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Phylogenetic analysis of the late Cambrian–early Ordovician genus *Parabolinella* Brøgger (Trilobita, Olenidae)

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Phylogenetic relationships among species of the family Olenidae (Trilobita, Ptychopariida) were traditionally established by the direct comparison of morphological features and the evaluation of stratigraphic placement. In this study, a cladistic analysis of *Parabolinella* Brøgger is conducted in order to test the supposed monophyly of the genus and to determine the relationships of its species. Twenty-one taxa (sixteen of this genus) from the late Cambrian and Tremadocian of Baltica, Avalonia, Laurentia, South China and the western margin of Gondwana were revised. Forty non-ordered characters were considered in the analysis, 34 belonging to the cephalon, four to the pygidium, and two to the thorax. Some of these characters were specially defined for this study. The phylogenetic analysis was performed under unweighted parsimony. The obtained tree is partially consistent with the stratigraphic record of the studied species and shows correspondence with global late Cambrian and early Ordovician palaeogeography. *Parabolinella* may have originated in deep water sites of the Oaxaca region, Mexico and then migrated to other regions. The genus diversified in outer shelf facies of the Baltica Province during the late Cambrian and Tremadocian, whereas it would have dispersed to the South China Province in early Tremadocian times.

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KEY WORDS Trilobita; Olenidae; *Parabolinella*; Furongian; Tremadocian; phylogeny

1. INTRODUCTION

The Olenidae is a widespread, biostratigraphically important family of trilobites that occurred in the Lower Palaeozoic. Although it is considered a natural, monophyletic group, many aspects of its systematics and evolutionary history still remain obscure. For example, relationships among the different subfamilies and lower taxa are not clearly resolved (e.g. Fortey, 1990); subfamiliar affinities of some genera were not properly determined (Robison and Pantoja-Alor, 1968; Nikolaisen and Henningsmoen, 1985), and many species lack an adequate definition.

Parabolinella Brøgger, 1882 is a genus of great phylogenetic significance and cosmopolitan distribution in the latest Furongian and Tremadocian. It has traditionally been regarded as a monophyletic taxon, but formal studies to test this assumption were never conducted.

The present paper reports a cladistic analysis on the genus *Parabolinella* and other related genera. Such analysis was conducted to clarify the position of *Parabolinella* within the family Olenidae and to determine the relationships among species belonging to this genus. Character states of possible phylogenetic significance are proposed for the first time, and these primary homology statements were evaluated through the cladistic analysis. The resulting tree is partially consistent with the stratigraphic record of the studied species and shows correspondence with global late Furongian and early Ordovician palaeogeography.

2. *PARABOLINELLA* BRØGGER: DEFINITION, DISTRIBUTION, AND PREVIOUS WORK ON PHYLOGENETIC AFFINITIES

Parabolinella has traditionally been defined as a Furongian–early Ordovician olenid having a subquadrate to subrectangular glabella, a well-developed preglabellar field, a bifurcated glabellar S1, 15 to 21 thoracic segments, and a small, entire, semi-elliptical pygidium with a length–width ratio less than 0.5 (Figure 1) (e.g. Harrington and Leanza, 1957; Henningsmoen, 1957; Rushton, 1988). It has been described from Scandinavia (e.g. Westergård, 1922; Henningsmoen, 1957; Terfelt and Ahlgren, 2009), Great Britain (South Wales,

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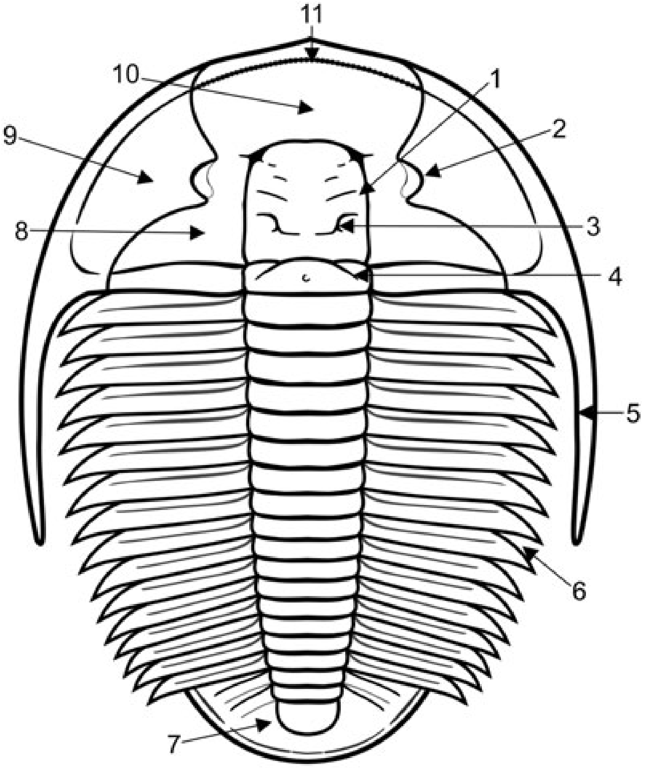

Figure 1. Schematic drawing of *Parabolinella* sp. Showing the characteristics of the genus. 1. Subquadrate to subrectangular glabella; 2. Moderately sized eyes, located not far from the glabella; 3. Bifurcated glabellar S1 furrow; 4. Composite occipital furrow; 5. Long genal spine; 6. 15 to 21 thoracic segments; 7. Small, entire, semi-elliptical pygidium; 8. Wide, subtriangular postocular cheeks; 9. Elongate librigenae; 10. Well-developed preglabelar field; 11. Pitted anterior border.

Owens *et al*., 1982; Lake District, Rushton, 1988; Breadstone, Gloucestershire, Fortey and Owens, 1997), North America (Vermont, Shaw, 1951; Nova Scotia, Henningsmoen, 1957; western Newfoundland, Fortey in Fortey *et al*., 1982; west of Mackenzie District, Ludvingsen, 1982; Oaxaca, Mexico, Robison and Pantoja-Alor, 1968), South America (northwestern Argentina and Bolivia, e.g. Kobayashi, 1936, 1937; Harrington, 1938; Harrington and Leanza, 1957; Pribyl and Vanek, 1980), and China (Jiangshan and Changshan counties, Lu and Lin, 1984; West Hunan, Peng, 1991). In addition, the genus has been cited from southern Tasmania (Bao and Jago, 2000), Kazakhstan and Russia (Henningsmoen, 1957).

Phylogenetic relationships among genera and species of Olenidae were conventionally established by the direct comparison of morphological features and the evaluation of stratigraphic placement. Westergård (1922) provided a pioneering scheme of phylogenetic relationships of the family, in which *Parabolinella* appears close to *Parabolina* Salter, 1866. Based on Westergård's statements, Harrington and Leanza (1952) discussed in more detail the evolutionary patterns of olenid genera and suggested that *Parabolinella* may be closely related to both *Parabolina* and *Bienvillia* Clark, 1924. Besides, *Parabolinella coelatifrons* Harrington and Leanza, 1957 was regarded as an intermediate form between *Parabolina* and *Parabolinella*, whereas *Parabolinella triarthroides* Harrington, 1938 was proposed as a transitional link between *Parabolinella* and *Bienvillia* (Harrington and Leanza, 1952). Henningsmoen (1957) also discussed the affinities of olenids and emphasized that *Parabolinella* and *Bienvillia* are 'sister groups', suggesting that these taxa were derived from *Parabolina* or *Parabolinites williamsoni* (Belt, 1868).

In addition, Rushton (1988) considered that *Parabolinella* is a conservative member of the family Olenidae that retains ancestral features such as: a well-developed preglabellar field; moderately sized eyes which are located not far from the glabella; wide, subtriangular postocular cheeks; elongate librigenae with long genal spine; continuing curvature of lateral margin (Figure 1); and a natant hypostome with entire posterior margin. However, he also indicated the presence of diagnostic, advanced characters, including a geniculate and bifurcate S1 furrow, a composite occipital furrow, an accessory glabellar furrow between S0 and S1, an inflated preglabellar field (in some species), and a pitted anterior border furrow (Figure 1). Compared with earlier olenid genera, *Parabolinella* has a higher number of thoracic segments and a smaller pygidium.

Although the studies cited above provided vital information about the definition and affinities of *Parabolinella*, there are only a few references in the literature about the relationships among the different species of the genus. There seems to be a consensus that *P. argentinensis* Kobayashi, 1936, *P. triarthra* (Callaway, 1877) and *P. limitis* Brøgger, 1882 constitute a homogeneous group (e.g. Harrington and Leanza, 1957, Henningsmoen, 1957), although it is not clear how these species relate to each other. Henningsmoen (1957) considered that *P. lata* Henningsmoen, 1957 was derived from this group.

3. MATERIALS AND METHODS

3.1. Terminals

Sixteen *Parabolinella* (ingroup) and five non-*Parabolinella* species (outgroup) were assayed for cladistic analysis.

3.1.1. Ingroup

Parabolinella species were included in the cladistic analysis, on the basis of the original descriptions and subsequent redescriptions existing in the scientific literature. Published illustrations of these species were also used to complete, where appropriate, the necessary information for the construction of the input matrix. The diagnosis of five species (*P. argentinensis*, *P. triarthroides, P. coelatifrons, Parabolinella* sp. nov. 1 and *Parabolinella* sp. nov. 2) were reviewed on the basis of material from different localities of Northwest Argentina Basin and Famatina,

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corresponding to the 'Harrington and Leanza Collection', which is included in the Invertebrate Palaeontology Collection, deposited in the Department of Geology (Palaeontology area), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (Curator, Dra. Beatriz Aguirre Urreta).

The species of *Parabolinella* included in this study are listed in Table 1. All of them occur in the late Furongian–Tremadocian of Baltica, Laurentia, South China, Avalonia and western Gondwana. Table 1 also shows the list of species originally described under open nomenclature, as well as those based on fragmentary and distorted material, which were excluded from the present analysis (see comments for each excluded species on Table 1). In addition, several species from China (*P. sayramensis* Xiang and Zhang, 1984; *P. lata* Xiang and Zhang, 1984; *P. xinjiangensis*, Xiang and Zhang, 1985; *P. ocellata* Lu and Lin, 1984) were synonymised with *P. contracta* Lu and Zhou, 1981 (see Rushton, 1988) and therefore were excluded from this analysis too.

3.1.2. Outgroups and rooting

In order to test the supposed monophyly of *Parabolinella* and to clarify its relationships with other olenid genera, multiple outgroups were used in the study. Three of them belong to *Bienvillia*: *B. tetragonalis* (Harrington, 1938), which was regarded by Harrington and Leanza (1957) as a descendant of *P. triarthroides*; *B. rectifrons* (Harrington, 1938); and *B. parchaensis* (Harrington and Leanza, 1957). In addition, because the genus *Parabolina* is a possible ancestor of *Parabolinella* (see Harrington and Leanza, 1952; Henningsmoen, 1957), the species *Parabolina (Neoparabolina) frequens argentina* (Kayser, 1876) was also added.

Olenus Dalman, 1827 is considered as the ancestral genus of Olenidae (Westergård, 1922; Harrington and Leanza, 1952). Since Fortey (1990) pointed out that the earliest *Olenus* species, which retains the rostral plate, forms the sister group of the rest of the family, the most parsimonious tree was rooted with *Olenus gibbosus* (Wahlenberg, 1818).

3.2. Characters

Since many *Parabolinella* species are only known from cranidia or cranidia + librigenae, a large majority of features considered in this analysis (33, see Appendix) belong to the cephalon. The morphology of the pygidium, which in other trilobite taxa is very informative, in this case is either homogeneous or unknown. Consequently, only six pygidial characters were coded. Similarly, only two thoracic characteristics and no hypostomal features were used in this study.

Many characters listed in the Appendix, such as those related with glabellar segmentation (car. #9, car. #10, car. #11, car. #12, car. #14) and the number of holaspid thoracic segments (car. #30) and pygidial axial rings (car. #26), are widely used in trilobite phylogenetic analyses (e.g. Cotton, 2001; Waisfeld *et al*., 2001; Lieberman, 2002; Zhou *et al*., 2009). In addition, some features were specifically utilized by Cotton (2001) and Waisfeld *et al*. (2001) in ptychopariid and shumardiid studies, respectively. With regard to the divergence of the anterior branch of the facial suture, Hughes and Rushton (1990) and Cotton (2001) coded it as two separate characters: the presence of a divergent facial suture, and its degree of divergence. However, these states are unified in a single character herein (char. #2), in order to minimize the missing entries in the matrix. The accessory lateral glabellar furrow described by Rushton (1988) as a characteristic of the genus, is not evident in most of the described species of *Parabolinella*, so this character was excluded from this study.

In addition, some common morphological features are used in this phylogenetic analysis for the first time (see Appendix): posterior width of fixed cheek (char. #20), width of palpebral area of fixed cheek (char. #31), length of palpebral lobe (char. #32), shape of anterior margin of glabella (char. #6), length of S2 furrow (char. #13), length of occipital ring (sag., from midpoint of S0) as proportion of the length of the glabella (sag., excluding occipital ring) (char. #15), length of posterior cephalic border as proportion of length of occipital ring (char. #21), shape of posterior branch of facial suture (char. #22), length of pygidium (sag.) as proportion of maximun width of pygidium (tr.) (char. #27), and direction of eye ridge (char. #29).

Primary homologies (Pinna, 1991) were established for forty informative morphological features (characters #0–#39, Appendix), and a data matrix was built (Table 2). Quantitative characters having non-overlapping ranges of variation were transformed into discrete ones. All multistate characteristics were treated *a priori* as unordered (non additive) in the absence of clear criteria for ordering them. Characters were considered unweighted.

3.3. Phylogenetic analysis

The cladistic analysis was performed with TNT 1.1 (Goloboff *et al*., 2008). Heuristic searches were performed using random addition sequences (RAS) followed by tree bisection–reconnection branch swapping (TBR). 1000 replicates were carried out, saving 25 trees per replicate.

The list of Synapomorphies were produced taking into account only the unambiguous changes in ancestral states (e.g. 0→1, but not 01→1; 01→2, but not 01→12).

Character indices were determined by exporting basic statistics (steps, minimum and maximum character lengths) from TNT to a spreadsheet. Consistency index (CI) and retention index (RI) were calculated for all informative characters.

Bremer support values (BS) (Bremer, 1994) were estimated by TBR swapping from the optimal tree, retaining suboptimal trees with increasing bounds, up to 1000 trees.

Table 1. List of species included in *Parabolinella* Brøgger. I = Species included in the analysis. '+': included, '-': not included. [1]see Harrington and Leanza, 1957; Waisfeld and Vaccari, 2003 and Pribyl and Vanek, 1980; [2]Tortello and Esteban, 2003; [3]Henningsmoen, 1957; [4]Callaway, 1877; [5]Fortey and Owens, 1997; [6]Lee and Chatterton, 2007; [7]Peng, 1991; [8]Lu and Lin, 1984; [9]Rushton, 1988; [10]Terfelt and Ahlgren, 2009. Cam. = Cambrian, Trem. = Tremadocian. *The descriptions of these species will be published elsewhere

Species	Procedence	Age	I	Comments
P. argentinensis Kobayashi (1936, Plate XV, figures 1–5).	**Bolivia**. Taraya and Palqui localities; **Argentine**. Eastern Cordillera, Santa Rosita Formation; Famatina range, Volcancito Formation **Mexico**. Oaxaca, Tiñu Formation **South Wales**. Carmarthen district.	**Furongian–Late Trem**. Argentine and Bolivia: Upper part of *Parabolina (N.) frequens argentina*, *Kainella meridionalis* and *Bienvillia tetragonalis-Conophrys minutula* Biozones.[1]	+	Material from Eastern Cordillera (Northwestern Argentina Basin) and Famatina was examined.
Parabolinella triarthroides Harrington (1938, Plate 7, figures 10–11).	**Argentine**. Eastern Cordillera, Santa Rosita Formation. **England**. River Calder, Lake District.	**Late Tremadocian**	+	Type and additional materials from Eastern Cordillera (Northwestern Argentina Basin) were revised.
P. coelatifrons Harrington and Leanza (1957, figures 39, 3a–h).	**Argentine**. Eastern Cordillera, Santa Rosita Formation.	**Furongian** inferior part of *Parabolina (N.) frequens argentina* Biozone, *Pseudorhaptagnostus (Machairagnostus)- Gymnagnostus* Subzone[2].	+	Type and additional materials from Eastern Cordillera (Northwestern Argentina Basin) were revised.
***Parabolinella* sp. nov. 1**	**Argentine**. Eastern Cordillera, Santa Rosita Formation. Probably South Wales and Bolvia.	**Furongian–Early Trem**. *Kainella meridionalis* Zone.	+	This species was defined based on material from the Early Tremadoc of Río San Pedro, Quebrada Colorada de Fundición and Santa Victoria (Eastern Cordillera, Northwestern Argentina Basin).*
***Parabolinella* sp. nov. 2**	**Argentine**. Eastern Cordillera, Santa Rosita Formation. Probably, Mexico (Oaxaca) and Bolivia.	**Tremadocian**	+	This species was defined based on material from Tremadoc of Purmamarca and Cerro Alto del Pajonal (Eastern Cordillera, Northwestern Argentina Basin).*
P. limitis Brøgger, 1882 (Henningsmoen (1957, Plate 1, figure 8; Plate 8; Plate 12, figures 1–5)).	**Scandinavia**. Norwegian: Oslo (Vekkerø, St. Olavs gate), Rigerike (Viul), Hadeland (Gran, Jaren). **Eastern Canada**. Nova Scotia.	**Late Tremadocian** Scandinavia: *Ceratopyge* Series.[3] Canada: *Asaphellus* Zone.[3]	+	
P. triarthra (Callaway (1877, Plate XXVI, figure 6)).	**England**. South Shropshire. **South Wales**. Carmarthen district. **Eastern Canada**. Nova Scotia. **Tasmania**. Birch Inlet.	**Furongian–Trem**. England: Shineton Shales.[4] Canada: *Asaphellus* Zone.[3]	+	
P. bolbifrons Fortey and Owens (1997, Plate 1, figures 1–8).	**England**. Breadstone Shales.	**Early Tremadocian** Lower Tremadocian, Cressagian stage.[5]	+	

P. prolata Robison and Pantoja-Alor, (1968, Plate 102, figures. 3, 6, 9).	**Mexico**. Oaxaca, Tiñu Formation **Canada**. Western District of Mackenzie	**Furongian–Early Trem**. Mexico: stratigraphic record delimited between *Cordylodus andresi* Zone and *Cordylodus proavus* Zone. Canada: *Missisquoia depressa* Subzone of *Parabolinella* Zone.[6]	+	= ***P. panosa***: synonymized by Chatterton and Speyer (in Whittington *et al*., 1997) and Lee and Chatterton (2007). Age from Mexico bounded by superimposing the profiles published by Robison and Pantoja-Alor (1968) and reviewed by Landing *et al*. (2007).
P. tumifrons Robison and Pantoja-Alor (1968, Plate 102, figures 10–16).	**Mexico**. Oaxaca, Tiñu Formation.	**Furongian–Early Trem**. Stratigraphic record delimited between *Cordylodus andresi* Zone and *Cordylodus proavus* Zone.	+	Age bounded by superimposing the profiles published by Robison and Pantoja-Alor (1968) and reviewed by Landing *et al*. (2007).
P. variabilis Robison and Pantoja-Alor (1968, Plate 102, figures 17–21).	**Mexico**. Oaxaca, Tiñu Formation.	**Furongian–Early Trem**. Stratigraphic record delimited between *Cordylodus andresi* Zone and *Cordylodus proavus* Zone.	+	Age bounded by superimposing the profiles published by Robison and Pantoja-Alor (1968) and reviewed by Landing *et al*. (2007).
P. hunanensis Peng (1991, Plate II, figures 4–5).	**China**. West of Hunan, Guotang Formation.	**Early Tremadocian** *Hysterolenus* Zone.[7]	+	
P. jiangnanensis Lu and Lin (1984, Plate VIII, Figures 10–13; Plate IX, figures 1–5).	**China**. Xiyangshan, Changshan County (Yinchupu Formation).	**Early Tremadocian** *Dichelepyge sinensis* Zone.[8]	+	
P. lata Henningsmoen (1957 Plate 8; Plate 12, figure 8).	**Scandinavia**. *Norwegian*: Royken (S. Bjerkåsholmen).	**Late Tremadocian** *Ceratopyge Limestone*.[3]	+	
***Parabolinella* new species** Terfelt and Ahlgren (2009, figures 6, 1–6).	**Sweden**. Southern Kinnekulle, Västergötland.	**Furongian** *Ctenopyge bisulcata* Zone.[11]	+	Not formally named, only known by cranidia, but with diagnostic characters.
P. contracta Lu and Zhou, in Lu et al., 1981	**China**. West of Nei Mongol, Hangula region **North Wales**. Bryn-llin-fawr.	**Furongian**[9]	+	Included in this analysis on the basis of descriptions and photographs of *P. ocellata*, accepting the synonymy proposed by Rushton (1988).
P. ocellata Lu and Lin (1984, Plate IX, figures 6–8).	**China**. Duibian, Jiangshan County and Xiyangshan, Changshan County (Yinchupu Formation).	**Early Tremadocian** *Dichelepyge sinensis* Zone.[8]	-	= *P. contracta*, synonymized by Rushton (1988).
P. chiliensis Chang and Fan, 1960	**China**	?	-	Only figures in list of Rushton (1988), without posterior references.
P. sayramensis Xiang and Zhang, 1984	**China**. *Xinjiang*: North Tianshan, Sayram Formation.	**Early Tremadocian**[9]	-	= *P. contracta*, synonymized by Rushton (1988).
P. xingjiangensis Xiang and Zhang, 1985	**China**. *Xinjiang*: western part of northern Tianshan.	**Furongian**[9]	-	= *P. contracta*, synonymized by Rushton (1988).
P. lata Xiang and Zhang, 1984(≠ *P. lata* Henningsmoen, 1957)	**China**. North Tianshan, Sayram Formation.	**Early Tremadocian**[9]	-	= *P. contracta*, synonymized by Rushton (1988).
P. borohoroensis Xiang and Zhang, 1985	**China**. *Xinjiang*: western part of northern Tianshan.	**Furongian**[9]	-	Assigned to *Parabolinites* by Rushton (1988).
***Parabolinella* sp. 1** Tortello and Esteban, 2007	**Argentina**. *Famatina range*: Volcancito Formation.	**Furongian**	-	Dubious assignment, based on distorted material.
***Parabolinella* sp. 2** Tortello and Esteban, 2007	**Argentina**. *Famatina range*: Volcancito Formation.	**Furongian**	-	Dubious assignment, based on distorted material.
P.? caesa Lake, 1913	**Wales**. Dolgelly District	**Furongian**[3]	-	Dubious assignment, based on fragmentary material.
P.? simplex (Salter, 1866)	**North Wales**.	**Furongian**[3]	-	Dubious assignment, based on fragmentary material.
P.? incerta Rasetti, 1945	**Canada**: Lèvis Formation, Quebec province.	?	-	Asigned to *Parabolinites* by Henningsmoen (1957).

(*Continues*)

Table 1. (Continued)

Species	Procedence	Age	I	Comments
P.? punctolineata Kobayashi, 1936	**Northwestern Canada**: Yukon-Alaska boundary region.	**Furongian**?^{3}	-	Dubious assignment, based on fragmentary and distorted material, without posterior references to Henningsmoen (1957).
P.? latilimbata Lu and Chen, *in* Yin and Lee, 1978	**China**. Sandu Formation.	**Furongian**^{10}	-	Belonging to the genus doubtful (Terfelt and Ahlgren, 2009)
P. bolati (Ergaliev, 1983)	**Kazakhstan**	?	-	= *P. contracta*, synonymized by Rushton (1988).
P. hecuba (Walcott, 1924)	**Canada**. British Columbia (Chushina Formation, act. part of Survey Peak Formation). **Probably Newfoundland**.	Tremadocian	-	Originally described as *Maxomia hecuba* and subsequently reassigned to *Parabolinella* by Harrington and Leanza (1957), known by two imperfect cranidia and posterior assignments unconvinced.
P.? rugosa Brøgger, 1882	**Scandinavia**. *Norwegian*: Vestfossen, Eiker (*Ceratopyge* Limestone); ? Røyken (S. Bjerkåsholmen) ? **Wales** (Tremadoc Slates)	Tremadocian	-	Dubious assignment, based on fragmentary material (see Shaw, 1951, Henningsmoen, 1957). Without posterior references.

Branch support was also calculated using Jackknife resampling (Lanyon, 1985) as incorporated in TNT (see Goloboff *et al.*, 2003). One thousand jackknife replicates were performed conducting a heuristic tree search consisting of ten replicates of Wagner trees (with random addition sequences) followed by TBR (saving ten trees per replicate). A probability of alteration equal to 7% (equivalent to three characters in this database) was used. The results shown are difference in the frequencies of GC (for Group present/Contradicted) developed by Goloboff *et al.* (2003). The difference in frequencies of GC was chosen because it is calculated as the difference between the frequency in which a given group is retrieved in the jackknife replicates and the most frequent contradictory group. This approach gives better measures for groups with low support (Goloboff *et al.*, 2003).

4. RESULTS

Only one most parsimonious tree of 176 steps was recovered (Figure 2). The retention index of this tree is 0.50, and the consistency index (excluding uninformative characters) is 0.35. In terms of the number of taxa, the value of the consistency index is slightly lower than expected in data sets of this size (Sanderson and Donoghue, 1989). However, it significantly exceeds consistency indices derived from similarly sized data matrices constructed from random data (consistency index of 0.16) at the 0.05 significance level (see Klassen *et al.*, 1991).

With regard to the topology of the tree, *Parabolina frequens argentina* is the sister group of all other species analyzed. These latter species are grouped into two subclades: one represented by *Bienvillia* spp. + *Parabolinella triarthroides*, and the other including all the other *Parabolinella* species. Therefore, the genus *Parabolinella* is not monophyletic as traditionally defined (Figure 2).

Parabolinella species, except *P. triarthroides*, constitute a monophyletic group supported by one nonhomoplastic synapomorphy: the presence of an adaxially bifurcated S1 furrow (char. #10, 0→1). *Parabolinella prolata* Robison and Pantoja-Alor, 1968, with one autapomorphy (posterior fixed cheek narrow, char. #20, 1→2), is the basal form of this group and sister of the rest of the *Parabolinella* species. This latter clade is defined by the presence of a weakly convex anterior cephalic border (char. #4, 0→1), pits on the anterior border furrow (char. #5, 0→1), and a caecate preglabellar field (char. #19, 0→1). The last two characters have been traditionally regarded as diagnostic features of the genus (e.g. Henningsmoen, 1957; Rushton, 1988).

It is interesting to note that the *Parabolinella* species known from China (*P. hunanensis* Peng, 1991; *P. contracta* Lu and Zhou, in Lu, Zhou and Zhou, 1981 and *P. jiangnanensis*

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Table 2. Input data matrix of 40 characters and 21 species. Numbers of characters (0–39) correspond to those indicated in the Appendix. Inapplicable characters are indicated by '-' and missing data by '?'. Character states listed as 'a' are polymorphic; 'a' = (1&2). Character states listed as 'b' and 'c' show an ambiguous condition between states; 'b' = (0&1) and c = (1&2)

											1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
Olenus gibbosus	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0
Parabolina frequens argentina	0	0	1	2	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1	2	1	0	1	2	0	0	1	1	0	0	?	1	2	0	0	0	1	0
Bienvillia tetragonalis	1	?	1	2	0	0	0	0	a	2	0	0	0	0	-	1	0	0	0	0	2	1	0	1	0	2	1	?	0	0	0	3	1	0	0	0	1	0	1	0
Bienvillia rectifrons	1	?	0	2	1	0	1	1	1	1	0	0	0	0	2	1	0	0	0	0	2	1	0	0	0	0	2	2	1	1	?	0	3	0	0	0	1	-	-	1
Bienvillia parchaensis	1	1	1	2	0	0	0	1	2	2	0	0	0	0	?	1	0	0	0	0	2	0	0	0	0	2	2	1	1	?	0	1	1	1	0	2	1	0	0	0
Parabolinella triarthra	1	0	1	1	1	1	0	1	2	0	1	1	0	1	0	1	1	2	0	0	1	1	0	1	0	1	3	1	0	0	2	2	1	0	0	0	1	0	1	1
Parabolinella bolbifrons	1	1	3	0	?	1	0	0	1	1	1	0	0	1	1	1	1	3	1	0	0	1	1	?	0	0	?	?	?	?	1	1	1	1	?	1	0	1	1	?
Parabolinella limitis	1	1	2	0	1	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0	1	2	1	1	0	?	?	?	0	1	?	2	1	0	?	0	0	0	0	?
Parabolinella jiangnanensis	1	1	2	2	0	0	1	1	1	1	1	1	0	0	1	0	1	1	0	1	1	0	1	1	0	0	1	1	0	0	0	1	1	0	0	1	0	1	1	0
Parabolinella contracta	1	0	1	2	0	0	1	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0	0	1	0	0	?	?	0	0	2	1	2	0	?	1	1	0	0	?
Parabolinella hunanensis	?	?	0	1	1	0	1	?	0	1	1	1	0	0	1	1	1	2	0	1	0	0	1	1	1	1	?	?	0	0	?	0	2	0	?	1	0	0	?	?
Parabolinella variabilis	1	?	c	0	0	1	1	1	0	1	1	0	1	0	1	0	0	1	0	1	1	2	1	1	0	?	3	0	0	0	?	1	2	0	2	1	0	0	1	0
Parabolinella tumifrons	1	?	0	0	1	1	1	1	0	2	1	0	b	1	2	0	0	1	0	1	1	2	0	1	0	?	?	?	1	?	?	1	1	0	?	1	1	0	1	?
Parabolinella lata	1	?	c	0	0	1	0	?	1	2	?	1	1	0	-	1	1	0	0	0	0	2	1	?	2	?	?	?	0	1	?	1	1	0	?	1	0	0	?	?
Parabolinella prolata	1	?	1	0	0	0	1	1	0	2	1	0	0	1	-	0	0	1	0	0	2	1	b	1	0	?	2	1	1	?	?	2	1	0	?	0	1	0	1	?
Parabolinella coelatifrons	0	0	1	0	1	1	1	1	0	1	1	1	0	0	2	0	1	1	0	1	0	1	0	1	1	0	2	1	0	0	0	2	1	0	1	0	1	1	1	0
Parabolinella triarthroides	1	?	1	0	0	1	b	1	1	1	0	0	0	1	2	1	1	1	0	0	1	1	0	1	0	0	?	?	1	0	1	2	1	0	?	0	1	0	?	?
Parabolinella argentinensis	1	0	3	0	0	1	0	0	1	0	1	1	0	0	0	1	1	2	0	1	0	2	1	1	0	1	3	1	0	0	2	1	1	0	3	1	1	0	1	0
Parabolinella sp. nov.	1	?	2	0	0	1	0	1	0	0	1	1	0	0	0	0	1	1	0	1	1	2	1	1	0	1	?	?	0	1	?	2	1	0	?	1	1	?	?	?
Parabolinella sp. nov.	1	1	3	0	0	1	0	0	1	1	1	1	0	1	0	1	1	2	1	1	0	2	1	1	0	1	3	1	0	1	2	2	1	0	?	0	0	0	?	?
Parabolinella new sp.	1	?	2	2	1	1	0	0	1	0	1	1	0	0	1	0	1	1	0	1	1	1	0	0	0	?	?	?	0	1	?	1	1	1	?	1	1	0	?	?

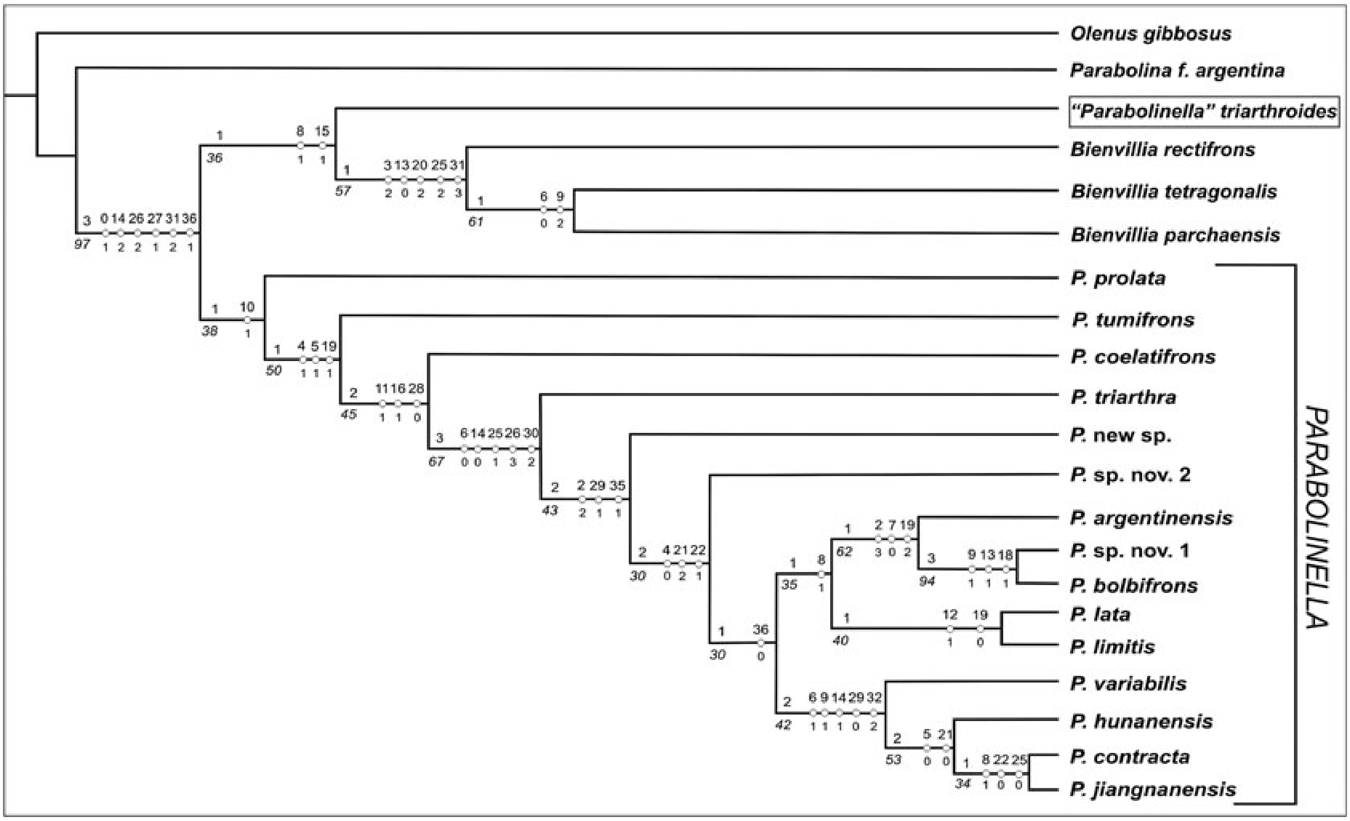

Figure 2. The single most parsimonious tree of length 176 steps. Numbers above and below white circles on branches represent characters and their corresponding states, respectively (characters according to Table 2). Numbers in bold above the nodes represent Bremer support values. Numbers in italics below the nodes represent GC Jacknife values.

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Lu and Lin, 1984; Table 1; Figure 2) constitute a monophyletic group, which is defined by a marginal furrow lacking pits (char. #5, 1→0) and a very short posterior cephalic border (char. #21, 2→0). *Parabolinella variabilis* Robison and Pantoja-Alor, 1968, from Mexico, is the sister species of this clade.

P. argentinensis; *P. bolbifrons* Fortey and Owens, 1997; *P.* sp. nov. 1; *P. lata*, and *P. limitis* form a clade with one synapomorphy: a parallel-sided glabella (char. #8, 0→1). Two subclades are distinguished within this group: the subclade including *P. argentinensis*, *P. bolbifrons* and *P.* sp. nov. 1, which are characterized by having a very divergent anterior branch of facial suture (char. #2, 2→3), a proportionately short glabella (char. #7, 1→0), and a well-developed preglabellar field (char. #17, 0→2); and the other subclade that includes *P. lata* and *P. limitis* which have a sinuous S2 furrow (char. #12, 0→1) and a smooth preglabellar field (char. #19, 1→0).

5. DISCUSSION

According to the present analysis, *Parabolinella triarthroides* is most closely related to *Bienvillia* than to other species of *Parabolinella*. These results agree with previous studies based on direct morphological comparison, which traditionally pointed out the similarities between these taxa. According to these results *P. triarthroides* should be included within the genus *Bienvillia*, and this latter genus regarded as the sister group of *Parabolinella*. The synapomorphies of the clade *Bienvillia* spp. + *P. triarthroides* include a parallel-sided glabella (char. #8, 0→1) and a short occipital ring (char. #15, 0→1). These synapomorphic characters are present in most species of *Bienvillia*, even in those ones not included in this study. However, this genus is characterized by having a poorly developed preglabellar field (char. #17, 0) (Table 2), which is not observed in *P. triarthroides* (char. #17, 0→1; Table 2; autapomorphy not shown in Figure 2). Thus, it would be necessary both to include a higher number of species of *Bienvillia* in the analysis in order to assess whether this relationship still remains, and to use a higher number of characters that could produce well-supported relationships. In view of the absence of clear synapomorphies and low support values, a traditional taxonomic treatment is adopted herein until additional data sources (more species and new characters) are examined.

Characters of *Parabolinella* that were considered as diagnostic by traditional taxonomy are regarded herein as synapomorphies of large groups of the genus. The presence of an adaxially bifurcate glabellar furrow S1, traditionally used to define *Parabolinella* (e.g. Henningsmoen, 1957; Rushton, 1988), is recovered as the only non-homoplastic synapomorphy of the genus. The presence of pits on the anterior cephalic border furrow and a striated preglabellar field (char. #5, 1 and char. #19, 1, respectively; Table 2; Figure 3) were optimized as synapomorphies in a basal position within the genus. Therefore, these features, which were considered as advanced characters by Rushton (1988), were probably acquired early in the evolution of the taxon, but later reversed to their primitive states in some derived species (e.g. the Chinese species group has an anterior marginal furrow lacking pits (char. #5, 0), and the *P. lata* and *P. limitis* clade shows a smooth preglabellar field (char. #19, 0)).

The relationships among the *Parabolinella* species obtained in the cladogram do not completely agree with those established from traditional morphological comparisons (e.g. Harrington and Leanza, 1957; Henningsmoen, 1957). In addition, the characters that support these groups do not always coincide with those found in the scientific literature (e.g. Harrington and Leanza, 1957; Henningsmoen, 1957; Rushton, 1988). This is the case, for example, of *P. triarthra*, which do not form a sister group with *P. argentinensis* and *P. limitis* in this phylogenetic hypothesis, as would be expected according to the descriptions of Harrington and Leanza (1957) and Henningsmoen (1957).

New characters with a phylogenetic signal arise from the present analysis, such as the degree of convexity of the anterior cephalic border in dorsal view (char. #4), length (exsag.) of posterior cephalic border as a proportion of length of occipital ring (char. #21), disposition of posterior branch of facial suture (char. #22), direction of eye ridge (char. #29), course of posterior margin of fixed cheeks (char. #35), and course of median part of occipital furrow (S0) (char. #36). On the other hand, some characters that have been usually used in direct morphological comparisons (glabellar shape, char. #8 and #6; glabellar segmentation, char. #9, #10, #11, #12, #13 and #14) are recovered herein as synapomorphies, whereas others (e.g. width of interocular cheeks, char. #31) seem to be not informative (Figure 2). Although the presence of a trisegmented occipital ring (char. #23) was considered as an advanced character of the group by some authors (see Rushton, 1988), it is recovered as an ambiguous character in this study (Figure 2). Depending on the optimization criterion used in the analysis (ARCTRAN or DELTRAN), it may be a plesiomorphy of *Parabolinella* + *Bienvillia* (including '*P.*' *triarthroides*) or a parallelism between species of *Parabolinella* and some species of the *Bienvillia* + '*P.*' *triarthroides* clade, respectively.

The bubble-head developments described in the preglabellar field of some *Parabolinella* specimens are not generally considered as homologous or analogous, because they are common structures in different trilobite lineages (Fortey and Owens, 1997). However, the presence of this character (char. #18, 1) shows a phylogenetic signal in this analysis, being recovered as a synapomorphy of *P. bolbifrons* and *P.* sp. nov. 1. In these two species, its position and anatomy is similar, differing only in its size.

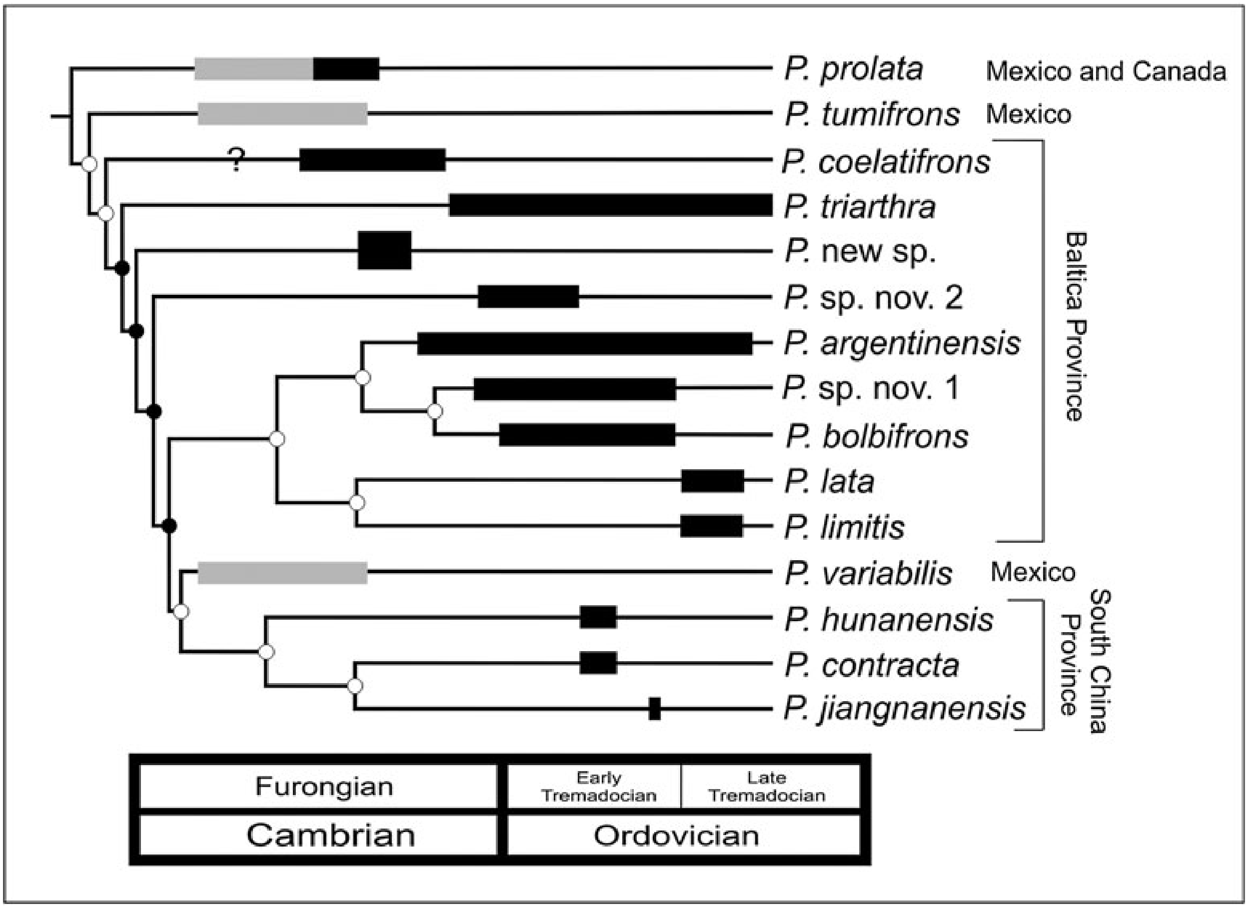

Figure 3. *Parabolinella* clade (based on the phylogenetic tree depicted in Figure 1), showing phylogenetic, stratigraphic and geographic relationships among its species. Black rectangles on branches correspond to the stratigraphic record; question mark indicates dubious records, and grey rectangles indicate stratigraphic ranges obtained by superimposing the profiles published by Robison and Pantoja-Alor (1968) and reviewed by Landing *et al.* (2007). Ranges assigned to *Parabolinella argentinensis*, *P.* sp. nov. 1 and *P.* sp nov. 2 are tentative and are under revision. On the right is indicated the palaeoprovince of each taxa. Black circles are inconsistent nodes, and white circles are consistent nodes.

Because thorax and pygidium characters are not known in several *Parabolinella* species, only a few features were used in this work, which have phylogenetic importance. They include the relative width (tr.) of the thoracic axis (tr.) (char. #25), the number of pygidial axial rings (excluding terminal piece) (char. #26), and the number of thoracic segments (char. #30). As noted by Rushton (1988), most derived species of *Parabolinella* present a high number of thoracic segments (char. #30) and a proportionately small pygidium (char. #27).

6. STRATIGRAPHIC FIT

In order to calculate indices of adjustment, a qualitative comparison of the stratigraphic fit to the tree obtained was made, pointing out those nodes that are consistent with the stratigraphic record (Figure 3). Absolute age range values could not be determined for all the species included in the study because the accurate stratigraphic position of some taxa is uncertain (e.g. *Parabolinella argentinensis*, *P. coelatifrons*, *P.* sp. nov. 2 and *P.* sp. nov. 1) or is being revised (*Parabolinella prolata*, *P. tumifrons* and *P. variabilis*; see Robison and Pantoja-Alor, 1968; Landing *et al.*, 2007).

With regard to the topology of the tree (Figure 3, based on the single most parsimonious tree shown in Figure 2), the Furongian species *P. prolata* is the basal species of *Parabolinella* (except '*P.' triarthroides*), being the oldest species of the genus (Table 1; Figure 3). Some typical characteristics of *Parabolinella* such as a pitted anterior marginal furrow and a striated preglabellar field are not present in this species, which is characterized by its tapering, anteriorly rounded glabella having only two pairs of lateral furrows. *Parabolinella tumifrons* Robison and Pantoja-Alor, 1968, restricted to the late Furongian–early Tremadocian of Mexico (Table 1; Figure 3) is younger than *P. prolata*, so this node is consistent with the stratigraphic record. *P. tumifrons* shares some morphological characteristics with *P. prolata*, such as similar glabellar segmentation and the absence of

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prominent eye ridges. In addition, the late Furongian age of *P. coelatifrons* is consistent with the tree obtained. As in the other basal species, the glabellar segmentation of *P. coelatifrons* is not conspicuous, consisting of two shallow furrows S1 and S2, and a very faint S3 which is visible only in well-preserved specimens.

The presence of three pairs of glabellar furrows and prominent eye ridges are ancestral conditions in Olenidae, as shown in *Olenus* (Table 2). However, basal species of *Parabolinella* are characterized by having only two pairs of glabellar furrows and faint or absent ocular ridges in the adult stage. In younger strata, derived species show an increase in the number of glabellar furrows, presenting three or four well-developed pairs in the holaspid stage, as well as visible ocular ridges.

Species from China (*P. hunanensis*, *P. contracta*, *P. jiangnanensis*), as well as *P. argentinensis*, *P.* sp. nov. 1, *P. bolbifrons*, *P. lata*, and *P. limitis* have a good stratigraphic fit (Figure 3). The latter group has a Furongian–Tremadocian record and is characterized by a parallel-sided glabella and a conspicuous glabellar segmentation consisting of three or more glabellar furrows (Figure 2; Table 2; Appendix 1). Two subclades are recognized in this group. In the first one, the latest Cambrian *P. argentinensis* (Table 1; Figure 3) shows a good fit in respect to its sister group (*P. bolbifrons* + *P.* sp. nov. 1), which has an early Ordovician occurrence (Table 1; Figure 3). Thus, the acquisition of a preglabellar boss is a derived character that is present in the species with the most recent records within the group. The other subclade (*P. lata* and *P. limitis*) is known from the late Tremadocian (Table 1; Figure 3). This derived group is characterized by a smooth preglabellar field, a feature that is regarded herein as a reversal. Finally, the type species *P. limitis* has a derivative position in the tree obtained, which coincides with its stratigraphic occurrence.

On the other hand, the positions of some species studied are inconsistent with the stratigraphic record. *Parabolinella triarthra* and *P.* sp. nov. 2 show basal positions in the tree, but their stratigraphic ranges are above that of *Parabolinella* new sp. from Scandinavia, which has a derived position in the clade (Table 1; Figure 3). Since the exact stratigraphic ranges of some taxa (*P. argentinensis*, *P.* sp. nov. 2 and *P.* sp. nov. 1) are under revision, some of these differences could be diminished in the future. In addition, it is important to note that several *Parabolinella* species have their first appearance within a relatively short time span, a complicating factor when discussing some evolutionary aspects of the genus.

7. PALAEOGEOGRAPHY

The resulting tree shows a high degree of correspondence with global late Furongian and early Ordovician palaeogeography (Figures 3, 4). With the exception of *Parabolinella variabilis* (sister of the species from China), distributions of the *Parabolinella* clades coincide with the trilobite provinces defined for the Cambrian–Ordovician transition (Baltica, Southeast China, North China, and North America; see Shergold, 1988). For example, the distribution of the monophyletic group: (*P. hunanensis*, (*P. contracta*, *P. jiangnanensis*)) is coincident with the Southeast China Province, whereas the occurrence of a large group composed of *P. coelatifrons*, *P. triarthra*, *P.* new sp. (Scandinavia), *P.* sp. nov. 2, *P. argentinensis*, *P.* sp. nov. 1, *P. bolbifrons*, *P. limitis*, and *P. lata* shows a high correspondence with high latitude regions of the Baltic Province *sensu* Shergold (1988). On the other hand, the most basal species of the genus (*P. prolata* and *P. tumifrons*) are from Canada and Mexico.

Most species of *Parabolinella* were described from poorly oxygenated to oxygen deficient outer shelf facies. *Parabolinella prolata*, from the Tiñu Formation (late Cambrian age, *Cordylodus andresi* Zone, *Cordylodus proavus* Zone) of Mexico and the Rabbitkettle Formation (latest Cambrian age, *Missisquoia depressa* Subzone of the *Parabolinella* Zone) of the Mackenzie Mountains, Canada, is the oldest and most basal species (with only one autapomorphy) in the genus, whereas the other plesiomorphic species, *P. tumifrons*, is known only from the Tiñu Formation. Thus, the genus may have originated in the Oaxaca region, Mexico, from deep, relatively cold water sites (Landing *et al.*, 2007). *P. prolata* would have rapidly dispersed to northern Laurentia, occupying a warmer-water environment dominated by mixed, carbonate-clastic deposition and normal oxygen conditions (Lee and Chatterton, 2007).

Similarly, *Parabolinella* would have dispersed into different parts of the Baltica Province in the latest Cambrian, reaching cold areas at high latitudes (Baltica, Avalonia and western Gondwana). Late in the Tremadocian, the genus is particularly diverse in these regions, which include highly dysoxic successions as the *Alum Shales* and equivalents. In addition, lower Tremadocian taxa from South China may have evolved from the original Mexican stock, giving rise to a set of species (e.g. *P. variabilis*) closely similar to *P. prolata* and *P. tumifrons*.

8. CONCLUSIONS

The monophyly of *Parabolinella* is considered doubtful because '*Parabolinella' triarthroides* is more closely related to species of *Bienvillia* than those of *Parabolinella*. '*Parabolinella' triarthroides* would have to be moved to *Bienvillia* in order to preserve the monophyly of *Parabolinella*, but further studies are being undertaken aiming to confirm these relationships.

The genus *Parabolinella* is defined by a single non-homoplastic synapomorphy: presence of a bifurcated glabellar furrow S1.

Characters usually regarded as diagnostic features of *Parabolinella* by traditional taxonomy were recovered herein as synapomorphies of major groups of the genus: presence of an adaxially bifurcated S1 furrow, a pitted cephalic anterior border furrow, and a striated preglabellar field.

New phylogenetically important characters emerge from this analysis: degree of convexity of anterior cephalic border, length

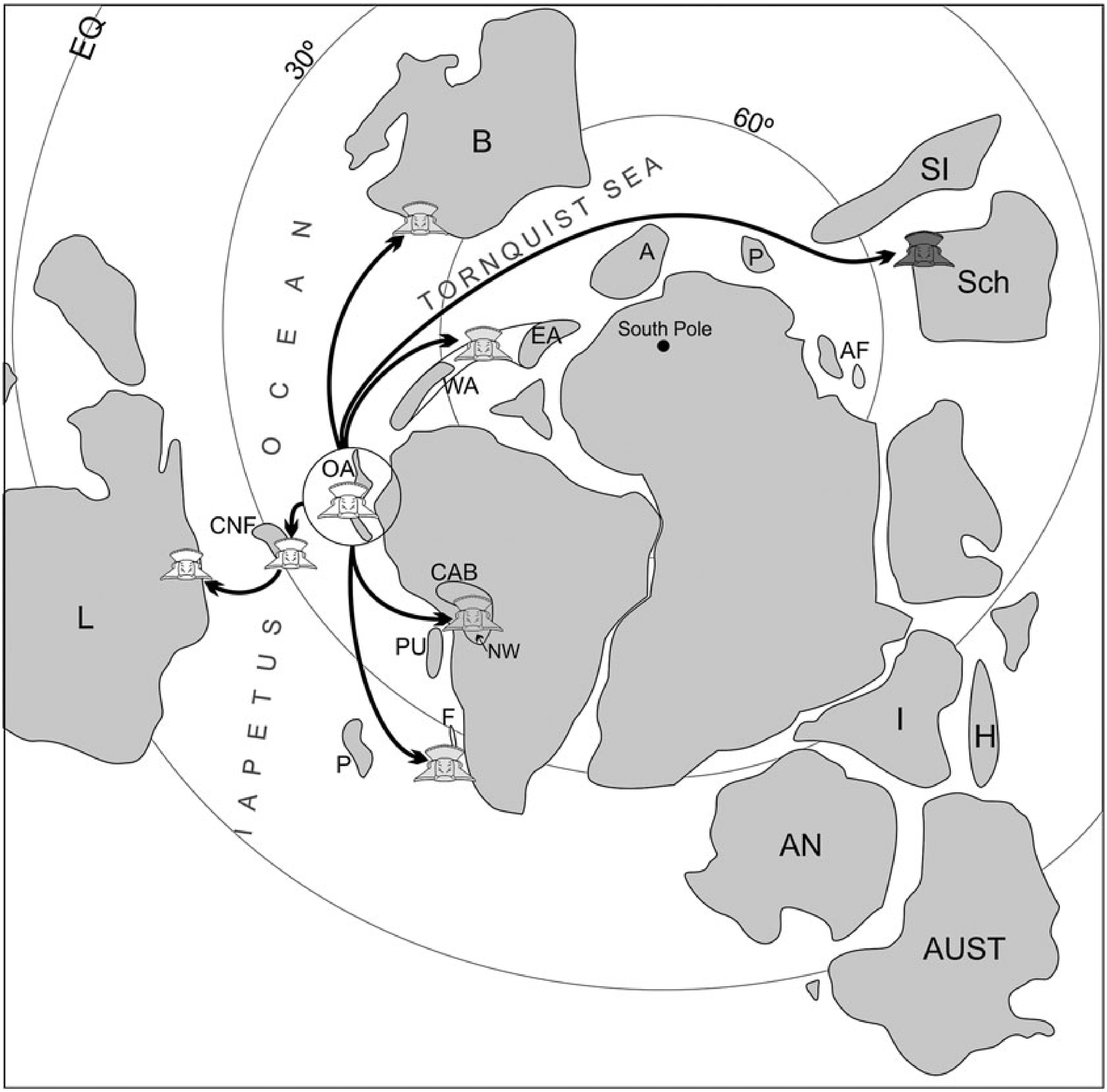

Figure 4. Early Ordovician (480 Ma) palaeogeographic reconstruction, showing *Parabolinella* genus distribution. Continental distribution modified from Cocks and Torsvik (2002). The circle marks the potential place of origin of the genus and the arrows show their possible dispersion. From this site of origin, the genus would have dispersed to other regions of the Baltica Province, western margin of Gondwana, Avalonia and Baltica (grey cranidia) and finally, to the South China Province (dark grey cranidia), which have a younger age. A: Armorican terrane, AF: Alpine terrane, AN: Antarctica, AUST: Australia, B: Baltica, CAB: Central Andean Basin, CNF: Central Newfoundland terrane, EA: Eastern Avalonia, F: Famatina, H: Himalayan terrane, I: India, L: Laurentia, NW: Northwestern Basin, OA: Oaxaca (Mexican terrane), P: Precordillera terrane, PU: Western Puna, Sch: South China, SI: Sibumasu, WA: Western Avalonia.

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of posterior cephalic border, disposition of posterior facial suture, direction of eye ridge, course of posterior margin of fixed cheeks, and course of median part of occipital furrow (S0).

The obtained tree is partially consistent with the stratigraphic record. On the other hand, the relative positions of the different species in the tree show a high degree of correspondence with global Furongian–early Ordovician palaeogeography. *Parabolinella* may have originated in deep, relatively cold water facies from the Oaxaca region, Mexico. From this site, it dispersed along the outer shelf facies of the latest Cambrian–Tremadocian in the Baltica Province and the earliest Tremadocian of South China.

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APPENDIX: CHARACTERS AND THEIR CORRESPONDING STATES USED IN THE PHYLOGENETIC ANALYSIS

0. Anterior margin of cranidium, medially. 0: transverse; 1: markedly concave forward.
1. Length of cephalon (sag.) as proportion of maximun width of cephalon (trans.). 0: short [0.3-0.49]; 1: half as long as wide or longer (≥ 0.5).
2. Condition of anterior branch of facial suture, measured as the angle formed by this and sagittal axis. 0: convergent ($\alpha \leq -5$º); 1: subparallel (10º $> \alpha > -5$ º); 2: moderately divergent (30º $> \alpha >$ 10º); 3: very divergent ($\geq$ 30º).
3. Positions of palpebral lobes. 0: at S2; 1: anterior to S2; 2: posterior to S2.
4. Degree of convexity of anterior cephalic border, in dorsal view. 0: strongly convex; 1: weakly convex.
5. Anterior border furrow. 0: without pits; 1: with pits.
6. Shape of anterior termination of glabella. 0: medially concave; 1: rounded.
7. Length of glabella (sag., excluding occipital ring) as proportion of length of cephalon (sag.). 0: short [0.5-0.6]; 1: long (>0.6).
8. Shape of glabella. 0: tapers forward; 1: approximately parallel-sided; 2: expands anteriorly.
9. Number of visible pairs of lateral glabellar furrows. 0: 4; 1: 3; 2: 2.
10. Condition of preoccipital furrow (S1). 0: simple; 1: adaxially bifurcate.
11. Shape of S1 furrow. 0: straight or simply curved; 1: sigmoid.
12. Shape of S2 furrow. 0: straight; 1: sinous.
13. Length of S2 furrow. 0: equal to S1; 1: shorter than S1.
14. Condition of S3 furrow. 0: furrows; 1: slits very short; 2: faint depressions.
15. Length of occipital ring (sag., from midpoint of S0) as a proportion of the length of the glabella (sag., excluding occipital ring). 0: long (> 0.25); 1: short (≤ 0.25).
16. Length of preglabellar field (sag.) as proportion of length of preglabellar area (sag.). 0: preglabellar field occupies a small part of preglabellar area (≤ 0.7). 1: preglabellar field occupies a higher proportion of preglabellar area (> 0.7).
17. Length of preglabellar field (sag.) as propotion of length of occipital ring (sag.). 0: short [0–0.8]; 1:

moderately long [0.8-1.5); 2: long [1.5-3); 3: very long (≥3).

18. Elevation of preglabellar field. 0: confluent with cheeks; 1: raised to form preglabellar boss.
19. Preglabellar field. 0: smooth; 1: striated; 2: crossed by furrows.
20. Width of fixed cheek posterior to eyes (trans.) as proportion of width of occipital ring (trans.) 0: wide (>0,85); 1: moderately wide [0.6-0.85]; 2: narrow (<0.6).
21. Length of posterior cephalic border as proportion of length of occipital ring. 0: very short (<0.4); 1: short [0.4-0.7]; 2: long (>0,7).
22. Posterior branch of facial suture. 0: straight or slightly sinuous; 1: very sinuous.
23. Occipital ring. 0: simple; 1: trisegmented.
24. Width of glabella (trans.) at base as proportion of length of glabella (sag. excluding occipital ring). 0: approximately equals [0.9-1.1]; 1: longer than width (<0.9), 1: wider than long (>1.1).
25. Width of thoracic axis (trans.) compared to width of whole segment (tr., excluding pleural spines) on anterior segments. 0: very narrow (< 1/3); 1: narrow (=1/3); 1: wide (>1/3).
26. Number of segments (excluding terminal piece) in pygidial axis. 0: ≥3; 1: 2; 3: 1.
27. Length of pygidium (sag.) as proportion of maximun width of pygidium (trans.). 0: long (> 0.4); 1: short [0.4-0.2].
28. Eye ridges. 0: present, 1: absent.
29. Direction of eye ridges. 0: eye-ridges run transversely; 1: eye-ridges run backwards and outwards obliquely.
30. Number of thoracic segments. 0: less than or equal to 15; 1: between 16 and 20; 2: 21 or more.
31. Width of interocular cheeks as proportion of width of glabella at eye line. 0: wide (>0.45); 1: moderately wide [0.45-0.3); 2: narrow [0.3-0.2); 3: very narrow (≤ 0.2).
32. Length of palpebral lobe as proportion of the length of glabella. 0: median (>0.35); 1: small [0.35-0.2]; tiny (<0.2).
33. Occipital node.
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; 2: absent.
39. Definition of posterior margin of pygidial axis. 0: well defined; 1: poorly defined.

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