dorsoplana* (Givetian of the Holy Cross Mts.; Gürich, 1896; Halamski, 2004a);
- species known from the Eifelian to Givetian interval in the study area, but from the Emsian to Eifelian in Europe: *Tyersella tetragona* (see text for details);
- species known solely from the Givetian both in the study area and in Europe: *Kransia subcordiformis* (Schmidt, 1941a; Halamski, 2004a);

Desquamatia cf. *subzonata* is known solely from the Givetian in the study area. *Desquamatia subzonata* is known from the upper Eifelian to Givetian of the Holy Cross Mts. (Biernat, 1964; Halamski, 2004a); it has not been reported from the Eifel heretofore, although Godefroid (1995) identified *D*. cf. *subzonata* from the upper Eifelian of southern Belgium.

As far as the material studied allows (given the locality and dating uncertainties discussed in the Introduction), one might conclude that the stratigraphic ranges of brachiopods in the study area are often the same as in Europe, but not seldom markedly different, when compared to Europe or other regions.

Finally, as far as the new species described in the present paper are concerned, *Spinatrypa ennigaldinannae* sp. nov.



Fig. 44. Rarefaction curves of the Maïder brachiopod assemblages: selected assemblages from northern Maïder (**A**); assemblages from southern Maïder (**B**; data after Halamski and Baliński, 2013); aggregated assemblages (**C**). Abbreviations of assemblages as in Figure 1 and Table 3.

is known from the Eifelian only, whereas *Prodavidsonia ebbighauseni* sp. nov. is known from the Eifelian and the Givetian.

Biogeography

In general, the Middle Devonian brachiopod fauna discussed herein has undeniable Rhenish affinities, as evidenced by numerous species in common between the Anti-Atlas on the one hand and the Eifel and the Holy Cross Mountains on the other (Tab. 3). Namely, having retracted the six species unfit for a detailed analysis (greyed cells in Table 3), the ratio of the species from Maïder present also in Europe (either in the Rhenish Slate Mts. or in the Holy Cross Mts.) has a minimum value of $47/81 \approx 58\%$, but could be as high (with the doubtful presences counted as presences) as $55/81 \approx 68\%$.

Region			Aggregated								
		no	rthern Maïo	ler		SO	uthern Maïo	ler	Maïder	Maïder	Maïder
Index	89	89 93		152	153	Af	Md	Mh	north	south	total
Simpson $1 - D$	0.65	0.79	0.93	0.04	0.40	0.92	0.78	0.78	0.93	0.94	0.96
Shannon H	1.41	1.99	3.04	0.11	0.70	2.84	1.99	1.82	3.20	3.17	3.61
Evenness e ^H / S	0.371	0.31	0.54	0.56	0.67	0.35	0.35	0.56	0.41	0.39	0.43
Berger- Parker	0.53	0.39	0.11	0.98	0.75	0.14	0.41	0.38	0.21	0.13	0.10
Chao1	14.3	33.0	50.0	2.0	3.0	66.5	22.0	11.3	70.3	67.5	93.5

Regional diversity indices and asymptotic estimators of species richness for the brachiopod fauna studied, for southern Maïder, and for Maïder as a whole. Absolute numbers of species and individuals are given in Table 3.



Fig. 45. Rank-abundance distributions (Whittaker plots) of selected assemblages (**A**) and of the aggregated samples (**B**) for northern Maïder, southern Maïder, and both regions together. Abbreviations of assemblages as in Figure 1 and Table 3.

This is in line with the conclusions made on the basis of the fauna from southern Maïder (Halamski and Baliński, 2013), but may be contrasted with the distinct Bohemian affinities of the late Emsian brachiopod faunas from Hamar Laghdad (Anti-Atlas, about 100 km NEE from the study area), described by Halamski and Baliński (2018b) and Mergl (2018). A detailed biogeographic study will be given separately.

CONCLUSIONS (BY ATH, AB & JK)

 A relatively diverse (60 species) Middle Devonian fauna is present in Jbel Issoumour (northern Maïder). It is described on the basis of a rich collection (over 1,200 specimens), made by the late Volker Ebbighausen. Given the circumstances, under which the collection was made and transferred to the Museum für Naturkunde in Berlin, details of outcrops and their stratigraphic assignments are less precise than it might be desired. Nonetheless, most of the fauna is assumed with reasonable certainty to have originated in the Taboumakhlouf Formation (upper Eifelian) and the overlying Bou Dib Formation (upper Eifelian to Givetian). Stratigraphic correlations are made mainly on the basis of co-occurring trilobites.

- 2. The Middle Devonian brachiopod fauna from northern Maïder, studied herein, 60 species and from southern Maïder, studied by Halamski and Baliński (2013), 62 species, totals 87 species. This is a rather low value in comparison with other coeval faunas and probably means that the sampling of the alpha-diversity of the region is still incomplete.
- Spinatrypa ennigaldinannae Halamski and Baliński sp. nov. [= Spinatrypa cf. trigonella sensu Halamski and Baliński, 2013 non S. trigonella (Davidson, 1882)] is characterised by transverse adult shells, typically about 16–18 mm wide and with 19–22 ribs. The age of the type level is late Eifelian.
- 4. Prodavidsonia ebbighauseni Halamski and Baliński sp. nov. differs from all the species of Prodavidsonia previously described in having a nearly flat (very weakly convex) dorsal valve and a convex ventral valve. The age of the type level is late Eifelian.
- 5. *Thomasaria simplex*, analysed on the basis of an uncommonly large sample (77 specimens), is shown to be extremely variable, especially in the interarea position, but also in the shape of the dorsal valve, tongue, and costation. The variability of this sample encompasses some taxa within that genus, described by previous authors as different from *T. simplex*.
- 6. As far as can be stated on the basis of the available material, the stratigraphic distributions of the brachiopods studied are largely the same as in Europe, but in some cases different from those in Europe or other regions.
- The brachiopod fauna is of clear Rhenish affinities with numerous species in common with the Eifel and the Holy Cross Mountains.

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Appendix 1

Biometric characteristics of selected species studied

Measurements in millimetres except as noted. Measurements in Roman typeface (those of the holotypes in boldface), statistics in Italics. Abbreviations: Har – area height; Jar – inclination of the interarea (in degrees); L – length; Ld – dorsal valve length; Nd – total number of ribs on the dorsal valve; Ndf – number of ribs on the fold of the dorsal valve; Ndl – number of ribs on the left flank of the dorsal valve; Ndr – number of ribs on the right flank of the dorsal valve; Nvl – number of ribs on the left flank of the ventral valve; Nvr – number of ribs on the right flank of the ventral valve; Nvr – number of ribs on the right flank of the ventral valve; Nvs – number of ribs on the sulcus of the ventral valve; R_{sd} – number of ribs per 5 mm at 5 mm from umbo on the dorsal valve; R_{ad} – number of ribs per 5 mm at 5 mm from umbo on the dorsal valve; (sd - mean); W – width; w – width of the sulcus; War – interarea width.

Skenidioides polonicus (Gürich, 1896)

	W	L	Ld	Т	Nd	W/L	Ld/L	Nd/W	T/L
MB.B.9458.1	5.5	4.7	3.7	2.4	24	1.17	0.79	4.36	0.51
MB.B.9458.2	5.9	4.9	4.5	2.7	23	1.20	0.92	3.90	0.55
MB.B.9458.3	6.0	5.4	4.9	2.9	19	1.11	0.91	3.17	0.54
MB.B.9458.4	6.6	6.1	5.0	3.6	23	1.08	0.82	3.48	0.59
MB.B.9458.5	6.9	5.6	4.7	3.0	26	1.23	0.84	3.77	0.54
MB.B.9458.6	5.7	3.7	3.7	2.3	21	1.54	1.00	3.68	0.62
MB.B.9458.7	5.0	4.1	3.6	2.4	18	1.22	0.88	3.60	0.59
MB.B.9458.8	4.8	4.1	3.5	2.8	18	1.17	0.85	3.75	0.68
MB.B.9458.9	4.3	3.6	3.1	2.0	19	1.19	0.86	4.42	0.56
MB.B.9458.10	4.4	3.6	3.4	2.0	23	1.22	0.94	5.23	0.56
MB.B.9458.11	6.8		5.0		22			3.24	
MB.B.9477	5.0	4.9	4.3	2.7	20	1.02	0.88	4.00	0.55
mean	5.58	4.61	4.12	2.62	21.3	1.197	0.881	3.883	0.571
sd	0.860	0.820	0.661	0.447	2.461	0.1256	0.0570	0.5462	0.0457
v	0.154	0.178	0.160	0.171	0.115	0.1050	0.0647	0.1407	0.0801

Costisorthis canalicula (Schnur, 1851)

	W	L	Т	W/L	T/L
MB.B.9394.1	16.2	14.6	8.6	1.11	0.59
MB.B.9394.2	15.9	14.3	7.2	1.11	0.50
MB.B.9394.3	14.7	13.5	7.8	1.09	0.58
MB.B.9394.4	13.8	13.3	8.2	1.04	0.62
MB.B.9394.5	12.9	11.8	6.3	1.09	0.53
MB.B.9394.6	15.8	14.2	8.4	1.11	0.59
MB.B.9394.7	14.9	13.0	6.7	1.15	0.52
MB.B.9394.8	13.9	12.2	7.8	1.14	0.64
MB.B.9394.9	12.9	11.6	7.4	1.11	0.64
MB.B.9394.10	12.9	10.9	6.3	1.18	0.58
MB.B.9465	23.0	19.7		1.17	
mean	15.17	13.55	7.47	1.120	0.578
sd	2.739	2.256	0.794	0.0382	0.0453
v	0.181	0.166	0.106	0.0342	0.0784

	W	L	Т	W/L	T/L
MB.B.9403.1	16.8	14.3	7.2	1.17	0.50
MB.B.9403.2	17.5	15.0	7.7	1.17	0.51
MB.B.9403.3	21.4	18.6	8.7	1.15	0.47
MB.B.9403.4	22.2	18.6	9.0	1.19	0.48
MB.B.9403.5	24.1	20.3	10.7	1.19	0.53
MB.B.9403.6	23.8	19.7	9.2	1.21	0.47
MB.B.9403.7	20.4	17.2	9.6	1.19	0.56
MB.B.9403.8	13.0	11.5	5.1	1.13	0.44
MB.B.9403.9	17.5	15.8	7.9	1.11	0.50
MB.B.9403.10	17.2	14.6	7.3	1.18	0.50
MB.B.9403.11	20.8	17.7	7.4	1.18	0.42
MB.B.9403.12	18.1	15.6	6.9	1.16	0.44
MB.B.9403.13	16.8	15.4	7.4	1.09	0.48
MB.B.9403.14	17.4	14.5	8.1	1.20	0.56
MB.B.9403.15	14.4	12.8	5.9	1.13	0.46
MB.B.9403.16	13.9	10.5	4.9	1.32	0.47
MB.B.9403.17	17.0	14.4	6.8	1.18	0.47
MB.B.9403.18	17.1	14.6	6.8	1.17	0.47
MB.B.9403.19	19.6	16.3	8.2	1.20	0.50
MB.B.9403.20	17.7	14.8	7.3	1.20	0.49
MB.B.9403.21	16.1	13.9	6.0	1.16	0.43
MB.B.9403.22	14.9	13.2	6.1	1.13	0.46
MB.B.9403.23	12.9	12.2	5.6	1.06	0.46
MB.B.9403.24	11.5	9.6	4.0	1.20	0.42
MB.B.9403.25	17.8	15.0	6.5	1.19	0.43
MB.B.9403.26	19.4	16.2	6.7	1.20	0.41
MB.B.9403.27	15.2	13.4	6.1	1.13	0.46
MB.B.9403.28	19.9	17.3	7.4	1.15	0.43
MB.B.9403.29	14.2	12.7	6.0	1.12	0.47
MB.B.9403.30	15.0	13.8	5.1	1.09	0.37
mean	17.45	14.98	7.05	1.164	0.469
sd	3.091	2.499	1.467	0.0482	0.0412
ν	0.177	0.167	0.208	0.0415	0.0879

Tyersella tetragona (Roemer, 1844)

Septalaria gracilis (Gürich, 1896)

	W	L	Т	W	Ndl	Ndf	Ndr	Nvl	Nvs	Nvr	W/L	Nd/W
MB.B.9425.1	10.6	8.1	7.0	6.9	8	6	8	9	7	8	1.31	0.65
MB.B.9425.2	13.9	12.8	9.8	9.8			11		9		1.09	0.71
MB.B.9425.3	10.3	8.8	7.7	8.3	8	7		9	8	9	1.17	0.81
MB.B.9425.4	9.4	8.2	5.8	6.8	10		9		9		1.15	0.72
MB.B.9426.1	12.3	9.6	7.1	9.3	9	9	9	10	8	9	1.28	0.76
MB.B.9426.2	12.0	10.5	9.0	9.5	6	7	6		6		1.14	0.79
MB.B.9426.3	11.7	9.8	8.5	7.3	12		10	9	10	10	1.19	0.62
MB.B.9426.4	11.8	10	8.1	9.8	8	11	10		10	9	1.18	0.83
MB.B.9426.5	10.3	9.7	8.0	8.5					8		1.06	0.83
mean	11.37	9.72	7.89	8.47	8.7	8.0	9.0	9.3	8.3	9.0	1.175	0.746
sd	1.279	1.332	1.112	1.152	1.75	1.79	1.51	0.43	1.25	0.63	0.0761	0.0710
v	0.113	0.137	0.141	0.136	0.201	0.23	0.17	0.05	0.15	0.07	0.0648	0.0951

Spinatrypa ennigaldinannae Halamski and Baliński sp. nov.

	W	L	Т	W	Nd	R	R.,	W/L	T/L	w/W
MB.B.9396.1	20.2	17	11.4	11.2	22	4.25	6.25	1.19	0.67	0.55
MB.B.9396.2	16.0	15.7	11.3	8.6	22	4.5	6	1.02	0.72	0.54
MB.B.9396.3	16.9	15.0	8.6	9.6	18	4	5	1.13	0.57	0.57
MB.B.9396.4	20.2	18.8	13.2	11.5	19	3	5	1.07	0.70	0.57
MB.B.9396.6	19.3	17.3	13.1	8.7	22	4	6	1.12	0.76	0.45
MB.B.9396.7	18.1	17.2	11.7	9.8	20	3.25	6	1.05	0.68	0.54
MB.B.9396.8	17.3	16.0	10.8	10.1	19	4		1.08	0.68	0.58
MB.B.9396.9	18.2	16.6	9.6					1.10	0.58	
MB.B.9396.10	16.0	15.3	8.7	12.3		3.5	4.5	1.05	0.57	0.77
MB.B.9396.11	16.8	15.8	8.8	9.2		3.5	6	1.06	0.56	0.55
MB.B.9396.12	17.8	17.0	10.1	11.8				1.05	0.59	0.66
MB.B.9396.13	19.6	16.9	9.5	9.4				1.16	0.56	0.48
MB.B.9396.14	17.8	16.9	8.8	11	22	4.75		1.05	0.52	0.62
MB.B.9396.15	15.2	14.9	8.2	7.9	20	4	6.5	1.02	0.55	0.52
MB.B.9396.16	16.9	15.9	8.2	9.4				1.06	0.52	0.56
MB.B.9396.17	13.4	13.9	8.1	7.7	18	4.25	5	0.96	0.58	0.57
MB.B.9396.18	12.9	11.3	7.8	8.0	16		6	1.14	0.69	0.62
MB.B.9396.19	13.4	12.5	8.0	8.4			5.5	1.07	0.64	0.63
MB.B.9396.20	14.8	13.9	7.4	8.2			5	1.06	0.53	0.55
MB.B.9396.21	12.1	12.4	6.1	7.5	13		4.75	0.98	0.49	0.62
mean	16.65	15.52	9.47	9.49	19.3	3.9	5.5	1.071	0.608	0.577
sd	2.355	1.860	1.861	1.437	2.65	0.49	0.62	0.0549	0.0751	0.0673
ν	0.141	0.120	0.151	0.138	0.14	0.13	0.11	0.0513	0.1235	0.1167

Spinatrypa globulina Copper, 1967

	W	L	Т	W	Nd	W/L	T/L	w/W
MB.B.9388.22	26	23.7	14.2	12.6	13	1.10	0.60	0.53
MB.B.9388.1	24.8	23.2	13.4	16.1	17	1.07	0.58	0.69
MB.B.9388.2	22.7	21.3	11.7	7.9	17	1.07	0.55	0.37
MB.B.9388.3	20.5	21.0	12.1	13.8	14	0.98	0.58	0.66
MB.B.9388.4	24.1	23.7	15.5	13.2		1.02	0.65	0.56
MB.B.9388.6	24.7	23.5	16.6	12.3	17	1.05	0.71	0.52
MB.B.9388.7	23.2	22.4	16.4	13.4	17	1.04	0.73	0.60
MB.B.9388.8	18.9	20.4	16.8	10.0		0.93	0.82	0.49
MB.B.9388.9	21.2	22.8	11.8	12.3	15	0.93	0.52	0.54
MB.B.9388.10	20.8	20.3	13.4		17	1.02	0.66	
MB.B.9388.11	23.6	22.6	12.5	10.9	15	1.04	0.55	0.48
MB.B.9388.12	21.6	19.0	10.8	10.6	13	1.14	0.57	0.56
MB.B.9388.13	19.5	19.5	11.2		14	1.00	0.57	
MB.B.9388.14	19.0	19.2	11.0		14	0.99	0.57	
MB.B.9388.15	18.7	16.0	9.6	14.5	11	1.17	0.60	0.91
MB.B.9388.16	20.8	17.8	9.6	14.0	14	1.17	0.54	0.79
mean	21.88	21.03	12.91	12.43	14.9	1.044	0.613	0.592
sd	2.257	2.223	2.322	2.072	1.85	0.0712	0.0796	0.1348
ν	0.103	0.106	0.180	0.167	0.124	0.0682	0.1299	0.2277

Prodavidsonia ebbighauseni Halamski and Baliński sp. nov.

	W	L	Т	W/L	T/L		W	L	Т	W/L	T/L
MB.B.9423.1	17.4	12.0	3.1	1.45	0.26	MB.B.9446.2	13.9	8.9	2.6	1.56	0.29
MB.B.9423.2	14.9	11.2	3.2	1.33	0.29	MB.B.9446.7	13.4	9.2	2.0	1.46	0.22
MB.B.9423.3	13.1	10.8	3.7	1.21	0.34	MB.B.9446.8	13.1	10.3	2.5	1.27	0.24
MB.B.9423.4	15.3	11.7	2.9	1.31	0.25	MB.B.9446.9	10.7	9.6	3.1	1.11	0.32
MB.B.9423.5	14.1	10.8	2.7	1.31	0.25	MB.B.9446.10	13.2	10.0	2.8	1.32	0.28
MB.B.9423.6	12.2	9.0	2.6	1.36	0.29	MB.B.9446.11	14.7	10.6	2.6	1.39	0.25
MB.B.9423.7	14.0	10.7	3.0	1.31	0.28	MB.B.9446.12	14.9	12.2	3.1	1.22	0.25
MB.B.9457.1	13.5	9.5	1.9	1.42	0.20	MB.B.9446.13	13.9	10.5	3.9	1.32	0.37
MB.B.9457.2	13.5	10.5	2.8	1.29	0.27	MB.B.9446.14	15.5	10.6	3.0	1.46	0.28
MB.B.9446.1	14.8	11.1	3.6	1.33	0.32	MB.B.9446.15	14.5	10.8	2.7	1.34	0.25
MB.B.9446.3	14.4	12.0	3.6	1.20	0.30	MB.B.9446.16	12.3	8.1	2.3	1.52	0.28
MB.B.9446.6	15.8	11.8	3.3	1.34	0.28	mean	14.19	10.4	2.92	1.348	0.277
MB.B.9446.4	15.2	11.2	3.1	1.36	0.28	sd	1.420	1.052	0.489	0.1067	0.0374
MB.B.9446.5	16.4	10.8	3.0	1.52	0.28	ν	0.100	0.100	0.167	0.0792	0.1351

Thomasaria simplex (Phillips, 1841)

	L	W	Т	War	Har	Jar	Ld	W/L	Har/Ld
MB.B.9408.1	13.9	17.9	9.6	13.2	5.9	100	12.5	1.29	0.47
MB.B.9408.2	19.0	25.8	18.2	19.7	11.6	60	19.2	1.36	0.60
MB.B.9408.3	10.5	14.5	10.1	11.8	7.9	68	10.5	1.38	0.75
MB.B.9408.4	8.4	11.9	6.6	8.7	4.4	75	8.4	1.42	0.52
MB.B.9408.5	7.7	9.9	6.2	7.5	4.4	64	7.7	1.29	0.57
MB.B.9408.7	10.5	16.3	8.7	11.5	5.9	69	10.5	1.55	0.56
MB.B.9408.9	8.6	13.5	8.1	10.8	6.1	65	8.6	1.57	0.71
MB.B.9408.10	9.4	14.1	8.7	11.4	6.1	80	9.1	1.50	0.67
MB.B.9408.11	10.0	15.1	9.9	11.5	6.5	62	9.7	1.51	0.67
MB.B.9408.12	10.4	14.9	9.7	10.5	7.0	68	10.4	1.43	0.67
MB.B.9408.13	10.6	15.3	9.2	11.7	6.1	73	10.6	1.44	0.58
MB.B.9408.14	11.3	14.4	10.9	10.4	7.4	56	11.3	1.27	0.65
MB.B.9408.15	10.7	16.1	9.4	13.3	8.9	42	10.7	1.50	0.83
MB.B.9408.16	11.6	16.9	10.0	10.7	5.5	64	11.6	1.46	0.47
MB.B.9408.17	11.3	15.8	9.7	13.5	6.3	98	10.5	1.40	0.60
MB.B.9408.18	11.8	16.3	9.8	10.7	5.4	82	11.6	1.38	0.47
MB.B.9408.19	11.3	16.3	10.9	13.0	8.7	57	11.3	1.44	0.77
MB.B.9408.20	11.0	17.0	9.0	10.7	5.5	80	11.0	1.55	0.50
MB.B.9408.21	11.5	16.8	10.2	13.5	8.8	48	11.5	1.46	0.77
MB.B.9408.22	12.1	17.3	11.3	13.4	6.7	69	12.1	1.43	0.55
MB.B.9408.23	13.6	19.5	13.8	14.9	8.9	63	13.6	1.43	0.65
MB.B.9408.24	12.5	19.0	11.5	13.2	7.4	86	12.5	1.52	0.59
MB.B.9408.25	15.5	19.9	16.5	14.5	10.8	84	15.5	1.28	0.70
MB.B.9408.26	15.9	20.6	17.8	16.7	11.1	82	15.9	1.30	0.70
MB.B.9408.27	15.5	21.7	15.0	17.5	9.1	76	15.5	1.40	0.59
MB.B.9408.28	17.2	24.1	17.3	19.7	12.3	71	17.2	1.40	0.72
MB.B.9408.29	18.4	25.4	19.3	21.7	12.2	76	18.4	1.38	0.66
MB.B.9408.30	18.6	25.3	18.4	19.0	12.1	89	18.6	1.36	0.65
MB.B.9408.31	18.5	26.3	19.2	21.6	13	67	18.5	1.42	0.70
MB.B.9408.32	11.4	15.3	8.2	11.3	4.8	93	10.6	1.34	0.45
MB.B.9408.33	11.6	14.6	8.5	10.9	4.3	82	11.6	1.26	0.37
MB.B.9408.34	13.3	16.4	7.4	10.1	3.8	115	11.7	1.23	0.32
MB.B.9408.35	12.8	16.9	9.2	10.6	4.1	108	11.5	1.32	0.36
MB.B.9408.36	14.2	17.5	9.5	12.1	3.6	116	12.4	1.23	0.29
MB.B.9408.37	14.4	18.1	9.6	12.3	4.3	118	12.6	1.26	0.34
MB.B.9408.38	13.4	18.4	10.1	13.0	5.5	94	12.9	1.37	0.43
MB.B.9408.39	14.6	17.4	9.2	10.2	4.6	108	12.6	1.19	0.37
MB.B.9408.40	15.1	18.5	11.3	13.7	3.8	112	13.2	1.23	0.29
MB.B.9408.41	14.9	18.4	10.3	11.4	4.6	112	13.5	1.23	0.34
MB.B.9408.42	17.2	20.4	11.2	14.4	4.8	110	14.7	1.19	0.33
MB.B.9408.43	18	21.0	12.0	14.9	5.9	141	14.3	1.17	0.41
MB.B.9408.44	19.8	20.7	18	19.3	12.5	81	15.8	1.05	0.79
mean	13.29	17.89	11.42	13.35	7.11	82.5	12.66	1.362	0.558
sd	3.128	3.644	3.608	3.390	2.778	21.486	2.83	0.1173	0.1529
ν	0.235	0.204	0.316	0.254	0.391	0.261	0.22	0.0861	0.2739