Application of morphometric techniques for taxonomic revision of *Berabichia oratrix* (Orłowski, 1985) (Trilobita, Cambrian) from the Holy Cross Mountains, Poland

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ABSTRACT

Detailed analysis of *c.* 900 trilobite specimens from the Cambrian Series 2 of the Holy Cross Mountains in Poland, assigned hitherto to *Comluella oratrix* Orłowski, 1985 and *Comluella igrzycznae* Orłowski, 1985, has shown that the two species constitute in fact a monospecific assemblage representing *Berabichia oratrix* (Orłowski, 1985). The differences pointed out in the original diagnoses are obviously caused by taphonomic processes. To test the hypothesis of a monospecific assemblage, six sagittal and exsagittal and five transverse parameters were measured and calculated for 182 best-preserved cranidia; from this dataset, 121 cranidia with the complete set of measurements were subjected to bivariate and multivariate morphometric analyses and discriminant analysis. Results of the morphometric analysis point to the significant role of tectonic deformation in the variation of the studied sample that could have led Orłowski (1985) to distinguish two separate species. Application of graphic techniques on photographs of distorted specimens lying in different directions with regard to the stress field allowed to obtain specimens statistically indistinguishable in terms of their sagittal and transverse proportions, thus confirming the tectonic overprint on the morphology of the analyzed trilobite sample.

KEY WORDS
Cambrian,
Trilobita,
Ellipsocephalidae,
morphometrics,
retrodeformation,
Holy Cross Mountains,
Poland.

RÉSUMÉ

Application des techniques morphométriques à la revision systématique de Berabichia oratrix *(Orłowski, 1985) (Trilobita, Cambrien) des Monts Sainte-Croix, Pologne.* L'analyse détaillée d'environ 900 spécimens de trilobites provenant de la Série 2 du Cambrien des Monts Sainte-Croix (Pologne), déterminés jusque-là comme *Comluella oratrix* Orłowski, 1985 et *Comluella igrzycznae* Orłowski, 1985, montre qu'il s'agit en fait d'un assemblage monospécifique de *Berabichia oratrix* (Orłowski, 1985). Il est certain que les différences indiquées dans les diagnoses originales sont dues à des processus taphonomiques. Pour vérifier l'hypothèse de la monospécificité de l'assemblage, six paramètres sagittaux et exsagittaux et cinq paramètres transversaux ont été mesurés et calculés pour les 182 cranidiums de suffisamment bon état de conservation. Les méthodes d'analyse morphométrique bivariée et multivariée ainsi que l'analyse discriminante ont été appliquées aux 121 cranidiums pour lesquels il a été possible d'effectuer la totalité des mesures. Les résultats de l'analyse morphométrique montrent que l'essentiel de la variation de l'échantillon étudié peut s'expliquer par la déformation tectonique, laquelle a pu amener Orłowski (1985) à distinguer deux espèces. L'application de techniques graphiques aux images de spécimens déformés différemment selon leur position par rapport au champ de tension a permis d'obtenir des spécimens statistiquement indistinguables en ce qui concerne leurs proportions sagittale et transversale. Cela confirme l'influence tectonique sur la morphologie de l'échantillon fossile étudié.

MOTS CLÉS
Cambrien,
Trilobita,
Ellipsocephalidae,
morphométrie,
rétrodéformation,
Monts Sainte-Croix,
Pologne.

INTRODUCTION

Ellipsocephalid trilobites occurring in the Cambrian Series 2 of the Holy Cross Mountains, Poland, include two species originally assigned to the genus *Comluella* Hupé, 1953: *C. oratrix* Orłowski, 1985 and *C. igrzycznae* Orłowski, 1985. Following a detailed revision of the family by Geyer (1990), the genus *Comluella* is now restricted to trilobites in which both the frontal area and the fixigenae and palpebral lobes combined slope down anteriorly and abaxially, i.e. they possess features that exclude the studied taxa from this genus. Moreover, Geyer (1990: 127) tentatively assigned these two Orłowski's species to *Ornamentaspis* Geyer, 1990. This genus includes a wide variety of species from a relatively long interval spanning the Cambrian Series 2-3 boundary interval (traditional Lower-Middle Cambrian boundary interval) in different palaeogeographic areas, that are grouped into one taxon by a uniform sagittal convexity of the cranidium, transversely convex fixigenae rising above the axial furrows and a mixed kingaspidoid and protolenoid pattern of the lateral glabellar furrows, i.e. features that also eliminate the studied species from the genus. Correct generic assignment is hindered by yet another issue. Orłowski (1985) differentiated between the two species by subtle differences in proportions, with cranidia and glabellae of *C. igrzycznae* generally relatively narrower transversely than those of *C. oratrix*. Qualitative distinguishing parameters include e.g., the presence (*C. oratrix*) or absence (*C. igrzycznae*) of a librigenal spine. However, careful examination of specimens housed in different museum collections indicated that the absence of a librigenal spine may be an artefact resulting from poor preservation. Therefore, a supposition was made that in reality the two taxa may be conspecific and the apparent disparity of the trilobites in question is an effect of post-burial processes, i.e. fossil preservation coupled with

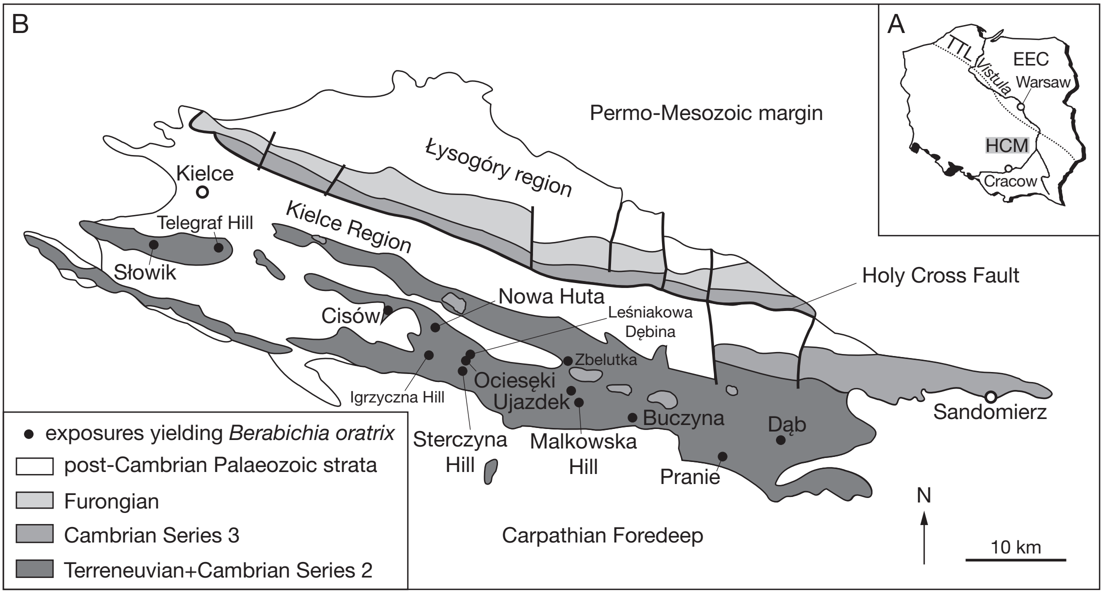

FIG. 1. — **A**, Sketch-map of Poland with location of the Holy Cross Mountains (**HCM**) in relation to the East European Craton (**EEC**) and the Teisseyre-Tornquist Line (**TTL**); **B**, geological sketch-map of the HCM showing the distribution of Cambrian deposits, compiled and modified from Samsonowicz (1962) and Orłowski (1975, 1992b), with location of the exposures yielding *Berabichia oratrix* (Orłowski, 1985).

tectonic deformations. This hypothesis was tested with bivariate and multivariate morphometric analyses and discriminant function (Hammer *et al.* 2001), as well as graphic techniques (Srivastava & Shah 2006).

GEOLOGICAL SETTING

The Holy Cross Mountains (HCM) are a small hilly area in south-central Poland (Fig. 1A) located between the towns of Kielce and Sandomierz. They comprise a *c.* 70 km long and 50 km wide belt of Palaeozoic rocks, surrounded by the Permo-Mesozoic Margin to the west, north and east, and Miocene deposits of the Carpathian Foredeep basin to the south (Fig. 1B). One of the last major structural reorganizations of the area was the Late Cretaceous-Early Palaeogene tectonic inversion and uplift (e.g., Kutek & Głazek 1972; Krzywiec *et al.* 2009) that resulted in partial removal of Permian and Mesozoic strata and exposure of the older rocks. The basement of the area belongs to the Trans-European Suture Zone, one of the main geotectonic domains in Europe (Berthelsen 1992), that separates the East European Craton from younger fold belts of Central and Western Europe. Based on different facies development, stratigraphy and tectonic evolution, the Palaeozoic rocks of the HCM are subdivided into the southern Kielce Region and the northern Łysogóry Region, separated by the WNW-ESE-oriented Holy Cross Fault, and considered either as tectono-stratigraphic (e.g., Czarnocki 1919) or palaeogeographic units (e.g., Belka *et al.* 2000, 2002; Nawrocki & Poprawa 2006 and references therein; Nawrocki *et al.* 2007) of proximal or exotic provenance.

The Cambrian of the area comprises siliciclastic facies with a total thickness estimated at 2500-3500 m (e.g., Orłowski 1988). All the studied specimens come from the Ociesęki Sandstone Formation exposed in the Kielce Region (Fig. 2). It is composed of fine sandstones and siltstones

TABLE 1. — Symbols applied for the measured and calculated linear dimensions of the *Berabichia oratrix* (Orłowski, 1985) dataset (after Shaw 1957).

Symbol	Parameter	Measurement direction
A1	total cranidial length	sagittal
B	total glabellar length	sagittal
B1	occipital-glabellar length	sagittal
C	palpebral length	exsagittal
D	occipital mid-palpebral distance	exsagittal
E	occipital width (calculated as B1–B)	sagittal
F1	frontal area length (calculated as A1–B1)	sagittal
J	palpebral cranidial width	transverse
K	occipital length	transverse
K1	palpebral glabellar width	transverse
(J–K1)/2	width of fixigena at mid-palpebral level (calculated)	transverse
L	length of posterior limb	transverse

with claystone intercalations (Orłowski 1975) that represent shallow-marine settings as supported by sedimentary structures and ichnofossils (Studencki 1988; Orłowski 1989, 1992a; Mizerski *et al.* 1999; Orłowski & Żylińska 2002). The strata in which the studied samples were collected belong to the Cambrian Series 2 *Holmia-Schmidtiellus* Assemblage Zone; its age is confirmed by holmiid trilobites (Czarnocki 1927, 1933; Samsonowicz 1959a; Orłowski 1985, 1987, 1988). This interval is roughly the equivalent of the Scandinavian traditional *Holmia kjerulfi*-group Zone (Kiær 1917; Bergström & Ahlberg 1981; Ahlberg *et al.* 1986; Moczydłowska 1991; Ebbestad *et al.* 2003; Żylińska 2013), now considered the lower part of the *H. kjerulfi*-'*O.*' *linnarssoni* Zone, following a recently proposed revised biostratigraphic scheme for the lower Cambrian of Scandinavia based on sequence stratigraphy (see discussion in Nielsen & Schovsbo 2011).

MATERIAL AND METHODS

The studied specimens are preserved as internal and external moulds, as well as imprints of external moulds, and are slightly flattened. A majority of them have suffered minor tectonic distortion. Disarticulated elements of the trilobite exoskeleton prevail, dominated by cranidia. Complete specimens and thoraces are sometimes slightly enrolled.

The specimens come from a number of localities in the Kielce Region of the HCM (Fig. 1B; see also Systematic Palaeontology); the exact locality is unknown in the case of some specimens, but the lithology of the rock slabs clearly shows characteristics of the Ociesęki Formation. A total of almost 900 specimens were studied; morphometric measurements were taken from the 182 best-preserved cranidia using vernier callipers with an accuracy of 0.01 mm. Five sagittal and exsagittal, as well as four transverse measurements were taken from each cranidium; another two were calculated from the original measurements (Table 1). A dataset comprising all measured and calculated parameters for 121 cranidia was subjected to bivariate and multivariate morphometric analyses using PAST software (Hammer *et al.* 2001). Photographs with a digital camera were made of individual specimens coated with ammonium chloride or rock slabs with several specimens; in the latter case, the trilobites were more distinctive by their reddish-brown colour contrasting with the surrounding light-coloured rock, therefore the rock slabs were left uncoated. Photographs of the rock slabs with several specimens were used in the graphic retrodeformation. Close-ups of uncoated individual specimens were made with a hand USB digital microscope. The names "*igrzycznae*" and "*oratrix*" used throughout refer to morphotypes that correspond to the species *sensu* Orłowski (1985).

TABLE 2. — Dimensional and morphological features distinguishing “*oratrix*” from “*igrzycznae*” (after Orłowski 1985).

	“*oratrix*”	**“*igrzycznae*”**
Dimensional features		
glabellar width (tr)	exceeding fixigenal width	much smaller than fixigenal width
glabellar length (sag)	4/5 cranidial length	3/4 cranidial length
occipital ring length (sag)	short	long
palpebral lobe length (exsag)	long, reaching posterior furrow	poorly marked
Morphological features		
librigenal spine	long, sharp, narrow	lacking
convexity of preglabellar field	medium	low or medium
number of thoracic segments	11	13
pleural spines	sharp, directed backwards	anterior two sharp and blunt, remaining sharp and short

VARIATION RESULTING FROM TAPHONOMY

Morphological features distinguishing “*igrzycznae*” from “*oratrix*” (Table 2) that could be affected firstly by taphonomic processes include: the presence or absence of the librigenal spine; the convexity of the preglabellar field; the number of thoracic segments; and the shape of pleural tips.

According to the original diagnosis, “*oratrix*” is characterized by the presence of a long, sharp and narrow librigenal spine (Orłowski 1985: 244), whereas in “*igrzycznae*” the librigenal spine is absent (Orłowski 1985: 245). The base of the spine in “*oratrix*” was located on the librigenae at the level of S1 on the glabella (Fig. 3); being relatively narrow, the spine could easily break off, resulting in specimens assigned to “*oratrix*” but without a librigenal spine (Fig. 4A). Moreover, the studied sample contains specimens labelled as *Comluella igrzycznae*, in which librigenal spines were recognized (Fig. 4B-F). The spines are rather poorly preserved and observed generally on imprints of external moulds and thus could have been easily omitted in the original study. Preservation of spines only on imprints is a common feature for the ellipsocephalids from the siliciclastic facies of the HCM and was already pointed out in recent systematic descriptions of Cambrian trilobites (e.g., Żylińska & Szczepanik 2009). Thus, both “*oratrix*” and “*igrzycznae*” probably had librigenae with a spine that could be broken off during taphonomic processes.

The facies in which “*oratrix*” and “*igrzycznae*” are preserved comprise fine-grained, strongly bioturbated sandstones with admixture of siltstones and could undergo different styles of compaction. The preglabellar field and other convex or concave elements in the cranidium may often be affected by variable compactional deformation, resulting in taxonomic confusions and morphological misinterpretations if the compressed features are considered primary (see e.g., Webster & Hughes 1999).

Relatively complete thoraces are rare in both morphotypes. The highest number of segments (eleven) in “*oratrix*” was observed only in one specimen (MWG ZI/29/1379). However, it is unclear if this is the maximal value, because the anterior and posterior parts of the specimen are too poorly preserved to allow a confident count (Fig. 5A, C). Up to thirteen thoracic segments are preserved in relatively complete specimens of “*igrzycznae*” (Fig. 5B, D-F). Therefore, it cannot be excluded that the total number of segments was thirteen in both morphotypes.

Orłowski (1985) stated that, contrary to “*oratrix*”, the first two pleural spines in the thoraces of “*igrzycznae*” are short and blunt. Re-examination of thoraces assigned to “*igrzycznae*” has shown that either the specimens have narrow, backward-directed spines (Fig. 5B, E) or they lack thoracic spines due to probably taphonomic factors.

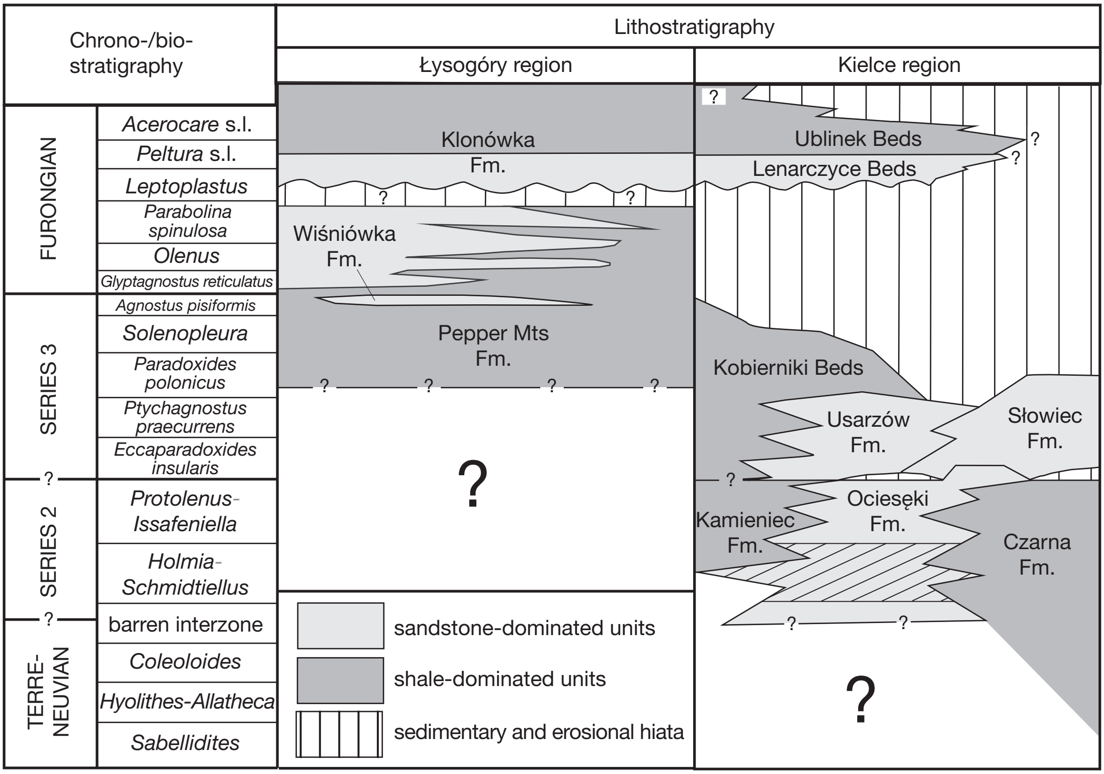

Fig. 2. — Lithostratigraphic scheme of the Cambrian in the HCM, modified after Żylińska & Szczepanik (2009). Informal lithostratigraphic units are in italics. The stratigraphic position of the analyzed trilobites in the Ocieseki Formation is marked by diagonal lines.

VARIATION RESULTING FROM TECTONIC DISTORTION

Tectonic deformations may often change fossil morphology significantly, resulting in exaggerated intraspecific variation or even assignment of the specimens to putatively different taxa (e.g., Hughes & Rushton 1990; Fortey & Owens 1992; Hughes & Jell 1992). Potentially, such situation could have occurred in the studied trilobite sample because Cambrian strata of the Kielce Region in the HCM, along with the fossils preserved in them, were subject to multiple tectonic deformations from the pre-Late Tremadocian Sandomirian phase (e.g., Gągała 2005). The studied trilobite specimens from Cisów give a good example, where a narrow (Fig. 6A-C) and a broad (Fig. 6D-F) morphotype are present. If so, then the difference in cranidial proportions between "*igrzycznae*" and "*oratrix*" are the result of various positions of the trilobite carapaces in relation to the stress field. In order to test this hypothesis, two tests were conducted: 1) morphometric measurements were subjected to statistical analysis (bivariate, multivariate, and discriminant function); and 2) digital images of the specimens were retrodeformed using a graphical method. Statistical analyses were conducted in PAST version 2.07 (Hammer *et al.* 2001); retrodeformation was performed using CorelDRAW© X3 software.

Statistical analysis

Bivariate analysis

This method (Hughes & Jell 1992) is commonly applied to reduce changes in the proportions of fossils caused by tectonic deformation. It compares pairs of parameters lying in one plane, i.e. with the same degree of deformation; therefore their mutual proportions remain unchanged. The bivariate method should generally be treated as the first step in the analysis of a tectonically deformed population.

When the observed variation in a sample is exclusively the effect of tectonic deformations, then the following properties of the variation are expected (Hughes & Jell 1992): 1) the correlation coefficient of two perpendicular dimensions should always be lower than the correlation coefficient of parallel dimensions; 2) ratios between dimensions should be independent of size; and 3) all variation should be continuous within the sample, provided that the specimens did not attain preferred orientation prior to deformation. When any of these properties is not met, morphological variation was present in the sample prior to deformation.

To test these predictions, we prepared scatter plots for pairs of variables. The study sample generally reveals high correlation with regard to parallel parameters and much lower in the case of perpendicular parameters (Table 3). There is distinct linear relationship between particular parameters (Fig. 7A-E). Pairs of parallel parameters generally exhibit high correlation (Table 3 and Fig. 7B, C) and cannot be used to differentiate the putative species distinguished by Orłowski (1985). The only exception is the total glabellar length compared to A1-B (occipital ring width and frontal area length combined) (Fig. 7A), which indicates some allometry in the bulk sample, but again no differentiation between the putative species of Orłowski (1985). Perpendicular parameters have relatively low correlation (Table 3 and Fig. 7D, E); in this comparison the putative species of Orłowski (1985) are relatively well distinguishable. The study sample contains cranidia scattered randomly on single rock slabs (Fig. 8) so that it is assumed that the sample did not attain a preferred orientation prior to deformation.

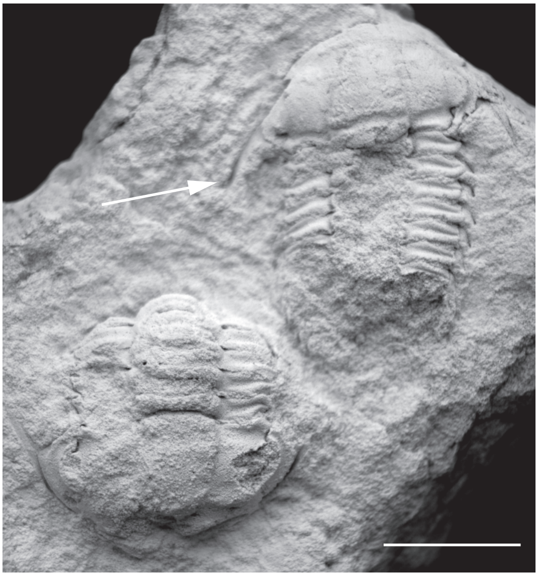

Fig. 3. — *Berabichia oratrix* (Orłowski, 1985), the holotype specimen is located in the upper right, original of Orłowski (1985: pl. 5, fig. 4) (MWG ZI/29/1340), from Igrzyczna Hill, HCM. **Arrow**, librigenal spine. Scale bar: 10 mm.

Table 3. — Correlation coefficients for particular parameters in the *Berabichia oratrix* (Orłowski, 1985) dataset at $p < 0.001$.

	A1	**B**	**C**	**J**	**K**	**K1**	**A1–B**	**(J–K1)/2**
A1	×	0.96	0.86	0.74	0.72	0.72	0.88	0.71
B		×	0.85	0.74	0.72	0.73	0.71	0.70
C			×	0.67	0.63	0.67	0.71	0.64
J				×	0.94	0.94	0.60	0.98
K					×	0.95	0.58	0.88
K1						×	0.58	0.85
A1–B							×	0.58
(J–K1)/2								×

Characteristics of the reduced major axes (RMA) for particular dimensional parameters were also determined (Table 4). They suggest allometry of some of the growth relationships, e.g., relationships which include width of fixigenae at mid-palpebral level and transverse occipital length usually show relatively large positive or negative values of the *y*-intercept. The analysis also shows positive allometry of the total glabellar length, although not when it is compared with glabellar width at mid-palpebral level or transverse occipital length. Therefore, the assumed allometry of the sample was further tested by calculating multivariate allometric coefficients (Hammer & Harper 2006); sagittal + exsagittal and transverse measurements were analyzed separately to exclude errors resulting from tectonic deformations. The results display that one lies well within the 95 % confidence intervals

Table 4. — RMA slopes and y-intercepts for selected pairs of parameters in the *Berabichia oratrix* (Orłowski, 1985) dataset.

Pairs of parameters	RMA slope	RMA y-intercept
B:C	0.46	0.31
B:J	1.98	0.56
B:(A1–B)	0.63	0.09
B:K	0.86	–0.30
B:K1	0.76	–0.19
B:(J–K1)/2	0.64	0.19
B:L	0.56	–0.14
C:(A1–B)	1.37	–0.33
C:J	4.27	–0.74
C:K	1.86	–0.87
C:K1	1.65	–0.70
C:(J–K1)/2	1.39	–0.23
C:L	1.21	–0.51
(A1–B):K	1.37	–0.42
(A1–B):(J–K1)/2	1.02	0.11
K:K1	0.88	0.07
K:L	0.65	0.06
K:(J–K1)/2	0.74	0.42

Table 5. — Eigenvalues and percentage of variation for principal components obtained from the measured parameters in the *Berabichia oratrix* (Orłowski, 1985) dataset.

Principal component	Eigenvalue	Percentage of variance
1	6.03671	75.459
2	0.896756	11.209
3	0.343867	4.2983
4	0.245838	3.073
5	0.202025	2.5253
6	0.142841	1.7855
7	0.0984646	1.2308
8	0.0334944	0.41868

of the allometric coefficients for three sagittal and exsagittal (Fig. 9A) and two transverse measurements (Fig. 9B), indicating that the parameters do not show significant departure from isometry. Exceptions are: K (transverse occipital length) and (J-K1)/2 (width of fixigena at mid-palpebral level), which display positive and negative allometry, respectively (Fig. 9B). A slight positive allometry is also apparent for B (total glabellar length) (Fig. 9A). Such allometric pattern suggests that with growth the glabella became slightly longer and posteriorly wider and the fixigenae became narrower at mid-palpebral level (Fig. 10). The putative species of Orłowski (1985) can only barely be distinguished on the scatter plot.

Multivariate analysis

This method (Hughes & Jell 1992; Hammer & Harper 2006) characterizes the main patterns of variation in a sample, allowing the analytical removal of variation related to tectonic deformations and that resulting from isometric growth. The remaining axes of variation typically describe patterns of variation related to allometric growth and biological variation, which can be used to determine the number of taxa within the sample.

Principal Component Analysis (PCA) is a standard ordination method that constructs hypothetical variables (principal components – PCs), each a linear combination of the original variables, accounting for the highest amount of variation within the dataset. It is commonly applied in analyses of fossil data (Hammer & Harper 2006) and has been employed in delimiting trilobite species (e.g., Hughes & Jell 1992; Hughes 1994; Webster 2009).

Each new parameter (PC) has a series of loadings which describe its relation to original variables. Each original variable has its own loading on each PC. The score on a PC for a given specimen is calculated as the sum of values of the original variables multiplied by their loadings. In practice, each PC describes a particular pattern of variation in the dataset (as revealed by the loadings of the original variables on that PC), and the relative 'importance' of that pattern of variation to the total variation within the sample is given by the per cent variance explained by that PC. The most apparent variation between the specimens is related to size, and a size-related vector is usually distinguished as the first PC (e.g., Hughes 1994); the subsequent PCs may thus represent morphological variation or that caused by tectonic deformation (Hughes & Jell 1992). Loadings of the PC corresponding to change of size during growth will have strong and positive values of all basic parameters (Hammer & Harper 2006). A PC that describes tectonic variation will be characterized by loadings of opposite sign for transverse and longitudinal original variables. Tectonic deformation, where present, typically has large impact on the observed morphological variation, and is therefore often described by one of the first PCs (Hughes & Jell 1992). Higher PCs describe the remaining patterns of variation in the

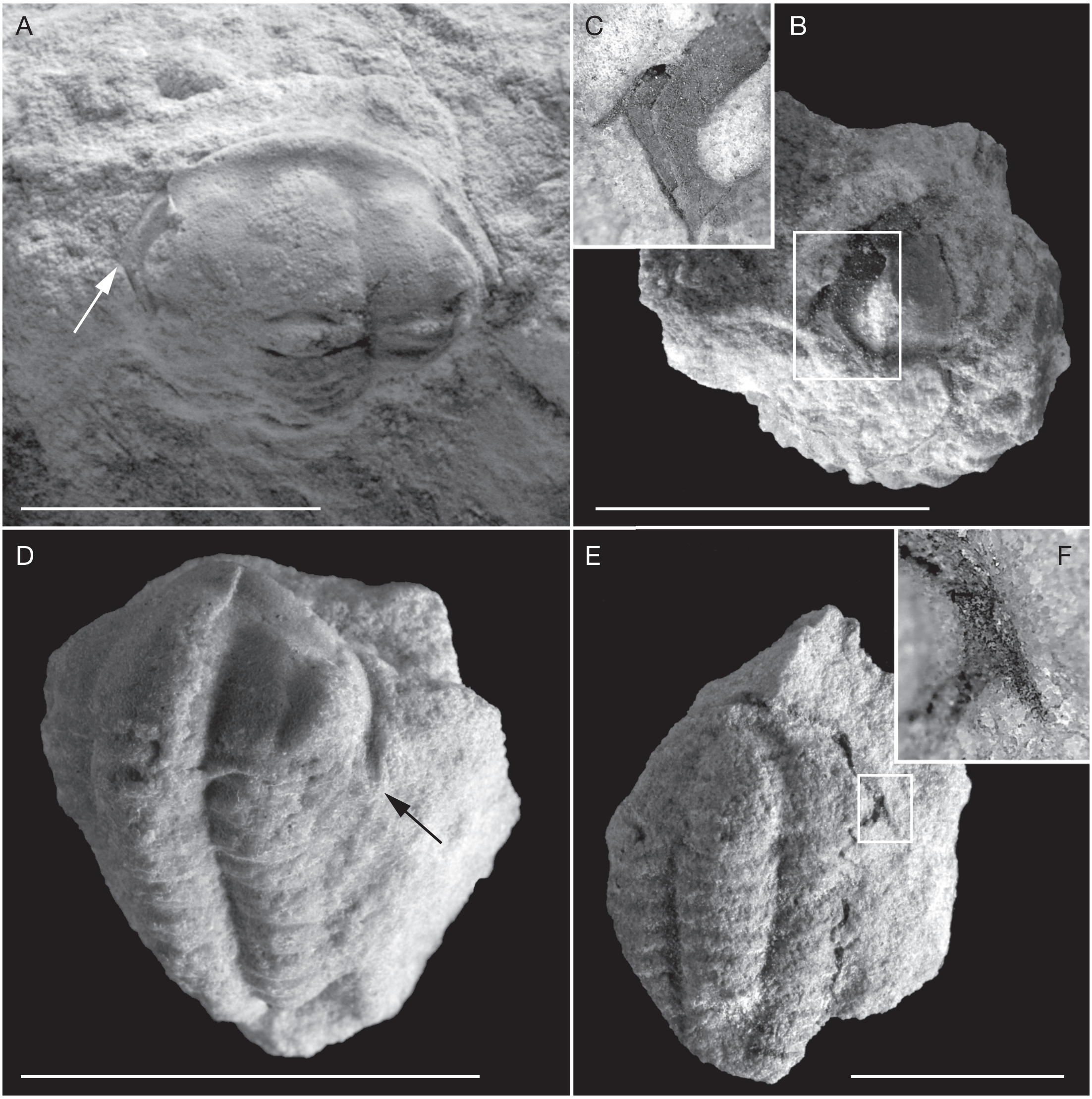

FIG. 4. — *Berabichia oratrix* (Orłowski, 1985): **A**, cephalon with fragmentary thorax, arrow points to the position of the broken-off librigenal spine (JN 006); **B-F**, specimens with librigenal spine, earlier identified as *Comluella igrzycznae*; **B**, almost complete, partly enrolled specimen (MWG ZI/29/1472); **C**, same specimen, close-up of librigena with spine; **D**, almost complete specimen, arrow points to the natural cast of the librigenal spine (MWG ZI/29/1438); **E**, almost complete specimen (MWG ZI/29/1471); **F**, same specimen, close-up of librigena with spine. All specimens from Sterczyna Hill, HCM. Scale bars: 10 mm.

sample, typically related to allometric growth and interspecific disparity. PCA of morphometric data is a powerful tool for identifying morphotypes that differ in shape. It should be noted that shape is only one component of morphology, and the species diagnosis should also be based on qualitative aspects of morphology.

For the PCA study of the analyzed population we selected eight parameters: the sagittal and exsagittal distances B, C, D, A1–B, and the transverse

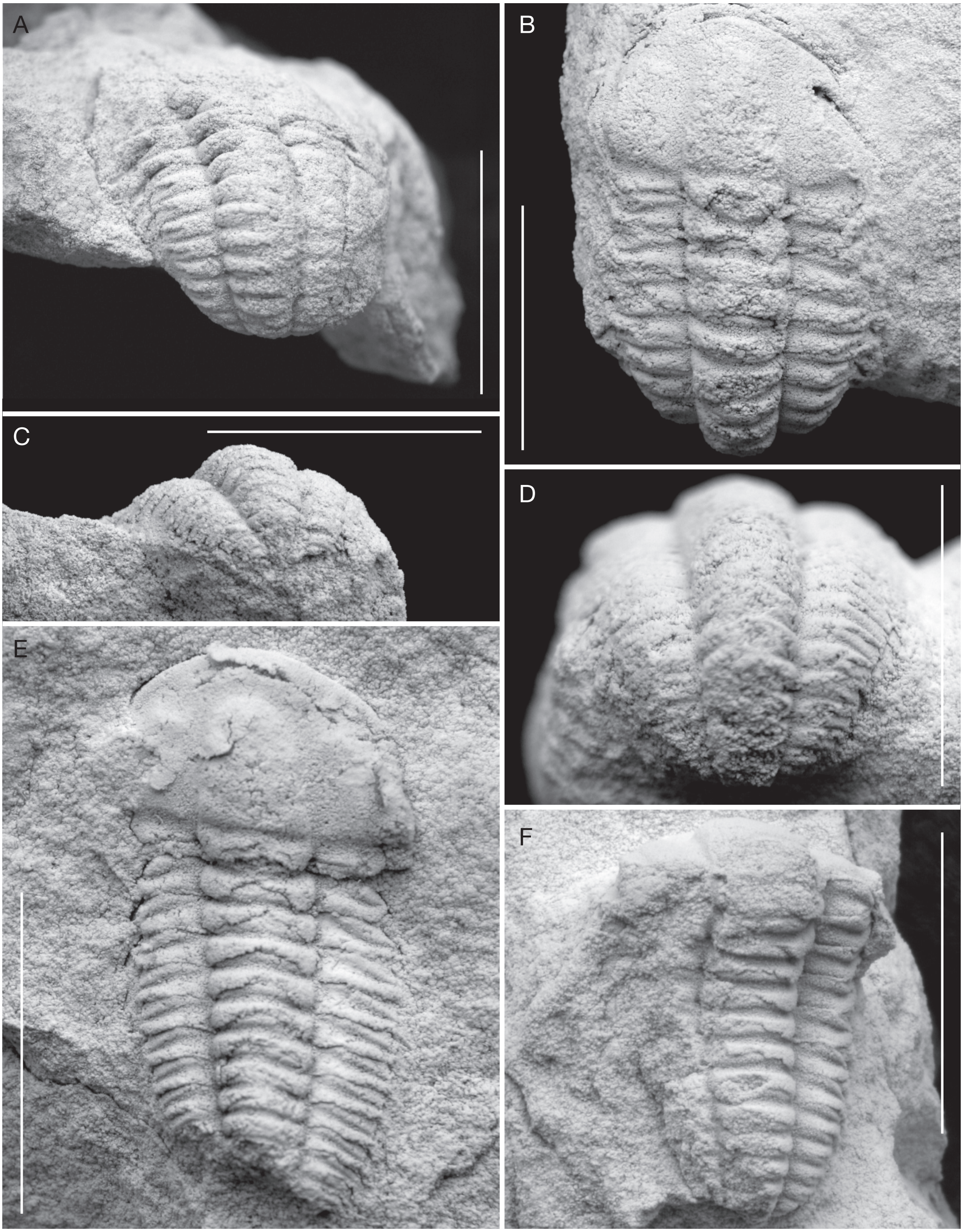

FIG. 5. — *Berabichia oratrix* (Orłowski, 1985): **A**, **C**, thorax from Sterczyna Hill, HCM (MWG ZI/29/1379) in dorsal (**A**) and lateral views (**C**); **B**, **D**, cephalon with thorax from Igrzyczna Hill, HCM; specimen identified earlier as the holotype of *Comluella igrzycznae*, original of Orłowski (1985: pl. 6, fig. 4a-b) (MWG ZI/29/1418) in dorsal (**B**) and lateral views (**D**); **E**, cranidium with thorax from Igrzyczna Hill, HCM; specimen earlier identified as *Comluella igrzycznae*, original of Orłowski (1985: pl. 6, fig. 5) (MWG ZI/29/1419), **F**, cranidium with incomplete thorax from Leśniakowa Dębina, HCM; specimen earlier identified as *Comluella igrzycznae* (MWG ZI/29/1434). Scale bars 10 mm.

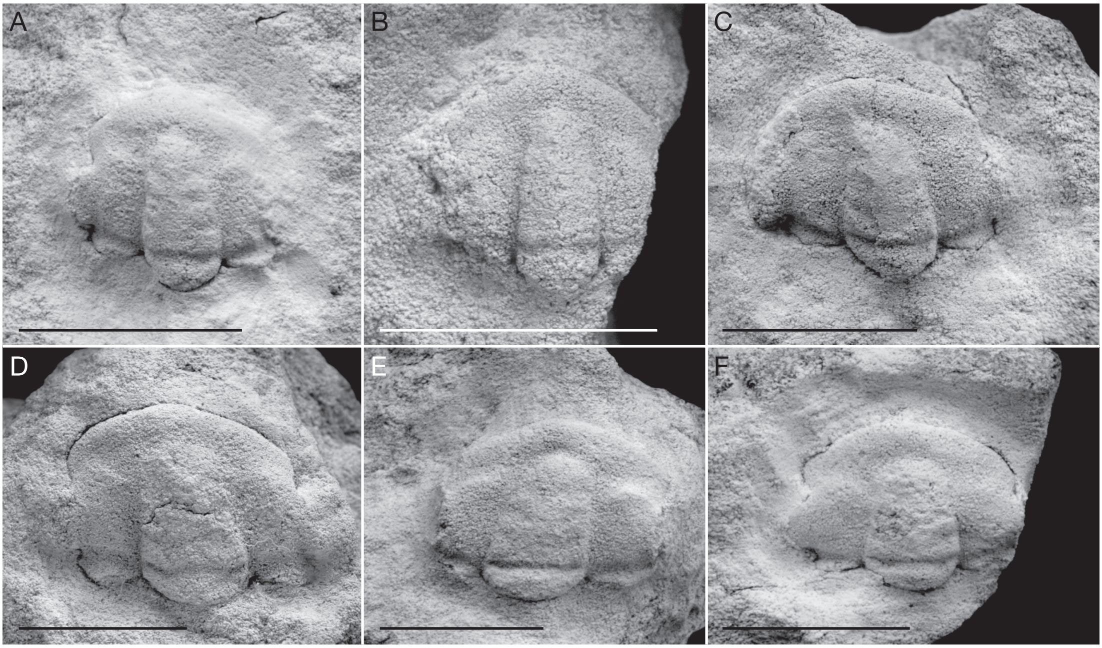

FIG. 6. — *Berabichia oratrix* (Orłowski, 1985) from Cisów, HCM: **A-C**, narrow morphotype ("*igrzycznae*"); **A**, cranidium (AK 12/TA4); **B**, cranidium (AK 12/TA34); **C**, cranidium (AK 12/TA1); **D-F**, broad morphotype ("*oratrix*"); **D**, cranidium (AK 12/TA16); **E**, cranidium (AK 12/TA23); **F**, cranidium (AK 12/TA22). Scale bars: 10 mm.

distances K, K1, (J-K1)/2, and L (see Table 1 for explanation of symbols). A correlation matrix was used in the analysis (Hammer *et al.* 2001). Of eight principal components, PC1 accounts for 75.46 % of the total variation (Table 5). It has the highest score on all parameters and positive loadings of all original variables (Tables 6 and 7) and is thus interpreted as related to size in an informal sense. Differences in the loading values (Table 6) result from differences in the absolute values of parameters: among the parameters measured sagittally, B attains the highest values and its loading is thus the largest for these parameters, whereas A1-B has the lowest values among the parameters measured transversely and thus its loading is the smallest. Similarly, K has the highest values among parameters measured transversely (and the highest of all values) and thus attains the largest loading, and L has the lowest values among parameters measured transversely and attains the smallest loading. A higher percentage of total variation, reaching over 95% was noted in populations without secondary deformations (see Hughes and Jell 1992 for relevant references). The value of variance on PC1 in the studied dataset is lower than values obtained for a tectonically deformed trilobite sample from the Himalaya (Hughes and Jell 1992). PC2 accounts for 11.21 % of the variation (Table 5). It is interpreted as variation resulting from tectonic deformation of the fossils, because all dimensions have similar loadings on this PC and loadings for original variables that were measured in transverse versus longitudinal directions are of opposite sign (Tables 6 and 7). Values of PC2 for the putative species are very well correlated ($r = 0.83$; $p < 0.0001$) with the B/K ratio (Fig. 11), which also points to changes in the proportions of the specimens resulting from tectonic deformation. Scores and loadings of all specimens on PC1 and PC2 (Fig. 12) show that larger values of sagittal parameters lead to higher PC2 values and larger transverse parameters give lower PC2 values. Specimens assigned

TABLE 6. — Loading values for particular parameters in relation to principal components in the *Berabichia oratrix* (Orłowski, 1985) dataset without standardization of variance (variance-covariance matrix).

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
B	0.369	0.289	–0.263	–0.208	–0.161	–0.084	–0.797	0.016
C	0.348	0.357	–0.065	–0.577	0.537	0.043	0.349	–0.054
D	0.337	0.387	–0.518	0.491	–0.268	–0.004	0.394	–0.016
A1-B	0.318	0.421	0.802	0.261	–0.098	0.038	–0.018	0.012
K1	0.681	–0.321	0.055	–0.296	–0.411	0.198	0.189	0.652
K	0.286	–0.365	0.067	–0.167	–0.317	0.164	0.092	–0.749
(J-K1)/2	0.256	–0.336	0.052	0.143	0.196	–0.831	0.040	0.055
L	0.171	–0.335	–0.064	0.423	0.545	0.483	–0.206	0.088

TABLE 7. — Loading values for particular parameters in relation to principal components in the *Berabichia oratrix* (Orłowski, 1985) dataset with standardization of variance (correlation matrix).

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
B	90.66	27.36	–15.45	–10.29	–7.23	–3.19	–25.00	0.23
C	85.54	33.85	–3.79	–28.60	24.11	1.63	10.94	–0.99
D	82.73	36.62	–30.40	24.34	–12.06	–0.2	12.36	–0.30
A1-B	77.51	39.87	47.04	12.93	–4.41	1.45	–0.58	0.21
K1	90.96	–30.43	3.20	–14.69	–18.48	7.49	5.90	11.93
K	91.00	–34.60	3.91	–8.28	–14.26	6.21	2.90	–13.70
(J-K1)/2	88.65	–31.85	3.06	7.09	8.83	–31.40	1.26	1.00
L	86.98	–31.69	–3.73	20.98	24.47	18.24	–6.46	1.62

to "*igrzycznae*" that have larger sagittal parameters and smaller transverse parameters are located in the upper part of the biplot, whereas specimens assigned to "*oratrix*" are located in the lower part of the biplot (Fig. 12). Higher PCs describe trivial proportions of the total variation in the sample and are inferred to relate to intraspecific variation (Fig. 13). The morphometric analyses demonstrate that the putative species recognized by Orłowski (1985) cannot be distinguished except along PC2, which relates to tectonic distortion so that the putative species must be regarded as tectonic variants of a single underlying morphotype and should be treated as conspecific.

Additional test using discriminant analysis

The assumption that the measured samples of "*oratrix*" and "*igrzycznae*" represent in reality one species was additionally tested with the use of discriminant analysis implemented using PAST (Hammer *et al.* 2001) in order to correct specimen assignment to particular species. Discriminant analysis projects a multivariate dataset onto a single axis in order to maximize separation between two *a priori* groups, in the studied case "*oratrix*" and "*igrzycznae*". The histogram of individuals projected onto the discriminant axis (Fig. 14) shows strong overlap of the two putative species. The parameters of the discriminant function [$v = -2.98B + 0.22C - 0.96D - 1.07(A1-B) + 2.59K + 2.84K1 - 0.21(J-K)/2 + 1.03L$] are influenced mainly by parameters of the glabella, i.e. its length (B) and widths (K and K1). A relatively wider and shorter glabella refers to specimens in the right part of the histogram ("*oratrix*" bars), whereas a relatively longer and narrower glabella refers to specimens in the left part of the histogram, occupied by "*igrzycznae*". The discriminant analysis indicated that 11.02% of the specimens were mis-classified; apparently they were mostly smaller specimens of "*oratrix*". The strong overlap of the two groups indicates that the *a priori* groups were not easily distinguished by the naked eye. After re-classification of the specimens to the putative species following discriminant analysis, PCA was conducted once again. The analysis failed again to support recognition of Orłowski's (1985) putative species as anything other than tectonic variants of one taxon (Fig. 15).

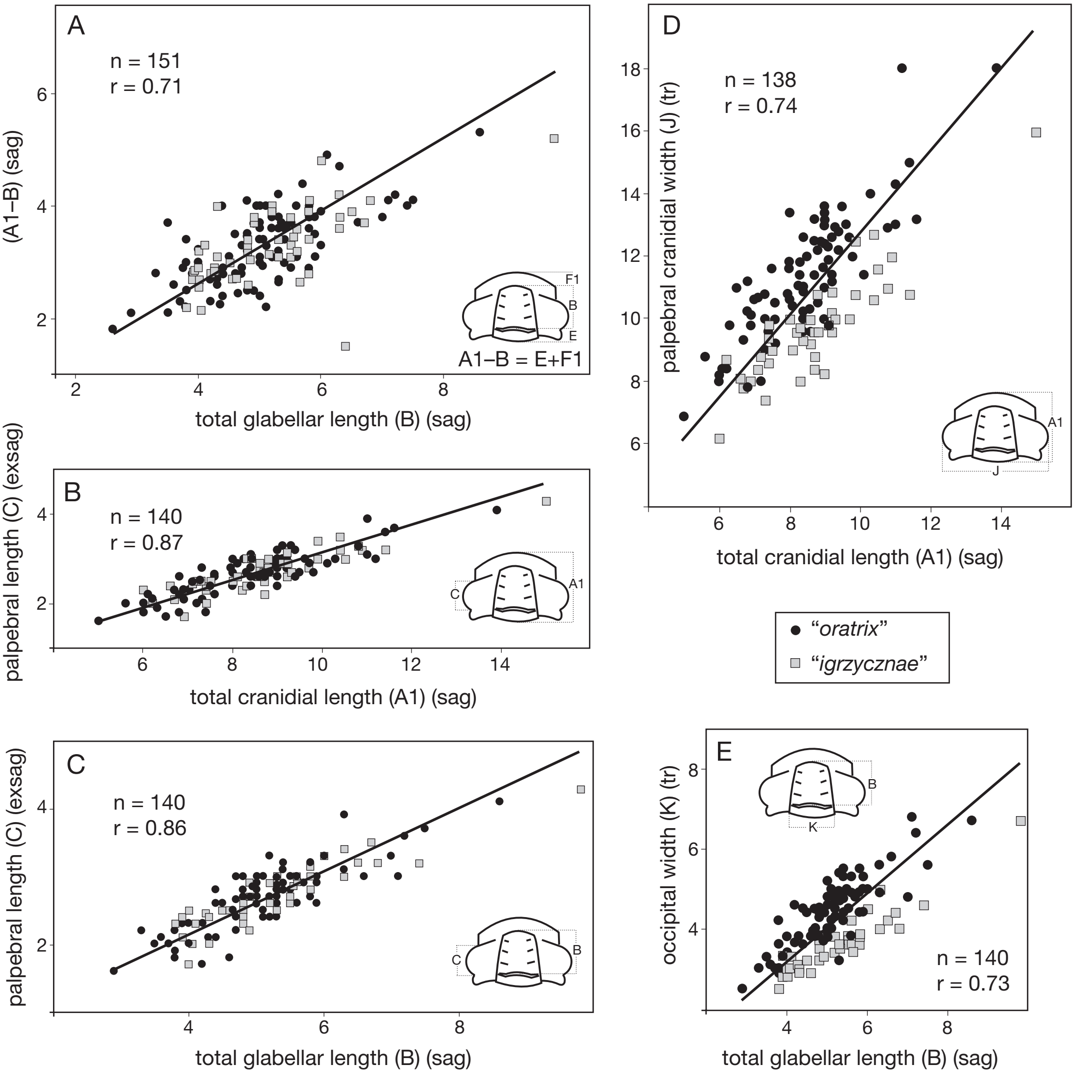

FIG. 7. — Scatter plots showing the relationships between selected sagittal, exsagittal and transverse parameters for the *Berabichia oratrix* (Orłowski, 1985) dataset: **A**, palpebral width at mid-palpebral level [(J–K1)/2] versus total glabellar length (B); **B**, total cranidial length (A1) versus palpebral length (C); **C**, total glabellar length (B) versus palpebral length (C); **D**, total cranidial length (A1) versus palpebral cranidial width (J); **E**, total glabellar length (B) versus occipital length (K). **Black lines**, reduced major axis; **n**, number of measured specimens; **r**, correlation coefficient.

GRAPHIC METHOD

Various methods of fossil restoration have been proposed since Lake (1943; see Hughes 1999 for a recent overview). Usually such techniques aim at restoring two-dimensional fossils on a bedding plane, presuming that the study area was subject to homogenous deformation (Cooper 1990). Measurements of fossils are used to calculate the strain ellipse; its axes show the direction and proportion of distortion. The strain ellipse is recognized graphically (Cooper 1990) or by calculating the extensions in various directions (Ramsay & Huber 1983). One of the methods applied is based on measuring a set of deformed

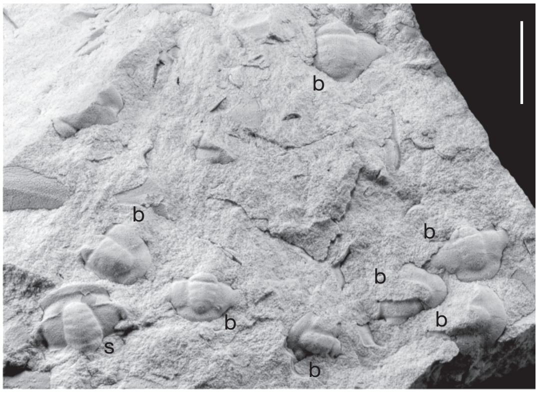

Fig. 8. — Slabs with trilobite cranidia orientated at different directions with regard to the stress field; locality unknown, HCM (MUZPIG 110.II.99); **b**, *Berabichia oratrix* (Orłowski, 1985); **s**, *Strenuella polonica* Czarnocki, 1926. Scale bar: 10 mm. The same slab is shown retrodeformed in Fig. 16B.

angles that have been equal to one another prior to the distortion (Lake 1943; Sdzuy 1962, 1966; Cooper 1990; Rushton & Smith 1993; Srivastava & Shah 2006); a special case occurs when the measured angle was originally a right angle.

The graphic method of fossil restoration (Srivastava & Shah 2006) applied in this study requires marking the axis of the specimen (or specimens) and the planes, which in an undistorted specimen should be located perpendicular to the plane of bilateral symmetry and lie at a different angle in distorted specimens. The retrodeformation technique restores the original rectangularity of planes in the specimen. In practice, such retrodeformations are conducted on photographs that are assumed to be perpendicular to the studied planes in the fossil. On the photographs the projections of the planes are straight lines and retrodeformation is based on manipulating the image in order to obtain right angles between these lines. The drawback of the method is a case when the vectors of maximal stress are parallel or normal to the symmetry axes; this will result in apparent lack of distortion. The best results are obtained when the rock slabs subject to retrodeformation techniques contain several specimens located at different directions in relation to the stress field. In effect, the retrodeformed images reveal fossils with original proportions and dimensions that can be used for taxonomic descriptions.

The studied material contains slabs that fulfil the criteria for successful graphic retrodeformation techniques (Srivastava & Shah 2006), i.e. contains slabs with several specimens that are located obliquely to each other and at different directions with regard to the stress field (Fig. 16A, C, E). The individual specimens belong to the two morphotypes "*oratrix*" and "*igrzycznae*"; additional specimens representing *Strenuella polonica* Czarnocki, 1926 were also subject to retrodeformation (Fig. 16G). It is worth noting that specimens of "*oratrix*" and "*igrzycznae*" were not observed to lie parallel to one another in the examined rock-slabs. For each relatively complete trilobite cranidium a sagittal line and a transverse line at the base of the cranidium were drawn. A reference circle was also added to each image. Retrodeformation shows that the putatively distinct "*oratrix*" and "*igrzycznae*" morphotypes lose their differences (Fig. 16B, D, F) and the distorted specimens of *S. polonica* represent a sample with more uniform shapes (Fig. 16H). Thus, earlier discrimination of two species was caused by not taking tectonic deformation into account.

INSTITUTIONAL ABBREVIATIONS

AK	Museum of the Geoscience Friends Association "Phacops" in Łódź [collection includes specimens collected by Katarzyna Pawłowska in 1953 in Cisów (Łobanowski 1955)];
IGPUW JN	Institute of Geology, Faculty of Geology, University of Warsaw (collection of specimens collected by JN for his M. Sc. thesis);
MUZPIG	Museum of the Polish Geological Institute – National Research Institute in Warsaw (1.II, 110.II and 113.II: collections of Jan Czarnocki; 8.II: collection of Jan Samsonowicz);
MWG	Museum of the Faculty of Geology, University of Warsaw (ZI/29: collection of Stanisław Orłowski; ZI/42: collection of Jan Samsonowicz);
UJ	Institute of Geological Sciences, Jagiellonian University in Cracow (collection of Michał Stachacz).

SYSTEMATIC PALEONTOLOGY

Class TRILOBITA Walch, 1771
Order REDLICHIIDA Richter, 1932
Suborder REDLICHIINA Richter, 1932

Superfamily Ellipsocephaloidea Matthew, 1887

Remarks

Assignment of the Ellipsocephaloidea to a higher level systematic rank is problematical. Many authors include them in the Redlichiina (Geyer 1990; Kaesler 1997: 429; Adrain 2011), whereas according to Fortey (1990) at least some ellipsocephaloids should be grouped among the Ptychopariina Richter, 1932 (see also Kaesler 1997: 302). Recently, Adrain (2011) suggested to abandon the suborder Ptychopariina Richter, 1932 and the order Ptychopariida Swinnerton, 1915.

Family Ellipsocephalidae Matthew, 1887
Subfamily Antatlasiinae Hupé, 1953

Genus *Berabichia* Geyer, 1990

Type species. — *Berabichia vertumnia* Geyer, 1990, from the Lemdad Formation (Cambrian Series 2, Sectigena Zone) in the Lemdad Syncline, High Atlas, Morocco, OD.

Remarks

Berabichia was introduced by Geyer (1990) for three species from the Anti-Atlas and High Atlas of Morocco, i.e. *B. vertumnia*, the type species, *B. stenometopa* Geyer, 1990 and *B. inopinata* Geyer, 1990, and six additional morphotypes in open nomenclature. *Berabichia inopinata*, differing from most of the remaining Moroccan taxa included in *Berabichia* in a rather homogenous overall convexity of the cephalon (Geyer 1990), was subsequently transferred to the genus *Epichalnipsus* Geyer, Popp, Weidner & Förster, 2004 (Geyer *et al.* 2004). A suggestion was made (Jell & Adrain 2003: 348, 436) that *Berabichia* is a junior subjective synonym of *Ptychoparopsis* Hupé, 1953. However, as pointed out by Geyer (1990), *Ptychoparopsis* is an unrecognizable taxon. Thus, *Berabichia* and *Ptychoparopsis* cannot be synonymized because no direct equalization has ever been proposed (G. Geyer, pers. comm.).

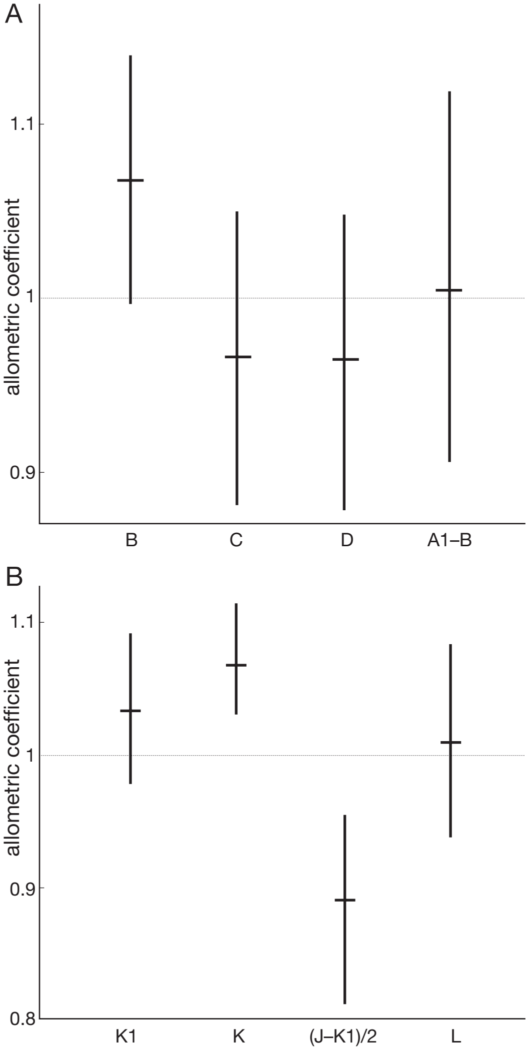

Fig. 9. — Multivariate allometric coefficients for the *Berabichia oratrix* (Orłowski, 1985) dataset: **A**, for sagittal parameters; **B**, for transverse parameters. For each variate, the 95% confidence interval is indicated by a vertical line. The allometric coefficient is shown by a horizontal line within the confidence interval.

The *Berabichia* group includes also *Chorbusulina wilkesi* Palmer & Gatehouse, 1972 and *Chorbusulina subdita* Palmer & Gatehouse, 1972 from

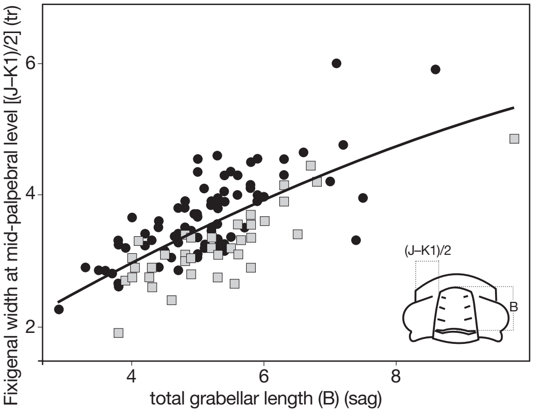

FIG. 10. — Scatter plot showing the relationship between total glabellar length (B) and fixigenal width at mid-palpebral level [(J–K1)/2] for the *Berabichia oratrix* (Orłowski, 1985) dataset; note slight allometry of the sample recording narrowing fixigenae in ontogeny. The exponential function [$y = -0.01765x^2 + 0.655x + 0.6173$] is based on a least-squares criterion and singular value decomposition, with mean and variance standardization for improved numerical stability (after Hammer *et al.* 2001).

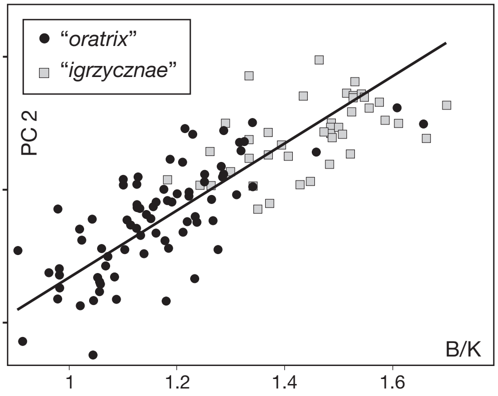

FIG. 11. — Scatter plot showing correlation between the B/K ratio and the PC2 values for the *Berabichia oratrix* (Orłowski, 1985) dataset. Black line is the reduced major axis.

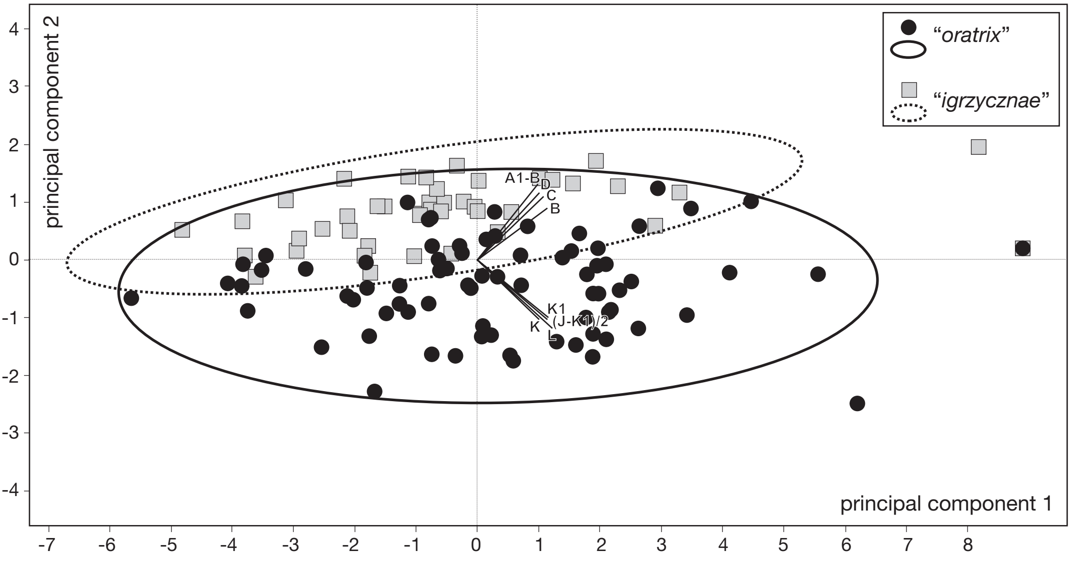

FIG. 12. — Biplot of scores and loadings on PC1 and PC2 of the *Berabichia oratrix* (Orłowski, 1985) dataset. PC1 is interpreted as a size axis, PC2 as a width/length difference axis. The lines represent loadings on each parameter. Ellipses mark the area of the 95% confidence interval.

the Lower Cambrian of the Argentina Range, Antarctica; *Proampyx rotundatus* (Kiær, 1917) from the Lower Cambrian of Sweden; and *Berabichia erratica* Geyer, Popp, Weidner & Förster, 2004 from Pleistocene erratic boulders collected in a gravel pit in northern Germany (Palmer & Gatehouse 1972; Geyer 1990; Palmer & Rowell 1995; Geyer *et al.* 2004). Geyer (1990: 79)

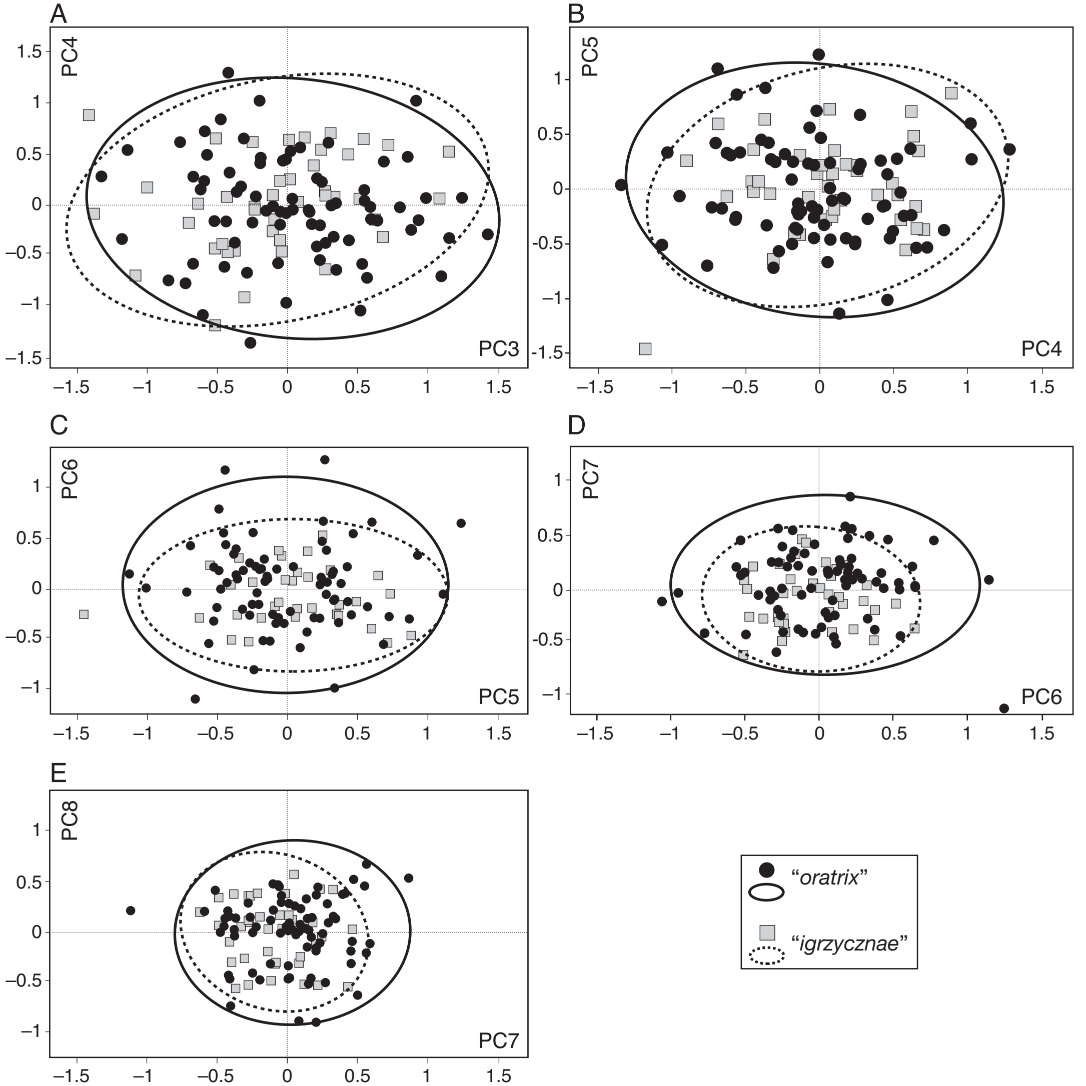

Fig. 13. — Scatter plots showing the relationships between principal components for the *Berabichia oratrix* (Orłowski, 1985) dataset: **A**, PC3 and PC4; **B**, PC4 and PC5; **C**, PC5 and PC6; **D**, PC6 and PC7; **E**, PC7 and PC8. Ellipses mark the area of the 95% confidence interval. PC3 to PC8 shown on the plots correspond to morphological variation and are devoid of variation resulting from size (PC1) and width/length difference (PC2).

suggested that *Strenuaeva kiaeri* Samsonowicz, 1959 (Samsonowicz 1959b: pl. 1, fig. 16a-c; *Ellipsocephalus kiaeri* of Orłowski 1985: 239, text-fig. 7, pl. 7, fig. 2) from the *Protolenus-Issafeniella* Zone of the HCM can be tentatively assigned to *Berabichia*; however, the only known specimen is strongly effaced, has very shallow lateral and axial furrows and might represent a tectonic variant of *Issafeniella orlowinensis* (Samsonowicz, 1959b) from the same interval (see Żylińska & Masiak 2007 and Żylińska & Szczepanik 2009 for comparison).

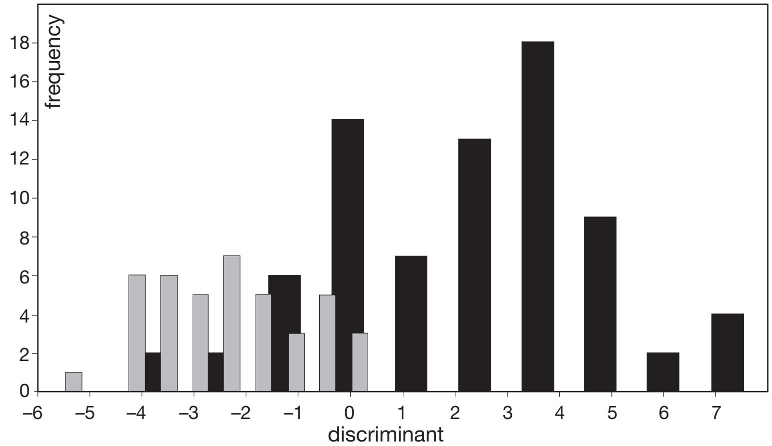

FIG. 14. — Histogram of discriminant projection values for the "*igrzycznae*" (grey bars) and "*oratrix*" (black bars) morphotypes. The cut-off point at v=0 separates "*igrzycznae*" (v < 0) from "*oratrix*" (v > 0).

Berabichia oratrix (Orłowski, 1985)
(Figs 3-6; 8; 16A-F; 17)

Comluella oratrix Orłowski, 1985: 244, text-fig. 14, pl. 5, figs 1-7, pl. 7, fig. 9.

Strenuaeva primaeva – Samsonowicz 1959b: 521, pl. 1, figs 1-9; 1962: 11, pl. 2, figs 1-4; 6-7, pl. 3, figs 3; 5.

Termierella sandomirensis – Samsonowicz 1962, pl. 1, fig. 7 only.

Comluella igrzycznae Orłowski, 1985: 245, text-fig. 15, pl. 6, figs 1-6.

Ornamentaspis? *oratrix* – Geyer 1990: 127.

Ornamentaspis? *igrzycznae* – Geyer 1990: 127.

HOLOTYPE OF *COMLUELLA ORATRIX*. — External mould of a cephalon with incomplete thorax (MWG ZI/29/1340; former number of the Institute of Geology collection: 1.607), figured by Orłowski (1985: pl. 5, fig. 4), illustrated herein in Figure 3.

HOLOTYPE OF *COMLUELLA IGRZYCZNAE*. — External mould of cephalon with thorax (MWG ZI/29/1418; former number of the Institute of Geology collection: 1.301), figured by Orłowski (1985: pl. 6, fig. 4a, b), illustrated herein in Figure 5B, D.

TYPE LOCALITY AND TYPE STRATUM. — Igrzyczna Hill, HCM; *Holmia-Schmidtiellus* Assemblage Zone, Cambrian Series 2 (middle part of the traditional Lower Cambrian).

AGE AND OCCURRENCE. — *Berabichia oratrix* is known from the Holy Cross Mountains, Poland, from the *Holmia-Schmidtiellus* Assemblage Zone, Cambrian Series 2 (Samsonowicz 1959b; Orłowski 1985).

EMENDED DIAGNOSIS. — A species of *Berabichia* with glabella *c.* 40% of palpebral cranidial width; front rounded to bluntly sub-triangular; occipital ring sagittally of slightly less than 20% of cephalic length; maximum fixigenal width slightly less than 60% of posterior glabellar width; palpebral lobes slightly more than 30% of cephalic length. Librigena with relatively long and slender spine.

MATERIAL EXAMINED. — 14 complete specimens, four cranidia with thoraces, eight thoraces, five cephala, over 840 detached cranidia, three detached librigenae; MWG ZI/29/1103, 1105, 1260, 1263, 1340-1483, 1514, 1526, 1530, 1569; MWG ZI/42/007, 021, 023, 067-072, 074-078, 081-089, 094, 100, 173, 178, 179, 182-188, 190, 191, 193, 195-198, 200, 201, 204, 205, 207-214, 216-218, 220, 223, 224, 227-233, 235-243, 252, 264, 267-272, 274-288; MUZPIG 1.II.8B, 23, 38, 42-45, 57, 59, 63, 64, 68, 73, 80, 85-89; MUZPIG 110.II.37, 38, 56, 62, 68, 70-72, 77, 78, 82, 86, 93, 95-99, 102, 105, 108, 110, 115-123, 126, 130, 133, 135, 141-146, 150, 151, 155-159, 164, 166, 170-174, 176, 177, 180, 182-184, 186, 188-203, 205, 213, 219, 229-231, 235; MUZPIG 113.II.2, 4, 8, 37; MUZPIG 8.II.30, 31; AK 300/CD 20-1, 12/TA 1–38; UJ 214P/T5, 6, 11, 12, 20, 23, 25; JN 033-043, 045-086. All specimens come from the local *Holmia-Schmidtiellus* Assemblage Zone of Cambrian Series 2 at Słowik, Telegraf Hill, Cisów, Nowa Huta, Igrzyczna Hill, Leśniakowa Dębina, Ociesęki, Sterczyna Hill, Zbelutka, Ujazdek, Malkowska Hill, Buczyna, Pranie, and Dąb, Holy Cross Mountains, Poland.

Measurements. — Cranidial length 4.4-13.9 mm, cranidial width across centre of palpebral lobes 5.8-18 mm. The holotype cranidium is 8 mm long and 10 mm wide across centre of palpebral lobes.

Description

Cephalon semi-elliptical, overall convexity relatively low; length 127 ± 18 % of palpebral cranidial width (n = 138). Glabella slightly elevated above the fixigenae, defined by distinct furrow, 78 ± 4 % of cephalic length (n = 151) and 39 ± 4 % of palpebral cranidial width (n = 135). Glabella tapering forwards, with rounded to bluntly subtriangular front. Three pairs of rather shallow, slightly backwardly directed lateral glabellar furrows. Occipital furrow narrow and deep, slightly sinuous. Occipital ring 17 ± 3% of cephalic length (n = 151). Occipital node or spine not developed. Fixigenae 67 ± 7% width of occipital ring (n = 123), 29 ± 3% of cephalic length (n = 121) and 57±3% of posterior glabellar width. Ocular ridges indistinct, straight, slightly backwardly directed, visible on the shell exterior only, located at level of S3 and separated from glabella by narrow furrows. Palpebral lobes 32 ± 3% of cephalic length (n = 140), strongly convex, reaching from ocular ridges to posterior border furrows. Palpebral furrow a shallow depression, narrower anteriorly and distinctly widening posteriorly. Palpebral lobes slightly upturned posteriorly. Frontal area 22 ± 4% of cephalic length (n = 147), entire, distinctly convex, without border furrow.

Librigena nearly flat, its width is less than one-third of transverse cranidial width across palpebral lobes, with sharp and slender librigenal spine whose base is at level of S1; librigenal spine slightly divergent from lateral margin, reaching to the level of the posterior part of second thoracic segment. In some cases, the spine is visible only on imprints of external moulds. Inner spine angle nearly rectangular. Librigenal border relatively wide and flat, separated from genal field by narrow furrow.

Thorax composed of up to 13 segments narrowing posteriorly, pleurae with distinct, long furrows, extending into backward-directed spines.

Pygidium small, sub-triangular, wider than long, axial piece strongly convex, reaching to posterior margin.

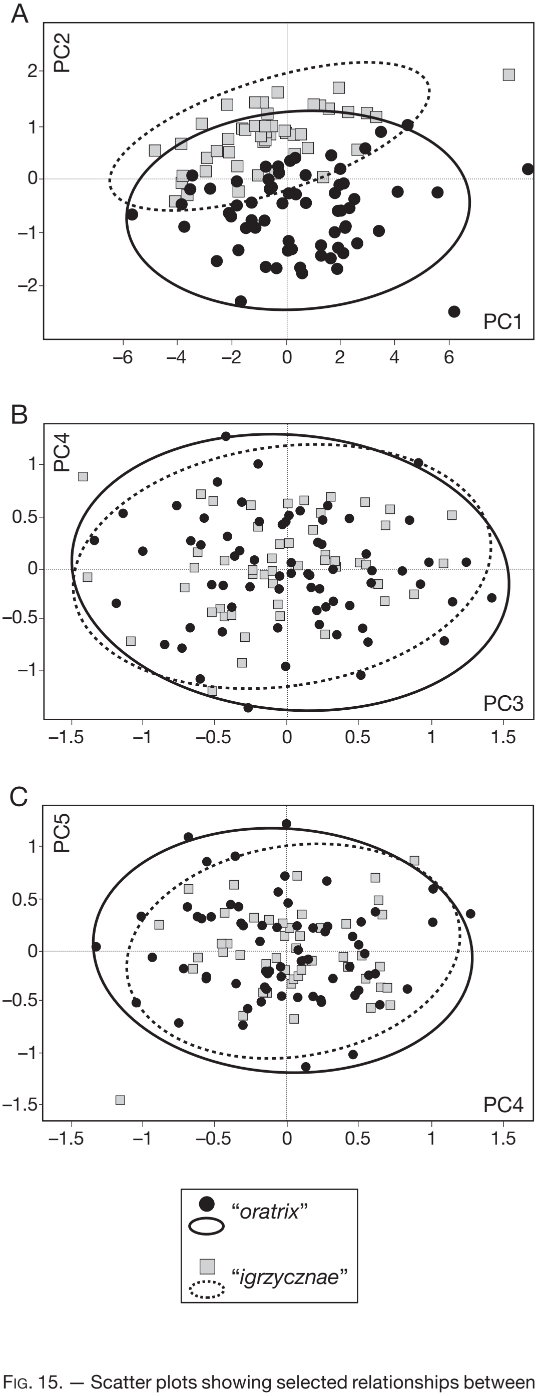

Fig. 15. — Scatter plots showing selected relationships between principal components for the *Berabichia oratrix* (Orłowski, 1985) dataset after discriminant analysis: **A**, PC1 and PC2; **B**, PC3 and PC4; **C**, PC4 to PC5. The ellipses mark the area of the 95% confidence interval.

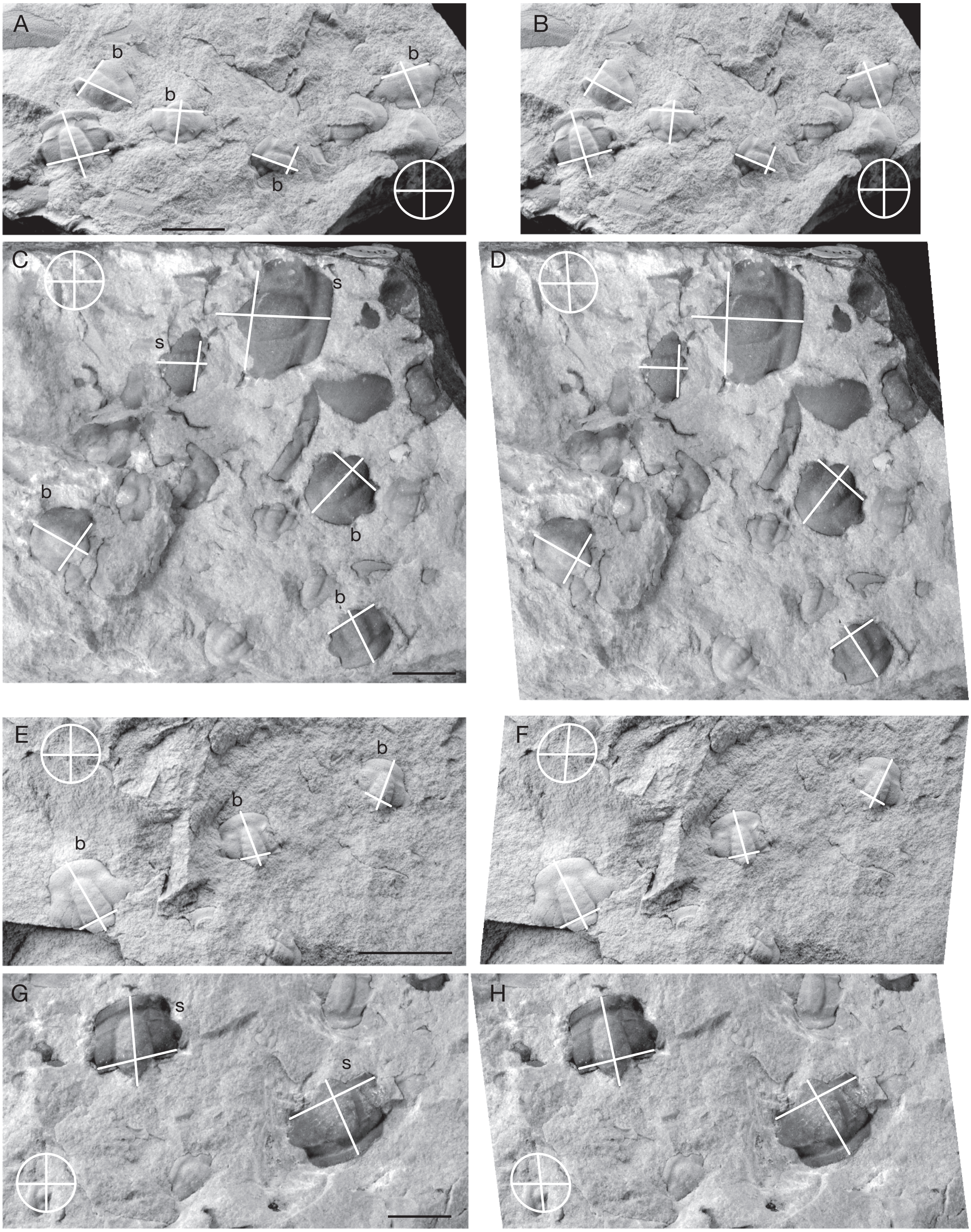

FIG. 16. — Slabs with trilobite cranidia located in different positions with regard to the stress field as preserved (**A**, **C**, **E**, **G**) and after retrodeformation (**B**, **D**, **F**, **H**); **A**, **B**, locality unknown, HCM (MUZPIG 110.II.99); **C**, **D**, Leśniakowa Dębina, HCM (MUZPIG 1.II.87); **E**, **F**, locality unknown, HCM (MUZPIG 110.II.173); **G**, **H**, Leśniakowa Dębina, HCM (MUZPIG 1.II.86). White circle is the reference circle, white ellipse is the strain ellipse. Abbreviations: **b**, *Berabichia oratrix* (Orłowski, 1985); **s**, *Strenuella polonica* Czarnocki, 1926. Scale bars: 10 mm.

Remarks

Assignment of this species to *Berabichia* Geyer, 1990 rather than *Ornamentaspis* Geyer, 1990 as tentatively suggested by Geyer (1990: 127) is justified by several cranidial features that include: a relatively flat cranidium with a tapering forwards glabella that has a rounded or bluntly sub-triangular anterior lobe, slightly upturned palpebral lobes, and a convex and entire frontal area; the lateral glabellar furrows in the studied specimens are oblique backwards, as in most species assigned to *Berabichia*, whereas in *Ornamentaspis* they attain a mixed kingaspidoid and protolenoid pattern (Geyer 1990). In the specimens studied the palpebral furrows are narrower forwards and distinctly wider backwards, a feature considered diagnostic of *Berabichia* (Geyer 1990: 78). As noted by Westrop & Landing (2000: 873), there is only subtle difference in palpebral furrow morphology between some species of *Berabichia* and *Antatlasia* Hupé, 1953. Nevertheless, the species which Westrop & Landing (2000) referred to (i.e. *B. inopinata*) was subsequently assigned to *Epichalnipsus* (see above) so that the palpebral furrow morphology can also be taken into consideration in the reassignment of the studied specimens to *Berabichia*. Morphometric analysis (see above) suggests that *C. igrzycznae* is a tectonically distorted morphological expression of *B. oratrix*. Other distinguishing features mentioned by Orłowski (1985: 245) in the original diagnoses have been caused by taphonomic processes (see above).

Berabichia oratrix is closest to *B. subdita* in most cranidial proportions and in the librigena (see Palmer & Gatehouse 1972: pl. 2, fig. 12). A significant difference is an elongated posteriorly occipital ring and test ornamentation in *B. subdita*. The external moulds of *B. oratrix* do not show any evidence of the test's ornamentation or prosopon. Similar proportions occur also in the type species *B. vertumnia*; the only significant difference between them is the width of the fixigenae, which reach 50-55% of posterior cranidial width in *B. vertumnia*, compared to almost 60% in *B. oratrix*. Compared with *B. stenometopa*, *B. oratrix* has a wider glabella at level of palpebral lobes, sagittally longer occipital ring, wider fixigenae and shorter palpebral lobes. *Berabichia wilkesi* is known from small, probably juvenile cranidia only, but the available specimens (Palmer & Gatehouse 1972: pl. 9, figs 1, 2) are distinguished by distinct ocular ridges and a relatively wide anterior border. From *B. erratica* it differs in much wider fixigenae and longer palpebral lobes; moreover, *B. erratica* differs from other species of the genus in its trend to a sub-arcuate anterior margin of the cephalon. *Berabichia rotundata* is distinguished from the studied species by a relatively longer frontal area, a bluntly rounded anterior lobe of the glabella and a slightly wider and shallower occipital furrow (Ahlberg & Bergström 1978: pl. 3, figs 1, 2).

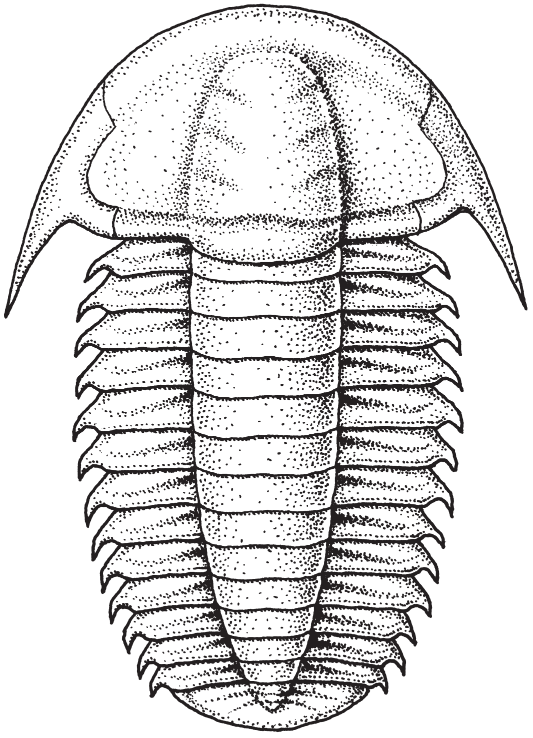

Fig. 17. — Reconstruction of *Berabichia oratrix* (Orłowski, 1985).

CONCLUSIONS

Detailed study of specimens hitherto assigned to *Comluella oratrix* Orłowski, 1985 and *Comluella igrzycznae* Orłowski, 1985 has shown that they belong to the genus *Berabichia* Geyer, 1990. Application of bivariate and multivariate morphometric analyses, along with discrimination function provide evidence that the taxa are in reality conspecific and that the differences distinguishing the two morphotypes are caused by post-sedimentary processes, i.e. fossil preservation and tectonic distortion. The latter was confirmed by restoration of distorted specimens using graphic retrodeformation techniques after Srivastava & Shah (2006). The studied specimens are thus assigned to *Berabichia oratrix* (Orłowski, 1985).

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