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ERESSELLA, A NEW UNCINULOID BRACHIOPOD GENUS FROM THE MIDDLE DEVONIAN OF EUROPE AND AFRICA

Adam T. HALAMSKI & Andrzej BALIŃSKI

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

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Abstract: *Eressella*, a new genus of rhynchonellide brachiopods belonging to the superfamily Uncinuloidea Rzhonsnitskaya, 1956, is described with *Rhynchonella coronata* Kayser, 1871, as the type and only species. It is characterised by a dorsibiconvex profile with a resupinate ventral valve, costae rounded posteriorly, but acute and developing ventrally directed spur-like protuberances anteriorly, small dental cavities, cardinal process multilobed posteriorly and massive anteriorly, and the presence of a septalium and thick dorsal median septum. Given the present state of flux in the systematics of the superfamily, it is conventionally placed within the family Uncinulidae Rzhonsnitskaya, 1956, although similarities with the subfamily Betterbergiinae Savage, 1996 and the family Eucharitinidae Sartenaer, 2015 are also noted. *Eressella coronata*, hitherto the only representative of the genus, is known from the Eifel Hills (Eifelian, mainly middle Eifelian), from central Poland (especially from the Eifelian of the Holy Cross Mts.), and from the Moroccan Anti-Atlas (late Eifelian to early Givetian, details uncertain).

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

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INTRODUCTION

Purpose of the present paper

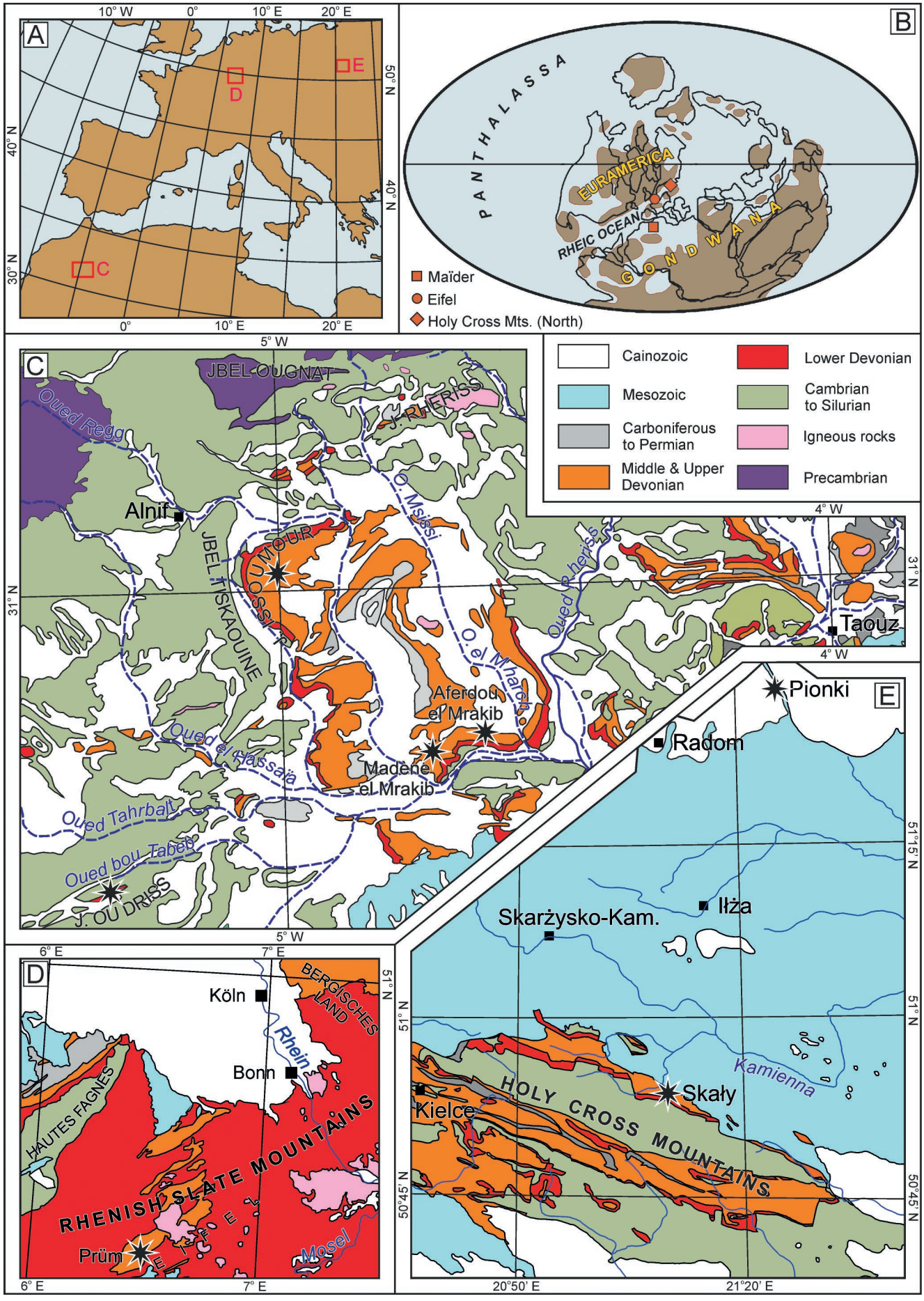
The Middle Devonian brachiopod species *Rhynchonella coronata* was originally described from the Eifel Hills in Germany (Kayser, 1871) and subsequently reported from the Holy Cross Mountains in Poland (first by Gürich, 1896) and from the Moroccan Anti-Atlas (first by Drot, 1971; Fig. 1). As aptly summarised by Drot (1971, p. 72), the species discussed is characterised by a peculiar external morphology and thus is unmistakably recognisable even without analysing the interiors, but its affinities at the genus level remain unclear. Halamski (2004, p. 139–140) concluded that *Rhynchonella coronata* should be placed within a new genus, but was unable to propose a formal description thereof, as the material at his disposal was too scarce.

The purpose of the present paper is therefore threefold: 1) to re-describe the morphology and the anatomy of *Rhynchonella coronata* on the basis of specimens from the Eifel, the Holy Cross Mts. and the Anti-Atlas (Fig. 1); 2) to introduce the new genus *Eressella*, typified by the above-mentioned species, and to elucidate its affinities; and 3) to discuss the stratigraphic distribution of the brachiopod species studied.

History of research

The Middle Devonian *Rhynchonella coronata* was first described by Kayser (1871). It need not be confused with the Jurassic species *Rhynchonella coronata* Moore, 1861, a probable representative of the genus *Holcorhynchia* (Ager, 1967, p. 153). *Rhynchonella coronata* Moore, 1861 and *Rhynchonella coronata* Kayser, 1871 are primary homonyms (Art. 53.3 of the ICZN). In the case of secondary homonyms no longer considered congeneric, the junior homonym is not to be rejected (Art. 59.2); however, the ICZN has no special provision for primary homonyms no longer considered congeneric. In the opinion of the present authors, the stability of nomenclature is best served by continuing the use of Kayser's specific name.

The characteristic external morphology of *Rhynchonella coronata* Kayser, 1871, namely the resupinate ventral valve with high costae and costellae commonly forming acute spur-like protuberances at lateral geniculation, reminiscent of a tiara or a crown (Fig. 2P), is reflected in the species name (Latin *coronatus*, crowned). The picturesque circumstances of the field studies of Emmanuel Kayser in the Eifel during the Franco-Prussian war were related by Alvarez *et al.* (1996, p. 75). The species discussed was then report-


A
B
C
D
E
PANTHALASSA
EURAMERICA
RHEIC OCEAN
GONDWANA
Maïder
Eifel
Holy Cross Mts. (North)
Cainozoic
Mesozoic
Carboniferous to Permian
Middle & Upper Devonian
Lower Devonian
Cambrian to Silurian
Igneous rocks
Precambrian
JBEL OUGNAT
J. RHERISS
Oued Regg
Alnif
JBEL TISKAOUINE
OUMOUR
OSSIT
O. Msissi
O. el M'harch
Oued R'heriss
Taouz
Aferdou el Mrakib
Madène el Mrakib
Oued el Hassaïa
Oued Tahrbalt
Oued bou Tabeb
J. OU DRISS
Pionki
Radom
Iłża
Skarżysko-Kam.
Kamienna
Skały
Kielce
HOLY CROSS MOUNTAINS
Köln
Bonn
Rhein
BERGISCHES LAND
HAUTES FAGNES
RHENISH SLATE MOUNTAINS
EIFEL
Prüm
Mosel

ed from the Northern region of the Holy Cross Mountains (Poland) by Gürich (1896), Sobolew (1904, 1909) and Siemiradzki (1909, 1922a, b).

The internal features of *Rhynchonella coronata* Kayser, 1871 were first investigated by Schmidt (1941), who transferred it to the genus *Uncinulus*. Biernat (1966) serially sectioned one of three shells at her disposal and agreed with such a classification. It is also under the same genus name that the species discussed was reported in a few regional geology papers dealing with the Eifel (Schwenzer, 1965), in an account of the drilling of a borehole in central Poland (Łobanowski and Przybyłowicz, 1979), and in a compilation of stratigraphically important species of the Polish Devonian (Biernat *in* Sarnecka, 2003, p. 205).

Drot (1971) was the first author to find the discussed brachiopod in Northern Africa. She sectioned one of eight poorly preserved specimens at her disposal and concluded that inclusion into any of the genera *Uncinulus*, *Kransia*, *Glossinotoechia*, and *Pseudoglossinotoechia* was an equally unsatisfying solution. She used the name "*Uncinulus*" *coronatus*.

In a compilation of Middle Devonian brachiopods from the Eifel, Jungheim (2000) included *Rhynchonella coronata* Kayser, 1871 within the genus *Kransia*, although without discussing the issue.

In an unpublished Ph.D. thesis, Halamski (2004, p. 139) used the name "*Kransia*" *coronata*, but stated clearly that a new genus (of the family Hebetoechiidae) should be proposed. Owing to the small quantity of specimens at his disposal (four shells from the Holy Cross Mts.), no formal nomenclatural act was attempted. In a paper dealing with brachiopods from the Moroccan Anti-Atlas, Halamski and Baliński (2013) used the name *Kransia*? *coronata*.

A few alleged subspecies of *Rhynchonella coronata* were described from Russia. Two of them come from the Eifelian of the Urals: *Hypothyridina* (?) *coronata alata* Khodalevitch, 1951 and *Hypothyridina* (?) *coronata tenuiplicata* Khodalevitch, 1951. *Uncinulus coronatus kitaticus* Rzhonsnitskaya, 1968 was described from the Givetian of Kuznetsk. The present authors follow Drot (1971, p. 72) and Erlanger (1994, p. 72) in considering them as separate species. Their revision should be conducted on the basis of representative collections from type strata and is beyond the scope of the present paper.

Material and methods

The collections investigated include the type collection of Kayser (MB) and Schultze's collection from the same area (MCZ). Only four shells from the Holy Cross Mts. (Gürich's collection, MGUWr; Biernat's collection, ZPAL) could be found. Particularly well preserved specimens come from the collection, established by the late Volker Ebbighausen in Morocco and bequeathed by him to the MB.

More precisely, the material investigated comes from the following outcrops.

Eifel. Prüm Syncline: "Crinoid Beds" [no further details are available for this collection] (coll. Kayser, MB); Schwirzheim (coll. Schultze in 1858, MCZ); Gondelsheim, Rommersheim, Oberlauch, Brühlbron (coll. Schmidt, SMF).

Holy Cross Mountains. Northern (or Łysogóry) region, Bodzentyn Syncline, Grzegorzowice-Skały section: outcrop 83 at Skały sensu Pajchlowa (1957) (coll. Biernat, ZPAL); Skały [details not available] (coll. Gürich, MGUWr).

Anti-Atlas. North-western Maïder, Jebel Issoumour [this oronym is spelt Issimour, Issomour, or Issoumour; the authors have chosen the latter variant used by du Dresnay *et al.* (1988)], outcrop 151 sensu Ebbighausen (unpublished), a continuous outcrop situated 3–8 km W–SW from Taboumakhlouf, "upper *Drotops* Beds" [Bou Dib Fm., Givetian] (coll. Ebbighausen, MB); *Drotops* Beds, Madène el Mrakib (coll. Ebbighausen, SMF); Aferdou el Mrakib (coll. Halamski and Baliński, ZPAL).

The stratigraphic setting of these outcrops is discussed in detail in a special chapter of the present paper. Collections that could not be used by the present authors include those of Sobolew (1904, 1909) and of Siemiradzki (1909, 1922a, b) from the Holy Cross Mts., that of Łobanowski and Przybyłowicz (1979) from a borehole in central Poland, and that of Drot (1971) from the Anti-Atlas.

The internal features of the species discussed have been studied on the basis of serial sections of five specimens: two from the Eifel (Schmidt, 1941, pl. 6, fig. 18 and Fig. 4B herein), two from the Anti-Atlas (Drot, 1971, text-pl. 1 and Fig. 4A herein), and one from the Holy Cross Mts. (Biernat, 1966, fig. 28). Sections made by the present authors were investigated, using the standard technique of 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.

Synonymies are commented upon by means of the usual signs (Richter, 1948; Matthews, 1973), as explained by Halamski (2009, p. 46–47). Measurements are given in the following way: (*a*–) *b*–*c* (–*d*) [*e*, *N*], with *a* – minimum value; *b* – first quartile; *c* – third quartile; *d* – maximum value; *e* – arithmetic mean; *N* – number of observations (not repeated, unless different from 35, the total number of measured specimens). In the main description, the values

Fig. 1. Geographic, palaeogeographic, and geologic setting of the brachiopods studied. **A.** Geographic map of Europe and northwestern Africa, showing the locations of the three detailed geologic maps (C to E). **B.** Devonian palaeogeography, showing the three faunas with *Eressella* [after Halamski and Baliński (2013), modified after Scotese and McKerrow (1990), Golonka *et al.* (2006), and Murphy *et al.* (2011)]. **C.** Geologic map of southeastern Anti-Atlas, Morocco (simplified after Hollard *et al.*, 1985). **D.** Geologic map of part of western Germany (simplified after Bundesanstalt für Geowissenschaften und Rohstoffe, 1993). **E.** Geologic map of the Holy Cross Mountains and its northern foreland (simplified after Samsonowicz, 1966 and Rühle *et al.*, 1977). Asterisks denote localities discussed in the text; squares denotes major towns (for reference purposes). Mountains in capitals, rivers and wadis in italics.

have been calculated on the basis of all measured specimens (Eifel and Maïder; $N = 35$), whereas a biometric comparison of European and African samples is given separately below. The raw data are given in the Appendix.

Institutional abbreviations: L, Prirodoznawčyj Muzej NANU (State Museum of Natural History, National Academy of Sciences of Ukraine; formerly Muzeum Przyrodnicze im. Dzieduszyckich), Lviv, Ukraine; MB, Museum für Naturkunde, Berlin, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Mass., United States of America; MGUWr, Muzeum Geologiczne Uniwersytetu Wrocławskiego (formerly Universität Breslau), Wrocław, Poland; PKUM, Geological Museum of Peking University, Beijing, China; SMF, Senckenberg, Frankfurt am Main, Germany; ZPAL, Instytut Paleobiologii PAN, Warszawa, Poland.

SYSTEMATIC PALAEONTOLOGY

Position of *Rhynchonella coronata* Kayser, 1871 among the rhynchonellides and value of external characters for elucidation of its systematic position

Rhynchonella coronata can be included in the superfamily Uncinuloidea on account of the costae and costellae being flattened and grooved on the anterior margin (Savage, in Savage *et al*., 2002). Such a feature of the radial ornamentation appears as a phylogenetically informative character, that is, not subject to homoeomorphy.

Classification at the family level is less evident because of the present state of flux in the taxonomy of Palaeozoic rhynchonellide. Savage (Savage *et al*., 2002) distinguished a few large families, among which Uncinulidae Rzhonsnitskaya, 1956, Hebetoechiidae Havlíček, 1960, Glossinotoechiidae Havlíček, 1992, and Eatoniidae Schmidt, 1965 have characters in common with *Rhynchonella coronata*. However, clear-cut characters distinguishing them are few. Sartenaer (2015) proposed three new small families, among which the Eucharitinidae Sartenaer, 2015, and restricted the circumscription of the Hebetoechiidae.

Among the uncinuloid brachiopods, a multilobed (at least partly) cardinal process is found in some genera of the family Uncinulidae Rzhonsnitskaya, 1956 (*Uncinulus* Bayle, 1878, *Eucharitina* Schmidt, 1955, *Flabellulirostrum* Sartenaer, 1971, *Taimyrrhynx* Havlíček, 1983), in three genera of the subfamily Betterbergiinae Savage, 1996 belonging to the family Hebetoechiidae (*Kransia* Westbroek, 1968, *Nalivkinaria* Rzhonsnitskaya, 1968, and *Primipilaria* Struve, 1992), and in *Glossinotoechia* Havlíček, 1959 (family Glossinotoechiidae). The cardinal processes of *Kransia* and *Uncinulus* are the most similar to that in *Eressella*, so these two groups (family Uncinulidae and subfamily Betterbergiinae; the latter should probably be separated from the Hebetoechiidae) may be considered as candidates for the closest relatives. However, a septalium that is massive, infilled by callus and dental plates obscured by thick umbonal shell deposits indicate a closer relationship with the family Uncinulidae.

Eucharitina Schmidt, 1955 (see Havlíček, 1961; Brice, 1991; García-Alcalde and Herrera, 2015; Sartenaer, 2015) is similar to *Eressella* gen. nov. on account of the concavo-convex shape. Savage (Savage *et al.*, 2002, p. 1092) described the cardinal process of *Eucharitina* as "multilobed posteriorly, but massively bilobed anteriorly", but the serial sections of *Eucharitina eucharis* (Havlíček, 1961, fig. 51), *E. oehlerti* (Brice, 1991, fig. 8), *E. bultyncki* (García-Alcalde and Herrera, 2015, figs 16–17) show that the pattern is in fact quite different, consisting of a few relatively large lobes; this perhaps might be better called a paucilobate cardinal process (Latin *pauci*, few). Given the differences of ornamentation and internal structures, the resemblance must be interpreted as resulting from convergence, all the more since the costae of *Eucharitina* are not grooved. The same should be said about *Eatonia* Hall, 1857, to which Williams and Breger (1916, p. 68) referred *Rhynchonella coronata* precisely on the basis of the "marginal recurvature in the pedicle valve". These authors were of opinion that "the internal features are of doubtful constancy among the different species" (Williams and Breger, 1916, p. 67). This is another example of external features being misleading for the establishment of the affinities of brachiopods (see Jin and Copper, 2000 for an example among Silurian Pentamerida and Halamski and Segit, 2006 among Devonian Terebratulida).

Other examples of homoeomorphic rhynchonellides having resupinate ventral valve and spur-like protuberances on the ventral valve are the Carboniferous pugnacoid *Pleuropugnoides* Ferguson, 1966 [material examined: *P. pleurodon* (Phillips, 1836), MB.B.10540–10544; Fig. 2S–T], the lower Permian wellerelloid *Antronaria* Cooper & Grant, 1976 (pl. 533, fig. 38), and the Lower Cretaceous hemithiridoid *Plicarostrum* Burri, 1953 (Burri, 1957, pl. 12, figs 1, 2). The repetitive occurrence of similar morphologies in several unrelated lineages indicates that such a shape has some adaptive significance. The interpretation thereof is difficult, especially given that no Recent brachiopod possesses these features (M.A. Bitner, pers. comm., March 2018).

Description

Order Rhynchonellida Kuhn, 1949
Superfamily Uncinuloidea Rzhonsnitskaya, 1956
Family Uncinulidae Rzhonsnitskaya, 1956

Eressella genus novum

Type species: *Rhynchonella coronata* Kayser, 1871, as below.
Species assigned: Type species only.
Diagnosis: Uncinuloid brachiopod with strongly convex dorsal valve and resupinate ventral valve; ornamentation of costae and costellae rounded posteriorly, high and acute near the lateral and antero-lateral commissures, flattened and grooved on the tongue; squama and glotta present; dental plates short, buried in umbonal callus, lateral umbonal cavities minute, ventral muscle field impressed, anteriorly divided by a median trough; dorsal median septum present;

septalium present, but buried in umbonal callus; cardinal process posteriorly multilobed, anteriorly forming a thick plate.

Etymology: Combined from *ereš*, Sumerian for 'queen' and the feminine suffix *-ella*.

Remarks: The combination of a dorsibiconvex shape with a resupinate ventral valve, ornamentation of the shell consisting of costae rounded posteriorly and developing spur-like protuberances on ventral flanks anteriorly, cardinal process multilobed (ctenophoridium-like) posteriorly and massive anteriorly, thick shell deposits obscuring dental plates and septalium, and the lack of median septum dividing the ventral muscle field is unique among the Rhynchonellida. A detailed analysis of the affinities of the new genus is given in the previous chapter.

Eressella coronata was attributed previously, with various degrees of confidence, to *Hypothyridina*, *Uncinulus* and *Kransia*. *Hypothyridina* has a cuboid shell shape, finer and more flattened ribs, and the dorsal median septum and septalium are weak to absent. *Uncinulus* has a ventral septum, whereas the dorsal septum is buried in the callus. *Kransia* is internally similar to *Eressella*, but the hinge plates are united anteriorly of the septalium, whereas in *E. coronata* they are supported by a median septum.

Veevers (1959) and Biernat (1966) stressed similarities between *E. coronata* and *Flabellulirostrum wolmericum* (Veevers, 1959) from the Frasnian of the Fitzroy Basin (Australia). The differences in internal structure concern the dental plates (present, although in some extent buried in umbonal callus in *Eressella*, absent in *Flabellulirostrum*; Sartenaer, 1971) and dorsal median septum (thick and low in *Eressella*, thinner and higher in *Flabellulirostrum*), but the main characters distinguishing between the two are external, as the latter (the type species of *Flabellulirostrum* Sartenaer, 1971) has a convex ventral valve and broad, lowly arched or flat costae (Veevers, 1959).

Eressella coronata (Kayser, 1871)
Figs 2–5

v*	1871	*Rhynchonella coronata* n. sp. – Kayser, pp. 512–513; pl. 9, fig. 5
v.	1896	*Rhynchonella* aff. *coronatae* Kays. – Gürich, p. 285; pl. 7, fig. 5
	1904	*Rhynchonella coronata* Kayser – Sobolew, p. 97; pl. 9, fig. 23.
	1909	*Rhynchonella coronata* Kayser – Sobolew, pp. 507–508.
	1909	*Rhynchonella* aff. *coronata* Kays. – Siemiradzki, p. 88.
	1922a	*Rhynch*[*onella*] *coronata* – Siemiradzki, p. 147.
vp	1922b	*Rhynchonella coronata* Kays. cfr. – Siemiradzki, p. 17.
v.	1941	*Uncinulus coronatus* (Kayser) – Schmidt, p. 24; pl. 2, fig. 24; pl. 4, fig. 73; pl. 6, fig. 18.
v.	1966	*Uncinulus coronatus* (Kayser) – Biernat, pp. 86–88; text-fig. 28; pl. 19, fig. 27–29.
	1971	"*Uncinulus*" *coronatus* (Kayser) – Drot, pp. 71–72; text-pl. 1; pl. 3, fig. 1 a–c.
	1979	*Uncinulus coronatus* (Kayser, 1871) – Łobanowski and Przybyłowicz, p. 390; pl. 1, fig. 1.
v.	2003	*Uncinulus coronatus* (Kayser) – Biernat in Sarnecka, pp. 205–206; pl. 155, figs 3–5 [**k** Biernat, 1966: pl. 19, figs 27–29].
v.	2013	*Kransia*? *coronata* (Kayser, 1871) – Halamski and Baliński, p. 265; fig. 13OO–SS.

Type material: Articulated shell MB.B.740.1 (lectotype selected herein, specimen figured by Kayser, 1871, pl. 9, fig. 5 and re-figured herein in Fig. 3Z–DD); ten articulated shells MB.B.740.2–11 (paratypes, three of them figured herein in Fig. 3A–O).

Type locality and stratum: "Prümer Mulde, Crinoidenschicht" (Kayser, 1871, p. 513): Eifel Mts., Prüm Syncline; middle or upper Eifelian.

Material: Eifel: Prüm Syncline – SMF XVII 754a–d; MCZ 190711–190722. Holy Cross Mountains: Skały Beds, Skały – ZPAL Bp VII/3–4, MGUWr 1973s (specimen figured by Gürich, 1896 and re-figured herein in Fig. 3EE––II). Anti-Atlas: Aferdou – ZPAL Bp 68/1/5/1, Madène el Mrakib – SMF 98178, Jbel Issoumour – MB.B.9422.

Description: Shell (13.1–) 16–18.7 (–22.8) mm in width [mean 17.5; $N = 35$] elliptic in outline, transverse [width-to-length ratio (1.13–) 1.22–1.31 (–1.49); mean 1.28], geniculately convexoconcave. Maximal width about midlength. Anterior commissure uniplicate, tongue narrowly trapezoidal to rectangular, moderately high to high, occupying (0.36–) 0.41–0.50 (–0.56) [mean 0.45] of the shell width. Squama and glotta present. Ventral valve resupinate, that is weakly convex in posterior region, then flattened and concave at flanks; lateral margins truncated. Distinct, rather deep, flat-bottomed sulcus appearing posteriorly to midlength of the valve, at about ⅛ to ¼ of the valve length. Dorsal valve strongly convex, somewhat flattened medially, anterior and lateral margins truncated; maximal thickness of the valve anteriorly. Low fold appearing in the umbonal region.

Ornamentation of costae and costellae arising most often by bifurcation, up to twice from a single costa, seldom by intercalation; costae and costellae separated by somewhat narrower furrows, (4–)5–6(–8) on the fold, (3–)4–5(–7) in the sulcus, (5–)8–10(–12) on each lateral flank. Costae rounded posteriorly, sharp and acute near anterior and lateral commissures, flattened and grooved on subvertical lateral flanks. Ventral flank costae frequently forming acute, ventrally directed spur-like protuberances at lateral geniculation (Fig. 2P–R).

Ventral interior: delthyrium closed by massive conjunct deltidial plates; dental plates short, poorly defined, buried in secondary shell deposit, slightly convergent ventrally, lateral umbonal cavities minute, largely infilled by callus;

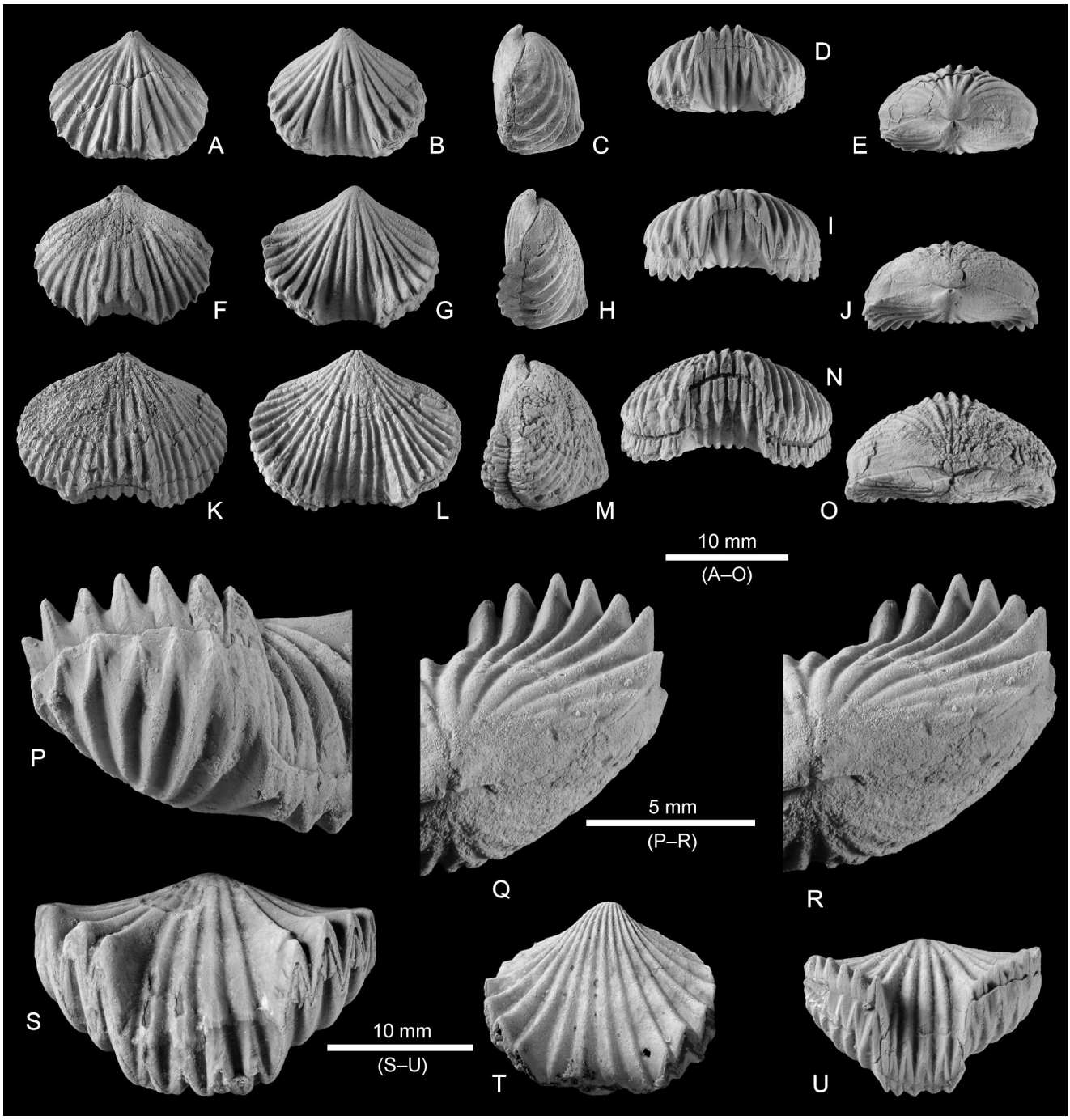


Fig. 2. *Eressella coronata* (Kayser, 1871) from Africa (Jebel Issoumour, locality 151 *sensu* Ebbighausen, unpublished) and representatives of the homoeomorphic pugnacoid genus *Pleuropugnoides* from the Carboniferous of England and China. **A–R, U.** *Eressella coronata* (Kayser, 1871) from Africa (Jebel Issoumour, locality 151 *sensu* Ebbighausen, unpublished). **A–E, F–J, K–O.** Articulated shells MB.B.9422.3,2,1 in dorsal, ventral, lateral, anterior, and posterior views. **P.** Fragment of the articulated shell MB.B.9422.4 in antero-lateral view to show acute spur-like protuberances of costae and costellae at the lateral commissure and flattening of the costae on the tongue (ventral valve upwards). **Q–R.** Fragment of the articulated shell MB.B.9422.4 in postero-ventral view (stereopair, ventral valve upwards). **U.** Articulated shell MB.B.9422.6 in anterior view. **S**, **T**. Two pugnacoid species showing resupinate ventral valve and acute spurs on ventral lateral ribs at anterior margin. **S**. *Pleuropugnoides pleurodon* (Phillips, 1836), anterior view of the articulated shell MB.B.10540; Lower Carboniferous, between Skipton and Grassington, England. **T**. *Pleuropugnoides calcaris* Sun & Baliński, 2012 from the Muhua Formation, Tournaisian, Muhua, China; ventral view of the silicified shell PKUM02-0415 (illustrated by Sun and Baliński 2012, fig. 9C2).

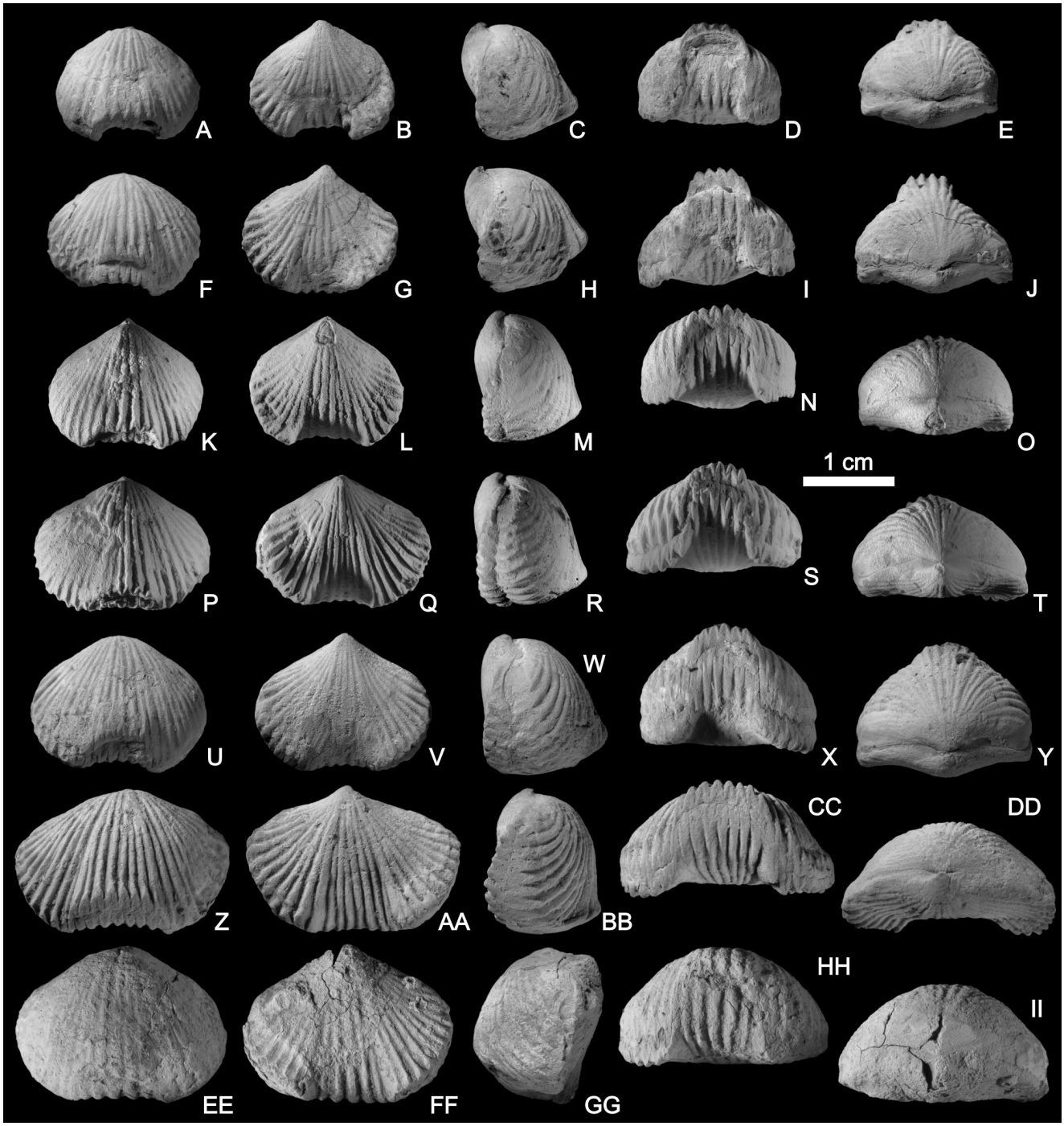


Fig. 3. *Eressella coronata* (Kayser, 1871) from Europe (A–DD, Eifel; EE–II, Holy Cross Mountains). Articulated shells in dorsal, ventral, lateral, anterior, and posterior views. **A–E, F–J, K–O.** Paratypes MB.B.740.12, 740.10, 740.4 from the Crinoid Beds of the Prüm Syncline, Eifel (coll. Kayser). **P–T, U–Y.** Shells MCZ 190712 and MCZ 190711 (serially sectioned, see Fig. 4A) from Schwirzheim, near Prüm (coll. Schultze). **Z–DD.** Holotype MB.B.740.1 from the Crinoid Beds of the Prüm Syncline, Eifel (coll. Kayser; specimen figured by Kayser, 1871, pl. 9, fig. 5). **EE–II.** Shell MGUWr 1973s from Skały (specimen figured by Gürich, 1896, pl. 7, fig. 5).

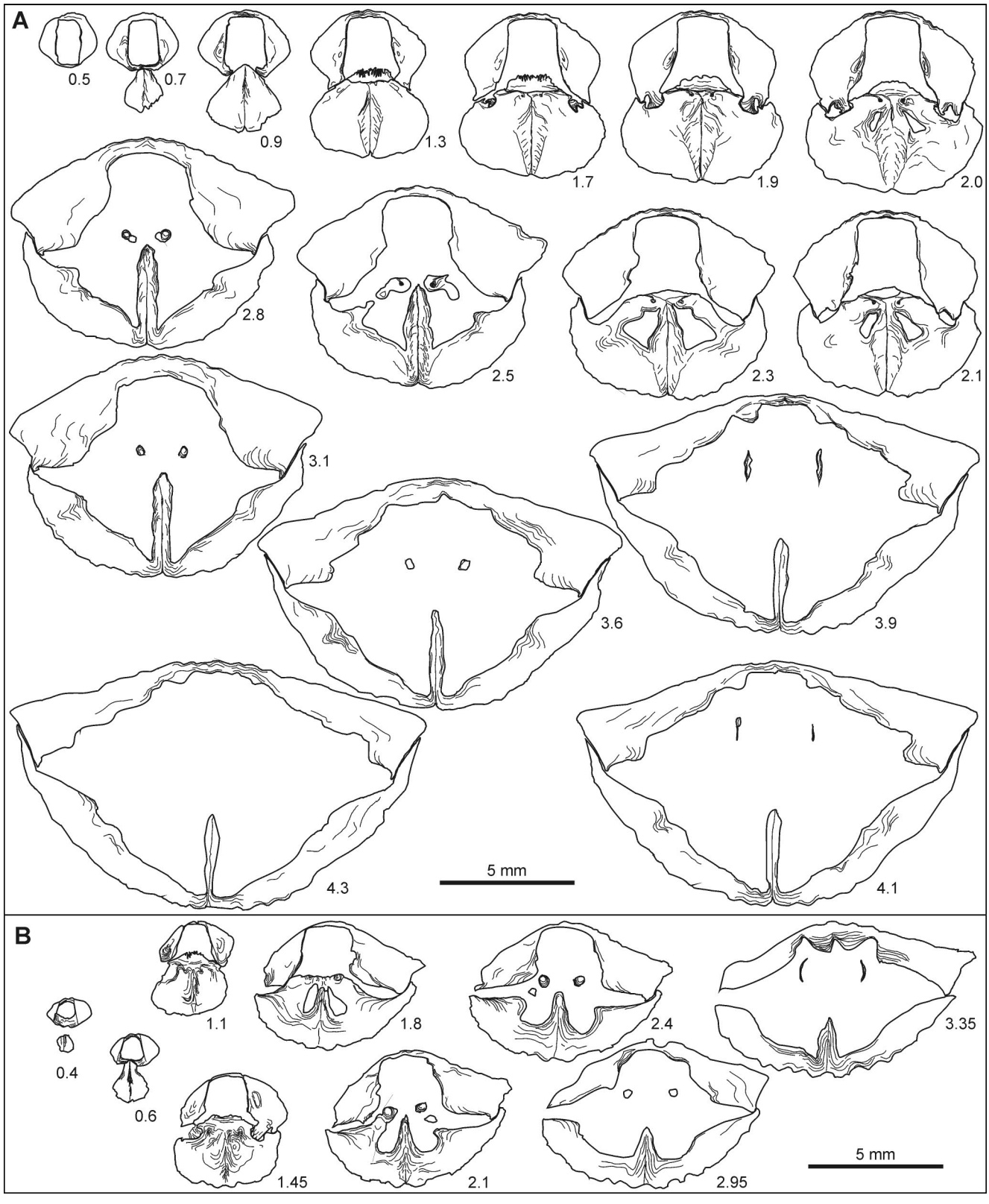


Fig. 4. Transverse serial sections of *Eressella coronata* (Kayser, 1871) through the shells MCZ 190711 from Schwirzheim near Prüm (coll. Schultze) **(A)** and MB.B.9422.6 from Jbel Issoumour (coll. Ebbighausen) **(B)**. Distances measured in millimetres from the tip of the ventral umbo.

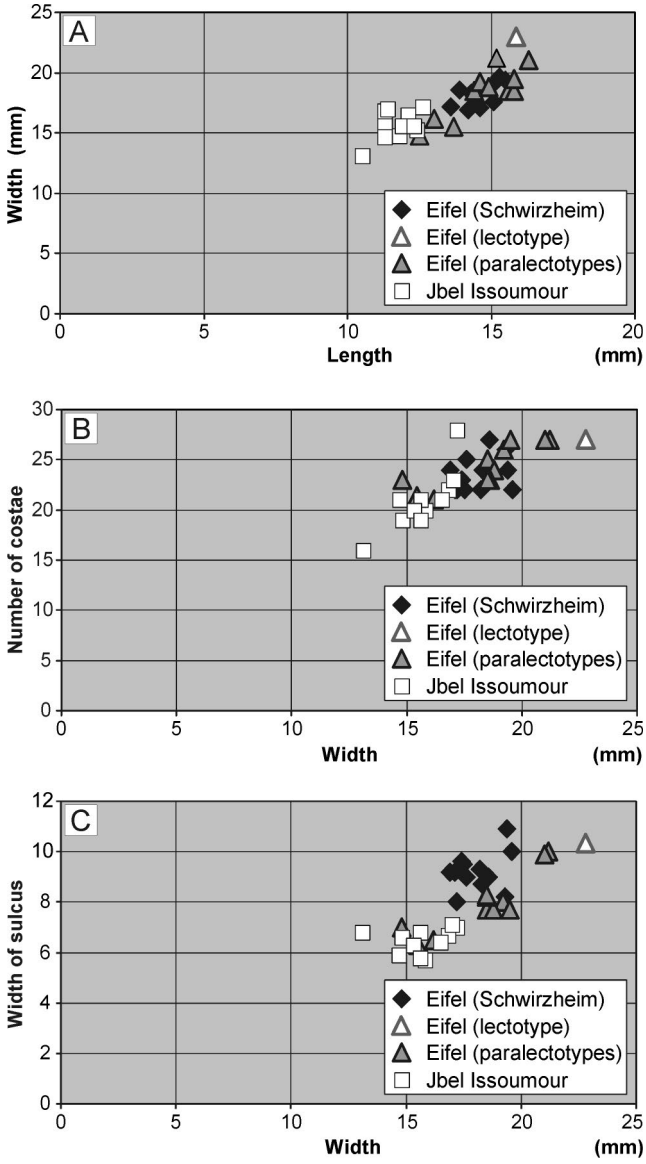


Fig. 5. *Eressella coronata* (Kayser, 1871). Scatter diagrams of shell width to shell length **(A)**, total number of costae to shell width **(B)** and sulcus width to shell width **(C)** for three samples (Eifel, Schwirzheim, $N = 12$; Eifel, Prüm Syncline, $N = 12$, including the holotype and 11 paratypes; Jebel Issoumour, $N = 11$). Raw data provided in the Appendix.

ventral muscle field wide, posteriorly deeply impressed, anteriorly divided by a median trough.

Dorsal interior: septalium present, but buried in umbonal callus; cardinal process posteriorly wide and multilobed, anteriorly, forming a thick raised plate covering the septalium; median septum thick, long; crura proximally rodlike, slightly diverging anteriorly and gently curved ventrally, distal blades flat to convex laterally.

Shell of both valves thick-walled.

Remarks: Biometrical comparison of samples from the Eifel (Kayser's collection from the "Crinoid Beds" from the Prüm Syncline and Schultze's collection from Schwirzheim near Prüm taken together; $N = 24$) and from Jebel Issoumour (Ebbighausen's collection; $N = 11$) shows that European representatives of *R. coronata* are larger (mean width 18.4 mm, compared to 15.7 mm in the African sample; Fig. 5A) and slightly less transverse (mean value 1.25, compared to 1.34). This results in a higher mean total number of costae and costellae in the Eifel sample (24; Africa – 21), but the ratio of number of costae to width is nearly the same in both cases (1.31 and 1.33, respectively; Fig. 5B). The ratio of the width of the tongue to the total width of the shell is slightly greater in the Eifel (0.47) than in Africa (0.41; Fig. 5C). Overall, it may be said that samples from the Eifel and from Jebel Issoumour are rather similar.

It may be noted that the feature given by Biernat (1966, p. 86) as "believed by Schmidt (1941: 24)" to be "characteristic for the species", namely twofold bifurcation of the costae limiting the fold, is in fact neither constant within the sample analysed, nor given as such by Schmidt (1941, p. 24).

Rhynchonella coronata sensu Siemiradzki (1922b) from Czarnów (L PZ-D *olim* 12904) is a representative of the Leiorhynchidae.

Distribution: Eifel, Germany; Łysogóry region of the Holy Cross Mts. and the environs of Radom (subsurface), Poland; Anti-Atlas, Morocco; Middle Devonian; never frequently. The stratigraphic distribution of this species is discussed in detail in the following chapter.

STRATIGRAPHY

Eifel, Germany

The stratigraphic distribution of *Eressella coronata* in the type area was described by Schmidt (1941, p. 24, 50–51). The details are not entirely clear, owing to her use of Happel and Reuling's (1937) stratigraphic units that subsequently proved to be assembled partly in the wrong order (Struve, 1961; see also Schwenzer, 1965, p. 263), but it is evident that *E. coronata* has a restricted stratigraphic distribution, being limited to the so-called "*ostiolatus*-Horizont" of the "Gondelsheim Beds". The *ostiolatus* horizon corresponds to a part of the Junkerberg Beds (middle Eifelian; Schwenzer, 1965 and references therein). However, some units between the *ostiolatus* Horizon and the Rommersheim Beds not listed by Schmidt (1941) have been relocated subsequently in the upper Eifelian and even to the Givetian (Schwenzer, 1965), so the upper limit of *E. coronata* in the Eifel is uncertain. According to Schwenzer (1965), in the Prüm Syncline *E. coronata* has been found in the Rechert, Nims, and Giesdorf horizons of the Junkerberg Beds (middle Eifelian). Apparently this species is unknown outside the Prüm Syncline (Frech 1886, p. 137).

Central Poland

In the Holy Cross Mountains, the species discussed is known solely from the Skały Beds at Skały (northern or Łysogóry region). Moreover, a single specimen was reported from the Pionki borehole, near Radom in the Mazovia Lowland (Senkowicz, 1973; Łobanowski and Przybyłowicz, 1979).

Holy Cross Mountains. According to Biernat (1966), *E. coronata* was found only in outcrop 83 *sensu* Pajchlowa (1957), belonging to set XVII. The data provided by Sobolew (1904) are slightly less precise ("crinoid limestone" over the "*Calceola* marls"), but still overall concordant with aforementioned stratigraphy. It follows that the stratigraphic position of *E. coronata* in the Grzegorzowice-Skały section is in the uppermost Eifelian (just below the Eifelian–Givetian boundary situated at about set XIX; Malec and Turnau, 1992, p. 80).

The data provided by Gürich (1896) are less clear. The species discussed is listed (Gürich, 1896, p. 50–51), along with several dozens of other species, some of which (like *Spirifer elegans sensu* Gürich, 1896 = *Mucrospirifer diluvianoides* Biernat, 1966) are restricted to a single, famous outcrop (SK-3 *sensu* Halamski, 2009; 73 *sensu* Pajchlowa, 1957), informally called "the fundamental pit" (a Konzentrat-Lagerstätte, see Halamski and Zapalski, 2005; corresponding to set XIV *sensu* Pajchlowa, 1957), the age of which is late Eifelian, corresponding to the Freilingen Beds of the Eifel (Adamczak, 1976; Dzik, 1981, Malec and Turnau, 1997; Halamski, 2005; Halamski and Racki, 2005). However, it is unclear how precise were the limits of the unit used by Gürich (1896).

In any case, in the Grzegorzowice-Skały section *E. coronata* is present in the uppermost Eifelian and perhaps also in the lower part of the upper Eifelian. The middle part of the Eifelian in the Skały section consists of dolomites of the Wojciechowice Formation (Kłossowski, 1985; Skompski and Szulczewski, 1994; Halamski and Racki, 2005; Narkiewicz and Narkiewicz, 2010; Wójcik, 2015): their fauna is scarce, so the lower limit of the species discussed is unclear.

Radom region. A single shell of *Eressella coronata* was reported from the Pionki 4 borehole (depth 1765.2––1759.3 m; Senkowicz, 1973; Łobanowski and Przybyłowicz, 1979). The "carbonate-terrigenous series" having yielded the brachiopod discussed was included by Turnau (1985, p. 357–358) within the Zwoleń Formation, but in a more recent work the "terrigenous suite" is considered to be an independent unit between the Czarnolas and Zwoleń formations (Turnau *et al.*, 2005, p. 122). The age of the marine strata with *E. coronata* was given as "Early Givetian or at most the latest Eifelian" (Łobanowski and Przybyłowicz, 1979, p. 388). However, this analysis largely relies on the age of the brachiopod-bearing sequence in the Holy Cross Mountains, misinterpreted by Biernat (1966) as Givetian (instead of Eifelian). An Eifelian age given in the preliminary description of the borehole record (Senkowicz 1973, p. 655) and indicated by a correlation provided by Turnau *et al.* (2005, fig. 2) appears more probable.

Anti-Atlas, Morocco

Eressella coronata (Kayser, 1871) is described herein from a locality in the Jebel Issoumour (northern Maïder), was described by Drot (1971) and by Halamski & Baliński (2013) from southern Maïder, and questionably reported from Jebel Ou Driss (southwest from Maïder) by Bultynck (1989).

Jebel Issoumour. Collecting localities of Volker Ebbighausen were usually described on cards kept in a separate archive, but for locality 151 the detailed data are lost (J. Bockwinkel, pers. comm., 11th Sep., 2017). If the "upper *Drotops* Beds" mentioned on the labels correspond to the locality figured and described by Struve (1995, p. 99, figs 25––26), then, according to a conodont-based age determination by Weddige (Struve 1995, p. 99) indicating the upper part of *kockelianus-australis* Zone till the lower part of the *ensensis* Zone, the level is late Eifelian in age. However, the *Drotops armatus* horizon belonging to the Bou Dib Formation (McKellar and Chatterton, 2009, p. 13), which is the higher of the two horizons with abundant *Drotops* fauna in the area (R. McKellar, pers. comm., 1st Dec., 2017), is interpreted as Givetian, according to Kaufmann (1998), Bultynck and Walliser (2000), and Campbell *et al.* (2002), as summarised by McKellar and Chatterton (2009, p. 63). This is based once more on a conodont-based age determination by Chatterton, indicating the lower *varcus* Zone (S. Gibb, pers. comm., 28th Feb., 2018). It may be mentioned that all the three species, noted by Weddige (Struve, 1995) as diagnostic for the Eifelian (*Polygnathus linguiformis linguiformis*, *Polygnathus pseudofoliatus*, *Icriodus struvei*), may be present in the lower Givetian (Bultynck, 2003; Narkiewicz and Bultynck, 2007; Walliser and Bultynck, 2011). However, the present authors do not intend to propose any solution to this apparent contradiction; one possibility, among others, might be that the two "upper *Drotops*" levels are not the same (M. Basse, pers. comm., 1st March, 2018).

Southern Maïder. The single specimen described by Halamski & Baliński (2013) was collected from a scree and its precise age cannot be determined. The age of the nearby outcrop TM 453 (El-Mrakib, southern Maïder; x = 566.5; y = 414.8), from which this species was reported by Drot (1971), was given as late Eifelian without any detailed argumentation; co-occurring *Spinella* sp. (Spiriferida) and *Calceola sandalina* (Rugosa) were listed (Drot, 1971, p. 71).

The material collected by V. Ebbighausen comes from the *Drotops* Beds at Madène el Mrakib. Halamski and Baliński (2013, p. 246) followed Struve (1990) in interpreting the age of these beds as Eifelian, although they noted the discrepancy in ages attributed to beds with *Drotops* to the north and south of Maïder.

Jebel Ou Driss. Bultynck (1989, p. 97) reports «cf. "*Uncinulus*" *coronatus*» (provisional identification by J. Godefroid) from an interval between samples ODE-3 and ODE-2. According to the correlation provided, this part of the section is well above the Eifelian–Givetian boundary. No description of the macrofauna is provided, so the interpretation of the open nomenclature used is unclear.

Summary of the stratigraphical distribution of *E. coronata*

In summary, the stratigraphic distribution of *Eressella coronata* in the three regions, from which it has been reported, is as follows:

– in the Eifel, mainly in the middle Eifelian, but with an uncertain upper limit;

– in the Holy Cross Mountains, in the upper (possibly only uppermost) Eifelian, but with an uncertain lower limit, due to extensive dolomitisation;
– in the Anti-Atlas, in the late Eifelian to early Givetian (at Jbel Issoumour and southern Maïder the identification of the brachiopod is certain, but the age is uncertain, whereas at Jbel Ou Driss the age determination is certain, but the identification of the brachiopod is not).

Such a pattern, if not simply the result of imprecise correlation, may be due either to imperfections of the fossil record or to regional diachronism. At present, neither of these two interpretations can be favoured.

CONCLUSIONS

Rhynchonella coronata Kayser, 1871 cannot be placed within any existing rhynchonellide genus. It is proposed as the type species of the new genus *Eressella*, characterised by a dorsibiconvex profile with a resupinate ventral valve, costae rounded posteriorly, acute and developing spur-like protuberances anteriorly, and a cardinal process multilobed posteriorly and massive anteriorly.

Eressella gen. nov. belongs to the superfamily Uncinuloidea on account of costae flattened and grooved on the anterior margin. It is further tentatively placed within the family Uncinulidae, although similarities with the subfamily Betterbergiinae (that probably should be separated from the Hebetoechiidae) are also noted.

The new genus and its only species is known from the Eifel (Eifelian, probably mainly, if not solely, middle Eifelian), from central Poland (in the Eifelian of the Holy Cross Mountains, probably mostly uppermost Eifelian), and from the Moroccan Anti-Atlas (late Eifelian to early Givetian, details uncertain).

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Appendix

Biometric characteristics of *Eressella coronata* (Kayser, 1871); measurements in millimetres

Specimen number	W	L	T	w	Dorsal valve			Ventral valve			W/L	w/W	C	C/W
					l	f	r	l	s	r				
MCZ 190711	19.3	15.2	11.7	8.2	10	6	10	10	5	10	1.27	0.42	26	1.35
MCZ 190712	16.9	14.2	10.6	9.2	9	6	9	8	5	8	1.19	0.54	24	1.42
MCZ 190713	19.4	15.5	10.4	10.9	9	6	–	10	5	10	1.25	0.56	24	1.23
MCZ 190714	17.6	15.1	12.1	9	9	7	9	10	6	10	1.16	0.51	25	1.42
MCZ 190715	18.6	13.9	11.6	9	9	7	11	11	6	10	1.34	0.48	27	1.45
MCZ 190716	17.2	13.6	12.4	8	9	5	8	8	4	9	1.26	0.47	22	1.28
MCZ 190717	18.3	14.3	12.2	8.7	10	6	8	8	5	8	1.28	0.48	24	1.31
MCZ 190718	19.6	15.3	13.6	10	8	6	8	9	5	8	1.28	0.51	22	1.12
MCZ 190719	18.2	14.5	12.9	9.3	8	5	9	7	4	8	1.26	0.51	22	1.21
MCZ 190720	17.5	14.5	12.4	9.5	8	7	7	8	6	8	1.21	0.54	22	1.26
MCZ 190721	17.1	14.6	12.2	9.2	8	6	8	10	5	9	1.17	0.54	22	1.29
MCZ 190722	17.4	14.5	12.6	9.6	8	5	10	8	4	8	1.2	0.55	23	1.32
MB.B.740.1	**22.8**	**15.9**	**11.9**	**10.3**	**9**	**8**	**10**	**9**	**7**	**10**	**1.43**	**0.45**	**27**	**1.18**
MB.B.740.2	21.2	15.2	14.8	10	10	8	9	8	7	10	1.39	0.47	27	1.27
MB.B.740.3	21	16.3	13	9.9	10	7	10	11	6	9	1.29	0.47	27	1.29
MB.B.740.4	18.5	14.4	13.6	7.7	9	7	9	9	6	9	1.28	0.42	25	1.35
MB.B.740.5	19.2	14.6	14.2	8	9	6	11	10	5	8	1.32	0.42	26	1.35
MB.B.740.6	18.8	14.9	12.4	7.7	8	6	10	10	5	8	1.26	0.41	24	1.28
MB.B.740.7	18.5	15.6	11.2	8.2	8	6	9	10	5	8	1.19	0.44	23	1.24
MB.B.740.8	18.5	15.8	11.4	8.3	8	6	9	9	5	9	1.17	0.45	23	1.24
MB.B.740.9	19.5	15.8	12	7.7	10	6	11	11	5	10	1.23	0.39	27	1.38
MB.B.740.10	16.2	13	11.7	6.5	7	6	8	8	5	8	1.25	0.40	21	1.30
MB.B.740.11	15.5	13.7	11.4	6.3	8	6	7	9	4	8	1.13	0.41	21	1.35
MB.B.740.12	14.8	12.5	10.6	7	9	6	8	8	5	9	1.18	0.47	23	1.55
Eifel, m	*18.40*	*14.70*	*12.20*	*8.7*	*8.8*	*6.3*	*9.0*	*9.1*	*5.2*	*8.8*	*1.250*	*0.472*	*24.0*	*1.311*
sd	*1.786*	*0.936*	*1.098*	*1.20*	*0.85*	*0.79*	*1.19*	*1.15*	*0.83*	*0.87*	*0.0730*	*0.0524*	*2.05*	*0.0932*
v	*0.097*	*0.064*	*0.090*	*0.137*	*0.097*	*0.13*	*0.13*	*0.13*	*0.16*	*0.098*	*0.058*	*0.111*	*0.085*	*0.071*
MB.B.9422.1	17.2	12.6	11.2	7	10	6	12	11	5	10	1.37	0.41	28	1.63
MB.B.9422.2	14.8	11.8	8.5	6.6	8	4	7	10	3	9	1.25	0.45	19	1.28
MB.B.9422.3	13.1	10.5	9	6.8	5	5	6	8	4	6	1.25	0.52	16	1.22
MB.B.9422.4	15.8	11.3	9.4	5.7	8	5	7	7	4	9	1.40	0.36	20	1.27
MB.B.9422.6	16.8	11.3	10	6.7	9	6	7	9	5	9	1.49	0.40	22	1.31
MB.B.9422.7	17	11.4	10.4	7.1	7	6	10	11	5	8	1.49	0.42	23	1.35
MB.B.9422.8	16.5	12.1	10.2	6.4	8	5	8	9	4	10	1.36	0.39	21	1.27
MB.B.9422.9	15.6	11.9	9.5	6.8	7	6	8	9	5	8	1.31	0.44	21	1.35
MB.B.9422.10	15.3	12.4	10.1	6.3	6	5	9	11	4	7	1.23	0.41	20	1.31
MB.B.9422.11	15.6	12.3	9.9	5.8	6	5	8	8	4	6	1.27	0.37	19	1.22
MB.B.9422.12	14.7	11.3	8.3	5.9	8	5	8	9	4	9	1.30	0.40	21	1.43

Specimen number	W	L	T	w	Dorsal valve			Ventral valve			W/L	w/W	C	C/W
					l	f	r	l	s	r				
J. Issoumour, m	*15.67*	*11.72*	*9.68*	*6.46*	*7.5*	*5. 3*	*8. 2*	*9. 3*	*4. 3*	*8. 3*	*1.338*	*0.414*	*20.9*	*1.330*
sd	*1.206*	*0.623*	*0.854*	*0.486*	*1.44*	*0.65*	*1.66*	*1.35*	*0.65*	*1.42*	*0.0914*	*0.0428*	*2.98*	*0.1158*
v	*0.0769*	*0.0531*	*0.0882*	*0.0752*	*0.19*	*0.12*	*0.20*	*0.15*	*0.15*	*0.17*	*0.0683*	*0.103*	*0.143*	*0.0870*
Total, m	*17.54*	*13.77*	*11.41*	*7.98*	*8.3*	*5.9*	*8.8*	*9.2*	*4.9*	*8.7*	*1.28*	*0.45*	*23.1*	*1.317*
sd	*2.058*	*1.638*	*1.563*	*1.456*	*1.21*	*0.87*	*1.40*	*1.20*	*0.89*	*1.08*	*0.089*	*0.0559*	*2.76*	*0.09949*
v	*0.12*	*0.12*	*0.14*	*0.18*	*0.15*	*0.15*	*0.16*	*0.13*	*0.18*	*0.13*	*0.069*	*0.12*	*0.12*	*0.076*

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 (of either a dorsal or a ventral valve); f – number of costae and costellae on the fold; r – number of costae and costellae on the right flank (of either a dorsal or a ventral valve); s – number of costae and costellae in the sulcus; C – total number of costae (value of another flank of the same valve taken twice if one of these values missing). Abbreviations: *m* – mean; *sd* – standard deviation; *v* – variation coefficient (= *sd* / *m*).