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MIDDLE DEVONIAN UNCINULOIDS (BRACHIOPODA, RHYNCHONELLIDA) FROM NORTH AFRICA AND CENTRAL EUROPE

Adam T. HALAMSKI[1*], Andrzej BALIŃSKI[1] & Ulrich JANSEN[2]

[1]*Institute of Paleobiology, Polish Academy of Sciences, ul. Twarda 51/55, 00-818 Warszawa, Poland; e-mails: ath@twarda.pan.pl, balinski@twarda.pan.pl*
[2]*Senckenberg Forschungsinstitut und Naturmuseum, Paläozoologie III, Senckenberganlage 25, 60325 Frankfurt am Main, Germany; e-mail: ulrich.jansen@senckenberg.de*
**Corresponding author*

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Abstract: The paper includes a taxonomic revision of four externally similar Middle Devonian rhynchonellide species from northwestern Africa (Maïder, Tindouf Syncline) and Central Europe (Eifel, Bergisches Land, Holy Cross Mts.), considered in recent papers as representatives of *Kransia* Westbroek, 1967 or *Nalivkinaria* Rzhonsnitskaya, 1968. All four possess a septalium and a multilamellate cardinal process, the assignment to *Nalivkinaria*, having a bifid cardinal process, is therefore clearly inappropriate. *Lebanzuella*? *issoumourensis* (Drot, 1971) is present in the Givetian of Africa; two subspecies, *L.*? *issoumourensis issoumourensis* from Jbel Issoumour and *L.*? *issoumourensis smarensis* ssp. nov. from Western Sahara, are distinguished by their biometric characteristics. The other two species are included in *Kransia* (*Fatimaerhynchia*) subgen. nov. differing from *Kransia* (*K.*) in the presence of a septalium; the occurrence of such a variable structure is considered to be justification for distinction at the subgenus level. *Kransia* (*Fatimaerhynchia*) *goldfussii* (Schnur, 1853) is an Eifelian species. *Kransia* (*Fatimaerhynchia*?) aff. *goldfussii* from the Givetian of Bilveringsen is a separate species (larger, more transverse, more strongly ornamented), which is not described because of insufficient material. *Kransia* (*Fatimaerhynchia*) *signata* (Schnur, 1851) is present in the Middle Devonian of Jbel Issoumour, the middle Eifelian of the Eifel and the (upper?) Givetian of the Holy Cross Mountains.

Key words: Systematics, Brachiopoda, Rhynchonellida, Devonian, Germany, Poland, Morocco.

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INTRODUCTION

Purpose of the present paper

In 1971, the French palaeontologist Jeannine Drot described a new brachiopod species, *Kransia* (?) *issoumourensis*, on the basis of nine specimens collected on the Jbel Issoumour in the eastern Anti-Atlas (Morocco). During the work on Middle Devonian faunas from northern Maïder (incl. Jbel Issoumour; ATH & AB) and from the south-western part of the Tindouf Syncline (UJ & ATH) it has been revealed that the above-mentioned species was one of the most common brachiopods at both localities (about two hundred and fifty and nearly five hundred specimens, respectively). Therefore, drawing up a joint treatment of this species seemed a more appropriate solution than producing separate accounts that would necessarily have to rely significantly on each other. It also appeared useful to revise externally similar species from Central Europe, first described as *Terebratula Goldfussii* Schnur, 1853 and *T. Wahlenbergii* var. *signata* Schnur, 1851.

The objectives of the present paper are therefore as follows: (i) to re-describe the Middle Devonian brachiopod originally described as *Kransia* (?) *issoumourensis* on the basis of new and much richer material, deciding in particular whether any of previous proposals on its assignment to the genera *Kransia* or *Nalivkinaria* are appropriate; (ii) to compare it with externally similar European species originally described as *Terebratula Goldfussii* Schnur, 1853 and *Terebratula Wahlenbergii* var. *signata* Schnur, 1851; (iii) to discuss the applicability of the presence of a septalium for distinguishing rhynchonellide genera and subgenera, proposing *Kransia* (*Fatimaerhynchia*) subgen. nov. as a result.

Institutional abbreviations are: GIUS, Uniwersytet Śląski, Sosnowiec, Poland; MB, Museum für Naturkunde, Berlin, Germany; MNHN, Muséum national d'Histoire naturelle, Paris, France; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany.

Other abbreviations: *s.n.*, *sine numero*, without a number (for specimens included in a museum collection but lacking an inventory number).

History of research

It would be tedious to repeat here the history of studies in the Rhenish Slate Mountains (Germany), where Devonian brachiopods were figured as early as the mid-seventeenth century (Worm, 1655, p. 83). Monographs and major papers of interest for the present work include: Schnur (1851, 1853), Torley (1934), and Schmidt (1941). Also for the history of palaeontological investigations in the Moroccan Anti-Atlas and in the Holy Cross Mts. of Poland, the reader may be referred, for example, to Halamski and Baliński (2013, pp. 243–245) for the former and to Halamski (2008, p. 43) for the latter.

On the other hand, it may be useful to enlarge upon the history of investigations of Devonian faunas in the southwestern part of the Tindouf Syncline and adjacent areas. The territory in question here is apparently most often referred to as Western Sahara (sometimes also West Sahara, former Spanish Sahara, now under the control of the Kingdom of Morocco). Care should be taken, however, to distinguish cases where Western Sahara denotes simply the western part of the Sahara Desert (as for example in Guerrak, 1988). In Western Sahara most attention was paid to the Middle and lowermost Upper Devonian reefs, beginning with Dumestre and Illing (1967). Earlier investigations were summarised by Wendt and Kaufmann (2006, p. 340). More recently, a geological expedition was organised by scientists from the Senckenberg Institute in cooperation with M. Bensaïd (Ministère de l'Énergie et des Mines, Rabat), A. El Hassani (University of Rabat) and E. Rjimati (Geological Survey of Laâyoune); it took place in 2002 (Königshof *et al.*, 2003). Results of the subsequent palaeontological studies were published by Königshof and Kershaw (2006), Ernst and Königshof (2008), and Schindler and Wehrmann (2011). It may be useful to recall that due to political circumstances this region was of limited access to Europeans and that getting the necessary authorisations for research involved His Majesty the King Mohammed VI of Morocco (Wendt and Kaufmann, 2006, p. 349). The conditions of geological work in Western Sahara were rather difficult, insofar as leaving footpaths was strongly unrecommended owing to the presence of landmines. A preliminary account of the entire brachiopod fauna collected during the 2002 expedition was presented at the Brachiopod Congress in Copenhagen (Schemm-Gregory and Jansen, 2005) and the descriptions of two species were published separately (*Paracrothyris* sp.: Schemm-Gregory and Jansen, 2008; *Cyrtospirifer tindoufensis*: Schemm-Gregory, 2011).

The Zemmour Noir, covered by the monumental work of Sougy (1964), is situated immediately to the south of that described previously. The wide array of geographical and geological data as well as the availability of Sougy's collections at the MNHN provide the reason why this monograph is a necessary reference for palaeontologists working in the Tindouf Syncline.

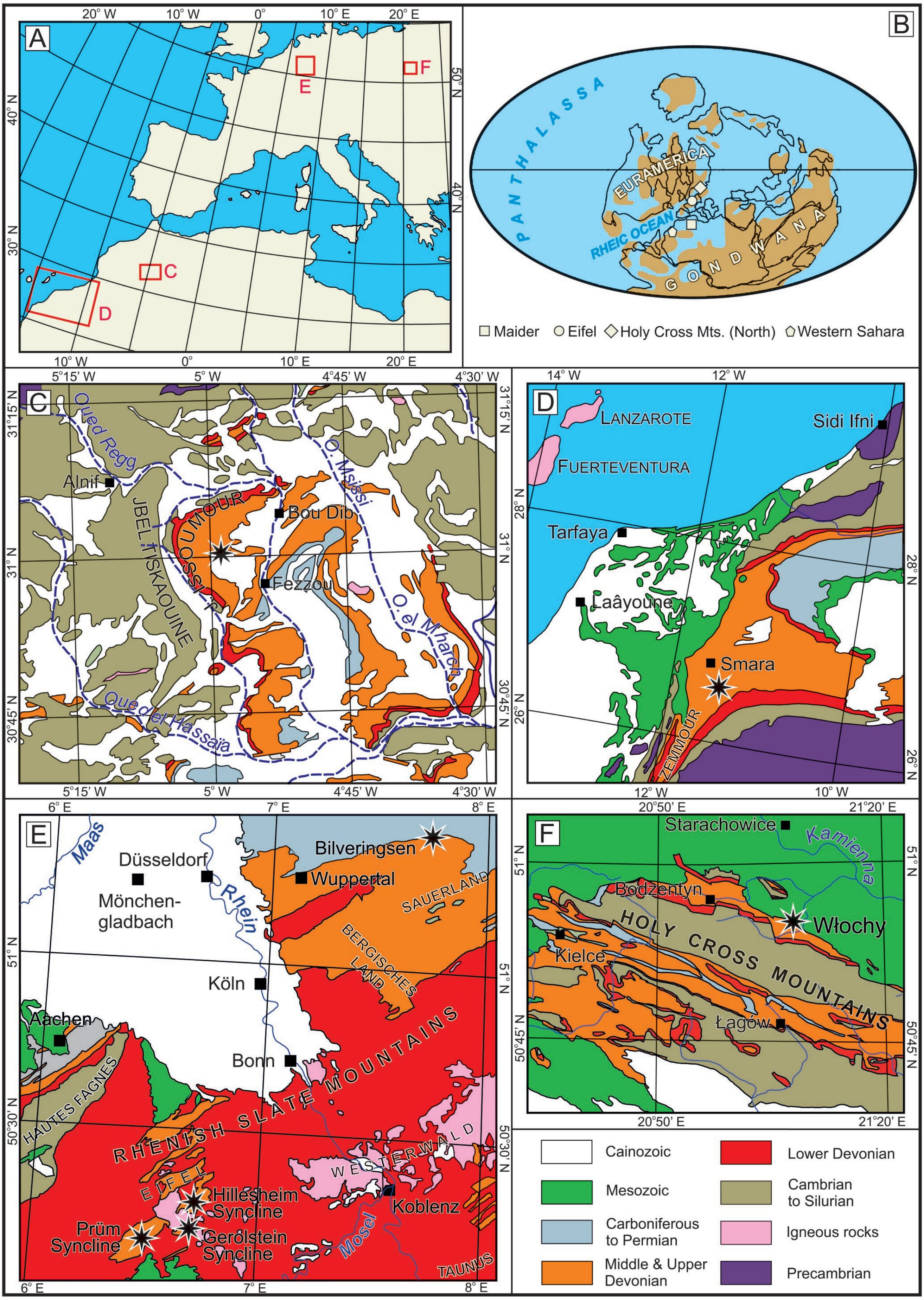
MATERIAL AND METHODS

The investigated collections of *Kransia* (?) *issoumourensis* include approximately topotypic (i.e., from the same area but not necessarily the same outcrop) collections from the Jbel Issoumour (coll. V. Ebbighausen, MB) and those from the environs of the town of Smara (coll. U. Jansen, 2002, SMF). The type material could not be traced in the MNHN. The material of *Terebratula goldfussii* and *T. signata* comes for the most part from the Eifel, was mostly investigated by Schmidt (1941), and along with some newer material is kept in the SMF. Two specimens of *T. signata* come from the Holy Cross Mts. The only available material of *K.* aff. *goldfussii* is Torley's collection from Bilveringsen (SMF).

Maïder (Fig. 1A–C). Maïder (Ma'der) is a Variscan syncline situated in the eastern part of the Anti-Atlas (Fig. 1C). The material studied, collected by V. Ebbighausen, comes from Jbel Issoumour and is described as follows: "Lesefunde Mergelhänge Jbel Issoumour 11 km SW Bou-Dib, Mittel-Devon". Unfortunately, no other data are available (see a few details on this collection in Halamski and Baliński, 2018, p. 30). The lithostratigraphy of the Maïder was elaborated by Hollard (1974) and the data on conodont stratigraphy were given by Kaufmann (1998).

Western Sahara (Fig. 1A–B, D). The material described in the present work was collected by U. Jansen in 2002 at two localities situated in the Sabkhat Lafayrina reef complex (Fig. 1D; Königshof and Kershaw, 2006; Ernst and Königshof, 2008): Bryo1 (26°32.877'N 11°29.657'W; including samples marked as SL) and locality 26 (26°33.069'N 11°29.526'W). Brachiopods were collected from Unit A *sensu* Königshof and Kershaw (2006), and the age of the strata might be late Givetian (Ernst and Königshof, 2008, p. 3). Additional material comes from locality 25 (26°31.425′N, 11°31.863′W), a detritic limestone bed containing corals and crinoids, situated in "Reef 7".

Fig. 1. Geographic, palaeogeographic, and geologic setting of the brachiopods studied. **A.** Geographic map of Europe and northwestern Africa showing the location of the four detailed geologic maps (C to F). **B.** Devonian palaeogeography showing the four areas discussed (after Halamski and Baliński, 2013; modified after Scotese and McKerrow, 1990; Golonka *et al.*, 2006 and Murphy *et al.*, 2011). **C.** Geologic map of the Maïder Syncline, Anti-Atlas, Morocco (simplified after Hollard *et al.*, 1985). **D.** Geologic map of the western part of the Tindouf Syncline and adjacent areas (simplified after Asch, 2005). **E.** Geologic map of part of western Germany (simplified after Bundesanstalt für Geowissenschaften und Rohstoffe, 1993). **F.** Geologic map of the Holy Cross Mountains (simplified after Samsonowicz, 1966). Asterisks denote localities (or groups of localities in C) discussed in the text; squares denote major towns (for reference purposes). Mountains in capitals, islands in small capitals, rivers and wadis in italics.


A
B
C
D
E
F
PANTHALASSA
EURAMERICA
RHEIC OCEAN
GONDWANA
Maider
Eifel
Holy Cross Mts. (North)
Western Sahara
Oued Regg
Alnif
Bou Dib
Fezzou
O. Msissi
O. el Mharch
Oued el Hassaïa
JBEL TISKAOUINE
OUMOUR
LANZAROTE
FUERTEVENTURA
Sidi Ifni
Tarfaya
Laâyoune
Smara
ZEMMOUR
Maas
Düsseldorf
Mönchen-gladbach
Rhein
Wuppertal
Bilveringsen
SAUERLAND
BERGISCHES LAND
Köln
Aachen
Bonn
HAUTES FAGNES
RHENISH SLATE MOUNTAINS
EIFEL
WESTERWALD
Hillesheim Syncline
Prüm Syncline
Gerolstein Syncline
Koblenz
Mosel
TAUNUS
Starachowice
Kamienna
Bodzentyn
Włochy
Kielce
HOLY CROSS MOUNTAINS
Łagów
Cainozoic
Mesozoic
Carboniferous to Permian
Middle & Upper Devonian
Lower Devonian
Cambrian to Silurian
Igneous rocks
Precambrian

Eifel (Fig. 1A, B, E). The Eifel is a low mountain range forming part of the Rhenish Massif (Fig. 1E). Middle Devonian strata crop out in several synclines (Struve *et al.*, 2008); the material studied here comes from the Prüm Syncline (locs. Lauch, Wetteldorf, Giesdorf, Gondelsheim, Schwirzheim), Hillesheim Syncline (Niederehe, Nollenbach-Ahütte), and the Gerolstein Syncline (Gees, Auburg).

Remscheid-Altena Anticline (Fig. 1A, B, E). Details on the quarry at Bilveringsen (Fig. 1E) and its fauna are given by May (1991, pp. 21–32). The age of the Massenkalk in this area is from the upper part of the *varcus* Zone to the *transitans* Zone (Clausen and Korn, 2008), meaning middle Givetian to early Frasnian. The rich brachiopod fauna could be studied thanks to the special preparation methods used by K. Torley (see Pfingsten, 1969).

Holy Cross Mountains (Fig. 1A, B, F). The Holy Cross Mountains (Góry Świętokrzyskie) form a small Palaeozoic outlier in central Poland (Fig. 1F). The extremely scarce investigated material comes from the Bodzentyn Syncline in the northern part of the area (Łysogóry Region; see Halamski, 2005; Halamski and Racki, 2005). Two specimens of *K. signata* come from a well in Włochy, probably from the Nieczulice Beds (outcrop Wł-st *sensu* Turnau and Racki, 1999, see especially figs 3B, 4).

No disarticulated valves of any brachiopod species studied herein were found, so interiors have been studied using the standard technique of serial sections and acetate peels. The latter were mounted between microscope slides and photographed under a binocular microscope. Images were imported to CorelDRAW and internal details were drawn using a digital drawing tablet.

The terminology used in the present work largely follows the revised *Treatise on Invertebrate Paleontology* (Williams and Brunton, 1997). As in many previous works, however, the coarse ribs of the external shell surface, are consistently termed 'costae' as the ontogenetic origin or hierarchical level of a rib is often unclear. Measurements are given in the following way: (*a*–) *b*–*c* (–*d*) [*e*], with *a* – minimum value; *b* – first quartile; *c* – third quartile; *d* – maximum value; *e* – arithmetic mean.

SYSTEMATIC PALAEONTOLOGY

General remarks on the Uncinuloidea

The species described in the present paper were assigned by previous workers to the genera *Uncinulus* Bayle, 1878, *Kransia* Westbroek, 1967 and *Nalivkinaria* Rzhonsnitskaya, 1968. *Uncinulus* Bayle, 1878 has a globular form and fine costation (Sartenaer, 2004), and is unrelated to the forms described here. *Kransia* (?) *issoumourensis* Drot, 1971 was originally described under that name by Drot (1971), whereas the assignment to *Nalivkinaria* was suggested in a preliminary publication by Schemm-Gregory and Jansen (2005). *Terebratula goldfussii* and *Terebratula wahlenbergii* var. *signata* (erroneously as "*signatus*") were listed as belonging to *Kransia* in the original discussion of this genus by Westbroek (1967, p. 82), along with a few other species reassigned subsequently to *Primipilaria* Struve, 1992, *Eressella* Halamski and Baliński, 2018, and possibly *Beckmannia* Mohanti, 1972. *Terebratula signata* was assigned to *Nalivkinaria* by Mohanti (1972).

Treating the three above-mentioned species as representatives of either *Kransia* or *Nalivkinaria* is unsatisfactory, insofar as all three possess a septalium and a multilamellate cardinal process. According to Mohanti (1972, p. 160, fig. 19) and in contrast to the earlier partly erroneous data in the original description (Westbroek, 1967); unfortunately the description given by Savage (2002) does not take into account the emended diagnosis provided by Mohanti (1972). *Kransia* does not have a true septalium, although its frequently cited type species *K. parallelepipeda* has never been revised (see Halamski and Baliński, 2013, p. 265). Furthermore, it is clear from the original description that *Nalivkinaria* has a massive bifid cardinal process and a peculiar pouch on each lateral flank of the shell (Rzhonsnitskaya, 1968). The brachiopods identified by Mohanti (1972, fig. 23) as *Nalivkinaria lacunosa* forma *tenuicostata* have neither and accordingly do not belong to *Nalivkinaria*, so that his conclusion on the placement of *Terebratula signata* within *Nalivkinaria* is based entirely on a misunderstanding.

Descriptions

Order Rhynchonellida Kuhn, 1949
Superfamily Uncinuloidea Rzhonsnitskaya, 1956

Remarks: According to the systematic treatment in the revised brachiopod volumes of the *Treatise on Invertebrate Paleontology*, *Lebanzuella* is included in the family Hebetoechiidae Havlíček, 1960 and the subfamily Hebetoechiinae Havlíček, 1960 (Savage, 2007, p. 2707) and *Kransia* in the family Hebetoechiidae Havlíček, 1960 and subfamily Betterbergiinae Savage, 1996 (Savage, 2002, p. 1111). The superfamily Uncinuloidea Rzhonsnitskaya, 1956 is a well-defined taxon, whereas its subdivisions are unsatisfactory. For example, the only consistent difference between the Uncinulidae Rzhonsnitskaya, 1956 and the Hebetoechiidae is apparently the shape (globose *vs*. dorsibiconvex), a rather weak criterion. These problems will be dealt with in detail in a future work; for the moment, the present authors deliberately refrain from using family- and subfamily-level taxa.

Genus *Lebanzuella* García-Alcalde, 1999

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

Lebanzuella? *issoumourensis* (Drot, 1971)
Figs 2–5

* 1971 *Kransia* (?) *issoumourensis* n. sp. – Drot, pp. 72–76; text-pl. 2; pl. 1, figs 4, 5.

v. 2005 *Nalivkinaria issoumourensis* – Schemm-Gregory and Jansen, p. 27.

Type material: Holotype MNHN *s.n.*, illustrated by Drot (1971, pl. 1, fig. 5), not found in 2012; paratypes, nine other specimens examined by Drot (including one illustrated; Drot, 1971, pl. 1, fig. 4), not found.
Type locality and stratum: Outcrop TM 585 *sensu* Drot (1971, p. 72), south from Taboumakhlouf, x = 540.7 y = = 446.9; Maïder, Anti-Atlas, Morocco. Lumachelle within Bou-Dib calcareous sandstones; Givetian.
Material: In total, 739 articulated shells (see details under subspecies).
Description: Shell subcircular to rounded pentagonal in outline, weakly transverse (width-to-length ratio usually about 1.1), markedly dorsibiconvex, moderately to very thick according to subspecies (see below), rather small to middle-sized according to subspecies (see below). Maximal thickness of the shell near the anterior commissure. Dorsal valve with a flat fold starting ca. 2–3 mm from the umbo; beak suberect to weakly incurved. Ventral valve with a flat-bottomed sulcus starting in the umbonal region. Anterior commissure uniplicate; tongue high, subtrapezoidal to rectangular (lateral slopes parallel to the symmetry plane), its width usually slightly less than half the shell width.

Ornamentation of distinct but rounded first and second order costae (costae and costellae, using the terminology of Williams and Brunton, 1997), starting between ¼ and mid-length of the shell; separated by furrows slightly narrower than the costae. Ornamentation on the fold consisting of two costae posteriorly, then dividing to form two bundles separated by a median furrow; thus 3–7, usually four costae at anterior margin. Costae in the sulcus usually three, seldom up to five, the median one often stronger than the others; parietal costae infrequent. Costae on each lateral flank (including those on the flanks of the fold if present) (4–)5–7(–9). Interspaces between costae prolonged to form marginal spines at the commissures.

Interior: Dental plates rarely well-developed (Fig. 3A), subparallel to weakly divergent ventrally in transverse serial sections, but mostly not recognized (Figs 3B, C, 4), probably obscured by umbonal callus and in part by secondary recrystallisation; lateral umbonal regions markedly thickened by secondary shell material; ventral muscle field deeply impressed, in some specimens divided by a low and short myophragm (Fig. 4A).

Dorsal median septum high, massively thickened posteriorly by secondary shell material, subtriangular and sharp, thinning anteriorly; hinge plates short, subhorizontal, supported by the median septum and thus forming a short (0.3–0.6 mm long) septalium (e.g., Fig. 3B, section at 4.1 mm; Fig. 4C, section at 2.5 mm), but frequently obscured by callus in sectioned specimens; cardinal process wide, multilobed (e.g., Fig. 3B, section at 1.8 mm; Fig. 4A, section at 1.3 mm); crura rod-like in cross section, slightly divergent anteriorly and distally bent toward the ventral valve.

Remarks: A detailed comparison of *Kransia* (?) *issoumourensis* with several externally similar species is given by Drot (1971, pp. 75–76). This species was assigned to *Kransia* Westbroek, 1967 by Drot (1971) and to *Nalivkinaria* Rzhonsnitskaya, 1968 by Schemm-Gregory and Jansen (2005). As stated above, both treatments are unsatisfactory because the type species of *Kransia* has no true septalium (Mohanti, 1972) and the type species of *Nalivkinaria* has a bifid cardinal process.

The discussed species is tentatively included herein in *Lebanzuella* García-Alcalde, 1999 on account of the pronounced similarity of internal structures (thick shell, stout septalium, multilamellar cardinal process, dental plates coalescent with shell wall) and general likeness of ornamentation (bifurcating costae, flattened and grooved on the paries geniculatus). The type species *Lebanzuella lebanza* (Binnekamp, 1965) comes from the upper part of the Lebanza Formation in the Cantabrian Mountains, to which Binnekamp (1965) assigned a middle Siegenian age. On the evidence of the brachiopod development, i.e., the evolutionary stage of *Schizophoria*, an early Siegenian age was later suggested by Renouf (1972) for this stratigraphic interval and further corroborated with additional data by Carls (1987) and Jansen (2001). The main difference from the distinctly older species is the ornamentation pattern consisting of two bundles of costae on the fold, present in *Lebanzuella*? *issoumourensis* and absent in *L. lebanza*. Moreover, the ventral valve is more flattened, the frontal aspect of shell is different in showing a more elevated fold and higher sulcus tongue, the cardinal process has more and more delicate lamellae, and the dorsal median septum is generally more developed.

A biometric comparison of our two samples (Issoumour and Smara; N = 40 for each) allows conclusions about the general similarity of shape, as expressed by nearly identical width-to-length ratios, (0.98–)1.07–1.12(–1.19) [mean 1.09] in the specimens from Issoumour and (0.95–)1.05–1.14(–1.23) [mean 1.08] in those from the Smara; likewise, the relative width of the tongue is (0.36–)0.43–0.51(–0.60) [mean 0.47] in Issoumour and (0.41–)0.48–0.54–(0.62) [mean 0.51] in Smara. On the other hand, shells from the Smara sample are smaller and significantly thicker than those from the Issoumour sample (see descriptions of subspecies for value ranges and Appendix for the raw data). The size of the studied samples allows checking the constancy of the above-mentioned differences, even if the thickness-to-length ratio is clearly more variable in the Issoumour sample than in the Smara sample. As a consequence, a formal distinction at the rank of subspecies is proposed for the specimens of the two samples as below.
Distribution: North Africa, in all cases probably Givetian (see details under respective subspecies). *Kransia* cf. *issoumourensis* was reported (without description) from faunistic intervals 21–22 (upper Givetian to Frasnian?) of the Asturo-Leonese Domain (Spain) by García-Alcalde (1996).

Lebanzuella? *issoumourensis issoumourensis* (Drot, 1971)
Figs 2A–T, 3, 5

* 1971 *Kransia* (?) *issoumourensis* n. sp. – Drot, pp. 72–76; text-pl. 2; pl. 1, figs 4, 5.

Type material, locality and stratum: as for the species.
Material: 250 articulated shells from outcrop "Maider (Marokko) (93) Lesefunde Mergelhänge Jbel Issoumour 11 km SW Bou-Dib, Mittel-Devon", Jbel Issoumour (coll. V. Ebbighausen), MB.B.9393.

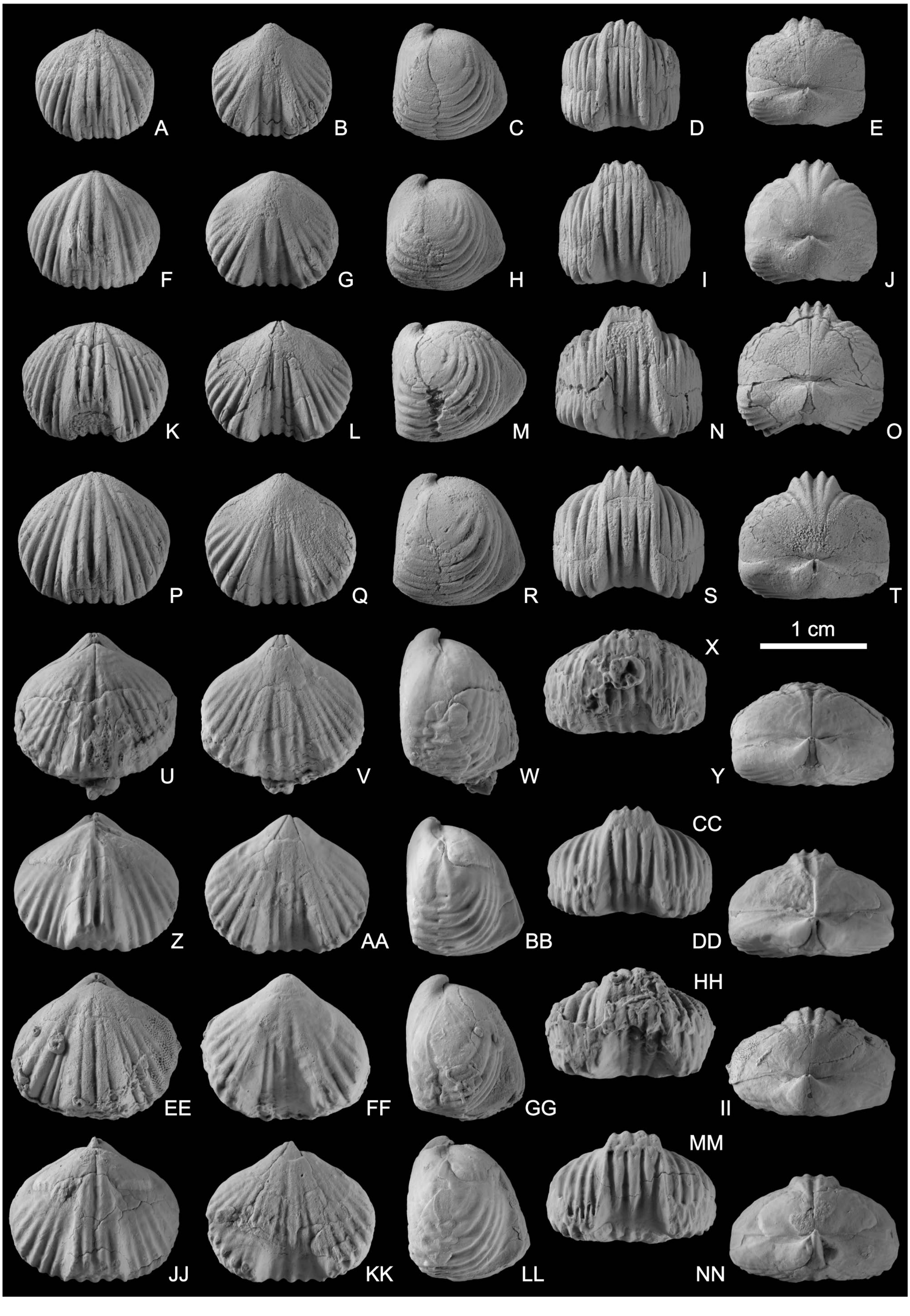


Fig. 2. *Lebanzuella*? *issoumourensis* (Drot, 1971) from the Givetian of North Africa [A–T, *Lebanzuella*? *issoumourensis issoumourensis* (Drot, 1971) from Jbel Issoumour; U–NN, *Lebanzuella*? *issoumourensis smarensis* ssp. nov. from Western Sahara]. Articulated shells in dorsal, ventral, lateral, anterior, and posterior views. **A–E, F–J, K–O**, **P–T.** Shells MB.B.9393.13, 9393.14, 9393.5, and 9393.18 from Jbel Issoumour (11 km SW Bou-Dib, coll. V. Ebbighausen). **U–Y**, **Z–DD**, **EE–II**, **JJ–NN.** Shells SMF 99605.9 (paratype), 99605.2 (holotype), 99605.11, and 99605.24 (paratypes) from locality Bryo1 near Smara (coll. U. Jansen).

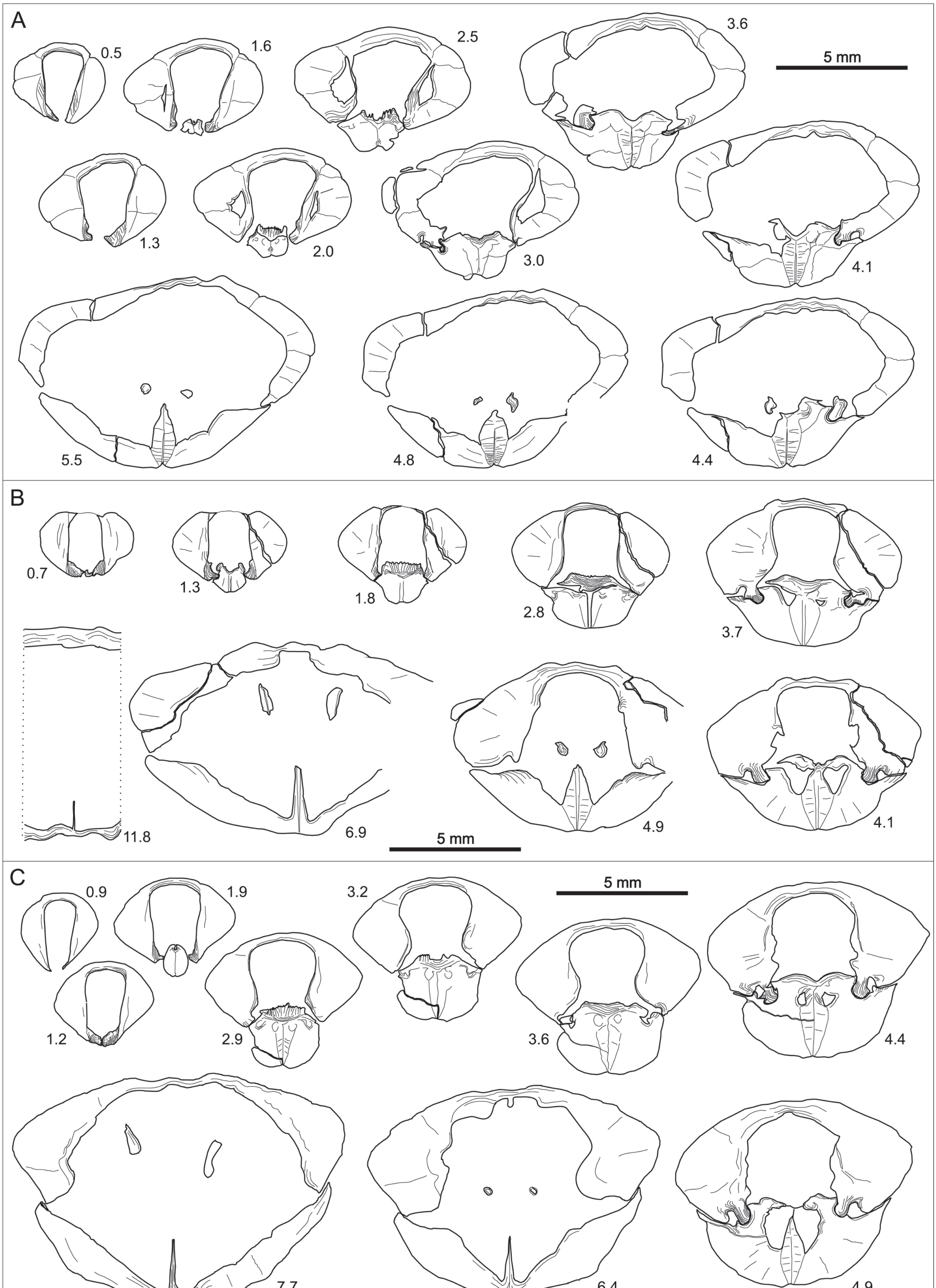


Fig. 3. Transverse serial sections of *Lebanzuella*? *issoumourensis issoumourensis* (Drot, 1971) through the shells MB.B.9393.41, 42, 43 **(A, B, C)** from Jbel Issoumour (11 km SW of Bou-Dib, coll. V. Ebbighausen). Distances measured in millimetres from the tip of the ventral umbo.

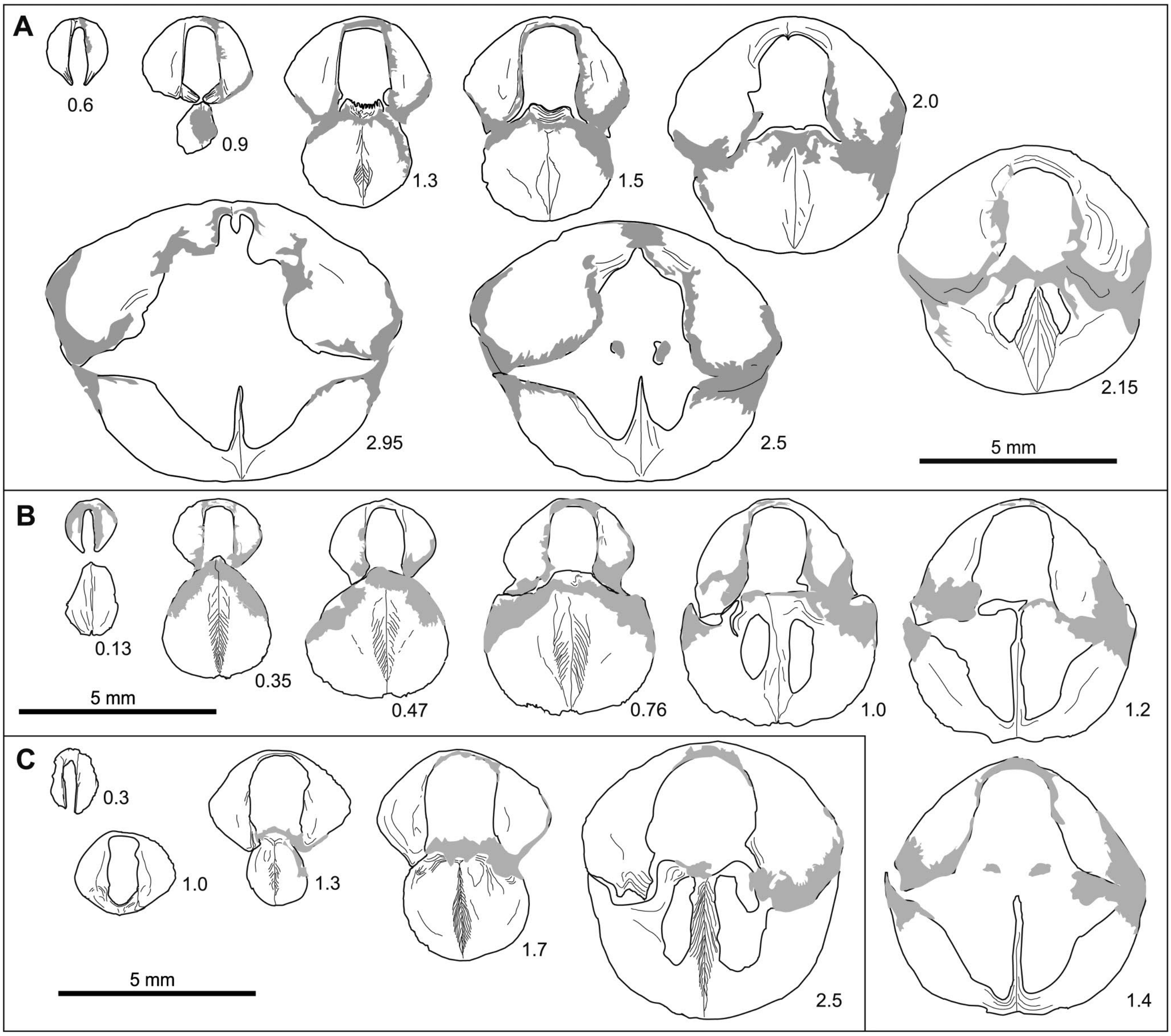


Fig. 4. Transverse serial sections of *Lebanzuella*? *issoumourensis smarensis* ssp. nov. through the shells SMF 99662 **(A)**, SMF 99663 **(B)**, and SMF 99664 **(C)**, all three from locality Bryo1, Western Sahara (specimens sectioned by the late M. Schemm-Gregory). Distances measured in millimetres from the tip of the ventral umbo. Greyed areas denote local recrystallization.

Description: Shell middle-sized (mean width 14.7 mm), moderately thick [thickness-to-length ratio (0.66–)0.74––0.86(–1.00), mean 0.80].
Distribution: North Africa, Maïder, Jbel Issoumour; probably Givetian.

Lebanzuella? *issoumourensis smarensis* ssp. nov.
Figs 2U–NN, 4, 5

v. 2005 *Nalivkinaria issoumourensis* – Schemm-Gregory and Jansen, p. 27.

Type material: Holotype (designated herein), articulated shell SMF 99605.2, illustrated in Fig. 2Z–DD. 488 other specimens (paratypes) from Western Sahara (456 from Bryo1, 28 from loc. 25, and 5 from loc. 26), SMF 99603–99610.

Type locality and stratum: Locality Bryo1 (26°32.877′N, 11°29.657′W) near Smara, Tindouf Syncline; Givetian.
Etymology: From the town of Smara (Arabic: as-Samāra; also: Semara, Esmara) near the type locality.
Diagnosis: Like *Lebanzuella*? *issoumourensis issoumourensis* (Drot, 1971), but with smaller and thicker shells.
Description: Shell rather small to middle-sized (mean width 12.7 mm), very thick [thickness-to-length ratio (0.95–) 1.05–1.14(–1.23), mean 1.08].
Distribution: North Africa, Tindouf Syncline, Smara region; probably Givetian.

Genus *Kransia* Westbroek, 1967

Type species: *Terebratula parallelepipeda* Bronn, 1834 in 1834–38 ["1835–37"] (see discussion in Mohanti, 1972; Halamski and Baliński, 2013, p. 265).

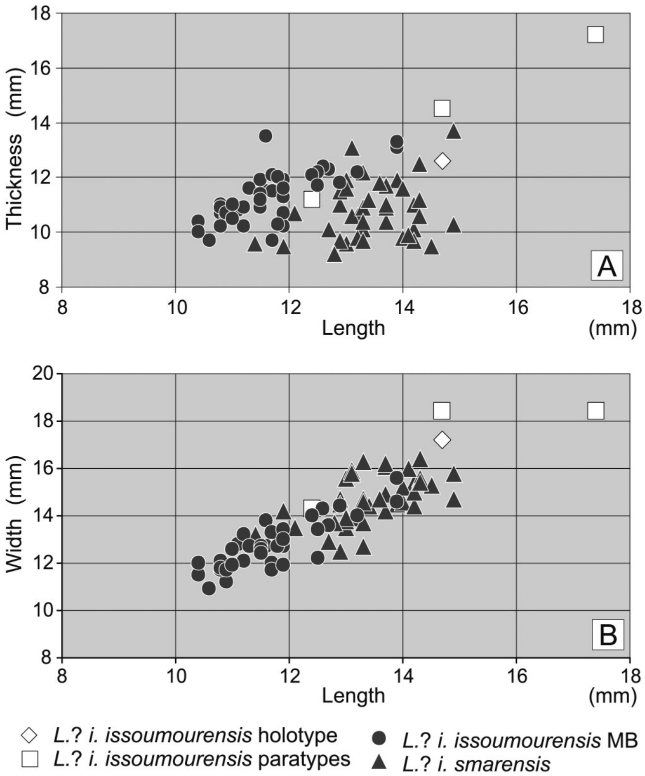


Fig. 5. *Lebanzuella*? *issoumourensis* (Drot, 1971). Scatter diagrams of shell width to shell length **(A)** and shell thickness to shell length **(B)** for the two subspecies studied: *Lebanzuella*? *issoumourensis issoumourensis* (Drot, 1971) from Jbel Issoumour, new data and the type material from the same area after Drot, 1971; *Lebanzuella*? *issoumourensis smarensis* ssp. nov. from Smara. Raw data provided in the Appendix.

Remarks: As shown by Mohanti (1972) and in contrast to partly erroneous data, based on earlier works quoted in Savage (2002), *K. parallelepipeda* does not have a true septalium. The subgenus *Kransia* (*Kransia*) is emended herein to contain only species lacking a true septalium, namely the type species and *Terebratula subcordiformis* Schnur, 1853, whereas the subgenus *Kransia* (*Fatimaerhynchia*) is proposed for species with a septalium, as below.

Subgenus *Kransia* (*Fatimaerhynchia*) nov.

Type species: *Terebratula wahlenbergii* var. *signata* Schnur, 1851.
Etymology: In honour of Fatima al-Fihri, credited for having founded the University of Al Quaraouiyine in Fes, Morocco in 859 AD.
Diagnosis: Like *Kransia* (*Kransia*), but with median septum supporting the hinge plates and thus forming a septalium.
Other species assigned: *Terebratula goldfussii* Schnur, 1851; *Uncinulus goldfussii* sensu Torley, 1934 (non Schnur, 1851) [tentatively assigned to the subgenus].
Remarks: The two species included in the new subgenus are characterised by external morphology and interior quite similar to that of *Kransia* (*Kransia*), the only major difference being the presence of a septalium. The taxonomic significance of the septalium in Mesozoic rhynchonellides was discussed in detail by Shi and Grant (1993), who concluded that "the septalium, although useful in a general sense, has proved to be a highly variable structure in the Jurassic rhynchonellides. In some groups, it proves a useful character, while in some others it varies even at the species level" (Shi and Grant, 1993, p. 3). Likewise, "all the elements that together constitute a septalium are capable of considerable variation in genus or even at the species level, although this by no means implies that they are useless for classification" (Shi and Grant, 1993, p. 16). According to Mohanti (1972), in *Kransia* this character is variable as well, because even if most often the septum does not touch the hinge plates, in some cases the two structures are in contact. All in all, even if the taxonomic identity of specimens studied in Mohanti (1972) should be re-investigated, the presence or absence of a septalium does not seem of such taxonomic weight that it may justify a distinction at the genus level; accordingly, a new subgenus within *Kransia* is proposed.

The two species described below differ from *Lebanzuella*? *issoumourensis* in their relatively thin-walled shell, well individualised dental plates, and longer septalium. Genera with notable similarity include *Tridensilis* Su, 1976 from the Emsian of China, alike externally but differing in a massive and trilobate cardinal process (a synonym of *Uncinulus* Bayle, 1878 according to Savage, 2002; valid genus according to Hou *et al.*, 2017) and *Glossinulina* Johnson, 1975 from the Emsian of Canada, quite alike internally but with very different ornamentation.

Kransia (*Fatimaerhynchia*) *goldfussii* (Schnur, 1853)
Figs 6A–J, 8A, B, 10

*p 1853 *Terebratula goldfussii* m. – Schnur, pp. 188–189; pl. 26, fig. 4a–g, m–p? [non fig. 4h–l: *K.* (*F.*) *signata*].

non 1934 *Uncinulus goldfussii* (Schnur) – Torley, p. 85; text-fig. A-19; pl. 3, figs 25–31.

1937 *Uncinulus goldfussii* (Schnur) – Schmidt, text-fig. 2.

v. 1941 *Uncinulus goldfussii* (Schnur, 1853) – Schmidt, pp. 24–25; pl. 1, fig. 16; pl. 4, fig. 70 [*ubi syn.*].

1967 *Kransia goldfussii* – Westbroek, pl. 3, fig. 3; pl. 14, fig. 3.

Type material: Lectotype, Goldfuß Museum, Steinmann Institute of Geology, Mineralogy and Palaeontology, University of Bonn *s.n.* (coll. J. Schnur), selected and illustrated by Schmidt (1941, pl. 4, fig. 70).
Type locality and stratum: "Im Kalk zu Schönecken, Gerolstein, und Pelm, etc.; nicht häufig" (Schnur, 1853, p. 189); Middle Devonian of the Eifel Synclines.
Material: Over 40 articulated shells (incl. 29 measurable specimens) from the Eifel: SMF 99590 (*olim* SMF XVII 345e), 99594, 99800 (*olim* SMF XVII 345n; Ahrdorf Fm, middle Eifelian, Gees, Trilobiten-Felder, coll. R. Richter 1913), 99591 (*olim* XVII 345g; "Gondelsheimer Schichten", Eifelian, Niederlauch, coll. T. Reuling), 99592 (*olim* XVII 345h; "Rommersheimer Sch.", today Junkerberg Fm, Auburg, coll. 1938), 99593, 99801 (*olim* XVII 345m;

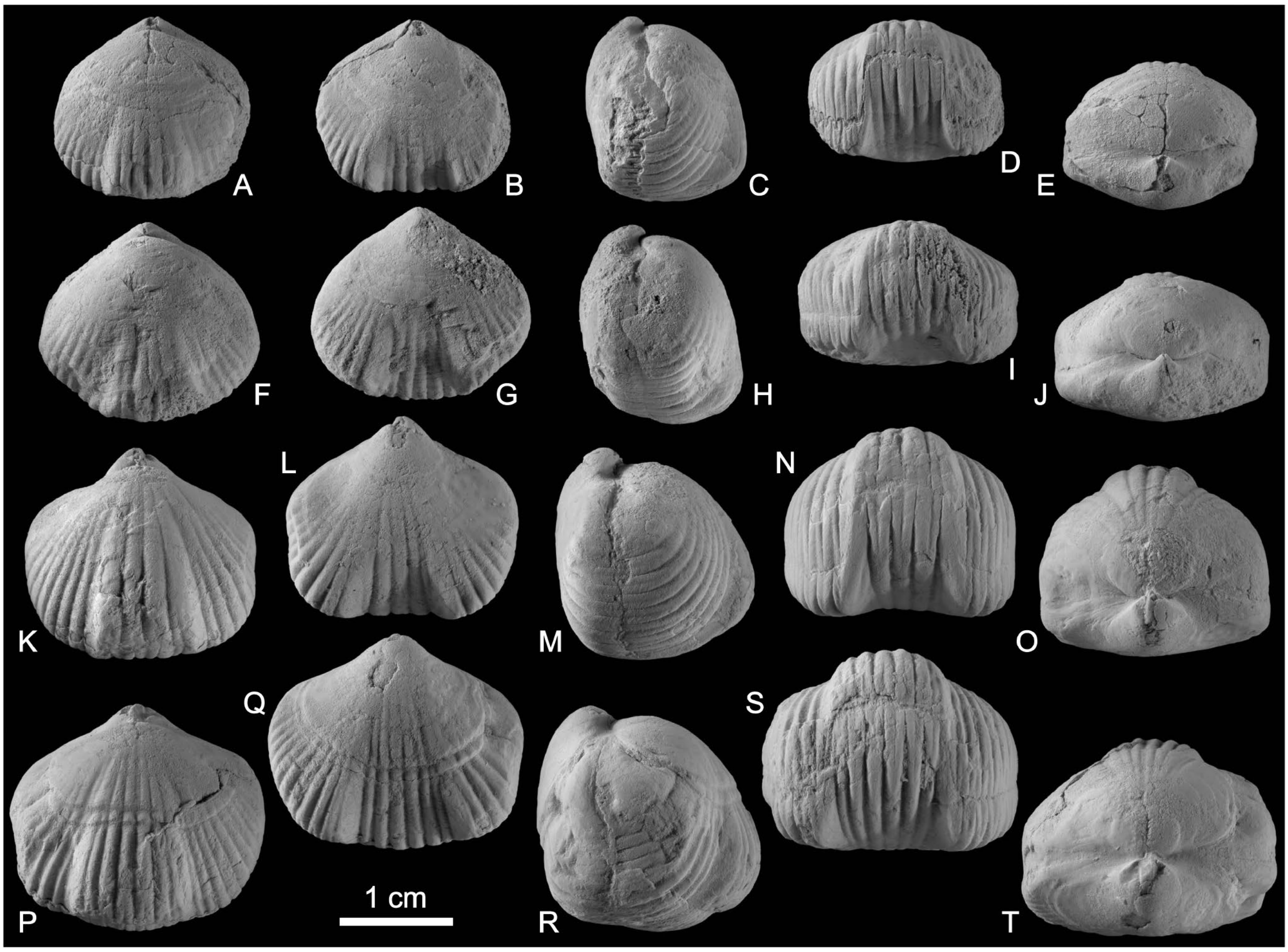


Fig. 6. *Kransia* (*Fatimaerhynchia*) *goldfussii* (Schnur, 1853) and *K.* (*F.*?) aff. *goldfussii* from the Eifelian and Givetian of Europe (A–J – Eifelian of the Eifel; K–T – Givetian of the Bergisches Land). Articulated shells in dorsal, ventral, lateral, anterior, and posterior views. **A–J.** *Kransia* (*Fatimaerhynchia*) *goldfussii* from Gees (coll. A. Lueken); A–E – shell SMF 99600 (Gees section, lower part); F–J – shell SMF 99601 (Gees, bed 1). **K–T.** *Kransia* (*Fatimaerhynchia*?) aff. *goldfussii* from Bilveringsen (coll. K. Torley); K–O, P–T – shells SMF 99598, 99599 (*olim* XVII 345d), illustrated by Torley (1934, figs 27, 29).

Ahrdorf Fm, Gees, Salmer Weg, Trilobiten-Felder, coll. Scholl 1935), SMF 99600–99601, 99651–99653, 99655, 99668–99672 (Ahrdorf Fm, Gees, coll. A. Lueken).

Description: Shell rounded to subpentagonal in outline, weakly transverse, width-to-length ratio (0.96–)1.05–1.13 (–1.28) [mean 1.10; N = 29], markedly dorsibiconvex, up to 19.4 mm in width, typically about 13–16 mm wide. Maximal thickness of the shell near mid-length or more anterior, but not immediately above the anterior commissure. Dorsal valve with a flat fold starting at about mid-length; beak erect to incurved; delthyrium partly closed by conjunct deltidial plates. Ventral valve with a flat-bottomed sulcus starting about mid-length. Anterior commissure uniplicate; tongue rather high, subtrapezoidal to rectangular, occupying (0.36–)0.44–0.51(–0.63) [mean 0.48] of the shell width. Squamae and glottae present.

Ornamentation of relatively weak costae, starting at about mid-length of the shell; separated by furrows slightly narrower than the costae. Costae (3–)4–5(–8) on the fold, (2–)3–4(–7) in the sulcus, (3–)5–6(–8) per flank, medianly furrowed on the paries geniculatus. Spine-like projections at the commissures.

Interior: Dental plates well-developed, thin, divergent ventrally in transverse serial sections; ventral muscle field impressed, in one of the two sectioned specimens (Fig. 8B) divided by a well-developed low and short myophragm.

Dorsal median septum thickened posteriorly, thinning anteriorly, high; hinge plates subhorizontal, supported by the median septum, forming a moderately short (1.1 mm long in the specimen shown in Fig. 8A) and narrow septalium (e.g., Fig. 8A, section at 2.05 mm); cardinal process wide, multilobed (e.g., Fig. 8A, section at 1.5 mm); crural bases closely set; crura rod-like in cross section, with distal parts divergent and bent toward the ventral valve.

Remarks: This species was first identified by Schnur (1851) as *Terebratula Wahlenbergii* Goldfuss in Roemer, 1843, a brachiopod described from the Devonian of Rübeland in the Harz (Roemer, 1843, p. 17). Two years later, he concluded that brachiopods from the Eifel and the Harz do not belong to the same species and proposed the name *Terebratula Goldfussii* for the former (Schnur, 1853, p. 188). The difference in the costation density (never more than eight costae per flank in *T. goldfussii*; 7–12 in *T. wahlenbergii*, Roemer, 1843) indicates Schnur (1853) was right.

Differences in external features of *K.* (*F.*) *goldfussii* and *Lebanzuella*? *issoumourensis* include the position of maximum thickness (closer to mid-length of the shell in the former, in the anterior region in the latter) and the costation (costae start later in the former; usually there is a distinct median dorsal furrow and a thicker median ventral costa in the latter; such a pattern is absent or indistinct in the former).

Kransia (*F.*) *goldfussii* differs from *K.* (*K.*) *parallelepipeda*, apart from the internal features mentioned earlier, in a thicker and generally more rounded shell with coarser costae, a more convex ventral valve, and more subtrapezoidal to rectangular sulcus tongue (arcuate in the latter).

Kransia (*Fatimaerhynchia*?) aff. *goldfussii* (Schnur, 1853)
Figs 6K–T, 10

v. 1934 *Uncinulus goldfussii* (Schnur) – Torley, p. 85; text-fig. A-19; pl. 3, figs 25–31.

Material: Seven articulated shells and one fragment from Bilveringsen, SMF 99595–99599, 99797–99799 (*olim* XVII 345a–d; coll. K. Torley).

Description: Shell 16.9–24.1 mm wide [mean 20.4 mm, $N = 7$], transversely pentagonal in outline, width-to-length ratio 1.11–1.49 [mean 1.23, $N = 6$], strongly dorsibiconvex, beak erect to incurved. Anterior commissure uniplicate; tongue subtrapezoidal, occupying 0.43–0.55 [mean 0.50, $N = 7$] of the shell width.

Ornamentation of relatively strong first- and second-order costae, starting at about 1/6 to 1/5 of the length of the shell, separated by furrows narrower than the costae. Costae on the fold in two bundles, 4–8 (most often 6), 3–7 in the sulcus, (3–)7–8(–9) on each lateral flank.

Interior: a high dorsal median septum (Torley, 1934, fig. A-19), otherwise unknown.

Remarks: Givetian brachiopods described by Torley (1934) as *Uncinulus goldfussii* are more angular in outline than both *Kransia* (*Fatimaerhynchia*) *goldfussii* from the type region and *K.* (*F.*) *signata*. The radial ornamentation starts earlier than in *K.* (*F.*) *goldfussii* from the type region, but not so close to the beak as in *K.* (*F.*) *signata*. Last, *K.* (*F.*?) aff. *goldfussii* from Bilveringsen is significantly larger and more transverse than *K.* (*F.*) *goldfussii* from the Eifel (the former usually about 20 mm wide, minimum recorded width 16.9 mm, mean width-to-length ratio 1.23; the latter usually 11–17 mm wide, maximum recorded width 19.4 mm, mean width-to-length ratio 1.10). As suggested already by Drot (1971, p. 76), they probably represent another species which is not described herein because of insufficient material and unknown internal features.

Distribution: Rhenish Slate Mountains, Remscheid-Altena Anticline, Bilveringsen; Massenkalk (middle Givetian to lower Frasnian).

Kransia (*Fatimaerhynchia*) *signata* (Schnur, 1851)
Figs 7, 8C, 9, 10

v* 1851 *Terebratula wahlenbergii* Gldf., var. *signata* nob. – Schnur, pp. 5–6.

1853 *Terebratula goldfussii* var. *signata* – Schnur, p. 189; pl. 26, fig. 4h–l.

1937 *Uncinulus signatus* (Schnur) – Schmidt, text-fig. 1.

v. 1941 *Uncinulus signatus* (Schnur 1853) – Schmidt, pp. 25–26; pl. 1, fig. 19; pl. 4, fig. 69.

1972 *Nalivkinaria signata* (Schnur, 1853) – Mohanti, fig. 24.

Type material: Lectotype, Goldfuß Museum, Steinmann Institute of Geology, Mineralogy and Palaeontology, University of Bonn *s.n.* (coll. J. Schnur), selected and illustrated by Schmidt (1941, pl. 4, fig. 69).

Type locality and stratum: Eifel; Eifelian, probably middle Eifelian. No data on the origin of the material described by Schnur (1851, 1853) are given in the original publication.

Material: Eifel: over 20 articulated shells (incl. 16 measurable ones): SMF 99656 (*olim* SMF XVII 545e; “Rommersheimer Sch.”, Schwirzheim, coll. T. Reuling 1924), SMF 99657 (Ost-Rommersheim), SMF 99658 (Giesdorf-Rommersheim), SMF 99659 (*olim* XVII 545r; “Gondelsheimer Sch.”, “ostiolatus-Hor.”, today Giesdorf Member of Junkerberg Fm, middle Eifelian, Oberlauch, coll. T. Reuling), SMF 99660 (*olim* XVII 545t; “Rommersheimer Sch.”, Wetteldorf-Niederhersdorf, coll. 1938), SMF 99661 (*olim* XVII 545w; “Rommersheimer Sch.”, Niederehe, coll. H. Schmidt 1937), SMF 99665, 99666 (Prümer Mulde), SMF 99667 (ostiolatus-Hor., Gondelsheim, coll. W. Struve), SMF 99654, 99655 (Junkerberg Fm, Hönselberg Mb, middle Eifelian, St. 736, south from the road Nollenbach-Ahütte, coll. W. Struve Oct. 1956), SMF 99803 (425 m NNW of Betterberg, Niederehe, “Crinoiden-Sch.”, coll. Rud. Richter 1949), SMF 99804 (750 m NE of H49, TK25 Schönecken, coll. Rud. Richter 1949), SMF 99802 (boundary interval Betterberg/Niederehe formations, ESE of Niederehe, coll. W. Struve, St. 58), SMF 99806 (Gondelsheim), SMF 99805 (unknown loc., Eifel). Holy Cross Mts.: one articulated shell GIUS 4-813 Ws and one fragmentary shell from a well in Włochy (yellow marls, set B of the Nieczulice beds, *hermanni-cristatus* Zone?). Maïder: Loose finds in marls at the slopes of Jbel Issoumour 11 km SW of Bou-Dib, Middle Devonian, MB.B.9392.1–55 (incl. 30 measured ones), coll. V. Ebbighausen; Jbel Issoumour, Taboumakhlouf, MB.B.9447.1; coll. V. Ebbighausen.

Description: Shell approximately elliptic to subcircular in outline, (14.0–)17.4–22.5(–26.2) mm wide [mean 19.9; $N = 47$], transverse, width-to-length ratio (1.06–)1.16–1.28(–1.52) [mean 1.22], strongly dorsibiconvex. Maximal thickness of the shell at about ¾–⅘ of its length. Dorsal valve with a distinct flat fold starting in the umbonal region. Ventral valve with a flat-bottomed sulcus starting in the umbonal region; beak erect to incurved; delthyrium partly closed by conjunct and delicate deltidial plates. Anterior commissure uniplicate, tongue high, subtrapezoidal to subrectangular, occupying (0.40–)0.47–0.54(–0.62) [mean 0.51] of the shell width.

Ornamentation of strong costae, starting in the umbonal region, separated by furrows narrower than the costae. Costae (5–)6–7(–8) on the fold and forming two bundles, (4–)5–6(–7) in the sulcus, (5–)7–8(–9) on each lateral flank, increasing in number by bifurcation in posterior regions of

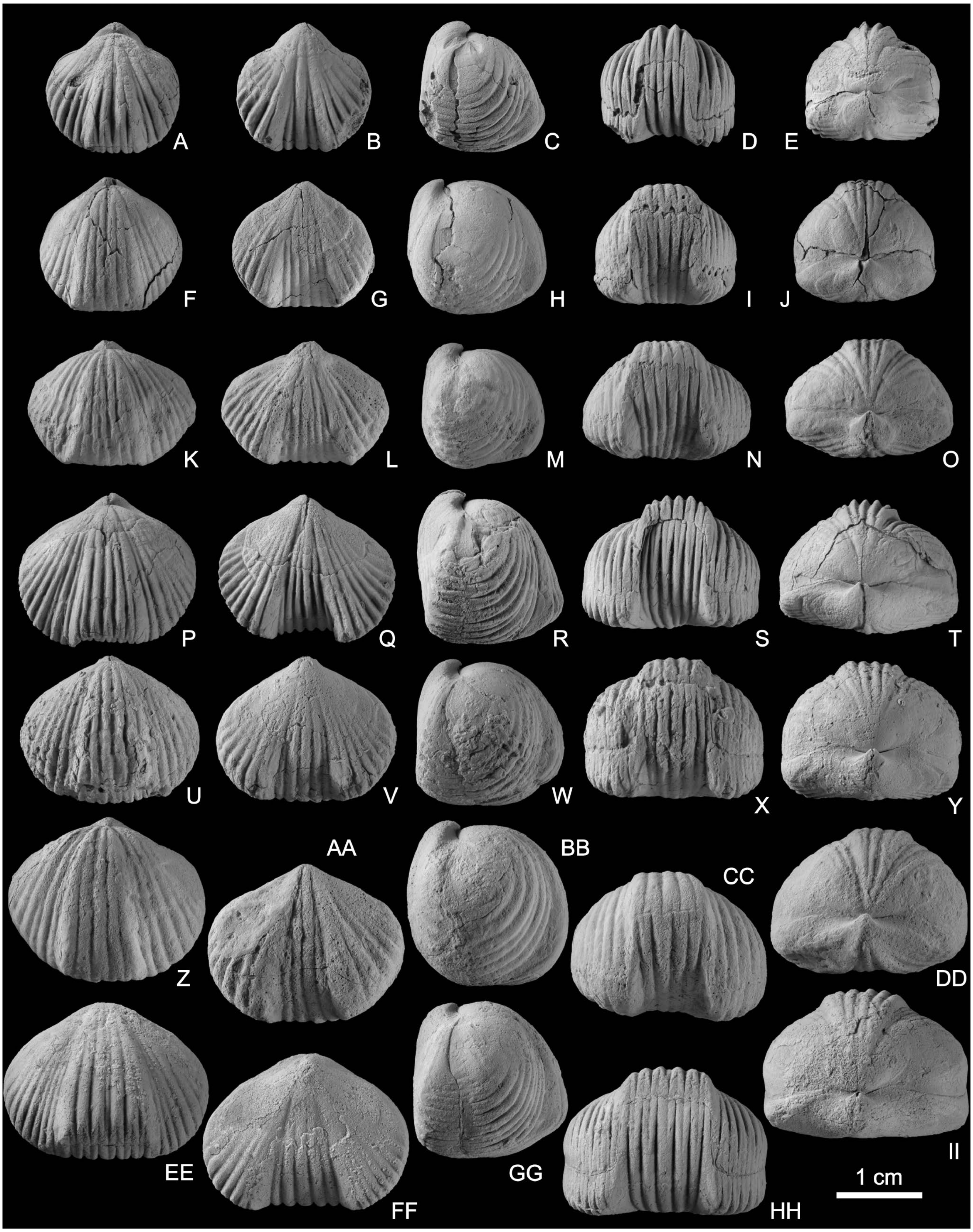


Fig. 7. *Kransia* (*Fatimaerhynchia*) *signata* (Schnur, 1851) from the Eifelian and Givetian of Europe and Africa (A–E, P–T, EE–II – Givetian? of Jbel Issoumour; F–O, Z–DD – Eifelian of the Eifel; U–Y – Givetian of the Holy Cross Mts.). Articulated shells in dorsal, ventral, lateral, anterior, and posterior views. **A–E, P–T, EE–II.** Shells MB.B.9392.31, 32 and MB.B.9447.1 from Jbel Issoumour (coll. V. Ebbighausen). **F–J.** Shell SMF 99657 from Ost-Rommersheim. **K–O.** Shell SMF 99658 from Giesdorf–Rommersheim. **U–Y.** Shell GIUS 4-813 Ws from Włochy (coll. G. Racki). **Z–DD.** Shell SMF 99656 (*olim* XVII 545e.1) from Schwirzheim (coll. T. Reuling).

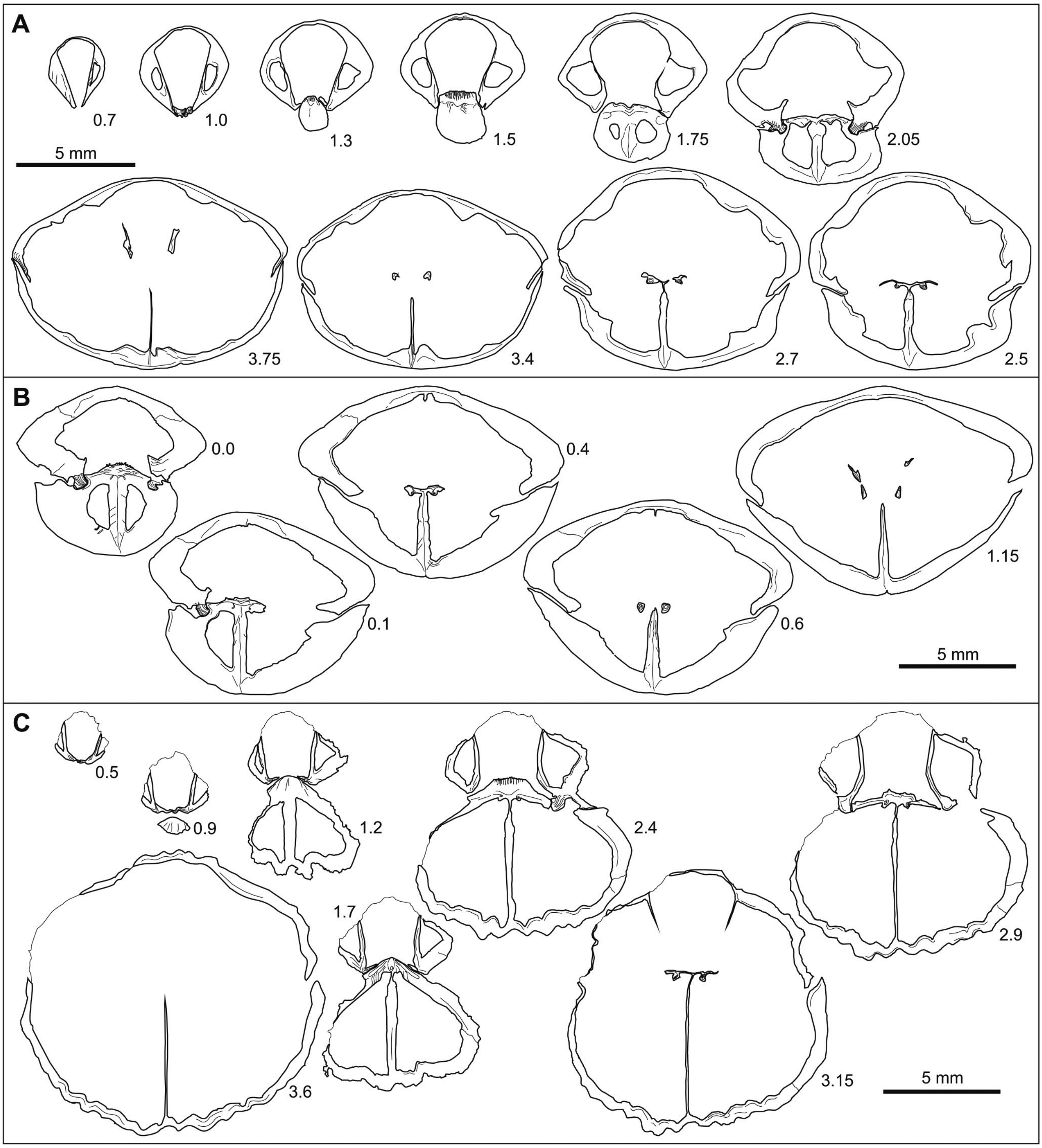


Fig. 8. Transverse serial sections of *Kransia* (*Fatimaerhynchia*) *goldfussii* (Schnur, 1853) through the shells SMF 99653 **(A)** from Gees (coll. A. Lueken) and SMF 99594 (*olim* XVII 345n) **(B)** from Gees (coll. R. Richter) and of *K.* (*F.*) *signata* (Schnur, 1851) through the shell SMF 99654 **(C)** from St. 736 (coll. W. Struve). Distances measured in millimetres from the tip of the ventral umbo (A, C) or from the first illustrated section (B, specimen sectioned by H. Schmidt, data on the distance between the section and the tip of the umbo not available).

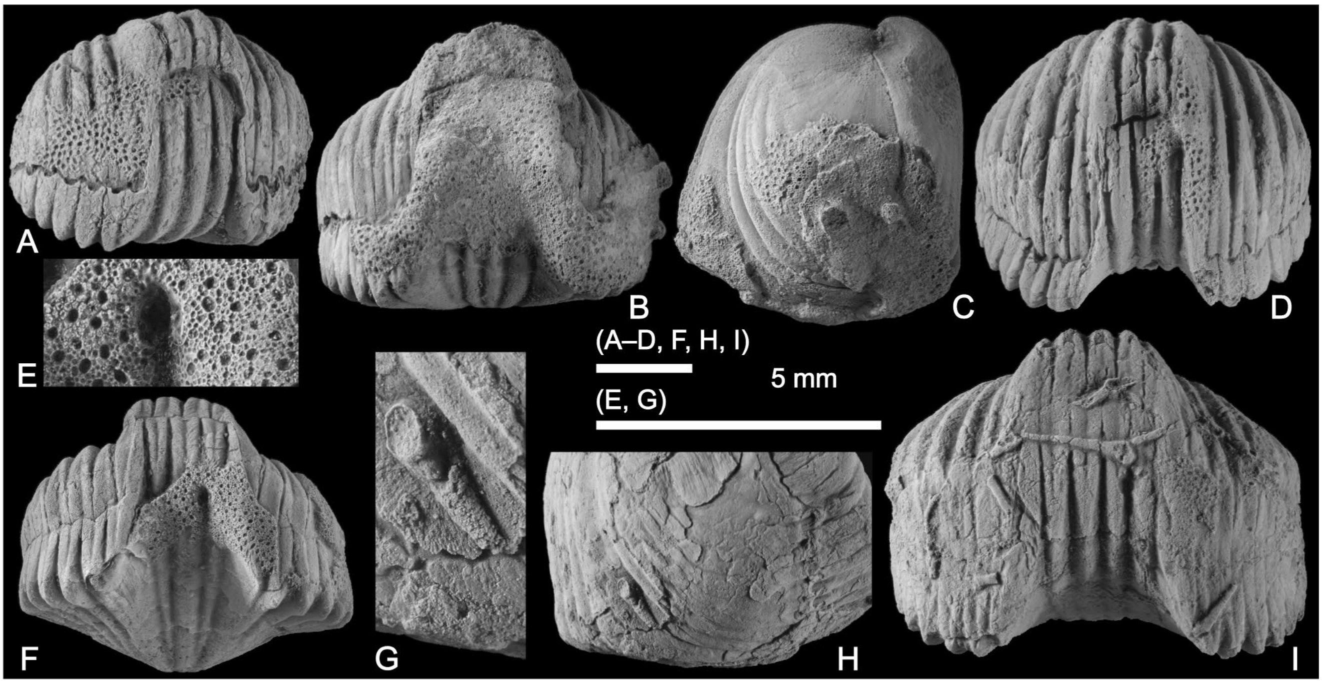


Fig. 9. Epizoans on *Kransia* (*Fatimaerhynchia*) *signata* (Schnur, 1851) from Jbel Issoumour. **A–F.** Trepostome bryozoan *Leioclema* sp. on shells MB.B.9392.27 (**A**, oblique antero-lateral view), MB.B.9392.5 (**B**, anterior view; **C**, lateral view), MB.B.9392.24 (**D**, anterior view), and MB.B.9392.33 (**F**, oblique antero-ventral view; **E**, enlargement of the bryozoan). **G–I.** Probable hederellids on shells MB.B.9392.9 (**H**, partial lateral view; **G**, enlargement of the epizoan) and MB.B.9392.11 (**I**, anterior view). Identifications by Andrej Ernst.

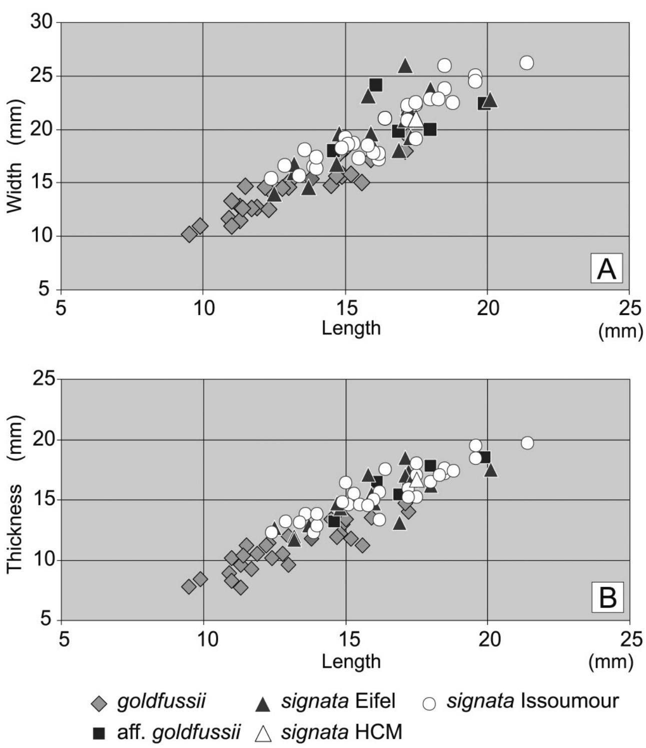


Fig. 10. *Kransia* (*Fatimaerhynchia*) *goldfussii* (Schnur, 1853), *Kransia* (*Fatimaerhynchia*?) aff. *goldfussii* (Schnur, 1853), and *Kransia* (*Fatimaerhynchia*) *signata* (Schnur, 1851). Scatter diagrams of shell width to shell length **(A)** and shell thickness to shell length **(B)**. Raw data provided in the Appendix.

shell; costae medianly furrowed on the paries geniculatus. Spine-like projections at the commissures.

Interior: Dental plates well-developed, thin, slightly divergent ventrally, lateral umbonal cavities well-developed; ventral muscle field impressed, myophragm not observed.

Dorsal median septum thick posteriorly, very thin and blade-like anteriorly, high; hinge plates subhorizontal, short and narrow, supported by the median septum, forming a fairly long (2.05 mm long in the specimen shown in Fig. 8C) and narrow septalium; cardinal process wide, multilobed (Fig. 8C, section at 2.4 mm); crural bases closely set, crura not preserved.

Remarks: The name "*signata*" was proposed for a "variety" of *Terebratula wahlenbergii* (Schnur, 1851), and Schnur (1853) and Kayser (1871) still considered it as a "variety". The first author to describe this brachiopod as a separate species was apparently Steininger (1853; *fide* Schmidt, 1941, material not seen). However, a variety name published before 1961, unless unambiguously proposed for an infrasubspecific entity (which is the case here, subspecies are never used by Schnur, 1851), has priority over a later species name (Art 45.1, 45.6.4 of the ICZN; ICZN, 1999), all the more that (Art. 45.6.4.1 of the ICZN; ICZN, 1999) it has been adopted as the valid name of the discussed species before 1985, in this case by Schmidt (1937, 1941).

The internal structure of the shell was studied on the basis of a single sectioned specimen coming from locality St. 736 (Hönselberg Mb, Junkerberg Fm, "vermutlich etwas vom tiefsten Rechert-Hzt."; Aufschluß 230 m NE Pkt 433,0, 145 m S Str. Nollenbach–Ahütte, R54480 H78035, coll. W.

Struve, Okt. 1956). It is fully concordant with the interior of a specimen coming from the Prüm Syncline sectioned by Mohanti (1972, fig. 24).

The two large samples (Eifel, N = 16 and Maïder, N = 30) are indistinguishable in shape (e.g., mean widths 19.5 and 20.0 mm, mean width-to-length ratios 1.22 in both cases); the single measurable specimen from the Holy Cross Mountains also falls within the variability limits of these samples.

Kransia (*Fatimaerhynchia*) *signata* (Schnur, 1851) differs from *K.* (*F.*) *goldfussii* and *K.* (*F.*?) aff. *goldfussii* in the costae and sulcus beginning in the umbonal region and a more rounded outline. Moreover, it differs from *K.* (*F.*) *goldfussii* in larger shell and more elevated fold. Apart from the presence of a septalium, it differs from *K.* (*K.*) *parallelepipeda* in larger shell, coarser costae and more angular sulcus tongue (more arcuate in the latter) .

Some shells of *K.* (*F.*) *signata* in the studied sample are encrusted by epizoans. These include trepostome bryozoans of the genus *Leioclema* Ulrich, 1882 (Fig. 9A–F) and possible hederellids (Fig. 9G–I). The location of *Leioclema* colonies approximately along the anterior commissure suggests brachiopods were overgrown *in vivo*.

Representatives of the Silurian to Carboniferous genus *Leioclema* were reported, among others, from the Lebanza Formation (Ernst *et al.*, 2012). Hederelloids (Taylor and Wilson, 2008) are a common group of Devonian epibionts, known for example from the Emsian to Eifelian of the Skały section of the Holy Cross Mts. (Kiepura, 1973). In a study of epizoans on the spiriferide *Paraspirifer* (*Laurentispirifer*) *bownockeri* (Stewart, 1927) from the approximately coeval (Givetian; age after Camp and Hatfield, 1991) Silica Formation Sparks *et al.* (1980) recovered hederellids as one of the most common epibionts of the above-mentioned brachiopod. Despite the numerical abundance, the present material is unsuitable for a quantitative study of the epifauna because aerial corrasion under desert conditions is likely to have removed a significant part of delicate organisms overgrowing the brachiopod shells.

Distribution: According to Struve *et al.* (2008, p. 330), in the Eifel the species discussed occurs in the Klausbach and Hönselberg members of the Junkerberg Formation (middle Eifelian). The stratigraphic position of the specimens from Włochy in the Holy Cross Mts. is the set B of the Nieczulice Beds, which are undoubtedly Givetian, probably upper Givetian (*hermanni-cristatus* Zone). *Kransia signata* is thus one of numerous Middle Devonian brachiopod species common to the Eifel, the Holy Cross Mountains, and Northern Africa (Halamski, 2004, 2008, 2009; Halamski and Baliński, 2013, 2018, 2019); however, as in the case of *Eressella coronata* (Kayser, 1871), local stratigraphic ranges are apparently in disagreement (Halamski and Baliński, 2018).

CONCLUSIONS

Kransia (?) *issoumourensis* Drot, 1971 is redescribed here on the basis of two rich collections, one approximately topotypic from Jbel Issoumour (Maïder) and one from the environs of Smara (Tindouf Syncline). It is tentatively reassigned to the genus *Lebanzuella* García-Alcalde, 1999. Two subspecies are recognised on the basis of biometric characteristics: *Lebanzuella*? *issoumourensis issoumourensis* from Jbel Issoumour with shells having a thickness-to-length ratio usually of about 0.8 and *L.*? *issoumourensis smarensis* ssp. nov. from Western Sahara with shells having the above-mentioned ratio usually of about 1.1.

Externally similar taxa *Terebratula goldfussii* Schnur, 1853 and *T. wahlenbergii* var. *signata* Schnur, 1851 do not belong to *Lebanzuella* because of differences in internal features. A new subgenus *Kransia* (*Fatimaerhynchia*), differing from the typical subgenus in the constant presence of a septalium, is proposed for placement of the two species.

Uncinulus goldfussii sensu Torley, 1934 from the Givetian to Frasnian Massenkalk of Bilveringsen represents a separate species, which is not formally described and named because insufficient material did not allow the investigation of internal structures. It is tentatively included in *Kransia* (*Fatimaerhynchia*).

Kransia (*Fatimaerhynchia*) *signata* occurs in the Eifel in the middle Eifelian. The age of the two specimens from Włochy in the Holy Cross Mountains is (late?) Givetian.

Acknowledgments

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Appendix

Biometric characteristics of studied species; measurements in millimetres

Lebanzuella? *issoumourensis smarensis* ssp. n.

Specimen number	W	L	T	w	l_{DV}	f	r_{DV}	l_{VV}	s	r_{VV}	W/L	w/W	T/L
SMF 99605.1	14.5	13.9	11.9	8.8	5	4	6	5	3	5	1.04	0.61	0.86
SMF 99605.2	**15.6**	**13**	**11.6**	**7**	**7**	**4**	**7**	**8**	**3**	**8**	**1.20**	**0.45**	**0.89**
SMF 99605.3	15.8	14.9	10.3	8.1	5	5	6	5	4	4	1.06	0.51	0.69
SMF 99605.4	14.9	13.7	10.4	6.8	6	4	8	5	4	7	1.09	0.46	0.76
SMF 99605.5	14.2	13.2	10.6	7.5	5	4	4	7	3	5	1.08	0.53	0.80
SMF 99605.6	15.4	14.2	10.1	8	6	5	7	7	4	7	1.08	0.52	0.71
SMF 99605.7	13.5	13	9.6	7.3	5	4	5	4	3	6	1.04	0.54	0.74
SMF 99605.8	14.7	12.9	9.7	7.9	6	4	5		3		1.14	0.54	0.75
SMF 99605.9	14.7	13.3	10.1	7.7	6	4	4	6	3	5	1.11	0.52	0.76
SMF 99605.10	15.9	13.1	10.6	8	5	4	5	6	3	5	1.21	0.50	0.81
SMF 99605.11	16.1	13.7	10.9	8	5	4	6	6	3	6	1.18	0.50	0.80
SMF 99605.12	15.6	14.3	12.5	8.5	5	4	6	8	4	7	1.09	0.54	0.87
SMF 99605.13	12.7	13.3	10.9	7.9	6	4	4	5	3	4	0.95	0.62	0.82
SMF 99605.14	14.6	14	11.6	7.2	6	4	6	6	3	6	1.04	0.49	0.83
SMF 99605.15	14.4	14.2	11	7.7	4	4	6	6	3	6	1.01	0.53	0.77
SMF 99605.16	15.2	14	9.8	8.4	5	4	4	8	3	6	1.09	0.55	0.70
SMF 99605.17	14.5	12.9	11	7.6	7	4	6	6	3	6	1.12	0.52	0.85
SMF 99605.18	14.7	14.9	13.7	7.1	5	4	6	8	3	7	0.99	0.48	0.92
SMF 99605.19	13.9	13.2	9.8	7.9	6	4	5		3	5	1.05	0.57	0.74
SMF 99605.20	14.2	11.9	9.5	6.4	6	4	7	6	3	6	1.19	0.45	0.80
SMF 99605.21	14.4	13.4	11.2	7.8	5	4	6	6	3	6	1.07	0.54	0.84
SMF 99605.22	15	14.2	9.7	7.6	5	4		6	3	6	1.06	0.51	0.68
SMF 99605.23	15.8	13.1	13.1	7.3		4		6	3		1.21	0.46	1.00
SMF 99605.24	16.2	13.7	11	7.4	6	4	7	6	3	6	1.18	0.46	0.80
SMF 99605.25	16.3	13.3	12.2	8.7	5	4	8		3	5	1.23	0.53	0.92
SMF 99605.26	15.3	14.5	9.5	6.3	5	4	5		3	5	1.06	0.41	0.66
SMF 99605.27	16	14.1	9.9	8.1	5	4	7	5	3	6	1.13	0.51	0.70
SMF 99605.28	12.5	12.9	11.5	6	6	4	5	6	3	6	0.97	0.48	0.89
SMF 99605.29	14.6	13.3	9.7	7.5	6	4	5	6	4	6	1.10	0.51	0.73
SMF 99605.30	16.4	14.3	10.6	7.9	7	5	6	6	4	7	1.15	0.48	0.74
SMF 99605.31	15.4	14.3	11.2	8.3	5	4	5	5	3	5	1.08	0.54	0.78
SMF 99605.32	14.2	13.7	11.7	7.3	6	4	6	7	3	6	1.04	0.51	0.85
SMF 99605.33	14.7	13.6	11.8	7.4	5	4	6		3		1.08	0.51	0.87
SMF 99605.34	12.9	12.7	10.1	6.9		4	5	5	3	5	1.02	0.53	0.80
SMF 99605.35	13.8	13	11.9	6.6	5	4	5		3	6	1.06	0.48	0.92
SMF 99605.36	13.5	12.1	10.7	5.8	6	4	6	6	3	6	1.12	0.43	0.88
SMF 99605.37	13.7	13.3	10.4	7.7	6	3	5	4	2	4	1.03	0.56	0.78
SMF 99605.38	13.2	11.4	9.6	7	6	4	5	4	3	5	1.16	0.53	0.84
SMF 99605.39	13.9	13	11.6	6.9	5	4	6	5	3	5	1.07	0.50	0.89
SMF 99605.40	13.7	12.8	9.2	7.2	5	4	5	4	3	4	1.07	0.53	0.72
SL, m	*14.67*	*13.46*	*10.81*	*7.49*	*5.5*	*4.1*	*5.7*	*5.9*	*3.1*	*5.7*	*1.091*	*0.511*	*0.804*
sd	*1.023*	*0.756*	*1.051*	*0.693*	*0.69*	*0.32*	*1.02*	*1.13*	*0.40*	*0.94*	*0.0671*	*0.0434*	*0.783*
v	*0.070*	*0.056*	*0.097*	*0.092*	*0.12*	*0.08*	*0.18*	*0.19*	*0.13*	*0.17*	*0.0615*	*0.0848*	*.0974*

Lebanzuella? *issoumourensis issoumourensis* (Drot, 1971)

Specimen number	W	L	T	w	l_{DV}	f	r_{DV}	l_{VV}	s	r_{VV}	W/L	w/W	T/L
MB.B.9439.1	11.5	10.4	10.4	4.9	5	4	6	6	3	6	1.11	0.43	1.00
MB.B.9439.2	13.6	12.7	12.3	7.0	7	4	6	8	3	7	1.07	0.51	0.97
MB.B.9439.3	15.6	13.9	13.1	8.3		6	8	8	5	8	1.12	0.53	0.94
MB.B.9439.4	14.6	13.9	13.3	7.2	6	4	6		3	7	1.05	0.49	0.96
MB.B.9439.5	13.8	11.6	13.5	7.0	8	4	6	7	3	8	1.19	0.51	1.16
MB.B.9439.6	12.8	11.1	10.8	5.3	7	4	7	7	3	7	1.15	0.41	0.97
MB.B.9439.7	12.1	10.8	10.7	5.8		4	7	7	3	6	1.12	0.48	0.99
MB.B.9439.8	13.4	11.9	11.9	8.0	7	5	8		4	7	1.13	0.60	1.00
MB.B.9439.9	12.0	11.7	9.7	5.5	5	4	5	7	3	5	1.03	0.46	0.83
MB.B.9439.10	14.4	12.9	11.8	7.4	7	6	7	6	5	7	1.12	0.51	0.91
MB.B.9439.11	12.7	11.6	11.5	5.0	5	4	6	6	3	6	1.09	0.39	0.99
MB.B.9439.12	13.2	11.2	10.9	6.5	6	4	7	7	3	8	1.18	0.49	0.97
MB.B.9439.13	12.4	11.5	11.9	6.3	6	4	6	6	3	7	1.08	0.51	1.03
MB.B.9439.14	14.3	12.6	12.4	6.0	6	4	7	7	3	6	1.13	0.42	0.98
MB.B.9439.15	11.8	10.8	11.0	6.5	6	4	7	6	3	6	1.09	0.55	1.02
MB.B.9439.16	10.9	10.6	9.7	6.3	5	4	6		3		1.03	0.58	0.92
MB.B.9439.17	12.7	11.9	10.2	6.0	5	4	6	5	3	5	1.07	0.47	0.86
MB.B.9439.18	11.2	10.9	10.6	4.9	6	4	5	7	3	8	1.03	0.44	0.97
MB.B.9439.19	13.3	11.7	12.1	4.8	7	4	8	9	3	6	1.14	0.36	1.03
MB.B.9439.20	12.1	11.2	10.2	5.5	5	4	5	6	3	7	1.08	0.45	0.91
MB.B.9439.21	12.0	10.4	10.0	5.1	7	4	7		3	8	1.15	0.43	0.96
MB.B.9439.22	12.7	11.8	12.0	5.7	6	4	6	6	3	7	1.08	0.45	1.02
MB.B.9439.23	11.7	10.8	10.9	5.4	6	4	6	7	3	7	1.08	0.46	1.01
MB.B.9439.24	12.2	12.5	12.2	6.7		5	7		4		0.98	0.55	0.98
MB.B.9439.25	13.4	11.9	10.7	7.0	5	4	6	7	3		1.13	0.52	0.90
MB.B.9439.26	11.8	10.8	10.2	6.4		5			4		1.09	0.54	0.94
MB.B.9439.27	14.0	12.4	12.1	6.6	7	6	7		5	7	1.13	0.47	0.98
MB.B.9439.28	12.7	11.3	11.6	6.5		4	6		3	6	1.12	0.51	1.03
MB.B.9439.29	11.7	10.9	10.7	4.2		4	6		3	7	1.07	0.36	0.98
MB.B.9439.30	13.4	12.5	11.7	6.7	6	4	6	6	3	7	1.07	0.50	0.94
MB.B.9439.31	11.7	11.7	11.5	5.0	6	4	7	7	3	6	1.00	0.43	0.98
MB.B.9439.32	12.7	11.5	10.9	5.4	7	4	7	6	3	6	1.10	0.43	0.95
MB.B.9439.33	11.9	11.0	10.5	5.7	7	5	6	7	4	7	1.08	0.48	0.95
MB.B.9439.34	12.7	11.8	10.3	6.6		4		7	3	5	1.08	0.52	0.87
MB.B.9439.35	14.0	13.2	12.2	6.2		5			4	7	1.06	0.44	0.92
MB.B.9439.36	12.6	11.0	11.0	4.8	6	4	6	5	3	5	1.15	0.38	1.00
MB.B.9439.37	13.0	11.9	11.3	5.5	5	4	5	5	3	5	1.09	0.42	0.95
MB.B.9439.38	12.6	11.5	11.4	5.5	5	4	5	6	3	5	1.10	0.44	0.99
MB.B.9439.39	12.4	11.5	11.2	6.5	6	4	6		3	7	1.08	0.52	0.97
MB.B.9439.40	11.9	11.9	11.6	5.5	7	4	7	7	3	7	1.00	0.46	0.97
Iss, m	*12.74*	*11.68*	*11.30*	*6.03*	*6.1*	*4.3*	*6.4*	*6.6*	*3.3*	*6.6*	*1.091*	*0.473*	*0.968*
sd	*1.012*	*0.854*	*0.940*	*0.917*	*0.86*	*0.60*	*0.82*	*0.91*	*0.60*	*0.94*	*0.0473*	*0.0568*	*.0560*
v	*0.079*	*0.0731*	*0.083*	*0.152*	*0.14*	*0.14*	*0.13*	*0.14*	*0.18*	*0.14*	*0.0434*	*0.1200*	*.0579*
Total, m	*13.70*	*12.57*	*11.05*	*6.76*	*5.8*	*4.2*	*6.0*	*6.2*	*3.2*	*6.1*	*1.091*	*0.492*	*0.886*
sd	*1.401*	*1.201*	*1.022*	*1.091*	*0.81*	*0.49*	*0.98*	*1.09*	*0.51*	*1.03*	*0.0577*	*0.0538*	*.1067*
v	*0.102*	*0.096*	*0.092*	*0.161*	*0.14*	*0.12*	*0.16*	*0.18*	*0.16*	*0.17*	*0.0529*	*0.1093*	*.1204*

Kransia (*Fatimaerhynchia*) *goldfussii* (Schnur, 1853)

Specimen number	W	L	T	w	l_{DV}	f	r_{DV}	l_{VV}	s	r_{VV}	W/L	w/W	T/L
SMF 99590	15.4	13.8	11.8	7.7	6	4	7	6	3	7	1.12	0.50	0.86
SMF 99800.1	12.8	11.3	7.7	4.6	7	4			3	6	1.13	0.36	0.68
SMF 99800.2	11.7	10.9	8.9	5.2	6	4	5	5	3	7	1.07	0.44	0.82
SMF 99800.3	15.8	14.9	13.6	9.3		6		7	5		1.06	0.59	0.91
SMF 99800.4	15.6	14.9	13	7.6		6	7		4		1.05	0.49	0.87
SMF 99800.5	12.7	11.9	10.5	8	6	4	7		3	6	1.07	0.63	0.88
SMF 99601	19.4	17.2	14	9.3	7	6	7	7	5	6	1.13	0.48	0.81
SMF 99600	17.2	15.9	13.5	9.2	6	6		8	5		1.08	0.53	0.85
SMF 99800.6	14.2	12.4	10.2	6.8	7	6	8				1.15	0.48	0.82
SMF 99800.7	11.5	11.3	9.6	5.9	4	4	4				1.02	0.51	0.85
SMF 99801	15	13	12	7.4	6	4	6	5	3		1.15	0.49	0.92
SMF 99593	18	17.1	14.7	10.2	7	7	7		6		1.05	0.57	0.86
SMF 99591	15	15.6	11.2	7	8	5	8	7	4		0.96	0.47	0.72
SMF 99800.8	18.2	15	13.4	10	7	8	8	9	7	7	1.21	0.55	0.89
SMF 99800.9	14.8	14.5	13.4	8.7		5	6		6		1.02	0.59	0.92
SMF 99800.10	14.6	13	9.6	7.2	4	4	5	5	3	5	1.12	0.49	0.74
SMF 99800.11	17.7	14.8	12.2			4	8	8	3		1.20		0.82
SMF 99800.12	11	11	8.3	4.2					2	4	1	0.38	0.75
SMF 99800.13	12.6	11.7	9.3	5	5	3	6	7	2	5	1.08	0.40	0.79
SMF 99800.14	11	9.9	8.4	4.6	3	3	4	3	2	4	1.11	0.42	0.85
SMF 99800.15	12.5	12.3	11.4	5.9		4	5		3		1.02	0.47	0.93
SMF 99592	13.3	11	10.2	5.8	4	3					1.21	0.44	0.93
SMF 99653	14.7	11.5	11.2	6.3	6	4	8	6	3	6	1.28	0.43	0.97
SMF 99672	14.5	12.8	10.5	7.4			6	7	3	7	1.13	0.51	0.82
SMF 99652	15.6	14.7	11.9	7.1		4	5	6	3		1.06	0.46	0.81
SMF 99671	14.6	12.2	11.2	6.2	5	5	5	5	4	6	1.20	0.42	0.92
SMF 99670	15.8	15.2	11.8	7.8	5	4	6	5	3	6	1.04	0.49	0.78
SMF 99668	12.6	11.4	10.4	5.8	5	4	6	5	3	4	1.11	0.46	0.91
SMF 99651	10.2	9.5	7.8	4.6	5	3	5	4	2		1.07	0.45	0.82
Eifel, m	*14.41*	*13.13*	*11.09*	*6.96*	*5.7*	*4.6*	*6.2*	*6.1*	*3.6*	*5.7*	*1.100*	*0.482*	*0.846*
sd	*2.339*	*2.100*	*1.930*	*1.713*	*1.28*	*1.28*	*1.28*	*1.51*	*1.33*	*1.10*	*0.0728*	*0.0638*	*.0698*
v	*0.162*	*0.160*	*0.174*	*0.246*	*0.23*	*0.28*	*0.21*	*0.25*	*0.37*	*0.19*	*0.0662*	*0.1324*	*.0826*

Kransia (*Fatimaerhynchia*) aff. *goldfussii* (Schnur, 1853)

Specimen number	W	L	T	w	l_{DV}	f	r_{DV}	l_{VV}	s	r_{VV}	W/L	w/W	T/L
SMF 99596	19.8	16.9	15.4	10	7	6	7	8	5	8	1.17	0.51	0.91
SMF 99595	21.3	17.2	16.6	10.6	8	6	8	8	5		1.24	0.50	0.97
SMF 99599	22.4	19.9	18.5	12.4		7	8	8	6		1.13	0.55	0.93
SMF 99797	24.1	16.1	16.5	11.8	8	8	8	9	7		1.50	0.49	1.02
SMF 99598	20	18	17.8	10	7	4	8	8	3	8	1.11	0.5	0.99
SMF 99798	18	14.6	13.2	9.1	7	6	7	6	5	8	1.23	0.51	0.90
SMF 99799	16.9		13	7.3	7	4	6	8	4	5		0.43	
Bilv., m	*20.36*	*17.12*	*15.86*	*10.17*	*7.3*	*5.9*	*7.4*	*7.9*	*5.0*	*7.3*	*1.229*	*0.498*	*0.95*
sd	*2.484*	*1.786*	*2.127*	*1.696*	*0.52*	*1.46*	*0.79*	*0.90*	*1.29*	*1.50*	*0.1412*	*0.0357*	*.0475*
v	*0.122*	*0.104*	*0.134*	*0.167*	*0.07*	*0.25*	*0.11*	*0.11*	*0.26*	*0.21*	*0.1149*	*0.0717*	*.0498*

Kransia (*Fatimaerhynchia*) *signata* (Schnur, 1851)

SMF 99656	22.8	20.1	17.5	10.0	7	5	7	7	4	8	1.13	0.44	0.87
SMF 99659	22.0	17.2	17.4	12.2	9	8	9	8	7	7	1.28	0.55	1.01
SMF 99661.1	23.8	18.0	16.2	11.6	7	7	7	7	6	7	1.32	0.49	0.90
SMF 99661.2	18.4	16.0	14.7	9.0	6	5	5	6	4	6	1.15	0.49	0.92
SMF 99806	20.9	17.1	17.0	9.8	9	7	8	9	6	8	1.22	0.47	0.99
SMF 99658	19.6	14.8	14.3	10.2	7	7	8	8	6	8	1.32	0.52	0.97
SMF 99660	16.0	13.2	12.0	6.7	6	5	6	6	4	6	1.21	0.42	0.91
SMF 99802	14.6	13.7	12.9	7.8	7	5	6	6	4	6	1.07	0.53	0.94
SMF 99804	16.8	13.2	11.7	7.9	6	7	6	7	5	8	1.27	0.47	0.89
SMF 99803	26.0	17.1	18.5	12.7	9	8	9	9	7		1.52	0.49	1.08
SMF 99666	14	12.5	12.7	8.3	6	6		6	5	6	1.12	0.59	1.02
SMF 99657	16.8	14.7	14.7	8.6	7	6	7	7	5	7	1.14	0.51	1.00
SMF 99805	19.3	17.3	16.6	10.2	8	7	8	7	6		1.12	0.53	0.96
SMF 99667	19.6	15.9	15.5	10.6		6	7	7	5		1.23	0.54	0.97
SMF 99661.3	23.2	15.8	17.1	12.4	7	7	8	7	6	6	1.47	0.53	1.08
SMF 99655	18.1	16.9	13.1	8.6	8	6	9	8	5	8	1.07	0.48	0.78
Eifel, m	*19.49*	*15.84*	*15.12*	*9.79*	*7.3*	*6.4*	*7.3*	*7.2*	*5.3*	*7.0*	*1.228*	*0.503*	*0.956*
sd	*3.443*	*2.052*	*2.169*	*1.792*	*1.10*	*1.02*	*1.23*	*0.98*	*1.01*	*0.91*	*0.1326*	*0.0448*	*.0792*
v	*0.177*	*0.130*	*0.143*	*0.183*	*0.15*	*0.16*	*0.17*	*0.14*	*0.19*	*0.13*	*0.1080*	*0.0889*	*.0829*
GIUS 4-813 Ws	21	17.5	16.7	10	6	6	6	8	5	10	1.20	0.48	0.95
MB.B.9392.1	21	16.4	17.5	11.2	5	4		7	3	7	1.28	0.53	1.07
MB.B.9392.2	22.3	17.5	17	12.1		6			5	8	1.27	0.54	0.97
MB.B.9392.3	18.7	15.3	15.5	9.9	5	5	4	5	4	7	1.22	0.53	1.01
MB.B.9392.4	17.2	16.2	13.3	9.4		5		5	4	6	1.06	0.55	0.82
MB.B.9392.5	17.7	16.2	15.6	9.2	6	5	5	6	4	7	1.09	0.52	0.96
MB.B.9392.6	25.9	18.5	17.2	12.5			7	8	4	10	1.40	0.48	0.93
MB.B.9392.7	26.2	21.4	19.7	15.1		6	9	8	6	8	1.22	0.58	0.92
MB.B.9392.8	22.2	17.2	15.9	9.8					5		1.29	0.44	0.92
MB.B.9392.9	23.8	18.5	17.6	13.3	8	7		9	6	9	1.29	0.56	0.95
MB.B.9392.10	25	19.6	19.5	12.7		6			5		1.28	0.51	0.99
MB.B.9392.11	22.5	17.5	18	10.8	6	5	7	9	4	8	1.29	0.48	1.03
MB.B.9392.12	16.5	13.9	12.3	8.9	8	5		7	4		1.19	0.54	0.88
MB.B.9392.13	16.3	14	12.8	8	8	5	7	8	4	9	1.16	0.49	0.91
MB.B.9392.14	22.8	18	16.5	10.3		5		8	4		1.27	0.45	0.92
MB.B.9392.15	22.5	18.8	17.4	12.8		6		7	5		1.20	0.57	0.93
MB.B.9392.16	19.1	17.5	15.2	10.6					5	7	1.09	0.55	0.87
MB.B.9392.17	18.1	13.6	13.8	8	7	5			4	8	1.33	0.44	1.01
MB.B.9392.18	17.8	16	15	10	5	6	5	5	5	6	1.11	0.56	0.94
MB.B.9392.19	19.2	15	16.4	8.1	8	4	8	9	3	9	1.28	0.42	1.09
MB.B.9392.20	18.6	15.1	14.6	9.8	8	6	7	8	5		1.23	0.53	0.97
MB.B.9392.21	20.8	17.2	15.2	10.1	8	6			5		1.21	0.49	0.88
MB.B.9392.22	22.8	18.3	17	14.1		6			5		1.25	0.62	0.93
MB.B.9392.23	18.2	14.9	14.8	8.7	6	6	8	8	5	7	1.22	0.48	0.99
MB.B.9392.24	17.3	15.5	14.6	7.7	6	4	6	7	3	7	1.12	0.45	0.94
MB.B.9392.25	15.4	12.4	12.3	6.9		5	8	8	4	9	1.24	0.45	0.99
MB.B.9392.26	18.5	15.8	14.5	10.3		4			3		1.17	0.56	0.92
MB.B.9392.27	16.6	12.9	13.2	6.7		4	7	8	3	8	1.29	0.40	1.02

MB.B.9392.28	24.5	19.6	18.4	14.4		7		10	6	10	1.25	0.59	0.94
MB.B.9392.29	17.4	14	13.8	7.9	6	6	6	6	5		1.24	0.45	0.99
MB.B.9392.30	15.6	13.4	13.1	8.4	6	6	6	8	5	7	1.16	0.54	0.98
Issoumour, m	*20.02*	*16.34*	*15.59*	*10.26*	*6.6*	*5.4*	*6.7*	*7.5*	*4.4*	*7.9*	*1.223*	*0.510*	*0.956*
sd	*3.201*	*2.216*	*2.055*	*2.258*	*1.204*	*0.884*	*1.345*	*1.371*	*0.898*	*1.182*	*0.0768*	*0.0548*	*.0587*
v	*0.159*	*0.136*	*0.132*	*0.220*	*0.182*	*0.165*	*0.202*	*0.184*	*0.202*	*0.151*	*0.0628*	*0.1074*	*.0614*
Total, m	*19.86*	*16.20*	*15.45*	*10.09*	*6.91*	*5.75*	*6.97*	*7.36*	*4.74*	*7.59*	*1.225*	*0.507*	*0.956*
sd	*3.227*	*2.136*	*2.069*	*2.076*	*1.174*	*1.037*	*1.303*	*1.203*	*1.010*	*1.209*	*0.097*	*0.051*	*0.065*
v	*0.163*	*0.132*	*0.134*	*0.206*	*0.170*	*0.180*	*0.187*	*0.163*	*0.213*	*0.159*	*0.0795*	*0.1001*	*.0680*

Measurements in Roman typeface (those of the holotype in boldface), statistics in Italics.
W – width of the shell; L – length of the shell; T – thickness of the shell; w – width of the sulcus; l – number of costae and costellae on the left flank (l_{DV} – of the dorsal valve, l_{VV} – of the ventral valve); f – number of costae and costellae on the fold; r – number of costae and costellae on the right flank (r_{DV} – of the dorsal valve, r_{VV} – of the ventral valve); s – number of costae and costellae in the sulcus;. Abbreviations: *m* – mean; *sd* – standard deviation; v – variation coefficient (= *sd* / *m*).