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Taxonomic revision of the Paradoxididae Hawle and Corda, 1847 from the Miaolingian (Cambrian) of the Holy Cross Mountains, Poland: a morphometric approach to simply deformed trilobites

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ABSTRACT:

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The taxonomy of simply deformed paradoxidids from the Miaolingian (Cambrian) of Słowiec Hill, Holy Cross Mountains, Poland, is revised based on morphometric analysis. The material represents two species: *Acadoparadoxides slowiecensis* (Czarnocki in Orłowski, 1965) and *Hydrocephalus*? *polonicus* (Czarnocki in Orłowski, 1965). A new assemblage zone based on the combined although not precisely known ranges of these two taxa is suggested replacing the previous *Paradoxides polonicus* Zone of Orłowski (1975, 1988, 1992a). The *Acadoparadoxides slowiecensis–Hydrocephalus*? *polonicus* Assemblage Zone corresponds to the middle and upper part of the Wuliuan Stage (lower Miaolingian).

Key words: Paradoxididae; Miaolingian; Cambrian; Holy Cross Mountains; Geometric morphometry; Simple deformation; Słowiec Hill.

This paper is dedicated to the memory
of Professor Stanisław Orłowski (1931–2021)

INTRODUCTION

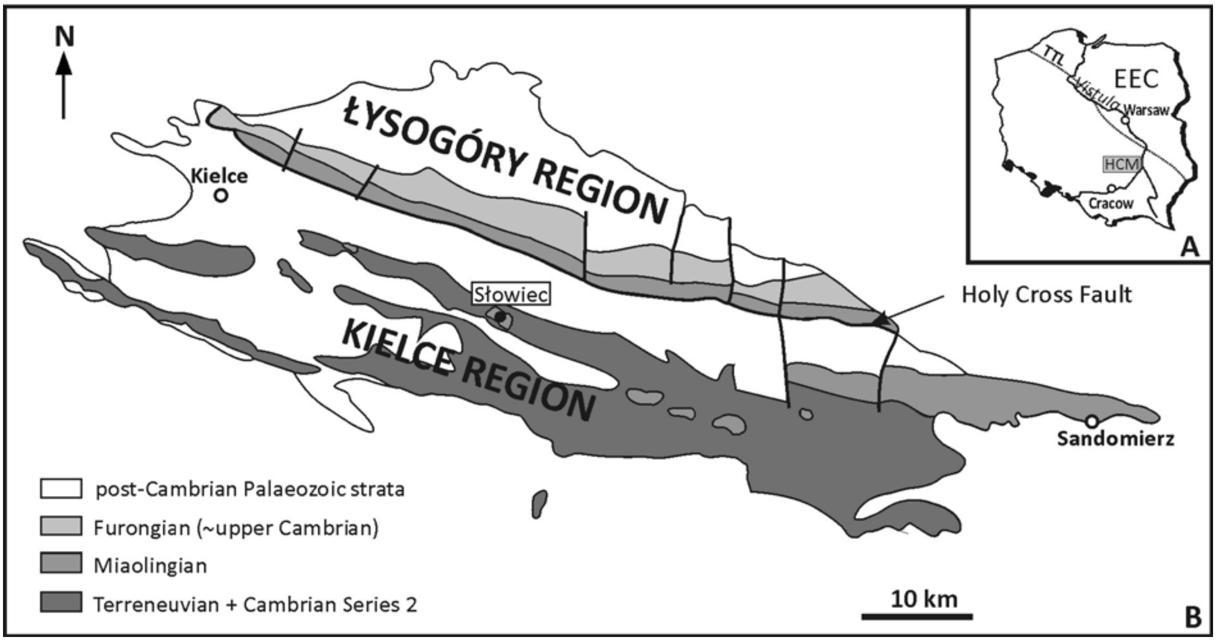
Tectonic deformation often leads to problems in determining the identity of a fossil sample. Since this problem is widely present when working with trilobite remains, the need for resolving such cases has resulted in the developing of tools that use morphometry to deal with such issues. The first attempts included linear measurements (e.g., Hughes and Jell 1992), but recent research has demonstrated how to use geometric morphometrics in this type of research (e.g., Nowicki and Żylińska 2019). This study follows the latter paper in reviewing simply deformed paradoxidiids from the Miaolingian (Cambrian) of the Holy Cross Mountains in central Poland. The endemic paradoxidiid assemblage from Słowiec Hill can be used as a good example of the use of a newly developed workflow for this type of data. Furthermore, the much needed redescription of species from this locality (the most recent study of the paradoxidiids from this locality was in Orłowski 1985) is the basis of a revision of the Cambrian biostratigraphic scheme for the Holy Cross Mountains, and allows for a discussion of the possible correlations.

GEOLOGICAL SETTING

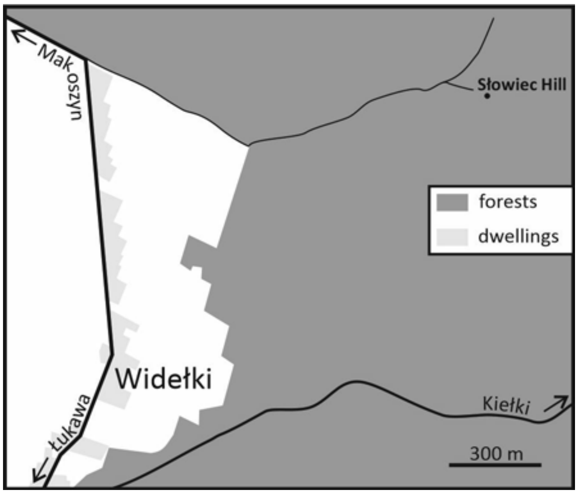
The entire material studied herein was collected over more than 50 years from loose sandstone blocks on the peak of the completely forested Słowiec Hill in the central part of the Palaeozoic exposure of the Holy Cross Mountains (Text-fig. 1). At 433 m above sea level, Słowiec Hill is one of the highest summits of the Orłowińskie Range, lying to the north-east of Widełki village (Text-fig. 2), c. 12 km to the north-west of Raków village and c. 10 km to the east of Daleszyce town. The forest covering Słowiec Hill and nearby summits is protected as part of the Cisów-Orłowiny Landscape Park.

The Cambrian succession of the Holy Cross Mountains is composed of siliciclastic facies, subdivided into several lithostratigraphic units (Orłowski 1975, 1988). The material studied comes from the Słowiec Sandstone Formation, a c. 100 m thick unit characterised by the predominance of light grey, in places yellowish or greenish, glauconite-bearing, coarse- to medium-grained, poorly sorted quartz sandstones, with clay clasts up to several centimetres in size (Orłowski 1975; Masiak and Żylińska 1994). Coarser grains occur often as distinct intercalations between the finer quartz grains. The rocks do not contain any trace fossils, as opposed to the common occurrence of ichnofossil assemblages in the underlying Ociesęki Sandstone Formation (e.g., Orłowski 1989, 1992b). As can be estimated from the sizes of the sandstone blocks observed on the peak of the hill, at least in part the predominantly light grey sandstones were thick-bedded. The fossils occur as internal or external moulds or their imprints, and in some cases abundant accumulations of sub-parallel oriented (possibly bedding-parallel) voids after fossils occur at one end of a sandstone block. Accordingly, a high-energy environment is postulated for the deposition of the strata, based on the predominance of coarse quartz grains, the presence of clay clasts, poor sorting, the preservation state of the fossils (isolated, crushed fragments), and the lack of trace fossils (e.g., Orłowski 1975; Masiak and Żylińska 1994; Kowalczewski *et al.* 2006). A common feature of the material is simple tectonic deformation; contrary to the statement of Orłowski (1965) that the fossils are undeformed, the available material shows that most fossils are subject to notable distortion.

This part of the Palaeozoic of the Holy Cross Mountains is located within the Kielce Region, also referred to as the Kielce Fold Zone (e.g., Konon 2008; Żelaźniewicz *et al.* 2011), which represents an exposed part of the sedimentary cover of the Małopolska Block, a crustal element within the Trans-European Suture Zone (Berthelsen 1992). Among the different views on the nature of this crustal block are those suggesting its proximal nature as part of the Baltica palaeocontinent (e.g., Nawrocki *et al.* 2007; Żelaźniewicz *et al.* 2009) or its exotic provenance as a terrane rifted from Gondwana and accreted to Baltica



Text-fig. 1. Geological sketch-map of the Holy Cross Mountains (HCM) showing the distribution of Cambrian deposits, modified from Orłowski (1975, 1992a), with location of Słowiec Hill. EEC – East European Craton, TTL – Teisseyre-Tornquist Line.



Text-fig. 2. Sketch-map of the Słowiec Hill area.

during the Cambrian (e.g., Belka *et al.* 2002). Recent interpretations postulate that the Małopolska Massif was not an individual terrane but part of the margin of Baltica, despite the Amazonian provenance of clastic material (Walczak and Belka 2017) that could have been supplied to lower Cambrian clastic sediments through the newly opening Tornquist Ocean (Aleksandrowski and Mazur 2017).

The biostratigraphic scheme of the Cambrian in the Holy Cross Mountains is based mainly on trilobites, supported in some intervals by acritarch assemblages (e.g., Szczepanik and Żylińska 2016; Nowicki and Żylińska 2019 and references therein). Members of the Paradoxididae have so far been recognised in the Kielce Region in the Cambrian Series 2–Miaolingian boundary interval of the Jugoszów-Usarzów succession and Brzechów (see Nowicki and Żylińska 2019 for a most recent taxonomic account) and in an apparently younger interval on Słowiec Hill (Orłowski 1965, 1985). A few poorly preserved specimens of *Paradoxides* sp. as well as *Ptychagnostus gibbus* (Linnarsson, 1869), *Peronospis fallax* (Linnarsson, 1869), *Solenopleura munsteri* Strand, 1929, and *Parasolenopleura linnarssoni* (Brøgger, 1878) have been reported from the upper Wuliuan strata of Pieprzowe Mts.[1] near Sandomierz town in the easternmost part of the Łysogóry Region (Orłowski 1964; Text-fig. 1). Revision of the paradoxidids from Słowiec Hill and evaluation of their stratigraphic significance, coupled with biostratigraphic analysis of other fossils present in this locality, are the topic of this contribution.

HISTORY OF RESEARCH ON THE PARADOXIDIDS FROM SŁOWIEC HILL

Paradoxidids from Słowiec Hill were mentioned more than a century ago in the classical monograph on the geology of the area (Czarnocki 1919), and the attribution of this part of the Cambrian succession to the traditional Middle Cambrian was based on the presence of *Paradoxides tessini* Brongniart, 1822 and *Paradoxides* sp. Later, Czarnocki (1927a, p. 196, 1927b, p. 87, 1933, p. 81) supplied more extensive faunal lists, where for the first time the endemic species ‘*Paradoxides polonicus* sp. n.’ and ‘*Paradoxides slowiecensis* sp. n.’ were mentioned, which were later formally named in Orłowski (1965). However, as is typical in Jan Czarnocki’s publications on the fossils from the Holy Cross Mountains, photographs or drawings of the specimens, or their descriptions, were never published; only faunal lists and similarities of the fossils to those known from other regions were presented in the publications mentioned above. Not much is left of Jan Czarnocki’s fossil collections, which were decimated, burnt, and deprived of museum labels following the Warsaw Uprising in 1944 during the Second World War; their scanty remains are presently housed in the Museum of the Polish Geological Institute – National Research Institute in Warsaw. A few specimens of the Cambrian trilobites from the Holy Cross Mountains (including those from Słowiec Hill) were offered by Jan Czarnocki to the U.S. Geological Survey in the early 1930’s; latex casts of these specimens with copies of museum labels were made available to Orłowski (1965, p. 135) by Allison R. (Pete) Palmer; presently these latex casts are in our possession.

The first person to illustrate the paradoxidids from Słowiec Hill was Orłowski (1957). He presented photographs of three newly collected cranidia which he designated as ‘*Paradoxides* forms of the *ölandicus* group’; furthermore, the succession on Słowiec Hill was postulated to encompass strata older than considered by Czarnocki (1927a, b, 1933). In a revision of the Słowiec Hill fauna, Orłowski (1965) provided the first formal descriptions and illustrations of *Paradoxides polonicus* and *Paradoxides slowiecensis*, the two forms mentioned earlier by Czarnocki (1927a, b, 1933). Unfortunately, an inconsistency arises from those descriptions. Firstly, the synonymy lists state

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[1] Gürich (1892, p. 70) noted the presence of *Paradoxides tessini* Brongniart, 1822 from Pieprzowe Mts., but the specimen has not been recovered in museum collections so this assignment cannot be confirmed.

that the taxonomic names of Czarnocki should have been treated as *nomina nuda* (Orłowski 1965). In spite of that, neotype specimens were selected for both species (Orłowski 1965, pp. 138, 139). The latter action was, regrettably, incorrect and therefore the designated neotypes should be considered as invalidly selected. Moreover, Czarnocki's name is given in parentheses both in the Polish and English versions of the text, in the captions to the plates and in the list of fauna from Słowiec Hill (Orłowski 1965, pp. 5, 138, 139, 144–146, respectively). Beside descriptions of the two taxa, formal descriptions and illustrations of '*Paradoxides* from the *oelandicus* group' were also included (with two specimens from the remnants of Jan Czarnocki's collection; Orłowski 1965, pp. 137, 138, pl. 2, figs 10, 11, pl. 3, figs 1, 2). Additionally, six paradoxidid taxa were described in open nomenclature (*Paradoxides* spp. A, B, C, and D – for various pygidia; *Paradoxides* sp. E – for hypostomata, and *Paradoxides* sp. F – for librigenae; Orłowski 1965, pp. 140, 141, pl. 4, figs 7–12; pl. 5, figs 7–11, pl. 6, figs 1–11). The most recent publication illustrating paradoxidids from Słowiec Hill is that by Orłowski (1985), in which the new species *Paradoxides socius* was introduced, generally differing from *Paradoxides slowiecensis* in a much broader glabella and broader fixigenae. The trilobite assemblage from Słowiec Hill was briefly mentioned in Żylińska and Szczepanik (2009), but the main focus of that study was on ellipsocephalids, mostly from the Cambrian Series 2, the paradoxidids from Słowiec Hill not being illustrated or discussed in detail.

MATERIAL

The studied material includes 266 specimens of isolated elements of the trilobite carapace: cranidia, pygidia, hypostomata, librigenae and parts of thoraces, housed in the Stanisław Józef Thugutt Geological Museum, Faculty of Geology, University of Warsaw. The primary collection is the original material of Stanisław Orłowski (142 labelled specimens, often containing several individuals of the same taxon on one rock slab; 204 trilobite elements in total; collection acronym MWGUW ZI/29). Additional material includes specimens from the teaching collection of the Department of Historical Geology, Regional Geology and Palaeontology at the Faculty of Geology, University of Warsaw (4 trilobite elements in total; presently reposited under collection acronym MWGUW ZI/66). The original material and these additional specimens were the basis of the morphometric analysis. Material collected in 2013–2016 by JN on Słowiec Hill (58 trilobite elements in total; presently reposited under collection acronym MWGUW ZI/66) was used as auxiliary in describing the taxa in the systematic part of this study. Several specimens (two labelled boxes: NMNH 85574 – *Paradoxides polonicus*; and NMNH 85575 – *Paradoxides slowiecensis*; each with crushed material that included several incomplete cranidia), originally labelled by Jan Czarnocki, and examined by JN in 2016 in the Museum of Natural History, Smithsonian Institution, Washington DC, USA, as well as the latex casts of specimens offered by Jan Czarnocki to the U.S. Geological Survey in the early 1930s (see above), were used to confirm the authorship of the taxonomic names.

The material includes both internal and external moulds, without the test preserved. Due to the coarse-grained character of the sandstones, reticulation is sparsely present, almost only on the hypostomata (*Paradoxides* sp. E of Orłowski 1965). For the same reason, the degree of compaction of the material studied is very low. The material is simply distorted by tectonic deformation, with the symmetry axes preserved as straight lines.

METHODOLOGY

Retrieving the true relations between distorted specimens of trilobites has been described in several papers (e.g., Hughes and Jell 1992; Żylińska *et al.* 2013). The main technique used in these publications was Principal Components Analysis (PCA) performed on linear measurements. Recent work on paradoxidids from the uppermost Cambrian Series 2 and lower part of the Miaolingian (middle Cambrian) of the Holy Cross Mountains (Nowicki 2016; Nowicki and Żylińska 2019) provided a similar usage of PCA, but with different type of data, i.e., the position of landmarks. Geometric morphometrics is a powerful tool, much more sensitive than classical morphometry, and therefore it can be effective in the analysis of groups with subtle differences between particular taxa, such as the paradoxidids (e.g., Geyer and Vincent 2015).

In both cases, PCA allows the splitting of variance into orthogonal components of which one may be interpreted as variance representing deformation. In linear measurements, the 'distortion component' is characterised by a high correlation with the proportions of the objects, usually defined as the quotient of the relatively largest sagittal parameter (along the axis; sag.) and relatively largest transversal parameter (perpendicular to the axis; tr.), and opposite signs of loadings for perpendicular parameters (e.g., Hughes and Jell 1992; Żylińska *et al.* 2013). In geometric morphometrics, the principal component that may be interpreted as tectonic distortion is also highly correlated with object proportions (defined as the quotient of maximum transverse width and maximum sagittal length). The second clue that allows the making of such an assumption is simple comparison of shapes that represent the minimum and maximum value of each component. Thus, the extreme shapes should represent narrow (elongated) and wide (squashed) forms of the analysed shape (e.g., Hughes and Jell 1992; Żylińska *et al.* 2013; Nowicki 2016; Nowicki and Żylińska 2019).

The mode of deformation is very important in dealing with this type of bias using morphometrics. All presented techniques make an assumption that the analysed objects are not bent with regard to their axis and the distortion attains the form of skewing or constriction. Bending of the symmetry axis (that often occurs in fine-grained clastic rocks) makes application of the presented methods inappropriate (see Geyer *et al.* 2019 for a thorough discussion). Usage of geometric morphometrics can also be limited by the deformation that may occur during compaction. Some structures may behave in different ways that change their outline in a significant way and implement additional bias (unrelated to taxonomy) to the sample (Webster and Hughes 1999). An example of such behaviour are the glabellae of paradoxidids described by Geyer and Vincent (2015) from Morocco.

Retrodeformation using PCA in geometric morphometrics was criticized by Angielczyk and Sheets (2007), but recent simulations have shown that combining the PCA technique with symmetry restoration can provide reliable results (Nowicki and Żylińska 2019).

The analysis presented herein was performed in a similar way as in our previous paper (Nowicki and Żylińska 2019); its main assumptions are briefly described below. Landmarks and semilandmarks were collected from the digital images of specimens (cranidia and pygidia) with restored axial symmetry following the methodology of Srivastava and Shah (2006). Photographs were taken after coating the specimens with ammonium chloride. Positions of points were collected from both sides of cranidia/pygidia with tpsDig software (Rohlf 2016), and in the case of missing landmarks/semilandmarks, the one lacking was estimated from the position of its pair on the other side of the cranidium/pygidium. Estimation of semilandmarks was possible due to the embedding of fans (radii of circles) on the photographs. The semilandmarks were located in homologous positions on both sides of the cranidia, defined by the intersection of the described curve and the symmetric radii. If both landmarks/semilandmarks were present, their position was averaged. The averaging/estimation was performed with *OSymm* function (Haber 2011), based on the algorithm presented in Klingenberg *et al.* (2002).

Further steps (including symmetrization) were performed with the R programming language (R Core Team 2016). Landmarks and semilandmarks were superimposed using Generalised Procrustes Analysis with the Procrustes distance criterion applied for sliding semilandmarks. The superimposition was performed with a *geomorph* package (Adams and Otárola-Castillo 2013; Adams *et al.* 2016). The same package was used to perform further analysis (PCA). Data manipulation and processing was performed using *morphoutils* package (Nowicki 2015).

FORMER CLASSIFICATION OF THE PARADOXIDIDS FROM SŁOWIEC HILL

Following previous taxonomic studies of the paradoxidids from Słowiec Hill (Orłowski 1965, 1985), the assemblage comprises three species based on cranidia (*Paradoxides polonicus*, *Paradoxides slowiecensis* and *Paradoxides socius*; see Systematic Part for details on the authorship of the taxonomic names), four taxa in open nomenclature based on pygidia (*Paradoxides* spp. A–D), hypostomata representing *Paradoxides* sp. E and librigenae representing *Paradoxides* sp. F.

The taxonomic assignment of the paradoxidid cranidia from Słowiec Hill was initially based on several morphological characters and differences in proportions (Table 1). Cranidia described as *Paradoxides polonicus* are well defined and can be clearly distinguished from other forms by the presence of wider palpebral lobes and a reduced preglabellar field (for details see Systematic Part). However, the differences between cranidia described as *Paradoxides slowiecensis* and *Paradoxides socius* are generally limited to differences in proportions, with the narrow form defined as *P. slowiecensis* and the wide form defined as *P. socius*. Such variance can be easily explained by tectonic deformation, and if this statement is true, then the subdivision into two taxa is unjustified. Tectonic deformation can be observed in most of the material from Słowiec Hill, including trilobites and brachiopods. On the contrary, cranidia described as *P. socius* seem to be undeformed or un-

	P. polonicus* vs. *P. slowiecensis	***P. polonicus* vs. *P. socius***	***P. slowiecensis* vs. *P. socius***
glabella	wider (tr.) in *P. polonicus*	differences in shape (no detailed description)	wider (tr.) in *P. socius*
palpebral lobes	wider (tr.) in *P. polonicus*	wider (tr.) and longer (sag.) in *P. polonicus*	–
fixigenae	–	wider (tr.) in *P. socius*	wider (tr.) in *P. socius*
anterior border	more distinct in *P. slowiecensis*	more distinct in *P. socius*	differences in shape (no detailed description)
preglabellar field	longer (sag.) in *P. slowiecensis*	–	–

Table 1. Diagnostic differences of paradoxidid cranidia from Słowiec Hill, based on Orłowski (1965, 1985).

recognisably deformed only, with the symmetry axis preserved intact. It is highly unlikely that only one group of fossils would evade deformation. It seems, therefore, that those cranidia were also deformed, but the axis of compression was parallel to the symmetry axis and deformation resulted in expanded cranidia with axial symmetry preserved.

A similar pattern can be observed in the pygidia of paradoxidids from Słowiec Hill. Specimens assigned by Orłowski (1965) as *Paradoxides* sp. C differ in a significant way from the other two types (*Paradoxides* sp. B and *Paradoxides* sp. D)[2], which can be distinguished only by different width to length proportions.

Paradoxides spp. E and F of Orłowski (1965), representing hypostomata and librigenae, respectively, do not display any morphological variation and, because they cannot be confidently assigned to any species, they are excluded from this analysis.

MORPHOMETRIC ANALYSIS

In order to check if the pattern of proportions is the only one that distinguishes the carapace elements, geometric morphometric analysis was applied. Two attempts with a different number of landmarks and semilandmarks were applied to the cranidia – differing in detail in the presence or absence of landmarks and semilandmarks on the anterior border furrow, and the number of semilandmarks on the anterior margin, palpebral lobes and frontal lobe of the glabella. The second attempt allowed for using cranidia with less detail preserved and, as a result, included more specimens in the analysis. The number of pygidia was not sufficient to perform a valid morphometric analysis.

Thirty-five cranidia of paradoxidids from Słowiec Hill were complete enough to collect a set of landmarks and semilandmarks with the anterior border furrow included. This was the analysis with a larger number of details but a smaller number of specimens included. The analysed material contained 22 cranidia labelled as *Paradoxides polonicus*, 7 cranidia labelled as *Paradoxides slowiecensis*, and 6 cranidia labelled as *Paradoxides socius*. The applied landmarks and semilandmarks are listed in Table 2 and in Text-fig. 3.

Number of landmark/ semilandmark	**General location**	**Description of the position on cranidium**
1	axis	posterior margin of the occipital ring
2	axis	deepest point of SO
3	axis	deepest point of S1
4	axis	deepest point of S2
5	axis	anterior margin of the glabella
6	axis	anterior border furrow
7	axis	anterior margin of the cranidium
8, 14	left and right side	juncture of SO and axial furrow
9, 15	left and right side	juncture of S1 and axial furrow
10, 16	left and right side	juncture of S2 and axial furrow
11, 17	left and right side	posterior tip of the palpebral lobe
12, 18	left and right side	anterior tip of the palpebral lobe
13, 19	left and right side	juncture of anterior border furrow and facial suture
20–24, 25–29	left and right side	anterior margin of the cranidium
30–33, 34–37	left and right side	anterior border furrow
38–42, 48–52	left and right side	external margin of the palpebral lobe
43–47, 53–57	left and right side	internal margin of the palpebral lobe
58–63, 64–69	left and right side	margin of the anterior part of the glabella

Table 2. Location of landmarks and semilandmarks on the cranidia studied. Analysis with anterior margin furrow included.

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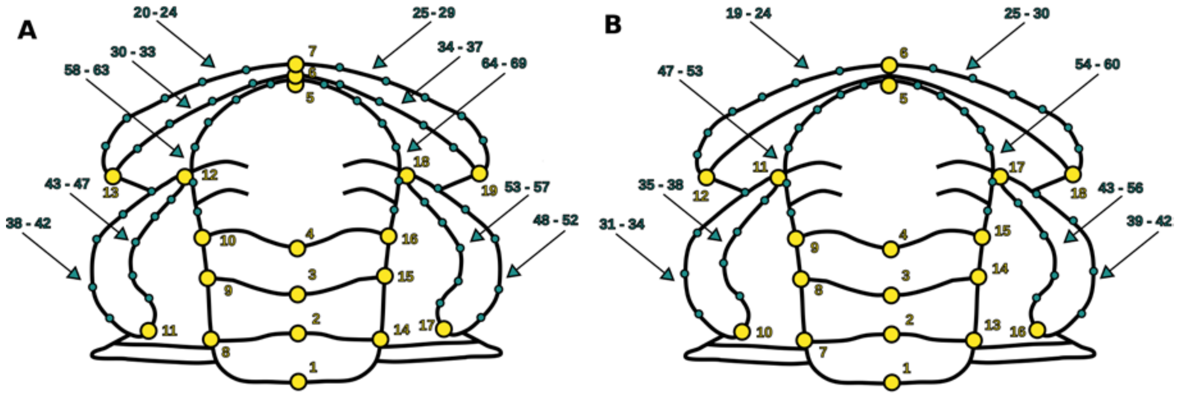
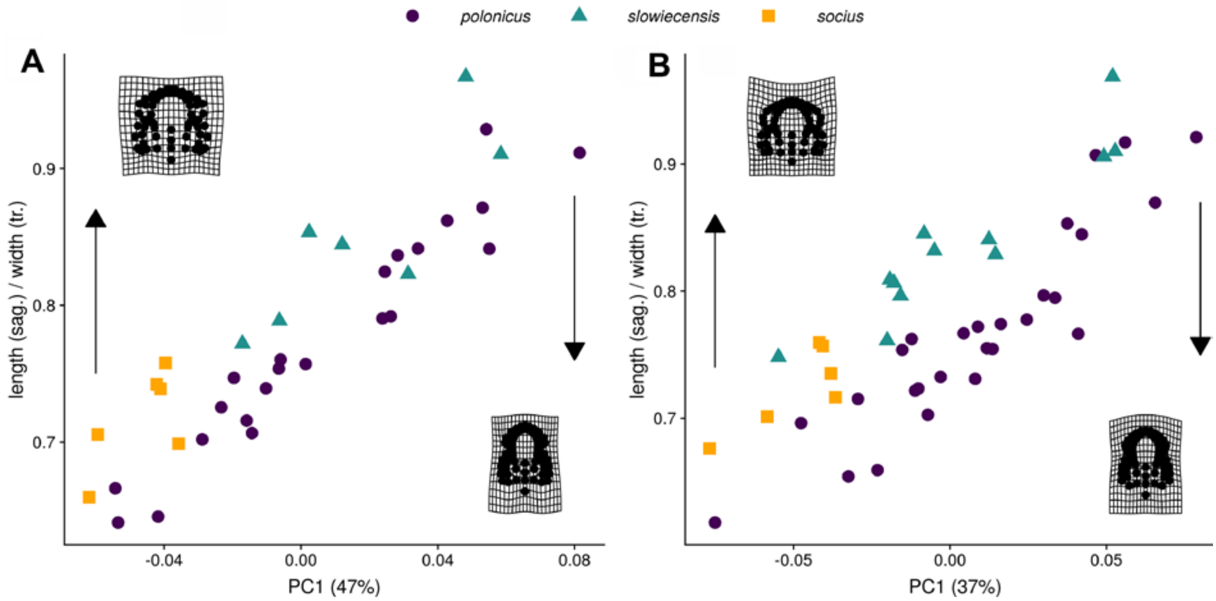
[2] A single pygidium described as *Paradoxides* sp. A in Orłowski (1965) is missing in the museum collections. Examination of the poor quality photograph from the original publication suggests that this specimen represents the B and D morphotypes, with the last segment of the thorax with pleurae preserved.

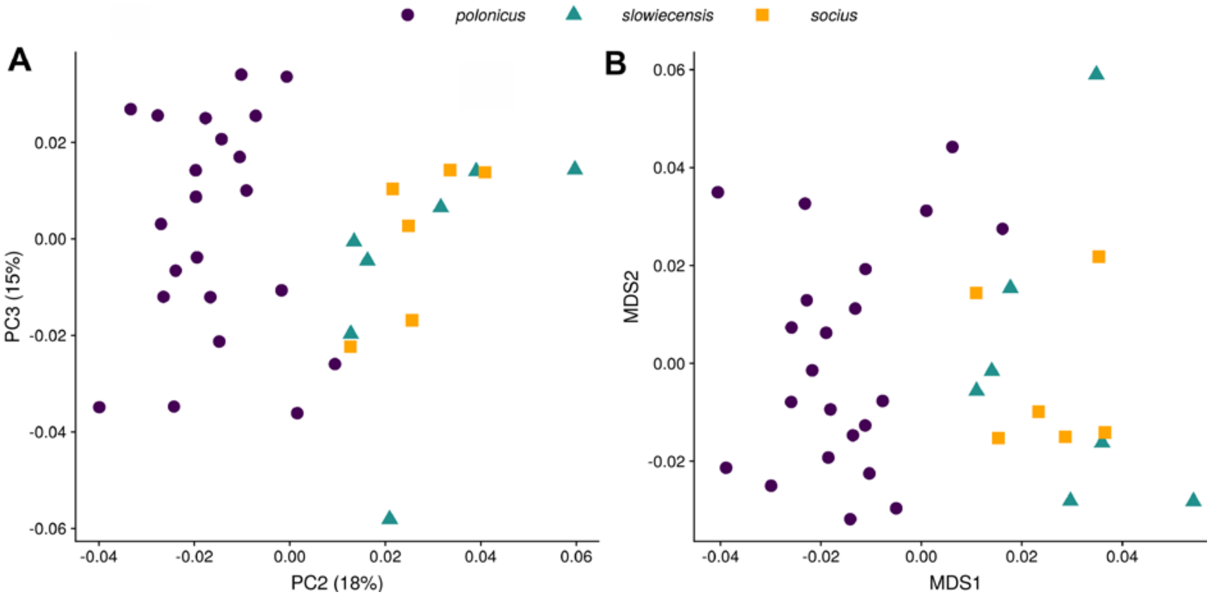


Text-fig. 3. Location of collected landmarks and semilandmarks on a paradoxidid glabella, A – anterior margin furrow included; B – anterior margin furrow excluded.



Text-fig. 4. Correlation of PC1 with glabellar proportions with thin plate splines showing cranidium shapes corresponding to the minimum and maximum value of PC1. A – less detailed analysis with more specimens included; B – more detailed analysis with less specimens included.

The first principal component represents 46.6% of the variation in the sample (Table 3) and, since it correlates with the length (sag.) to width (tr.) proportions (r = 0.91, p-value > 0.0001; Text-fig. 4A), it can be interpreted as a component that represents variation related to the deformation. The remaining principal components represent unbiased morphological variation. As can be seen on the scatterplot of PC2 (18.4%) and PC3 (15.1%) (Text-fig. 5A), cranidia of *P. polonicus* form one consistent group, whereas those representing *P. slowiecensis* and *P. socius* form a second consistent group. Picturing the whole remaining variance (all PCs except PC1) using Nonmetric Multidimensional Scaling (NMDS) performed with the vegan package (Oksanen *et al.* 2016) following the recommendations of Minchin (1987), reveals the same pattern (Text-fig. 5B). Both groups (*P. polonicus* and *P. slowiecensis* + *P. socius*) are slightly mixed in the right part of the first plot (Text-fig. 5A) and (in the same way) in the right part of the second plot (Text-fig. 5B). This pattern is related to the size of the specimens. The major characters that distinguish those two groups (including the size of the preglabellar field and the shape of the palpebral lobes) are not well ex-



Text-fig. 5. Scatter plots for less detailed analysis with more specimens showing: A – the relationship of PC2 and PC3; and B – visualization of PCA (with PC1 excluded) using NMDS.

Component	Eigenvalue	Proportion of variance	Cumulative proportion of variance
PC1	0.00153	46.6%	46.6%
PC2	0.00060	18.4%	65.0%
PC3	0.00050	15.1%	80.2%
PC4	0.00024	7.4%	87.5%
PC5	0.00008	2.4%	89.9%
PC6	0.00007	2.2%	92.1%
PC7	0.00005	1.4%	93.5%
PC8	0.00003	1.0%	94.5%
PC9	0.00003	0.8%	95.3%
PC10	0.00002	0.8%	96.1%

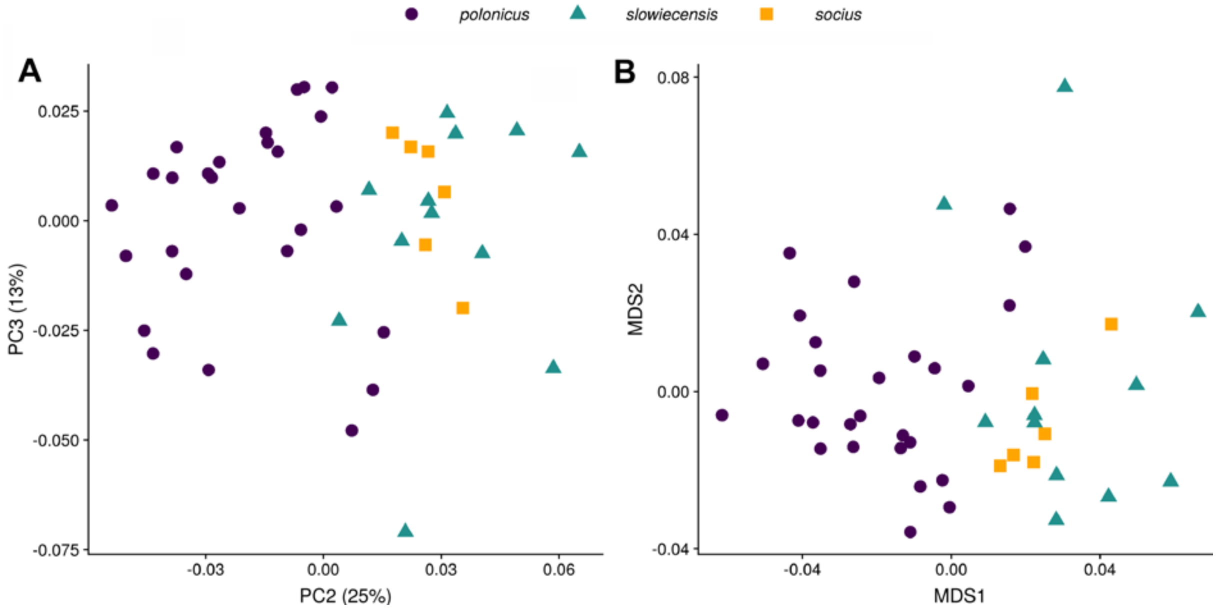
Table 3. Eigenvalues and proportion of variance for the first ten PCs obtained for the specimens studied. Analysis with anterior margin furrow included.

Number of landmark/ semilandmark	General location	Description of the position on cranidium
1	axis	posterior margin of the occipital ring
2	axis	deepest point of SO
3	axis	deepest point of S1
4	axis	deepest point of S2
5	axis	anterior margin of the glabella
6	axis	anterior margin of the cranidium
7, 13	left and right side	juncture of SO and axial furrow
8, 14	left and right side	juncture of S1 and axial furrow
8, 15	left and right side	juncture of S2 and axial furrow
10, 16	left and right side	posterior tip of the palpebral lobe
11, 17	left and right side	anterior tip of the palpebral lobe
12, 18	left and right side	juncture of anterior border furrow and facial suture
19–24, 25–30	left and right side	anterior margin of the cranidium
31–34, 39–42	left and right side	external margin of the palpebral lobe
35–38, 43–46	left and right side	internal margin of the palpebral lobe
47–53, 54–60	left and right side	margin of the anterior part of the glabella

Table 4. Location of landmarks and semilandmarks on the cranidia studied. Analysis with anterior margin furrow excluded.

pressed in the juvenile forms (see lower part of plots in Text-fig. 5), thus morphometrics is not able to properly recapture these differences. Nevertheless, those juvenile specimens can be assigned to one of those groups using other characters, including the shape of the glabella (more pyriform in the *P. polonicus* group; see Systematic Part below).

A similar pattern can be observed in the analysis without the anterior margin furrow included (less detailed analysis using a larger number of specimens). In this group, 27 cranidia of *P. polonicus* have been included, together with 12 of *P. slowiecensis* and 6 of



Text-fig. 6. Scatter plots for more detailed analysis with less specimens showing: A – relationship of PC2 and PC3; and B – visualization of PCA (with PC1 excluded) using NMDS.

Component	Eigenvalue	Proportion of variance	Cumulative proportion of variance
PC1	0.00144	37.4%	37.4%
PC2	0.00097	25.2%	62.5%
PC3	0.00051	13.3%	75.9%
PC4	0.00029	7.5%	83.4%
PC5	0.00015	3.8%	87.2%
PC6	0.00009	2.3%	89.4%
PC7	0.00008	2.1%	91.5%
PC8	0.00006	1.5%	93.0%
PC9	0.00005	1.3%	94.4%
PC10	0.00004	0.9%	95.3%

Table 5. Eigenvalues and proportion of variance for the first ten PCs obtained for the specimens studied. Analysis with anterior margin furrow excluded.

P. socius (overall 45 cranidia). The applied landmarks and semilandmarks are listed in Table 4 and shown in Text-fig. 3. Again, PC1 (37.4% of total variance, see Table 5) is highly correlated with the length (sag.) to width (tr.) proportions ($r = 0.81$, p-value < 0.0001; see Text-fig. 4B). As previously, two major groups can be observed. The first one contains only cranidia of *P. polonicus* and the second one cranidia of both *P. slowiecensis* and *P. socius* (Text-fig. 6A – scatterplot of PC2 *vs* PC3; Text-fig. 6B – data visualised using NMDS). In addition, small specimens from both groups are not well distinguishable.

In both cases, excluding the PC containing the variance related to deformation resulted in removing the differences between the cranidia previously assigned to *P. slowiecensis* and *P. socius*. The differences between these two species were restricted only to the length (sag.) to width (tr.) proportions, and those differences are connected not with true morphological variation, but rather with post-mortem tectonic deformation. The lack of other characters that can be described by morphometrics or by classical palaeontological comparison clearly shows that the cranidia previously assigned to *P. slowiecensis* and *P. socius* in fact belong to a single species.

SYSTEMATIC PART

Class Trilobita Walch, 1771
Order Redlichiida Richter, 1932
Family Paradoxididae Hawle and Corda, 1847
Genus *Acadoparadoxides* Šnajdr, 1957

TYPE SPECIES: *Paradoxides sacheri* Barrande, 1852, from the Cambrian of Bohemia; by subsequent designation of Šnajdr (1957, p. 238).

DIAGNOSIS: For characters defining *Acadoparadoxides*, see Geyer and Vincent (2015).

REMARKS: For discussion about the internal systematics of *Acadoparadoxides* see Nowicki and Żylińska (2019).

Acadoparadoxides slowiecensis (Czarnocki in Orłowski, 1965)

(Text-figs 7 and 8)

1927a. *Paradoxides slowiecensis* sp. n.; Czarnocki, p. 741.
1927b. *Paradoxides slowiecensis*; Czarnocki, p. 196.
1933. *Paradoxides slowiecensis*; Czarnocki, p. 81.
part 1957. *Paradoxides* forms of the *ölandicus* group; Orłowski, figs 1–3 (non figs 4, 6 = *Acadoparadoxides kozlowskii*; non fig. 5 = *Acadoparadoxides samsonowiczi*).
1965. *Paradoxides slowiecensis* (Czarnocki); Orłowski, pp. 5, 139, 140; pl. 5, figs 1–6.
1965. *Paradoxides* from the *oelandicus* group; Orłowski, pp. 137, 138; pl. 2, figs 10, 11; pl. 3, figs 1, 2.
?1965. *Paradoxides* sp. A; Orłowski, p. 140; pl. 4, figs 7, 8.
1965. *Paradoxides* sp. B; Orłowski, pp. 140, 141; pl. 4, figs 9–12.
1965. *Paradoxides* sp. D; Orłowski, p. 141; pl. 5, figs 7–11.
1985. *Paradoxides slowiecensis* Orłowski, 1965; Orłowski, pp. 258, 259; text-fig. 5c; pl. 5, figs 6–10.
1985. *Paradoxides socius* sp. n.; Orłowski, pp. 258, 259; text-fig. 5b; pl. 6, figs 1–6.
1990. *Paradoxides slowiecensis* Orłowski, 1965; Bednarczyk *et al*., p. 60; pl. 18, fig. 1.

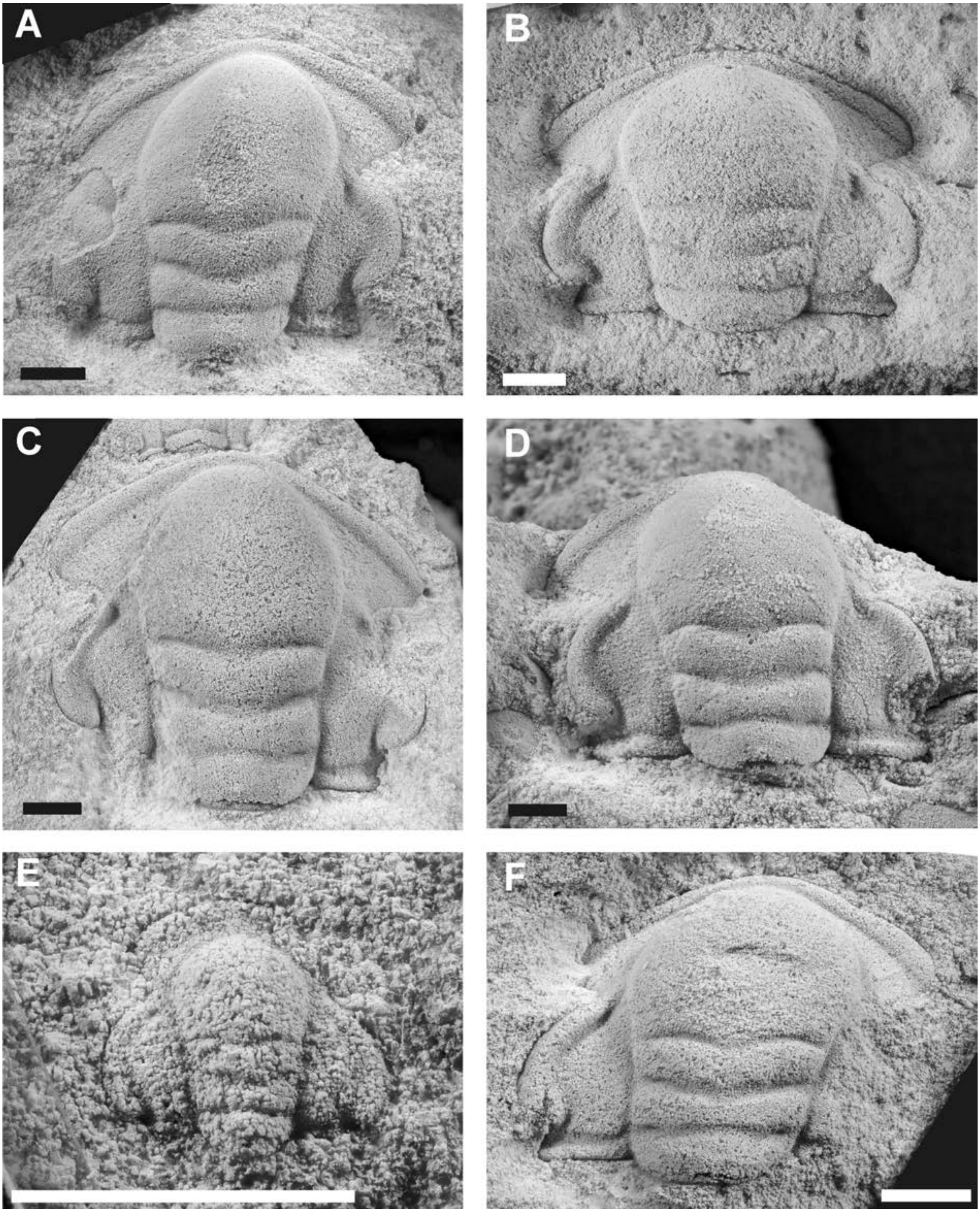
TYPES: As lectotype is selected cranidium MWGUW ZI/29/1847, invalidly designated as neotype by Orłowski (1965, p. 139). This specimen is illustrated in: Orłowski (1965, pl. 5, fig. 1, as UW 250), Orłowski (1985, pl. 5, fig. 10, as 2.250), Bednarczyk *et al.* (1990, pl. 18, fig. 1, as IGP UW 250), and Text-fig. 7A herein.

OTHER MATERIAL: 56 cranidia: MWGUW ZI/29/1827–1846, 1848–1882, 1972; 15 pygidia: MWGUW ZI/29/1898–1902, 1904, 1905, 1908, 1910, 1912–1914, 1917–1919.

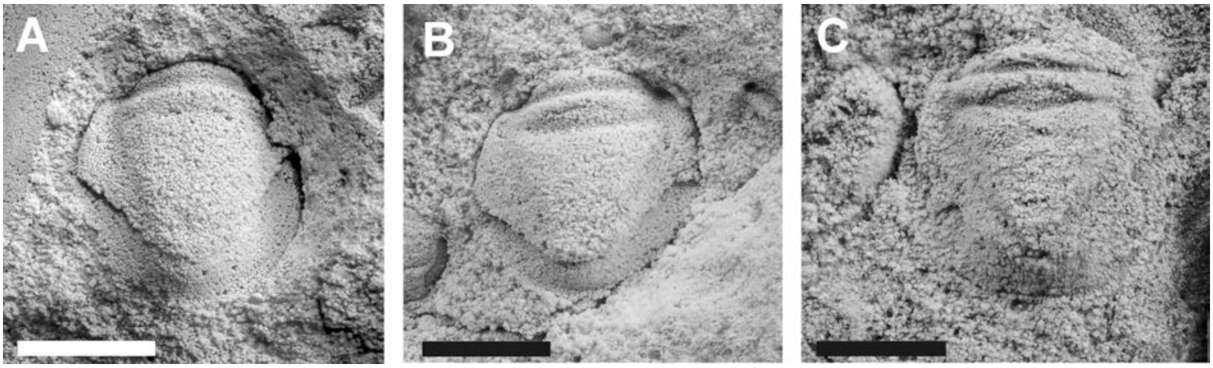
DESCRIPTION: Cranidium wider (tr.) than long (sag.), 96 to 142% of total cranidial length; exact proportions cannot be provided since the material is deformed. Glabella pyriform, broadening (tr.) more or less evenly from the occipital ring to the frontal lobe, sometimes frontal lobe becomes slightly bulb-shaped. S0, S1, S2 distinct, joining in the middle part of glabella. S0 on its sides directed posteriorly, in the middle part slightly arched anteriorly. S1 directed posteriorly. S2 bent on the sides, with arcs directed anteriorly. S3 and S4 present, but short and indistinct. Occipital ring quite long (sag.), with small node at two-thirds of its length (sag.). L1 wider (tr.) than occipital ring; L2 wider (tr.) than L1. Both L1 and L2 equal or slightly shorter (sag.) than occipital ring. Frontal lobe large, half of the glabellar length (sag.), oval. Glabella surrounded by marginal furrow, distinct in the posterior part, vanishing anteriorly. Posterior margin straight, posterior border narrow (exsag.). Posterior width (tr.) of the cranidium equal or slightly larger than width (tr.) in the middle part of the palpebral lobes. Palpebral lobes large (exsagittal length 31 to 49% of total cranidial length; exact proportions cannot be provided since the material is deformed); relative size becoming smaller during ontogeny; extending from the posterior border furrow to the frontal lobe of the glabella, which is met between S3 and S4. Palpebral lobes arched, with a narrower curvature in the anterior part. Width (tr.) largest in the posterior parts, slightly narrowing anteriorly. Furrows between palpebral lobes and fixigenae shallow in the middle and deeper in the posterior and anterior parts. Fixigenae narrower (tr.) than glabellar width across occipital ring. Posterior branch of the facial suture short. Anterior part of the cranidium wide (tr.), similar to the cranidial width (tr.) across the centres of the palpebral lobes. Anterior border in front of the glabella narrow (sag.), broadening (exsag.) towards the suture. Preglabellar field narrow (sag.), broader in juvenile specimens. Anterior part of the facial suture slightly bent. Preocular field small.

Pygidium small, oval, with similar length (sag.) and width (tr.). Axial part with single axial ring surrounded with furrows. Single, indistinct pair of pleural furrows. Rhachis triangular in outline, quite long (sag.), almost reaching to posterior margin. Platform poorly preserved in the studied specimens, slightly extending outside rhachis. Axial furrow moderately well developed. Posterior and lateral margins of the pygidium curved.

REMARKS: Following the morphometric analysis of cranidia with application of landmarks and semilandmarks, *Paradoxides slowiecensis* and *Paradoxides socius*, the two previously described species (Orłowski 1965, 1985) form a uniform group. Following priority rules, they are assigned to a single species named *Acadoparadoxides slowiecensis*. The authorship expressed as ‘Czarnocki in Orłowski, 1965’ follows Recommendation 51E of the ICZN.



Text-fig. 7. Cranidia of *Acadoparadoxides slowiecensis* (Czarnocki in Orłowski, 1965) from the Słowiec Sandstone Formation of Słowiec Hill, Holy Cross Mountains, Poland. A – MWGUW ZI/29/1847, lectotype, original of Orłowski (1957, fig. 1; 1965, pl. 5, fig. 1; 1985, pl. 5, fig. 10) and Bednarczyk *et al.* (1990, pl. 18, fig. 1); B – MWGUW ZI/29/1862, holotype of *Paradoxides socius* Orłowski, 1985; original of Orłowski (1985, pl. 6, fig. 5a–b); C – MWGUW ZI/29/1827; D – MWGUW ZI/29/1849, original of Orłowski (1985, pl. 5, fig. 9); E – MWGUW ZI/29/1832; F – MWGUW ZI/29/1851. Scale bars equal 5 mm.



Text-fig. 8. Pygidia of *Acadoparadoxides slowiecensis* (Czarnocki in Orłowski, 1965) from the Słowiec Sandstone Formation of Słowiec Hill, Holy Cross Mountains, Poland. A – MWGUW ZI/29/1898; B – MWGUW ZI/29/1904; C – MWGUW ZI/29/1900. Scale bars equal 5 mm.

The species can be assigned to *Acadoparadoxides* due to the following features: presence of large, arched palpebral lobes, the width (tr.) of the cranidium being similar in the anterior part and in the middle of the palpebral lobes, the presence of a preglabellar field, and the presence of indistinct S3 and S4 and a quite broad (exsag.) anterior border. The pygidia described by Orłowski (1965) as *Paradoxides* spp. B and D also form a single group. They are also assigned to *Acadoparadoxides* due to their oval shape, their rhachis reaching almost to the posterior margin, and the presence of a platform. In the analysed material from Słowiec Hill, only one morphotype of cranidium and only one morphotype of pygidium can be assigned to *Acadoparadoxides*, and this allows combining the two elements in a single species, i.e., *A. slowiecensis*.

The cranidia of *A. slowiecensis* differ from the acadoparadoxidines and acadoparadoxidine-related taxa from Scandinavia, i.e., *Acadoparadoxides oelandicus* (Sjögren, 1872), *Acadoparadoxides pinus* (Westergård, 1936) and *Acadoparadoxides torelli* (Westergård in Asklund and Thorslund, 1935) in a wider (tr.) anterior of cranidium in *A. slowiecensis* (in the Scandinavian taxa this parameter is smaller than the transverse width in the middle of the palpebral lobes). Also, the palpebral lobes are slightly thinner (tr.) in *A. slowiecensis*. The width (tr.) of the anterior part of the cranidium also allows for distinguishing this taxon from the species known from the Czech Republic, i.e., *Acadoparadoxides sacheri* (Barrande, 1852) and *Acadoparadoxides sirokyi* (Šnajdr, 1986), but the most important differentiating character is the width (tr.) and length (exsag.) of the palpebral lobes, which is much larger in the taxa from the Czech Republic.

Acadoparadoxides slowiecensis resembles acadoparadoxidine taxa known from Gondwana and Avalonia. In general, the configuration of the elements on the cranidia is similar to taxa described from Morocco, i.e., *Acadoparadoxides pampalius* Geyer and Vincent, 2015, *Acadoparadoxides levisettii* Geyer and Vincent, 2015, *Acadoparadoxides nobilis* (Geyer, 1998), *Acadoparadoxides* cf. *mureroensis* (Sdzuy, 1958), *Acadoparadoxides ovatopyge* Geyer and Vincent, 2015, and south-eastern Newfoundland, i.e., *Acadoparadoxides harlani* (Green, 1834). The main difference between *A. slowiecensis* and the Moroccan species is the broader (exsag.) anterior border in the latter ones (although this character is overemphasized by compaction in the Moroccan specimens, which are preserved in shales). Specimens of *A. slowiecensis* are very similar to the specimens of *A. harlani* illustrated by Geyer and Landing (2001) of the same size class, but the shape of the posterior part of the palpebral lobes, which is more curved in Polish species, is a good character differentiating those taxa.

Pygidia assigned to *A. slowiecensis* are completely different from the ones known in Scandinavian forms. Also, in taxa from the Czech Republic (although quite similar in their oval outline) the pygidia have a much larger pleural field than the pygidia of *A. slowiecensis*. Pygidia of *A. harlani* also have a similar outline, but their rhachis is narrower (tr.) than in *A. slowiecensis*. Pygidia of *A. levisettii* and *A. nobilis* from Morocco can be distinguished by their pyriform outline. Pygidia of other Moroccan taxa (*A. pampalius, A.* cf. *mureroesis* and *A. ovatopyge*) have a similar outline, but the field between the rhachis and the posterior margin is better developed in those species than in *A. slowiecensis*. A species most similar to *A.*

slowiecensis is *Acadoparadoxides*? sp. B in Geyer and Vincent (2015), but in *A. slowiecensis* the rhachis seems to be slightly wider (tr.).

The cranidia of *A. slowiecensis* differ from those of *Hydrocephalus*? *polonicus* (the second paradoxidid species from Słowiec Hill; see below) in the following characters: in *H.*? *polonicus* the preglabellar field and anterior border in front of the glabella are absent (in adult specimens) and present in *A. slowiecensis*; the glabella of *A. slowiecensis* widens (tr.) more or less evenly towards the anterior, whereas in *H.*? *polonicus* the margins are subparallel; the palpebral lobes of *A. slowiecensis* are slightly narrower (tr.) and become even narrower (tr.) in the anterior part, whereas in *H.*? *polonicus* the palpebral lobes have a constant width (tr.); the width (tr.) of the anterior part of the cranidium compared to the width (tr.) across the centres of the palpebral lobes is larger in *A. slowiecensis*. The pygidium of *A. slowiecensis* has a suboval outline, whereas the pygidium of *H.*? *polonicus* is roughly subrectangular; it is wider (tr.) than long (sag.) in *H.*? *polonicus* and of a more subquadrangular shape in *A. slowiecensis*. The posterior margin is curved in *A. polonicus* and nearly straight in *H.*? *polonicus*. The rhachis is much more distinct in *A. slowiecensis* than in *H.*? *polonicus*.

Cranidia of *A. slowiecensis* can be distinguished from *Acadoparadoxides samsonowiczi* (Orłowski, 1959a) and *A. kozlowskii* (Orłowski, 1959a), species occurring in strata representing the Cambrian Series 2–Miaolingian boundary interval in the Holy Cross Mountains (Nowicki and Żylińska 2019), by the following features: a narrower (exsag.) anterior border in *A. slowiecensis*; palpebral lobes in *A. kozlowskii* and *A. samsonowiczi* being more curved and narrower in the anterior part; a more strongly reduced preglabellar field in *A. slowiecensis*; pygidia of *A. samsonowiczi* and *A. kozlowskii* having much more distinct platforms, clearly defined from the pleural field; and pygidium of *A. kozlowskii* having a different, pyriform outline.

OCCURRENCE: Miaolingian (*Acadoparadoxides slowiecensis–Hydrocephalus*? *polonicus* Assemblage Zone) in the Słowiec Sandstone Formation from Słowiec Hill, central part of the Holy Cross Mountains, Poland.

Genus *Hydrocephalus* (Barrande, 1846)

TYPE SPECIES: *Hydrocephalus carens* (Barrande, 1846) from the Cambrian of Bohemia, OD.

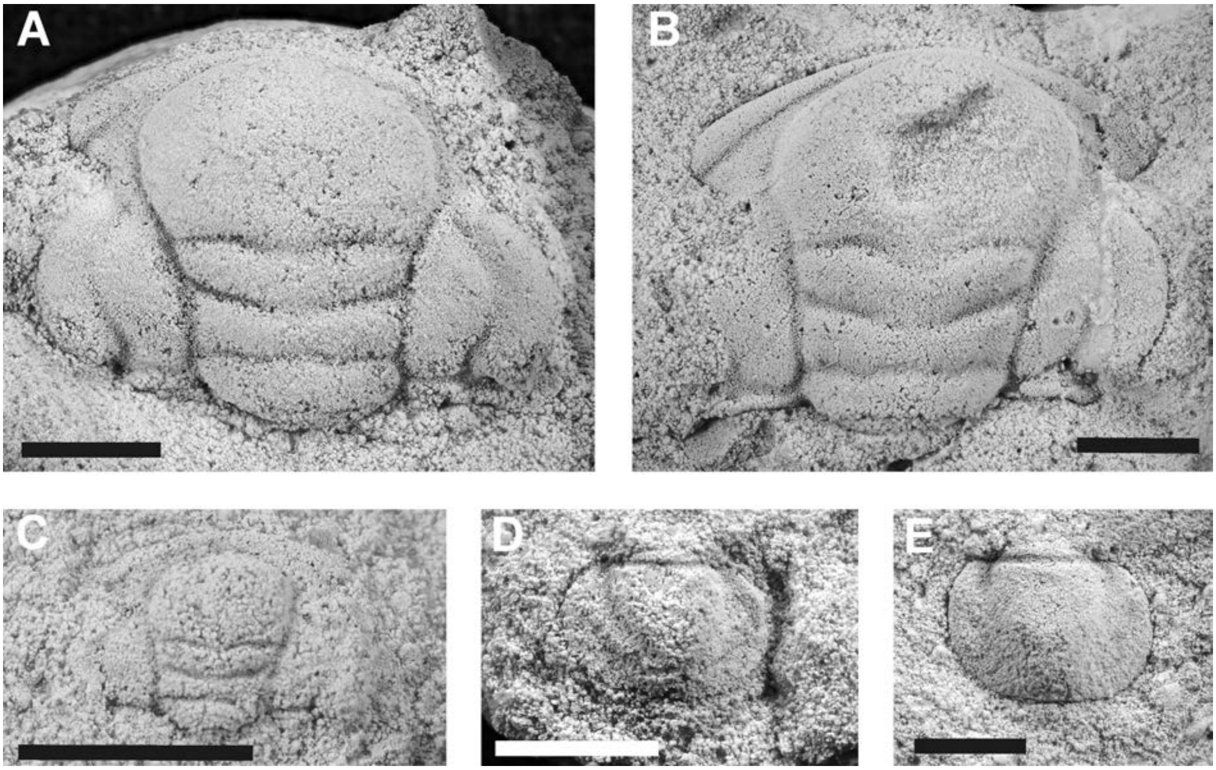
DIAGNOSIS: We follow the diagnosis provided by Dean and Rushton (1997) and emended by Rushton and Weidner (2007) and Rushton *et al.* (2016).

REMARKS: *Hydrocephalus* is one of the genera created in the 19th century (Barrande 1846) and included in the systematics of the Paradoxididae proposed by Šnajdr (1957, 1958). Currently, it is possible to distinguish three groups of species assigned to this genus: (1) the taxa from Bohemia (including the type species *Hydrocephalus carens*, *Hydrocephalus minor* Boeck, 1827, *Hydrocephalus mandiki* Kordule, 1990, and representatives of the genus *Rejkocephalus* Kordule, 1990, whose taxonomy remains problematic); (2) various species assigned to *Hydrocephalus* in the 20th century, e.g., *Hydrocephalus hicksii* (Salter, 1865) (presently *Mawddachites hicksii*; see Fletcher 2007) from different locations around the world, and *Hydrocephalus donayrei* Liñán and Gozalo, 1986 from Spain; and (3) two species from Scandinavia, i.e., *Hydrocephalus vikensis* Rushton and Weidner, 2007, and *Hydrocephalus spinulosus* Rushton, Weidner and Ebbestad, 2016. The second group contains several species that require revision and its members should not be used for characterising the genus *Hydrocephalus*. In turn, the species of the third group which were assigned to the genus require significant emendation of the diagnosis of *Hydrocephalus*. Differences between the taxa from the type locality and from Scandinavia include longer and thicker palpebral lobes, and shorter posterior branches of the facial sutures in the latter ones (Rushton and Weidner 2007). The presence of these differences questions the internal homogeneousness of the hydrocephalines. The Scandinavian taxa may represent a different, unrelated clade, possibly ancestors of *Paradoxides sensu stricto* (see Rushton 2006). Establishing a new genus for the Scandinavian hydrocephalines should be considered, but this would require additional research and is beyond the scope of this paper. This potential new genus would include *H. vikensis*, *H. spinulosus* and *Hydrocephalus*? *polonicus* (described below). Also, the phylogenetic position of *Acadoparadoxides torelli* and *Eccaparadoxides*? *thorslundi* Rushton, Weidner and Ebbestad, 2016 should be taken into consideration, since those species may be closely related to this group.

Hydrocephalus? *polonicus*
(Czarnocki in Orłowski, 1965)

(Text-fig. 9)

1927a. *Paradoxides polonicus* sp. n.; Czarnocki, p. 741.
1927b. *Paradoxides polonicus*; Czarnocki, p. 196



Text-fig. 9. Cranidia (A–C) and pygidia (D, E) of *Hydrocephalus*? *polonicus* (Czarnocki in Orłowski, 1965) from the Słowiec Sandstone Formation of Słowiec Hill, Holy Cross Mountains, Poland. A – MWGUW ZI/29/1895, lectotype, original of Orłowski (1965, pl. 3, fig. 3; 1985, pl. 5, fig. 2) and Bednarczyk *et al.* (1990, pl. 17, fig. 10); B – MWGUW ZI/29/1896, original of Orłowski (1985, pl. 5, fig. 4); C – MWGUW ZI/29/2188; D – MWGUW ZI/29/1903; E – MWGUW ZI/29/1911, original of Orłowski (1965, pl. 6, fig. 1 and pl. 7, fig. 2a, b, as *Paradoxides* sp. C). Scale bars equal 5 mm.

1933. *Paradoxides polonicus*; Czarnocki, p. 81.
1957. *Paradoxides polonicus* Czarn.; Orłowski, p. 770.
1965. *Paradoxides polonicus* (Czarnocki); Orłowski, pp. 5, 138, 139; pl. 3, figs 3–8, pl. 4, figs 1–6.
1965. *Paradoxides* sp. C; Orłowski, p. 141; pl. 6, figs 1, 2.
1985. *Paradoxides polonicus* Orłowski, 1965; Orłowski, pp. 258, 259; fig. 5a, pl. 5, figs 1–5.
1990. *Paradoxides polonicus* Orłowski, 1965; Bednarczyk *et al*., p. 59; pl. 17, fig. 11.
non 1990. *Paradoxides* cf. *polonicus* Orłowski, 1965; Samson *et al*., pp. 1467, 1468; fig. 6I–U (= *Paradoxides* sp.).

NEOTYPE: Cranidium MWGUW ZI/29/1895, designated by Orłowski (1965, p. 138); illustrated in: Orłowski (1965, pl. 3, fig. 3, as UW 222), Orłowski (1985, pl. 5, fig. 2, as 2.222), Bednarczyk *et al.* (1990, pl. 17, fig. 10, as IGP UW 222), and Text-fig. 9A herein.

OTHER MATERIAL: 48 cranidia: MWGUW ZI/29/1891–1894, 1896, 1897, 2156–2158, 2160–2198; 7 pygidia: MWGUW ZI/29/1903, 1906, 1907, 1909, 1911, 1915, 1916.

DESCRIPTION: Cranidium wider (tr.) than long (sag.), 99 to 168% of total cranidial length, exact proportions cannot be provided, since the material is deformed. Glabella pyriform, with subparallel sides from occipital ring to S2 and strongly widening (tr.) forward, large, domed frontal lobe and the lobe posterior to it, reaching the anterior margin. L0, L1 and L2 of similar width (tr.) and length (sag.), L2 can be slightly wider (tr.). Small node located in the centre of the occipital ring. S0, S1 and S2 distinct, deep, shallower in the middle part. S0 straight, with small bending in the middle part, directed anteriorly from the lateral margins. S1 straight, directed backwards, connected in the middle of glabella. S2 arched anteriorly, connected in the middle of glabella. S3 and S4 only sometimes developed, indistinct, short. Glabella surrounded by furrow, which is distinct in the posterior part and disappearing anteriorly. Palpebral lobes long (exsagittal length 39 to 66% of total cranidial length, exact proportions cannot be provided, since the material is deformed), wide (tr.), arched, extending from posterior border furrow to the frontal lobe of glabella (almost reaching it near S3 and S4). Width of palpebral lobes constant almost throughout except for slightly narrower anteriormost part. Palpebral furrows poorly marked. Fixigenae narrower than glabella across occipital ring. Posterior border narrow (exsag.). Cranidial width (tr.) across posterior border and occipital ring similar to the width (tr.) across centres of palpebral lobes; width (tr.) across anterior ends of facial suture smaller. Preocular field small. Preglabellar field developed only in juvenile individuals. Anterior border narrow (exsag.), completely fading in front of glabella, slightly wider (exsag.) on the sides. Both anterior and posterior branches of facial suture short.

Pygidium small, subrectangular in outline, wider (tr.) than long (sag.). Axial part suboval, single axial ring poorly marked, defined by weak furrow. Single, poorly marked pair of pleural furrows. Rhachis long (sag.), almost reaching to posterior margin. Axial furrow only developed in the anterior part; platform indistinguishable from rhachis in the posterior part. Posterior margin almost straight to weakly curved, lateral margins weakly curved in the middle part, with advanced curvature anteriorly and posteriorly.

REMARKS: Similarly as in *A. slowiecensis* (described above), uniting cranidia and pygidia into a single species was appropriate because of the presence of a single type of cranidium and a single type of pygidium that could be assigned to *Hydrocephalus sensu lato* in the assemblage from Słowiec Hill. Assignment to this genus is suggested due to the presence of a pyriform glabella, absence of a preglabellar field in mature specimens, and a wide (tr.) pygidium with a straight posterior margin. In fact, the specimens from the Holy Cross Mountains do not readily fit the diagnosis provided by Dean and Rushton (1997). The concept of *Hydrocephalus* was later extended by Rushton and Weidner (2007) and Rushton *et al.* (2016) to include two species from Scandinavia to this genus. Here, we follow this approach, although it has to be emphasised that the present generic concept obviously requires a review. *Hydrocephalus*? *polonicus* may in fact be a member of the 'Scandinavian' group, not related to the hydrocephalines from Bohemia, and representing a separate new taxon (see above).

Hydrocephalus? *polonicus* differs from *H. vikensis* and *H. spinulosus* in having a more strongly reduced preglabellar field, palpebral lobes with a stronger curvature posteriorly and of equal width (tr.) along the entire length. In addition, the posterior branch of the facial suture is shorter and the posterior part of the glabella is slightly wider (tr.) in *H.*? *polonicus.* Pygidia of the three species are very similar, although *H.*? *polonicus* has a slightly larger axial part. The outline of the pygidium in the Scandinavian species is subhexagonal.

Compared to the Bohemian taxa *Hydrocephalus carens* and *H. minor*, *H.*? *polonicus* has a reduced preglabellar field, longer (exsag.), wider (tr.) and more strongly curved palpebral lobes and much shorter posterior branches of the facial sutures. Its pygidium has a larger axial part in comparison to the pleural part and slightly differs in the shape of the outline.

For comparison with *Acadoparadoxides slowiecensis*, the other paradoxidid from Słowiec Hill, see under that species.

OCCURRENCE: Miaolingian (*Acadoparadoxides slowiecensis–Hydrocephalus*? *polonicus* Assemblage Zone) in the Słowiec Sandstone Formation from Słowiec Hill, central part of the Holy Cross Mountains, Poland.

AGE OF THE SŁOWIEC HILL FAUNAL ASSEMBLAGE

The age of the rocks exposed on Słowiec Hill is poorly constrained due to a number of factors. They include lack of section; the occurrence of only isolated and mostly fragmented sclerites of trilobite exoskeletons; the trilobite species being mostly of endemic aspect at species level; the occurrence of only few specimens of brachiopod taxa with low stratigraphic significance (Orłowski 1965; Jendryka-Fuglewicz 1992); and lack of auxiliary acritarch data (Żylińska and Szczepanik 2009). Although the samples in the repository occasionally contain several individuals on one rock slab, the majority of samples preserve only remains of a single taxon; only in two cases a single rock slab yields two taxa (MWGUW ZI/29/1947 – *Hydrocephalus*? *polonicus* and *Parasolenopleura linnarssoni*; MWGUW ZI/29/1972 – *Acadoparadoxides slowiecensis* and *Solenopleura minima* Orłowski, 1985).

The trilobite taxa recognised from the rocks on Słowiec Hill include representatives of the families Paradoxididae (Orłowski 1965, 1985 and this study), Ellipsocephalidae Matthew, 1887 (Orłowski 1965; Żylińska and Szczepanik 2009), Solenopleuridae Angelin, 1854[3] (Orłowski 1965, 1985), and Dorypygidae Kobayashi, 1935 (Orłowski 1985). The ellipsocephalids from Słowiec Hill include 11 taxa, i.e., *Ellipsocephalus hoffi* (Schlotheim, 1823), *Geyerorodes usarzowi* (Orłowski, 1985), *Kingaspidoides jugoszowi* (Orłowski, 1959b), *K. sanctacrucensis* (Czarnocki, 1927a), *K. sandomiri* (Orłowski, 1959b), *Kingaspis guerichi* (Orłowski, 1959b), *Latikingaspis samsonowiczi* (Orłowski, 1964), *Latoucheia* (*Latoucheia*) *longa* (Orłowski, 1959b), *Ornamentaspis henningsmoeni* (Orłowski, 1964), *O. hupei* (Orłowski, 1964), *O. opatowi* (Orłowski, 1985), and *O. puschi* (Orłowski, 1959b) (Orłowski 1965; Żylińska and Szczepanik 2009; taxonomic names modified in part after Özdikmen 2009). All these taxa occur abundantly in the Jugoszów−Usarzów section in the *Acadoparadoxides samsonowiczi–Acadoparadoxides kozlowskii* Assemblage Zone, representing the Cambrian Series 2–Miaolingian boundary interval, i.e., corresponding to the Moroccan Cambrian Stage 4 *Morocconus notabilis* Zone and a barren interval in Scandinavia (see Żylińska and Szczepanik 2009; Nowicki and Żylińska 2019). Some of the recognised ellipsocephalids have been shown to occur in the lowermost part of the Słowiec Formation (in Brzechów and on Konarska Hill; Żylińska and Masiak 2007; Żylińska and Szczepanik 2009) as well, corresponding to the *Morocconus notabilis* Zone of Moroccan Atlas ranges, which probably spans the Cambrian Stage 4–Wuliuan boundary (Geyer 2019). Therefore it is assumed that the ellipsocephalids had quite long ranges in the interval encompassing Cambrian Stage 4 and the Wuliuan, although redeposition of at least some of the trilobite remains cannot not be excluded. The solenopleurids *Parasolenopleura linnarssoni*, *Solenopleura munsteri* and *Solenopleura trapezoides* Orłowski, 1985, the alleged ptychopariid ‘*Solenopleura*’ *minima*, and the dorypygid *Kootenia enigmatica* Orłowski, 1985[4] (Orłowski 1965, 1985) are the only groups of trilobites from the Cambrian of the Holy Cross Mountains awaiting a modern and much-needed revision. Such revision requires more abundant and better preserved material, which due to the deterioration of most exposures will probably never be accessible. In any case, the solenopleurids, if actually representing the mentioned species, suggest a correlation into the lower part of the *Paradoxides paradoxissimus* Superzone in Scandinavia (e.g., Axheimer and Ahlberg 2003), i.e., the upper Wuliuan (Geyer 2019; Nielsen and Ahlberg 2019). *Kootenia enigmatica* is known from only three poorly preserved pygidia and shows some similarity to *Kootenia westergaardi* Thorslund, 1949 from the *Acadoparadoxides*? *pinus–Pentagnostus praecurrens* Zone of the *Acadoparadoxides oelandicus* Superzone in Jämtland, Sweden (Thorslund 1949), and to *Kootenia* n. sp. from the Kalby Member at Læså (Berg-Madsen 1981; presently considered as a weathered equivalent of the Exsulans Limestone from the *Paradoxides paradoxissimus* Superzone – see Nielsen and Schovsbo 2006; Nielsen and Ahlberg 2019). Its presence on Słowiec Hill suggests an age corresponding to the middle and/or upper Wuliuan.

The remaining fauna includes rare brachiopods: Orłowski (1965) described and illustrated *Lingulella vistulae* (Gürich, 1892) and *Acrothele* sp., whereas Jendryka-Fuglewicz (1992) mentioned *Acrothele granulata* Linnarsson, 1876, *Acrotreta*? sp., *Lingulella vistulae* and *Mickwitzia* sp. The taxa all have wide stratigraphic ranges and cannot be used to refine the stratigraphic position of the rocks exposed on Słowiec Hill. *Acrothele granulata* is known from the lower Miaolingian *Acadoparadoxides oelandicus* Superzone and younger beds in Scandinavia (e.g., Henningsmoen 1952), whereas the endemic *Lingulella vistulae* has been recognised in the Cambrian Stage 4–Wuliuan boundary interval in the Jugoszów-Usarzów section and in the upper Wuliuan of the Pieprzowe Mts. (Gürich 1892; Orłowski 1964; Jendryka-Fuglewicz 1992).

Therefore, the biostratigraphy of this part of the Cambrian succession in the Holy Cross Mountains is best defined by paradoxidids. However, usage of a taxon-range zone, i.e., the *Paradoxides polonicus* Zone of Orłowski (1975, 1988, 1992a; even with the eponymous taxon’s name modified according to the new analysis), basing the biostratigraphic description on a single paradoxidid species seems to be oversimplified. Because the stratigraphic relations between the two paradoxidid species described herein remain unknown, the *Acadoparadoxides slowiecensis–Hydrocephalus*? *polonicus* Assemblage Zone is proposed herein, defined by the combined, but in fact unknown ranges of the two taxa.

The *Paradoxides polonicus* Zone was previously thought to be an equivalent of the upper Wuliuan to middle Drumian *Paradoxides paradoxissimus*

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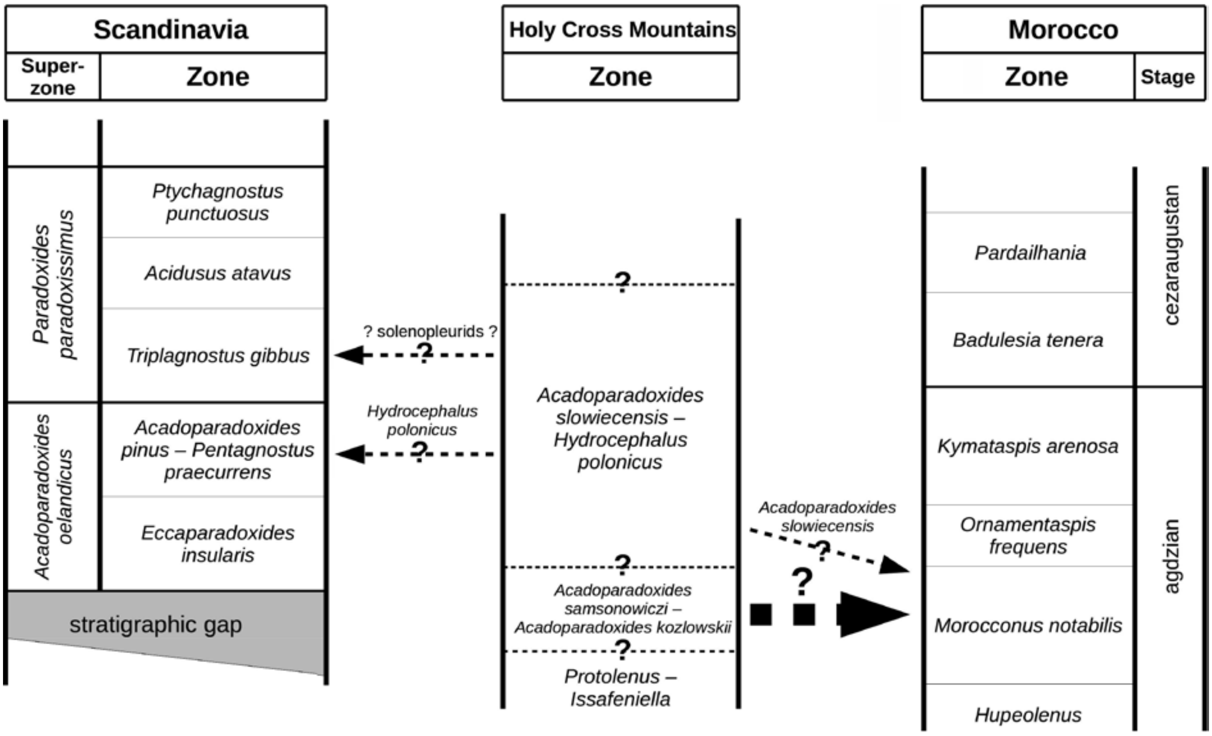
[3] *Solenopleura minima*, another species mentioned by Orłowski (1985) as belonging to the Solenopleuridae, most likely represents a ptychoparioid, but a larger collection and detailed research are required to confirm this assumption.

[4] Czarnocki (1927a, p. 196) referred a single, spinose pygidium from Słowiec Hill to *Paradoxides lamberti* sp. n. The only spiny pygidium from this locality belongs to *Kootenia enigmatica*, and it is quite possible (but presently cannot be confirmed) that *Paradoxides lamberti nomen nudum* refers to that taxon.



Text-fig. 10. Correlation of the position of the Słowiec Hill fauna with stratigraphic schemes for Scandinavia and Morocco (after Sundberg *et al.* 2016).

Superzone of Scandinavia (Orłowski 1992a), based on the assumed close evolutionary relationship of *P. polonicus* with *Paradoxides paradoxissimus* Wahlenberg, 1818. According to the present study, *H.*? *polonicus* is completely unrelated to *P. paradoxissimus*, but resembles rather the Scandinavian hydrocephalines, i.e., *Hydrocephalus vikensis* and *H. spinulosus* (Rushton and Weidner 2007; Rushton *et al.* 2016), the precise links of which with the Bohemian hydrocephalines still require a detailed study (see above). The Scandinavian taxa come from the middle Wuliuan *Acadoparadoxides*? *pinus–Pentagnostus praecurrens* Zone of the *Acadoparadoxides oelandicus* Superzone (Rushton and Weidner 2007; Rushton *et al.* 2017; Geyer 2019; Nielsen and Ahlberg 2019). Thus, the hydrocephaline from Słowiec Hill may suggest correlation with this stratigraphic interval (Text-fig. 10).

In turn, the second paradoxidid from Słowiec Hill, *Acadoparadoxides slowiecensis*, shows clear links with the early group of acadoparadoxidines *sensu* Nowicki and Żylińska (2019), characterised by species with a wider (tr.) anterior part of the cranidium, shorter and thinner (tr.) palpebral lobes, and rounded, suboval or pyriform pygidia. It is most similar to *Acadoparadoxides harlani* and *Acadoparadoxides*? sp. B of Geyer and Vincent (2015). Rough correlation based on these relationships indicates a stratigraphic level coeval with the lower *Acadoparadoxides harlani* Zone of western Avalonia and the uppermost *Morocconus notabilis* Zone of Morocco, i.e., a stratigraphic interval that occurs just above the Cambrian Stage 4–Wuliuan boundary (Sundberg *et al.* 2016; Geyer 2019; Text-fig. 10). In general, acadoparadoxidines range up to the top of the *Acadoparadoxides*? *pinus–Pentagnostus praecurrens* Zone in Scandinavia and to the top of the *Kymataspis arenosa* Zone in Morocco, thus they do not appear in the upper Wuliuan.

Following this analysis, most elements of the faunal assemblage on Słowiec Hill are of middle and/or upper Wuliuan aspect. In the Kielce Region, the Słowiec Sandstone Formation represents the final stage of basin infill. It thus evidently postdates the Usarzów Sandstone Formation exposed in the Jugoszów-Usarzów succession (Nowicki and Żylińska 2019). At present, a wide stratigraphic interval encompassing both the middle and upper Wuliuan is suggested for the *Acadoparadoxides slowiecensis–Hydrocephalus*? *polonicus* Assemblage Zone. This implies that *Acadoparadoxides slowiecensis* might be a relic of the early acadoparadoxidines which thrived in the middle Wuliuan. If so, then at least part of the Słowiec Hill strata were formed during the same stratigraphic interval as part of the Łysogóry Region Pieprzowe Mts. Formation with trilobites. On the other hand, the fauna from Słowiec Hill has not been found in a measurable section. Because it is impossible to prove that both paradoxidid species co-occurred, it cannot be excluded that they represent different stratigraphic intervals, even with a stratigraphic gap between them. The available data do not allow a more precise biostratigraphic resolution (Text-fig. 10).

CONCLUSIONS

Geometric morphometry with application of landmarks and semilandmarks has been proved an appropriate tool in the study of simply deformed members of the Miaolingian paradoxidid assemblage from Słowiec Hill in the Holy Cross Mountains. The analysed specimens have been assigned to two taxa, i.e., *Acadoparadoxides slowiecensis* (Czarnocki in Orłowski, 1965) and *Hydrocephalus*? *polonicus* (Czarnocki in Orłowski, 1965). *Paradoxides* spp. E and F of Orłowski (1965) are left in open nomenclature, as it is impossible to attribute them to any of the species mentioned above.

The former *Paradoxides polonicus* Zone of Orłowski (1975, 1988, 1992a) is revised herein into the *Acadoparadoxides slowiecensis–Hydrocephalus*? *polonicus* Assemblage Zone, defined by the combined ranges of both zonal index species. A biostratigraphic analysis of all taxa present in rocks on Słowiec Hill suggest that the *Acadoparadoxides slowiecensis–Hydrocephalus*? *polonicus* Assemblage Zone corresponds to the middle and upper Wuliuan. A more precise correlation with Baltic (Scandinavia), Avalonian (Newfoundland) and Gondwanan (Morocco, Iberia) schemes is not possible at present.

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REFERENCES

Adams, D.C., Collyer, M., Kaliontzopoulou, A. and Baken, E. 2016. Package ‘geomorph’. Software for geometric morphometric analyses for 2D/3D landmark data. Available at: http://cran.r-project.org/packages/geomorph/index.html.

Adams, D.C. and Otárola-Castillo, E. 2013. geomorph: an R Package for the collection and analysis of geometric morphometric shape data. *Methods in ecology and evolution*, **4**, 393–399.

Aleksandrowski, P. and Mazur, S. 2017. On the new tectonic solutions in ‘Geological Atlas of Poland’. *Przegląd Geologiczny*, **65**, 1499–1510. [In Polish with English abstract]

Angelin, N.P. 1854. Palaeontologia Scandinavica. Pars I: Crustacea Formationis Transitionis. Fasc. II, 21–92. T.O. Weigel; Leipzig (“Lipsiae”).

Angielczyk, K.D. and Sheets, H.D. 2007. Investigation of simulated tectonic deformation in fossils using geometric morphometrics. *Paleobiology*, **33**, 125–148.

Asklund, B. and Thorslund, P. 1935. Fjällkedjerandens berggyggnad i norra Jämtland och Ångermanland. *Sveriges Geologiska Undersökning C*, **382**, 1–110.

Axheimer, N. and Ahlberg, P. 2003. A core drilling through Cambrian strata at Almbacken, Scania, S. Sweden: trilobites and stratigraphical assessment. *GFF*, **125**, 139–156.

Barrande, J. 1846. Notice Préliminaire sur le Systême Silurien et les Trilobites de Bohême, 97 pp. C.L. Hirschfeld; Leipzig (“Leipsic”).

Barrande, J. 1852. Systême Silurien du Centre de la Bohême, 935 pp. Private edition by J. Barrande; Prague, Paris.

Bednarczyk, W., Lendzion, K. and Orłowski, S. 1990. Rodzina Paradoxididae Hawle et Corda, 1847. In: Pajchlowa, M. (Ed.), Budowa geologiczna Polski. Tom III. Atlas skamieniałości przewodnich i charakterystycznych. Część 1a. Paleozoik starszy (z proterozoikiem górnym). Ryfej, Wend, Kambr, 58–61. Wydawnictwa Geologiczne; Warszawa.

Belka, Z., Valverde-Vaquero, P., Dörr, W., Ahrendt, H., Wemmer, K., Franke, W. and Schäfer, J. 2002. Accretion of first Gondwana-derived terranes at the margin of Baltica. In: Winchester, J.A., Pharaoh, T.C. and Verniers, J. (Eds), Palaeozoic Amalgamation of Central Europe. *Special Publications of the Geological Society of London*, **201**, 19–36.

Berg-Madsen, V. 1981. The Middle Cambrian Kalby and Borregård Members of Bornholm, Denmark. *Geologiska Föreningens i Stockholm Förhandlingar*, **103**, 215–231.

Berthelsen, A. 1992. From Precambrian to Variscan Europe. In: Blundell, D., Freeman, R. and Müller, S. (Eds), A Continent Revealed: The European Geotraverse, 153–164. Cambridge University Press; Cambridge.

Boeck, C.P.B. 1827. Notizer til Læren om trilobiterne. *Magazin for Naturvidenskaberne*, **8** (1), 11–44.

Brøgger, W.C. 1878. Om paradoxidesskiferene ved Krekling. *Nyt Magazin for Natursvidenskaberne*, **24**, 18–88.

Brongniart, A. 1822. Les Trilobites. In: Brongniart, A. and Desmarest A.-G., Histoire naturelle des crustacés fossiles, sous les rapports zoologiques et géologiques, 1–65. F.-G. Levrault; Paris.

Czarnocki, J. 1919. Stratygrafja i tektonika Gór Świętokrzyskich. *Prace Towarzystwa Naukowego Warszawskiego*, **28**, 1–172.

Czarnocki, J. 1927a. Kambr i jego fauna w środkowej części Gór Świętokrzyskich. *Sprawozdania Państwowego Instytutu Geologicznego*, **4** (1/2), 189–208.

Czarnocki, J. 1927b. Le Cambrien et la faune cambrienne de la partie moyenne du massif de Swiety Krzyz (S^{te} Croix). Congrès Geológique International, Compte-rendue de la XIVe session, en Espagne, 1926, Madrid, 735–750.

Czarnocki, J. 1933. Odsłonięcia kambru okolic Ociesęk i Orłowin jako zabytek w znaczeniu naukowem. *Zabytki Przyrody Nieożywionej*, **2**, 78–85.

Dean, W.T. and Rushton, A.W.A. 1997. Superfamily Paradoxidoidea Hawle and Corda, 1847. In: Kaesler, R.L. (Ed.), Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita, Revised, volume 1: Introduction, Order Agnostida, Order Redlichiida, 470–481. Geological Society of America and University of Kansas Press; Boulder and Lawrence.

Fletcher, T.P. 2007. Correlating the zones of '*Paradoxides hicksii*' and '*Paradoxides davidis*' in Cambrian Series 3. *Memoirs of the Association of Australasian Palaeontologists*, **33**, 35–56.

Geyer, G. 1998. Intercontinental, trilobite-based correlation of the Moroccan early Middle Cambrian. *Canadian Journal of Earth Sciences*, **35**, 374–401.

Geyer, G. 2019. A comprehensive Cambrian correlation chart. *Episodes*, **42** (4), 321–332.

Geyer, G. and Landing, E. 2001. Middle Cambrian of Avalonian Massachusetts: stratigraphy and correlation of the Braintree trilobites. *Journal of Paleontology*, **75**, 116–135.

Geyer, G., Nowicki, J., Żylińska, A. and Landing, E. 2019. Comment on: Álvaro, J.J., Esteve, J. & Zamora, S. 2019. Morphological assessment of the earliest paradoxidid trilobites (Cambrian Series 3) from Morocco and Spain [Geological Magazine]. *Geological Magazine*, **156**, 1691–1707.

Geyer, G. and Vincent, T. 2015. The *Paradoxides* puzzle resolved: the appearance of the oldest paradoxidines and its bearing on the Cambrian Series 3 lower boundary. *Paläontologische Zeitschrift*, **89**, 335–398.

Green, J. 1834. Descriptions of some new North American trilobites. *American Journal of Science*, **25**, 334–337.

Gürich, G. 1892. Ueber eine cambrische Fauna von Sandomir in Russisch-Polen. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **1892** (1), 69–70.

Haber, A. 2011. OSymm. Available at: http://life.bio.sunysb.edu/morph/morphmet/OSymm.R.

Hawle, I. and Corda, A.J.C. 1847. Prodrom einer Monographie der böhmischen Trilobiten, *Königliche Böhmische Gesellschaft der Wissenschaften*, *Abhandlungen*, **5**, 1–176.

Henningsmoen, G. 1952. Early Middle Cambrian fauna from Rogaland, SW Norway *(Paradoxides oelandicus stage = 1c a)*. *Norsk Geologisk Tidsskrift*, **30**, 13–32.

Hughes, N.C. and Jell, P.A. 1992. A statistical/computer-graphic technique for assessing variation in tectonically deformed fossils and its application to Cambrian trilobites from Kashmir. *Lethaia*, **25**, 317–330.

Jendryka-Fuglewicz, B. 1992. Comparative analysis of brachiopods from the Cambrian deposits of the Holy Cross Mountains and the Precambrian Platform in Poland. *Przegląd Geologiczny*, **40**, 150–155. [In Polish]

Klingenberg, C.P., Barluenga, M. and Meyer, A. 2002. Shape analysis of symmetric structures: quantifying variation among individuals and asymmetry. *Evolution*; *International Journal of Organic Evolution*, **56**, 1909–1920.

Kobayashi, T. 1935. The Cambro-Ordovician formations and faunas of South Chosen. Palaeontology. Part III. Cambrian fauna of South Chosen with a special study of the Cambrian trilobite genera and families. *Journal of the Faculty of Science, Imperial University of Tokyo, section 2*, **4**, 49–344.

Konon, A. 2008. Tectonic subdivision of Poland: Holy Cross Mountains and adjacent areas. *Przegląd Geologiczny*, **56**, 921–926. [In Polish with English abstract]

Kordule, V. 1990. *Rejkocephalus*, a new paradoxidid genus from the Middle Cambrian of Bohemia (Trilobita). *Věstník Ústředního Ústavu Geologického*, **65**, 55–60.

Kowalczewski, Z., Żylińska, A. and Szczepanik, Z. 2006. Kambr w Górach Świętokrzyskich. In: Skompski, S. and Żylińska, A. (Eds), 77 Zjazd Naukowy Polskiego Towarzystwa Geologicznego, Ameliówka k. Kielc 28–30 czerwca 2006 r., 14–27. Wydawnictwa Geologiczne; Warszawa.

Liñán, E. and Gozalo, R. 1986. Trilobites del Cámbrico inferior y medio de Murero (Cordillera Ibérica). *Memorias del Museo Paleontológico de la Universidad de Zaragoza*, **2**, 1–104.

Linnarsson, J.G.O. 1869. Om Vestergötlands cambriska och siluriska aflagringar. *Kungliga Vetenskaps-Akademiens Handlingar*, **8** (2), 1–89.

Linnarsson, J.G.O. 1876. On the Brachiopoda of the *Paradoxides* Beds of Sweden. *Bihang till Kungliga Svenska Vetenskaps-Akademiens Handlingar*, **3** (12), 1–34.

Masiak, M. and Żylińska, A. 1994. Burgess Shale-type fossils in Cambrian sandstones of the Holy Cross Mountains. *Acta Palaeontologica Polonica*, **39**, 329–340.

Matthew, G.F. 1887. Illustrations of the fauna of the St. John Group. No. IV. On the smaller-eyed trilobites of Division I, with a few remarks on the species of the higher divisions of the group. *Canadian Record of Science*, **2**, 357–363.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio*, **69**, 89–107.

Nawrocki, J., Dunlap, J., Pecskay, Z., Krzemiński, L., Żylińska, A., Fanning, M., Kozłowski, W., Salwa, S., Szczepanik, Z. and Trela, W. 2007. Late Neoproterozoic to Early Palaeozoic palaeogeography of the Holy Cross Mountains

(Central Europe): an integrated approach. *Journal of the Geological Society*, *London*, **164**, 405–423.

Nielsen, A.T. and Ahlberg, P. 2019. The Miaolingian, a new name for the 'Middle' Cambrian (Cambrian Series 3): identification of lower and upper boundaries in Baltoscandia. *GFF*, **141**, 162–173.

Nielsen, A.T. and Schovsbo, N.H. 2006. Cambrian to basal Ordovician lithostratigraphy in southern Scandinavia. *Bulletin of the Geological Society of Denmark*, **53**, 47–92.

Nowicki, J. 2015. morphoutils – utility functions for geometric morphometrics. Available at: https://github.com/jakubnowicki/morphoutils.

Nowicki, J. 2016. Taxonomic revision of the Cambrian trilobite family Paradoxididae Hawle et Corda, 1847 from the Holy Cross Mountains (Poland) with the application of morphometric analysis, 192 pp. Unpublished Doctoral Thesis, University of Warsaw. [In Polish]

Nowicki, J. and Żylińska, A. 2019. The first occurrence of the earliest species of Acadoparadoxides outside Gondwana (Cambrian; Holy Cross Mountains, Poland). *Geological Magazine*, **156**, 1027–1051.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. and Wagner, H. 2016. vegan: Community Ecology Package. Available at: https://cran.r-project.org/web/packages/vegan/index.html.

Orłowski, S. 1957. On the presence of Paradoxides ölandicus Beds in the Holy Cross Mountains. *Bulletin de l'Académie Polonaise des Sciences*, *Série des sciences chimiques*, *géologiques et géographiques*, **5**, 769–772.

Orłowski, S. 1959a. Paradoxidae from lower Middle Cambrian Strata in the vicinity of Sandomierz (Central Poland). *Bulletin de l'Académie Polonaise des Sciences*, *Série des sciences chimiques*, *géologiques et géographiques*, **7**, 441–446.

Orłowski, S. 1959b. Ellipsocephalidae from the Lower Beds of the Middle Cambrian in the Vicinity of Sandomierz (Central Poland). *Bulletin de l'Académie Polonaise des Sciences*, *Série des sciences chimiques*, *géologiques et géographiques*, **7**, 515–520.

Orłowski, S. 1964. Middle Cambrian and its fauna in the eastern part of the Holy Cross Mts. *Studia Geologica Polonica*, **16**, 5–94. [In Polish with English abstract]

Orłowski, S. 1965. A revision of the Middle Cambrian fauna from the Słowiec Hill (Holy Cross Mountains). *Biuletyn Geologiczny UW*, **6**, 136–146. [In Polish with extensive English abstract]

Orłowski, S. 1975. Cambrian and Upper Precambrian lithostratigraphic units of the Holy Cross Mts. *Acta Geologica Polonica*, **25**, 431–448. [In Polish with English abstract]

Orłowski, S. 1985. New data on the Middle Cambrian trilobites and stratigraphy in the Holy Cross Mts. *Acta Geologica Polonica*, **35**, 251–263.

Orłowski, S. 1988. Stratigraphy of the Cambrian system in the Holy Cross Mts. *Kwartalnik Geologiczny*, **32**, 525–532.

Orłowski, S. 1989. Trace fossils in the Lower Cambrian sequence in the Świętokrzyskie Mountains, Central Poland. *Acta Palaeontologica Polonica*, **34**, 211–231.

Orłowski, S. 1992a. Cambrian stratigraphy and stage subdivision in the Holy Cross Mountains, Poland. *Geological Magazine*, **129**, 471–474.

Orłowski, S. 1992b. Trilobite trace fossils and their stratigraphical significance in the Cambrian sequence of the Holy Cross Mountains, Poland. *Geological Journal*, **27**, 15–34.

Özdikmen, H. 2009. Nomenclatural changes for twenty trilobites genera. *Munis Entomology & Zoology*, **4**, 155–171.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. Available at: http://www.r-project.org.

Richter, R. 1932. Crustacea (Paläontologie). In: Dittler, R., Joos, G., Korschelt, E., Linck, G., Oltmanns, F. and Schaum, K. (Eds), Handwörterbuch der Naturwissenschaften, Zweite Auflage, 840–864. Gustav Fischer; Jena.

Rohlf, F.J. 2016. TPS software series. Available at: http://life.bio.sunysb.edu/morph/.

Rushton, A.W.A. 2006. Revision of the middle Cambrian trilobite *Paradoxides jemtlandicus*. *Geological Magazine*, **143**, 771–776.

Rushton, A.W.A. and Weidner, T.R. 2007. The Middle Cambrian paradoxidid trilobite *Hydrocephalus* from Jämtland, central Sweden. *Acta Geologica Polonica*, **57**, 391–401.

Rushton, A.W.A., Weidner, T. and Ebbestad, J.O.R. 2016. Paradoxidid trilobites from a mid-Cambrian (Series 3, stage 5) limestone concretion from Jämtland, central Sweden. *Bulletin of Geosciences*, **91**, 515–552.

Salter, J.W. 1865. A monograph of the British trilobites from the Cambrian, Silurian and Devonian formations. Monographs of the Palaeontolographical Society, 81–128. The Palaeontographical Society; London.

Samson, S., Palmer, A.R., Robison, R.A. and Secor Jr., D.T. 1990. Biogeographical significance of Cambrian trilobites from the Carolina slate belt. *Bulletin of the Geological Society of America*, **102**, 1459–1470.

Schlotheim, E.F. 1823. Nachträge zur Petrefactenkunde, 114 pp. Becker'sche Buchhandlung; Gotha.

Sdzuy, K. 1958. Neue Trilobiten aus dem Mittelkambrium von Spanien. *Senckenbergiana lethaea*, **39**, 235–253.

Sjögren, A. 1872. Om några försteningar i Ölands Kambriska lager. *Geologiska Föreningens i Stockholm Förhandlingar*, **1** (5), 67–80.

Šnajdr, M., 1957. O nových trilobitech z českého kambria. *Věstnik Ústředniho Ústavu Geologického*, **32**, 235–244.

Šnajdr, M. 1958. Trilobiti českého středního kambria. *Rozpravy Ústředniho Ústavu Geologického*, **24**, 1–280.

Šnajdr, M. 1986. Two new paradoxid trilobites from the Jince Formation (Middle Cambrian, Czechoslovakia). *Věstnik Ústředniho Ústavu Geologického*, **61**, 169–174.

Srivastava, D.C. and Shah, J. 2006. Digital method for strain estimation and retrodeformation of bilaterally symmetric fossils. *Geology*, **34**, 593–596.

Strand, T. 1929. The Cambrian beds of the Mjøsen district in Norway. *Norsk Geologisk Tidsskrift*, **10**, 308–366.

Sundberg, F.A., Geyer, G., Kruse, P.D., McCollum, L.B., Pegel', T.V., Żylińska, A. and Zhuravlev, A.Yu. 2016. International correlation of the Cambrian Series 2–3, Stages 4–5 boundary interval. *Australasian Paleontological Memoirs*, **49**, 83–124.

Szczepanik, Z. and Żylińska, A. 2016. The oldest rocks of the Holy Cross Mountains, Poland – biostratigraphy of the Cambrian Czarna Shale Formation in the vicinity of Kotuszów. *Acta Geologica Polonica*, **66**, 267–281.

Thorslund, P. 1949. Notes on *Kootenia* sp. n. and associated *Paradoxides* species from the lower Middle Cambrian of Jemtland, Sweden. *Sveriges Geologiska Undersökning, ser. C*, **410**, 3–8.

Wahlenberg, G. 1818. Petrifacta telluris Svecanae. *Acta Societas Regiae Scientiarum*, **8**, 1–116. [for 1921]

Walch, J.E.I. 1771. Die Naturgeschichte der Versteinerungen zur Erläuterung der Knorrischen Sammlung von Merkwürdigkeiten der Natur, 250 pp. Felßecker; Nürnberg.

Walczak, A. and Belka, Z. 2017. Fingerprinting Gondwana versus Baltica provenance: Nd and Sr isotopes in Lower Paleozoic clastic rocks of the Małopolska and Łysogóry terranes, southern Poland. *Gondwana Research*, **45**, 138–151.

Webster, M. and Hughes, N.C. 1999. Compaction-related deformation in Cambrian olenelloid trilobites and its implications for fossil morphometry. *Journal of Paleontology*, **73**, 355–371.

Westergård, A.H. 1936. *Paradoxides oelandicus* Beds of Öland. *Sveriges Geologiska Undersökning C*, **394**, 1–66.

Żelaźniewicz A., Aleksandrowski, P., Buła, Z., Karnkowski, P.H., Konon, A., Oszczypko, N., Ślączka, A., Żaba, J. and Żytko, K. 2011. Regionalizacja tektoniczna Polski, 60 pp. Komitet Nauk Geologicznych PAN; Wrocław.

Żelaźniewicz, A., Buła, Z., Fanning, M., Seghedi, A. and Żaba, J. 2009. More evidence on Neoproterozoic terranes in Southern Poland and southeastern Romania. *Geological Quarterly*, **53**, 93–124.

Żylińska, A., Kin, A. and Nowicki, J. 2013. Application of morphometric techniques for taxonomic revision of *Berabichia oratrix* (Orłowski, 1985) (Trilobita, Cambrian) from the Holy Cross Mountains, Poland. *Geodiversitas*, **35**, 505–528.

Żylińska, A. and Szczepanik, Z. 2009. Trilobite and acritarch assemblages from the Lower–Middle Cambrian boundary interval in the Holy Cross Mountains (Poland). *Acta Geologica Polonica*, **59**, 413–458.

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