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The first occurrence of the earliest species of *Acadoparadoxides* outside West Gondwana (Cambrian; Holy Cross Mountains, Poland)

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Abstract – Two hundred and eighty specimens of paradoxidids from two localities in the Holy Cross Mountains (Poland) have been reanalysed using morphometric techniques. Revision of the dataset provided evidence for the presence of two endemic taxa: *Acadoparadoxides kozlowskii* (Orłowski, 1959) and *Acadoparadoxides samsonowiczi* (Orłowski, 1959), both belonging to the earliest group of *Acadoparadoxides*, initially considered to be present only in Gondwanan successions. Thus, this is the first description of the members of this group outside West Gondwana. The taxonomic revision, and the presence of representatives of the earliest acadoparadoxidines coupled with the absence of taxa typical of Scandinavia that were previously described from this locality have resulted in the modification of the biostratigraphic scheme hitherto used in the Holy Cross Mountains. The newly established *A. samsonowiczi – A. kozlowskii* Assemblage Zone is correlated with the *Morocconus notabilis* Zone of Morocco, and thus represents the Cambrian Series 2 and 3 boundary interval. Links with West Gondwana challenge the existing palaeogeographic interpretations for the southern part of the Holy Cross Mountains and point to an urgent need to revise the position of the Małopolska Block during the middle Cambrian.

Keywords: Paradoxididae, Trilobita, Cambrian, Holy Cross Mountains, biostratigraphy, palaeogeography.

1. Introduction

Recent work on early paradoxidids has resulted in the description of several new species from the Anti-Atlas (Morocco), all belonging to the genus *Acadoparadoxides* (Geyer & Vincent, 2015). Those species together with some taxa from other localities (Spain, Turkey, Newfoundland) form a consistent group (sometimes referred to as the *Acadoparadoxides mureroensis* clade (see e.g. Geyer & Vincent, 2015), to be verified in the future with phylogenetics). Until now, this group has never been reported from palaeogeographic areas outside West Gondwana and Avalonia. The Holy Cross Mountains (central Poland), especially their southern region, represent part of the Małopolska Block, a terrane usually reconstructed as being an element of the Baltica palaeocontinent, but with an unclear provenance and a widely disputed age of accretion (e.g. Nawrocki *et al*. 2007; Walczak & Belka, 2017). Previous descriptions of paradoxidids from this area included several species, among which four represented taxa typical of Baltica. This paper provides a revision of this material and shows for the first time the presence of the earliest group of acadoparadoxidines outside West Gondwana coupled with the lack of Scandinavian trilobite taxa. Such revision was possible due to the application of morphometric techniques (geometric morphometrics), a very useful tool becoming increasingly popular in modern palaeontology. This approach included a new application of retrodeformation techniques (since the material from Poland is significantly distorted) that comprises the adaptation of methods used in classical morphometry (e.g. Hughes & Jell, 1992; Żylińska, Kin & Nowicki, 2013) to landmark data.

2. Geological setting and review of the trilobite assemblages

The analysed material was collected in the central and eastern part of the Holy Cross Mountains. This hilly area located within the Trans-European Suture Zone is subdivided into the Kielce and Łysogóry regions, separated by the Holy Cross Fault (Fig. 1). The main outcrops (including Brzechów and Jugoszów–Usarzów) of the traditional 'Middle' Cambrian are situated in the southern Kielce Region, which represents an exposed part of the sedimentary cover of the Małopolska Block. During the Cambrian, this crustal element was either a small terrane believed to be the proximal part of the Baltica palaeocontinent (e.g. Nawrocki *et al.* 2007) or an exotic terrane rifted from Gondwana and accreted to Baltica during the Cambrian (e.g. Belka *et al.* 2002).

The Cambrian succession of the Holy Cross Mountains is developed in siliciclastic facies. The analysed material comes from two lithostratigraphic formations: the Słowiec Sandstones and the Usarzów Sandstones

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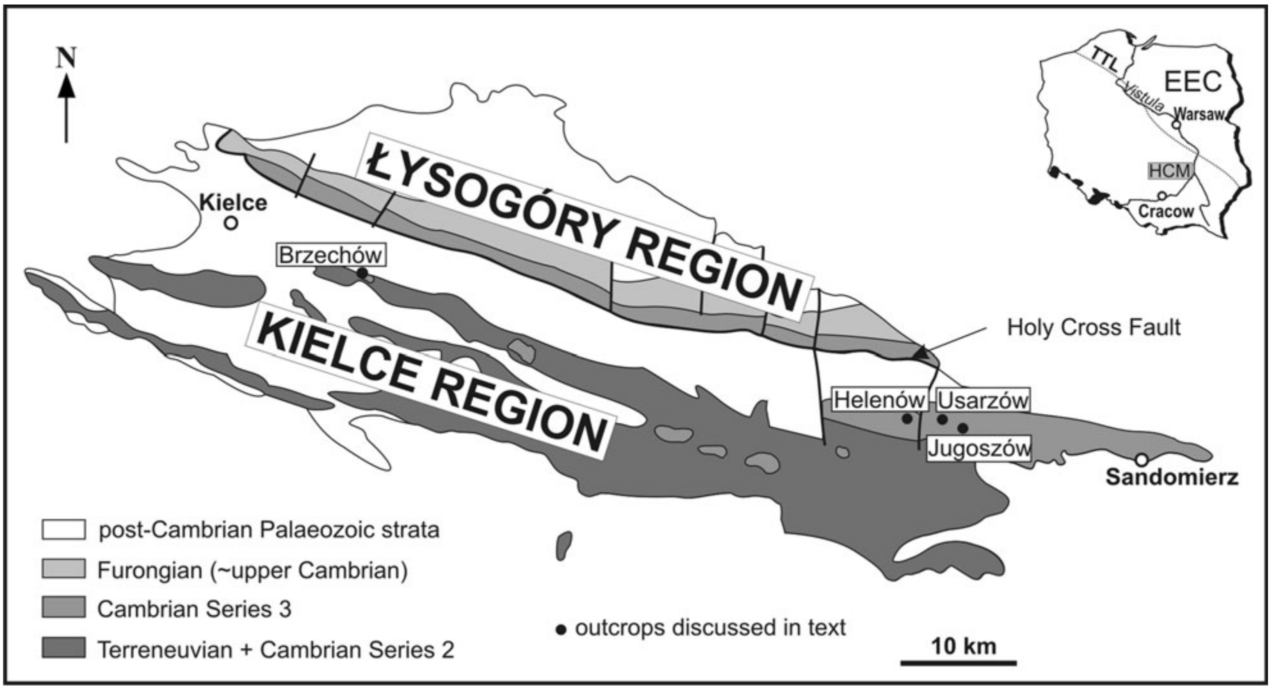

Figure 1. Geological sketch map of the Holy Cross Mountains (HCM) showing the distribution of Cambrian deposits, modified from Orłowski (1975, 1992), with location of the studied outcrops. EEC – East European Craton; TTL – Teisseyre–Tornquist Line.

(Orłowski, 1975). Both formations were deposited in a shallow marine environment; for instance, a typical occurrence of the Słowiec Formation bears evidence of a relatively high-energy setting, whereas the lower part of the unit, which occurs in Brzechów, was deposited in calmer conditions (e.g. Kowalczewski, Żylińska & Szczepanik, 2006). The Usarzów Sandstones developed in a rather low-energy environment (e.g. Kowalczewski, Żylińska & Szczepanik, 2006).

The first locality with paradoxidid remains, situated near Brzechów village, lies in the western part of the Holy Cross Mountains, *c.* 10 km to the east of Kielce city (Fig. 2). Cambrian rocks form the core of an inverted anticline and build the bottom of a WNW–ESE-oriented valley mostly covered by fields and grasslands. There is no exposure and the specimens may be found only in loose sandstone blocks on the fields, especially after spring ploughing. The sandstone bedrock was discovered in the mid-1960s by Wiesław Bednarczyk, but presently the location of the trenches made by him cannot be reconstructed (Żylińska & Masiak, 2007). In 2006 another trench was dug close to where the loose blocks with fossils could be found, but it exposed only shales that, based on a low-diversity and low-frequency acritarch assemblage, were assigned to the traditional 'Middle' Cambrian; a more precise stratigraphic resolution was not possible and the relation of these rocks to the sandstones yielding macrofossils was not recognized (Żylińska & Szczepanik, 2009). The diverse and unique assemblage of fossils found in Brzechów includes trilobites (Czarnocki, 1927*a*, *b*; Bednarczyk, 1970; Żylińska & Masiak, 2007), brachiopods (Bednarczyk, 1970), imprints of soft-bodied animals (Czarnocki, 1927*a, b*; Stasińska, 1960; Masiak & Żylińska, 1994) and other remains of organisms (A.Ż., unpublished data). Two species from the Family Paradoxididae Hawle & Corda, 1847 have been described from this locality: *Paradoxides oelandicus* Sjögren, 1872 by Bednarczyk (1970) and *Paradoxides* (*Acadoparadoxides*) cf. *mureroensis* (Sdzuy, 1958) by Żylińska (in Żylińska & Masiak, 2007). The first taxon was the basis for correlating the rocks from this locality with the Scandinavian *Acadoparadoxides oelandicus* Superzone (Bednarczyk, 1970). Besides

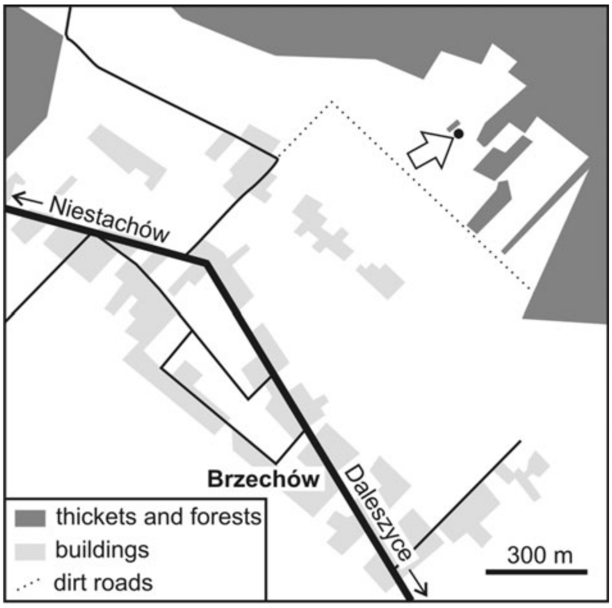

Figure 2. Sketch map of the Brzechów area with location of the Brzechów outcrop.

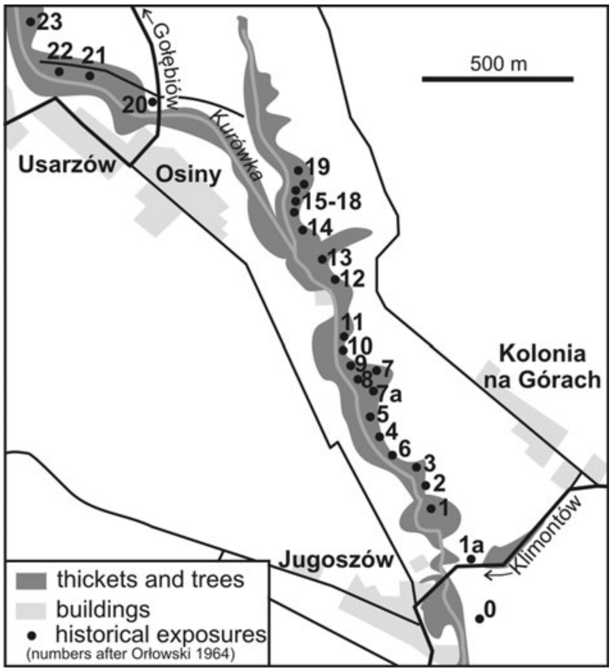

Figure 3. Sketch map of the Jugoszów–Usarzów section, modified from Orłowski (1964).

paradoxidids, the trilobites from Brzechów include representatives of the Family Ellipsocephalidae Matthew, 1887 (*Kingaspidoides sanctacrucensis* (Czarnocki, 1927*a*) and *Issafeniella orlowinensis* (Samsonowicz, 1959)), the Family Palaeolenidae Hupé, 1953 (*Palaeolenus medius* (Bednarczyk, 1970)) and a member of the *Conomicmacca*/*Myopsolenites* clade (*Myopsolenites kielcensis* (Bednarczyk, 1970)) (see revision in Żylińska & Masiak, 2007 and remarks on *Myopsolenites kielcensis* in Elicki & Geyer, 2013 and Geyer, 2016). The two latter species are important for biostratigraphy, as their presence had led to the correlation of the Brzechów sandstones with the Moroccan *Morocconus notabilis* Zone (Żylińska & Masiak, 2007). The co-occurrence of *Acadoparadoxides oelandicus* with *Acadoparadoxides* cf. *mureroensis* was additional evidence that the stratigraphic interval represented by the Brzechów sandstones was older than the oldest traditional 'Middle' Cambrian strata from Scandinavia, and the base of the *Eccaparadoxides insularis* Zone in the Holy Cross Mountains was thus placed earlier than in Scandinavia (Żylińska & Masiak, 2007; Żylińska & Szczepanik, 2009).

The second locality, Jugoszów–Usarzów, comprises numerous small outcrops in the eastern part of the Holy Cross Mountains, described in detail by Orłowski (1959*a*, *b*, 1964). The Jugoszów–Usarzów section *sensu stricto* is composed of 25 small outcrops along the Kurówka stream (Fig. 3). Additional outcrops are located in the close vicinity, near Sternalice, Słoptów and Helenów villages (Fig. 4), of which the presently non-existing Sternalice outcrop had yielded abundant specimens of trilobites. Previously described taxa (Orłowski, 1959*a*, 1964; Żylińska & Szczepanik, 2009) include eight species of paradoxidids, of which four were known also from Scandinavia, i.e. *Acadoparadoxides oelandicus*, *Acadoparadoxides pinus* (Westergård, 1936), *Acadoparadoxides torelli* (Westergård in: Asklund & Thorslund, 1935) and *Eccaparadoxides insularis* (Westergård, 1936); one was known from Gondwanan successions, i.e. *Acadoparadoxides* cf. *mureroensis*; and three were endemic taxa, i.e. *Paradoxides czarnockii* Orłowski, 1959, *Paradoxides kozlowskii* Orłowski, 1959 and *Paradoxides samsonowiczi* Orłowski, 1959. Besides paradoxidids, the strata exposed in the Jugoszów–Usarzów section and the nearby localities yield numerous trilobites of the Family Ellipsocephalidae (12 species; Żylińska & Szczepanik, 2009). Their presence and diversity are similar to those from Gondwanan and Avalonian successions rather than from Baltica (Żylińska & Szczepanik, 2009; Żylińska, 2013*a*). Other faunal elements known from the succession include brachiopods (Orłowski, 1964; Jendryka-Fuglewicz, 1992), primitive echinoderms (Orłowski, 1964; Dzik & Orłowski, 1995), and hyoliths and pelagiellids (Orłowski, 1964).

The hitherto used biostratigraphic scheme for the interval exposed in Brzechów and Jugoszów–Usarzów includes two biozones derived from Scandinavia: the *Paradoxides insularis* and the *Paradoxides pinus* zones (e.g. Orłowski, 1992). The range of the first zone was later extended below to include the part of the Cambrian succession that was correlated with the *Morocconus notabilis* Zone from Morocco (Żylińska & Masiak, 2007; Żylińska & Szczepanik, 2009), but was absent in Scandinavia (e.g. Nielsen & Schovsbo, 2015). The lowermost part of this zone was to be represented in Brzechów, whereas the remaining part was supposed to occur in Jugoszów–Usarzów.

3. Material and methodology

3.a. Material

Most of the analysed material was collected by Stanisław Orłowski and is now reposited in the Stanisław Józef Thugutt Geological Museum, Faculty of Geology, University of Warsaw. Additional material from Brzechów was collected by Wojciech Kozłowski and is reposited in the collection of the Department of Historical and Regional Geology, Institute of Basic Geology at the Faculty of Geology, University of Warsaw. Orłowski's collection includes 280 specimens of paradoxidids from Brzechów and Jugoszów–Usarzów. Except for two partial carapaces, all specimens are isolated sclerites: cranidia, pygidia, hypostomata and parts of thoraces. The material is preserved as both internal and external moulds and has experienced significant tectonic deformation, which, however, is simple; the axes of the specimens have not been bent and remain straight (Fig. 5a). Moreover, the specimens are only marginally affected by compaction (Fig. 5b). The former determination of the material includes the following

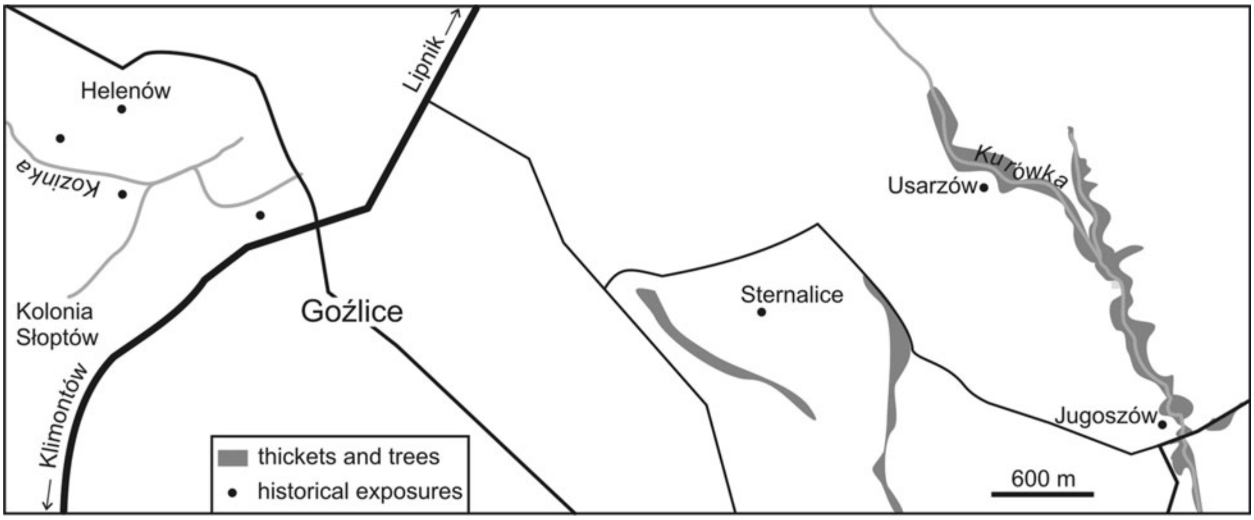

Figure 4. Sketch map of the Jugoszów–Usarzów locality with historical outcrops and sections (after Orłowski 1964).

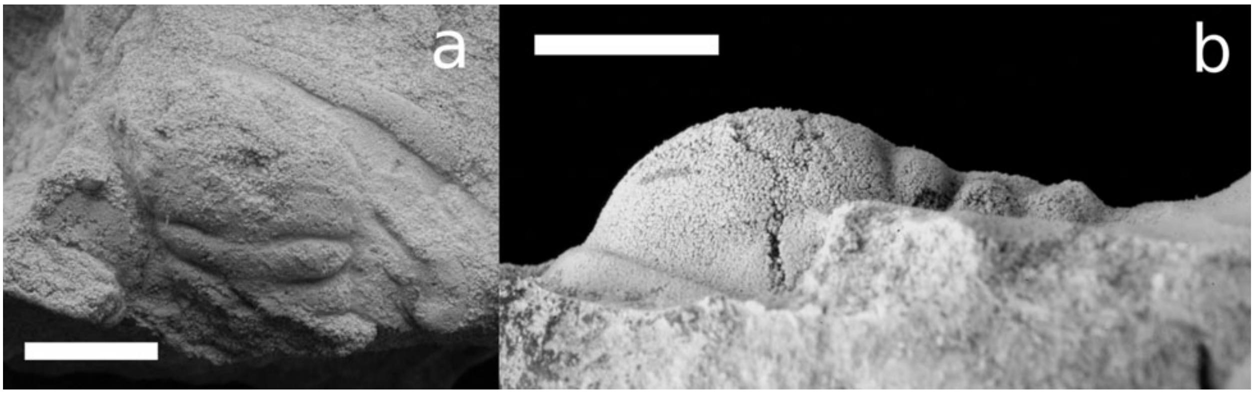

Figure 5. Examples of the style of deformation expressed by trilobite cranidia from the study area. (a) Strongly skewed specimen of *Acadoparadoxides* sp., MWGUW ZI/29/3252; (b) Side view of cranidium of *Acadoparadoxides kozlowskii* (Orłowski, 1959) with very low degree of compaction, original of Orłowski (1964), pl. 2, fig. 2, and Żylińska & Szczepanik (2009), pl. 4, fig. 9; MWGUW ZI/29/3210. Scale bars equal 5 mm.

species (names as on labels): *Paradoxides* (*Acadoparadoxides*) cf. *mureroensis*, *Paradoxides* (*Acadoparadoxides*) *oelandicus*, *Paradoxides* (*Acadoparadoxides*) *pinus*, *Paradoxides* (*Eccaparadoxides*) *insularis*, *Paradoxides* (*Eccaparadoxides*) *torelli*, *Paradoxides czarnockii*, *Paradoxides kozlowskii* and *Paradoxides samsonowiczi*. Kozłowski's collection contains nine specimens from Brzechów (isolated cranidia, pleurae, and one incomplete pygidium). Likewise, the material is preserved as internal and external moulds, and is distorted. The specimens were labelled as *Paradoxides* (*Acadoparadoxides*) cf. *mureroensis* and *Paradoxides* (*Acadoparadoxides*) *oelandicus*.

3.b. Methodology

Revision of distorted material requires special tools to remove the deformation and restore the original relations between the specimens. There are numerous cases in which retrodeformation techniques have been successfully applied to tectonically deformed trilobites (e.g. Hughes & Jell, 1992; Żylińska, Kin & Nowicki, 2013). Similar tools have already been used to evaluate some features in the Paradoxididae (Esteve, 2014; Rushton, Weidner & Ebbestad, 2016); however, the outcome of these analyses, which used linear measurements, had rather minor influence on the research results, especially in the latter cited paper. A principal component analysis (PCA) was not able to show differences between trilobite species distinguished by qualitative features (including the well-known and well-defined taxa in Rushton, Weidner & Ebbestad, 2016). Although the analyses were not free from technical mistakes (e.g. Rushton, Weidner & Ebbestad, 2016 included overlapping measurements in the PCA) which could have influenced the obtained results, above all, traditional morphometric analyses are obviously insufficient for this group. One reason may be the subtlety of the differences between particular paradoxidid species (e.g. Geyer & Vincent, 2015). A possible solution is the application of a more sensitive method, i.e. geometric morphometrics (e.g. Zelditch, Swiderski & Sheets, 2012). The risk of potential inconsistencies in this case is that the 'noise' coming from preservation may be overrepresented and may obscure the true morphological variation in the sample.

In geometric morphometrics, PCA may be used in a similar way to its use in classical morphometrics (e.g. Hughes & Jell, 1992; Żylińska, Kin & Nowicki, 2013). One of the components may be interpreted as resulting from deformation caused by tectonics and be removed from the analysed sample to bring back the original variance. The component can be detected manually, by visualizing shapes that correspond to the maximal/minimal value of the component, or by examining the correlation between the components and the length:width proportions. In the latter case, high correlation may suggest that this component represents tectonic deformation. After removing the 'tectonic' component, the remaining components can be analysed with various tools, including cluster analysis and distance visualizations, such as Nonmetric Multidimensional Scaling (NMDS).

Angielczyk & Sheets (2007) presented a comprehensive validation of numerical retrodeformation techniques in geometric morphometrics. They recognized PCA as a method that does not successfully remove tectonic variance from the dataset. The major problem with PCA application was the distribution of tectonic variance between several components. Removal of only one component did not significantly improve the outcome, whereas removal of more than one component resulted in also throwing out part of the variance that was not connected with deformation. It should be noted, however, that the cited study was based on a single dataset and did not consider a combination of retrodeformation techniques. The latter approach may be a possible solution for the problem of distribution of tectonic variance by joining PCA with another technique: reflection and averaging of bilaterally symmetric landmarks, i.e. symmetrization. To test this approach, we performed a simulation using the R programming language (R Core Team, 2016) – the geomorphotest package (Nowicki, 2016). As a measure of efficiency of retrodeformation we used a correlation (Pearson's r coefficient) of the Euclidean distances between retrodeformed specimens in a principal component (PC) space and the distances between non-deformed specimens. This statistic was selected because the clustering methods that were to be used to determine the classification of the specimens were based on the distances between the specimens. The test sample contained 1000 datasets, each with 30 specimens. Each specimen had 20 landmarks and was characterized by axial symmetry. The test was repeated nine times, with different deformation ranges. We followed the deforming procedure used by Angielczyk & Sheets (2007) – application of a deformation matrix in the form:

$$\begin{vmatrix} a\cos\Theta & \sin\Theta \\ \sin\Theta & (1/a)\cos\Theta \end{vmatrix}$$

where coefficient a is a normal strain and Θ is a shear strain.

In the first three approaches, deformation was restricted to the applied matrices; in the next six approaches some amount of random noise was added to the deformation. Noise was added to the deformation coefficients as a random value, different for each landmark and each coefficient, and derived from normal distribution with a mean 0 and a standard deviation of 0.01 for groups 4–6 and 0.03 for groups 7–9 (Θ was converted to radians). The angle of the deformation was applied randomly to each specimen within each dataset. Coefficient a was derived from the interval 0.95–1. For groups 1, 4 and 7, Θ was derived from the interval 1–10°. For groups 2, 5 and 8, Θ was derived from the interval 10–20°. For groups 3, 6 and 9, Θ was derived from the interval 1–20°. The deformation parameters are summarized in Table 1. In the simulations we intentionally ignored variation related to ontogenetic development. In the Paradoxididae, the shape of the glabella (an element considered in Section 5 of this paper) is quite stable during late ontogeny (more mature meraspid and holaspid stages; see illustrations in Westergård, 1936; Šnajdr, 1958). In our analysis, only PC3 (5.1 % of variance) and PC8 (0.9 % of variance) may be correlated with the size of the cranidia, although this correlation is weak (for PC3: $r = -0.379$, p-value = 0.0354; for PC8: $r = -0.384$, p-value = 0.0327). Also, in general, the paradoxidids have a similar ontogenetic development in mature stages (reduction of the relative sizes of the pre-glabellar field and the palpebral lobes) and the species from Poland follow this trend. Ontogenetic allometry is therefore unlikely to account for the interspecific differences documented herein.

Table 1. Parameters of deformation in the simulated landmark sets

Group ID	a	Θ	Deformation noise (standard deviation)	Deformation angle
1	0.95–1	1–10°	0	random
2	0.95–1	10–20°	0	random
3	0.95–1	1–20°	0	random
4	0.95–1	1–10°	0.01	random
5	0.95–1	10–20°	0.01	random
6	0.95–1	1–20°	0.01	random
7	0.95–1	1–10°	0.03	random
8	0.95–1	10–20°	0.03	random
9	0.95–1	1–20°	0.03	random

Removing the PC with the highest correlation with the length:width proportions from the sets without symmetrization does not improve the correlation of the distances between the specimens in the non-deformed sets and the retrodeformed sets (Fig. 6). In most cases, both the correlation of the deformed set and the correlation of the retrodeformed set are close to 0; therefore, this technique does not improve the outcome in comparison to the non-retrodeformed samples. A meaningful improvement may be observed in the datasets with symmetrization (Fig. 7). In the three groups with no deformation noise (groups 1–3), this improvement may be observed in almost all cases, and the best outcome appears with higher Θ values. The same pattern may be observed in groups with higher values

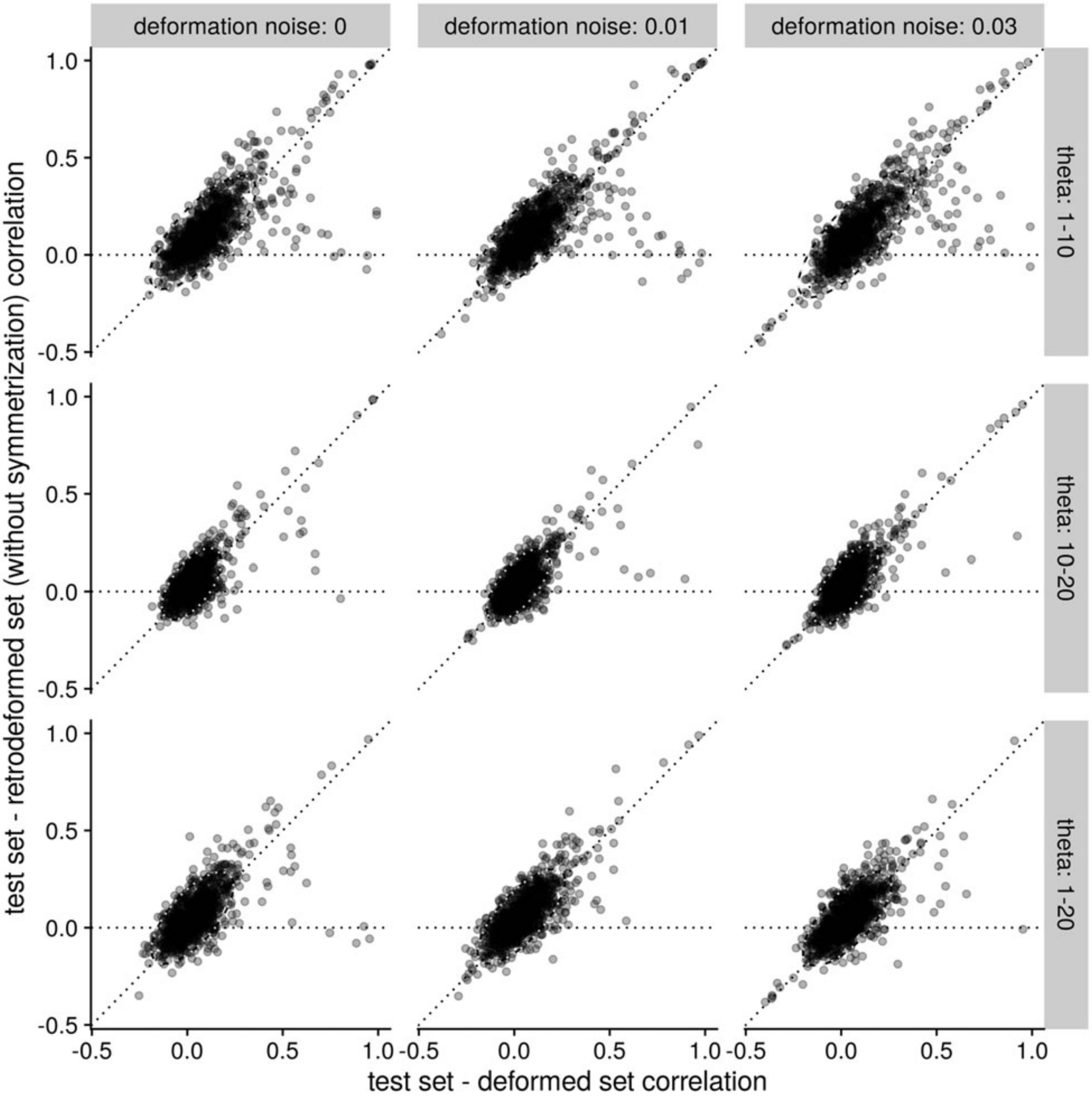

Figure 6. Comparison of the correlation with distances between the specimens in non-deformed sets. *x*-axis: correlation with deformed sets; *y*-axis: correlation with sets retrodeformed without symmetrization. Ellipses represent the 95 % confidence interval.

of the deformation noise (groups 4–6). In the groups with intermediate levels of deformation noise (0.01), the results remain promising: most cases show quite high improvement of correlation in comparison to the sets without retrodeformation. Unfortunately, in the third group (7–9), with the highest amount of noise added to the deformation, only part of the sets was successfully retrodeformed, but even in this case, almost all sets displayed better performance than in the non-retrodeformed sets.

The results clearly show that removal of a PC that is best correlated with the length:width proportions does not improve the outcome when the axial symmetry is not restored in the specimens before the procedure. Symmetrization improves the results, but can be safely applied only to data in which deformation is relatively simple, without a high amount of noise added to the deformation. Such simple deformation may be found in sandstones. On the other hand, it seems that in fine-grained rocks (shales), the complexity of deformation, which often includes bending and flattening, precludes usage of the described technique. The problem of combined retrodeformation in datasets with ontogenetic variance, and also the validation of more complex outputs of retrodeformation is beyond the scope of this paper, but successful application in this case may be taken as encouragement for solving these issues.

Due to the poor preservation of the studied specimens, only three cranidia were sufficiently complete to provide data for geometric morphometrics analysis. To overcome this problem, the analysis focused exclusively on the glabellae and aimed at detecting

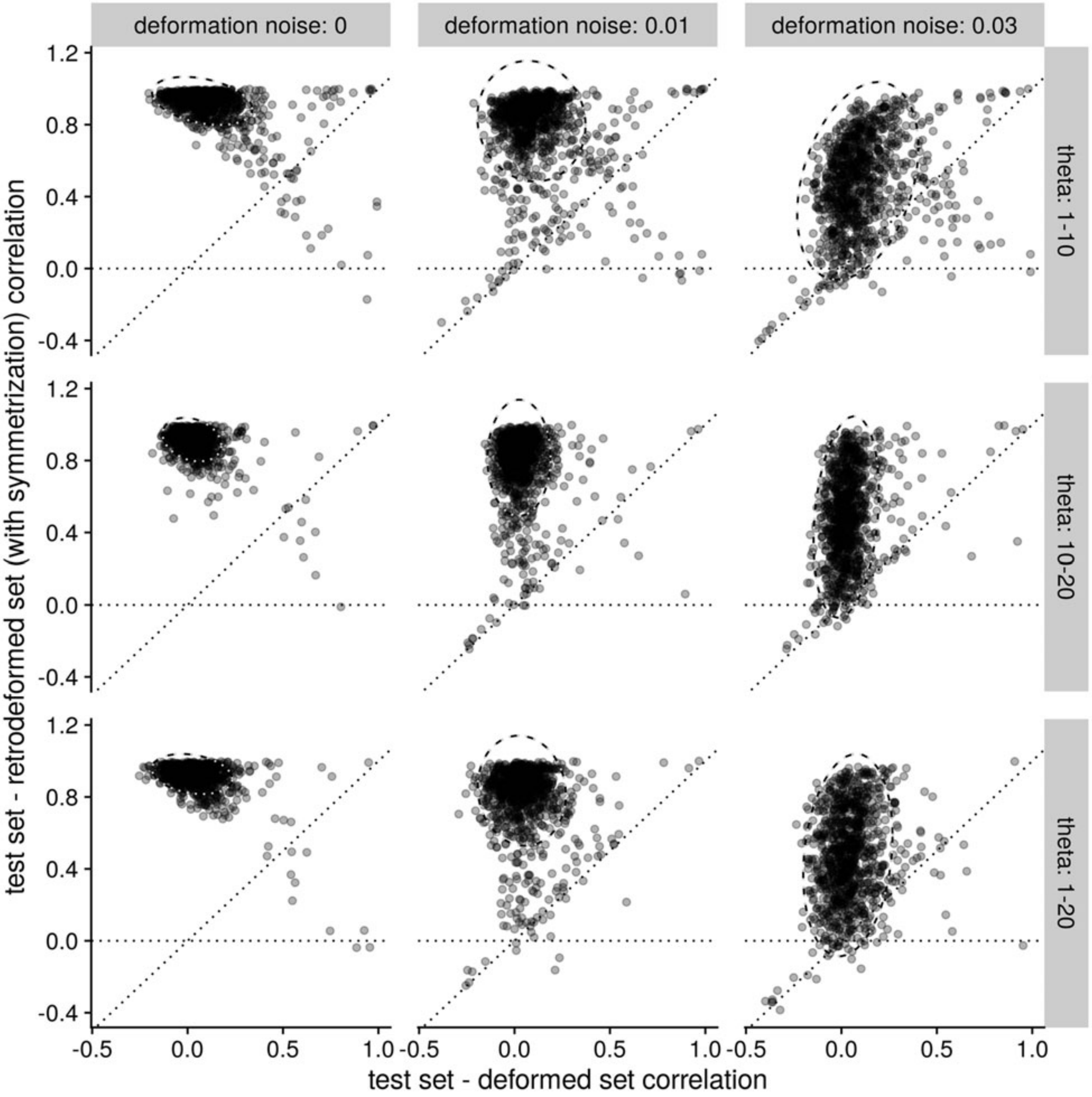

Figure 7. Comparison of the correlation with distances between the specimens in non-deformed sets. x-axis – correlation with deformed sets; y-axis: correlation with sets retrodeformed with symmetrization. Ellipses represent the 95 % confidence interval.

differences among them. Twenty-seven specimens from various outcrops in the Jugoszów–Usarzów locality and four specimens from Brzechów comprised a dataset sufficient to acquire landmarks from the glabellae. Data for the analyses were collected from digital photographs of the specimens (coated with ammonium chloride before photographing) using TPS software (Rohlf, 2016). Each photograph was preprocessed before landmark acquisition by restoring the symmetry of the cranidia (using a technique similar to that presented by Srivastava & Shah, 2006) in order to allow for estimation of the missing landmarks. The specimens were not fully retrodeformed; instead, only the axis of symmetry was restored by shearing the photographs. A dataset of 11 landmarks and 26 semi-landmarks was collected from each glabella (Table 2; Fig. 8). In the analysis, we used landmarks situated on both sides of the glabellae to avoid the transfer of variance from the glabellar sides to the axial landmarks. This was crucial, since the applied retrodeformation techniques are based on the assumption that the axis of symmetry is preserved as a straight line. All further actions were performed using the R programming language (R Core Team, 2016). Pairs of landmarks/semi-landmarks on the opposite sides of the glabella were averaged, or, if only one landmark/semi-landmark of the pair was preserved, the missing landmark/semi-landmark was estimated (according to the positions of all existing landmarks) using the algorithm proposed by Klingenberg, Barluenga & Meyer (2002). Both actions were performed using the *OSymm* function (Haber, 2011). Averaging of the semi-landmarks

Table 2. Location of landmarks and semi-landmarks on the glabella of the studied paradoxidids

Number of landmark/semi-landmark	General location	Description of position on glabella
1	axis of symmetry	posterior margin of occipital ring
2	axis of symmetry	deepest point of SO
3	axis of symmetry	deepest point of S1
4	axis of symmetry	deepest point of S2
5	axis of symmetry	anterior margin of glabella (frontal lobe)
6	left side	juncture of SO and axial furrow
9	right side	juncture of SO and axial furrow
7	left side	juncture of S1 and axial furrow
10	right side	juncture of S1 and axial furrow
8	left side	juncture of S2 and axial furrow
11	right side	juncture of S2 and axial furrow
12 – 13	left side	margin of L1
14 – 15	right side	margin of L1
16 – 17	left side	margin of L2
18 – 19	right side	margin of L2
20 – 28	left side	margin of the anterior part of glabella
29 – 37	right side	margin of the anterior part of glabella

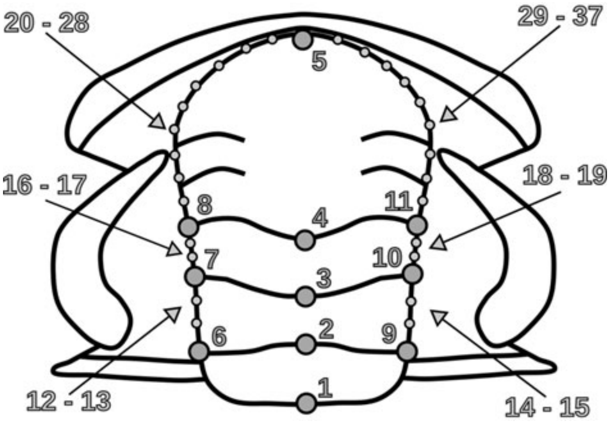

Figure 8. Location of collected landmarks and semi-landmarks on a paradoxidid glabella.

was possible due to embedding of fans (radii of circles) on the photographs. Since axial symmetry was restored in the specimens, the semi-landmarks were located in homologous positions on both sides of the glabellae (in a single specimen; the homology between specimens was achieved with sliding semi-landmarks), defined by the intersection of the described curve and the symmetric radii. Landmarks and semi-landmarks were superimposed (Generalized Procrustes Analysis). Semi-landmarks were slided with the Procrustes distance criterion applied. Both actions were performed using the *geomorph* package (Adams & Otárola-Castillo, 2013; Adams *et al.* 2016). The same package was used for PCA application. Major data manipulation, including symmetrization, was performed using the *morphoutils* package (Nowicki, 2015).

4. Revision of former taxonomic assignments

Among the taxa described in the previous papers (Orłowski, 1959*a*, 1964; Bednarczyk, 1970; Żylińska & Masiak, 2007; Żylińska & Szczepanik, 2009) occurring in Jugoszów–Usarzów (eight species) and Brzechów (two species), most taxa were diagnosed based only on cranidia, with the exception of two endemic species represented only by pygidia (*Paradoxides kozlowskii* and *Paradoxides samsonowiczi*). Except for a relatively detailed description of the differences between specimens assigned previously to *Paradoxides* (*Acadoparadoxides*) *oelandicus* and *Paradoxides* (*Acadoparadoxides*) cf. *mureroensis* given by Żylińska & Masiak (2007), none of the cited papers presents a comparison between the paradoxidid species, therefore the diagnostic features extracted from Orłowski (1959*a*) are compared in Table 3. Specimens assigned by Orłowski (1964) to *Paradoxides torelli* are the only ones that differ significantly from the remaining paradoxidids; however, they are very poorly preserved and were not included in the comparison. Their species assignment is not possible; additionally, Weidner, Rushton & Ebbestad (2014) have shown that they definitely cannot be attributed to *Acadoparadoxides torelli* as currently known from Scandinavia. Differences between the types of cranidia (excluding the specimens assigned to *P. torelli*) described by Orłowski (1959*a*) are doubtful. The major character emphasized by Orłowski (1959*a*) for cranidia assigned to *Paradoxides insularis* and *Paradoxides czarnockii* was the presence of the S3 and S4 glabellar furrows. In reality, these furrows are present also on the glabellae of specimens assigned by Orłowski to *Paradoxides oelandicus* and *Paradoxides pinus* (Orłowski 1959*a*, pl. 1, figs 2, 4, 6, 7). In all cases, the furrows are not well marked, unlike in the type specimens of *Eccaparadoxides insularis* from Sweden, in which they are clearly developed (e.g. Westergård 1936, pl. 7 figs 1, 2a, 5, 8, 9). This difference is evidently not caused by variable preservation of the material from the Holy Cross Mountains and the material from Scandinavia. Another difference between *Eccaparadoxides insularis* from Scandinavia and the paradoxidid species in question is the disparity in the length:width proportions of the cranidia. All cranidia assigned by Orłowski (1959*a*) to *Paradoxides insularis* show traces of

Table 3. Diagnostic differences between the specimens of *Paradoxides oelandicus*, *Paradoxides pinus*, *Paradoxides insularis* and *Paradoxides czarnockii* from the Holy Cross Mountains after Orłowski (1959*a*)

	P. oelandicus	*P. pinus*	*P. insularis*	*P. czarnockii*
cranidial width (tr.) versus cranidial length (sag.)	–	similar	–	similar
shape of glabella	elongated, widening anteriorly, domed	widening anteriorly, slightly domed	short (sag.), wide (tr.), pyriform, domed	elongated, widening anteriorly, domed
glabellar furrows	2 pairs joined medially; shallower in the middle part	2 pairs joined medially	4 pairs: S1 and S2 joined medially; S3 and S4 shallow, indistinct, short	4 pairs: S1 and S2 joined medially, shallower in the middle part; S3 and S4 shallow, indistinct, short
palpebral lobes	large, extending from posterior margin furrow to anterior part of glabella above S2	large, strongly curved, extending from posterior margin furrow to anterior part of glabella above S2	large, strongly curved, extending from posterior margin furrow to anterior part of glabella between S3 and S4	large, strongly curved, extending from posterior margin furrow to anterior part of glabella near S3
anterior border	distinct, wide (sag./exsag.), wider (exsag.) abaxially	distinct, wide (sag./exsag.)	distinct, wide (sag./exsag.), wider (exsag.) abaxially	distinct, wide (sag./exsag.), wider (exsag.) abaxially
pre-glabellar field	narrow (sag.) or absent ('in form of furrow between anterior border and glabella')	–	narrow (sag.)	narrow (sag.)

Table 4. Diagnostic differences between the specimens of *Paradoxides* (*Acadoparadoxides*) cf. *mureroensis* and *Paradoxides* (*Acadoparadoxides*) *oelandicus* from the Holy Cross Mountains after Żylińska & Masiak (2007)

	P. (A.) cf. mureroensis	*P. (A.) oelandicus*
shape of anterior border	more curved	less curved
width of fixigenae (tr.)	narrower	wider
width of glabella in the middle of the palpebral lobes (tr.)	narrower	wider
shape of frontal lobe of glabella	more rounded	less rounded
shape of S1 and S2 furrows	curving posteriorly in the middle of the glabella	straight

tectonic shortening along the axis, therefore this character is inappropriate for distinguishing between the taxa.

All the characters listed for specimens from Brzechów assigned to *Paradoxides* (*Acadoparadoxides*) *oelandicus* and *Paradoxides* (*Acadoparadoxides*) cf. *mureroensis* by Żylińska & Masiak (2007) follow the same pattern: the specimens assigned to *Paradoxides* (*Acadoparadoxides*) cf. *mureroensis* are always narrower (Table 4). Owing to the presence of tectonic deformation, these differences are insufficient to distinguish between the taxa. The difference in the shape of glabellar furrows can be noted on only one specimen and seems to be rather an artefact than a true character.

Pygidia from Jugoszów–Usarzów were assigned to two distinct morphotypes. *Paradoxides kozlowskii* differs from *Paradoxides samsonowiczi* in the expression of several characters so that in this case the differentiation described by Orłowski (1959*a*, 1964) appears to be correct. A single pygidium from Brzechów (Żylińska & Masiak, 2007, fig. 11j) is unfortunately incomplete; the posterior part is missing, making a precise taxonomic assignment impossible.

None of the pygidia from Jugoszów–Usarzów can be assigned to Scandinavian species that were described on the basis of cranidia. Moreover, the previously suggested diversities of cranidia and of pygidia are not compatible with one another. The diversity of the pygidia suggests that there should be two morphotypes of cranidia, whereas the number of distinguished morphotypes of cranidia is much larger. Cranidia assigned by Orłowski (1959*a*, 1964) to *Paradoxides torelli* may be excluded from this analysis. Their abundance is very low (unlike the abundance of pygidia and other morphotypes of cranidia). Additionally, they bear features that appear to suggest their assignment to different genera than the pygidia (see Section 7 below).

5. Morphometric analysis

In order to determine morphotypes in tectonically deformed specimens, a PCA was performed using landmarks and semi-landmarks on the glabellae. In the first analysis, 27 specimens from Jugoszów–Usarzów were processed. Previous assignments of the analysed dataset include (names according to labels): 13 specimens of *Paradoxides* (*Acadoparadoxides*) *oelandicus*, six specimens of *Paradoxides* (*Acadoparadoxides*) *pinus*, four specimens of *Paradoxides* (*Acadoparadoxides*) cf.

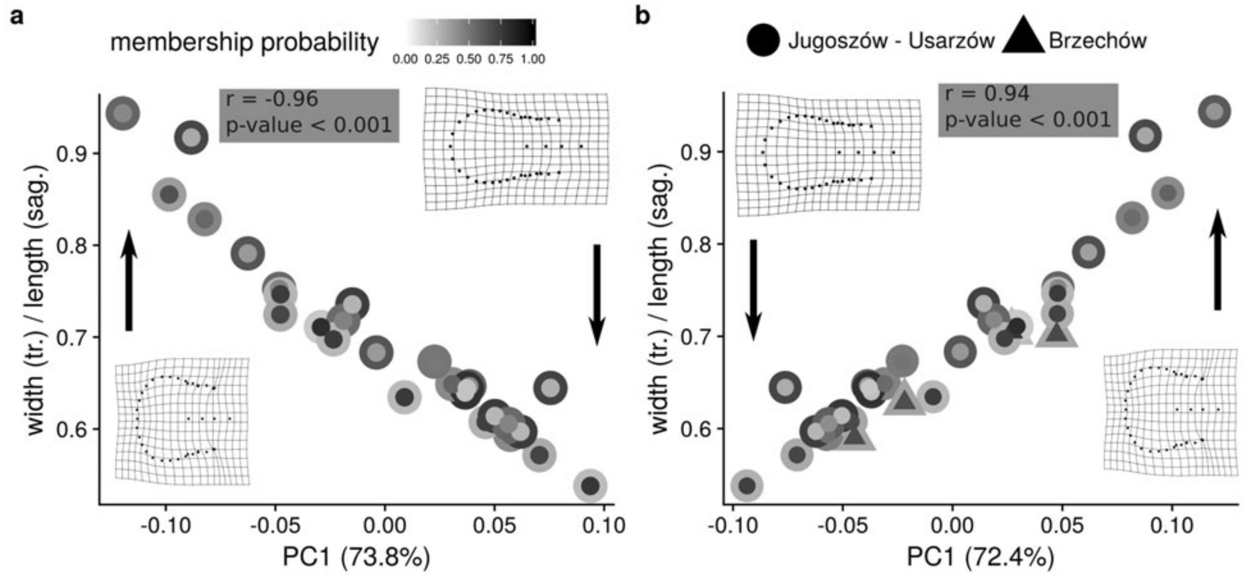

Figure 9. Correlation of PC1 with glabellar proportions with thin plate splines showing glabellar shapes corresponding to the minimum and maximum value of PC1, for (a) specimens from Jugoszów–Usarzów, and (b) specimens from Jugoszów–Usarzów and Brzechów combined. Inner circle represents the probability of being a member of morphotype A (*Acadoparadoxides samsonowiczi*); outer circle represents the probability of being a member of morphotype B (*Acadoparadoxides kozlowskii*).

Table 5. Eigenvalues and proportion of variance for the first ten PCs obtained for specimens from Jugoszów–Usarzów

Component	Eigenvalue	Proportion of variance	Cumulative proportion
PC1	0.0593	73.82 %	73.82 %
PC2	0.0227	10.81 %	84.63 %
PC3	0.0150	4.70 %	89.33 %
PC4	0.0108	2.44 %	91.77 %
PC5	0.0098	2.01 %	93.78 %
PC6	0.0090	1.69 %	95.46 %
PC7	0.0074	1.15 %	96.61 %
PC8	0.0064	0.87 %	97.48 %
PC9	0.0051	0.54 %	98.02 %
PC10	0.0048	0.48 %	98.50 %

mureroensis, three specimens of *Paradoxides* (*Eccaparadoxides*) *insularis* and one specimen of *Paradoxides czarnockii*. The first component is responsible for 74 % of variance (Table 5) in the sample and is associated with the length:width proportions of the glabella (correlation: $r = -0.96$; Fig. 9a); thus it may be treated as variance caused primarily by tectonic deformation. After removing PC1, the rest of the components represent a sufficient approximation of the diversity of the glabellae (as proven in the simulations). The diversity of the pygidia suggested that at least two morphotypes of cranidia should be detectable in the sample. Since PC2 was not connected with deformation (correlation with the length:width proportions of the glabella: $r = 0.23$, p-value = 0.24) nor with ontogeny (correlation with centroid sizes: $r = 0.03$, p-value = 0.87) and represented 10.81 % of the variation, it should contain the major morphological diversity. To discover the morphotypes that would potentially be present in the sample, we applied a fuzzy C-Means Clustering algorithm (for details see description of the *cmeans* function in Meyer *et al*. 2017). To check the best number of clusters we performed 1000 repetitions of the procedure, each time calculating the partition coefficient, the partition entropy and the proportion exponent (for details see description of the *fclustIndex* function in Meyer *et al*. 2017). All indexes confirmed that the best outcome is obtained for two clusters (Fig. 10a). Fuzzy clustering allowed including all PC (except PC1) in the analysis and emphasized the presence of uncertainty in assigning the cranidia. As expected, PC2 was the component that subdivided the sample into two clusters. In the case of several specimens with middle values of PC2 it was not possible to validate their membership (the probabilities of belonging to both clusters were around 0.5), but in most cases the characters located on the other parts of the glabellae allowed such assignment. In two cases (specimens MWGUW ZI/29/3289 and MWGUW ZI/29/3323), characters other than the glabella suggested the assignment to morphotype B, despite the slightly higher probability of being the member of the morphotype A cluster; in the systematic part this is expressed with a question mark. Assignment of one specimen (MWGUW ZI/29/3378) remains unclear. As shown on the PC2 and PC3 scatterplot, the first group (morphotype A) contains widening-forward glabellae, with rather straight lateral margins, and the second group (morphotype B) contains glabellae with (sub)parallel lateral margins in the posterior portion and a bulb-shaped frontal portion (Fig. 11a). It should be emphasized that in this case the number of morphotypes of cranidia in the analysed succession corresponds with the number of morphotypes of pygidia. Both morphotypes of pygidia and both morphotypes of cranidia occur in the lower part of the Jugoszów–Usarzów succession, whereas pygidia described as *Paradoxides kozlowskii* and cranidia with bulb-shaped glabellae occur in its upper part.

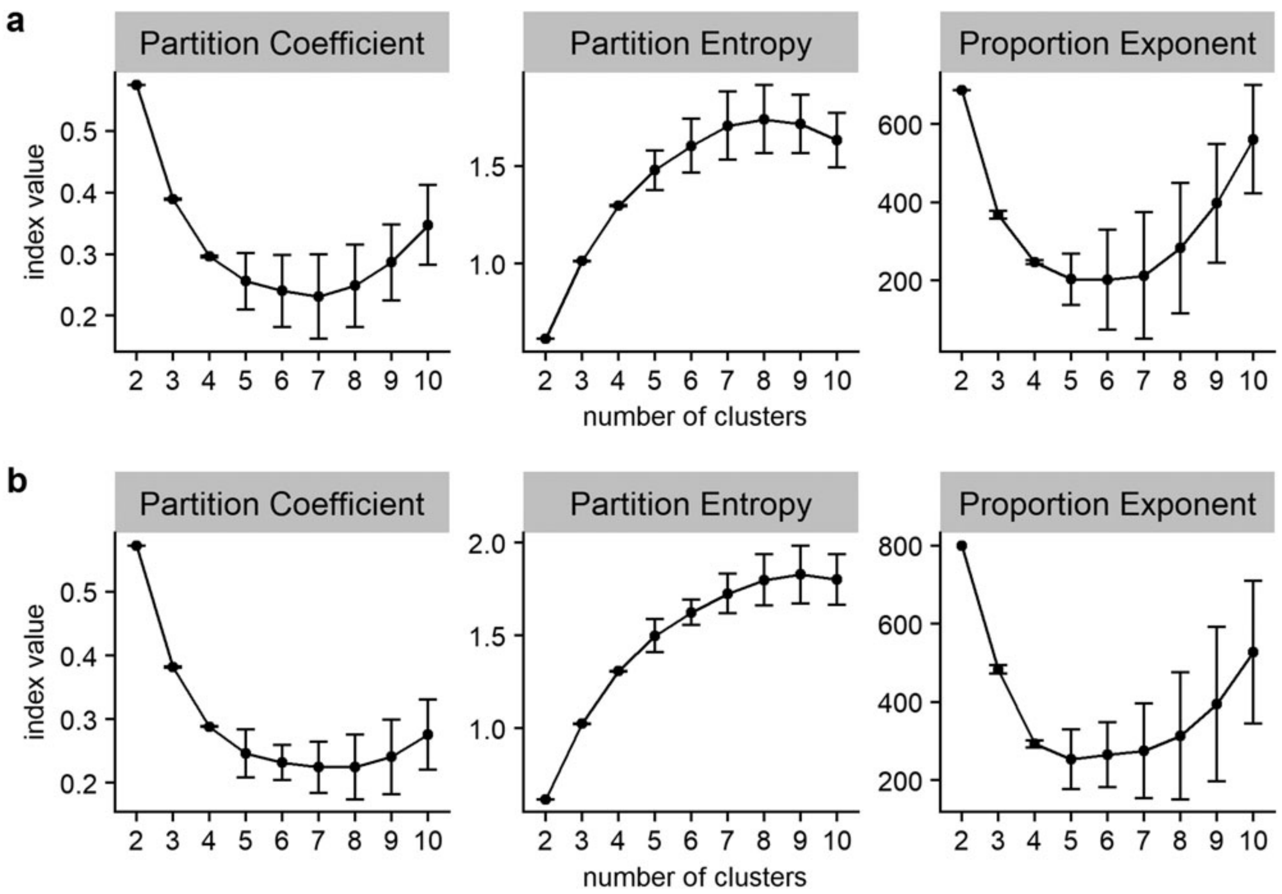

Figure 10. Results of 1000 tests of fuzzy c-means clustering validate indexes (partition coefficient: highest best; partition entropy: lowest best; and proportion exponent: highest best) for (a) specimens from Jugoszów–Usarzów, and (b) specimens from Jugoszów–Usarzów and Brzechów combined. Points indicate the mean values, error bars indicate the range of ±3 standard deviations.

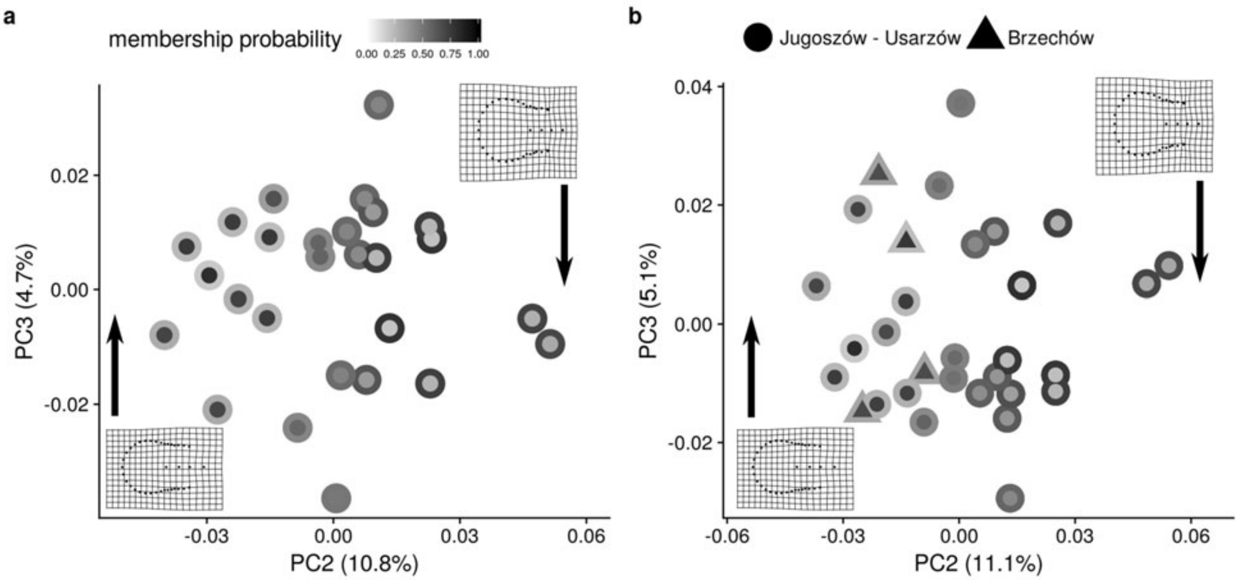

Figure 11. Scatterplots showing the relationship of PC2 and PC3 with thin plate splines showing glabellar shapes corresponding to the minimum and maximum value of PC2. (a) Specimens from Jugoszów–Usarzów; (b) specimens from Jugoszów–Usarzów and Brzechów combined. Inner circle represents the probability of being a member of morphotype A (*Acadoparadoxides samsonowiczi*); outer circle represents the probability of being a member of morphotype B (*Acadoparadoxides kozlowskii*).

Table 6. Eigenvalues and proportion of variance for the first ten PCs obtained for specimens from Jugoszów–Usarzów and Brzechów combined

Component	Eigenvalue	Proportion of variance	Cumulative proportion
PC1	0.0568	72.39 %	72.39 %
PC2	0.0222	11.05 %	83.44 %
PC3	0.0151	5.14 %	88.58 %
PC4	0.0108	2.62 %	91.20 %
PC5	0.0098	2.14 %	93.34 %
PC6	0.0088	1.75 %	95.09 %
PC7	0.0072	1.18 %	96.26 %
PC8	0.0063	0.88 %	97.15 %
PC9	0.0049	0.54 %	97.69 %
PC10	0.0047	0.50 %	98.19 %

Four specimens from Brzechów (two previously assigned to *Paradoxides* (*Acadoparadoxides*) *oelandicus* and two previously assigned to *Paradoxides* (*Acadoparadoxides*) cf. *mureroensis*)) were added to the analysed sample, and the PCA was repeated (Table 6). The interpretations are robust: the first component still has the same features that allow it to be interpreted (with the same reservations as in the previous analysis) as resulting from tectonic deformation (correlation: $r = 0.94$; Fig. 9b). Moreover, the subdivision between the two morphotypes of glabellae is also present. All specimens from Brzechów can be assigned to morphotype A, with specimens having a glabella that widens forwards and has straight lateral margins. This assignment can be seen on the scatterplot of PC2 and PC3 (Fig. 11b). In this case, PC2 is still uncorrelated with deformation (correlation with the length:width proportions of the glabella: $r = 0.27$, p-value = 0.14) or ontogeny (correlation with centroid sizes: $r = 0.16$, p-value = 0.38). Again, fuzzy clustering provided the best results for two clusters (Fig. 10b). The PCA scores from the full set of specimens with PC1 excluded have also been visualized using NMDS (Fig. 12). The stress for the scaling was 0.13, which is an acceptable value (Clarke, 1993). The absence of the 'bulb-shaped' glabellae in Brzechów may suggest that the strata containing only one morphotype (glabellae with parallel sides) are older than the strata from the Jugoszów–Usarzów succession, which conforms with the conclusions in Żylińska & Masiak (2007) and Żylińska & Szczepanik (2009).

As mentioned earlier, ontogenetic development is unlikely to have influenced the outcome of the morphometric analysis. Sizes of the glabellae (sagittal length of the glabella with occipital ring) included in the analysis varied from 7 to 30 mm for morphotype A and from 6 to 34 mm for morphotype B.

The presence of two species (and one additional taxon, previously described as *Paradoxides torelli* in the studied samples) is supported by the diversity of both cranidia and pygidia. The differences in the cranidia are very subtle, so assignment is often difficult. The differences in the pygidia are much more obvious. It is important to emphasize that the preservation of the material does not allow for a more detailed description, but it cannot be excluded that the true diversity is higher. Recognition of cryptic species may be possible only with careful and precise collection of samples from the continuous section, such as the one described from Morocco by Geyer & Vincent (2015); thus the diversity presented herein seems to be the best hypothesis based on presently available data.

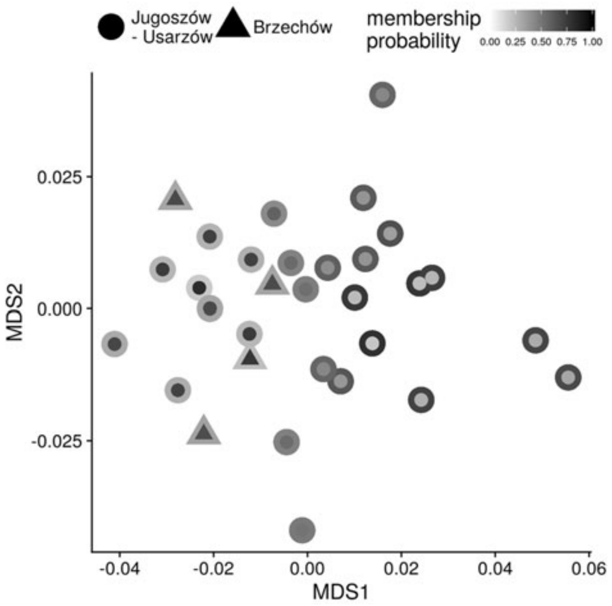

Figure 12. Visualization of PCA (with PC1 excluded) using NMDS for the studied specimens. Inner circle represents the probability of being a member of morphotype A (*Acadoparadoxides samsonowiczi*); outer circle represents the probability of being a member of morphotype B (*Acadoparadoxides kozlowskii*).

6. Institutional abbreviations and terminology

MWGUW: Stanisław Józef Thugutt Geological Museum (Muzeum Geologiczne im. Stanisława Józefa Thugutta), Faculty of Geology, University of Warsaw, Warsaw, Poland; **WK**: collection of Wojciech Kozłowski in the archives of the Department of Historical and Regional Geology, Institute of Basic Geology, Faculty of Geology, University of Warsaw, Warsaw, Poland. The terminology used herein follows that used in Whittington (1997).

7. Systematic descriptions

Class TRILOBITA Walch, 1771
Order REDLICHIIDA Richter, 1932
Family PARADOXIDIDAE Hawle & Corda, 1847
Genus *Acadoparadoxides* Šnajdr, 1957

Type species. *Paradoxides sacheri* (Barrande, 1852) from the Cambrian of Bohemia; SD by Šnajdr (1957, p. 146).

Diagnosis. For characters defining *Acadoparadoxides*, see Geyer & Vincent (2015).

Remarks. Modern ideas about *Acadoparadoxides* in general follow the original concept of Šnajdr (1957, 1958), modified by Sdzuy (1967) and Šnajdr (1986, 1987), although the subdivision between *Acadoparadoxides* (*Acadoparadoxides*) and *Acadoparadoxides* (*Baltoparadoxides*) as indicated in the treatise (Dean & Rushton, 1997, pp. *O*474–5) has recently been criticized by Geyer & Vincent (2015). This paper generally follows the summarized concept provided by the latter authors, although another subdivision within this genus that may have strong impact on biostratigraphic interpretations is demonstrated below.

Species assigned to this genus from Morocco (Geyer, 1993, 1998; Geyer & Vincent, 2015), Spain (Sdzuy, 1958), Turkey (Dean, 2005), Newfoundland (Geyer & Landing, 2001) and possibly Siberia (specimens described as other genera in Solov'ev, 1969; see discussion in Geyer & Vincent, 2015) differ significantly from the taxa described from the Czech Republic (Šnajdr, 1957, 1958, 1986, 1987) and from Scandinavia (e.g. Weidner, Rushton & Ebbestad, 2014). The main differences are as follows: the species from Bohemia and especially the species from Scandinavia have the anterior part of the cranidial border narrower (tr.) in comparison to the total width (tr.) of the cranidium in the middle point of the palpebral lobes; and the palpebral lobes of the Czech and Scandinavian taxa are wider (tr.), longer (exsag.) and more strongly curved. Important differences are displayed between the pygidia of Scandinavian species and other acadoparadoxidines. The variety of Scandinavian pygidia includes rounded or slightly elongated forms with spines (*Acadoparadoxides oelandicus* and *Acadoparadoxides bidentatus* (Westergård, 1936)); hexagonal forms with an optional indentation in the posterior margin (*Acadoparadoxides torelli* (Westergård in: Asklund & Thorslund, 1935)); and elongated forms with an indentation in the posterior margin (*Acadoparadoxides pinus* (Westergård, 1936)). In comparison, acadoparadoxidines from other regions have rounded, suboval or pyriform pygidia without spines. Geyer & Vincent (2015) proposed a cladogram for acadoparadoxidine pygidia that includes only non-Scandinavian species. This grouping seems to be quite well defined, although it has not been tested with phylogenetic analysis. Phylogenetic relations between this group and the Scandinavian acadoparadoxidines remain unclear and in fact the latter group has many characters in common with the genus *Eccaparadoxides* Šnajdr, 1957, especially with the Scandinavian species *Eccaparadoxides insularis* and *Eccaparadoxides*? *thorslundi* Rushton, Weidner & Ebbestad, 2016, and with the Scandinavian taxa assigned to *Hydrocephalus* (i.e. *H. vikensis* Rushton & Weidner, 2007 and *H. spinulosus* Rushton, Weidner & Ebbestad, 2016). True relations between Scandinavian taxa need a phylogenetic revision, but it is probable that *A. torelli*, *E*?. *thorslundi*, *H. vikensis* and *H. spinulosus* may form one clade.

A possible revised internal subdivision of *Acadoparadoxides* should be developed with phylogenetic data. Until then, informal grouping may be applied, with the major groups described as follows:

1. The earliest acadoparadoxidines comprising species with a wider (tr.) anterior part of the cranidium, smaller and thinner (tr.) palpebral lobes and pygidia that are rounded, suboval or pyriform. This group includes: *Acadoparadoxides briareus* Geyer, 1993, *Acadoparadoxides levisettii* Geyer & Vincent, 2015, *Acadoparadoxides* cf. *mureroensis*, *Acadoparadoxides nobilis* Geyer, 1998, *Acadoparadoxides ovatopyge* Geyer & Vincent, 2015 and *Acadoparadoxides pampalius* Geyer & Vincent, 2015, from Morocco and partially from Spain*; *Acadoparadoxides deani* Geyer & Vincent, 2015 from Turkey; and *Acadoparadoxides harlani* (Green, 1834) from Newfoundland. Some Siberian species may be included in this group, but a major revision of this material is necessary. The species from the Holy Cross Mountains presented herein also fit well in this group and are the first taxa assigned to this group that come from outside Gondwana.

2. The later group of acadoparadoxidines is much more diverse. It includes species with a narrower (tr.) anterior part of the cranidium and wider (tr.), longer (exsag.) and slightly more curved palpebral lobes. The pygidia in the Bohemian taxa (*Acadoparadoxides sacheri* and *Acadoparadoxides sirokyi* (Šnajdr, 1986)) are rounded and quite similar to the later species from the first group (e.g. *Acadoparadoxides harlani*). The pygidia of the Scandinavian forms include various shapes: rounded or slightly elongated forms with spines, hexagonal forms with a variably present indentation in the posterior margin, and elongated forms with an indentation in the posterior margin. It is probable that this group contains several clades, and a phylogenetic analysis should be performed to resolve this problem. Nevertheless, these species differ significantly from representatives of the first group.

The relations, both phylogenetic and palaeobiogeographic, between these two groups remain unclear.

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*We follow here the description of taxa provided by Geyer & Vincent (2015), despite a paper published recently by Álvaro, Esteve & Zamora (2017). The latter paper suggests that all the species from Morocco *sensu* Geyer & Vincent (2015), except *A. nobilis*, together with the material from Spain form a single taxon, *Acadoparadoxides mureroensis*. This assumption is based on the inability to detect differences with application of geometric morphometrics. Such a conclusion is inappropriate, since not detecting the differences is not a proof of conspecificity, but only a proof that the applied technique does not detect differences (separately from the presence/absence of differences). Such a case should be treated similarly to the case of not rejecting the null hypothesis in statistics – it is not equal to the confirmation of the null hypothesis. Moreover, the analysis presented in the cited paper (Álvaro, Esteve & Zamora, 2017) ignores deformation related to compaction, such as bending of the axis and changes in the shape of the glabella. Not detecting the taxa postulated by Geyer & Vincent (2015) may be an outcome of the overprinting of the biological signal by taphonomy (tectonic deformation and compaction), as well as ignoring some differences described in the original paper in the morphometric analyses (including the position and shape of the anterior branch of the facial suture).

Only their stratigraphic relations can be described, as reflected in the names of the groups (earlier versus later acadoparadoxidines), but the nature of how the older group was replaced by the younger group remains unknown. In Scandinavia, the lack of the earliest acadoparadoxidines could be caused by palaeobiogeographic factors (true absence of this group in Baltica), or by the lack of strata of similar age to the interval with the earliest acadoparadoxidines in Morocco, Spain and the Holy Cross Mountains (Hawke Bay unconformity; e.g. Nielsen & Schovsbo, 2015). Moreover, data about the later acadoparadoxidines from Morocco have never been published. In a broader view, the middle Cambrian fauna of Baltica (Scandinavia) and West Gondwana (Morocco) clearly seems to reflect different palaeobiogeographic regions, and the fossils from the Holy Cross Mountains are more closely related to the fauna from Morocco (see palaeobiogeographic part of the discussion).

Acadoparadoxides kozlowskii (Orłowski, 1959)
Figures 5b, 13

pars 1957 *Paradoxides* forms of the *ölandicus group*; Orłowski, figs 4, 6 (non figs 1–3 = *Acadoparadoxides slowiecensis*; non fig. 5 = *Acadoparadoxides samsonowiczi*).

pars 1959*a Paradoxides oelandicus* Sjögren, 1872; Orłowski, pp. 441–2, pl. 1, figs 1–3 (non fig. 4 = *Acadoparadoxides samsonowiczi*; non fig. 5 = Paradoxididae gen. et sp. indet.).

pars 1959*a Paradoxides pinus* Holm; Orłowski, p. 442, pl. 1, fig. 6 (non fig. 7 = *Acadoparadoxides samsonowiczi*; non fig. 8 = Paradoxididae gen. et sp. indet.).

1959*a Paradoxides insularis* Wgård [*sic*]; Orłowski, p. 443, pl. 2, figs 2, 3.

1959*a Paradoxides kozlowskii* n. sp.; Orłowski, p. 444, pl. 2, figs 6a, b, 7.

pars 1964 *Paradoxides oelandicus* Sjögren; Orłowski, pl. I, figs 3, 4, 6–8 [non fig. 5 = *Acadoparadoxides samsonowiczi*; non figs 1, 9–11 = Paradoxididae gen. et sp. indet.).

1964 *Paradoxides pinus* Holm; Orłowski, pl. II, figs 1–3.

1990 *Paradoxides kozlowskii* Orłowski, 1959; Bednarczyk, Lendzion & Orłowski, p. 58, pl. XVI, fig. 9.

2009 *Paradoxides* (*Acadoparadoxides*) *oelandicus* (Sjögren, 1872) [*sic*]; Żylińska & Szczepanik, pl. 4, fig. 7.

2009 *Paradoxides* (*Eccaparadoxides*) *insularis* Westergård, 1936; Żylińska & Szczepanik, pl. 4, fig. 8.

2009 *Paradoxides* (*Eccaparadoxides*) *pinus* Westergård, 1936; Żylińska & Szczepanik, pl. 4, fig. 9.

pars 2013*a Paradoxides* (*Acadoparadoxides*) *oelandicus* Sjögren, 1872; Żylińska, fig. 7A (non fig. 6F = *Acadoparadoxides samsonowiczi*).

2013*a Paradoxides* (*Eccaparadoxides*) *insularis* Westergård, 1936; Żylińska, fig. 7D.

2013*a Paradoxides* (*Eccaparadoxides*) *pinus* Westergård, 1936; Żylińska, fig. 7G.

Holotype. Pygidium MWGUW ZI/29/3217, illustrated as specimen no. 465 in Orłowski (1959*a*, pl. II, fig. 7) and Bednarczyk, Lendzion & Orłowski (1990, pl. XVI, fig. 9).

Other material. Thirty-seven cranidia: MWGUW ZI/29/3210, ZI/29/3211, ZI/29/3220, ZI/29/3222, ZI/29/3244, ZI/29/3250, ZI/29/3254, ZI/29/3255, ZI/29/3260, ZI/29/3280, (?) ZI/29/3289, ZI/29/3292, ZI/29/3298, ZI/29/3301, ZI/29/3305, ZI/29/3311, ZI/29/3316, ZI/29/3320, (?) ZI/29/3323, ZI/29/3324, ZI/29/3325, ZI/29/3328, ZI/29/3334, ZI/29/3338, ZI/29/3340, ZI/29/3343, ZI/29/3348-ZI/29/3350, ZI/29/3355, ZI/29/3357, ZI/29/3370, ZI/29/3392, ZI/29/3397, ZI/29/3406, ZI/29/3416, ZI/29/3428; eleven pygidia: MWGUW ZI/29/3266, ZI/29/3272, ZI/29/3286, ZI/29/3304, ZI/29/3319, ZI/29/3322, ZI/29/3335, ZI/29/3379, ZI/29/3383, ZI/29/3395, ZI/29/3413.

Occurrence. Cambrian Series 2 and 3 boundary interval (*Acadoparadoxides samsonowiczi – Acadoparadoxides kozlowskii* Assemblage Zone) in the Usarzów Sandstone Formation from the Jugoszów–Usarzów locality, eastern part of the Holy Cross Mountains, Poland.

Description. Cranidium wider (tr., measured across the widest point of the palpebral lobes) than long (sag.), *c.* 140 % of the cranidial length (sag.). Presence of tectonic deformation precludes providing exact range of proportions. Glabella pyriform, widening in the anterior part, anteriorly to S2. Occipital ring with small node at two-thirds of its length (sag.) from SO. Width (tr.) of L1 similar to or slightly larger than width (tr.) of occipital ring. Width (tr.) of L2 similar to or slightly larger than L1. Anterior part of glabella widens (tr.) forwards, widest (tr.) slightly anterior to S4; shape suboval, domed. In the widest (tr.) part reaching *c.* 132–150 % of the width (tr.) of the occipital ring. SO with lateral sections straight; central portion curving anteriorly. S1 bent adaxially, joined in the middle of glabella. S2 arched towards the anterior, also connected across the glabella. SO, S1 and S2 distinct, deep; S1 and S2 shallower and wider (sag.) in the middle part. Anterior margin of S1 in the middle part of glabella occasionally bent forward. S3 and S4 furrows indistinct, shallow and short. Posterior border furrow broad (exsag.). Posterior branch of facial suture shorter than anterior branch, rarely preserved, ε located very close to the posterior border furrow. Palpebral lobes well developed (32–46 % of the cranidial length (sag.)), arched, extending from posterior border furrow to S4. Palpebral lobes widest (tr.) in posterior part, narrower anteriorly, in anterior part forming a small arc towards the glabella. Palpebral furrows indistinct, slightly deeper in the posterior and

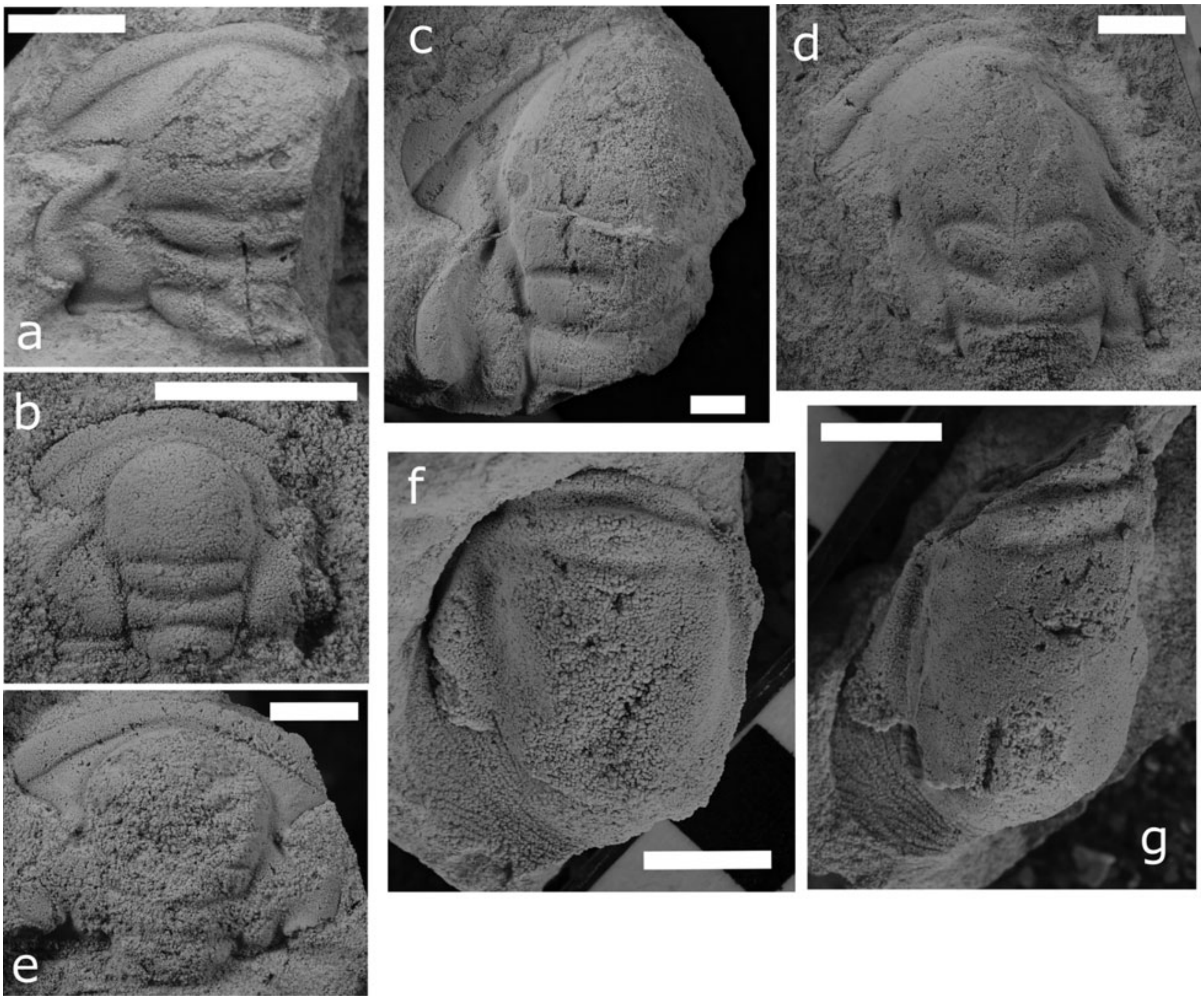

Figure 13. *Acadoparadoxides kozlowskii* (Orłowski, 1959). (a) MWGUW ZI/29/3210, original of Orłowski (1964), pl. 2, fig. 2 and Żylińska & Szczepanik (2009), pl. 4, fig. 9; (b) MWGUW ZI/29/3348, original of Orłowski (1964), pl. 2, fig. 3; (c) MWGUW ZI/29/3280; (d) MWGUW ZI/29/3311, original of Orłowski (1959*a*), pl. 1, fig. 1; (e) MWGUW ZI/29/3222, original of Orłowski (1964), pl. 2, fig. 1a–b; (f) MWGUW ZI/29/3266; (g) MWGUW ZI/29/3272, original of Orłowski (1959*a*), pl. 2, fig. 6a–b. Scale bars equal 5 mm.

anterior parts. Larger specimens with relatively smaller and less arched palpebral lobes (Fig. 13c). Fixigenae relatively wide (tr.), of more than half glabellar width (measured across the middle of the palpebral lobes). Anterior branches of facial sutures long, directed outwards and slightly forwards from anterior tips of ocular sutures, turning inwards to the front slightly posterior to anterior border furrow. Width (tr.) of anterior part of cranidium similar to width (tr.) of cranidium across centre of palpebral lobes, *c.* 129–156 % of the cranidial width (tr.) between the most abaxial positions of the ocular sutures. Anterior border wider (exsag.) than pre-glabellar field, slightly narrower (sag.) in front of glabella. Pre-glabellar field narrow (sag.), narrower (sag.) than the anterior border. Anterior border furrow distinct, slightly bent in the abaxial parts.

Pygidium pyriform, widening (tr.) posteriorly. Axial part wide (tr.) (wider than the pleural part), with single axial ring defined by furrows. Platform large, extending almost to posterior margin, with a constant width (tr.). Rhachis poorly marked on the available specimens, reaching three-quarters of pygidial length (sag.). Single pair of pleural furrows on pleural field. Lateral pygidial margins directed strongly backwards, curving strongly adaxially at the end of the platforms creating lobes on both sides. Posterior margin wide (tr.), straight or with small median indentation.

Remarks. Due to the mode of preservation (isolated elements), a reconstruction of the entire exoskeleton was not possible. However, the overlapping stratigraphic ranges of one cranidium morphotype and one pygidium morphotype (the pygidia were described by Orłowski 1959*a* as *Paradoxides kozlowskii*) in the upper part of the Jugoszów–Usarzów section allow a connection of these elements. As a result, they were assigned to *Acadoparadoxides kozlowskii*. The other cranidial and pygidial morphotypes are classified together as *Acadoparadoxides samsonowiczi* (see below for detailed description and discussion). Other parts of the exoskeleton were not diverse enough to discriminate them and to assign them to the described species.

Both *Acadoparadoxides kozlowskii* and *A. samsonowiczi* can be included in the earlier group of acadoparadoxidines as described above. Species from the Holy Cross Mountains are very similar to the taxa described from the Anti-Atlas of Morocco (Geyer, 1998; Geyer & Vincent, 2015) and from Spain (Sdzuy, 1958). From the Scandinavian (*A. oelandicus*, *A. pinus*, *A. torelli*) and Bohemian groups (*A. sacheri*, *A. sirokyi*), the cranidia of the species from the Holy Cross Mountains differ in possessing a wider (tr.) anterior part of the cranidium and narrower (tr.) palpebral lobes. The pygidia of the Polish species differ from the variety of Scandinavian morphotypes, whereas the pygidia of the Czech taxa have a more rounded shape compared to the Polish species.

Some specimens described herein as *Acadoparadoxides kozlowskii* were assigned by Orłowski (1959*a*) to *Paradoxides insularis*. This assignment is considered incorrect, because they differ from *Eccaparadoxides insularis* from Scandinavia (Westergård, 1936) in possessing a much wider (tr.) anterior border and much less distinct S3 and S4 furrows. In addition, the pygidium of the Polish species differs in shape from the elongated pygidium of *E. insularis* with a deep indentation on the posterior margin.

Acadoparadoxides kozlowskii is closely related to a number of Moroccan species (Geyer, 1998; Geyer & Vincent, 2015), although in some aspects it differs significantly enough to be distinguished from them. The material from Morocco is preserved in muddy fine-grained sandstones, thus the compaction of this material is much more extreme (the specimens are almost flat), likewise the preservation results in a different mode of deformation that includes cracking and bending of the test. These factors hamper comparisons and preclude the usage of advanced morphometric techniques (e.g. geometric morphometrics) in such comparisons. *Acadoparadoxides kozlowskii* differs from *Acadoparadoxides pampalius* in possessing slightly longer palpebral lobes that reach a bit further anteriorly. Palpebral lobes of the Polish species are also narrower (tr.) in the anterior part and slightly more bent. The anterior part of the glabella of *A. kozlowskii* is wider (tr.) in comparison to the rest of the glabella, but because this element is usually strongly deformed by compaction in the Moroccan specimens, this character should be treated with caution in the comparisons. The widest (tr.) part of the pygidium in *A. kozlowskii* is situated more posteriorly; the platform of *A. pampalius* is much shorter (sag.). *Acadoparadoxides kozlowskii* differs from *Acadoparadoxides levisettii* in the proportions of the anterior border width (tr.) versus the cranidial width (tr.) in the middle point of the palpebral lobes – in the Polish species these parameters are almost equal, whereas in the Moroccan species the anterior border width (tr.) is distinctly larger. The palpebral lobes are slightly shorter (exsag.) in *A. levisettii*. The pygidia are quite similar, but *A. kozlowskii* has a much longer (sag.) platform. The Polish species differs from *Acadoparadoxides* cf. *mureroensis* from Morocco in having slightly longer (exsag.) palpebral lobes. The pygidia of the two taxa differ distinctly in their outline, which is pyriform in *A. kozlowskii* and suboval in *A.* cf. *mureroensis*. From *Acadoparadoxides nobilis*, the species differs in a wider (tr.) posterior part of the glabella and less distinct curvatures on the outer parts of the anterior border. The pygidium of *A. nobilis* has a much larger posterior part of the pleural field, a very distinct indentation in the posterior margin and a shorter (sag.) platform. *Acadoparadoxides kozlowskii* has more arched palpebral lobes than *Acadoparadoxides ovatopyge*. In addition, the Polish species has more subparallel lateral margins of the glabella along L1. Pygidia of the two species differ in outline (pyriform in *A. kozlowskii*; suboval in *A. ovatopyge*), and the Moroccan species has a shorter (sag.) platform.

Differences between the cranidia of *A. kozlowskii* and *A. samsonowiczi* are not very distinct. The anterior part of glabella of *A. kozlowskii* expands laterally stronger than in *A. samsonowiczi*. The widest (tr.) part of the glabella in *A. kozlowskii* is located slightly anterior to S4, whereas in *A. samsonowiczi* it may sometimes lie slightly more posteriorly, between S3 and S4. The palpebral lobes of *A. kozlowskii* are slightly longer (tr.) and their anterior end lies closer to S4. The anterior margin of S1 is more strongly curved anteriorly in the median part of the glabella of *A. kozlowskii*. The adaxial curvature of the anterior branch of the facial suture lies closer to the anterior border furrow in *A. kozlowskii* (compare Fig. 13a, b, e with Fig. 14e). Pygidia of the two species can be easily distinguished by comparing their outlines: the pygidium of *A. kozlowskii* is pyriform, whereas that of *A. samsonowiczi* is suboval. In the latter species the widest (tr.) part of the pygidium lies in its middle, whereas in *A. kozlowskii* it is situated near the posterior end of the pygidium. The posterior margin of the pygidium of *A. samsonowiczi* is gently curved in comparison to the straight margin in *A. kozlowskii*. The differences between *A. kozlowskii* and *Acadoparadoxides slowiecensis* (Czarnocki, 1927*a, b*) (another acadoparadoxidine from the Holy Cross Mountains, previously known as *Paradoxides slowiecensis*; a revision will be provided in a subsequent paper – J. Nowicki & A. Żylińska in prep.) include: a wider (sag., exsag.) anterior border in *A. kozlowskii*; a less curved and wider (tr.) anterior part of the palpebral lobes in *A. slowiecensis*; a pre-glabellar field in adult specimens that is less reduced in *A. kozlowskii*; the pygidium with a larger, more distinct platform and a different, pyriform outline in *A. kozlowskii* compared to the suboval outline in the pygidial platform in *A. slowiecensis*.

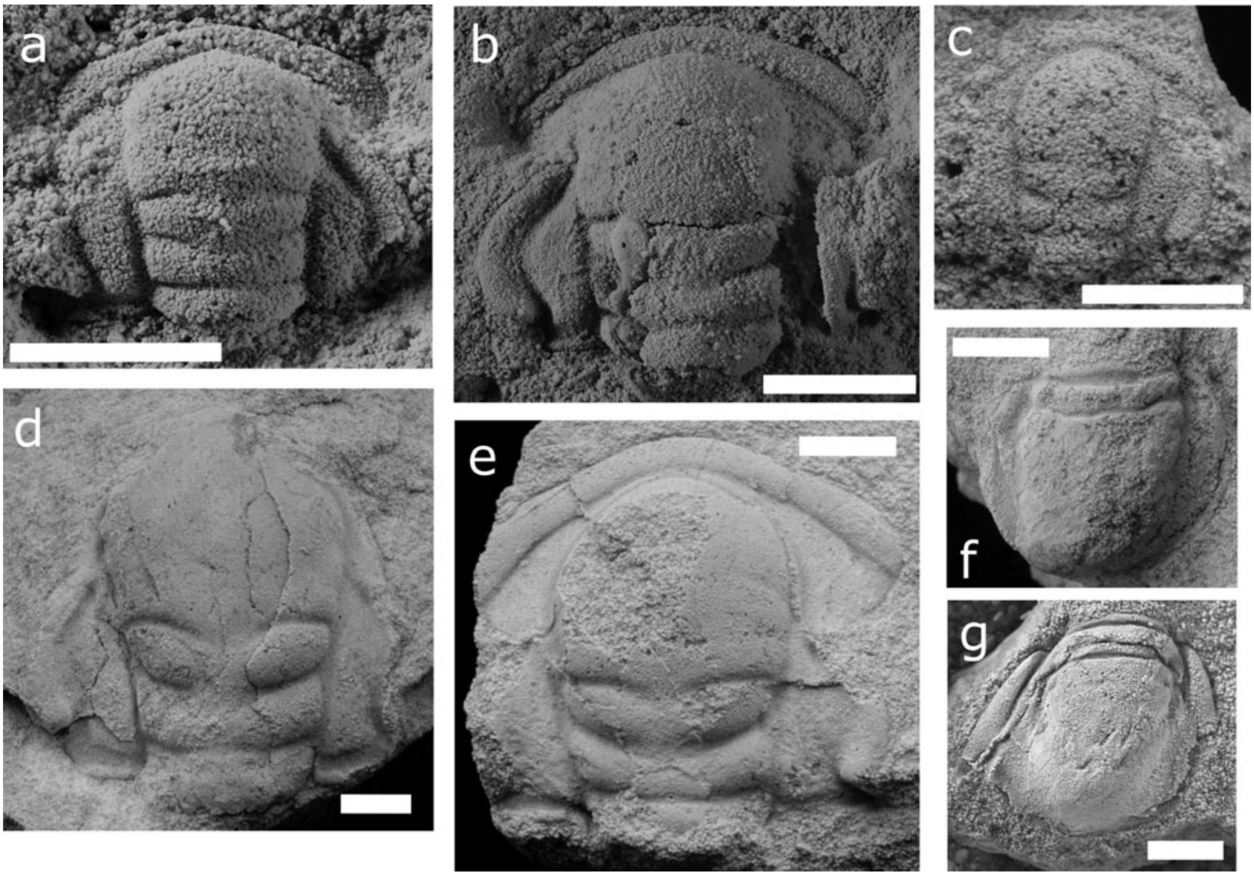

Figure 14. *Acadoparadoxides samsonowiczi* (Orłowski, 1959). (a) WK40, original of Żylińska & Masiak (2007), fig. 11c; (b) MWGUW ZI/29/0972, original of Żylińska & Masiak (2007), fig. 11a–b; (c) MWGUW ZI/29/0959, original of Żylińska & Masiak (2007), fig. 11g and Nawrocki *et al.* (2007), fig. 8.15; (d) MWGUW ZI/29/3288, original of Orłowski (1964), pl. 1, fig. 5; (e) MWGUW ZI/29/3212, original of Orłowski (1959*a*), pl. 2, fig. 4a–b and Żylińska & Szczepanik (2009), pl. 4, fig. 10; (f) MWGUW ZI/29/3246, original of Orłowski (1964), pl. 2, fig. 9; (g) MWGUW ZI/29/3218, original of Orłowski (1959*a*), pl. 2, fig. 8a–b (holotype). Scale bars equal 5 mm.

Acadoparadoxides samsonowiczi (Orłowski, 1959)
Figure 14

pars 1957 *Paradoxides* forms of the *ölandicus* group; Orłowski, fig. 5 (non figs 1–3 = *Acadoparadoxides slowiecensis*; non figs 4, 6 = *Acadoparadoxides kozlowskii*).

pars 1959*a Paradoxides oelandicus* Sjögren, 1872; Orłowski, pp. 441–2, pl. I, fig. 4 (non figs 1–3 = *Acadoparadoxides kozlowskii*; non fig. 5 = Paradoxididae gen. et sp. indet.).

pars 1959*a Paradoxides pinus* Holm; Orłowski, p. 442, pl. I, fig. 7 (non fig. 6 = *Acadoparadoxides kozlowskii*; non fig. 8 = Paradoxididae gen. et sp. indet.).

1959*a Paradoxides czarnockii* n. sp.; Orłowski, pp. 443–4, pl. II, figs 4, 5.

1959*a Paradoxides samsonowiczi* n. sp.; Orłowski, p. 445, pl. II, fig. 8a, b.

pars 1964 *Paradoxides oelandicus* Sjögren; Orłowski, pl. I, fig. 5 (non figs 3, 4, 6–8 = *Acadoparadoxides kozlowskii*; non figs 1, 9–11 = Paradoxididae gen. et sp. indet.).

1964 *Paradoxides czarnockii* Orłowski, 1959; Orłowski, pl. II, figs 6, 7.

1964 *Paradoxides samsonowiczi* Orłowski, 1959; Orłowski, pl. II, figs 8, 9.

1970 *Paradoxides oelandicus* Sjögren; Bednarczyk, p. 34, pl. 1, fig. 1.

1990 *Paradoxides czarnockii* Orłowski, 1959; Bednarczyk, Lendzion & Orłowski, p. 58, pl. XVI, fig. 6.

1990 *Paradoxides samsonowiczi* Orłowski, 1959; Bednarczyk, Lendzion & Orłowski, p. 58, pl. XVII, fig. 11.

2007 *Acadoparadoxides oelandicus* (Sjögren); Nawrocki *et al.*, fig. 8b.14.

2007 *Acadoparadoxides* cf. *mureroensis* (Sdzuy); Nawrocki *et al.*, fig. 8b.15.

2007 *Paradoxides* (*Acadoparadoxides*) cf. *mureroensis* (Sdzuy, 1958); Żylińska & Masiak, pp. 679, 681, fig. 11d, g.

2007 *Paradoxides* (*Acadoparadoxides*) *oelandicus* Sjögren, 1872; Żylińska & Masiak, pp. 681, 682, fig. 11a–c, e, i (non fig. 11f, h = Paradoxididae gen. et sp. indet.).

?2007 *Paradoxides* (*Acadoparadoxides*) sp.; Żylińska & Masiak, p. 682, fig. 11j.

2009 *Paradoxides* (*Acadoparadoxides*) *czarnockii* Orłowski, 1959a; Żylińska & Szczepanik, pl. 4, fig. 10.

pars 2013*a* *Paradoxides* (*Acadoparadoxides*) *oelandicus* Sjögren, 1872; Żylińska, fig. 6F (non fig. 7A = *Acadoparadoxides kozlowskii*).

2013*a* *Paradoxides* (*Acadoparadoxides*) *czarnockii* Orłowski, 1959; Żylińska, fig. 7J.

Holotype. Pygidium MWGUW ZI/29/3218, illustrated as specimen no. 3 in: Orłowski (1959*a*, pl. II, fig. 8a, b), and Bednarczyk, Lendzion & Orłowski (1990, pl. XVII, fig. 11).

Other material. Thirty-seven cranidia: WK36, WK40, WK59, MWGUW ZI/29/0959, ZI/29/0961, ZI/29/0962, ZI/29/0972, ZI/29/3212, ZI/29/3248, ZI/29/3249, ZI/29/3257, ZI/29/3259, ZI/29/3263, ZI/29/3288, ZI/29/3293, ZI/29/3294, ZI/29/3297, ZI/29/3299, ZI/29/3303, ZI/29/3307-ZI/29/3310, ZI/29/3312, ZI/29/3317, ZI/29/3318, ZI/29/3331, (?) ZI/29/3333, ZI/29/3346, ZI/29/3359, ZI/29/3369, ZI/29/3375, ZI/29/3387, ZI/29/3415, ZI/29/3419, ZI/29/3425, ZI/29/3443; five pygidia: MWGUW ZI/29/3245, ZI/29/3246, ZI/29/3247, ZI/29/3281, ZI/29/3313.

Occurrence. Cambrian Series 2 and 3 boundary interval (*Acadoparadoxides samsonowiczi* – *Acadoparadoxides kozlowskii* Assemblage Zone) in the Słowiec Sandstone Formation from Brzechów, central part of the Holy Cross Mountains, Poland; and Usarzów Sandstone Formation from the Jugoszów–Usarzów locality, eastern part of the Holy Cross Mountains, Poland.

Description. Cranidium wider (tr., measured across the widest point of the palpebral lobes) than long (sag.), around 140 % of the cranidial length (sag.). The presence of tectonic deformation precludes providing the exact range of proportions. Glabella with straight borders, widening (tr.) anteriorly quite evenly. Occipital ring with small node in the centre (tr.), in two-thirds of its length (sag.) from SO. LO is the narrowest (tr.) of the glabellar lobes, L1 slightly wider (tr.), L2 also wider (tr.), anterior part of glabella widest (tr.) anteriorly to S3, often (but not always) posteriorly to S4. Anterior part of the glabella suboval in outline, domed, widest (tr.) part reaching *c.* 130–151 % of the width (tr.) of the occipital ring. SO straight laterally, in the middle part arched anteriorly. SO, S1 and S2 distinct, deep. S1 transglabellar, shallowing medially and broadening (exsag., sag.). S2 also transglabellar, shallowing and broadening in the middle of the glabella. S3 and S4 shallow, indistinct and short. Posterior branches of facial sutures short, ε located very close to posterior border furrow. Palpebral lobes well developed (36–46 % of the cranidial length (sag.)), arched, extending from near posterior border furrow to frontal lobe of glabella, adjacent to S3 and S4, widest in posterior part and narrowing anteriorly. Palpebral lobes between S3 and S4 slightly curved forward to form arches directed to glabella. Palpebral furrows indistinct, slightly deeper in the posterior and anterior parts. Fixigenae quite wide (tr.), more than half glabellar width (measured across the middle of the palpebral lobes). Anterior branches of facial suture longer than posterior parts, directed abaxially and slightly anteriorly from anterior ends of ocular suture, then curving adaxially transversely opposite S4. Anterior width of the cranidium around 129–156 % of the cranidial width (tr.) between the most abaxial positions of the ocular sutures. Anterior border wider (exsag.) than pre-glabellar field, slightly narrower (sag.) in front of glabella. Preglabellar field narrower (sag.) than anterior border. Anterior border furrow distinct, with small bendings in the abaxial parts.

Pygidium suboval, widest (tr.) in the middle part. Axial part wide (tr.) (wider than the pleural part) with one axial ring moderately well defined by with furrows. Platform distinct, large (reaching almost to posterior margin of pygidium), with constant width (tr.). Rhachis indistinct, four-fifths of pygidial length (sag.). Pleural field with single pair of pleural furrows. Pygidial margin curved subevenly for the entire length.

Remarks. The correlation between morphotypes of pygidia and cranidia from the Jugoszów–Usarzów locality has been described in the remarks under *Acadoparadoxides kozlowskii*. Specimens from Brzechów have been assigned to *A. samsonowiczi*, but this assignment is uncertain because of the lack of complete pygidia. The only known pygidium from this locality lacks the posterior part, which is crucial for the determination. The cranidia from Brzechów fit well into the morphotype described as *A. samsonowiczi*, although the differences in the acadoparadoxidine cranidia are less distinct. Thus a diagnosis based solely on the cranidia is less reliable. This is also the reason for choosing the name for the species after the name given to the pygidia (*Paradoxides samsonowiczi*) and not for cranidia that were described in the same paper (Orłowski, 1959*a*) as *Paradoxides czarnockii*.

Acadoparadoxides samsonowiczi is closely related to *A. kozlowskii* and can also be assigned to the earliest group of acadoparadoxidines. The reasons for this assignment and the differences between this group and the species of *Acadoparadoxides* from Scandinavia and Bohemia are given in the remarks for *A. kozlowskii*. The differences between *A. samsonowiczi* and *Eccaparadoxides insularis* are also presented therein.

Like *Acadoparadoxides kozlowskii*, *A. samsonowiczi* resembles the species from Morocco (Geyer, 1998; Geyer & Vincent, 2015). The differences between the cranidia are subtle and difficult to recognize due to the different mode of preservation. Cranidia of *A. samsonowiczi* differ from *A. pampalius* in a less widening (tr.) anterior part of glabella. Also the anterior parts of the facial sutures have a different shape, bending towards the anterior much more anteriorly in *A. pampalius*. Palpebral lobes of *A. samsonowiczi* are slightly narrower (tr.) in the anterior part. Pygidia are similar in outline, but in *A. samsonowiczi* the platform is distinctly longer (sag.), almost reaching to the posterior margin of the pygidium. The cranidia of *A. samsonowiczi* differ from those of *A. levisettii* in proportions of the width (tr.) of the anterior margin of cranidium versus cranidial width (tr.) in the middle of the palpebral lobes. In the Polish species these dimensions are similar, whereas in the Moroccan species the anterior width (tr.) is larger. The curve in the anterior part of the facial suture is situated more anteriorly in *A. levisettii* (according to the position of the anterior border furrow). Pygidia differ in shape (suboval in *A. samsonowiczi* versus pyriform in *A. levisettii*). Moreover, the platform in the pygidium of the Moroccan species is shorter. The pygidial posterior margin in *A. samsonowiczi* lacks an indentation, which is sometimes developed in *A. levisettii*. The Polish species differs from *A.* cf. *mureroensis* from Morocco in possessing a less wide (tr.) anterior part of glabella. The pygidium of *A. samsonowiczi* has a longer (sag.) platform. The widest part of the pygidium is situated more posteriorly in *A.* cf. *mureroensis*. From *A. nobilis* the species from Poland differs in the shape of the anterior branch of the facial suture (in a similar way to *A. pampalius* and *A. levisettii*). The curvature in the outer part of the anterior margin furrow is slightly less distinct in *A. samsonowiczi*. The anterior part of the glabella is wider (tr.) in *A. nobilis*. The pygidia differ distinctly in their outline (pyriform with an indentation on the posterior margin in the Moroccan species versus suboval in the Polish species). The platform is longer (sag.) in *A. samsonowiczi*. From *A. ovatopyge*, the cranidia of *A. samsonowiczi* differ in possessing a smaller width (tr.) of the anterior part of the glabella and in the shape of the anterior branches of the facial sutures (similarly to the other Moroccan species). The pygidia are very similar, but those of the Polish species have a longer (tr.) platform.

The differences between *A. samsonowiczi* and *A. kozlowskii* have been pointed out in the description of the latter species. The differences between cranidia of *A. samsonowiczi* and *A. slowiecensis* are very similar to those between *A. kozlowskii* and *A. slowiecensis*. The pygidium of *A. samsonowiczi* is more similar to the pygidium of *A. slowiecensis*, but has a more circular outline in the latter species and the platform is distinctly larger in *A. samsonowiczi*.

Genus *Hydrocephalus* Barrande, 1846

Type species. *Hydrocephalus carens* Barrande, 1846 from the Cambrian of Bohemia, OD.

Hydrocephalus? sp.
Figure 15

1959*a* *Paradoxides torelli* Holm; Orłowski, p. 443, pl. II, fig. 1.

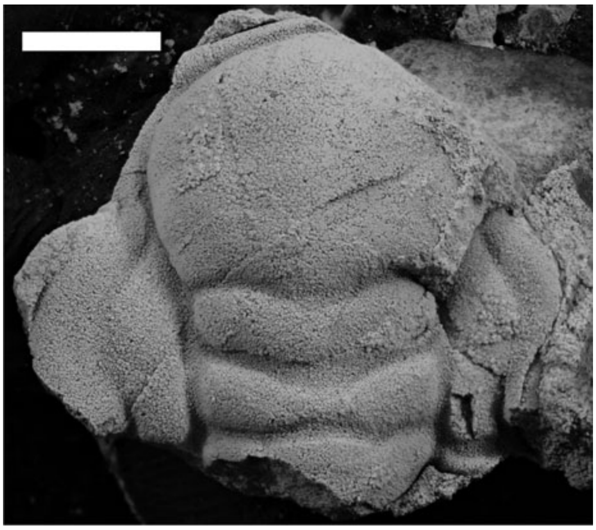

Figure 15. *Hydrocephalus*? sp. MWGUW ZI/29/3341, original of Orłowski (1964), pl. 2, fig. 4. Scale bar equals 5 mm.

pars 1964 *Paradoxides torelli* Holm; Orłowski, pl. II, fig. 4 (non fig. 5 = Paradoxididae gen. et sp. indet.).

Material. Two fragmentary cranidia; MWGUW ZI/29/3341 and ZI/29/3414.

Occurrence. Cambrian Series 2 and 3 boundary interval (*Acadoparadoxides samsonowiczi* – *Acadoparadoxides kozlowskii* Assemblage Zone) in the Usarzów Sandstone Formation from the Jugoszów–Usarzów locality, eastern part of the Holy Cross Mountains, Poland.

Description. Specimens known only from fragments of cranidia, which show glabellae, fixigenae, palpebral lobes and part of the anterior margin. Glabella pyriform, strongly widening (tr.) anteriorly from S2. Small node situated on occipital ring, near its posterior margin. Widths (tr.) of LO, L1 and L2 similar. Anterior part large, suboval, domed, widest anterior to S4. SO distinct, deep, straight laterally, curving anteriorly in the median part. S1 and S2 distinct, deep, transglabellar, shallow in the middle of the glabella. S1 straight, directed posteriorly from near axial furrows, in the middle part almost orthogonal to axis. S2 arched anteriorly. S3 and S4 short and indistinct. Posterior border furrow wide (exsag.). Length of posterior branches of facial sutures unknown. Fixigenae wide (tr.), up to 60 % of glabellar width (tr.) (measured across the middle of the palpebral lobes). Palpebral lobes of smaller specimen long, with nearly equal curvature of abaxial and adaxial margins, but with small additional flexure in the anterior parts, widest in the central section, tapering towards both ends. Palpebral furrow quite shallow, but well defined. Palpebral lobes extend from posterior margin furrows to glabella at L4. Palpebral lobes of larger specimen shorter and narrower in relative size, but similar in shape. Anterior margin unknown except for the part in front of the glabella, which tapers distinctively towards the sagittal line. Pre-glabellar field absent.

Remarks. Two specimens from the Jugoszów–Usarzów locality do not fit with the characters seen in *Acadoparadoxides samsonowiczi* and *A. kozlowskii*. The differences include the shape of the palpebral lobes (wider in the smaller specimen and more reduced in the larger specimen compared to the two acadoparadoxidine species) and the anterior margin (which is distinctly wider in the two species). In addition, the glabellae of these two specimens are narrower (tr.) in the posterior parts.

Weidner, Rushton & Ebbestad (2014) pointed out that specimens described previously by Orłowski (1959*a*, 1964) as *Paradoxides torelli* do not match the characters of this species. The shape of the anterior border, the palpebral lobes of the larger specimen and the shape of the glabella suggest that these specimens may be assigned to *Hydrocephalus*, although poor preservation precludes a confident assignment. Moreover, the genus *Hydrocephalus* is in need of a revision (J. Nowicki, unpub. Ph.D. thesis, Univ. Warsaw, 2016; J. Nowicki & A. Żylińska in prep.), and this assignment should be regarded as an interim solution.

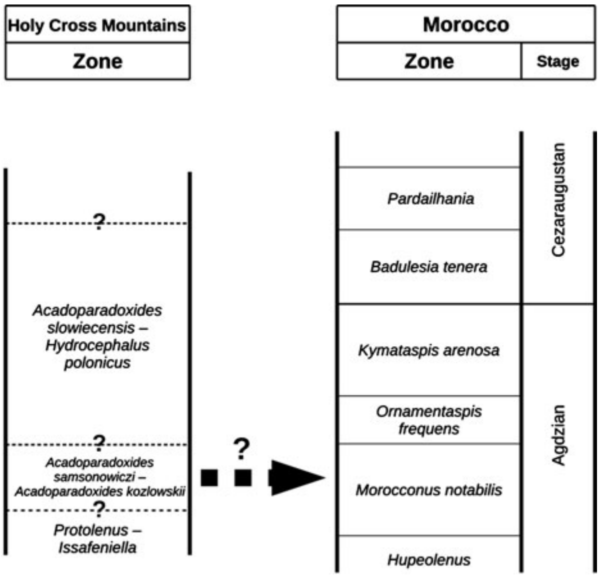

Figure 16. Revised biostratigraphic scheme for the Cambrian Series 2 and 3 boundary interval in the Holy Cross Mountains (Poland) and its correlation with the biostratigraphic scheme for the same interval in Morocco (right column; Geyer & Landing, 2006). The name of the uppermost zone in the Holy Cross Mountains is after J. Nowicki (unpub. Ph.D. thesis, Univ. Warsaw, 2016) and J. Nowicki & A. Żylińska (in preparation).

8. Implications for biostratigraphy and palaeobiogeography

8.a. Biostratigraphy

Revision of the paradoxidids from Brzechów and from the Jugoszów–Usarzów locality has major impact on the biostratigraphic scheme for the Holy Cross Mountains in the analysed stratigraphic interval. The former biozones, *Eccaparadoxides insularis* and *Ptychagnostus praeccurens* – *Acadoparadoxides pinus* (see e.g. Orłowski, 1992; Żylińska, 2013*a*), cannot be used further, since the species that were used to define them are not present in the analysed succession. The traditional 'Middle' Cambrian interval of the Holy Cross Mountains is replete with endemic trilobite species, and the paradoxidids also follow this trend. Correlation on the species level is impossible, so a new local biozonation has to be developed. The new scheme is also based on paradoxidids, the remaining trilobites being of much lower stratigraphic resolution (Żylińska & Szczepanik, 2009). Although the previous scheme included two zones, the boundary between them cannot be maintained; according to the revised systematics, it would be determined by the last appearance datum (LAD) of *A. samsonowiczi* so that the stability of this boundary is questionable. Placing the zonal boundary on the first appearance datum (FAD) of *A. kozlowskii* is also inappropriate. This bioevent probably lies between the interval represented in Brzechów and the interval represented in the Jugoszów–Usarzów locality, and its true position remains unrecognized. Moreover, the material from Brzechów, assigned to *A. samsonowiczi*, consists only of cranidia so that the assignment of these specimens is less confident. The present state of knowledge allows determining the *Acadoparadoxides samsonowiczi* – *Acadoparadoxides kozlowskii* Assemblage Zone encompassing both ranges of these species. The paradoxidids are accompanied by several other trilobite species. *Conomicmacca kielcensis* and '*Palaeolenus*' *medius* occur only in Brzechów and may suggest the lower part of the *Acadoparadoxides samsonowiczi* – *Acadoparadoxides kozlowskii* Assemblage Zone.

Correlation of the *Acadoparadoxides samsonowiczi* – *Acadoparadoxides kozlowskii* Zone is difficult, but not impossible. It has been done partly by Żylińska & Masiak (2007), Żylińska & Szczepanik (2009) and summarized in Żylińska (2013*a*) (see also Sundberg *et al.* 2016). Correlation of the Brzechów trilobites with the *Morocconus notabilis* Zone of Morocco is also supported by the revised paradoxidids. Both *A. samsonowiczi* and *A. kozlowskii* fit very well in the earliest group of acadoparadoxidines described above. These species are endemic; however, they are closely related to the Moroccan species described by Geyer & Vincent (2015). This relationship and the differences between the forms from the Holy Cross Mountains and Scandinavia also permit correlation of the Jugoszów–Usarzów succession with the *Morocconus notabilis* Zone (Fig. 16). The occurrence of acadoparadoxidines in the upper part of the *Morocconus notabilis* Zone in the Anti-Atlas successions (Geyer & Vincent, 2015) suggests that the analysed sequence from the Holy Cross Mountains may be related to this part. Exact correlation is impossible, but the presented resolution is sufficient to show that the analysed interval is older than considered previously (e.g. Orłowski, 1992) and, according to the recent report on the Cambrian Series 2 and 3 boundary (Sundberg *et al.* 2016), in fact at least partially represents Cambrian Series 2 if the FAD of *Oryctocephalus indicus* is chosen to define the base of Series 3. Therefore, the boundary between Cambrian Series 2 and 3 in the Holy Cross Mountains would fall within the newly proposed *Acadoparadoxides samsonowiczi – Acadoparadoxides kozlowskii* Zone, but cannot be precisely indicated. The absence of *Acadoparadoxides* cf. *mureroensis* in the Holy Cross Mountains confirms that this species is not as widely dispersed as assumed previously by some authors (Gozalo *et al.* 2013). New data from the Holy Cross Mountains support rather the view presented by Geyer & Vincent (2015).

8.b. Palaeobiogeography

The faunistic connection of the paradoxidids from the Holy Cross Mountains with taxa from West Gondwana fits well in the general trend of biogeographic affinities of the trilobites from the studied interval. The diversity of the ellipsocephalids is very similar to that known from West Gondwanan and Avalonian successions (Żylińska & Szczepanik, 2009; Żylińska, 2013*a*); of similar affinities is also *Conomicmacca kielcensis* from Brzechów (Geyer & Landing, 2004; Żylińska & Masiak, 2007; Elicki & Geyer, 2013). Since there are no direct faunal links with Baltica, the occurrence of such exotic fauna has to be resolved. Fairly recent palaeogeographic reconstructions by Torsvik & Cocks (2013) indicate that the distance between the present Anti-Atlas region and the putative location of the Małopolska Block near the western margin of Baltica does not support the possibility of dispersion that would lead to the presence of Gondwana-derived fauna in the Holy Cross Mountains succession. The position of the Małopolska Block in the neighbourhood of Baltica, proven in various ways (Nawrocki *et al.* 2007), is still a matter of discussion (e.g. Walczak & Belka, 2017). The position of Gondwana and Baltica presented by Torsvik & Cocks (2013) is also questionable, due to the extreme movement of West Gondwana from low latitudes that favoured the existence of a carbonate platform (e.g. Landing *et al.* 2013) with archaeocyathan reefs (Kerner & Debrenne, 2013) in Cambrian Epoch 2 to the South Pole in Cambrian Epoch 3 (Torsvik & Cocks, 2013). It is possible that the spatial relations between Baltica, the Małopolska Block and West Gondwana were different than previously believed. The dispersal of Gondwana/Avalonia-related trilobite taxa into the Małopolska Block could have been maintained by oceanic currents (Żylińska, 2013*a, b*), and if so, then the Małopolska Block should have faced West Gondwana. The occurrence of paradoxidids similar to those present in the Anti-Atlas successions in the Cambrian of the Holy Cross Mountains provides additional evidence for this interpretation. The possible configuration of Baltica with the adjacent Małopolska Block and with West Gondwana would include a different position of the Małopolska Block near Baltica, or Baltica facing Gondwana with its western margin; and a position of Baltica closer to the Atlas sector of West Gondwana in the Cambrian. The latter configuration implies the location of an oceanic current similar to that presented by Servais *et al.* (2014), but allowing for the transportation of trilobite larvae from the Gondwanan margin into the Baltic realm. The existence of a current transporting larvae is supported by the presence of the Gondwana-related species such as *Rectifrontinella olhae* Konstantinenko, 2001 (a member of the *Conomicmacca*/*Myopsolenites* clade: see Żylińska & Masiak, 2007), in the Ukraine (Carpathian Foredeep) (Drygant & Konstantinenko, 2001). The hypothesis of long transportation of paradoxidid larvae is also supported by a recent study by Laibl, Esteve & Fatka (2017), in which protaspids of Bohemian paradoxidids are interpreted as lecitotrophic larvae. This mode of life would make the larvae more able to survive transport and allow them to reach distant continental shelves like those of Baltica.

An alternative concept of the palaeogeographic position of the Małopolska Block during the Cambrian also does not resolve the apparent disparate distribution of the fauna. In this view, the Małopolska Block was a part of the Cadomian orogen bordering Amazonia that rifted from Gondwana before the early Cambrian and accreted to Baltica during Furongian–Tremadocian times (Sandomierz Phase) (Belka *et al.* 2002). This concept is supported by geochemical data (Walczak & Belka, 2017), suggesting a Gondwanan affinity of the detritic material with cooling ages similar to those of the Amazonian terrane basement, and by geophysical data that allow for a Cadomian interpretation of the Małopolska Block basement (Narkiewicz & Petecki, 2017). Nawrocki *et al.* (2007) also indicated a non-Baltic (Cadomian) age of the material from the middle Cambrian and younger strata, but their interpretation assumed supply of this type of material from the Uralid margin of Baltica and not from Gondwana. The data from Walczak & Belka (2017) are incomplete, as not all Cambrian localities have been analysed, for instance the Słowiec Hill. Belka *et al.* (2002) and Walczak & Belka (2017) also use the biogeographic interpretation of Cambrian brachiopods as evidence for early Cambrian connections with Gondwana and Avalonia, but the present knowledge about this group definitely does not allow such interpretation (Bassett, Popov & Holmer, 2002; Winrow & Sutton, 2014). Nevertheless, the possibility of West Gondwanan affinities of the Małopolska Block should be reconsidered, since the trilobite fauna has strong connections with taxa from this realm. Palaeomagnetic data support the position of the Małopolska Block close to Baltica, but the accuracy of this method for the Cambrian was questioned (Landing *et al.* 2013) and the confidence interval of the latitude was estimated to be *c.* 20° and (in some cases) even 40° (Smith, 2001). Because Walczak & Belka (2017) suggest that the Małopolska

Block was not in the vicinity of the West African part of Gondwana during the Cambrian, the scenario with the position of the Małopolska Block as an independent terrane situated in Cambrian Epoch 2 in closer proximity to Gondwana still requires a mechanism for the dispersal of fauna, of which oceanic currents seem the most probable factors. The conclusions drawn by Walczak & Belka (2017) and herein are based on completely different data. The problem of the configuration of palaeogeographic elements in the Cambrian seems to be still an open case, and one of the further research topics should be the revision of brachiopods and further work on the revision of the trilobites.

9. Conclusions

Revised paradoxidids from the Holy Cross Mountains imply several important changes in the interpretation of the succession previously described as the traditional 'Middle' Cambrian:

(1) The previous descriptions of eight species have been corrected; they have been replaced by two species (*Acadoparadoxides kozlowskii* and *Acadoparadoxides samsonowiczi*). Moreover, one taxon is retained in open nomenclature (*Hydrocephalus*? sp.). Both acadoparadoxidines represent an earliest group of *Acadoparadoxides* and are closely related to the taxa from the Gondwanan realm rather than from Baltica (Scandinavia). Members of this clade have been described outside Gondwana for the first time.

(2) Due to the absence of diagnostic taxa, the previous *Eccaparadoxides insularis* and *Acadoparadoxides pinus* – *Pentagnostus praeccurrens* zones have been replaced by the *Acadoparadoxides samsonowiczi* – *Acadoparadoxides kozlowskii* Assemblage Zone.

(3) The *A. samsonowiczi* – *A. kozlowskii* Assemblage Zone can be correlated with the Moroccan *Morocconus notabilis* Zone, and thus points to an interval located near the Cambrian Series 2 – 3 boundary defined by the FAD of *Oryctocephalus indicus* Reed, 1910. Defining the precise position of this boundary within the *A. samsonowiczi* – *A. kozlowskii* Zone is impossible. Former correlations with the Scandinavian *Acadoparadoxides oelandicus* Superzone have to be disclaimed.

(4) The presence of Gondwana-related paradoxidids is consistent with the present knowledge about other trilobites from this interval in the Holy Cross Mountains. Thus, the palaeogeographical position of the Małopolska Block has to be revised. The hypothesis presented herein assumes a position closer to the Gondwana margin (but does not conclude on the distance from Baltica) and the influence of oceanic currents in the distribution of trilobite larvae from Gondwana to the Małopolska Block.

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