Comparing phylogenetics and linear morphometrics to solve the generic assignment of *Parabolinella*? *triarthroides* Harrington (Trilobita, Olenidae)

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Abstract.—The use of different methodological approaches together with an exhaustive qualitative study has helped to recognize important morphological traits to distinguish species in a systematic and phylogenetic framework. *Parabolinella triarthroides* Harrington, 1938 was described based on two cranidia from the Quebrada de Coquena, Purmamarca, Jujuy province. The generic assignment of *P. triarthroides* has been questioned by a phylogenetic analysis, which resolves this species as the sister group of *Bienvillia* Clark, 1924. To explore the generic assignment of this species, a revision of the type material, plus a morphometric analysis including specimens of *Parabolinella* Brøgger, 1882 and *Bienvillia* were performed. In addition, the original matrix used in the published phylogeny was reviewed and enlarged, including more species of *Bienvillia*. Continuous characters were coded in different ways in order to compare how they could affect the ordering of specimens and their phylogenetic relationships. Finally, both methodologies were compared, especially in regard to the behavior of the quantitative characters included in the analyses. From the combined analyses, it is shown that similarities between the cranidium of *P. triarthroides* and all other *Parabolinella* species are true homologies instead of a by-product of evolutionary convergence. Therefore, *P. triarthroides* should be considered a member of this genus. Finally, this study demonstrates that the best strategy for solving systematic problems in groups where the morphological variation is the only source of information (i.e., fossil taxa without living representatives) is the implementation of an integrative approach, combining different methodological techniques and a good description of specimens.

Introduction

Morphometrics and systematic biology share a common interest in the analysis of morphology and the nature of morphological variation (MacLeod, 2002), although both fields have a history of complex dialogue, which derives, at least partially, from the underlying differences in their theoretical bases (Rae, 2002; Jensen, 2003; Clouse et al., 2011). The use of ratios (i.e., quotients between morphometric measurements) has become thoroughly ingrained into scientific methodology (Atchley et al., 1976), in part given their capability to present, in concise and easily interpretable ways, quantities that are otherwise non-comparable (Leirmann et al., 2004). Consequently, their use is extensive throughout taxonomic and systematic literature (Reyment et al., 1984; Winston, 1999; Schuh, 2000). Among these fields, the purpose behind the use of ratios is either to control the body size component in the observed variation of an anatomical feature (Atchley et al., 1976) or to represent shapes or proportions (Baur and Leuenberger, 2011) that are useful to identify and describe living organisms. Morphometrics can be an important tool in systematic studies given that it incorporates strong elements of quantification and formal hypothesis testing (MacLeod, 2002), and linear morphometrics have proven to be valuable tools for the resolution of taxonomic problems (e.g., Hughes, 1994; Żylińska et al., 2013). On the other hand, the use

of ratios as cladistic characters has raised an intense debate. Most of the criticisms are related to several undesirable statistical properties that violate the fundamental principle of character independence of cladistics studies. Furthermore, Mongiardino Koch et al. (2015) stated out that the often-arbitrary choice between which measurement is used as numerator and which as denominator affects the phylogenetic outcome of the analysis, so the use of log-transformed ratios would be a suitable solution. Nonetheless, many authors continue to use ratios as continuous characters without any sort of modification. In addition, they have proven to be useful in fossil taxa, in which the morphological variation is the only source of information (e.g., Prevosti, 2010; Escapa and Catalano, 2013; Mannion et al., 2013; Monti and Confalonieri, 2014).

Parabolinella triarthroides Harrington, 1938 (p. 194, pl. 7, figs. 10, 11) was first described based on two cranidia from the Quebrada Coquena, Purmamarca, Jujuy Province. In its original description, Harrington (1938) mentioned a simple preoccipital furrow (S1) in the type specimens of *P. thriarthroides*, which is the only character that distinguishes this species from the rest of the species of *Parabolinella* Brogger, 1882 (Harrington and Leanza, 1957). The generic assignment of *P. triarthroides* has been questioned by a phylogenetic analysis, which resolved this species as the sister group of *Bienvillia* Clark, 1924 and recovered a bifurcate preoccipital furrow as the only nonhomoplasic

synapomorphy of the genus *Parabolinella* (excluded *P.? triarthroides*) (Monti and Confalonieri, 2013).

The aim of this study is to solve the generic assignment of this species, performing a revision of the type material and a morphometric analysis of *P. triarthroides*, *Parabolinella*, and *Bienvillia* specimens. The original matrix used in a previous phylogenetic analysis (Monti and Confalonieri, 2013) was reviewed in light of the revision of the type material and was enlarged to include more species of *Bienvillia*. Continuous characters were coded in different ways in order to compare how they could affect the results. Because the variables used in the morphometric analysis were also treated as characters in the phylogenetic analysis, both results were compared and the behavior of these variables was analyzed. This study points to the importance of combining different methodological approaches with exhaustive qualitative analyses, which are necessary to recognize morphological traits and to solve systematic problems.

Materials and methods

Materials.—Studied specimens correspond to previously collected material from Ordovician outcrops in the Cordillera Oriental Argentina, at Purmamarca region and Quebrada Moya, Jujuy Province (Monti et al., 2016). Also more than 250 specimens from the "Harrington and Leanza Collection" (Harrington and Leanza, 1957) were reviewed (Supplementary dataset 1). These samples consist of specimens from Cambro-Ordovician units exposed at different localities in the Cordillera Oriental: quebradas Huasamayo, Rupasca, and San Gregorio (Alfarcito area); Bocoyá River and Nazareno River (Iruya Region); Quebrada Colorada de Fundición and Santa Victoria River (Santa Victoria region); Negrito River (tributary of Santa Cruz River), La Caldera region; Reyes River, Cumbre de Castillejo region; Quebrada de Coquena (Purmamarca region); and Quebrada del Barranco (Pascha area).

We measured 136 specimens (ingroup) and 6 (outgroup) to construct the input matrix for the phylogenetic analysis (Supplementary dataset 1). From these, 90 more-complete specimens were included in the morphometric analysis, given that the method does not allow the existence of missing entries (Supplementary dataset 1, 2). The sample for the morphometric analysis includes 28 specimens of *Bienvillia*: *B. parchaensis* (Harrington and Leanza, 1957) (5); *B. rectifrons* (Harrington, 1938) (7); *B. tetragonalis* (Harrington, 1938) (9), *B. jana* Waisfeld and Vaccari, 2006 (5); and *B. kichka* Waisfeld and Vaccari, 2006 (2). The sample for morphometric analysis also includes 57 specimens of *Parabolinella*: *P. clarisae* Monti, Benítez, and Ramírez, 2016 (28); *P. pompadouris* Monti, Benítez, and Ramírez, 2016 (8); *P. argentinensis* Kobayashi, 1935 (13); *P. coelatifrons* Harrington and Leanza, 1957 (6); and *P. limitis* Brøgger, 1882 (2) (Supplementary dataset 2). In this analysis, the types of *P. triarthroides* described by Harrington (1938) (CPBA 5, type and CPBA 54, paratype) and other specimens of this species from the type locality (CPBA 9; Waisfeld and Vaccari, 2003, pl. 32, figs. 15, 16) were also included. Nine additional species of *Parabolinella*, whose characters were analyzed and coded on the basis of published descriptions and figures (see Monti and Confalonieri, 2013) also

were added: *P. jianganensis* Lu and Lin, 1984; *P. ocellata* Lu and Lin, 1984; *P. prolata* Robison and Pantoja-Alor, 1968; *P. tumifrons* Robison and Pantoja-Alor, 1968; *P. variabilis* Robison and Pantoja-Alor, 1968; *P. bolbifrons* Fortey and Owens, 1997; *P. lata* Henningsmoen, 1957; *P. triarthra* (Callaway, 1877) *Parabolinella* new sp., and *P. limitis*) were incorporated in the cladistic analysis. All the specimens included in the analyses are holaspids and they are preserved as imprints and molds (internal and external). Most of them have suffered minor tectonic distortion. Disarticulated elements of the trilobite exoskeleton prevail, dominated by cranidia.

Morphometric analysis.—Eleven measurements from the above-mentioned 90 specimens corresponding to *P.? triarthroides* and different species of *Parabolinella* and *Bienvillia* were taken for the analyses (Table 1, Fig. 1, Supplementary dataset 2). With the aim of ordering the specimens according to the morphometric variability observed, three different Principal Component Analyses (PCA) were performed from the variance-covariance matrix: (1) using the set of logarithm transformed raw data, (2) using the logarithm of the raw data corrected by the geometric mean (hereafter called GMD) (Mosimann size variables) (see Mosimann and James, 1979; Meachen-Samuels and Van Valkenburgh, 2009), and (3) using the logarithm of nine new variables generated from the relationship of the original ones (hereafter called RD) (Table 1). It is important to note that all of the preceding analyses were also carried out with the correlation matrices (instead of variance-covariance matrices) of the untransformed data, although they are not shown in detail because outcomes regarding the separation of both genera and the variables of importance to distinguish them were very similar to those obtained with the variance-covariance matrices of the log-transformed data (see Supplementary datasets 3, 4). The analyses were performed with the software R version 3.2.2 (R Development Core Team, 2015) using the package vegan 2.3-1 (Oksanen et al., 2015). For GMD and RD analyses, confidence intervals of the eigenvectors of each variable were

Table 1. Description of the variables used in each morphometric analysis.

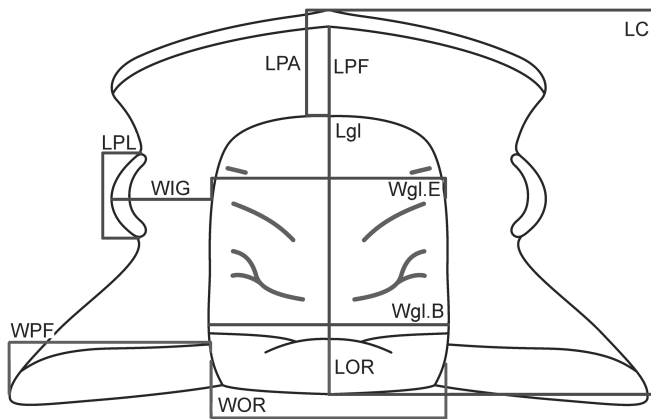| Dataset	Variables	Description
GMD	LPA	Length of the Preglabellar Area
	LPF	Length of the Preglabellar field
	LPL	Length of the Palpebral Lobes
	LC	Length of the Cranidio
	Lgl	Length of the glabella
	LOR	Length of the Occipital Ring
	WglE	Width of the glabella (Eyes)
	WglB	Width of the glaballa (Base)
	WOR	Width of the Occipital Ring
	WPF	Width of the Posterior Fixinae
	WIG	Width of the Interocular Genae
RD	Lgl/LC	Length of the glabella/ Length of the Cranidia
	LOR/Lgl	Length of the Occipital Ring/Length glabella
	LOR/WOR	Length of the Occipital Ring/Width of the Occipital Ring
	Lgl/WglB	Length glabella/Width glabella (Base)
	LPL/Lgl	Length Palebral Lobes/ Length glabella
	WIG/WglE	Width of the Interocular Genae/Width of the glebella (Eyes)
	WPF/WOR	Width of the Posterior Fixigenae/Width of the Occipital Ring
	LPF/LOR	Length of the Preglabellar Field/ Length of the Occipital Ring
	LPF/LPA	Length of the Preglabellar Field/ Length of the Preglabellar Area

Figure 1. Schematic representation of the cranidium of *Parabolinella* sp. showing the measurements used in the morphometric analyses. 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.); Wgl.B, Width of the glabella (at the Base) (tr.); WPF, Width of the Posterior Fixigenae (tr.); WIG, Width of the Interocular Genae (tr.); Wgl.E, Width of the glabella (at the Eye line) (tr.); LPA, Length of the Preglabellar Area (sag.); LPF, Length of the Preglabellar Field (sag.).

estimated by one thousand replicates of bootstrap PCA with R package bootSVD version 0.5 (Fisher, 2015). To compare the effectiveness of both GMD and RD transformations in reducing size effects, the first axis of the PCA was correlated with two variables that estimate size (Log of the Length of the Cephalon [LC] and Log of the Geometric Mean [GM]). Finally, a Discriminant Analysis was conducted for the two genera, excluding the types of *P.? triarthroides*. In order to classify the type specimens of *P.? triarthroides*, the values of the discriminant function for these specimens were calculated with the Microsoft Excel spreadsheet using canonical coefficients. These last two analyses were carried out with Infostat version 2015 (Di Rienzo et al., 2015).

Cladistic analysis.—The matrix used in the phylogenetic analysis of the genus *Parabolinella* (Monti and Confalonieri, 2013) was reviewed, especially the characters coded for *P.? triarthroides*. Two new taxa belonging to the genus *Bienvillia* (*B. kicka* and *B. jana*) were added. The matrix has 40 characters, of which fifteen are continuous and the rest are discrete. In the original matrix (Monti and Confalonieri, 2013), the continuous characters were coded as discrete (12 were expressed as ratios and three as meristic), but in the present study they were coded as continuous, as implemented in TNT (Goloboff et al., 2006). Two strategies were used for coding these continuous characters (Table 2, Supplementary dataset 5): the first one considers their original definition and characters are coded as ratios (hereafter called CPR); the second one considers the use of the raw data corrected for size by the geometric mean (hereafter CPGM) (Mosimann size variables) (see Mosimann and James, 1979; Meachen-Samuels and Van Valkenburgh, 2009). In both strategies the median was used as the statistical descriptor because it has the advantage of being less affected by extreme values of frequency distribution. Also, to solve the scaling problem, the continuous characters were standardized to range 0–1, so the maximum internal steps are equivalent to one step of a discretely coded character (i.e., a change between the two most dissimilar

states in each continuous character has the same cost as one step in a discrete character). Because the arbitrary election of the numerator and denominator of the ratio character may affect the results obtained, the ratio variables were transformed with logarithm to minimize this effect (Mongiardino Koch et al., 2015).

Continuous (CPR or CPGM) and discrete (DP) partitions were used combined and separated in the cladistic analyses (Table 2, Supplementary dataset 5). Heuristic searches were performed with TNT (Goloboff et al., 2008), using random addition sequences (RAS) followed by tree bisection–reconnection branch swapping (TBR). One thousand replicates were carried out, saving 25 trees per replicate. Maximum parsimony and implied weighting (concavity constants from $k = 3$ to $k = 14$) were used as optimality criteria. The trees obtained with the different types of coding were compared using unweighted SPR distances (Goloboff, 2007) and the number of coincident internal nodes in the strict consensus tree. These values were taken to represent the degree of discordance between each continuous dataset and the discrete partition. Additionally, the mean value of these measurements was interpreted as the average topological difference resulted from choosing a different way to code the continuous characters.

Branch support was calculated by means of Bremer Support values (BS) (Bremer, 1994) through the search of suboptimal trees by TBR swapping. Also, jacknife resampling (Lanyon, 1985) was calculated using TNT (see Goloboff et al., 2003). One thousand jacknife replicates were performed, conducting a heuristic tree search consisting of 10 replicates of Wagner trees (with random addition sequences) followed by TBR (saving 10 trees per replicate). A probability of alteration equal to 10% (equivalent to four characters in this database) was used. The differences in GC frequencies (for Group present/ Contradicted) are also shown because they give better measures for groups with low support (Goloboff et al., 2003).

Because the list of synapomorphies depends on the optimal solution, when more than one most parsimonious tree was obtained, the common synapomorphies of all trees were considered on the strict consensus. Those quantitative characters that were important to distinguish both genera in the morphometric analysis were optimized on trees in order to analyze their phylogenetic signal, and to compare both kinds of analyses (i.e., morphometric vs. phylogenetic analyses).

Repository and institutional abbreviation.—Studied specimens are deposited in the Invertebrate Paleontology Collection, Department of Geology (Paleontology area), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, under repository abbreviations CPBA.

Systematic paleontology

Class Trilobita Walch, 1771
Order Ptychopariida Swinnerton, 1915
Suborder Olenina Burmeister, 1843
Family Olenidae Burmeister, 1843
Subfamily Oleninae Burmeister, 1843
Genus *Parabolinella* Brøgger, 1882

Table 2. List of characters used in the cladistic analysis indicating each partition and the character states (only for the qualitative partition). The characters also used as variables in the morphometric analysis are indicated on the right with the acronyms used in Table 1.

Continuous Partition: ratios (CPR)

0	Length of glabella (sag. excluding occipital ring) as proportion of length of cephalon (sag.)	Lgl/LC
1	Length of the occipital ring (sag.) as proportion of the Length of the glabella (sag., excluding the occipital ring)	LOR/Lgl
2	Length of preglabellar field (sag.) as proportion of length of preglabelar area (sag.)	LPF/LPA
3	Length of preglabellar field (sag.) as proportion of length of occipital ring (sag.)	LPF/LOR
4	Width of fixed cheek posterior to eyes (tr.) as proportion of width of occipital ring (tr.)	WPF/WOR
5	Length of posterior cephalic border as proportion of length of occipital ring (sag.)	
6	Width of glabella at base (tr.) as proportion of length of glabella (sag. excluding occipital ring)	LglB/Lgl
7	Width of thoracic axis (tr.) compared to width of whole segment (tr., excluding pleural spines) on anterior segments	
8	Length of pygidium (sag.) as proportion of maximun width of pygidium (tr.)	
9	Width of interocular genae as proportion of width of glabella at eye line	WIG/WglE
10	Length of palpebral lobes (exasag.) as proportion of the length of glabella (sag.)	LPL/Lgl
11	Number of visible pairs of lateral glabellar furrows	
12	Number of segments (excluding terminal piece) in pygidial axis	
13	Number of thoracic segments	

Continuous Partition: Geometric Mean (CPGM)

0	Length of Cephalon (sag.)	LC
1	Length of glabella (sag., excluding occipital ring)	Lgl
2	Length of the occipital ring (sag.)	LOR
3	Length of preglabellar area (sag.)	LPA
4	Length of preglabellar field (sag.)	LPF
5	Width of the posterior fixigenae (tr.)	WPF
6	Length of porterior border (exasag.)	
7	Width of the glabella at the base (tr.)	WglB
8	Width of the thoracic axis (tr.)	
9	Length of the pygidium (sag.)	
10	Width of interocular genae (tr.)	WIG
11	Length of palpebral lobes (exasag.)	LPL
12	Number of visible pairs of lateral glabellar furrows	
13	Number of segments (excluding terminal piece) in pygidial axis	
14	Number of thoracic segments	

Qualitative Partition (DP)

15	Anterior margin of cranidium, medially. 0: transverse; 1: concave forward, 2: convex
16	Condition of anterior branch of facial suture, measured as the angle formed by this and sagittal axis. 0: convergent ($\alpha \leq -5°$); 1: subparalell ($10° > \alpha > -5°$); 2: moderately divergent ($30° > \alpha > 10°$); 3: very divergent ($\geq 30°$).
17	Positions of palpebral lobes. 0: center to S2; 1: center anterior to S2; 2: center posterior to S2
18	Degree of convexity of anterior cephalic border, in dorsal view. 0: strongly convex; 1: more weakly convex.
19	Anterior border furrow. 0: without pits; 1: with pits.
20	Shape of anterior termination of glabella. 0: medially concave; 1: rounded.
21	Shape of the glabella. 0: tapered forward; 1: approximately parallel-sided; 2: tapered backward; 3: expands anteriorly
22	Condition of preoccipital furrow (S1). 0: simple; 1: adaxially bifurcate.
23	Shape of S1 furrows. 0: straight or simply curved; 1: sigmoid.
24	Shape of S2 furrows. 0: straight; 1: sinuous.
25	Length of S2 furrows. 0: equal to S1; 1: shorter than S1.
26	Condition of S3 furrow. 0: furrows; 1: slits very shorts; 2: faint depressions.
27	Elevation of preglabellar field. 0: confluent with cheeks; 1: raised to form preglabellar boss.
28	Preglabellar field. 0: smooth; 1: striated.
29	Posterior branch of facial suture. 0: straight or slightly sinuous; 1: very sinuous.
30	Occipital ring. 0: simple; 1: trisegmented.
31	Eye ridges. 0: elevated, well developed, 1:barely visible.
32	Direction of eye ridges. 0: eye-ridges run transversely; 1: eye-ridges run backwards and outwards obliquely.
33	Occipital node. 0: conspicuous 1: barely visible 2: absent
34	Medial portion of posterior margin of pygidium. 0: curved, convex; 1: subangular, convex; 2: transverse; 3: concave.
35	Course of posterior margin of fixed cheeks. 0: transverse; 1: curved back distally; 2: curved forward.
36	Course of occipital furrow medially (S0). 0: transverse; 1: convex forward.
37	Posterior border furrow of cranidium. 0: deep, ends near the genal angle; 1: distally faint.
38	Length of genal spines. 0: short; 1: long.
39	Definition of posterior margin of pygidial axis. 0: well defined; 1: poorly defined.

Type species.—*Parabolinella limitis* Brøgger, 1882 (Bassler, 1915) from upper Tremadocian of Scandinavia.

Remarks.—*Parabolinella* is a monophyletic group supported by one nonhomoplastic synapomorphy, the presence of an adaxially bifurcated S1 furrow; palpebral lobes centered to S2; anterior termination of the glabella rounded, S2 furrows shorter than S1, the preglabellar field occupies a larger proportion of the preglabellar area (sag.), a well-developed preglabellar field (sag.), and a short (sag.) glabella with a narrow base (tr.).

Parabolinella triarthroides Harrington, 1938
Figure 2.1, 2.2

1938 *Parabolinella triarthroides* Harrington, p. 194, pl. 7, figs. 10,11.

1957 *Parabolinella triarthroides*; Harrington and Leanza, p. 105, figs. 39.1a, 39.1b.

1988 *Parabolinella triarthroides*; Rushton, p. 686, fig. 3c.

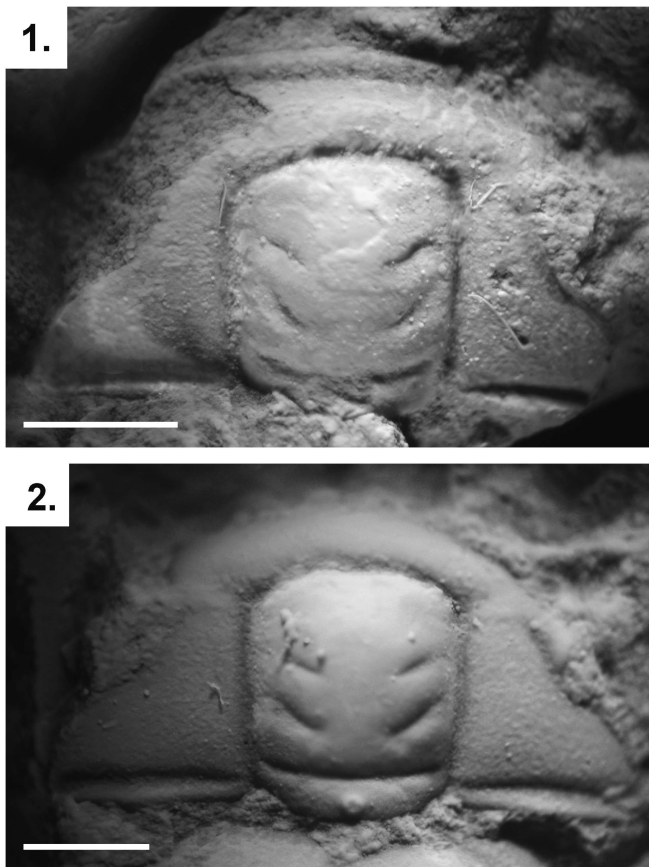2003 *Parabolinella triarthroides*; Waisfeld and Vaccari, p. 330, pl. 32, figs. 14–18.

Figure 2. *Parabolinella triarthroides* (Harrington, 1938) from the Quebrada Coquena, Purmamarca, Jujuy: (**1**) dorsal view of the cranidium holotype (CPBA 5); (**2**) dorsal view of the cranidium paratype (CPBA 54). Scale bars represent 1 mm.

Holotype.—Cranidium (CPBA 5, Fig. 2.1) from the late Tremadocian from the Quebrada Coquena, Purmamarca, Jujuy (Harrington, 1938, pl. 7, fig. 10).

Remarks.—Harrington (1938) mentioned a simple preoccipital furrow (S1) in the type specimens of *P. thriarthroides*. Later, based on that description, Harrington and Leanza (1957) proposed that this species was an intermediate form between the genera *Parabolinella* and *Bienvillia*. The generic assignment of *P. triarthroides* has been questioned by a phylogenetic analysis, which resolved this species as the sister group of *Bienvillia* Clark, 1924. This analysis recovered a bifurcate preoccipital furrow as the only nonhomoplasic sinapomorphy of the *Parabolinella* genus (excluded *P.? triarthroides*) (Monti and Confalonieri, 2013). The holotype of *P. triarthroides* is poorly preserved and the nature (simple or bifurcate) of the preoccipital furrow (S1) cannot be determinate on this specimen (Fig. 2.1). Nevertheless, the paratype has a bifurcate preoccipital, which is suggested on its left side (Fig. 2.2). Moreover other specimens assigned to this species also have a conspicuous bifurcate preoccipital furrow (Waisfeld and Vaccari, 2003). Additionally, *P. tirarthroides* has a developed preglabellar area (sag.) and preglabellar field (sag.), a wide posterior fixigenae (tr.), a large glabella and cranidium, and a higher ratio between the width of the interocular genae and the width of glabella (at the eye line) (tr.). All these characters justify the inclusion this species in *Parabolinella*.

Results

Morphometric analysis.—The first axis of the PCA performed with the log-transformed raw data accounts for 90.58% of the total variability. Because all the variables are negatively correlated with this axis, it explains the variation related to size (Fig. 3.1). Both genera are distributed evenly over the axis, meaning that the two groups do not show differences in size, although *Bienvillia* has a smaller range of size variation (Fig. 3.1). The PC2 explains 7.08% of the total variability. Both genera appear separated by this axis, *Bienvillia* is located in the positive values of this axis while *Parabolinella*, including the type specimens of *P.? triarthroides*, is in the negative values (Fig. 3.1). Although no variable significantly correlates with PC2, LPA and LPF are those that most contribute to this axis (Table 3). Because LPA and LPF have negative values of the eigenvectors, specimens of *Parabolinella*, which lie in the negative region of the PC2, have a more-developed preglabellar field and preglabellar area (Fig. 3.1). Finally the third axis, which explains 0.835% of the total variability, describes variation within each genus.

The PCA performed with GMD clearly differentiates both genera, and the type specimens of *P.? triarthroides* are located within the range of variation of *Parabolinella* (Fig. 3.2). The PC1 positively correlates with WPF, LPA, and LPF, and negatively correlates with the LOR, LC, Lgl, WOR, and Wgl.B (Table 4). The positive values of the first axis include specimens with a smaller glabella and occipital ring, wider posterior fixigenae (tr.), and a more developed preglabellar area and preglabellar field (sag.). The negative values of the first axis include specimens with a more-developed axis of the cephalon (bigger glabella and occipital ring), narrower posterior fixigenae (tr.), and shorter preglabellar area and preglabellar field (sag.). Both genera can be distinguished by the first axis, while they are evenly distributed over the second one (Fig. 3.2). Species of *Parabolinella* are located on the positive values of the first axis. This genus is characterized by a wider posterior fixigenae and more-developed preglabellar area and preglabellar field (Fig. 4.1). On the contrary, species of *Bienvillia* are located completely on the negative values of the first axis. This genus has a bigger axis of the cephalon (larger and wider glabella and occipital ring), narrower posterior fixigenae (tr.), and shorter preglabellar area (sag.) and preglabellar field (sag.) (Fig. 4.2). The specimens of *P.? triarthroides* are included within the range of variation of *Parabolinella* (Fig. 3.2). Therefore, *P.? triarthroides* and *Parabolinella* share a similar cranidium morphology.

When RD was used, similar results to GMD analysis were obtained. The specimens of *Bienvillia* are located on the negative values of the PC1, while those of the *Parabolinella* genus are mostly found on the positives values. Even if an overlapping zone can be recognized, the types of *P.? triarthroides* are located on the most-positive values of the PC1 (Fig. 3.3). Some differences on the variables that contribute to the PC1 axis are observed, compared to the GMD analysis. In addition, confidence intervals for the loadings of these variables were bigger than those obtained with GMD (Tables 4, 5). The PC1
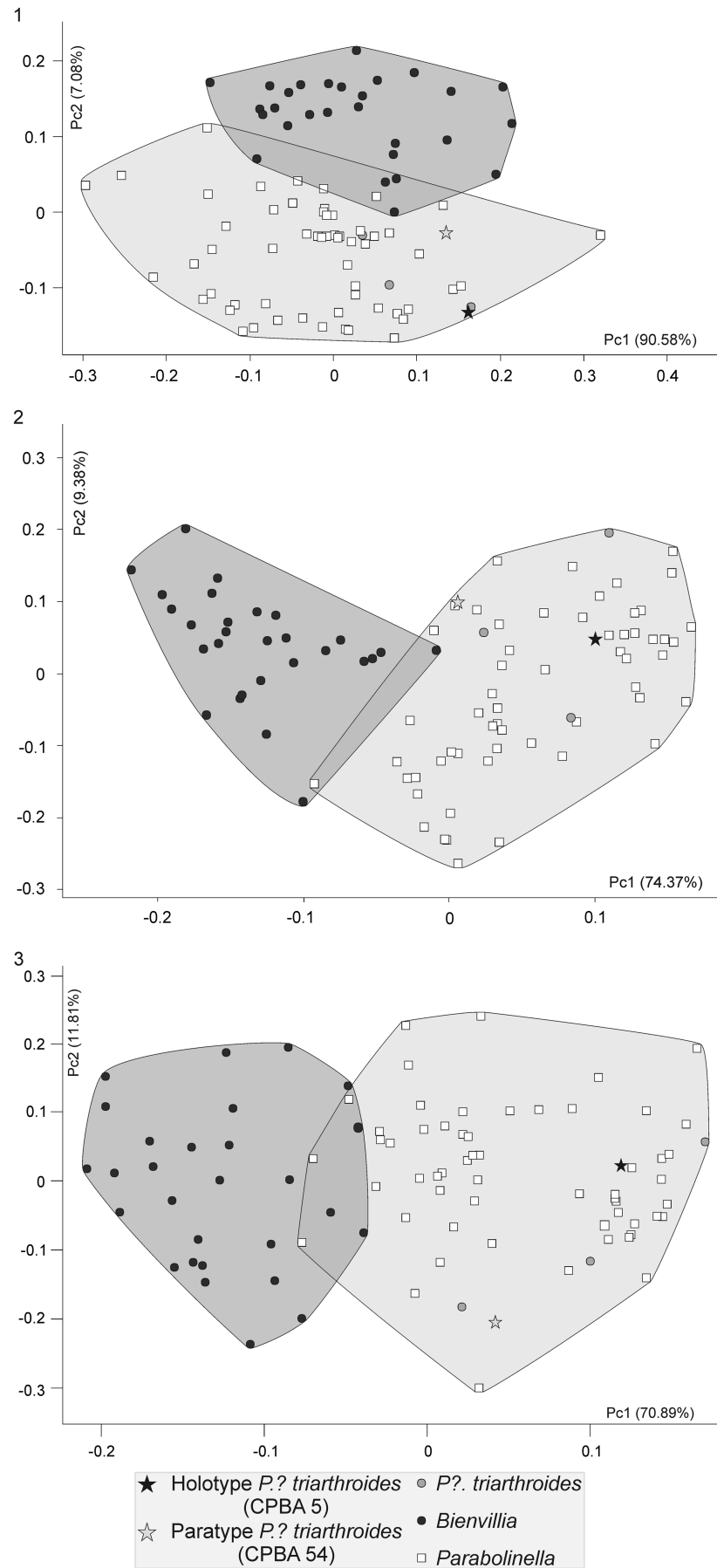
positively correlates with LPF/LOR, LPF/LPA, WPF/WOR, and WIG/Wgl.E; and negatively correlates with Lgl/LC (Table 5). Specimens located on the positive side of this axis have higher values for these variables. Specimens assigned to *Parabolinella* are mostly located in the positive values of the PC1 (Fig. 3.3), therefore they are characterized by a more developed preglabellar field related to the length of the occipital ring (sag.), more developed preglabellar field related to the length of the preglabellar area (sag.), wider posterior fixigenae related to the width of the occipital ring (tr.), wider interocular genae related to the width of the glabella (at the eye line) (tr.), and shorter glabella related to the length of the cranidium (sag.) (Fig. 4.1). On the other hand, specimens of the genus *Bienvillia* have a poorly developed preglabellar field related to the lengths of the occipital ring (sag.) and preglabllar area (sag.), narrower posterior fixigenae related to the width of the occipital ring (tr.), narrower interocular genae related to the width of the glabella (at the eye line) (tr.), and larger glabella related to the length of the cranidium (sag.) (Figs. 3.3, 4.2).

Both methods are equally effective in reducing the size effect. They do not show any correlation between the PC1 and the variables that estimate size (Coefficient of Pearson correlation: PC1 [RD] vs. Log LC: 0.02 [p = 0.822];

PC1 [RD] vs. Log GM: 0.09 [p = 0.397]; PC1 [GMD] vs. Log LC: 0.06 [p = 0.548]; PC1 [GMD] vs. Log GM: 0.13 [p = 0.235]).
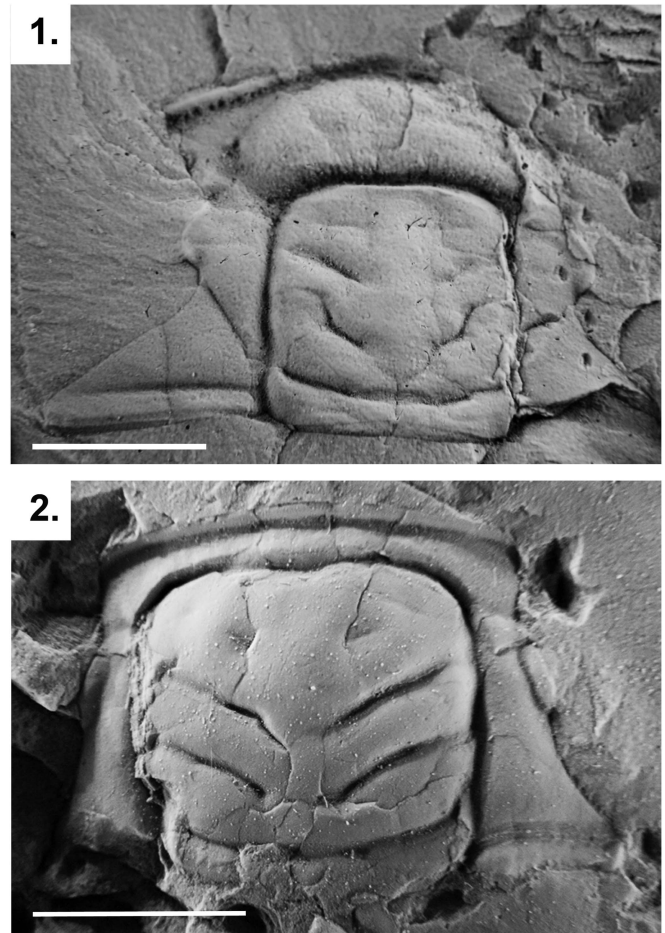

Figure 4. Cranidia of two specimens representing *Parabolinella* Brøgger, 1882 and *Bienvillia* Clark, 1924: (**1**) *Parabolinella pompadouris* Monti et al., 2016 from the Bocoyá River (CPBA 4036); (**2**) *Bienvillia tetragonalis* Harrington, 1938 from the Quebrada Rupasca (Holotype, CPBA 705). Scale bars represent 5 mm.

Table 3. Eigenvalues and correlation coefficients for each variable with the two first components of the PCA obtained with log-transformed data (Fig. 3.1). Abbreviations of variables according to Figure 1 and Table 1. Asterisks indicate significant correlation.

Variable	Eigenvalue		Correlation	
	PC1	PC2	PC1	PC2
LOR	−0.2861	0.2407	0.9533*	0.2242
LC	−0.2976	0.0779	0.9948*	0.0728
Lgl	−0.2934	0.2262	0.9731*	0.2096
LPL	−0.2705	0.2028	0.9401*	0.1971
WOR	−0.3112	0.2321	0.9749*	0.2033
WglB	−0.2944	0.2526	0.9671*	0.2320
WPF	−0.3206	−0.2299	0.9618*	−0.1929
WIG	−0.2846	−0.0795	0.9691*	−0.0756
WglE	−0.3054	0.2791	0.9633*	0.2461
LPA	−0.3223	−0.4714	0.9196*	−0.3760
LPF	−0.3251	−0.6056	0.8840*	−0.4602

Table 4. Eigenvalues with confidence intervals at 95% and correlation coefficients for each variable with the two first components of the PCA obtained with the data corrected by the geometric mean (Fig. 3.2). Abbreviations of variables according to Figure 1 and Table 1. Asterisks indicate significant correlation.

Variable	Eigenvalue						Correlation	
	PC1	Lower limit	Upper limit	PC2	Lower limit	Upper limit	PC1	PC2
LOR	−0.2325	−0.2807	−0.1838	−0.1428	−0.3899	0.1370	−0.7316*	−0.1594
LC	−0.0669	−0.0877	−0.0457	−0.0087	−0.1123	0.0961	−0.6607*	−0.0306
Lgl	−0.2144	−0.2384	−0.1890	−0.0855	−0.1785	0.0243	−0.9000*	−0.1275
LPL	−0.2041	−0.2664	−0.1397	0.7873	0.5004	0.9410	−0.5737	0.7858*
WOR	−0.2114	−0.2354	−0.1878	−0.2331	−0.3163	−0.1247	−0.8618*	−0.3375
WglB	−0.2398	−0.2600	−0.2198	−0.1639	−0.2215	−0.0782	−0.9008*	−0.2186
WPF	0.2471	0.1884	0.3041	−0.4237	−0.7499	−0.0221	0.7270	−0.4429
WIG	0.0805	0.0244	0.1381	0.2433	−0.2212	0.6976	0.3030	0.3258
WglE	−0.2605	−0.2840	−0.2351	−0.1209	−0.2303	−0.0049	−0.8898*	−0.1468
LPA	0.4844	0.4465	0.5200	0.1328	−0.1263	0.3589	0.9601*	0.0936
LPF	0.6178	0.5938	0.6385	0.0151	−0.1474	0.1683	0.9854*	0.0085

Figure 3. Scatter plot of the two first components of the PCAs: (**1**) analysis using log-transformed raw data; (**2**) analysis using log-transformed data corrected by the geometric mean (GMD); (**3**) analysis using log-transformed ratio variables (RD). Black circles: *Bienvillia* Clark; white squares: *Parabolinella* Brogger; black star: Holotype of *P.? triarthroides* (CPBA 5); gray star: *P.? triarthroides* (CPBA 54); gray circle: *P.? triarthroides*.

Table 5. Eigenvalues with confidence intervals at 95% and correlation coefficients for each variable with the two first components of the PCA obtained with ratio variables (Fig. 3.3). Abbreviations of variables according to Figure 1 and Table 1. Asterisks indicate significant correlation.

Variable	Eigenvalue						Correlation	
	PC1	Lower limit	Upper limit	PC2	Lower limit	Upper limit	PC1	PC2
LOR/Lgl	−0.0454	−0.1134	0.0306	−0.4423	−0.7301	−0.0463	−0.1886	0.7504*
Lgl/LC	−0.1325	−0.1942	−0.0630	0.0775	−0.0185	0.1555	−0.8456*	−0.2019
LPL/Lgl	0.0321	−0.0323	0.0946	−0.3170	−0.7759	0.1913	0.1004	0.4052
Lgl/WglB	0.0198	−0.0141	0.0526	0.0398	−0.0859	0.1596	0.1421	−0.1165
LOR/WOR	−0.0436	−0.1030	0.0260	−0.4988	−0.8082	−0.0687	−0.1767	0.8254*
WPF/WOR	0.4429	0.2176	0.6396	−0.1841	−0.4093	0.1015	0.9140*	0.1558
WIG/WglE	0.3397	0.1626	0.4951	−0.5578	−0.9295	−0.0573	0.7712*	0.5169
LPF/LOR	0.8060	0.3712	1.1832	0.3163	0.0516	0.5116	0.9797*	−0.1569
LPF/LPA	0.1328	0.0554	0.1995	−0.0490	−0.1751	0.1008	0.6453*	0.0972

The discriminant analysis results were quite similar. In both cases the two groups show significant differences and the discriminant functions were equally efficient in classifying the specimens. The total error from the cross-classification table is 3.53% with both datasets (GMD and RD). To avoid redundancy, only the values of the discriminant function obtained with GMD are shown: centroid values are −3.08 and 1.51 for *Bienvillia* and *Parabolinella*, respectively, and the discriminant scores for the holotype and paratype of *P.? triarthroides* are 1.287 and −0.793, respectively, suggesting that they should be classified as *Parabolinella*.

Cladistic analysis.—Revision of the type material of *P.? triarthroides* reveals that this species has a bifurcate preoccipital (S1). Thus the original matrix from Monti and Confalonieri (2013) was accordingly modified for this qualitative character (Ch. 22, state 1 instead of 0 for *P.? triarthroides*, see Table 2 and Supplementary dataset 5). The analyses performed including all 40 characters (Table 2, Supplementary dataset 5) and with the two treatments of continuous characters (ratios vs. geometric mean) show similar results. In both cases, the species of *Parabolinella* constitute a monophyletic group, even with different conditions of analysis (without implied weighting and with different function of k), and *P.? triarthroides* is always recovered within this group. Among all the trees recovered with these different conditions, only those with highest similitude index (similarity = 0.95; Supplementary dataset 6.1) are shown: the topology in Figure 5 (CPR + DP matrix), which was obtained applying either maximum parsimony or implied weighting (k = 11–14), and the topology in Figure 6 (CPGM + DP matrix), which was obtained applying implied weighting (k = 10–14). When the analysis was performed only with the continuous partition, *Parabolinella* was never recovered as a monophyletic clade (Fig. 7). When the CPR matrix was used, two very similar trees were recovered (similarity = 0.9), independently of the conditions of analysis (i.e., without implied weighting and with different functions of k); and when the CPGM matrix was used, three slightly different topologies were obtained (similarity = 0.6, 0.65, and 0.8). For comparison purposes, only the topologies obtained with k = 11 are reported for each kind of partition (Fig. 7). The comparison of topologies through unweighted SPR distances obtained from CPR vs. CPGM matrices indicates that they are very different (similarity = 0.3–0.55, Supplementary dataset 6.3). Furthermore, the consensus tree displays only from two to five shared

internal nodes, out of a total of 20 (Supplementary dataset 6.5). The topologies obtained with the discrete partition are very different to those obtained with CPR and CPGM (the maximum of similarity is 0.35 for CPR, Supplementary dataset 6.5) (Fig. 7). The topologies obtained from CPR are slightly more consistent with the discrete partition than those obtained from CPGM (mean of similarity 0.2755 and 0.1196 for each strategy, respectively, see Supplementary dataset 6.5). Finally the tree obtained from the complete matrix, but using CPGM, shows slightly higher support values than including CPR (Figs. 5 and 6).

When all characters are included in the analysis, the discrete partition controls the structure of the tree (Figs. 5–7). The topologies obtained for each complete matrix (with CPR or CPGM data) do not differ so widely with the use of different k values. As mentioned above, when the analyses were performed with the complete dataset, the genus *Parabolinella* was always recovered as a monophyletic group and the differences are within the *Parabolinella* clade (Figs. 5, 6).

The *Parabolinella* clade is supported by four synapomorphies within the discrete partition: the presence of an adaxially bifurcated S1 furrow (Ch. 22, 0 → 1), which is the only non-homoplastic character; the palpebral lobes centered to S2 (Ch. 17, 0 → 1); the anterior termination of glabella rounded (Ch. 20, 0 → 1); and the S2 furrows shorter than S1 (Ch. 25, 0 → 1) (Figs. 5, 6; Table 2). Within the continuous partition, four additional synapomorphies emerge with CPR and with CPGM, although they are not the same. Considering CPR, the synapomorphic transformations are: shorter glabella related to the length of the cephalon (Ch. 1, 0.68 → 0.63); the preglabellar field occupies a larger proportion of the preglabellar area (sag.) (Ch. 3, 0.69 → 0.72); preglabellar field well developed related to length of the occipital ring (sag.) (Ch. 4, 0.58 → 0.94); posterior cephalic border shorter as a proportion of length of occipital ring (Ch. 6, 0.58–0.59 → 0.54–0.57) (Fig. 5). The first three of these synapomorphies also are recovered as characters of importance to distinguish the two genera in the morphometric analysis. On the other hand, the synapomorphies of the genus for CPGM are: a well-developed preglabellar area (sag.) and preglabellar field (sag.) (Ch. 3, 0.51 → 0.69-0.73; Ch. 4, 0.35 → 0.48–0.55); and a short (sag.) glabella with a narrow base (tr.) (Ch. 1, 1.97 → 1.92; Ch. 7, 2.1–2.18 → 2.06) (Fig. 6). In this case, all four synapomorphies found coincide with variables that allow separation of both genera in the morphometric analysis.
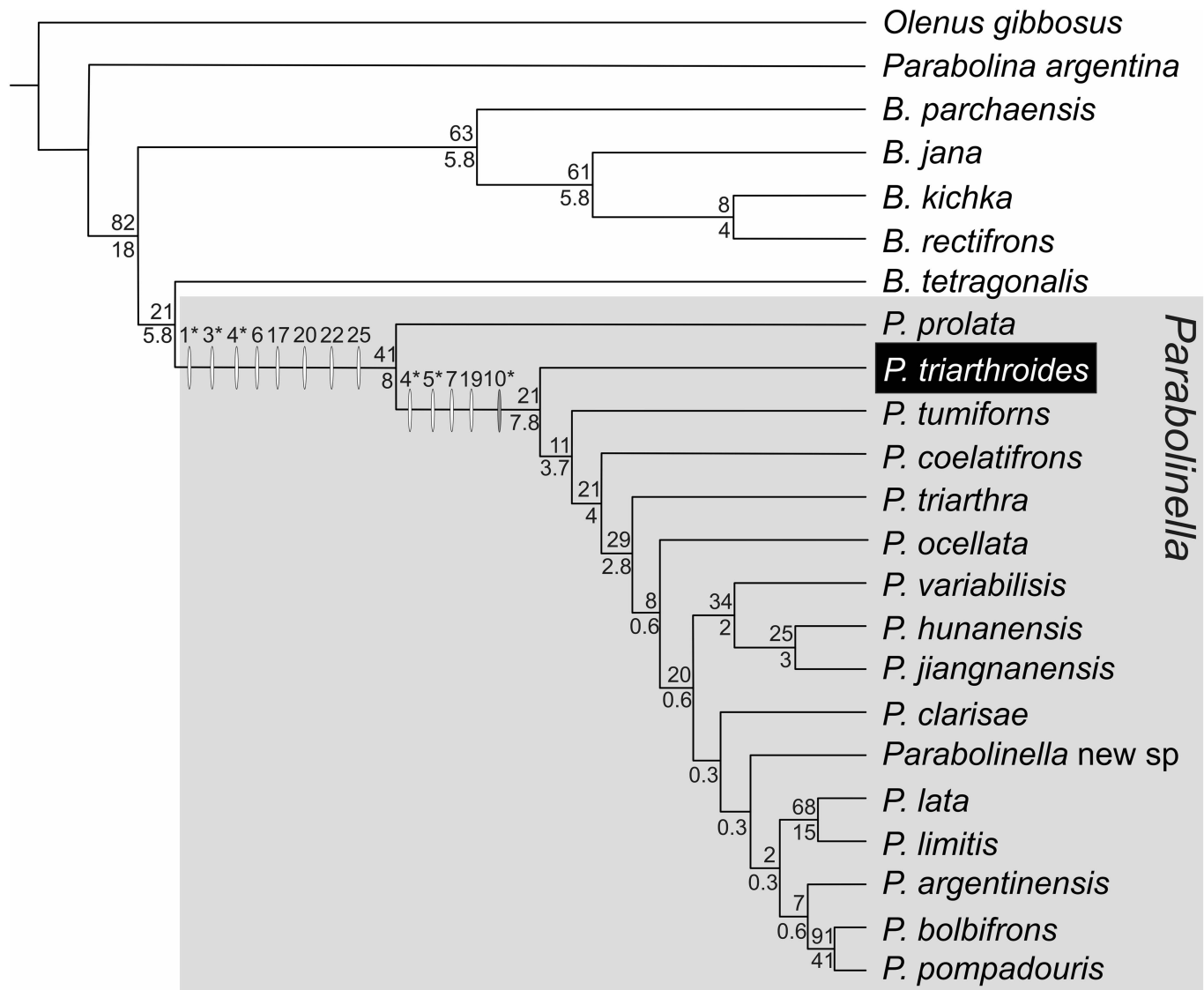
Figure 5. Topology obtained applying maximum parsimony and implied weighting (k = 11–14) from the complete dataset with continuous partition code as ratios (DP + CPR); fit: 6.79 (for k = 11); length: 146.276; CI: 0.346; RI: 0.526. Synapomorphies are indicated with white ovals over the branches and changes in the range of the continuous characters are represented with gray ovals. Numbers above the ovals are characters in Table 2. Asterisks indicate those characters that allow differentiation of the two genera in the morphometric analysis: Ch. 1: Lgl/LC, Ch. 3: LPF/LPA, Ch. 4: LPF/LOR; Ch. 5: WPF/WOR; Ch. 10: WIG/Wgl.E (acronyms as Table 1). Numbers above branches are the GC Jacknife values; numbers below branches are the Bremer Support in units of fit ×100. Synapomorphies of *Parabolinella* genus: Ch. 1, 0.68 → 0.63; Ch. 3, 0.69 → 0.72; Ch. 4, 0.58 → 0.94; Ch. 6, 0.58-0.59 → 0.54–0.57; Ch. 17, 0 → 1; Ch. 20, 0 → 1; Ch. 22, 0 → 1; Ch. 25, 0 → 1. Synapomorphies of *Parabolinella* (expect *P. prolata*): Ch. 4, 0.95 → 1–1.22; Ch. 5, 0.58 → 0.67-0.8; Ch. 7, 1.08 → 1.01; Ch. 19, 0 → 1. Change of range: Ch. 10, 0.3–0.43 → 0.37–0.43.

Other characters that emerge from the morphometric analysis also show some phylogenetic signal; they are recovered as synapomorphies of all *Parabolinella* species, except for *P. prolata* Robison and Pantoja-Alor, 1968. Both matrices entail the wider posterior fixigenae (tr.) (CPR, Ch. 5, 0.58 → 0.67-0.8; CPGM, Ch. 5, 1.23 → 1.31–1.33) (Figs. 5, 6); and only for CPGM, a shorter cranidium (sag.) (Ch. 0, 3.01–3.05 → 2.8–2.99) (Fig. 6). Finally, it is important to note that the width of interocular genae related to the width of the glabella at the eye line (Ch. 10 of CPR, see Table 2) and the length of the occipital ring (Ch. 2 of CPGM, see Table 2) show changes in their ranges on the basal nodes of the *Parabolinella* clade, although they are not recovered as

synapomorphies. Therefore, *Parabolinella* (except *P. prolata*) have higher interocular genae ratio (Ch. 10, 0.3–0.43 → 0.37–0.43) (Fig. 5) and larger occipital ring (Ch. 2, 0.41–0.46 → 0.34–0.46) (Fig. 6).

Discussion

Quantitative characters are important tools for the discrimination of species, especially in fossils in which the morphology is the only data available to distinguish biological units. Multiple approaches are necessary to understand how these characters vary within and between species (e.g., MacLeod, 2002; Hopkins
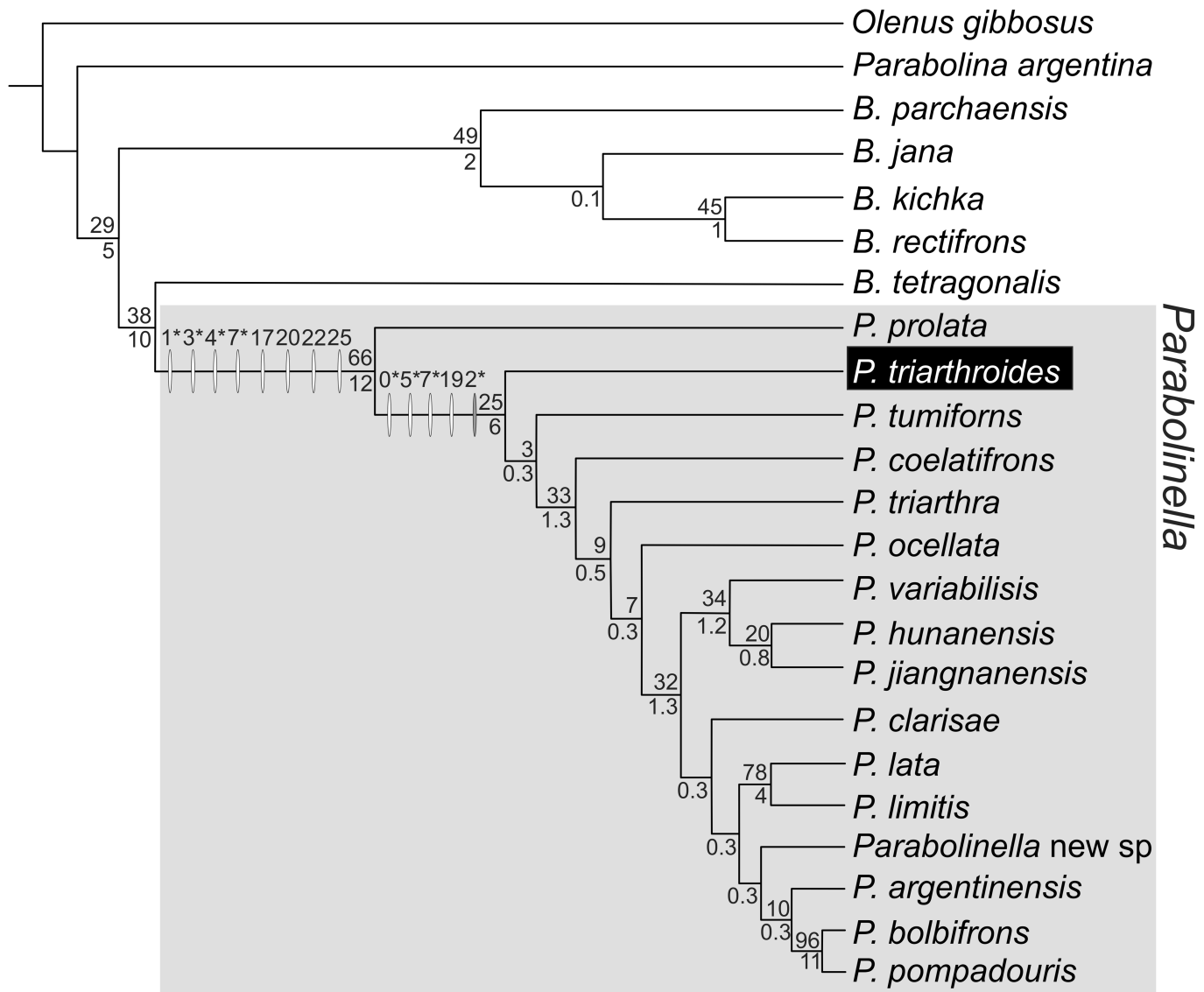
Figure 6. Topology obtained applying implied weighting (k = 10–14) from the complete dataset with continuous partition code as data corrected by the geometric mean (DP + CPGM); fit: 7.08 (for k = 11); length: 150.590; CI: 0.337; RI: 0.525. Synapomorphies are indicated with white ovals over the branches and changes in range of the continuous characters are represented with gray ovals. Numbers above the ovals are characters in Table 2. Asterisks indicate those characters that allow differentiation of the two genera in the morphometric analysis: Ch. 0: LC, Ch. 1: Lgl, Ch. 2: LOR, Ch. 3: LPA; Ch. 4: LPF, Ch. 5: WPF; Ch. 7: Wgl.B (acronyms as Table 1). Numbers above branches are the GC Jacknife values; numbers below branches are the Bremer Support in units of fit ×100. Synapomorphies of *Parabolinella* genus: Ch. 1, 1.97 → 1.92; Ch. 3, 0.51 → 0.69–0.73; Ch. 4, 0.35 → 0.48–0.55; Ch. 7, 2.1–2.18 → 2.06; Ch. 17, 0 → 1; Ch. 20, 0 → 1; Ch. 22, 0 → 1; Ch. 25, 0 → 1. Synapomorphies of *Parabolinella* (expect *P. prolata*): Ch. 0, 3.01–3.05 → 2.8–2.99; Ch. 5, 1.23 → 1.31–1.33; Ch. 7, 1.08 → 1.01; Ch. 19 0 → 1; change of range: Ch. 2, 0.41–0.46 → 0.34–0.46.

and Webster, 2009; Monti et al., 2016). Morphometrics can help distinguish patterns of morphological variation in a given group; however, cladistics provides an evolutionary hypothesis for this group, which indicates how these variations would have evolved. Both methods are complementary and necessary to propose a more integral approach and more rigorous taxonomic decisions (MacLeod, 2002).

The present study demonstrates that log-transformed raw data can be used to differentiate *Parabolinella* from *Bienvillia*, although it is difficult in this kind of analysis to recognize variables of importance that can be used to directly distinguish both genera. Only two characters emerged from this analysis: the length of preglabellar area and preglabellar field. However, when data are corrected (using geometric means and ratios), both genera can be readily distinguished and new variables of importance that allow their differentiation can be recognized.

All the analyses performed here gave similar results in relation to the position of *P.? triarthroides*, which is located within the most extreme forms of the genus *Parabolinella*. All the analyses also allow separation of the two genera; however,

Figure 7. Topologies obtained with each partition: (**1**) continuous partition coded as ratios (CPR) applying implied weighting (k = 12–3), fit: 1.48 (for k = 11), length: 33.130, CI: 0.44, RI: 0.548; (**2**) continuous partition coded as data corrected by the geometric mean (CPGM) applying implied weighting (k = 14–4), fit: 7.08 (for k = 11), length: 35.371, CI: 0.412, RI: 0.578; (**3**) qualitative partition; fit: 4.8 (for k = 11), length: 106, CI: 0.34, RI: 0.565.
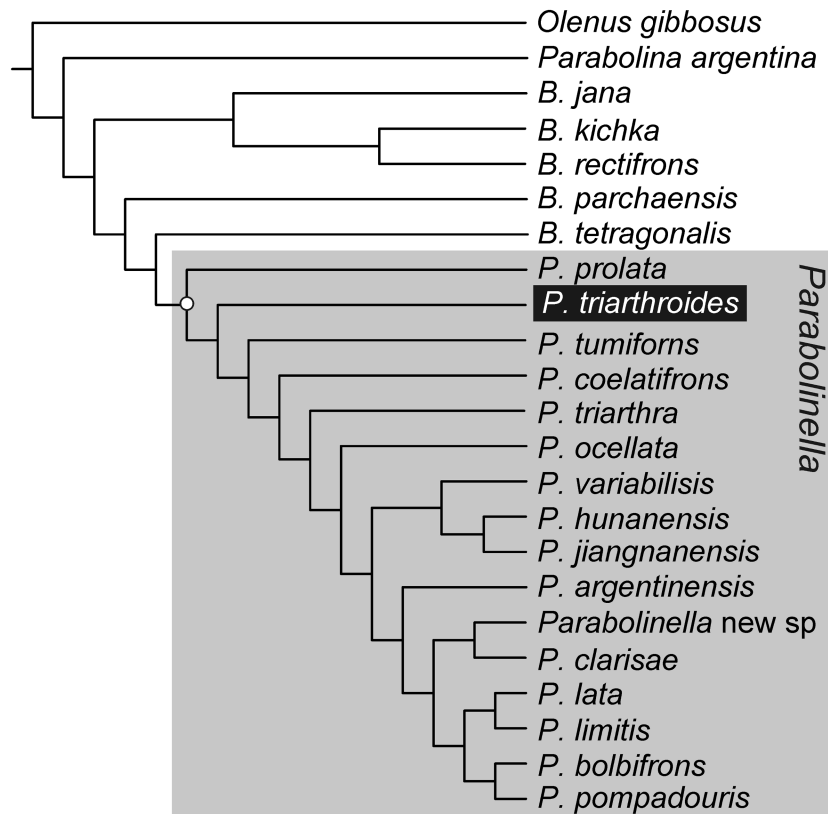
1. Continuous partition: ratios
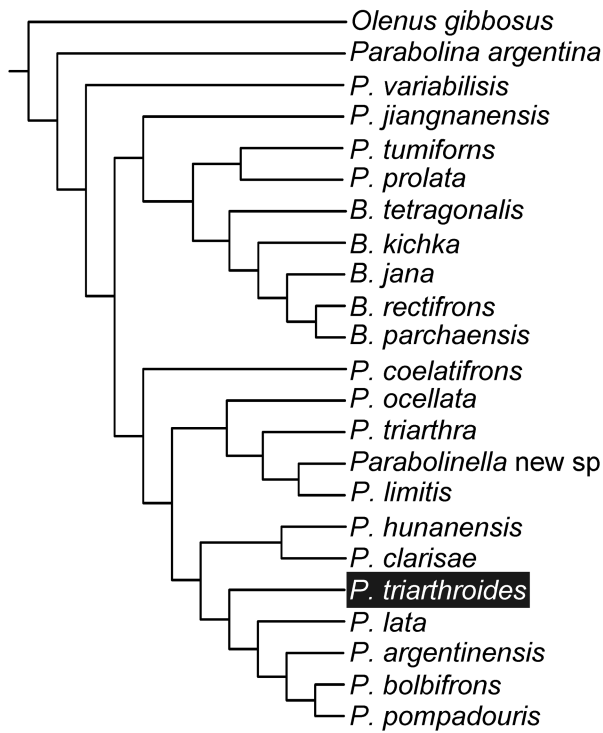
2. Continuous partition: geometric mean
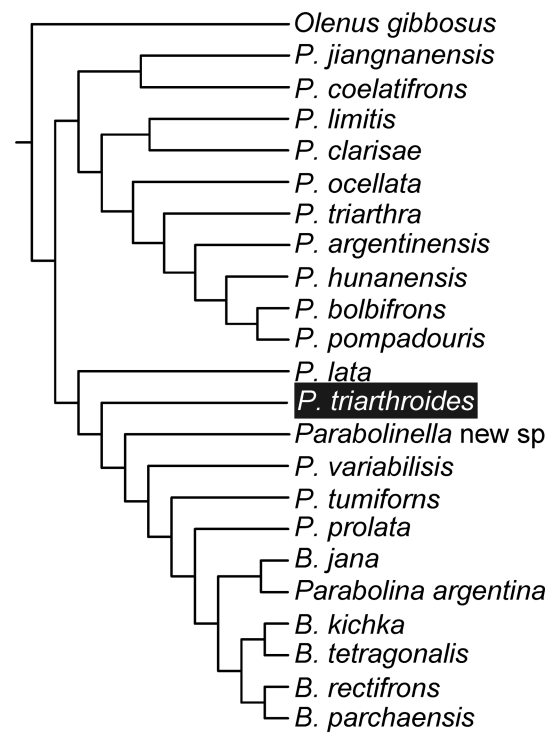
3. Qualitative partition

correction with the geometric mean provides more useful characters with smaller confidence intervals (Tables 4, 5) for differentiating them. Particularly, importance of the length and width of the occipital ring and the relative size of the cranidium could be revealed. These two characters could not otherwise be identified in the analysis with the ratios. A possible explanation for this result may be the fact that the geometric mean is a more holistic measurement because it includes all the variables to calculate a size estimator for the specimen. However, ratio variables can be affected by the relationship between the two original variables, if they co-vary. An example of this situation could be the width of the interocular genae. This character is not recovered as important to distinguish both genera when data were corrected by the geometric mean. However, when using ratios, the width of the interocular genae related to the width of the glabella (at the eye line) is strongly correlated with PC1. Through the combination of both results, the width of glabella (at the eye line) is shown to be the character that differentiates both genera, instead of the width of the interocular genae. Even if the size effect could not be completely eliminated from the analyses, both corrections applied to reducing size effects proved to be equally effective in the sense that they revealed the morphological differences of both genera.

This study also confirms that the general morphology of the cranidium of *Parabolinella* differs from that of *Bienvillia* in having a more-developed preglabellar area (sag.) and pregla-bellar field (sag.), wider posterior fixigenae (tr.), larger glabella and cranidium, and higher ratio between the width of the interocular genae and the width of glabella (at the eye line) (tr.) (Fig. 4). The first three characters have been used to justify the inclusion of *P.?* *triarthroides* in *Parabolinella* (e.g., Harrington and Leanza, 1957). In addition, the types of *P.?* *triarthroides* show a similar morphology to the genus *Parabolinella*, and they are located far from the overlapping zone. Therefore, the morphology of *P.?* *triarthroides* cannot be considered as inter-mediate, as proposed by Harrington and Leanza (1957). These authors arrived at this conclusion based on the original description of *P.?* *triarthroides* made by Harrington (1938), who reported the presence of a simple preoccipital furrow (S1) in this species. Indeed, in a previous phylogenetic analysis, this character was also identified the most significant difference between *P.?* *triarthroides* and the rest of the species of *Parabolinella* (Monti and Confalonieri, 2013). However, despite the importance of this character for the genus diagnosis, the correction of the original matrix regarding this particular character (from simple to bifurcated for *P. triarthroides*) does not produce a substantial change in the results of the cladistics analysis compared with the previous work (tree not shown). In this context, the combination between the codification of the continuous characters and the inclusion of more species of *Bienvillia* were key strategies to solve the position of *P.?* *triarthroides*. Therefore, the implementation of different methodologies (morphometric and phylogenetic approaches, based on raw and corrected data) gave a better understanding of how the quantitative characters and their codification may affect the proposed relationships between the species, as well as the clue to observe with more detail more specimens, and to uncover possible reasons of the discrepancies: the

misidentification of one character (simple instead of bifurcated furrow).

Both types of continuous partitions recovered as synapo-morphies of *Parabolinella* the following characters: larger preglabellar area (sag.) and preglabellar field (sag.), and shorter glabella (sag.). One more character was recovered as a syna-pomorphy of the genus, but it is different according to the type of coding. When quantitative characters are coded as ratio variables, there is more consistency between the qualitative and quantitative partitions, but characters coded as geometric means gave better-supported clades. Many authors have pointed out that the use of ratios may fail to eliminate the allometric effect, and at the same time can create new relationships between previously uncorrelated characters (e.g., Corruccini, 1977; Albrecht et al., 1993).

Another problem could be that some measurements can be repeated in more than one character, violating the fundamental principle of character independence. There is a long debate in the scientific literature about the best way of coding quantitative characters, but no consensus on how to solve this problem has been yet reached (e.g., Corruccini, 1977; Hills, 1978; Albrecht et al., 1993; MacLeod, 2002; Rae, 2002; Jansen, 2003; Clouse et al., 2010; De Bivort et al., 2010). For instance, different techniques were proposed to adjust ratios that maximize the reduction of size information (Corruccini, 1977; Hills, 1978; Albrecht et al., 1993), and to eliminate co-varying continuous characters from the data matrix (Clouse et al., 2010; De Bivort et al., 2010). In the present study, the main difference between both ways of coding is that the use of geometric means has the primary function to eliminate size effect while the use of ratios reflects shapes; relative proportions or positions of different structures of the cranidium morphology (see Albrecht et al., 1993 for a similar distinction). Likewise, both types of coding used here are intuitive and easily understandable, being an advantage when interpreting results. Their performance was very similar. Therefore, there is not definite answer on how to code characters and which way will be better in each case, so further research will be necessary to explore the best way of coding in every particular dataset.

Finally, some characters of importance to distinguish the two genera in the morphometric analysis also have evolutionary importance because they are recovered as synapomorphies of *Parabolinella* (e.g., the length of the preglabellar area [Ch. 3], the length of the preglabellar field [Ch. 4], and the length of the glabella [Ch.1]), both expressed as ratios or as data corrected by the geometric mean (Table 2, Figs. 5, 6). The width of the glabella at the base (Ch. 7) is also added to the list of synapomorphies when using CPGM. Regarding the width of the posterior fixigenae (Ch. 5) and the length of the cranidium (Ch. 0), they show some phylogenetic signal because they are recovered as synapomorphies of all of the *Parabolinella* species, except *P. prolata* (Figs. 5, 6). Lastly, the other char-acters that emerge from the morphometric analysis are those that change in their ranges on the basal nodes of the *Parabolinella* clade (for CPR, Ch. 10 [WPF/WOR] and for CPMG Ch. 2 [LOR]; see Table 2; Figs. 5, 6), although they are not recovered as synapomorphies. In this sense, the two types of analysis are complementary: the range of the morphological variation for each genus and the position of the type material of

P.? triarthroides can be set from the morphometric analysis; however, without a phylogenetic context, the morphological similarities can also be interpreted as the result of convergence. When combining the analyses, the similarities between the cranidium of *P.? triarthroides* and the rest of the species of *Parabolinella* can be interpreted as evidence of homology rather than as the result of convergent evolution. Summarizing, based on the general morphology of the cranidium, the qualitative characters, and the phylogenetic analysis, *P. thriartroides* should be left within the genus *Parabolinella*.

As a more general conclusion, the results here presented lead to the suggestion that that the analysis of qualitative characters that emerge from direct observation of the specimens will be the first step to consider for elaborating generic diagnoses. Morphometric analyses will be a useful complementary approach to easily identify recognizable quantitative characters that all the species included in a particular genus will share. Finally, phylogenetic analyses will allow assessment of the evolution of those diagnostic characters and testing of their importance as true synapomorphies defining natural groups.

Conclusions

Both methodologies, together with a good description of the specimens, are complementary and necessary to propose a more integral analysis and to make taxonomic decisions. The combined analyses show that the similitudes observed among the cranidia of *P. triarthroides* and the rest species of *Parabolinella* are not the product of evolutionary convergence. Therefore, *P. triarthroides* should be included in the genus *Parabolinella*, as traditionally has been considered.

In regard to the morphometric analysis, the two ways of taking size differences into consideration are equally effective, and the results are similar. But the analysis carried out with the data corrected by the geometric mean provides more characters of importance for differentiating the genera and is more effective in classifying with the discriminant function. On the other hand, the cladistic analysis based on characters coded as ratios exhibit more consistency between qualitative and quantitative partitions.

The general morphology of the cranidium of *P. triarthroides* is within the range of variation of the *Parabolinella* genus. *Parabolinella* (including *P. triarthroides*) is a monophyletic group supported by one nonhomoplastic synapomorphy, the presence of an adaxially bifurcated S1 furrow, the palpebral lobes centered to S2, the anterior termination of glabella rounded, S2 furrows shorter than S1, the preglabellar field occupying a larger proportion of the preglabellar area (sag.), a well-developed preglabellar field (sag.), and a short (sag.) glabella with a narrow base (tr.).

Acknowledgments

Accessibility of supplemental data

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.27qj6

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