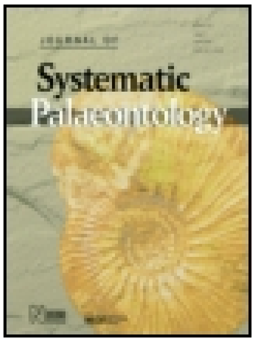

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Morphometrics of *Leptoplastides marianus* (Hoek) (Trilobita, Olenidae) from the Tremadocian of north-western Argentina: taxonomic implications

Daniela S. Monti*

Instituto de Ecología, Genética y Evolución de Buenos Aires, CONICET-UBA, Departamento de Ecología Genética y Evolución, Facultad de ciencias Exactas y Naturales, UBA, Intendente Güiraldes 2160, Ciudad Universitaria, Buenos Aires, C1428EGA, Argentina

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Morphometrics can be an important tool in systematic studies, providing taxonomists with strong elements of quantification and formal hypothesis testing. Here, these tools are tested for the trilobite *Leptoplastides marianus* (Hoek) which was originally described on the basis of three deformed specimens from west Tarija, Bolivia. Following the conclusions of Harrington & Leanza, a wide range of morphological variation is accepted for this species, and the name was applied to a large number of specimens from north-western Argentina. Based on specimens collected from the quebrada Moya (Huacalera, Jujuy), as well as on material in the Harrington & Leanza collections in the University of Buenos Aires, traditional morphometric and geometric morphometric methods were used to evaluate the variation of the cranidial shape of *L. marianus* sensu Harrington & Leanza. The results allow discrimination between two clearly different morphotypes. The name *L. marianus* should be restricted to the type specimens, given the deformation of these materials. In addition, *L. argentinensis* and *L. granulosus* are both valid names for the two morphotypes recognized in the present paper.

Keywords: geometric morphometrics; traditional morphometrics; Olenidae; *Leptoplastides*; Ordovician; Tremadocian

Introduction

The processes determining species boundaries have emerged as a major topic in modern systematics (e.g. Sites & Marshall 2003). Several methods for species delimitation have been developed based on the analysis of genetic data (e.g. Puorto *et al*. 2001; Templeton 2001; Wiens & Penkrot 2002; Morando *et al*. 2003; Pons *et al*. 2006). From a taxonomic point of view, the delimitation of a species has traditionally relied on one or more qualitative or quantitative characters that do not overlap with those of other species. In other words, morphological variation is characterized by gaps between taxa, and the presence of these gaps makes each taxon uniquely diagnosable (see Otte & Endler 1989). However, the fact that individuals of a species differ from each other and characters vary along a continuum highlights the importance of considering intraspecific variation when delimiting species boundaries. It is worthy of note that intraspecific variation is usually difficult to identify, especially in fossil taxa without living representatives.

Morphometrics can be an important tool in systematic studies given that it incorporates strong elements of quantification and formal hypothesis testing (MacLeod 2002). Linear and geometric morphometrics have proved to be valuable tools for the resolution of taxonomic problems (e.g. Hughes 1994; Adrain & Westrop 2006; Webster 2009; Hopkins & Webster 2009; Gendry *et al*. 2013; Pandey & Parcha 2013; Żylińska *et al*. 2013). In particular, geometric morphometrics has been used to distinguish interspecific disparity from intraspecific variation, leading to more robust species delimitation, diversity estimates, biostratigraphical correlation and detection of evolutionary patterns in a phylogenetic context (e.g. Hughes 1994; Hughes & Chapman 2001; Crônier *et al*. 2005; Adrain & Westrop 2006; Webster 2007, 2009, 2011; Hopkins & Webster 2009; Abe & Lieberman 2012; Gendry *et al*. 2013).

Geometric morphometric approaches provide taxonomists with additional characters concerning the shape of certain structures which may help in taxon delimitation (e.g. Mutanen & Pretorius 2007). Unfortunately, although these methods are capable of mathematically estimating the best discriminator among species they often fail to make accurate identifications (or diagnoses), rendering them useless from a biological point of view (Zelditch *et al*. 2004).

The olenid trilobite *Leptoplastides marianus* (Hoek) was described based on three specimens from Cuesta de Erquis, west Tarija, Bolivia (Hoek in Steinmann & Hoek 1912, p. 226, pl. 7, figs 1–3, referred to *Parabolinopsis mariana*). These specimens show some degree of

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*Email: danielamonti@ege.fcen.uba.ar

deformation and the illustrations in the original description are reconstructed. Later, Kobayashi (1937, p. 479, pl. 4, figs 15–17) redescribed this species and provided photographs of the type material. This author mentioned as diagnostic characters the presence of a smooth glabella, tiny palpebral lobes close to the glabella, truncated (almost rectangular) pleural endings, 13 thoracic segments, and two? axial rings on the pygidium. The latter two characters were subsequently emended by Harrington & Leanza (1957), who observed 14 thoracic segments and two pygidial axial rings.

Kobayashi (1935) erected the new genus *Andesaspis* to accommodate a single species, *Andesaspis argentinensis* Kobayashi, 1935 (pl. 11, figs 1, 2), which was described on the basis of material from the early Tremadocian of the Pascha area, Salta province, Argentina. A lectotype for this species was subsequently designated by Harrington & Leanza (1952, p. 196): the cranidium illustrated by Kobayashi (1935, pl. 11, fig. 1). Harrington (1938, pp. 213–214; pl. 8, figs 13, 18, 21) described the species *Protopeltura granulosa* Harrington based on material from the Ruspasca Formation (Alfarcito area). This author recognized the following diagnostic characters for the species: presence of a granular sculpture on the external surface, a glabella with two furrows, 12 thoracic segments and spine-like pleural ends. Finally, after examining a large number of specimens (about 800), Harrington & Leanza (1957) concluded that both *A. argentinensis* and *P. granulosa* were junior synonyms of *L. marianus*. In regard to *L. granulosus*, they considered that the characteristic glabellar granules are present in the types of this species, but absent in most of the samples collected from the type locality, which also exhibit a smooth glabella or one with shallow depressions. Moreover, these authors pointed out that the specimens that had been assigned to *L. granulosus* have 14 thoracic segments and two pygidial rings, instead of 12 and four, respectively, as described previously by Harrington (1938); they even attributed the difference in the shape of the pleural endings to poor preservation of the type specimens of *L. marianus* (Harrington & Leanza 1957, pp. 92–93). With reference to *L. argentinensis*, Harrington & Leanza (1957, p. 93) considered that its cranidium and librigena were indistinguishable from those of *L. marianus*, emphasizing that specimens with this morphology were found combined with *L. granulosus*-like pygidia in numerous localities. Recently, Waisfeld & Vaccari (2003) proposed restricting the name *L. marianus* to the type specimens because comparisons are hampered by the poor preservation of this material. In addition, they identified *L. granulosus* and *L. argentinensis* as distinct species based on the different position of the palpebral lobes (more anteriorly placed in *L. granulosus*), the length of the preglabellar field (shorter in *L. granulosus*), the width of the posterior fixigena (wider in *L. granulosus*), and the position and direction of the genal spines. Thus, they accepted *L. granulosus* as a valid taxon for the specimens from the type locality (Alfarcito area) (Waisfeld & Vaccari 2003, pl. 30, figs 8–10) and suggested a revision of *L. argentinesis*. They also mentioned that the material from Tortello & Rao (2000, figs 3J–R) from the Lampazar and Cardonal formations (Angosto de Lampazar, Pascha area) should be included in *L. argentinesis*. On the other hand, Tortello & Aceñolaza (2010) considered that the morphology of the holotype of *L. marianus*, in spite of showing transverse deformation, is similar to that of *L. argentinensis*, especially in the degree of development of the preglabellar field and palpebral lobes, shape of the truncated anterior margin of the glabella and features of the librigena. They agreed with Waisfeld & Vaccari (2003) in recognizing *L. granulosus* as a valid species, but they considered *L. argentinensis* as a junior synonym of *L. marianus* (cf. Harrington & Leanza 1957).

To summarize, the name *L. marianus* has been applied to a large number of specimens from north-western Argentina following the conclusions of Harrington & Leanza (1957) of a wide morphological variation in this species. However, there has yet to be a major revision of such material with particular focus on inter- or intraspecific variations. In the present work, the variation of cranidial shape in *L. marianus* sensu Harrington & Leanza is quantified using morphometric tools to test the hypothesis that there are two different morphotypes. Also, the holotype of *L. marianus* is retro-deformed to evaluate the validity of the proposed synonymy. Accordingly, the diagnosis and systematics of the morphospecies are revised, and the usefulness of morphometric methodology for species discrimination is discussed.

Geological setting

The Upper Cambrian–Lower Ordovician successions from north-western Argentina are included in the Central Andean Basin, a retroarc foreland basin located at mid to high palaeolatitudes on the western margin of Gondwana (Astini 2003, 2008; Egenhoff 2007). Deposits exposed along the Western Cordillera of Argentina encompass a wide range of marine and transitional environments, from estuaries or deltas to deep marine (below storm wave base) settings (Astini *et al*. 2004; Buatois *et al*. 2006; Egenhoff 2007). They correspond to the Santa Rosita and Acoite formations (and lateral equivalents) included in the Santa Victoria Group (Turner 1960; Astini *et al*. 2004; Buatois *et al*. 2006).

Material and methods

Eight samples were collected from Ordovician outcrops in the Argentinian Cordillera Oriental at quebrada Moya, Sierra de Zenta, Jujuy province. In addition, more than 200 specimens from the collection described by Harrington & Leanza (1957) were also examined. These samples consist of specimens from Tremadocian units exposed at different localities in the Cordillera Oriental: quebradas Huasamayo, Rupasca and San Gregorio (Alfarcito area), quebrada Pocoy (Huichaira area), Iturbe River (Azul Pampa area), quebrada Yacoraite (West of Huacalera area), Negrito River (tributary of the Santa Cruz River), quebrada de los Chanchos and road to La Caldera (La Caldera area), Angosto de Pascha, quebrada del Toro (Pascha area) (Fig. 1).

Specimens used for this study are preserved as imprints, as well as internal and external moulds. Most have suffered minor tectonic distortion and there is a predominance of disarticulated elements of the exoskeleton, mainly cranidia. Only holaspids were included in the analyses. To obtain a reference value of the error introduced by taphonomy, the variance within the same type of lithology of the two proposed morphospecies was compared with the total observed variance of the sample. In this context, the variance observed in moulds and casts was also compared between specimens with the two types of preservation collected from the same locality. In the absence of other variables like lithology or taxonomy, the variance observed in the sample was attributed to differences in preservation. For each locality, 10 pseudo-replicates of this procedure were carried out.

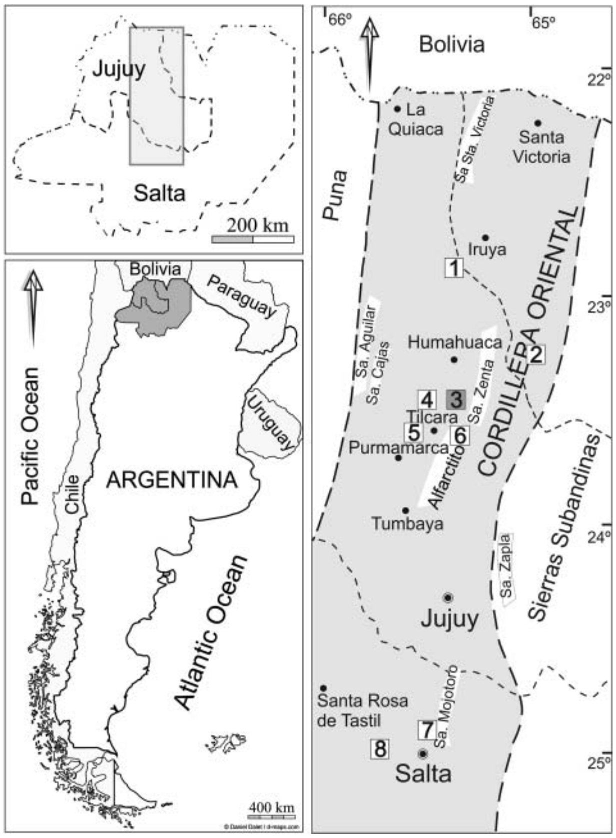

Figure 1. Map showing the location of the Western Cordillera of Argentina indicating the provenance of the specimens: 1, Azul Pampa area, northern margin of the Iturbe River, 3.7 km north-west of Azul Pampa; 2, Negrito river (tributary of Santa Cruz river), west of San Antonio de la Nueva Oran city; 3, Quebrada Moya, eastern margin of the Rio Grande, 5 km south-east of Uquía; 4, Quebrada Yacoraite (west of Huacalera area), western margin of the Rio Grande, 8 km south-east of Uquía; 5, Quebrada Pocoy (upper quebrada Huichaira), 10 km west of Tilcara city; 6, Alfarcito area, eastern side of quebrada de Humahuaca, 3 km east of Tilcara city; 7, La Caldera area, western margin of La Caldera river, 15–20 km north of Salta; 8, Pascha area, Angosto de Pascha, upper quebrada de Incamayo.

In addition, the study incorporated the holotype of *Protopeltura granulosa* (CPBA 679) and two more specimens: the lectotype of *Andesaspis argentinensis* (USNM PAL 94138) from an online photograph, and the holotype of *Leptoplastides marianus*. As mentioned above, the latter specimen is tectonically deformed but it was retro-deformed based on Kobayashi's photograph (1937, pl. 4, fig. 15) and then included in the study. Retro-deformation was performed with Photoshop, taking into account the bilateral symmetry of the cranidium. Thus, the two main axes (the sagittal and the wider transverse axes) were set so that they became orthogonal to each other (Fig. 2), obtaining 10 retro-deformed reconstructions of the holotype of *L. marianus*. To obtain a reference measure of the retro-deformation error, the variance of the pseudo-replicates was compared with the total observed variance of the sample and with the variance of the 10 pseudo-replicates of the same specimen.

Traditional morphometrics

Measurements were taken on 80 specimens, including those assigned to *Leptoplastides marianus* by Harrington & Leanza (1957) and the types of *Protopeltura granulosa* and *Andesaspis argentinensis*. Eleven morphometric variables were determined (Fig. 3A; Table 1). In addition, measurements were made on the 10 pseudo-replicates corresponding to the retro-deformed reconstructions of the holotype of *L. marianus.* For both samples, the mean and standard deviation of each variable were calculated and the variances of the two groups for each variable were compared. Three data matrices were constructed: the first matrix included data from the specimens of *L. marianus* sensu Harrington & Leanza; the second matrix also contained the mean values from the pseudo-replicates of the holotype of *L. marianus*; and the third matrix included data from the 80 specimens of *L. marianus* sensu Harrington & Leanza and the individual (non-averaged) data from the pseudo-replicates. To summarize the variation observed in *L. marianus*, a principal component analysis (PCA) was performed from the variance-covariance matrix of the log-transformed data using the software R

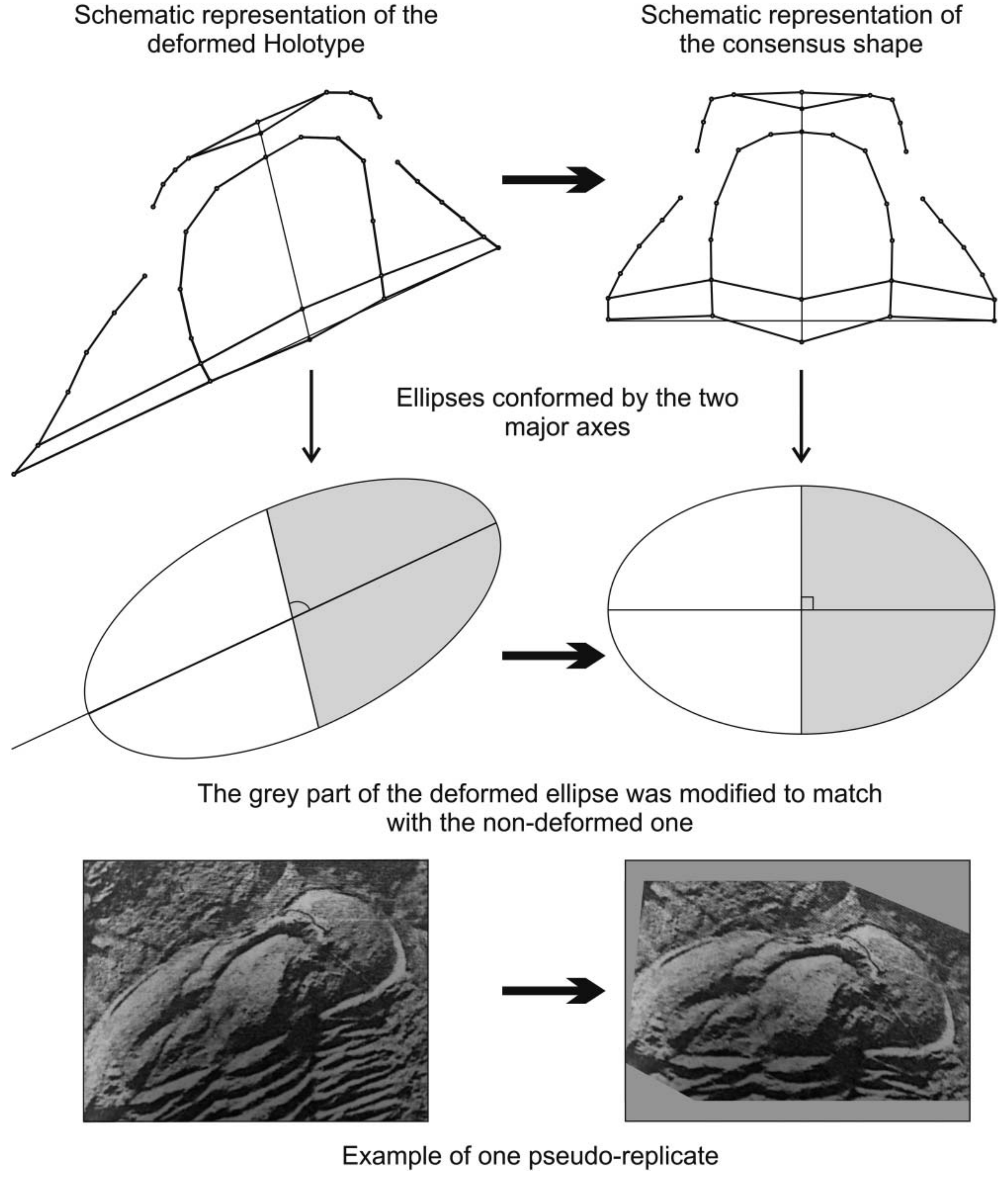

Figure 2. Image showing the steps followed to obtain the retro-deformed reconstructions of the holotype of *Leptoplastides marianus* (Hoek).

(R Development Core Team 2010). To avoid the size effect, the values of linear variables were corrected by the geometric means (Mosimann's size variables) (see Mosimann & James 1979; Meachen-Samuels & Van Valkernburh 2009) and a new PCA was performed from the variance-covariance matrix of the log-transformed corrected data. The first analysis (raw data) was carried out on the matrix with the 80 specimens, while the second

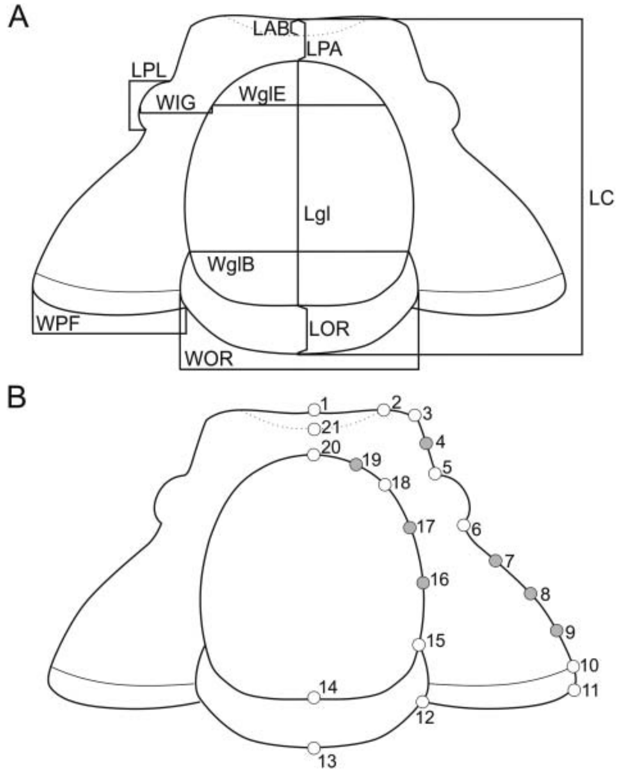

Figure 3. Schematic diagram of the cranidium of *Leptoplastides marianus* sensu Harrington & Leanza, showing the data sets used in the morphometric analyses. **A,** measurements used in the classic morphometric analysis; **B,** landmark distributions used in the geometric morphometric analysis. Abbreviations: LOR, length of the occipital ring (sag.); LC, length of the cranidium (sag.); Lgl, length of the glabella (sag.); LPL, length of the palpebral lobes (exasag.); WOR, width of the occipital ring (tr.); WglB, width of the glabella (base) (tr.); WPF, width of the posterior fixigena (tr.); WIG, width of the interocular gena (tr.); WglE, width of the glabella (eyes) (tr.); LPA, length of the preglabellar area (sag.); LAB, length of the anterior border (sag.).

Table 1. Description of variables used in traditional morphometric analysis.

Variable	Description
LAB	Length of the anterior border
LPA	Length of the preglabellar area
LPL	Length of the palpebral lobes
LC	Length of the cranidium
Lgl	Length of the glabella
LOR	Length of the occipital ring
WglE	Width of the glabella (eyes)
WglB	Width of the glabella (base)
WOR	Width of the occipital ring
WPF	Width of the posterior fixinae
WIG	Width of the interocular genae

(corrected data) was performed using the three matrices mentioned above. Finally, a discriminant analysis was conducted using the two predefined morphotypes as a classifier with the original matrix (without the holotype of *L. marianus*). To position the holotype of *L. marianus* in the discriminant space, the value of the discriminant function was calculated with Microsoft Excel using the canonical coefficients and considering the mean values of the 10 retro-deformed pseudoreplicates as representative of this specimen.

Geometric morphometrics

Digital images of 66 cranidia of *Leptoplastides marianus* sensu Harrington & Leanza, including the types of *Protopeltura granulosa* and *Andesaspis argentinesis*, were taken. In cases where one-half of the cranidium was incomplete, the other half was reflected, to increase the amount of data. A total of 14 landmarks (type I and II landmarks of Bookstein 1991) and seven semi-landmarks (type III landmark of Bookstein 1991; see Bookstein 1997) were digitized (Fig. 3B; Table 2) with tpsDig 2.16 (Rohlf 2010a). The criterion used for sliding semi-landmarks was minimum bending energy (BE: Bookstein 1996, 1997; Green 1996; Bookstein *et al.* 2002), which consists in sliding semi-landmark points along the contour of each specimen to minimize the bending energy necessary to produce the change in the outline relative to the reference form (Bookstein 1997; Gunz *et al*. 2005; Pérez *et al.* 2006). A generalized least-squares Procrustes analysis (GLS, also called a generalized Procrustes analysis, GPA: Goodall 1991; Rohlf 1999) was performed to estimate a mean shape and to align the specimens. Then, each individual landmark configuration of the aligned specimens was compared to the consensus, using the thin-plate splines (TPS) deformation method, which allows the visualization of the direction and degree of shape change relative to a mean consensus form. Thus, the partial warp scores were computed for each individual (including the non-uniform component and two uniform components) and subsequently stored in a single matrix (weight matrix, WM). These analyses were carried out with the program TpsRelW 1.49 (Rohlf 2010b). The 10 retro-deformed pseudo-replicates corresponding to the holotype of *L. marianus* were treated with the same procedures, but separately. In this way, a consensus form was generated for the holotype of *L. marianus*.

An exploratory analysis was made for the 66 specimens of the relationship between shape and size. For this purpose, the centroid size (CS), defined as the square root of the squared distance between each landmark and the centroid of the landmark configurations summed over all landmarks, was calculated for each specimen. In the presence of allometry, CS will be related to any function expressing ‘shape’. To evaluate the proportion of shape

Table 2. Description and type of landmarks used in geometric morphometric analysis. The asterisk indicates semi-landmarks.

Landmark	Description	Type of homology
1	Maximum of anterior curvature of the cranidium	2
2	Point where the anterior border furrow cuts the anterior margin of the cranidium	1
3	Anterolateral corner of the cranidium	2
4	Anterior branch of the facial suture	3*
5	Most distal anterior point of the palpebral lobe	2
6	Most posterior point of the palpebral lobe	2
7, 8, 9	Posterior branch of the facial suture	3*
10	Intersection between the posterior border furrow and the posterior branch of the facial suture	1
11	Posterolateral corner of the cranidium	2
12	Intersection between the posterior margin of the fixigena and the occipital ring	1
13	Posterior margin of the occipital ring at the sagittal plane	1
14	S0 at the sagittal plane	1
15	Intersection between S0 and axial furrows	1
16, 17	Axial furrow	3*
18	Point of the maximum convexity of the glabella	2
19	Preglabellar furrow	3*
20	Preglabellar furrow at the sagittal plane	1
21	Anterior border furrow at sagittal plane	1

that was explained by size, the partial warp scores (calculated as explained above) were regressed against the logarithm of the CS. This analysis was performed for all data and for each group, separately. Because the regression model assumes linearity of the relationship between size and shape, the residuals from the regression line are the deviations of an individual from the mean shape expected for its size. In this way, the sum-squared residual (SSresidual) can be used to estimate shape deviations not attributable to allometry. The shape variation explained by allometry (SSmodel) will be the difference between the sum-squared total (SStotal) of the sample and the SSresidual. The ratio of SSmodel to SStotal gives the proportion of total variance explained by allometry. A permutation test (10,000 replicates of bootstrap resampling) was applied to test for significance of the multivariate regression. These analyses were performed with the program TpsRegr 1.41 (Rohlf 2011).

A relative warp analysis (RWA) was made from the WM to quantify and visualize the shape variation of *Leptoplastides marianus* sensu Harrington & Leanza with TpsRelW 1.49 (Rohlf 2010b). In this case three matrices were also used, one including the 66 specimens of *L. marianus* sensu Harrington & Leanza, and the other two containing the retro-deformed type specimen of *L. marianus* (one including the 10 pseudo-replicates mentioned above and the other only the consensus form). To quantify the differences among the previously defined groups, the partial Procrustes distance between the consensus configurations of each species was calculated. The significance of the observed difference between the species means was tested using a bootstrap-based approach with Goodall's F-test (Goodall 1991; Dryden & Mardia 1998). The observed F-value was compared to the range of F-values obtained by randomly assigning specimens to samples (1600 replicates) using TwoGroup8 software (Sheets 2014). For details of the methodology used, see Webster & Sheets (2010) and Webster (2011). In addition, a canonical variate analysis (CVA) based on Procrustes coordinates was conducted with MorphoJ 1.02E (Klingenberg 2011).

To recognize variables easily determined in new material and identify diagnostic characters that could discriminate between the two groups, a correlation analysis was performed between the first axes of the RWA and the linear variables corrected for size (LOR, LC, Lgl, LPL, WOR, WglB, WPF, WGI, WglE, LPA and LAB) and the ratio variables (Lgl/WglB, LOR/WOR, LPA/LC, LAB/LPF, WIG/WglE, WPF/WglB, LOR/LC, LPL/Lgl, Lgl/LC) (see Table 1). The correlation analysis was carried out with InfoStat (Di Rienzo *et al*. 2014).

Systematic palaeontology

Studied specimens are deposited in the Invertebrate Paleontology Collection, Department of Geology (Paleontology area), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires. In the descriptions and the diagnoses, the proportions expressed as percentages are medians, with the range of values in parentheses. All measurements were obtained from digital images using the Measure Tool of Adobe Photoshop.

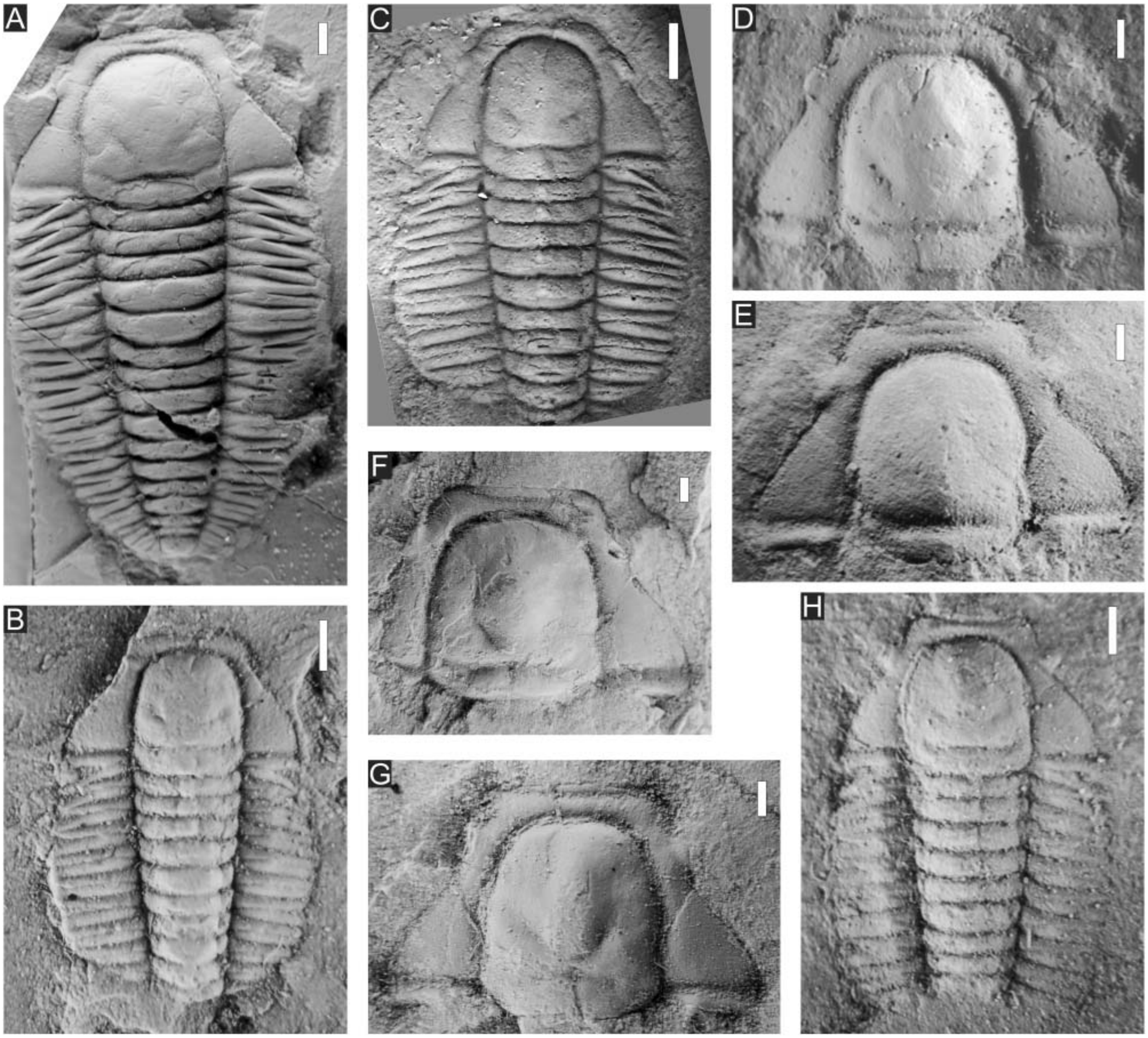

Figure 4. *Leptoplastides granulosus* (Harrington) from the Alfarcito area. **A–C,** type locality, quebrada Rupasca, Upper Tremadoc; **A,** cranidium-thorax in dorsal view, holotype, CPBA 679; **B,** cranidio-thorax, CPBA 740; **C,** cranidium and partial thorax, CPBA 712. **D–G,** quebrada San gregorio, Lower Tremadoc; **D,** cranidium, CPBA 1316; **E,** cranidium, CPBA 1310; **F,** cranidium, CPBA 1302; **G,** cranidium, CPBA 1301; **H,** cranidium-thorax, CPBA 1311. Scale bars = 1 mm.

Class **Trilobita** Walch, 1771
Order **Ptychopariida** Swinnerton, 1915
Suborder **Olenina** Burmeister, 1843
Family **Olenidae** Burmeister, 1843
Subfamily **Pelturinae** Hawle & Corda, 1847
Genus ***Leptoplastides*** Raw, 1908

Type species. *Concoryphe salteri* Callaway, 1877 by original designation.

Leptoplastides granulosus (Harrington, 1938)
(Figs 4, 6A)

1938 *Protopeltura granulosa* Harrington: 213, pl. 8, figs 13, 18, 21.
1957 *Parabolinopsis mariana* (Hoek) [*partim*]; Harrington & Leanza: 90, figs 29, 30.2–30.6, 30.10.
2003 *Leptoplastides granulosa* (Harrington); Waisfeld & Vaccari: 328, pl. 30, figs 8–10.
2005 *Leptoplastides marianus* (Hoek); Zeballo & Tortello: 135 figs. 4M, P–R.

Holotype. By original designation, CPBA 679 (Harrington 1938, pl. 8, fig. 21), from the late Tremadocian of the quebrada Rupasca, Alfarcito area, Jujuy.

Other material. CPBA 686, 687, 709, 712, 715, 718, 719, 721, 722, 733, 735, 736, 738–740, 742, 744, 746–750, 753, 754, 756, 760, 765–767, 769, 771–773, 775, 777, 779, 781, 782, 817–819, 821–825, 827, 830, 833–838, 840–844, 845, 847–853, 856–859, 1301, 1302, 1305, 1308–1311, 1315–1318, 1322, 1323, 1325–1329, 1360, 1367, 1368, 1371, 1374, 1376, 1378, 1386, 2638, 2706–2711, 2716, 2718, 2779, 2801, 2818, 4168–4170, 4172, 4173, 4175, 4177, 4178, 4180, 4183–4187, 4189, 4193, 4194, 4200, 4202, 4210.

Diagnosis. *Leptoplastides* that combines a short preglabellar field, tiny palpebral lobes, closed to the glabella, located anteriorly and oblique to the axial furrow with a robust glabella, relatively large and a convex posterior section of the facial suture.

Occurrence. Upper part of the Rupasca Formation (*Bienvillia tetragonalis*-*Conophrys minutula* Zone, late lower Tremadocian), quebradas Rupasca, San Gregorio and Huasamayo (Alfarcito area), Jujuy. *Leptoplastides granulosus* also occurs in the Tremadocian of Iturbe River in the Azul Pampa area (J.Hum-5, and J.Hum-6 of Harrington & Leanza 1957), and Negrito River, Santa Cruz River area (S.Ora-5 of Harrington & Leanza 1957).

Remarks. *Leptoplastides granulosus* shows great morphological variation in the general shape of the cranidium. However, the combination of unique features, given in the diagnosis, allows it to be distinguished from other species of *Leptoplastides*. Therefore, in accordance with the proposal of Waisfeld & Vaccari (2003), subsequently followed by Tortello & Aceñolaza (2010), *L. granulosus* is considered here a valid taxon.

Leptoplastides granulosus differs from *L. argentinensis* (Kobayashi) in having a very convex, more rounded and larger glabella, shorter palpebral lobes, located anteriorly and positioned obliquely with respect to the axial furrow, a shorter preglabellar field and convex posterior section of the facial suture.

Like most of the species of the genus, *Leptoplastides granulosus* shows some ontogenetic variability. Specimens of the late meraspid and early holaspid stages have two or three glabellar furrows, an occipital node and strong ocular ridges, but these characters are not observable in the late holaspid stage. Zeballo & Tortello (2005) pointed out some of these differences, along with others such as the presence of striae on the librigena and a lower external genal angle in younger specimens from Alfarcito that can be assigned to this species.

Specimens resembling *L. granulosus* from the type locality were illustrated by Harrington (1938, pl. 8, figs 13, 18, 21; referred to as *Protopeltura granulosa*), Harrington & Leanza (1957, figs 29, 30.2–30.6, 30.10; referred to as *Parabolinopsis mariana*), Zeballo & Tortello (2005, fig. 4M, P–R; referred to as *Leptoplastides marianus*) and Waisfeld & Vaccari (2003, pl. 30, figs 8–10; referred to as *Leptoplastides granulosus*). The proposal of Tortello & Aceñolaza (2010, p. 159) of a poorly preserved specimen from the upper Tremadocian of Sierra de Santa Bárbara (F. G. Aceñolaza & González 1977, fig. 1.2) as conspecific with *L. granulosus* is confirmed here.

Leptoplastides argentinensis (Kobayashi, 1935) (Figs 5, 6B)

1935 *Andesaspis argentinensis* Kobayashi: 204, pl. 11, figs 1, 2 only.
1937 *Andesaspis argentinensis* Kobayashi; Harrington: 111, pl. 7, figs 8–10.
1938 *Andesaspis argentinensis* Kobayashi (*partim*); Harrington: pl. 8, figs 10, 14, 15.
1957 *Parabolinopsis mariana* (Hoek) (*partim*); Harrington & Leanza: 90, figs 30.1, 30.7–30.9.
1957 *Leptoplastides marianus* (Hoek) (*partim*); Henningsmoen: 266.
1980 *Leptoplastides marianus* (Hoek) (*partim*); Pribyl & Vanek: pl. 7, figs 4, 5.
1998 *Leptoplastides marianus* (Hoek); Rao & Tortello: 39, fig. 4G–J.
2000 *Leptoplastides marianus* (Hoek); Tortello & Rao: 72, fig. 3J–R.
2002 *Leptoplastides marianus* (Hoek); Tortello, Esteban, & Aceñolaza: figs 3n, 4a–c.
2003 *Leptoplastides marianus* (Hoek); G. F. Aceñolaza, Aráoz, Vergel, Tortello, & Nieva: pl. 1, figs d, e.
2013 *Leptoplatides marianus* (Hoek); Tortello, Zeballo, & Esteban: 144, fig. 6.1–11.

Type. Lectotype, designated by Harrington & Leanza (1952, p. 196): cranidium illustrated by Kobayashi (1935, pl. 11, fig. 1) from the early Tremadocian of the Pascha area, Salta. USNM PAL 94138 (Fig. 6B).

Diagnosis. *Leptoplastides* with a moderately developed preglabellar field, tiny palpebral lobes, located at the midpoint (sag.) of the glabella, subparallel to the axial furrows and almost triangular fixigena, posterior branch of the facial suture straight to concave.

Material. CPBA 1400, 1401, 1405–1407, 1411–1420, 1422, 1423, 1425, 1429–1432, 1830, 1839, 1843, 1895, 1924, 2912, 2955, 3171, 3332–3346, 3348, 3350, 3574, 3384, 3887, 3895, 3574, 4367, 19378, 19494, 21910 (1–6), 21911 (1–2), 21912 (1–2), 21914 (1–2), 21915, 21916 (1–2), 21917 (1–3).

Occurrence. Lower Tremadocian of quebrada de los Chanchos (Gallinato) and road to La Caldera, La Caldera area, quebrada Moya, Abra Zenta (Tortello & Aceñolaza 2010), quebrada Incamayo, Santa Victoria area. The species also occurs in the Lower Tremadocian of quebrada

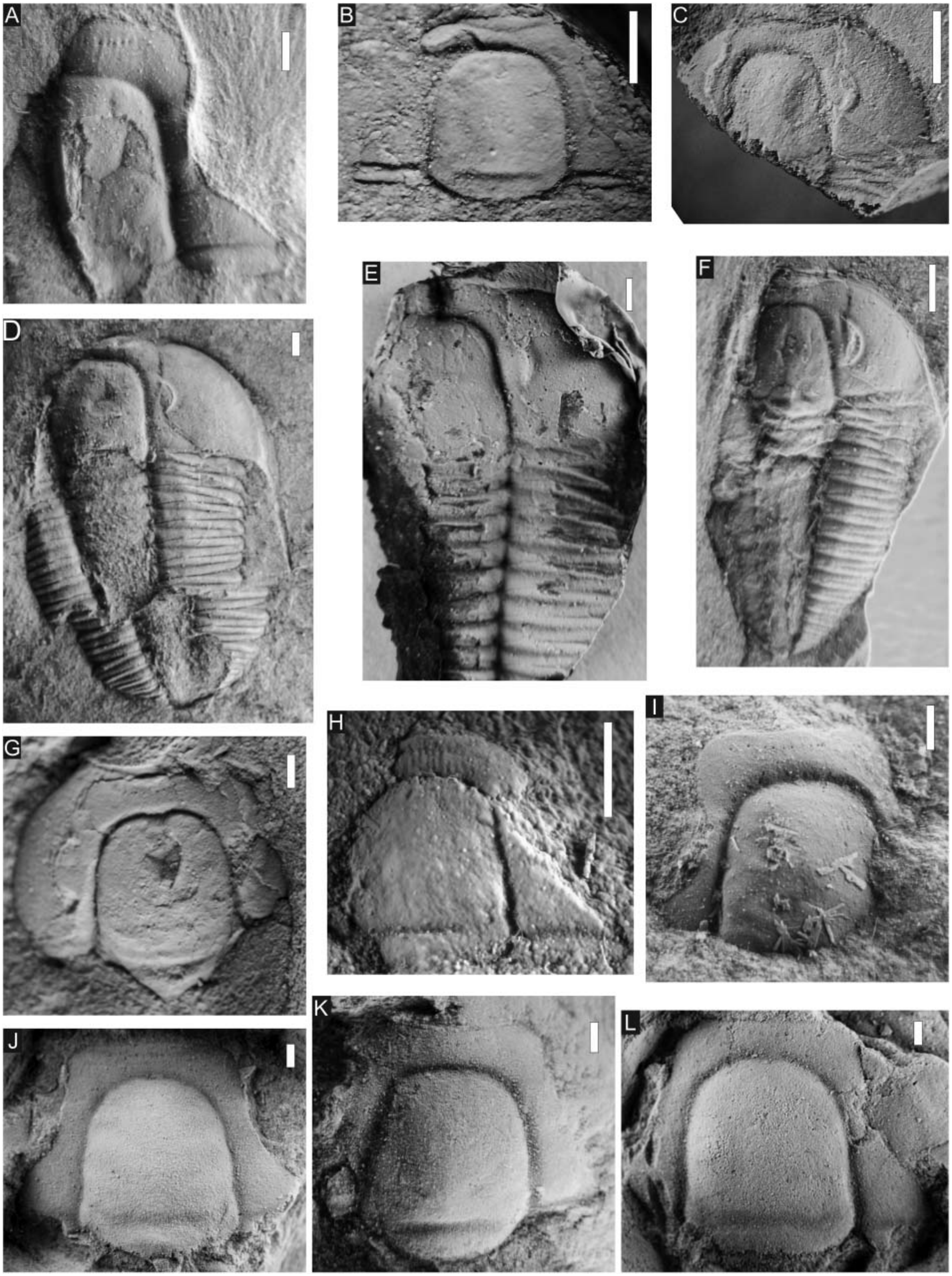

Figure 5. *Leptoplastides argentinensis* (Kobayashi). **A–I,** quebrada Moya, Lower Tremadoc; **A,** partial cranidium, CPBA 21910-3; **B,** cranidium, CPBA 21917-1; **C,** cephalon, CPBA 21910-5; **D,** cephalon-thorax, CPBA 21910-1; **E,** cephalon-thorax, CPBA 21914-2; **F,** right side of cephalothorax, CPBA 21911-2; **G,** cephalon, CPBA 21911-1; **H,** partial cranidium, CPBA 21910-6; **I,** partial cranidium, CPBA 21914-1. **J–L,** La Caldera area, quebrada de los Chanchos, Lower Tremadoc; **J,** cranidium, CPBA 1401; **K,** cranidium, CPBA 1420; **L,** cranidium, CPBA 1422. Scale bars = 1 mm.

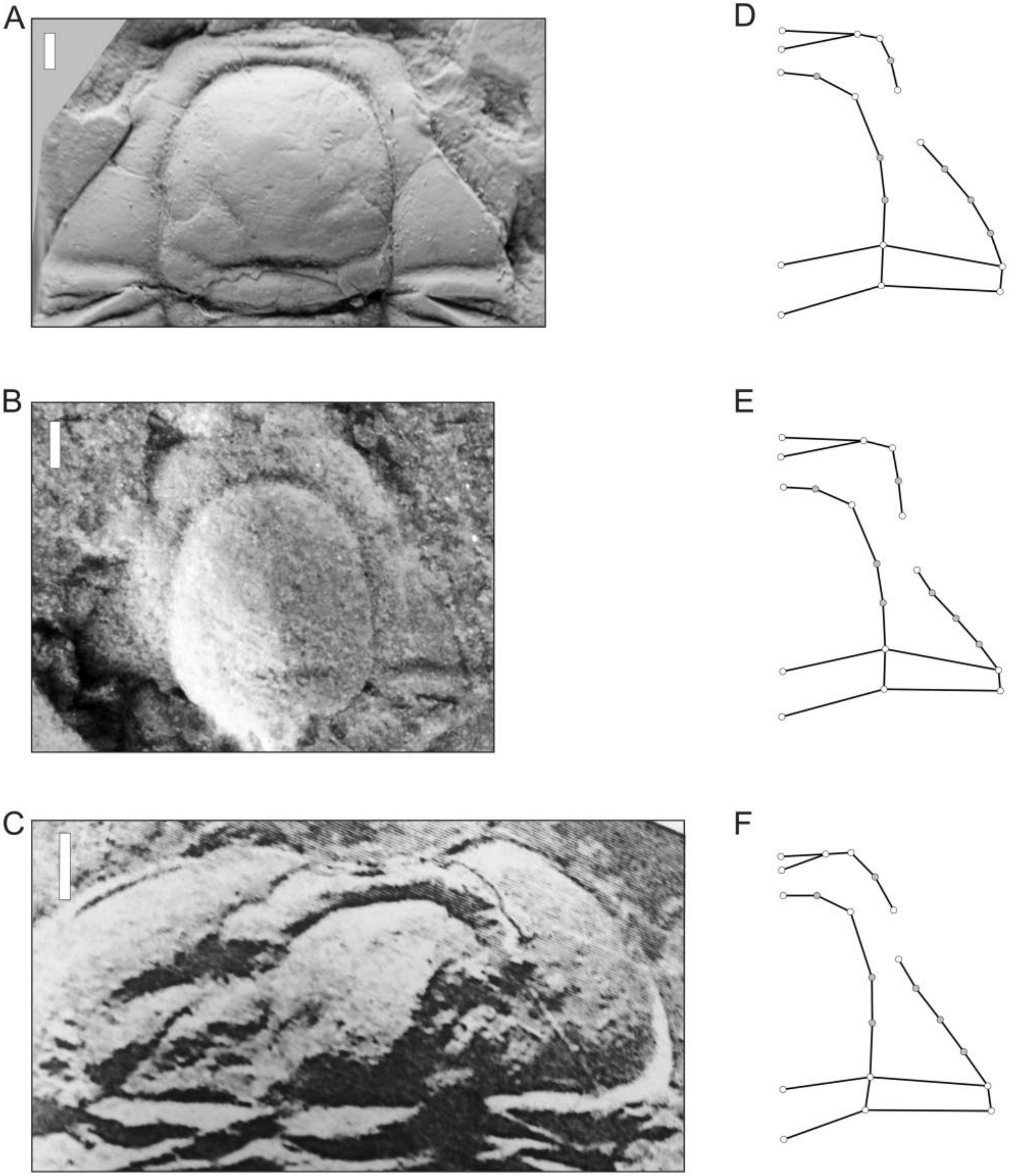

Figure 6. Comparison of the types and consensus shapes for each taxon recognized. **A,** holotype of *Leptoplastides granulosus* (Harrington). **B,** lectotype of *L. argentinenesis* (Kobayashi) (modified from the online catalogue of the Smithsoninan Collection: nmnhpaleobiology_3038433; courtesy of the Smithsonian Institution). **C,** retro-deformed holotype of *L. marianus* (Hoek). **D,** consensus shape of *L. granulosus*. **E,** consensus shape of *L. argentinensis*. **F,** consensus shape of the 10 retro-deformed pseudo-replicates of the holotype of *L. marianus*. Scale bars: A = 0.69 mm; B = 0.98 mm; C = 4.08 mm.

Toro (Pascha area), Lampazar and Cardonal formations, Angosto de Lampazar (Pascha area) and east of Cerro Gólgota, Rosario de Lerma, Salta (Rao & Tortello 1998; Tortello & Rao 2000).

Remarks. Tortello & Aceñolaza (2010) followed Harrington & Leanza (1957) in regarding *Leptoplastides argentinensis* as a junior synonym of *L. marianus*, arguing from the similar morphology, especially with respect to the degree of the preglabellar field and the palpebral lobes. However, both characters were analysed here and this hypothesis is not corroborated. *Leptoplastides argentinensis*, unlike the retro-deformed type of *L. marianus*, shows a more developed preglabellar field, and larger palpebral lobes.

Leptoplastides argentinensis shows some variations in different aspects of its morphology, as previously stated (e.g. Robison & Pantoja-Alor 1968; Tortello & Aceñolaza 2010). The specimens studied here show variability related to the degree of development of the preglabellar field and glabellar segmentation (while most of the specimens have a smooth glabella, some show indications of a pair of glabellar furrows). Robison & Pantoja-Alor (1968) suggested that this variability is related to ontogenetic development. They noted that late meraspids/early holaspids have visible glabellar furrows, a moderately defined anterior border furrow, a narrow and elevated anterior border, and a conspicuous occipital node, which disappears or becomes faint in larger holaspids. This ontogenetic variability is also documented in other species of the genus, such as *L. salteri* (Callaway, 1877) from the late Tremadocian of England (Fortey & Owens 1991).

Leptoplastides argentinensis differs from the type species of the genus, *L. salteri* (Callaway) from the Tremadocian of Shropshire, UK (Fortey & Owens 1991, figs 8c–j, 9), because the former has a more developed preglabellar field, more posteriorly located genal spines, and a pygidium with marginal spines (cf. Henningsmoen 1957; Rao & Tortello 1998; Tortello & Aceñolaza 2010).

Results

Traditional morphometrics

The first axis of the PCA with the raw data accounts for 94.29% of total variability and shows a strong influence of size. All of the variables are positively correlated with this axis (Fig. 7A, B). Therefore, larger specimens have positive values on PC1, while smaller specimens have negative values. All of the specimens are evenly scattered along this axis, indicating that the two morphotypes do not differ in size. The two primary axes of the PCA obtained from the corrected data account for 61.91% of total variability. Although the two morphotypes can be recognized, they show some overlap (Fig. 7C). The first axis, which explains 40.16% of the variability, correlates positively with the length of the palpebral lobes (LPL), the length of the preglabellar area (LPA), and the length of the anterior border (LAB) (0.25, 0.49 and 0.57, respectively). It correlates negatively with the length of the occipital ring (LOR) (−0.51) (Fig. 7D). Therefore, specimens with a well-developed preglabellar area (sag.) and anterior border (sag.), and with longer palpebral lobes (exasag.), are located on the positive side of the axis, while specimens with a poorly developed preglabellar area (sag.) and anterior border (sag.), and with shorter palpebral lobes (exasag.), are placed on the negative side of the axis (Fig. 7C, D).

The second axis correlates positively with the length of the palpebral lobes (LPL) (0.68) and negatively with the length of the occipital ring (LOR) and the length of the anterior border (LAB) (−0.37 and −0.51, respectively) (Fig. 7D). Specimens with well-developed palpebral lobes (exasag.), a longer anterior border (sag.), and a shorter occipital ring (sag.), lie on the positive side of the axis, while specimens with less-developed palpebral lobes (exasag.), a shorter occipital ring (sag.), and a longer anterior border (sag.) (Fig. 7C), are on the negative side of the axis. Specimens assigned to *Leptoplastides argentinensis* are located in the positive half, while those morphologically similar to *L. granulosus* are found in the negative half. This indicates that *L. argentinensis* specimens, unlike those of *L. granulosus*, are characterized by having a relatively well-developed preglabellar area (sag.), longer palpebral lobes (exasag.) and a shorter occipital ring (sag.) (Fig. 7C, D).

When the retro-deformed holotype of *L. marianus* was included in the PCA, it was placed in the range of variation of *L. granulosus* (Fig. 8A). However, when the 10 retro-deformed pseudo-replicates were included, they formed a third group separated from the other two morphotypes that overlapped with the group of *L. granulosus* (Fig. 8C). The discriminant function separates the two morphotypes, with centroid values of −1.28 and 1.73 for *L. granulosus* and *L. argentinensis*, respectively. However, a total error of 8.75% is obtained from the cross-classification table. The discriminant score for the retro-deformed holotype of *L. marianus* is −0.9699, suggesting that it may be classified as *L. granulosus.*

Geometric morphometrics

The first axis of the RWA accounts for 33.50% of the total shape variance and clearly separates the two morphotypes (Fig. 9A). This axis relates primarily to variation in the relative size and shape of the frontal region and posterior wing. The most remarkable difference in morphology along the axis is the shape of the anterior and posterior branches of the facial suture. In addition, the relative size and position of the palpebral lobes vary

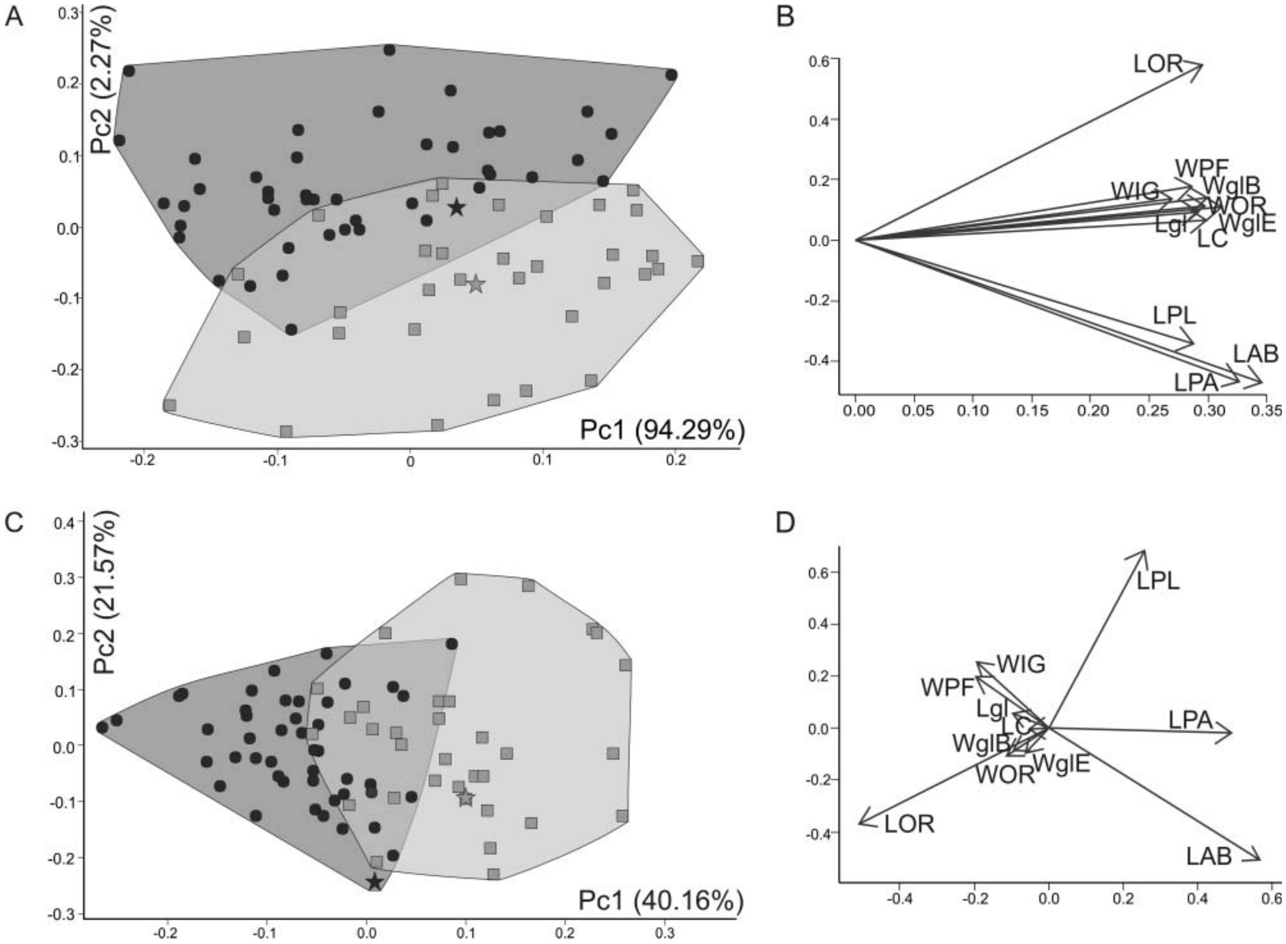

Figure 7. Scatter plot of the two first components of the principal component analysis (PCA) performed with morphometric variables. **A,** raw data; **C,** data corrected by geometric means; black circles, *Leptoplastides granulosus* (Harrington); black star, holotype of *L. granulosus* (CPBA 679); grey square, *Leptoplastides argentinensis* (Kobayashi); grey star, holotype of *L. argentinensis* (USNM PAL 94138). **B, D,** biplots of the eigenvectors. For abbreviations see Table 1.

along this axis. Specimens with positive score values show an almost concave posterior branch of the facial suture and longer palpebral lobes (exasag.), which are parallel to the axial furrow and placed at the middle point of the glabella (sag.). The anterior branch of the facial suture tends to be subparallel, and the preglabellar field is more developed (Fig. 9A). Specimens with negative score values of relative warp 1 (RW1) have a clearly convex posterior branch of the facial suture and a shorter preglabellar field (sag.). The anterior branch of the facial suture tends to be convergent and the palpebral lobes are shorter (exasag.), oblique with respect to the axial furrow and anterior to the middle point of the glabella (sag.) (Fig. 9A).

Almost all of the specimens assigned to *Leptoplastides granulosus* have negative scores and the type specimen of this species is found among the most extreme forms, while all the specimens assigned to *L. argentinensis* have positive scores (Fig. 9A). The second axis of the RWA explains 15.76% of total shape variance and relates primarily to variation in the width of the posterior fixigeanae and the length of the preglabellar field. Both morphotypes are evenly scattered along this axis (Fig. 9A). Hence, *L. granulosus* is characterized by having a relatively larger axial lobe of the cranidium, a clearly convex posterior branch of the facial suture, a shorter preglabellar field (sag.), an anterior branch of the facial suture that tends to be convergent, and shorter palpebral lobes, oblique with respect to the axial furrow and close to the anterior end of the glabella (sag.). On the other hand, *L. argentinensis* shows a relatively smaller glabella and occipital ring, a posterior branch of the facial suture with a tendency to be concave, and longer palpebral lobes (exasag.) that are parallel to the axial furrow and located at the middle point of the glabella (sag.). The anterior branch of the facial suture is subparallel and a preglabellar field more developed.

When the holotype of *L. marianus* is included in the analysis as the consensus of all pseudo-replicates, it is placed within the variational range of *L. granulosus* (Fig. 9B). However, when the individual pseudo-

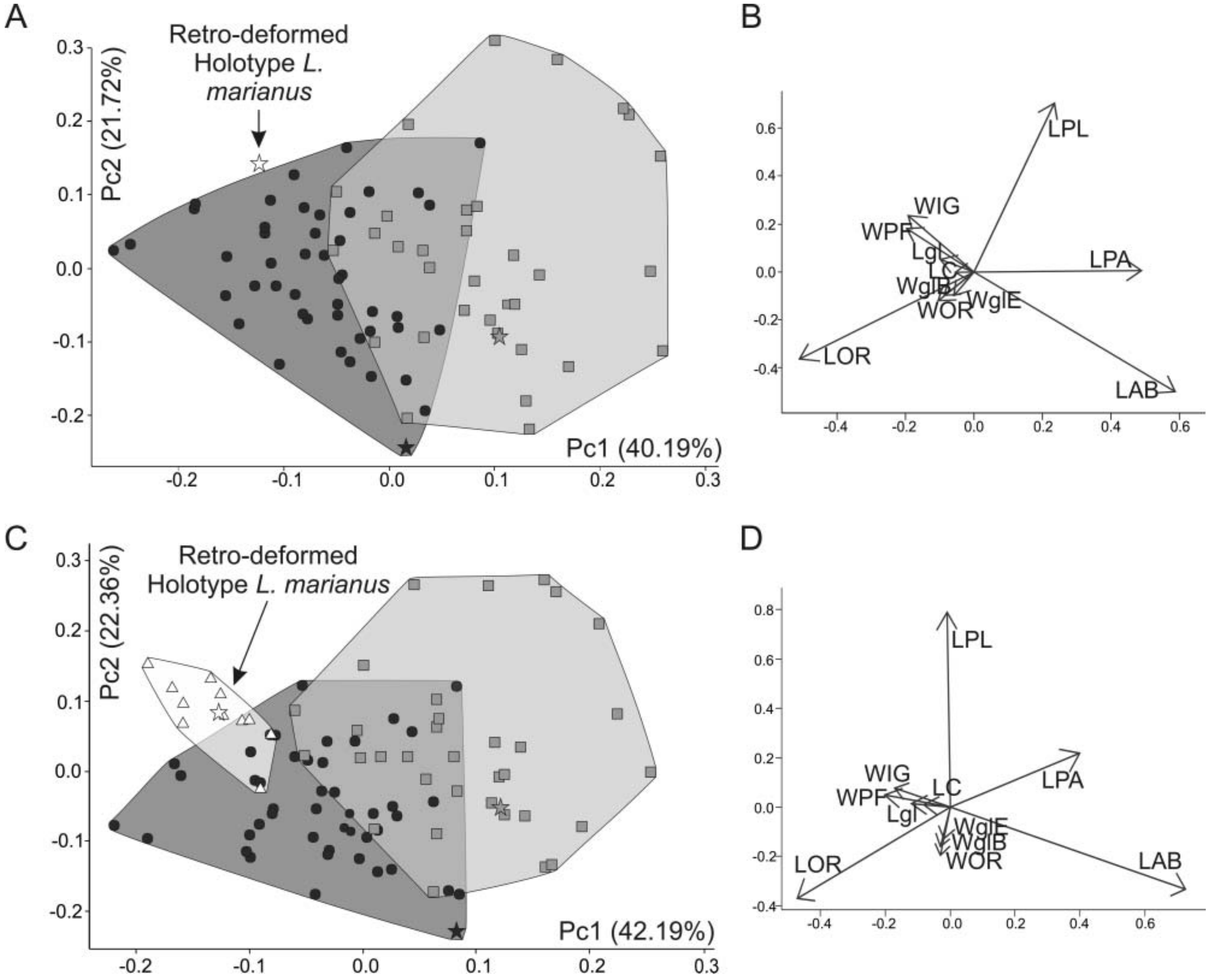

Figure 8. Scatter plot of the two first components of the principal component analysis (PCA) performed with the matrix including the retro-deformed holotype of *Leptoplastides marianus*. **A,** including the average measurements; **C,** including the average measurements and the 10 pseudo-replicates; black circles, *Leptoplastides granulosus* (Harrington); black star, holotype of *L. granulosus* (CPBA 679); grey square, *Leptoplastides argentinensis* (Kobayashi); grey star, holotype of *L. argentinensis* (USNM PAL 94138); white triangles, pseudo-replicates of the *L. marianus* type; white star, average measurements of the holotype of *L. marianus*. **B, D,** biplots of the eigenvectors. For abbreviations see Table 1.

replicates are incorporated into the analysis these are separated as a third group (Fig. 9C). This new group shows some subtle differences, including an anterior branch of the facial suture clearly convergent, an almost straight posterior branch, and palpebral lobes located closer to the glabella and even more anterior than in *L. granulosus* (Fig. 9C). Goodall's F-test shows significant differences in mean shape between the two morphotypes (distance between medians 0.0644–0.0913 at 95% of confidence; F $= 17.04$; $p = 0.0006$, permutation test, 1600 replicates). Furthermore, the CVA based on the Procrustes coordinates show significant differences between the two groups (Mahalanobis distance $= 6.9121$, $p < 0.0001$, permutation test 1000 replicates; Procrustes distance 0.0748, $p < 0.0001$, permutation test 1000 replicates).

In analysing the linear variables, RW1 shows a significant positive correlation with LPA and LAB, and a significant negative correlation with LOR, LC, Lgl, LPL, WOR, WglB and WIG. However, it is worthy of note that the Pearson's correlation coefficient is smaller than $|0.61|$ in all cases (Table 3). With regard to the ratio variables, RW1 shows a significant positive correlation with LPA/LC and LPL/Lgl, and a significant negative correlation with LOR/WOR, WIG/WglE, and LOR/LC (Table 3).

Leptoplastides granulosus shows a statistically significant regression between shape and size (4.83% of the total variance; permutation test $p = 0.0423$), with larger specimens having a more developed preglabellar field and a less-convex posterior branch of the facial suture than smaller ones. On the other hand, specimens of *L.*

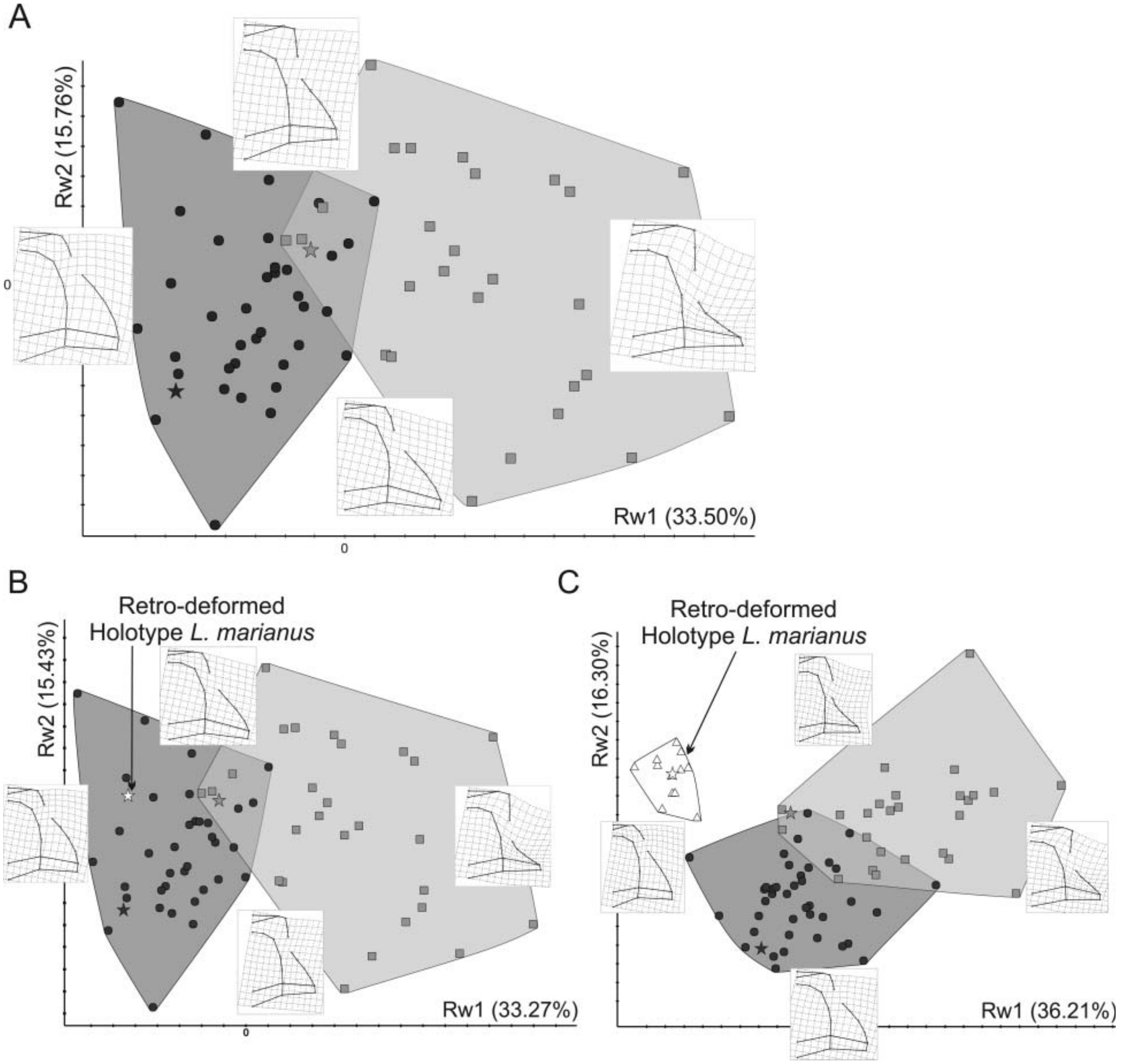

Figure 9. Distribution of specimens in the two primary axes of the relative warp analysis. **A,** including 66 specimens; **B,** including the consensus form of the holotype of *Leptoplastides marianus* (Hoek); **C,** including consensus form and the 10 pseudo-replicates of the holotype of *L. marianus*. Thin-plate spline indicates the extreme shape for each axis. Black circles, *Leptoplastides granulosus* (Harrington); black star, holotype of *L. granulosus* (CPBA 679); grey square, *Leptoplastides argentinensis* (Kobayashi); grey star, holotype of *L. argentinensis* (USNM PAL 94138); white triangles, pseudo-replicates of the *L. marianus* type; white star, average measurements of the holotype of *L. marianus*.

argentinensis showed a non-significant regression between shape and size (5.97% of the total variance; permutation test $p = 0.1306$), suggesting that there is not enough evidence to support any association between shape and size. Nevertheless, the range of size included in each case is different: the cranidium length range of *L. granulosus* (0.195–1.306 cm) is wider than that of *L. argentinensis* (0.252–1.279 cm).

Discussion

The results obtained from the different analyses carried out in this study allow discrimination between two morphotypes, supporting their separation as two species (*Leptoplastides granulosus* and *L. argentinensis*). The distortion of the holotype of *L. marianus* prevented it from being included *a priori* in the analyses. However,

Table 3. Coefficient of Pearson's correlation for each linear variable corrected for size and ratio variables with the relative warp 1 (RW1). The asterisk indicates significant correlations.

Relative warp analysis (RWA) axis	Variable	Pearson coefficient	*P* value
RW1	LOR	−0.61	<0.0001*
RW1	LC	−0.41	0.0007*
RW1	Lgl	−0.31	0.012*
RW1	LPL	0.58	<0.0001*
RW1	WOR	−0.42	0.0005*
RW1	Wgl.B	−0.41	0.0007*
RW1	WPF	−0.12	0.328
RW1	WIG	−0.37	0.0024*
RW1	Wgl.E	0.17	0.1748
RW1	LPA	0.53	<0.0001*
RW1	LAB	0.38	0.0015*
RW1	Lgl/WglB	0.08	0.502
RW1	LOR/WOR	−0.44	0.0002*
RW1	LPA/LC	0.58	0.0002*
RW1	LAB/LPF	−0.11	0.38
RW1	WIG/WglE	−0.35	0.0035*
RW1	WPF/WglB	0.1	0.4478
RW1	LOR/LC	−0.56	<0.0001*
RW1	LPL/Lgl	0.62	<0.0001*
RW1	Lgl/LC	−0.08	0.5222

after quantifying the variation in cranidium shape of the sample and confirming the existence of the two morphotypes, a second analysis was undertaken to determine the position in the morphospace of the retro-deformed holotype of *L. marianus.*

It is interesting to note that the holotype of *L. marianus* (in both the geometric and linear morphometry data sets) is not placed within the range of variation of *L. argentinensis*, as proposed by Tortello & Aceñolaza (2010), but instead falls within the range of variation of *L. granulosus*. These authors considered that the morphology of the holotype of *L. marianus* is similar to that of *L. argentinensis*, especially in the degree of development of the preglabellar field and palpebral lobes. Regarding the first character in the types of *L. marianus*, *L. argentinensis* and *L. granulosus*, the length of the preglabellar field occupies respectively 9.8, 9.8 and 6.5% relative to the length of the cranidium (excluding the anterior cephalic border) (Fig. 6A–C). Also, as stated by Harrington & Leanza (1957, p. 91), the preglabellar field of the holotype of *L. marianus* is raised by the distortion of the specimen and therefore its real sagittal length could be even longer. The differences observed in the length of the preglabellar area are due to the length of the anterior cephalic border, which is much smaller in *L. marianus*, perhaps because of the poor preservation. On the other hand, the length of the palpebral lobes occupies about 21, 19 and 15% of the length of the cephalon in the types of *L. marianus*, *L. argentinensis* and *L. granulosus*, respectively (Fig. 6A–C). In the analysis of linear morphometrics this character is important to order the variation among the specimens, and the three types clearly occupy different zones of the morphospace. With regard to the qualitative characters, even if the position of the palpebral lobes and the outline of the posterior facial suture of *L. marianus* and *L. argentinensis* are comparable, the geometric morphometric analyses show differences between the two types, especially explained by RW1 which exposes changes in these characters (Fig. 9B, C).

When the types of *Leptoplastides argentinensis* and *L. granulosus* were compared with the consensus shape or the mean measurements of the sample, some differences due to intraspecific variations could be recognized. In *L. granulosus* these differences are minor, and the holotype is very similar to the consensus shape, while the lectotype of *L. argentinensis* does not occupy the centre of the distribution for this species (Figs 6A, B, D, E, 9B, C). Even if the lectotype of *L. argentinesis* shows a preglabellar field that is shorter than the median value for the morphospecies (9.8% vs 16%), this character statistically differs between the two species and is considered here a diagnostic character.

Another point to emphasize is that when the pseudoreplicates were analysed separately they formed a distinct grouping different from *Leptoplastides granulosus* and *L. argentinensis*. This may be a consequence of how PCA axes are defined: the first axis is a built-in function of the highest differences observed among all the specimens in the sample, which are arranged in an increasing order along this axis; the second axis is orthogonal to the first axis and considers the variance not explained by the first axis, and so on. If the analysis is restricted to two morphotypes, the highest differences on the axes are those leading to their separation. If a single specimen of a slightly different morphotype is included, it may be overlooked by the analysis. However, the differences among the three morphotypes may become evident if many specimens of the third morphotype are incorporated in the analysis. In any case, it is risky to assume that *L. marianus* corresponds to a third morphotype. Firstly, the data from the holotype of *L. marianus* may be inaccurate because they were obtained from a retro-deformed image, which can be affected by different error sources. Secondly, but not less importantly, no additional material has been recognized to be included in a third morphotype. The fact that the holotype of *L. marianus* is deformed makes it difficult to identify specific diagnostic characters and thus to assign it to any species. Although Tortello & Aceñolaza (2010) considered the specimens of *L. argentinensis* to belong to *L. marianus*, this is not supported by the results obtained here. Indeed, the retro-deformed holotype of *L. marianus* does not provide conclusive evidence to include it within the variation range of *L. granulosus* for assessing synonymy. Moreover, the shape of the glabella, which was proposed by Kobayashi (1937) as a diagnostic character, is shared by the two morphotypes distinguished by the analysis. Based on the considerations mentioned above, the name *L. marianus*, which is widely used in the scientific literature to refer to a large number of specimens, should be restricted to the three type specimens, as previously proposed by Waisfeld & Vaccari (2003). In line with this conclusion, *Leptoplastides granulosus* and *Leptoplastides argentinensis* are recognized as valid names for the two morphotypes distinguished in this work.

Although both morphometric approaches were able to separate the two species, the area of overlap was greater for the traditional than for the geometric analyses. Moreover, differences between the two morphospecies were better identified by the geometric analyses since these allowed inclusion of characters of the cranidium, such as the shape of the facial suture and the relative position of the palpebral lobes. Traditional morphometric analyses revealed differences in the degree of development of the preglabellar area (sag.), the length of the palpebral lobes (exasag.), and the length of the occipital ring (sag.). The former two characters were also important for species discrimination in the geometric morphometric analysis, and the correlations between these three variables and the first RWA axis showed the highest Pearson's correlation coefficient ($> |0.5|$; Table 3). These characters were considered differences between the two species by Waisfeld & Vaccari (2003), who also proposed the width of the posterior fixigena as a difference. However, the results obtained here do not support this statement (95% confidence interval (CI): 0.23–0.31 for *Leptoplastides argentinensis* vs 0.16–0.22 for *L. granulosus*). As noted above, geometric morphometric analysis allows a clearer separation between the two species and recognizes differences between them, such as the position of the palpebral lobes (previously highlighted as a difference by Waisfeld & Vaccari 2003), the relative size of the axial lobe of the cranidium, and the direction of the facial suture. The ratio characters that distinguished *L. argentinensis* from *L. granulosus* were: the length of the preglabellar area relative to the length of the cranidium (95% CI: 0.17–0.18 vs 0.13–0.14, respectively), the width of the interocular gena relative to the width of the glabella (eyes) (95% CI: 0.31–0.34 vs 0.35–0.40, respectively), the length of the occipital ring relative to the length of the cranidium (95% CI: 0.14–0.16 vs 0.17–0.18, respectively), and the length of the palpebral lobes relative to the length of the glabella (95% CI: 0.30–0.36 vs 0.26–0.28, respectively). In his original description, Harrington (1938) recognized the presence of a granular sculpture on the external surface as a diagnostic character of the species *Protopeltura granulosa.* As noted by Harrington & Leanza (1957), this character is present in the holotype but is absent in most of the samples collected from the type locality. The granular sculpture is present only in well-preserved specimens, across different localities. Moreover, in the analyses carried out here, specimens with this character are evenly scattered along the axes. Therefore, observed sculpture variation is probably a taphonomic artifact.

Allometric growth has been well documented in several species of olenids (e.g. Kim *et al*. 2002) at different stages of development (ontogenetic allometry: Cook 1966). The present study involved holaspids and focused on static allometry, which deals with covariation of traits within a particular ontogenetic stage of a single species (Cook 1966; individual allomorphosis sensu Gould 1966). This type of allometry was not specifically explored in other olenid species. An exploratory analysis performed in other olenid species from the Cordillera Oriental, such as *Jujuyaspis keideli* (Monti 2013), suggests that this type of allometry is present in holaspids. In particular for the genus *Leptoplastides*, morphological variation attributable to ontogenetic allometry has been reported for different species (e.g. Robison & Pantoja-Alor 1968; Fortey & Owens 1991), and is generally associated with qualitative characters, such as the degree of segmentation of the glabella, the degree of definition of the anterior border furrow, the degree of development of the anterior border, and the presence of an occipital node; the cranidia of late holaspids tend to be smoother. The results presented here suggest that *L. granulosus* exhibits allometric growth whereas *L. argentinensis* does not, possibly because cranidium length range in *L. granulosus* (0.195–1.306 cm) is greater than that of *L. argentinensis* (0.252–1.279 cm). A larger sample is needed for more definitive conclusions. With regard to *L. granulosus*, it is pertinent to mention that the late meraspids/early holaspids, unlike the late holaspids, exhibit a more developed preglabellar area and a more concave posterior branch of the facial suture.

Morphological data are the cornerstone of almost all systematic descriptions, with morphological features defining the basic units of biology such as species and other monophyletic taxa (Nelson 1989). However, the use of morphology as the only species identification method may be a difficult task. Taking into account the theoretical correspondence between morphology and genetics, one would expect to find morphological gaps supporting the separation of these units, but a continuity of variation is often observed between morphological traits, particularly in small taxonomic units. Another constraint may be imposed by intraspecific variation, which is common in extant species. In fossil taxa without living representatives, not only intraspecific variation but also tectonic deformation complicates this issue even further. In this scenario morphometrics provides useful tools for the identification of sources of variation (e.g. Lawing & Polly 2010), which contribute to more informative analyses allowing species diagnosis, as evidenced in this study.

The results of this work constitute a new example of the contribution of morphometrics to taxonomic studies. Using different sources of variation allows the distinction of different morphological groups that share some degree of cohesion. The study of classic variables helps to identify morphometric variables that are useful in the diagnoses of species.

Conclusions

The name *Leptoplastides marianus* should be restricted to the three type specimens of Cuesta de Erquis, Bolivia, due to the deformation of these materials. *Leptoplastides argentinensis* and *L. granulosus* are both valid names for the two morphotypes recognized in the present paper. *Leptoplastides argentinensis* is characterized by the presence of a proportionally smaller glabella and occipital ring compared to the size of the cranidium, a posterior branch of the facial suture ranging from almost straight to concave, large palpebral lobes (exasag.) located subparallel to the axial furrow and at the midpoint of the glabella (tr.), an anterior branch of the facial suture that tends to be subparallel, and a barely more developed preglabellar area. *Leptoplastides granulosus* has a relatively larger axial lobe of the cranidium, a clearly convex posterior branch of the facial suture, small palpebral lobes located obliquely to the axial furrow and close to the anterior part of the glabella, a subparallel to convergent anterior branch of the facial suture, and a very short (sag.) preglabellar area. *Leptoplastides granulosus* shows allometric growth: the late meraspids/early holaspids have a better developed preglabellar (sag.) area and a more convex anterior section of the facial suture, while the late holaspids show a shorter preglabellar area (sag.) and a less convex posterior section of the facial suture.

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Supplemental data

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References

Abe, F. R. & **Lieberman, B. S.** 2012. Quantifying morphological change during an evolutionary radiation of Devonian trilobites. *Paleobiology*, **38**, 292–307.

Aceñolaza, F. G. & **González, O. E.** 1977. El Ordovícico de la zona de Arroyo Volcán, en la sierra de Santa Bárbara, Provincia de Jujuy. *Revista del Instituto de Geología y Minería de Jujuy*, **2**, 125–137.

Aceñolaza, G. F., **Aráoz, L.**, **Vergel, M. D. M.**, **Tortello, M. F.** & **Nieva, S. M.** 2003. Paleontology and biostratigraphy of the Lower Ordovician strata cropping out at the Abra de Zenta (Cordillera Oriental, Jujuy and Salta provinces), NW Argentina. *Serie Correlación Geológica*, **17**, 23–28.

Adrain, J. M. & **Westrop, S. R.** 2006. New earliest Ordovician trilobite genus *Millardicurus*: the oldest known hystricurid. *Journal of Paleontology*, **80**, 650–671.

Astini, R. A. 2003. The Ordovician Proto-Andean basins. Pp. 295–409 in J. L. Benedetto (ed.) *Ordovician fossils of Argentina*. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba.

Astini, R. A. 2008. Sedimentación, facies, discordancias y evolución paleoambiental durante el Cambro-Ordovícico. Pp. 50–73 in B. Coira & E. Zapettini (eds) *17° Congreso Geológico Argentino*. Jujuy.

Astini, R. A., **Waisfeld, B. G.**, **Toro, B. A.** & **Benedetto, J. L.** 2004. El Paleozoico inferior y medio de la región de Los Colorados, borde occidental de la Cordillera Oriental (provincia de Jujuy). *Revista de la Asociación Geológica Argentina*, **59**(2), 243–260.

Bookstein, F. L. 1991. *Morphometric tools for landmark data: geometry and biology*. Cambridge University Press, Cambridge, 435 pp.

Bookstein, F. L. 1996. Applying landmark methods to biological outline data. Pp. 59–70 in K. V. Mardia, C. A. Gill & I. L. Dryden (eds) *Image fusion and shape variability*. Leeds University Press. Leeds.

Bookstein, F. L. 1997. Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. *Medical Image Analysis* **1**(3), 97–118.

Bookstein, F. L., **Streissguth, A. P.**, **Sampson, P. D.**, **Connor, P. D.** & **Barr, H. M.** 2002. Corpus callosum shape and neuropsychological deficits in adult males with heavy fetal alcohol exposure. *Neuroimage*, **15**(1), 233–251.

Buatois, L. A., **Zeballo, F. J.**, **Albanesi, G. L.**, **Ortega, G.**, **Vaccari, N. E.** & **Mángano, M. G.** 2006. Depositional environments and stratigraphy of the Cambrian–Tremadocian Santa Rosita Formation at the Alfarcito area, Cordillera Oriental, Argentina: integration of biostratigraphic data within a sequence stratigraphic framework. *Latin American Journal of Sedimentology and Basin Analysis*, **13**, 65–94.

Burmeister, H. 1843. *Die organisation der Trilobiten, aus ihrem lebenden Verwandten entewickelt; nebst einer systematischen übersicht aller zeither beschriebenen*. Arten, Berlin, 147 pp.

Callaway, C. 1877. On a new area of Upper Cambrian rocks in south Shropshire, with a description of a new fauna. *Quaternary Journal of the Geological Society, London*, **33**, 652–672.

Cook, A. G. 1966. Genetical aspects of metrical growth and form in animals. *Quarterly Review of Biology*, **41**, 131–190.

Crônier, C., **Auffray, J.-C.** & **Courville, P.** 2005. A quantitative comparison of the ontogeny of two closely related Upper Devonian phacopid trilobites. *Lethaia*, **38**, 123–135.

Di Rienzo, J. A., **Casanoves, F.**, **Balzarini, M. G.**, **Gonzalez, L.**, **Tablada, M.** & **Robledo, C. W.** 2014. *InfoStat versión 2014*. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. [updated at http://www.infostat.com.ar, accessed 14 April 2016].

Dryden, I. L. & **Mardia, K. V.** 1998. *Statistical shape analysis*. John Wiley and Sons, Chichester, 347 pp.

Egenhoff, S. O. 2007. Life and death of a Cambrian–Ordovician basin: an Andean three-act play featuring Gondwana and the Arequipa-Antofalla terrane. *Geological Society of America, Special Papers*, **423**, 511–524.

Fortey, R. A. & **Owens, R. M.** 1991. A trilobite fauna from the highest Shineton Shales in Shropshire, and the correlation of the latest Tremadoc. *Geological Magazine*, **128**, 437–464.

Gendry, D., **Courville, P.**, **Saucède, T.**, **Laffont, R.** & **Paris, F.** 2013. Contribution of morphometrics to the systematics of the Ordovician genus *Neseuretus* (Calymenidae, Trilobita) from the Armorican Massif, France. *Journal of Paleontology*, **87**, 456–471.

Goodall, C. 1991. Procrustes methods in the statistical analysis of shape. *Journal of the Royal Statistical Society, Series B (Methodological)*, **53**, 285–339.

Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biological Reviews*, **41**, 587–638.

Green, W. D. K. 1996. The thin-plate spline and images with curving features. Pp. 79–87 in K. V. Mardia, C. A. Gill & I. L. Dryden (eds) *Image fusion and shape variability*. Leeds University Press, Leeds.

Gunz, P., **Mitteroecker, P.** & **Bookstein, F. L.** 2005. Semilandmarks in three dimensions. Pp. 73–98 in D. E. Slice (ed.) *Modern morphometrics in physical anthropology*. Kluwer Academic / Plenum Publishers, New York.

Harrington, H. J. 1937. On some fossils from northern Argentina. *Geological Magazine*, **74**, 97–124.

Harrington, H. J. 1938. Sobre las faunas del Ordovícico Inferior del norte argentino. *Revista Museo de La Plata (n.s.) Sección Paleontología*, **4**, 209–289.

Harrington, H. J. & **Leanza, A. F.** 1952. La clasificación de los 'Olenidae' y de los 'Ceratopygidae' (Trilobita). *Revista de la Asociación Geológica Argentina*, **7**, 190–205.

Harrington, H. J. & **Leanza, A. F.** 1957. *Ordovician trilobites of Argentina*. Department of Geology, University of Kansas, Special Publication, Lawrence, 276 pp.

Hawle, I. & **Corda, A. J. C.** 1847. Prodrom einer Monographie der bohmischen Trilobiten. Abhandlungen Koeniglichen Böhmischen Gesellschaft der Wissenschaften, 5. *Folge*, **5** (5), 1–176.

Henningsmoen, G. 1957. The trilobite family Olenidae. *Skrifter utgitt av det Norske Videnskaps-Akademi I Oslo. 1. Mathematics and Natural Sciences*, **1**, 1–303.

Hopkins, M. J. & **Webster, M.** 2009. Ontogeny and geographic variation of a new species of the corynexochine trilobite Zacanthopsis (Dyeran, Cambrian). *Journal of Paleontology*, **83**, 524–547.

Hughes, N. C. 1994. Ontogeny, intraspecific variation, and systematics of the Late Cambrian trilobite *Dikelocephalus*. *Smithsonian Contributions to Paleobiology*, **79**, 1–89.

Hughes, N. C. & **Chapman, R. E.** 2001. Morphometry and phylogeny in the resolution of paleobiological problems – unlocking the evolutionary significance of an assemblage of Silurian Trilobites. Pp. 29–54 in J. M. Adrain, G. D. Edgecombe & B. S. Lieberman (eds) *Fossils, phylogeny, and form*. Kluwer Academic/Plenum Publishers, New York.

Kim, K., **Sheets, H. D.**, **Haney, R. A.** & **Mitchel, C. E.** 2002. Morphometric analysis of ontogeny and allometry of the Middle Ordovician trilobite *Triarthrus becki*. *Paleobiology*, **28**, 364–377.

Klingenberg, C. P. 2011. MorphoJ: an integrated software package for geometric morphometrics. *Molecular Ecology Resources*, **11**(2), 353–357.

Kobayashi, T. 1935. On the *Kainella* fauna of the basal Ordovician age found in Argentina. *Japanese Journal of Geology and Geography*, **12**, 59–67.

Kobayashi, T. 1937. The Cambro–Ordovician shelly faunas of South America. *Journal of the Faculty of Science, Imperial University of Tokyo, Section II*, **4**, 369–522.

Lawing, A. M. & **Polly, P. D.** 2010. Geometric morphometrics: recent applications to the study of evolution and development. *Journal of Zoology*, **280**(1), 1–7.

MacLeod, N. 2002. Phylogenetic signals in morphometric data. Pp. 100–138 in N. MacLeod & P. L. Forey (eds) *Morphology, shape and phylogeny*. Taylor & Francis, London.

Meachen-Samuels, J. & **Van Valkenburgh, B.** 2009. Cranio-dental indicators of prey size preference in the Felidae. *Biological Journal of the Linnean Society*, **96**, 784–799.

Monti, D. S. 2013. Análisis morfogeométrico de *Jujuyaspis keideli* Kobayashi (Trilobita, Olenidae) del Ordovícico Temprano del Noroeste Argentino. *Ameghiniana*, **50**(6r: suplemento resúmenes), R31.

Morando, M., **Avila, L. J.** & **Sites, J. W.** 2003. Sampling strategies for delimiting species: genes, individuals, and populations in the *Liolaemus elongatus-kriegi* complex (Squamata: Liolaemidae) in Andean-Patagonian South America. *Systematic Biology*, **52**, 159–185.

Mosimann, J. E. & **James, F. C.** 1979. New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution*, **33**, 444–459.

Mutanen, M. & **Pretorius, E.** 2007. Subjective visual evaluation vs. traditional and geometric morphometrics in species delimitation: a comparison of moth genitalia. *Systematic Entomology*, **32**, 371–386.

Nelson, G. 1989. Species and taxa: systematics and evolution. Pp. 63–81 in D. Otte & J. A. Endler (eds) *Speciation and its consequences*. Plenum, New York.

Otte, D. & **Endler, J. A.** 1989. *Speciation and its consequences*. Sinauer Associates, Sunderland, 679 pp.

Pandey, S. & **Parcha, S. K.** 2013. Systematics, biometry of the species *Opsidiscus* from the Middle Cambrian succession of the Spiti Basin, India. *Journal of the Geological Society of India*, **82**, 330–338.

Pérez, S. I., **Bernal, V.** & **González, P.** 2006. Differences between sliding semi-landmark methods in geometric morphometrics, with an application to human craniofacial and dental variation. *Journal of Anatomy*, **208**, 769–784.

Pons, J., **Barraclough, T. G.**, **Gomez-Zurita, J.**, **Cardoso, A.**, **Duran, D. P.**, **Hazell, S.**, **Kamoun, S.**, **Sumlin, W. D.** & **Vogler, A. P.** 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology*, **55**, 595–609.

Pribyl, A. & **Vanek, J.** 1980. Ordovician trilobites of Bolivia. *Rozpravy Ceskoslovenské Akademie Ved*, **9**, 1–90.

Puorto, G., **da Graça Salomão, M.**, **Theakston, R. D. G.**, **Thorpe, R. S.**, **Warrell, D. A.** & **Wüster, W.** 2001. Combining mitochondrial DNA sequences and morphological data to infer species boundaries: phylogeography of lance-headed pitvipers in the Brazilian Atlantic forest, and the status of *Bothrops pradoi* (Squamata: Serpentes: Viperidae). *Journal of Evolutionary Biology*, **14**, 527–538.

R Development Core Team. 2010. *R: a language and environment for statistical computing*. R foundation for statistical computing, Vienna, Austria. [updated at http://www.r-project.org, accessed 4 April 2016].

Rao, R. I. & **Tortello, M. F.** 1998. Tremadocian conodonts and trilobites from the Cardonal Formation, Incamayo Creek, Salta Province, northwestern Argentina. *Palaeontologia Polonica*, **58**, 31–45.

Raw, F. 1908. The trilobite fauna of the Shineton Shales. *Reports of the British Association for the Advancement of Science*, **1907**, 511–513.

Robison, R. A. & **Pantoja-Alor, J.** 1968. Tremadocian trilobites from the Nochixtlán region, Oaxaca, Mexico. *Journal of Paleontology*, **42**, 767–800.

Rohlf, F. J. 1999. Shape statistics: Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology*, **39**, 40–59.

Rohlf, F. J. 2010a. *Tpsdig version 2.16*. Department of Ecology and Evolution, State University of New York, New York. [updated at http://life.bio.sunysb.edu/morph/, accessed 5 May 2016].

Rohlf, F. J. 2010b. *Tpsrelw version 1.49*. Department of Ecology and Evolution, State University of New York, New York. [updated at http://life.bio.sunysb.edu/morph/, accessed 5 May 2016].

Rohlf, F. J. 2011. *TpsRegr, ver. 1.41*. Department of Ecology and Evolution, State University of New York, New York. [updated at http://life.bio.sunysb.edu/morph/, accessed 5 May 2016].

Sheets, H. D. 2014. *TwoGroup8*. Department of Physics, Canisius College, Buffalo, New York. [updated at http://www3.canisius.edu/~sheets/IMP 8.htm, accessed 10 May 2016].

Sites, J. W. & **Marshall, J. C.** 2003. Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology and Evolution*, **18**, 462–470.

Steinmann, G. & **Hoek, H.** 1912. Das Silur und Kambrium des Hochlandes von Bolivia und ihre Fauna. *Neues Jahrbuch für Geologie, Mineralogie und Paläontologie*, **34**, 176–252.

Swinnerton, H. H. 1915. II. Suggestions for a revised classification of trilobites. *Geological Magazine*, Decade 6, **2**(11), 538–545.

Templeton, A. R. 2001. Using phylogeographic analyses of gene trees to test species status & processes. *Molecular Ecology*, **10**, 779–791.

Tortello, M. F. & **Aceñolaza, G. F.** 2010. Trilobites tremadocianos de Abra de Zenta (Cordillera oriental, provincias de Jujuy y Salta). *Revista de la Asociación Geológica Argentina*, **66**(1–2), 156–163.

Tortello, M. F. & **Rao, R. I.** 2000. Trilobites y conodontes del Ordovícico Temprano del Angosto de Lampazar (provincia de Salta, Argentina). *Boletín Geológico y Minero*, **111**(2), 61–84.

Tortello, M. F., **Esteban, S. B.** & **Aceñolaza, F. G.** 2002. Trilobites from the base of the Ordovician System in Northwestern Argentina. Pp. 131–142 in F. G. Aceñolaza (ed.) *Aspects of the Ordovician System in Argentina*. INSUGEO, Correlación Geológica, 16.

Tortello, M. F., **Zeballo, F. J.** & **Esteban, S. B.** 2013. Trilobites tremadocianos en facies de lutitas oscuras del Miembro Alfacito (Formación Santa Rosita), quebrada de Moya, Jujuy, Argentina. *Ameghiniana*, **50**, 137–152.

Turner, J. C. M. 1960. Estratigrafía de la sierra de Santa Victoria y adyacencias. *Boletín de la Academia Nacional de Ciencias de Córdoba*, **41**(2), 163–196.

Waisfeld, B. G. & **Vaccari, N. E.** 2003. Trilobites. Pp. 295–409 in J. L. Benedetto (ed.) *Ordovician fossils of Argentina*. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba.

Walch, J. E. I. 1771. *Die Naturgeschichte der Versteinerungen, Dritter Theil*. Felßecker, Nürnberg, 235 pp.

Webster, M. 2007. Ontogeny and evolution of the Early Cambrian trilobite genus *Nephrolenellus* (Olenelloidea). *Journal of Paleontology*, **81**, 1168–1193.

Webster, M. 2009. Systematic revision of the Cambrian trilobite *Bathynotus* Hall, 1860, with documentation of new occurrences in western Laurentia and implications for intercontinental biostratigraphic correlation. *Memoirs of the Association of Australasian Palaeontologists*, **37**, 369–406.

Webster, M. 2011. The structure of cranidial shape variation in three early ptychoparioid trilobite species from the Dyeran–Delamaran (traditional 'lower–middle' Cambrian) boundary interval of Nevada, USA. *Journal of Paleontology*, **85**, 179–225.

Webster, M. & **Sheets, H. D.** 2010. A practical introduction to landmark-based geometric morphometrics. Pp 163–188 in J. Alroy & G. Hunt (eds) *Quantitative methods in paleobiology*. Paleontological Society Papers Volume 16. Yale University Printing and Publishing Services, New Haven, Connecticut.

Wiens, J. J. & **Penkrot, T. A.** 2002. Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards. *Systematic Biology*, **51**, 69–91.

Zeballo, F. J. & **Tortello, M. F.** 2005. Trilobites del Cámbrico Tardío–Ordovícico Temprano del área de Alfarcito, Tilcara, Cordillera Oriental de Jujuy, Argentina. *Ameghiniana*, **42**, 127–142.

Zelditch, M. L., **Swiderski, D. L.**, **Sheets, H. D.** & **Fink, W. L.** 2004. *Geometric morphometrics for biologists: a primer*. Elsevier, Amsterdam, 437 pp.

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