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RESEARCH PAPER

Diversity of the *Schizophoria* lineage (Brachiopoda: Orthida) in the Lower and Middle Devonian of Poland and adjacent areas

Adam T. Halamski

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Abstract The nominative subgenus of *Schizophoria* (Brachiopoda, Orthida) is represented in the Lower and Middle Devonian of Poland and of the western Ukraine by six taxa: late Emsian *Schizophoria* (*S.*) *interstrialis*, late Eifelian *S.* (*S.*) *schnuri biscissa*, early Givetian *S.* (*S.*) *schnuri schnuri*, middle to late Givetian *S.* (*S.*) *schnuri prohibita* ssp.n., middle Givetian *S.* (*S.*) *parvaepunctata* and late Givetian *S.* (*S.*) sp.n. (unnamed for lack of sufficient material). Morphotypes referable to *S.* (*S.*) *schnuri biscissa* and to *S.* (*S.*) *schnuri junkerbergiana* co-occur in the same outcrop (not necessarily in the same levels), wherefore the separation of these subspecies may be maintained only if they are considered as chronosubspecies (unverifiable on the studied material) but not as geographic variants (hypothesis falsified by the studied material). A lectotype for *S.* (*S.*) *interstrialis* and a neotype for *S.* (*S.*) *parvaepunctata* are selected. Punctae diameter and density (either an important systematic character according to some authors or devoid of such value according to other ones) were investigated: they show important within-individual and within-sample variation, wherefore they cannot serve to distinguish related species. On the contrary, punctae character combinations are sufficiently constant to help differentiate subgenera or groups of species. In the studied material, three clusters are distinguished on the basis of the punctae characteristics: *S.* (*Pachyschizophoria*) and *S.* (*S.*) *parvaepunctata* differ between each other and from all other investigated species of *S.* (*Schizophoria*); the latter are indistinguishable on the sole basis of punctae characteristics.

Keywords Brachiopoda · Orthida · *Schizophoria* · Holy Cross Mountains · Volhynia · Middle Devonian · Taxonomy · Punctae distribution

Kurzfassung Die nominative Untergattung von *Schizophoria* (Brachiopoda, Orthida) ist im Unter- und Mitteldevon Polens und der westlichen Ukraine durch sechs Taxa vertreten: *Schizophoria* (*S.*) *interstrialis* aus dem oberen Emsium, *Schizophoria* (*S.*) *schnuri biscissa* aus dem oberen Eifelium, *S.* (*S.*) *schnuri schnuri* aus dem unteren Givetium, *S.* (*S.*) *schnuri prohibita* ssp.n. aus dem mittleren bis oberen Givetium, *S.* (*S.*) *parvaepunctata* aus dem mittleren Givetium, und *S.* (*S.*) sp.n. (nicht benannt wegen des nicht ausreichendes Material) aus dem späten Givetium. Die zu *S.* (*S.*) *schnuri biscissa* und *S.* (*S.*) *schnuri junkerbergiana* beziehenden Morphotypi kommen zusammen an derselben Lokalität vor (aber nicht notwendigerweise in demselben Stratum), darum können sie nur als Chronosubspecies (nicht belegbar nach dem untersuchten Material) unterschieden werden, aber nicht als geographische Varianten (Hypothese widerlegt nach dem untersuchten Material). Ein Lectotypus für *S.* (*S.*) *interstrialis* und ein Neotypus für *S.* (*S.*) *parvaepunctata* werden ausgewählt. Der Durchmesser und die Dichte der Poren (nach einigen Autoren ein gutes taxonomisches Merkmal und nach anderen nicht), werden untersucht: Die Variation innerhalb eines Individuums und einer Probe ist bedeutend, darum kann sie nicht benutzen werden, um die verwandte Arten zu unterscheiden. Im Gegenteil, Porenmerkmalekombinationen sind genügend fest, darum kann sie helfen, um die Untergattungen oder die Artgruppen zu unterscheiden. In dem untersuchten Material

A. T. Halamski (✉)
Polish Academy of Sciences,
Institute of Paleobiology,
Twarda 51/55, 00-818 Warszawa,
Poland
e-mail: ath@twarda.pan.pl

werden drei Gruppen nach Porenmerkmale unterschieden: *S.* (*Pachyschizophoria*) und *S.* (*S.*) *parvaepunctata* unterscheiden sich voneinander und von den übrigen untersuchten Arten von *S.* (*Schizophoria*); diese können allein den Porenmerkmale unterschieden werden.

Schlüsselwörter Brachiopoda · Orthida · *Schizophoria* · Heiligkreuzgebirge · Volhynien · Mitteldevon · Taxonomie · Porenverteilung

Introduction

Schizophoria (Brachiopoda, Orthida) is a cosmopolitan genus of long stratigraphic range (Upper Silurian to Lower Carboniferous). The aim of the present paper is to give a systematic account of the Lower and Middle Devonian representatives of its nominative subgenus from Poland and western Ukraine (the acme interval of its diversity in these areas). This allows to confirm the existence of an evolutionary lineage previously described from the Eifelian to lower Givetian of the Eifel and to find its continuation (*Schizophoria schnuri prohibita* ssp.n.) in the middle to upper Givetian. Moreover, the validity of the punctae distribution as a systematic criterion, either an important systematic character according to some authors or devoid of such value according to other ones, is assessed.

Geological setting

The investigated material comes from the Lower and Middle Devonian strata cropping out in two geographic regions: the Holy Cross Mountains (Góry Świętokrzyskie) in central Poland and the Povcha-Mizoch (Pełcza-Mizocz)[1] Range (Povcha Upland according to other authors) in Volhynia (western Ukraine; Fig. 1).

The Holy Cross Mountains belong to the Middle Polish Anticlinorium and form a Palaeozoic horst that can be further subdivided into two regions (Stupnicka 1992 and references therein), Łysogóry (or Northern) and Kielce (or Southern; north and south of the Holy Cross Dislocation, respectively, Fig. 1B). Fossil faunas of the two regions are notably different. Stratigraphic details for the Middle Devonian of the Northern Region are to be found in Halamski (2005 and references therein) and Halamski and Racki (2005). Orthide brachiopods were monographed by Biernat (1959) and Halamski (2009). Stratigraphic details for the Middle Devonian of the southern region and the Lower Devonian of both regions are to be found in Racki (1993a, 2005) and Halamski and Racki (2005). Brachiopods from the Kielce Region were described by Racki (1993b).

Late Emsian to earliest Eifelian Grzegorzowice Formation and late Eifelian to early Givetian Skały beds crop out in several sections belonging to the Bodzentyn Syncline situated in the Łysogóry Region. Late Emsian limestones and marls crop out near Grzegorzowice (Pajchlowa 1957; Malec 1999) and yielded *Schizophoria* (*S.*) *interstrialis* Biernat, 1954. Late Eifelian ('Freilingian') brachiopod shales are known from a famous outcrop at Skały known informally as the 'fundamental (or brachiopod) pit' (73 sensu Pajchlowa 1957; brachiopod shales sensu Biernat 1959; SK-3 sensu Halamski 2009; faunistic list given by Halamski and Zapalski 2006). It yielded a rich collection of *Schizophoria* (*S.*) *schnuri biscissa* Struve, 1965. A younger, early Givetian level with *Schizophoria* (*S.*) *schnuri schnuri* Struve, 1965 crops out at Błonia Sierżawskie near Świętomarz (outcrop SW-2 sensu Halamski 2009; stratigraphy discussed by Halamski and Segit 2006). A roughly coeval level with the same species was encountered in a well in Włochy near Skały.

Middle to late Givetian Laskowa Góra Beds (set A sensu Racki 1993a) crop out in the eastern wall of the Józefka quarry (formerly Józefka Hill) at Górno (Radlin Syncline, a subordinate element of the Kielce-Łagów Synclinorium, Kielce Region). *Schizophoria* (*S.*) *schnuri prohibita* ssp.n. is accompanied by several species of brachiopods (representatives of Pugnacidae, Hypothyridinidae, Reticulariidae, Atrypida and possibly Cyrtospiriferidae; Baliński and Halamski, unpublished data), as well as crinoids and rarer corals, bivalves and orthocone nautiloids. Conodont assemblages indicate an interval between Middle *varcus* and *disparilis* Zones (Racki, unpublished data). Approximately coeval rocks were cropping out in the southern part of a trench dug along the road from Górno to Daleszyce about 100 m east from the above-mentioned locality; at present, only the northern part of the trench showing the Frasnian part of the section is accessible. This trench corresponds to outcrop V sensu Małkowski (1981) and to the type outcrop of *Biernatella lentiformis* Baliński, 1995 (Baliński 1995b). Approximately coeval strata crop out also in Laskowa (in geological papers this locality is most often incorrectly reported as Laskowa Góra) near Kielce.

Late Givetian Chęciny Beds cropping out at the eastern hill in Trzemoszna (south-east from Daleszyce, Gałęzice-Bolechowice Syncline, Kielce Region) yielded three poorly preserved specimens of *Schizophoria* (*S.*) sp.n. (*S.* aff. *macfarlanei* sensu Racki 1993b).

The Middle Devonian of Volhynia is known from two isolated outcrops in the vicinity of Povcha (Pełcza) (von Kelus 1939; Samsonowicz 1950; Fig. 1C). Givetian deposits surrounded by a continuous Cretaceous and Neogene cover cropped out (localities inaccessible at present; D. Drygant,

[1] Ukrainian toponyms are transcripted according to the Ukrainian National Transliteration standard. Polish equivalents (official before 1939) are given in parentheses.

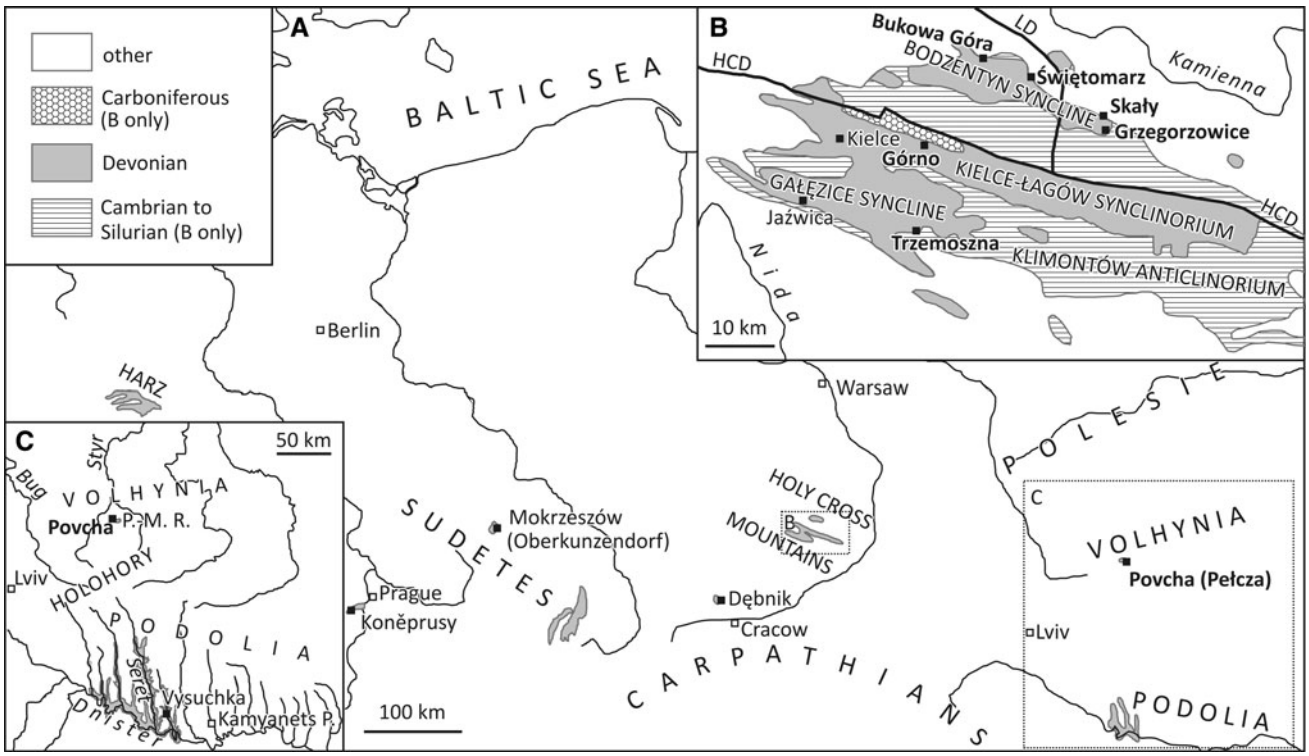


Fig. 1 Geographic and geologic setting of the studied fauna. *A* Topography of central Europe and localisation of Devonian outcrops. *B* Geologic map of the Palaeozoic core of the Holy Cross Mountains. *C* Topography of Podolia and Volhynia and localisation of Devonian outcrops. *Hollow squares* major cities. *Black squares* Devonian localities either discussed (in *boldface*) or mentioned (in *Roman typeface*) in the text. Rivers in *italics*. Present place names given first, former ones in parentheses. *HCD* Holy Cross Dislocation, *LD* Łysogóry Dislocation, *P.-M. R.* Povcha-Mizoch Range. Redrawn and modified after Dupret and Blieck (2009), von Gaertner and Walther (1971), Kozłowski (1929), Nikiforova et al. (1985) and Samsonowicz (1950, 1966)

pers. comm. 2010) at Biła Debra near Tartak and at Kamieniarnia (Samsonowicz 1950: fig. 1). They have been dated to the Middle Givetian (Middle *varcus* Zone; Drygant 2010) and yielded *Schizophoria* (*S.*) *parvaepunctata* von Kelus, 1939 accompanied by numerous other brachiopods, e.g. *Diazoma volhynica* (von Kelus, 1939) and *Desquamatia parazonata* (von Kelus, 1939).

Systematic part

Institutional abbreviations: GIUS, Geological Institute of the Silesian University, Sosnowiec, Poland; MWG, Museum of the Faculty of Geology, Warsaw University, Warsaw, Poland; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Phylum Brachiopoda Duméril, 1805 (‘1806’)
Subphylum Rhynchonelliformea Williams et al., 1996
Classis Rhynchonellata Williams et al., 1996
Order Orthida Schuchert & Cooper, 1931
Family Schizophoriidae Schuchert & LeVene, 1929
Genus *Schizophoria* King, 1850

Type species: *Conchyliolithes Anomites resupinatus* Martin, 1809.

Diagnosis: see Jansen (2001).

Remarks: The present paper is limited to the Lower and Middle Devonian representatives of the subgenus *S.* (*Schizophoria*) for the following reasons. First, in Poland and adjacent areas only two Devonian taxa not belonging to the nominative subgenus of *Schizophoria* have been found up to now: *S.* (*Eoschizophoria*) *fragilis* Kozłowski, 1929 from the Zlichovian of Podolia (type locality: Vysuchka) was described in detail by Kozłowski (1929) and by Nikiforova et al. (1985), whereas the material of *S. vulvaria* (von Schlotheim, 1820), *S.* aff. *vulvaria* (von Schlotheim, 1820) and *S. striatula* (von Schlotheim, 1820), all three sensu Łobanowski (1971) (possibly a single species belonging to *Pachyschizophoria* on account of the slender shape of the ventral muscle field and the convexly curved brachiophore plates; U. Jansen, pers. comm. 2012), from the upper Emsian of Bukowa Góra (northern region of the Holy Cross Mts.) was not available for restudy. Moreover, the morphology, systematics and evolution of the subgenera

S. (*Pachyschizophoria*) and *S.* (*Rhenoschizophoria*) were described in detail by Jansen (2001).

There exist two contrasting approaches to the taxonomy of Middle Devonian species of *Schizophoria* in Europe. Struve (1963, 1965) described the *S. schnuri* complex with five subspecies (both chronosubspecies and geographic variants); small representatives of the genus with different ornamentation were segregated as *S. pygmaea*, whereas *S. striatula* and *S. excisa* were restricted to their type samples from the Frasnian. On the contrary, Pocock (1966) merged *S. striatula* with *S. schnuri* except the subspecies *S. schnuri blankenheimensis* that she considered as conspecific to *S. pygmaea* on account on the existence of intermediary forms.

The facts observed in the Holy Cross Mountains incline the present author to prefer the former approach, although with some reservations. In effect, the general appearance of stratigraphically separated (Eifelian versus Givetian) samples of *Schizophoria* is strikingly different. Moreover, samples from a given level in the Holy Cross Mountains are remarkably similar to those from coeval levels of both the Holy Cross Mts. and the Eifel. Last, *Schizophoria striatula* is known only from its limited type material (from the Frasnian), wherefore its variability and internal structures are unknown; using this name for brachiopods of different (Middle Devonian) age will rather increase confusion than serve clarity. Middle Devonian reports of *Schizophoria striatula* (e.g. Baranov 2008) are herein considered doubtful.

Struve's approach is therefore followed with a large *S. schnuri* complex with several subspecies. *S. pygmaea* does not occur in Poland and will not be dealt with here. Following Jansen (2001: 17), subspecies are considered here as stratigraphically segregated populations differing by morphological trends rather than discrete characters (in which case they would have to be described as separate species). Consequently, such morphoclines arranged along chronoclines are observable only on large samples of adult individuals. On the contrary, the interpretation of certain samples as geographic variants (Struve 1965) is falsified (see below, under *S. schnuri biscissa*, for details).

Subgenus *Schizophoria* (*Pachyschizophoria*) Jansen, 2001

Type species: *Hysteriolithes vulvarius* von Schlotheim, 1820.

Diagnosis, species assigned: see Jansen (2001).

Remarks: Representatives of this subgenus do not occur in the studied material (but see above, under remarks on the genus *Schizophoria*). A Spanish taxon is described here solely for comparison of the punctae distribution.

Schizophoria (*Pachyschizophoria*) cf. *vulvaria* (von Schlotheim, 1820) (Fig. 8D, F)

Material: one specimen ZPAL 64/A from the upper Emsian of the Cabo la Vela section (La Ladrona Formation, Cantabrian Mts., Spain).

Description: Punctae in the central region of the shell ca. 15–45 μm in diameter, rather sparsely distributed, ca. 120 per mm^2; in marginal region of remarkably different sizes, ca. 15–90 μm in diameter (Fig. 8D).

Subgenus *Schizophoria* (*Schizophoria*) King, 1850

Type species: as for the genus

Diagnosis: see Jansen (2001).

Remarks: According to Jansen (2001), the subgenus *S.* (*Schizophoria*) originated in the Lochkovian from an unidentified representative of the subgenus *S.* (*Eoschizophoria*). In the Lower Devonian the former subgenus is represented by the *S. praecursor* group (a single species, *S. interstrialis*, in the described material) and an offline, namely *S. antiqua* (the opinion of Pocock 1966 on the presence of this taxon in the Frasnian seems doubtful). The group of *S. schnuri*, descending from the *S. praecursor* group (Jansen 2001), is abundant in the Middle Devonian (see below). Other Middle Devonian taxa include (among others, see Stigall Rode 2005 for a detailed list of taxa from the USA) *S. parvaepunctata* (see below) as well as solely North American *S. macfarlanei* (Meek, 1868), *S. ferronensis* Imbrie, 1959 and *S. mesacarina* Imbrie, 1959, and finally *S. traversensis* Grabau, 1931, *S. excellens* Grabau, 1931 and several other taxa of uncertain status from South China (Grabau 1931–33). A further continuation of the evolutionary line of *S. praecursor*–*S. schnuri* may be found in the Upper Devonian and is most probably represented by the lower Frasnian taxa described from the Russian Platform (*S. kremsi* Ljaschenko, 1959, *S. uchtensis* Ljaschenko, 1959 and others; Ljaschenko 1959). The specimen from the Barvaux Formation (Frasnian, Belgium) figured by Mottequin (2008: fig. 22F–J) under the name *Schizophoria* gr. *striatula* may also belong to this group, whereas the other putatively conspecific one from the Grand Breux Fm. (Frasnian, Belgium: Mottequin 2008: fig. 22A–E) does probably not. The widely used name *S. striatula* relates, in fact, to a single, poorly located specimen of dubious affinities (Struve 1965). The Upper Devonian representatives of *Schizophoria* in Poland are known from three groups of localities: Dębnik Anticline near Cracow (Baliński 1995a, 2002, 2006); Mokrzeszów (Oberkunzendorf) and other localities in the Świebodzice (Freiberg in Schlesien) Depression in the Sudetes (Dames 1868; Gunia 1968); last, Jaźwica and Kadzielnia quarry in

Kielce (southern region of the Holy Cross Mountains; Racki 1993b). They are infrequent and usually poorly preserved, wherefore an inquiry upon the younger members of the discussed lineage has not been attempted.

Schizophoria (*Schizophoria*) *interstrialis* Biernat, 1954 (Figs. 2K–Y; 4D, I–K, P–R; 8E)

v* 1954 *Schizophoria interstrialis* n. sp.—Biernat, p. 496–499, text-figs. 5–7, pl. 1: 1–4

Type material: Biernat (1954) stated that 'the specimen' illustrated in pl. 1: 1–4 and text-figs. 5–7 is the holotype. In fact, six different specimens (syntypes) are concerned. The specimen ZPAL Bp I/2/1 (new number, material unnumbered in the original work) represented by Biernat (1954, pl. 1: 1–4) and in the present paper (Fig. 2P–T) is selected herein as the lectotype. The paralectotypes ZPAL Bp I/2/2–5 are illustrated herein in Fig. 4D, I–K, P–R.

Material: Four subcomplete specimens, one fragmentary dorsal valve, seven internal moulds of ventral valves and about 20 fragmentary and/or crushed shells, collection number ZPAL Bp I/2, all from the late Emsian Grzegorzowice Formation in Grzegorzowice.

Description: Shell medium-sized (up to 31 mm in width), transverse, dorsibiconvex, subelliptic in outline.

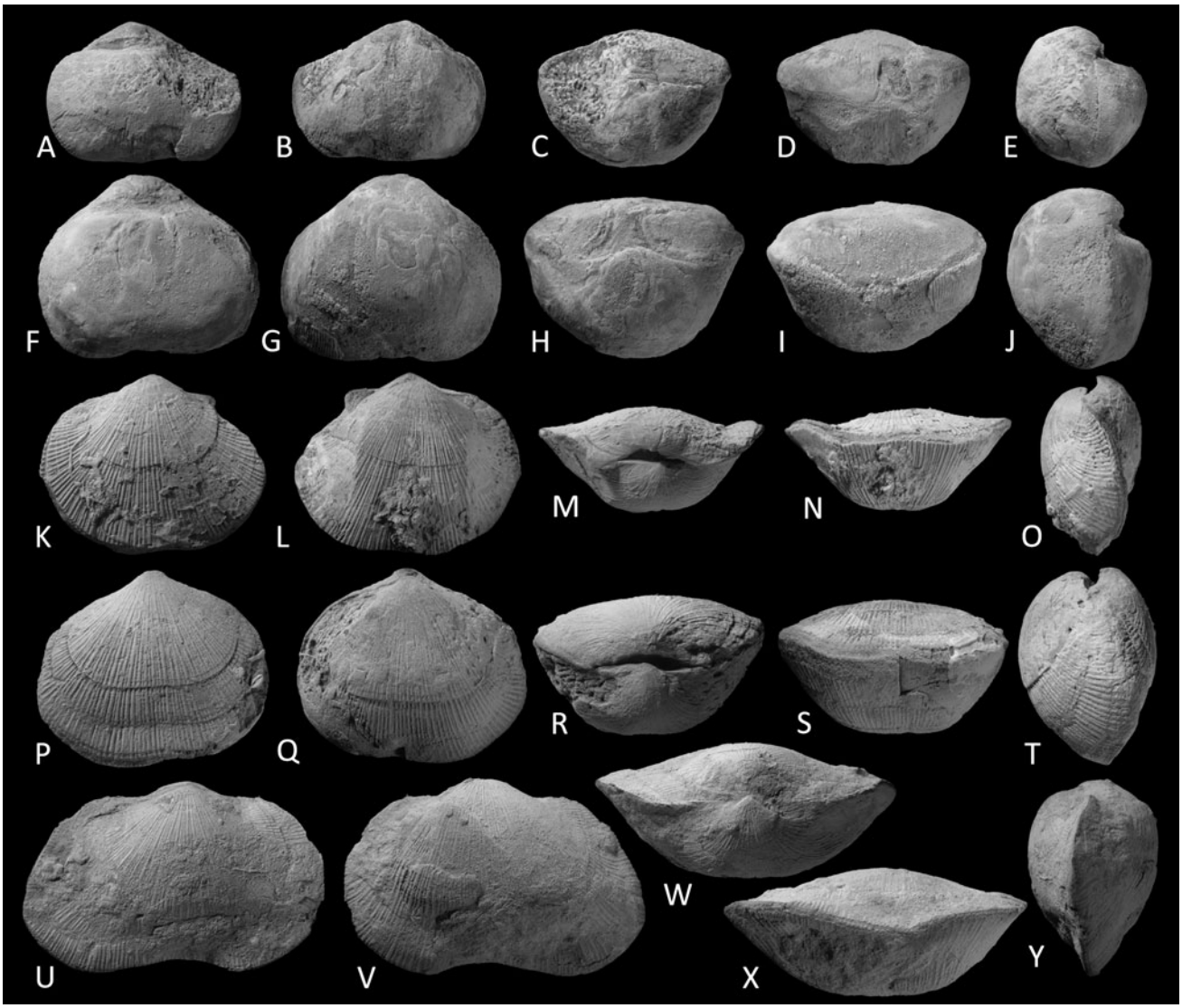


Fig. 2 External morphology of *Schizophoria* (*Schizophoria*). Articulated shells in dorsal, ventral, posterior, anterior and lateral views. All specimens shown ×1.5. *A–J Schizophoria* (*S.*) sp.n. Trzemoszna, eastern hill, rubble; Chęciny Beds, upper Givetian. *A–E* Specimen GIUS 4/219/S-2. *F–J* Specimen GIUS 4/219/S-1; figured by Racki (1993b: fig. 1H, I). *K–Y Schizophoria* (*S.*) *interstrialis* Biernat, 1954. Grzegorzowice; Grzegorzowice Formation, upper Emsian. *K–O* Lectotype ZPAL Bp IV/2/1. *P–T* Specimen ZPAL Bp IV/2/6. *U–Y* Specimen ZPAL Bp 64/3/1

Maximal width about midlength of the shell, sometimes slightly more anteriorly. The width of the area usually about half the width of the shell. Anterior commissure either rectimarginate or with a very wide (2/3–3/4 of the shell width) and very shallow (dorsal) deflection. Dorsal valve strongly convex, slightly flattened medially in posterior region, more anteriorly with an incipient rather narrow sulcus; dorsal beak quite thick, markedly incurved. Dorsal interarea apsacline to orthocline. Ventral valve weakly convex. Ventral interarea apsacline.

Ornamentation parvicostellate. Costellae arising by intercalation, more seldom by bifurcation. In central region of both valves costellae are of very different thicknesses, while at anterior margin they are of about the same width, moderately coarse, 2–3 per mm. Growth lines usually not observed.

Dorsal interior. Cardinal process rather small, supported by a small shaft. Brachiophores not preserved. Dental sockets of moderate size. Posterior adductor scars parallel, narrow, separated by a broad and low median ridge. Anterior adductor scars diverging, separated by a much narrower median wall.

Ventral interior poorly preserved. Muscle field length up to half the valve length, its maximal width situated markedly anteriorly, length to width ratio 1:1–1.5:1.

Punctae medium-sized, ca. 20–30 μm in diameter, distributed moderately densely, ca. 170 per mm^2.

Remarks: The comparison of *Schizophoria interstrialis* with other representatives of the *S. praecursor* group is given in Table 1.

García-Alcalde (2001) listed a *Schizophoria* aff. *interstrialis* from the latest Emsian of the Cantabrian Zone, and Jansen (2001) reported a 'representative of the *praecursor* group' from the uppermost upper Emsian of the Dill Syncline (Kieselgallen-Schiefer). In both cases neither figures nor description were provided, so no inference on relationships of these taxa with the approximately coeval *S.* (*S.*) *interstrialis* is possible.

Fig. 3 External morphology of *Schizophoria* (*Schizophoria*), continued. Articulated shells in dorsal, ventral, posterior, anterior and lateral views. All specimens shown ×1.25. *A–O Schizophoria* (*S.*) *parvaepunctata* von Kelus, 1939. Povcha (Pełcza) region, details unknown; Givetian. *A–E* Juvenile specimen MWG 02619/3. *F–J* Specimen MWG 02619/2. *K–O* Neotype MWG 02619/1. *P–II Schizophoria* (*S.*) *schnuri biscissa* Struve, 1965. Skały, 'fundamental pit'; Skały beds, upper Eifelian. *P–T* Specimen ZPAL Bp 64/3/1. *U–Y* Specimen ZPAL Bp 64/3/2. *Z–DD* Specimen ZPAL Bp 64/3/3. *EE–II* Specimen ZPAL Bp 64/3/4

Schizophoria (*Schizophoria*) *schnuri* Struve, 1965

Remarks: Various (partly unidentified at subspecific level) representatives of the *S. schnuri* complex were reported from the Eifel (Struve 1965), the Ardennes (Hubert et al. 2007), Holy Cross Mts. (Halamski 2009), Moravia (Havlíček 1977) and Burma (Anderson et al. 1969).

Schizophoria (*Schizophoria*) *schnuri biscissa* Struve, 1965 (Figs. 3P–II; 4C, F–H, M–O; 8A)

v. 2009 *Schizophoria* (*Schizophoria*) *schnuri biscissa* Struve, 1965—Halamski, p. 85–87, text-fig. 17, pls. 14: 1, 2, 12, 13, 18–20; 15: 1–10 [*ubi syn.*]

Material: several dozens of articulated shells, numerous separate dorsal and ventral valves from outcrop SK-3 sensu Halamski (2009), collection numbers ZPAL Bp IV and ZPAL 64/3.

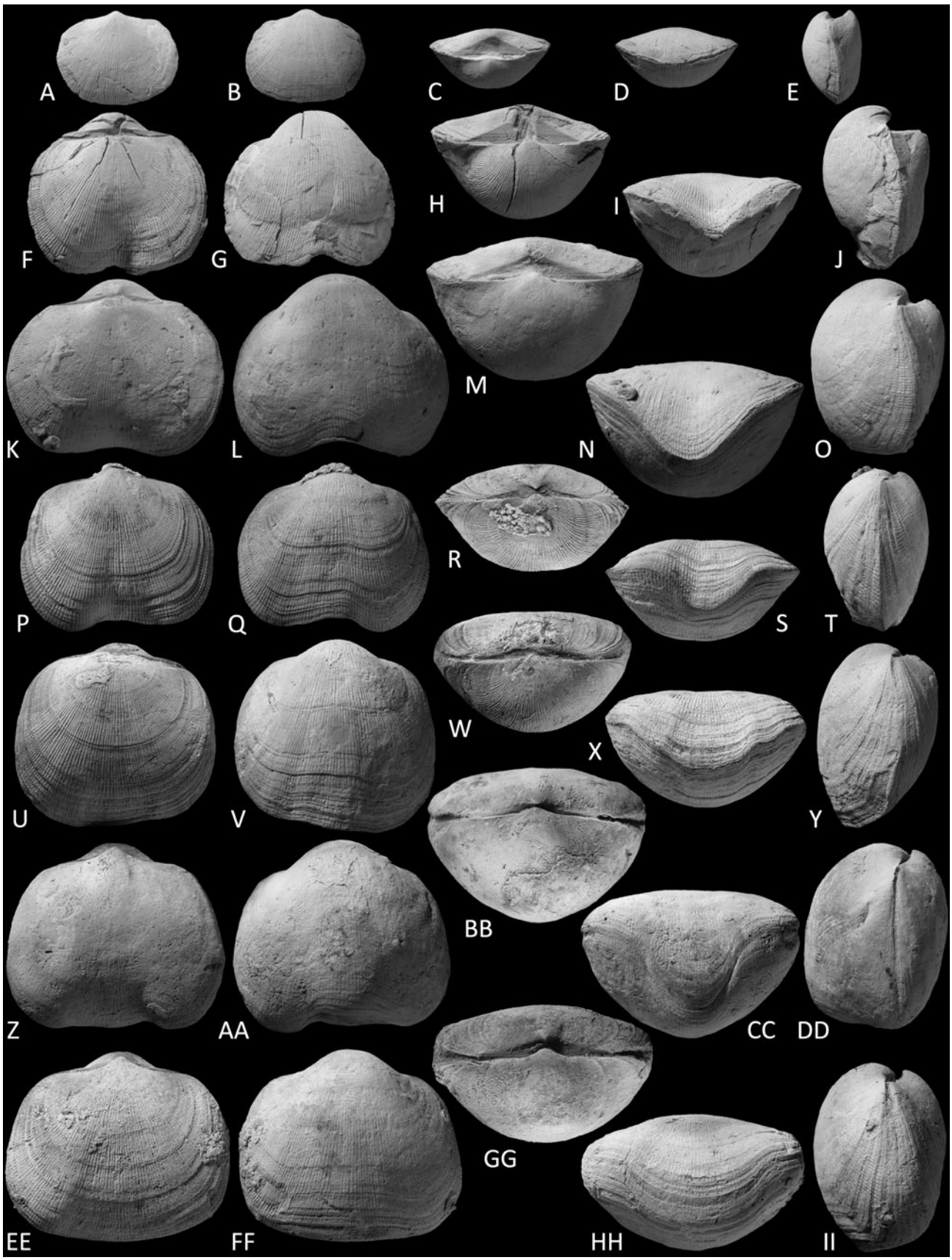
Description: Morphology and anatomy, see Biernat (1959) and Halamski (2009).

Punctae medium-sized, ca. 13–27 μm in diameter, distributed moderately densely, ca. 215–400 per mm^2.

Remarks: *Schizophoria schnuri biscissa* differs from the following two subspecies of *S.* (*S.*) *schnuri* in its subtrapezoidal outline, the maximal width of the shell situated anteriorly and in slightly finer costellae (2–4 per mm at anterior margin compared with 2–3 in *S.* (*S.*) *schnuri schnuri* Struve, 1965 and *S. schnuri prohibita* subsp. nov.).

Table 1 Comparison of Early Devonian species of *Schizophoria* from central Europe

Taxon character	*S.* (*S.*) *zephyrina* (Barrande, 1879)	*S.* (*S.*) *praecursor* (Barrande, 1879)	*S.* (*S.*) *interstrialis* Biernat, 1954
Occurrence	Koněprusy Limestone, Bohemia (Pragian)		Grzegorzowice, Poland (upper Emsian)
Shape	Subequally biconvex	Dorsibiconvex	Strongly dorsibiconvex
Anterior commissure	Rectimarginate	Slightly deflected	Slightly deflected
Dorsal valve	Neither sulcus nor fold	A small convexity, not a true fold	Sulcus
Ornamentation	Costellae of subequal size	Slightly accentuated primaries	Slightly accentuated primaries
Characters given after	Havlíček (1977)	Havlíček (1977)	Present work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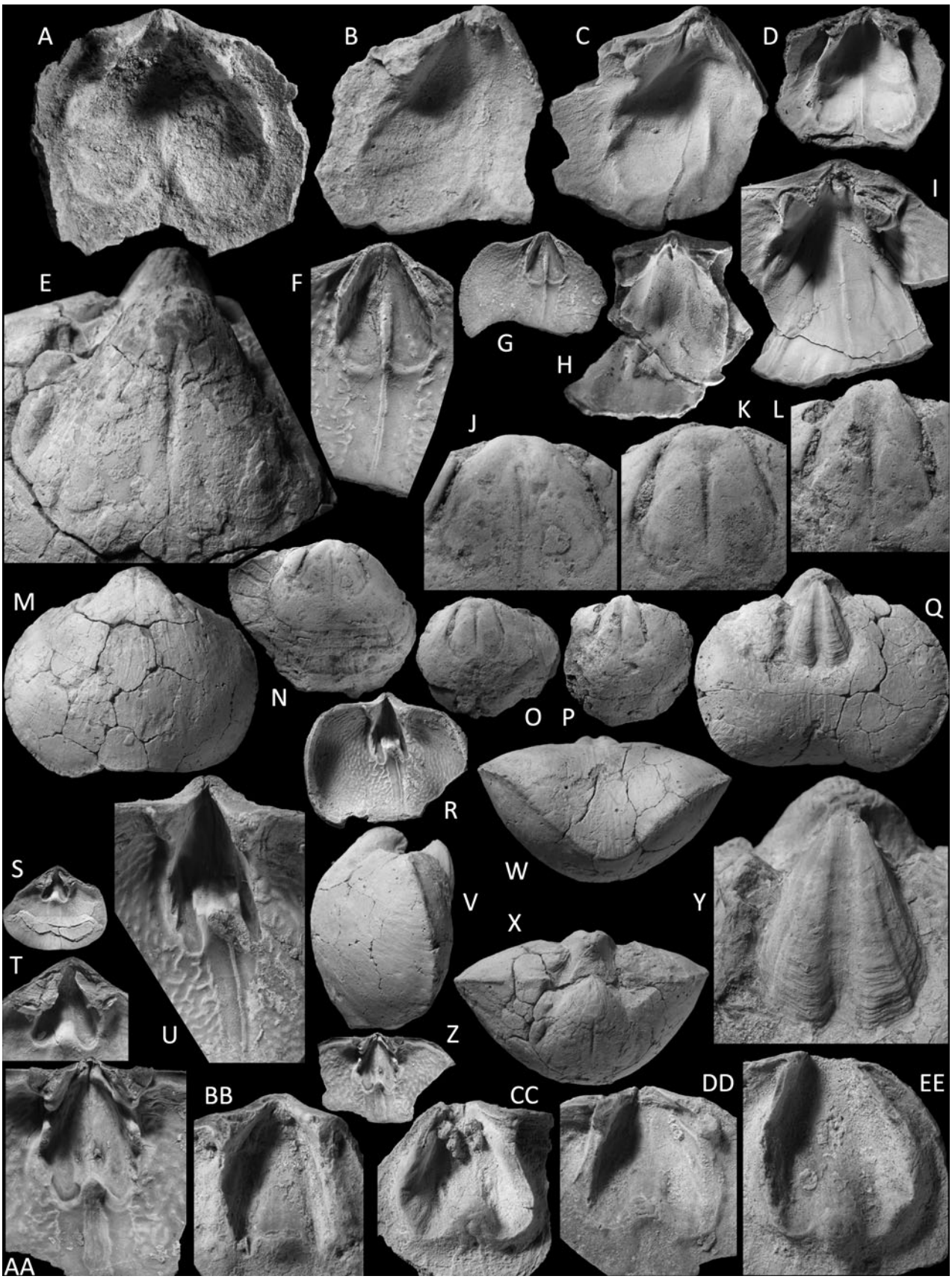
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◀ **Fig. 4** Internal morphology of *Schizophoria* (*Schizophoria*). Entire or subentire valves (*G*, *M–S*, *V–X*, *Z*), natural size; fragmentary muscle fields and enlargements of muscle fields (*A–F*, *H–L*, *T–U*, *Y*, *AA–EE*), ×2.5. *A–C*, *E*, *M*, *Q*, *V–Y*, *BB–EE Schizophoria* (*S.*) *schnuri prohibita* ssp.n. *A*. Górno, Józefka quarry; Laskowa Góra beds, upper Givetian (stratotopotypic paratype). *B–C*, *E*, *M*, *Q*, *V–Y*, *BB–EE* Górno, trench (approximately topotypic paratypes). *A–C* Dorsal muscle fields ZPAL Bp 64/1/1/6 and 64/1/2/7,8. *E*, *M*, *Q*, *V–Y* Internal mould ZPAL Bp 64/1/2/2 in dorsal (*M*), lateral (*V*), anterior (*W*), posterior (*X*) and ventral (*Q*) views with enlargements of the dorsal (*E*) and ventral (*Y*) muscle fields. *BB–EE* Ventral muscle fields ZPAL Bp 64/1/2/3–6. *D*, *S–T Schizophoria* (*S.*) *schnuri schnuri* Struve, 1965. Błonia Sierżawskie near Świętomarz, lower Givetian. *D* Dorsal muscle field ZPAL Bp 64/2/1/1. *S–T* Ventral interior ZPAL Bp 64/2/1/2 and enlargement of the muscle field. *I*, *F–G*, *R*, *U*, *Z–AA Schizophoria* (*S.*) *schnuri biscissa* Struve, 1965. Skały, 'fundamental pit'; Skały beds, upper Eifelian. *I* Dorsal muscle field ZPAL Bp 64/3/5. *F*, *G* Dorsal interior and enlargement of the muscle field ZPAL Bp 64/3/6. *R*, *U* Ventral interior and enlargement of the muscle field ZPAL Bp 64/3/7. *Z*, *AA* Ventral interior and enlargement of the muscle field ZPAL Bp 64/3/8. *H*, *J–L*, *N–P Schizophoria* (*S.*) *interstrialis* Biernat, 1954. Grzegorzowice; Grzegorzowice Formation, upper Emsian. *H* Dorsal muscle field ZPAL Bp IV/2/2 (paralectotype); specimen figured by Biernat (1954: text-fig. 6). *J*, *N*; *K*, *O*; *L*, *P* Three moulds of ventral interiors ZPAL IV/2/3–5 (paralectotypes) and enlargements of muscle fields; specimens figured by Biernat (1954: text-fig. 7)

A large part of specimens from outcrop SK-3 at Skały conforms closely to the description of *S.* (*S.*) *schnuri biscissa* Struve, 1965. However, a certain number of specimens are referable rather to *S.* (*S.*) *schnuri junkerbergiana* Struve, 1965; For example, a very large shell figured by Biernat (1959, pl. 8: 1–5) has the maximal width at midlength and a very narrow deflection of the anterior commissure, both characters diagnostic for the latter subspecies. Some intermediary forms between the morphotypes corresponding to both subspecies are figured in Fig. 5. *S.* (*S.*) *schnuri biscissa* and *S.* (*S.*) *schnuri junkerbergiana* cannot therefore be interpreted as geographic variants.

It should be reminded that the available samples from the outcrop SK-3 have not been collected bed by bed; what is more, co-occurrence of *Primipilaria praeprimipilaris* Struve, 1992 and *P. primipilaris* (von Buch, 1834) evidences that several distinct levels are indeed present (Halamski 2005). The co-occurrence of the two above-mentioned morphotypes of *Schizophoria* in the studied material does not prove their co-occurrence in vivo (but does not disprove it either). Three different, equally tenable interpretations may therefore be proposed: either *S. schnuri biscissa* and *S. schnuri junkerbergiana* are ecologic variants that did not co-occur in vivo (and should not be distinguished taxonomically) or two extremes of a continuous variation series co-occurring in vivo (same conclusion), or else two chronosubspecies, therefore necessarily overlapping in some point of a timescale (and should be distinguished). The latter conclusion seems to emerge from the analysis of the Eifel data (Struve 1965: fig. 4); it is, however, not testable on the available data from the single, stratigraphically imprecise (even if large) sample from the Holy Cross Mts.

The sample from the 'fundamental pit' at Skały is therefore identified as *S. schnuri biscissa*, according to the morphology of most specimens; the remaining individuals are referred to as *S.* (*S.*) *schnuri* ssp. indet., either morphotype *junkerbergiana* (Fig. 5A) or intermediate between the two above-mentioned ones (Fig. 5B–D).

Schizophoria (*Schizophoria*) *schnuri schnuri* Struve, 1965 (Figs. 4D, S, T; 6A–T; 8B)

v. 2005 *Schizophoria schnuri* (Schlottheim)—Zapalski, fig. 4D

vp 2009 *Schizophoria* (*Schizophoria*) cf. *schnuri* Struve, 1965—Halamski, p. 87; text-fig. 17; pl. 14: 11, 17; 15: 11–15; non 16: 10, 14, 15, 23, 24 [*ubi syn.*]

Material: about 20 articulated shells, one dorsal and one ventral valve from outcrop SW-2 sensu Halamski (2009), collection numbers ZPAL Bp 48/28 and ZPAL Bp 64/2/1; a single specimen from a well in Włochy, ZPAL Bp 64/2/2/1.

Description: Shell medium-sized (up to 32 mm in width), transverse, dorsibiconvex, subelliptic in outline. Maximal width at about midlength of the shell. Posterior margin straight, attaining up to 3/4 of the shell width; anterior commissure uniplicate, linguiform extension moderately wide (1/3–1/2 of the shell width), low to moderately high, rounded. Dorsal valve convex, elliptic to parabolic in anterior view, the umbonal region not seldom extending more posteriorly than the ventral umbo, dorsal beak rather thick, markedly incurved. Dorsal interarea apsacline to orthocline. Ventral valve moderately convex in the umbonal region, with an incipient sulcus extending anteriorly from midlength. Ventral interarea apsacline.

Ornamentation of moderately coarse radial costellae, 2–3 per mm, either of approximately the same thickness (aequicostellate) or some of them finer than the other (parvicostellate), separated by somewhat wider furrows. Costellae arising by bifurcation and intercalation. Growth lines very fine, rarely preserved.

Ventral interior: teeth moderately strong, muscle area wide.

Dorsal interior: the single juvenile dorsal valve has a relatively small and narrow muscle area; the scars are separated by a broad median elevation with a faint and narrow median ridge.

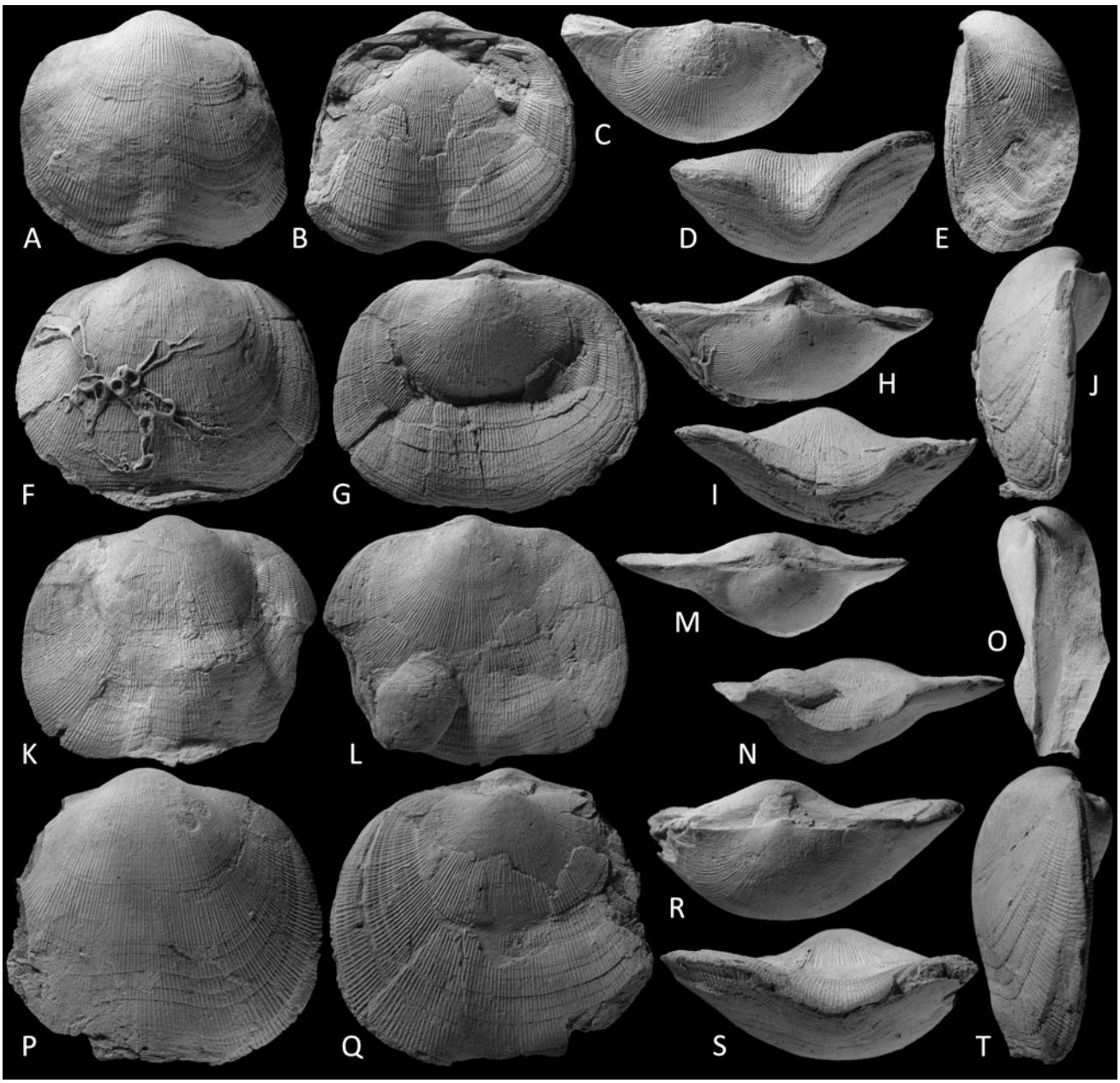


Fig. 5 *Schizophoria* (*S.*) *schnuri* Struve, 1965 (ssp. indet.). Individuals of intermediate morphology between *S.* (*S.*) *schnuri biscissa* Struve, 1965 and *S.* (*S.*) *schnuri junkerbergiana* Struve, 1965 in dorsal, ventral, posterior, anterior and lateral views. All specimens from the 'fundamental pit' in Skały (Skały beds, upper Eifelian) and shown natural size. *A–E* Articulated shell (*junkerbergiana*-morphotype) ZPAL Bp 64/3/9. *F–J* Articulated shell (intermediate morphotype) ZPAL Bp 64/3/10. *K–O* Articulated shell (intermediate morphotype) ZPAL Bp 64/3/11. *P–T* Articulated shell (intermediate morphotype) ZPAL Bp 64/3/12

Punctae medium-sized, ca. (15–)21–27 µm in diameter, distributed moderately densely, ca. 205–270 per mm^2.

Remarks: The sample from Błonia Sierżawskie was previously described by Zapalski (2005) and Halamski (2009) on the basis of limited material as *Schizophoria schnuri* and *Schizophoria* (*S.*) cf. *schnuri*, respectively. A larger sample allowed a precise identification. The differences with *S. schnuri prohibita* ssp.n. are discussed below.

Schizophoria (*Schizophoria*) *schnuri prohibita* ssp.n. (Figs. 4A–C, E, M, Q, V–Y, BB–EE; 7A–II; 8C, E)

vp 2009 *Schizophoria* (*Schizophoria*) cf. *schnuri* Struve, 1965—Halamski, p. 87; text-fig. 17; pl. 16: 10, 14, 15, 23, 24; non 14: 11, 17; 15: 11–15

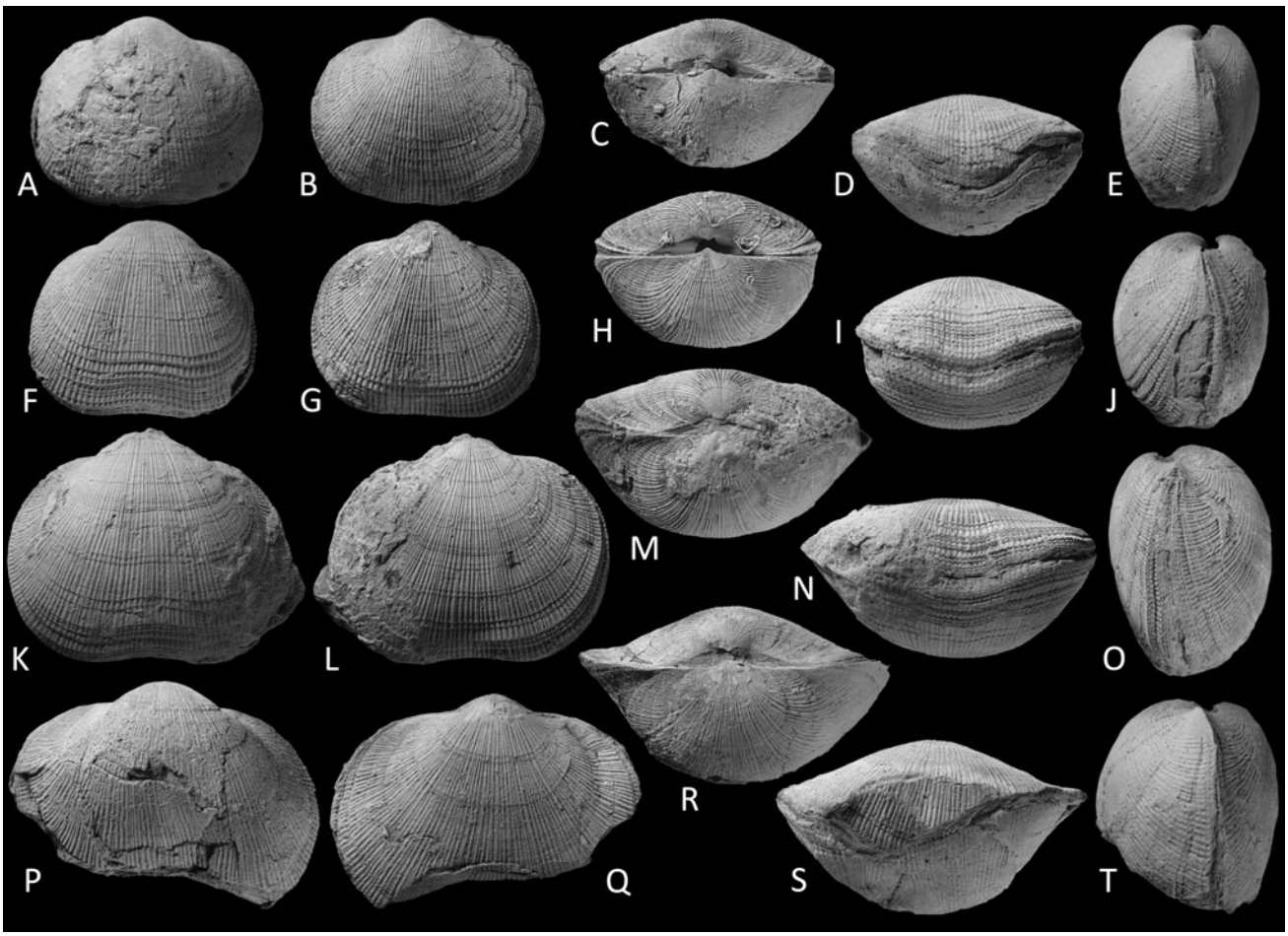


Fig. 6 External morphology of *Schizophoria* (*Schizophoria*), continued. Articulated shells in dorsal, ventral, posterior, anterior and lateral views. All specimens shown ×1.5. *A–T Schizophoria* (*S.*) *schnuri schnuri* Struve, 1965. Błonia Sierżawskie near Świętomarz; Skały beds, lower Givetian. *A–E* Specimen ZPAL Bp 64/2/1/3. *F–J* Specimen ZPAL Bp 64/2/1/4. *K–O* Specimen ZPAL Bp 64/2/1/5. *P–T* Specimen ZPAL Bp 64/2/1/6

Diagnosis: *Schizophoria schnuri* rounded-subrectangular in outline, with wide tongue and dorsal muscle field wider than long.

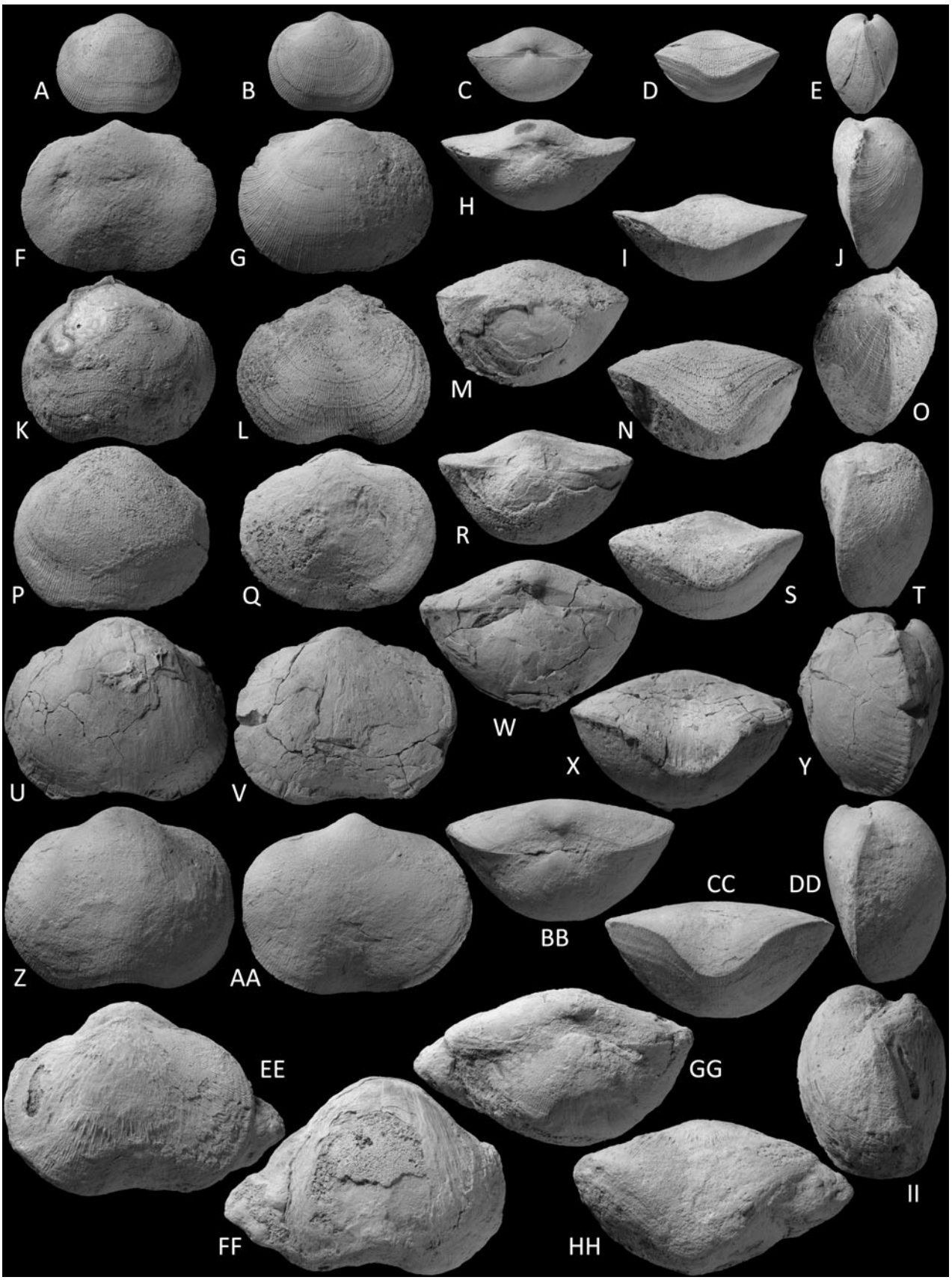
Locus typicus: Józefka quarry (eastern wall), Górno, Holy Cross Mts.

Stratum typicum: Laskowa Góra beds, upper Givetian.

Derivatio nominis: *prohibitus*, in Latin 'forbidden'—in allusion to the difficult access to the type outcrop.

Type material: Holotype, articulated shell ZPAL Bp 64/1/1/1 (Fig. 7Z–DD; stratotopotypic paratypes, four articulated shells from the type outcrop ZPAL Bp 64/1/1/2–5 (Fig. 7F–T, EE–II); approximately stratotopotypic paratype ZPAL Bp 64/1/2/1 from the outcrop in Górno (Fig. 5U–Y); non-topotypic paratype from Laskowa Góra ZPAL Bp 64/1/3/1 (Fig. 7A–E); one complete internal mould (approximately topotypic paratype) ZPAL Bp 64/1/2/2 (Fig. 4E, M, Q, V–Y); four ventral muscle fields (approximately topotypic paratypes) ZPAL Bp 64/1/2/3–6 (Fig. 4BB–EE); three dorsal muscle fields, one stratotopotypic paratype ZPAL Bp 64/1/1/6 (Fig. 4A) and two approximately topotypic paratypes ZPAL 64/1/2/7,8 (Fig. 4B, C); several more fragmentarily preserved stratotopotypic paratypes, collection ZPAL Bp 64/1/1; a single non-topotypic paratype from Nieczulice, ZPAL Bp 48/28/3/1.

Description: Shell rather large to large (up to 41.2 mm in width), transverse, dorsibiconvex, subrectangular in outline with markedly rounded postero-lateral and antero-lateral extremities. Maximal width at about midlength of the shell. Posterior margin straight, attaining up to 3/4 of the shell width; anterior commissure usually slightly indented, uniplicate, linguiform extension moderately wide (1/3–1/2 of the shell width), seldom more, low to moderately high, rounded. Dorsal valve strongly convex, semi-elliptic to parabolic in anterior view, the umbonal region not seldom extending more posteriorly than the ventral umbo, dorsal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◀ **Fig. 7** External morphology of *Schizophoria* (*Schizophoria*), continued. Articulated shells in dorsal, ventral, posterior, anterior and lateral views. All specimens shown natural size. *A–Y Schizophoria* (*S.*) *schnuri prohibita* ssp.n. *A–E* Non-topotypic paratype from Laskowa Góra quarry, Laskowa Góra beds, upper Givetian. *F–T*, *EE–II* Topotypic paratypes from Górno, Józefka quarry; Laskowa Góra beds, upper Givetian. *U–Y* Approximately topotypic paratypes from Górno, trench. *A–E* Paratype ZPAL Bp 64/1/3/1. *F–J* Paratype ZPAL Bp 64/1/1/2. *K–O* Paratype ZPAL Bp 64/1/1/3. *P–T* Paratype ZPAL Bp 64/1/1/4. *U–Y* Paratype ZPAL Bp 64/1/2/1. *Z–DD* Holotype ZPAL Bp 64/1/1/1. *EE–II* Paratype ZPAL Bp 64/1/1/5

beak rather thick, markedly incurved. Dorsal interarea apsacline to orthocline. Ventral valve moderately convex in the umbonal region, with a very broad, shallow sulcus extending anteriorly from midlength. Ventral interarea apsacline.

Ornamentation of moderately coarse radial costellae, 2–3 per mm, most often of approximately the same thicknesses, seldom parvicostellate, separated by somewhat wider furrows. Costellae arising by bifurcation and intercalation, the former apparently more frequent. Growth lines not observed.

Ventral interior: teeth relatively high, narrow, divergent at 75°. The muscle field is about 15 mm wide and 14 mm long, bisected by an indentation ca. 3 mm long. A low and rather thin median septum prolongs the indentation posteriorly to about half the length of the muscle field.

Dorsal interior: unknown.

Punctae medium-sized, ca. (13–20)–27 μm in diameter, distributed moderately densely, ca. 185–205 per mm^2.

Remarks: The above-described middle to late Givetian form is quite similar to the early Givetian *Schizophoria* (*S.*) *schnuri schnuri* (see above). The mean size of the shell in the Górno sample is smaller than that of *S.* (*S.*) *schnuri schnuri* from Świętomarz, but this is due to ecologic factors as *S.* (*S.*) *schnuri schnuri* from the Eifel is up to 38.9 mm wide. The shape of shells from both samples is quite the same. On the contrary, dorsal muscle fields of specimens from Górno are wider than long whereas those from the Świętomarz sample are longer than wide (compare Figs. 3B and 4A herein and pl. 14: 1, 2, 12 in Halamski 2009; corresponding data for the Eifel are unfortunately not available). Given the stratigraphic gap separating the two samples, the Górno material is described here as a new subspecies in the *Schizophoria* (*S.*) *schnuri* lineage.

Schizophoria (*Schizophoria*) sp.n. (Fig. 2A–J)

? 1970 *Schizophoria striatula*—Dürkoop, p. 181–183, pl. 14: 7–10

v. 1993b *Schizophoria* aff. *mcfarlanei* (Meek, 1868)—Racki, p. 300, fig. 1H–I

Material: two fragmentarily preserved shells and one fragment from the eastern hill at Trzemoszna, Givetian; GIUS 4-219.

Description: Shell small (up to 22 mm in width), transverse (width to length ratio 1.18–1.36), ventribiconvex, often teardrop-shaped in outline with approximately straight anterior margin, sometimes more transverse. Maximal width usually at about midlength (anterior or posterior to it, according to the individual). Hinge line attaining ca. 0.6 of the total width of the shell. Anterior commissure broadly and shallowly uniplicate, sulcus very wide (0.8–0.9 of the shell width), relatively shallow. Dorsal valve relatively low, broadly triangular in anterior view. Ventral valve very high, parabolic in anterior view; umbo thick, incurved, extending over the hinge line; sulcus very shallow, apparent only in the proximity of the anterior margin. Ventral interarea anacline, dorsal area very high, nearly flat, slightly hypercline.

Ornamentation of fine, rounded, tubular radial costellae, 3–4 per mm, separated by narrower furrows.

Dorsal interior: trace of an elongate (about half of the shell length, length to width ratio 1.5) and deeply medially indented (over 1/3 of its length, Fig. 2F) muscle area. Interior otherwise unknown.

Shell structure: not studied.

Remarks: The Givetian to Frasnian *Schizophoria* (*S.*) *macfarlanei* (Meek, 1868) has a very characteristic strongly dorsibiconvex shell (Meek 1868: 88, pl. 12, 1; Shimer and Shrock 1944: pl. 140: 1–3; Stigall Rode 2005: 151, fig. 5.5–5.7). Its conspecificity with the described material may be excluded.

Schizophoria striatula sensu Dürkoop, 1970 from the Middle Devonian of Rukh (Afghanistan) resembles *Schizophoria* (*S.*) sp.n. described here in external form of the shell and the narrow, deeply indented dorsal muscle field (Dürkoop 1970: pl. 14, 7–10) but the position of the dorsal interarea is different (hypercline in the described material and anacline in that from Afghanistan).

Schizophoria macfarlanii var. *galeatiformis* Grabau, 1931 from the 'late Middle Devonian of South China' (Grabau 1931–33: 70–71, pl. 7: 8, 9, 14) is rather similar to *Schizophoria* (*S.*) sp.n. in lateral profile; the differences include the position of the area and the shape of the valves (longer than wide).

The described material represents probably a new species which is not named due to lack of sufficient material.

Schizophoria (*Schizophoria*) *parvaepunctata* von Kelus 1939 (Fig. 3A–O)

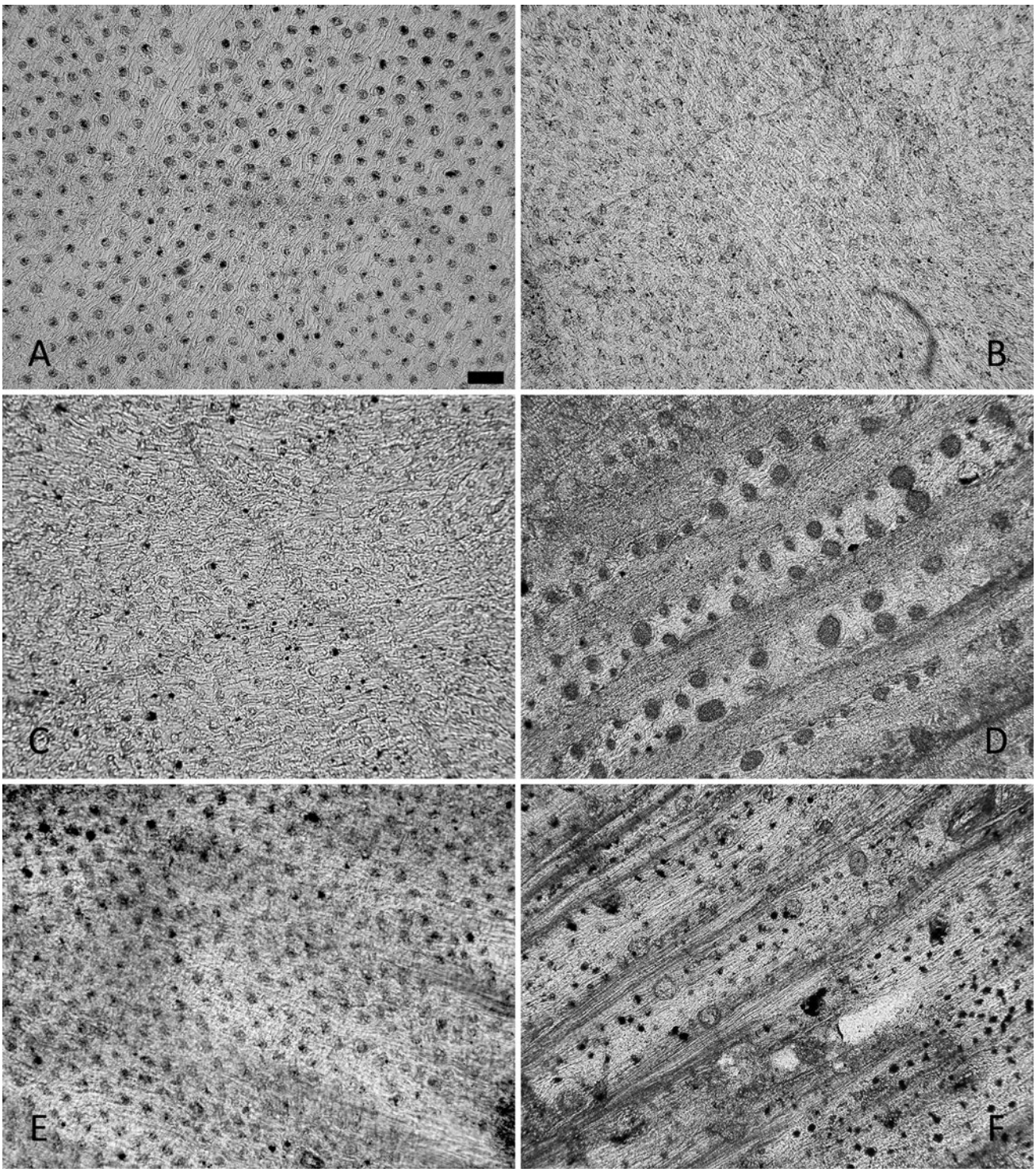

Fig. 8 Tangential sections of *Schizophoria* shells. *Scale bar* 100 µm. **a** *Schizophoria* (*S.*) *schnuri biscissa* Struve, 1965. Skały, 'fundamental pit'; Skały beds, upper Eifelian. Thin section ZPAL 64/3/S1. **b** *Schizophoria* (*S.*) *schnuri schnuri* Struve, 1965. Błonia Sierżawskie near Świętomarz; Skały beds, lower Givetian. Thin section ZPAL 64/2/S1. **c** *Schizophoria* (*S.*) *schnuri prohibita* ssp.n. Górno, Józefka quarry; Laskowa Góra beds, upper Givetian. Thin section ZPAL 64/1/S1. **d, f** *Schizophoria* (*Pachyschizophoria*) cf. *vulvaria* (von Schlotheim, 1820). Cabo la Vela section, Cantabrian Mts., Spain; La Ladrona Formation, upper Emsian. Thin sections ZPAL 64/A/S1,2. **e** *Schizophoria* (*S.*) *interstrialis* Biernat, 1954. Grzegorzowice; Grzegorzowice Formation, upper Emsian. Thin section ZPAL 64/4/S1

* 1939 *Schizophoria resupinata* var. *parvaepunctata*—Kelus, p. 33–36; text-fig. 25e; pl. 2: 18–21

v. *1950* *Schizophoria striatula* var. *parvaepunctata* Kelus—Samsonowicz, p. 410, 412, 413, 418, 419

Type material: The original specimens of von Kelus (1939) were destroyed during World War II. The specimen MWG 02619/1, an (approximate) topotype from J. Samsonowicz's collection (illustrated herein in Fig. 3K–O), is selected herein as the neotype.

Material: five articulated shells MWG 02619/1–5.

Description: Shell medium-sized (up to 29.6 mm in width), slightly to distinctly transverse, strongly dorsibiconvex, elliptic in outline. Maximal width approximately at midlength, maximal thickness posteriorly. Posterior margin straight, attaining ca. 0.6–0.65 of the shell width; anterior commissure uniplicate, tongue relatively narrow to relatively wide, high, subtriangular. Dorsal valve strongly convex, semi-elliptic to parabolic in anterior view, the umbonal region often extending more posteriorly than the ventral umbo, dorsal beak rather fine, markedly incurved. Dorsal interarea apsacline to orthocline. Ventral valve moderately convex in the umbonal region, with a very broad, shallow to occasionally deeper sulcus extending anteriorly from midlength. Ventral interarea apsacline. Delthyrium and notothyrium rather narrow, not exceeding 1/5 of the width of the interarea.

Ornamentation of fine, rounded, tubular radial costellae, 3–5 per mm, separated by somewhat wider furrows. Costellae arising by both bifurcation and intercalation. Growth lines rather strong, 2–4 per 5 mm in posterior and central region, much denser in the anterior region of the adults.

Punctae very small, ca. 5–9 μm in diameter, distributed moderately densely, ca. 190 per mm^2.

Distribution of punctae[2] as a systematic criterion

Punctae or pores are shell perforations found in several unrelated groups of articulates: enteletaceans among orthides, retziidines among athyridides, spiriferinides, terebratulides and thecideides, as well as in a few genera of rhynchonellides (Rudwick 1970; Williams 1997). The spatial pattern of their distribution has been shown to be both of some systematic value (Foster 1974: fig. 25, density; fig. 26, pore size) and influenced by external factors (Ackerly et al. 1993).

In particular, concerning orthides, Leidhold (1925) suggested that punctae distribution might be a valuable systematic criterion (among others, in *Schizophoria*). Despite several reservations, Kozłowski (1929), Schuchert and Cooper (1932) and Cloud (1942) concluded that at least in some cases this was actually the case. On the contrary, in a part of a study of Devonian fauna of Volhynia dealing with representatives of the genus *Schizophoria*, von Kelus (1939) arrived to an opposite conclusion on account of high within-individual and (presumed) intraspecific variation. This result must, however, be considered unsound, as his '*Schizophoria striatula*' included at least three different taxa (*S. schnuri*, *S. parvaepunctata* and an unidentified Frasnian species from Boulonnais). Biernat (1959), despite detailed studies of a very large material (over 10,000 specimens), was unable to give any definite conclusions, stating that "problems of the systematic significance of punctae still require further work" (Biernat 1959: 8). It has therefore seemed interesting to reassess the value of the above-mentioned criterion in a sample consisting of all the representatives of a genus (namely *Schizophoria*) within a given period and including, in particular, the intraspecific variation within more narrowly defined taxa.

Tangential sections were made from shells of *Schizophoria* (*S.*) *schnuri biscissa*, *S.* (*S.*) *schnuri schnuri* and *S.* (*S.*) *schnuri prohibita* (see descriptions above). The original sections of *S.* (*S.*) *interstrialis* by Biernat were used too. No material of *S.* (*S.*) *parvaepunctata* or *Schizophoria* (*S.*) sp.n. was available for sectioning, nonetheless corresponding values for the former species could have been estimated from the description and figure (25e) in von Kelus (1939). For comparison, two shells of *Schizophoria* (*Pachyschizophoria*) cf. *vulvaria* from the upper Emsian of the Cabo la Vela section (La Ladrona Formation, Cantabrian Mts., Spain) have also been sectioned. Sections were examined under Zeiss biologic light microscope: puncta diameter was measured using a 40× objective, whereas punctae density was counted under a 16× objective on a surface of 0.37 mm^2 on each section. Two counts were made per individual. The results are presented in the systematic descriptions above and summarised in Table 2.

The results may be systematised as follows: three groups of taxa can be distinguished according to the punctae characteristics. *Schizophoria* (*Pachyschizophoria*) cf. *vulvaria* is characterised by relatively large and sparsely

[2] It may be noted that the name of this anatomic structure is taken from Latin *puncta* 'the action of pricking' (first declension, feminine), much rarer than usual *punctum* 'the action or the mark of pricking' (second declension, neuter; Gesner 1749: 1178; Plezia 1959: 389). Both forms have been used by palaeontologists. The former one, namely *puncta*, plural *punctae*, although less correct from a strictly linguistic point of view, has been recommended by the editors of the *Treatise* (Williams and Brunton 1997: 436) followed by a majority of modern authors; it is also used in the present text.

Table 2 Numeric characteristics of punctae distribution in selected species of *Schizophoria*

Subgenus	Group	Species	Individual	Puncta diameter (in μm)	Punctae density (per mm^2)	Variation within taxa	
						Puncta diameter	Punctae density
Schizophoria (*Pachy-schizophoria*)	–	*Schizophoria* (*P.*) cf. *vulvaria*	A	15–45 (–90)	120	15–45 (–90)	120
		Cantabrian Mts., upper Emsian					
Schizophoria (*Schizophoria*)	*S.* (*S.*) *praecursor*	*Schizophoria* (*S.*) *interstrialis*	B	20–30	170	20–30	170
		Grzegorzowice, upper Emsian					
	S. (*S.*) *schnuri*	*Schizophoria* (*S.*) *schnuri biscissa*	C	13–18 (–23)	215–240	13–27	215–400
			D	15–24	365–400		
		Skały, upper Eifelian	E	(13–) 15–27	260–275		
		Schizophoria (*S.*) *schnuri schnuri*	F	(15–) 21–27	205–270	15–27	205–270
		Świętomarz, lower Givetian					
		Schizophoria (*S.*) *schnuri prohibita*	G	13–20 (–27)	185–205	13–27	185–205
		Górno, upper Givetian					
	–	*Schizophoria* (*S.*) *parvaepunctata*	H	5–9	190	5–9	190
		Pełcza, Givetian					

Values have been rounded. See text for further explanations

distributed punctae (diameter up to 45 μm in the central region of the valve, up to 90 μm in marginal region). *Schizophoria* (*S.*) *parvaepunctata* is characterised by very small (less than 10 μm in diameter) and moderately densely distributed (190 per mm^2) punctae. *Schizophoria* (*S.*) *interstrialis* and all the subspecific variants of *Schizophoria* (*S.*) *schnuri* have medium-sized punctae (15–30 μm in diameter) of moderately dense distribution (185–400 per mm^2). The intraspecific variability of these characters is quite important.

The punctae distribution in *Schizophoria* (*Pachy-schizophoria*) cf. *vulvaria* is certainly the most unusual among the patterns described here, as it is quite different from both the above-mentioned fossil material and recent taxa. In effect, the distribution of the punctae was studied in some detail in recent terebratulides, and it has been shown that in all studied species the pattern of the spatial positioning of the punctae was similar, consisting of more or less uniformly sized punctae disposed without significant changes in density (Foster 1974: fig. 3). A similar pattern may be observed in numerous published illustrations of both fossil and Recent terebratulides (a few examples may be quoted: Recent *Gryphus vitreus*, Ruggiero 1983: pl. 1, fig. 3; Recent *Argyrotheca cuneata*, Ruggiero 1987: pl. 2, figs. 1–7; Recent *Megathiris detruncata*, Benigni 1987: fig. 6; Ruggiero 1987: pl. 5, figs. 1–3; Recent *Phaneropora galatheae*, Bitner 2008: fig. 15; Eocene *Magella australis*, Bitner 1996: pl. 23, fig. 3 and unpublished data; several Cretaceous representatives of genera *Sellithyris*, *Rectithyris*, *Concinnithyris*, and others, Gaspard 1970). Thecideids seem to have a slightly less regular yet broadly similar pattern (Jurassic *Rioultina wapiennensis*, Krawczyński 2008: pl. 2, figs. 4, 6; Recent *Thecidellina minuta*, Bitner 2010: fig. 5). On the contrary, *Schizophoria* (*P.*) cf. *vulvaria* is characterised by an unusual pattern consisting in punctae of very different sizes (the largest ones being up to six times wider than the smallest) intermingled among one other (Fig. 8D). The only analogue found for such a distribution is that found in Middle Devonian *Levenea depressa* Wang, 1956 from Kwangsi (now Guangxi), South China (Wang, 1956: pl. 3, fig. D6; the image is, unfortunately, poorly legible). This shows that shell structure in brachiopods is still relatively poorly studied. Lack of data on punctae size and density has recently been stressed also by Pérez-Huerta et al. (2009).

Conclusions

1. The nominative subgenus of the genus *Schizophoria* in the Lower and Middle Devonian of Poland (Łysogóry and Kielce Regions, Holy Cross Mts.) and of western Ukraine (Volhynia) is represented by the following taxa:

(a) *Schizophoria* (*Schizophoria*) *interstrialis* in the upper Emsian of Grzegorzowice (Łysogóry Region);

(b) *Schizophoria* (*S.*) *schnuri biscissa* in the upper Eifelian of Skały (Łysogóry Region); some morphotypes from the same outcrop are referable to *S.* (*S.*) *schnuri junkerbergiana*, wherefore the separation of these subspecies may be maintained only if they are considered as chronosubspecies (unverifiable on the studied material) but not as geographic variants (hypothesis falsified by the studied material);
(c) *Schizophoria* (*S.*) *schnuri schnuri* in the lower Givetian of Błonia Sierżawskie near Świętomarz and of Włochy (Łysogóry Region);
(d) *Schizophoria* (*S.*) *schnuri prohibita* ssp.n. in the middle to upper Givetian of Górno (Kielce Region) and of Nieczulice (Łysogóry Region);
(e) *Schizophoria* (*S.*) sp.n. (unnamed for lack of sufficient material) in the upper Givetian of Trzemoszna (Kielce Region);
(f) *Schizophoria* (*S.*) *parvaepunctata* in the middle Givetian of Povcha (Volhynia).

2. Within the genus *Schizophoria*, punctae diameter and density may serve as a systematic criterion between groups of species but not within a lineage of closely related taxa. *S.* (*Pachyschizophoria*) and *S.* (*S.*) *parvaepunctata* differ between one another and from all other investigated species of *S.* (*Schizophoria*); the latter are indistinguishable on the sole basis of punctae characteristics.
3. The punctae distribution pattern in *Schizophoria* (*Pachyschizophoria*) cf. *vulvaria* consists of intermingled punctae of very different diameters. Such a condition is apparently very rare among brachiopods.

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