Systematic, morphometric and palaeobiogeographic study of *Blainia gregaria* Walcott, 1916 (Trilobita, Ptychopariida), Middle Cambrian of the Precordillera of western Argentina

OSVALDO L. BORDONARO[1]*, BRIAN R. PRATT[2] and VIRGINIA ROBLEDO[3]

[1]*Centro Científico Tecnológico, IANIGLA, Parque General San Martín, 5500 Mendoza, Argentina*
[2]*Department of Geological Sciences, University of Saskatchewan, Saskatoon, Saskatchewan, S7N 5E2, Canada*
[3]*Instituto Superior del Profesorado San Pedro Nolasco, Universidad del Aconcagua, Mendoza, Argentina*

The ptychoparioid trilobite *Blainia gregaria* Walcott, 1916 is described for the first time from the late middle Cambrian (Series 3) of the Argentine Precordillera. It occurs commonly in the upper part of La Laja Formation, a carbonate platform succession that crops out in the Precordillera Oriental of San Juan where it reaches a thickness of some 600 m. Sections were sampled on cerro Tres Marías in Sierra de Marquesado and in quebrada de Zonda at the northern termination of Sierra Chica de Zonda. More than 1200 specimens were recovered from 22 stratigraphic levels over a thickness of 155 m, located in the uppermost 15 m of the Soldano Member, the approximately 100 m thick Rivadavia Member, and in the lower 40 m of the Juan Pobre Member. Our biometric study dealt with 205 cranidia and 365 pygidia from cerro Tres Marías. Measured dimensions of a subset of this collection provide bivariate datasets that in some characters show broad scatter plots and relatively low linear correlation coefficients, indicative of rather wide intraspecific morphological variation. Six morphotypes (three cranidial and three pygidial), recognized mainly on the basis of shape, occur together in the same collections. This evidence for an unusually high degree of variability leads to a proposed synonymy of some 30 previously named species in North America belonging to two genera, *Blainia* Walcott, 1916 and *Glyphaspis* Poulsen, 1927, the latter considered a junior synonym. The biogeographic distribution of *B. gregaria*, as redefined here, shows that it was an endemic Laurentian species that inhabited the inner parts of the carbonate platform that rimmed the craton and mantled portions of its interior. Its presence in western Argentina is further evidence for the very close faunal relationship between the Precordilleran terrane, known as Cuyania, and Laurentia during the Cambrian. Copyright © 2012 John Wiley & Sons, Ltd.

1. INTRODUCTION

Palaeontologists have struggled for almost two centuries to appreciate morphological variation and incorporate it in their definition of fossil species. For much of this time, a typological thinking was dominant, in that a rather narrow latitude was allowed, especially with extinct taxonomic groups that could not be well informed by living analogues. This often resulted in the naming of a great number of species on the basis of small differences exhibited by a few specimens in unique or scattered collections. Individual preferences of palaeontologists also played a role, causing some fossil groups to experience 'splitting' more than others. The modern tendency is to accept some degree of intraspecific variation, depending of course on the taxonomic group. Commonly, however, the amount of variation allowed is subjective. This can be alleviated where morphometric analysis of large collections can show a continuum of variability during growth. All the same, it is impossible for most fossil deposits to separate putative variation within a single population from that exhibited by successive populations as a whole. Moreover, variation, if present, might have been more pronounced in one taxon than another, even related, species.

Our study of La Laja Formation (Middle Cambrian, Series 3) of the Precordillera of San Juan, Argentina (Pratt and Bordonaro, 2007; Bordonaro *et al.*, 2008; Bordonaro and Pratt, 2008, unpublished data) permitted the recovery of abundant specimens of a distinct but generalized ptychoparioid trilobite taxon from a limited stratigraphic interval in two closely spaced sections. This large collection offers the opportunity to investigate the nature of possible intraspecific variation by means of standard description coupled with a

*Correspondence to: O. L. Bordonaro, Centro Científico Tecnológico, IANIGLA, c.c. 131, Parque General San Martín, 5500 Mendoza, Argentina.
E-mail: obordona@mendoza-conicet.gov.ar

simple bivariate morphometric analysis. The specimens exhibit a similarity to species hitherto placed in two genera, *Blainia* Walcott, 1916 and *Glyphaspis* Poulsen, 1927, known from many localities in North America. Our results suggest that the trilobites belong to a single species, *Blainia gregaria* Walcott, 1916, that exhibits an unusually large degree of morphological variation. Consequently, we are able to propose a synonymy of some 30 species belonging to these two genera. Their occurrences in La Laja Formation further links the Cambrian trilobite fauna of the Precordillera with that of Laurentia.

2. STRATIGRAPHIC SETTING

La Laja Formation (Borrello, 1962; emended by Bordonaro, 1980) comprises the middle Cambrian (Series 3) interval of a broad, west-facing carbonate platform succession of early Palaeozoic age that constitutes the core of the Precordilleran terrane (Keller, 1999; Bordonaro, 2003). It is exposed throughout the Precordillera Oriental of San Juan where it reaches a stratigraphic thickness of slightly more than 600 m (Figure 1). Baldis and Bordonaro (1981) defined four units, El Estero, Soldano, Rivadavia and Juan Pobre members. These consist of a suite of limestone lithofacies deposited in the interior part of the platform (Pratt and Bordonaro, 2007; Gomez *et al.*, 2007). Our study is based on two stratigraphic sections, one located on cerro Tres Marías at the northern end of Sierra de Marquesado, and the other mainly along the southern wall of quebrada de Zonda in the northern termination of Sierra Chica de Zonda. These sections are 10 km apart.

3. MATERIALS AND METHODS

Specimens of *Blainia gregaria* Walcott, 1916 were collected in the upper 15 m of the Soldano Member, sporadically through the 100 m thick Rivadavia Member, and in the lower 40 m of the Juan Pobre Member. The collection of 1202 specimens (570 from cerro Tres Marías and 632 from quebrada de Zonda) comprises 563 pygidia and 639 cranidia. Measurements were made on the 205 cranidia and 365 pygidia from cerro Tres Marías recovered from 22 stratigraphic levels over a thickness of 155 m. Most specimens came from gently weathered surfaces of thin-bedded, slightly argillaceous lime mudstones in the basal few metres of the Juan Pobre Member; no articulated specimens were found. For comparison, co-occurring pygidia belonging to *Kochaspis coosensis* Resser, 1938 were also collected. Specimens are not flattened by compaction or tectonically distorted. Measurements were taken with a digital caliper, and reliable values were obtained from 88 cranidia and 104 pygidia. A series of widths and lengths of cranidial and pygidial features were measured in holaspides of various sizes (Tables 1 and 2).

Bivariate analysis of these dimensions examines relationships between pairs of these features during growth. Bivariate plots accompanied by the linear, or Pearson's, correlation coefficient (R) and the coefficient of determination (R^2) show the relationships of morphometric proportions (e.g. Hammer and Harper, 2006). The former is a statistical index that measures the strength of the linear relationship between two quantitative variables and is independent of their scale. Values equal to or nearly equal to 0 indicate little or no linear correlation, while values around −1 indicate a negative or inverse correlation of dimensions, and those around 1 indicate a positive correlation. The coefficient of determination shows the proportion of variance that can be explained by the linear relationship. A value of 0 indicates no correlation while a value of 1 indicates complete correlation.

When the Pearson coefficient is high (greater than 0.8) it indicates that growth was the principal control on the variation among the measured dimensions (e.g. Labandeira and Hughes, 1994). If it describes a straight line from the origin with a slope of 1 this is isometric growth, whereas if the slope is greater or less than 1 then this is allometric growth. A low correlation coefficient (less than 0.8) indicates that the control exerted by growth on the dimensions was more variable. It is important to note that the morphological continuity of a population is a positive sign of the integrity of a species (Labandeira and Hughes, 1994; Hughes, 1994a, b; Melzak and Westrop, 1994; Chirivella Martorell *et al.*, 2003; Dies and Gozalo, 2004). In addition, bivariate analysis can be used to calculate the effects of tectonic deformation on fossils (Hughes and Jell, 1992).

In addition, visual (non-statistical) comparison focused on a number of characters that were not measured. With cranidia, this was the nature of the preglabellar field, while with pygidia, it was the outline and shape of the posterior border.

4. MORPHOMETRIC ANALYSIS

In the bivariate plots of the various dimensions measured (Figures 2A–2F) the slope of the lines indicates more or less an isometric increase in the size of the pygidium and glabella in the holaspid stages, whereas the sizes of the frontal area and palpebral lobe are somewhat allometric. Pygidial length versus width for all specimens (Figure 2A) has a high Pearson's coefficient and a high coefficient of determination (R = 0.95 and R^2 = 0.81) indicating that these aspects vary together with growth, as expected. Comparison of length of the frontal area versus its width gives even higher coefficients (R = 0.95 and R^2 = 0.91; Figure 2B), as does glabellar length versus cranidial length (R = 0.97 and R^2 = 0.95;
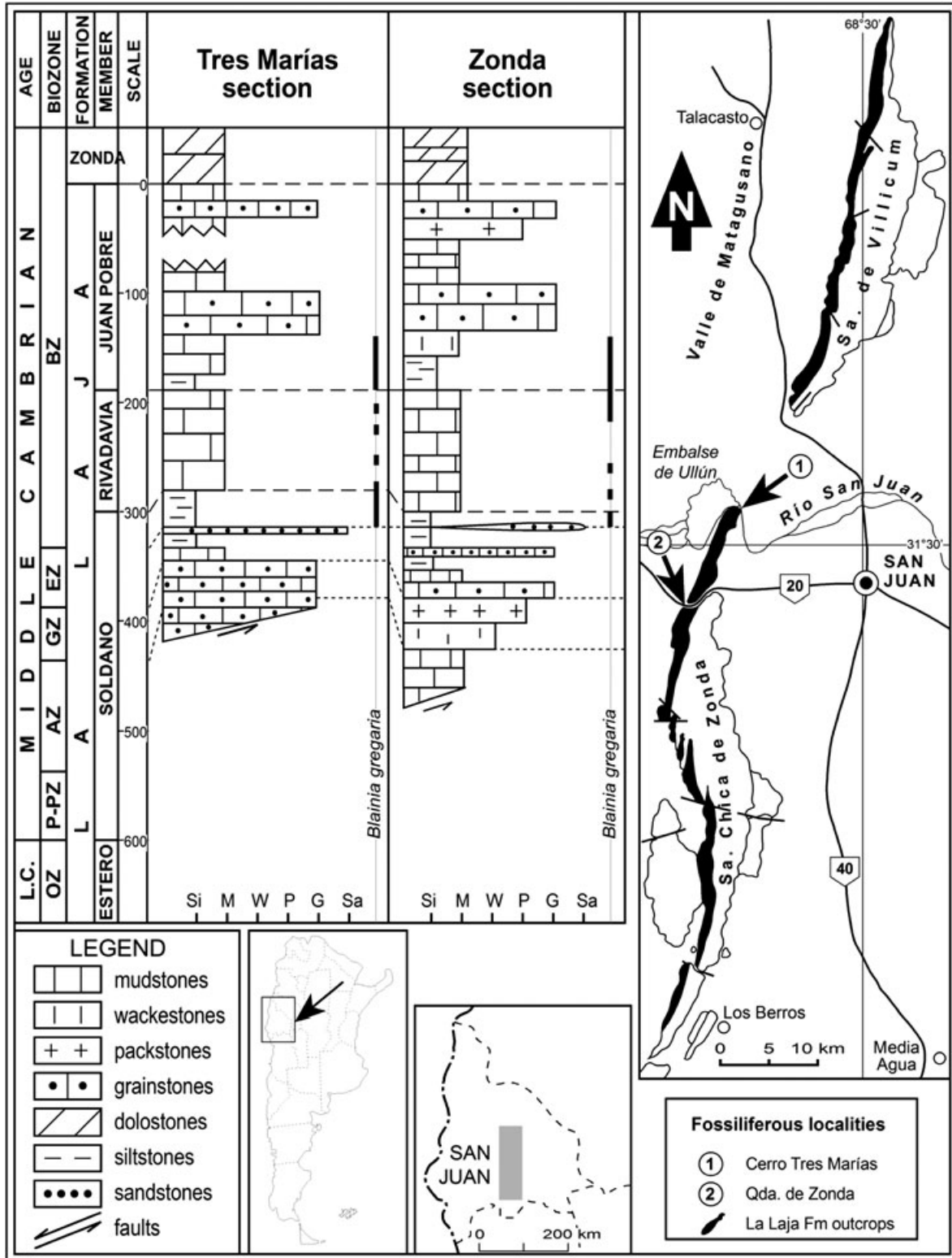
Figure 1. Stratigraphic sections of La Laja Formation at cerro Tres Marías and in quebrada de Zonda at the northern tip of Sierra Chica de Zonda, and location map of these sections west of San Juan. The subdivisions of La Laja Formation are those erected by Bordonaro (1980). The stratigraphic distribution of *Blainia gregaria* is shown by the line to the right of each profile (solid = collected; dotted = inferred). Tight recumbent folds in the Soldano Member in quebrada de Zonda have been approximately restored. Biostratigraphic zonation for Laurentia: OZ = *Olenellus* Zone; P–PZ = *Plagiura–Poliella* Zone; AZ = *Albertella* Zone; GZ = *Glossopleura* Zone; EZ = *Ehmaniella* Zone; BZ = *Bolaspidella* Zone. L.C. = Lower Cambrian.

Table 1. Dimensions of cranidial characters (in millimetres) of specimens of *Blainia gregaria*. Abbreviations: cl = cranidial length; pll = palpebral lobe length; fcw = fixed cheek width; fal = frontal area length; faw = frontal area width; gl = glabellar length; gw = glabellar width

IANIGLA-PI	Cranidium			Frontal area			Glabella		
	pll	fcw	c l	fal	faw	fal/faw	gl	gw	gl/gw
0004				10.00	3.50	0.35			
0049				10.20	3.00	0.30			
0268				9.20	3.50	0.34			
0284				10.00	3.40	0.34			
0284′				9.30	2.80	0.30			
1841			10.94	8.91	3.75	0.42	7.19	5.09	1.41
1842	4.53	2.66	10.67	10.85	3.28	0.30	7.39	4.76	1.55
1843	2.91	1.67					6.32	3.61	1.75
1844				11.34	3.97	0.35			
1845	1.67	1.03		3.57	1.51	0.42			
1846			5.71	5.22	1.70	0.33	4.01	2.38	1.68
1850	1.84	1.31					2.71	1.90	1.43
1853				4.64	1.50	0.32			
1866							7.04	3.87	1.82
1867	2.13	1.43	6.57	5.74	2.17	0.38	4.40	2.38	1.85
1871 (a)	3.46	1.84	8.24	7.97	2.20	0.28	6.04	3.66	1.65
1878	6.10	3.49	10.77	12.24	2.39	0.20	8.38	7.48	1.12
1880	2.11	1.39	6.01	3.14	2.24	0.71	3.77	2.79	1.35
1881	4.04	2.07							
1887	1.47	1.16		4.73	1.92	0.41			
1888	2.36	2.07					3.95	3.16	1.25
1989	1.60	0.68					1.85	1.57	1.18
1890	2.20	1.60					3.71	1.78	2.08
1900	3.81	2.20							
1906				13.04	4.09	0.31			
1909	0.69	0.29					1.33	0.74	1.80
1915	1.58	1.12							
1921							6.27	5.63	1.11
1926	3.25	1.34							
1930	1.75	1.04					2.54	1.77	1.44
1931							2.13	1.63	1.31
1932	1.54	1.08							
1964							6.23	4.16	1.50
1937	1.23	0.94							
1938							1.98	1.08	0.00
1939	2.65	1.92							
1940				4.34	1.88	0.43			
1943			5.29	4.39	1.44	0.33	3.85	2.20	1.75
1946	2.97	1.12							
1948							3.40	1.94	1.75
1949	2.76	1.65		7.46	2.39	0.32			
1953	3.13	1.93	7.93	9.17	1.77	0.19	6.16	4.30	1.43
1954	4.46	2.09							
1955	3.53	1.50	9.11	7.70	2.90	0.38	6.21	3.37	1.84
1956	2.44	1.57							
1957	2.96	1.81							
1958	3.49	2.90							
1960	3.22	1.58							
1962	3.37	1.98							
1975	2.35	1.75							
1976	1.21	0.99		3.25	0.90	0.28			
1980				3.88	1.08	0.28			
1981			1.94	6.49	1.37	0.21	0.57	2.65	0.22
1982	1.99	1.46					3.76	2.47	1.52
1983	1.48	1.68		5.66	1.39	0.25			

(Continues)

Table 1.   (Continued)

IANIGLA-PI	Cranidium			Frontal area			Glabella		
	pll	fcw	c l	fal	faw	fal/faw	gl	gw	gl/gw
1984	1.78	1.44		3.27	1.10	0.34			
1993	3.17	2.02							
1996	1.37	1.22					3.07	1.83	1.68
1997							4.06	3.26	1.25
1998	3.07	2.20					5.79	3.53	1.64
1999			6.5	6.36	1.90	0.30	4.60	3.73	1.23
2000	1.82	1.16					3.63	1.97	1.84
2001	3.2	2.01							
2002	1.77	1.31	4.6	4.04	1.39	0.34	3.21	2.02	1.59
2003				4.14	1.66	0.40			
2004	1.48	0.89					2.68	1.77	1.51
2005				3.61	1.55	0.43			
2011	1.10	0.72							
2012	2.34	1.34	6.96	6.41	2.27	0.35	4.69	3.39	1.38
2020	1.35	0.91	3.88	3.97	1.31	0.33	2.57	1.70	1.51
2021	2.41	1.33							
2028	2.36	1.35	5.97	7.45	1.35	0.18	4.62	3.46	1.34
2029	3.94	2.22	9.59	11.38	3.96	0.35			
2030	2.22	1.58					2.62	2.54	1.03
2031	1.71	0.93					2.48	2.16	1.15
2032	1.02	0.49					1.51	0.85	1.78
2033							5.44	4.08	1.33
2034	3.87	2.73					5.80	3.61	1.61
2035	1.13	0.85		2.47	0.75	0.30	1.81	1.41	1.28
2036	2.05	1.48					3.28	2.63	1.25
2037	3.43	2.16					4.56	3.39	1.35
2040	4.21	1.91	7.9	9.13	2.33	0.26	5.57	4.44	1.25
2041	1.81	1.02	4.15	3.48	0.91	0.26	3.24	1.78	1.82
2061	1.44	0.75	3.39	3.76	0.85	0.23	2.54	1.55	1.64
2062			8.83	7.92	2.54	0.32	6.29	3.48	1.81
2063	3.07	2.11		7.64	3.13	0.41			
2064	2.29	1.60							
2065	2.10	1.24	5.73	4.89	1.75	0.36	3.98	1.89	2.11

Figure 2C). Similarly, specimens attributed to *Glyphaspis tetonensis* Resser, 1938 by Melzak and Westrop (1994), which we consider a synonym of *B. gregaria* (see below), show a high coefficient of the length of the preglabellar field versus cranidial length. However, comparison of other cranidial dimensions (Figures 2D–2E) gives somewhat lower coefficients: length versus width of glabella (R = 0.88 and R^2 = 0.77); and length of the palpebral lobe versus length of the glabella (R = 0.86 and R^2 = 0.75). These values indicate a relatively wide intraspecific variation of some attributes but not others.

Besides the variation in measured parameters, three end-member cranidial morphotypes are identified on the basis of intergrading differences in the preglabellar field (Figure 3). Type 1 exhibits a relatively long frontal area with broad, shallow anterior border furrow that widens medially towards the anterior glabellar furrow, forming a plectrum-like depression. Type 2 has a slightly shorter frontal area with moderately short anterior border furrow exhibiting a gently curved medial

inflection. Type 3 shows a moderately short frontal area with an evenly curved, shallow anterior border furrow.

Of the three pygidial morphotypes (Figure 4), type 1 is sub-elliptical to semi-circular in outline and lacks a median indentation. Type 2 has a sub-pentagonal outline and a shallow median indentation, while type 3 is semi-circular to sub-pentagonal in outline and has a deep median indentation. It is not possible to assign each to a specific cranidial morphotype because all these sclerites occur together, and articulated specimens are lacking.

For each of three pygidial morphotypes comparison of length versus width (Figure 2F) gives individually high correlation coefficients and coefficients of determination: R = 0.91 to 0.94 and R^2 = 0.83 to 0.89. The coincidence of these regression lines is evidence that the three morphotypes belong to the same species, despite the difference in the shape of the posterior border, while pygidia of *Kochaspis coosensis*, which exhibit a pair of large posteriorly directed marginal spines (Figures 6.16, 6.17), produces a different

Table 2. Dimensions of pygidial characters (in millimetres) of specimens of *Blainia gregaria*. Abbreviations: pl = pygidial length; pw = pygidial width

| IANIGLA-PI	Pygidium			IANIGLA-PI	Pygidium		
	pl	pw	pl/pw		pl	pw	pl/pw
1848	11.61	11.36	1.02	1985	8.09	15.30	0.53
1864	5.32	9.47	0.56	1986	7.22	10.34	0.70
1865	4.60	6.88	0.67	1987	1.96	2.12	0.92
1868	6.32	9.51	0.66	1988	5.74	10.29	0.56
1869	8.71	15.74	0.55	1989	5.67	7.69	0.74
1870	9.63	14.91	0.65	1990	4.63	8.64	0.54
1871(b)	5.75	9.13	0.63	1991	6.64	10.37	0.64
1873	9.65	12.73	0.76	1992	13.94	24.45	0.57
1874	4.88	8.61	0.57	1994	6.14	5.65	1.09
1875	8.05	14.87	0.54	2006	4.41	6.14	0.72
1876	6.06	10.77	0.56	2007	3.19	5.57	0.57
1877	6.51	13.09	0.50	2008	4.06	5.83	0.70
1879	5.34	11.11	0.48	2009	7.31	11.96	0.61
1892	8.80	9.14	0.96	2010	5.32	8.98	0.59
1894	8.47	13.38	0.63	2013	3.63	6.11	0.59
1896	6.95	12.25	0.57	2014	6.01	10.21	0.59
1898	4.25	8.56	0.50	2015	2.71	4.96	0.55
1899	7.06	11.80	0.60	2016	5.46	6.84	0.80
1902	5.50	10.92	0.50	2018	9.57	15.30	0.63
1903	2.69	4.29	0.63	2019	3.50	6.02	0.58
1904	2.86	4.44	0.64	2022	7.45	9.86	0.76
1905	5.83	10.42	0.56	2023	3.70	6.08	0.61
1908	9.36	14.66	0.64	2024	3.32	5.92	0.56
1911	2.02	3.44	0.59	2025	5.28	9.36	0.56
1913	5.43	9.55	0.57	2026	4.53	8.47	0.53
1914	2.45	3.50	0.70	2027	8.18	11.57	0.71
1916	1.99	3.36	0.59	2038	14.01	22.21	0.63
1917	3.02	5.40	0.56	2039	5.58	9.69	0.58
1918	1.80	3.66	0.49	2042	4.13	8.10	0.51
1919	2.51	4.44	0.57	2043	6.37	11.27	0.57
1920	4.55	8.02	0.57	2044	4.86	9.16	0.53
1922	8.72	9.48	0.92	2045	7.62	12.44	0.61
1924	2.88	3.96	0.73	2046	8.81	15.55	0.57
1935	3.97	5.35	0.74	2047	4.61	8.21	0.56
1936	4.97	7.21	0.69	2048	7.79	12.22	0.64
1941	4.15	6.21	0.67	2049	7.73	11.99	0.64
1944	4.07	7.62	0.53	2050	5.63	10.56	0.53
1945	2.96	3.82	0.77	2051	7.03	8.35	0.84
1950	5.33	8.25	0.65	2052	5.85	8.14	0.72
1951	5.31	8.31	0.64	2053	6.89	10.33	0.67
1952	7.01	11.30	0.62	2054	4.16	7.78	0.53
1963	5.84	9.31	0.63	2055	3.40	6.26	0.54
1964	3.69	6.59	0.56	2056	4.45	6.79	0.66
1965	5.99	12.36	0.48	2057	4.19	8.20	0.51
1967	3.76	5.22	0.72	2058	6.28	6.51	0.96
1968	5.31	8.70	0.61	2059	7.30	7.09	1.03
1970	3.45	6.31	0.55	2066	5.36	7.50	0.71
1971	4.72	7.38	0.64	2067	5.63	9.65	0.58
1973	3.36	6.17	0.54	2068	4.66	9.27	0.50
1974	3.51	6.01	0.58	2069	8.57	16.64	0.52
1978	4.36	7.26	0.60	2070	4.74	5.38	0.88
1979	1.40	3.68	0.38	2071	5.94	7.87	0.75
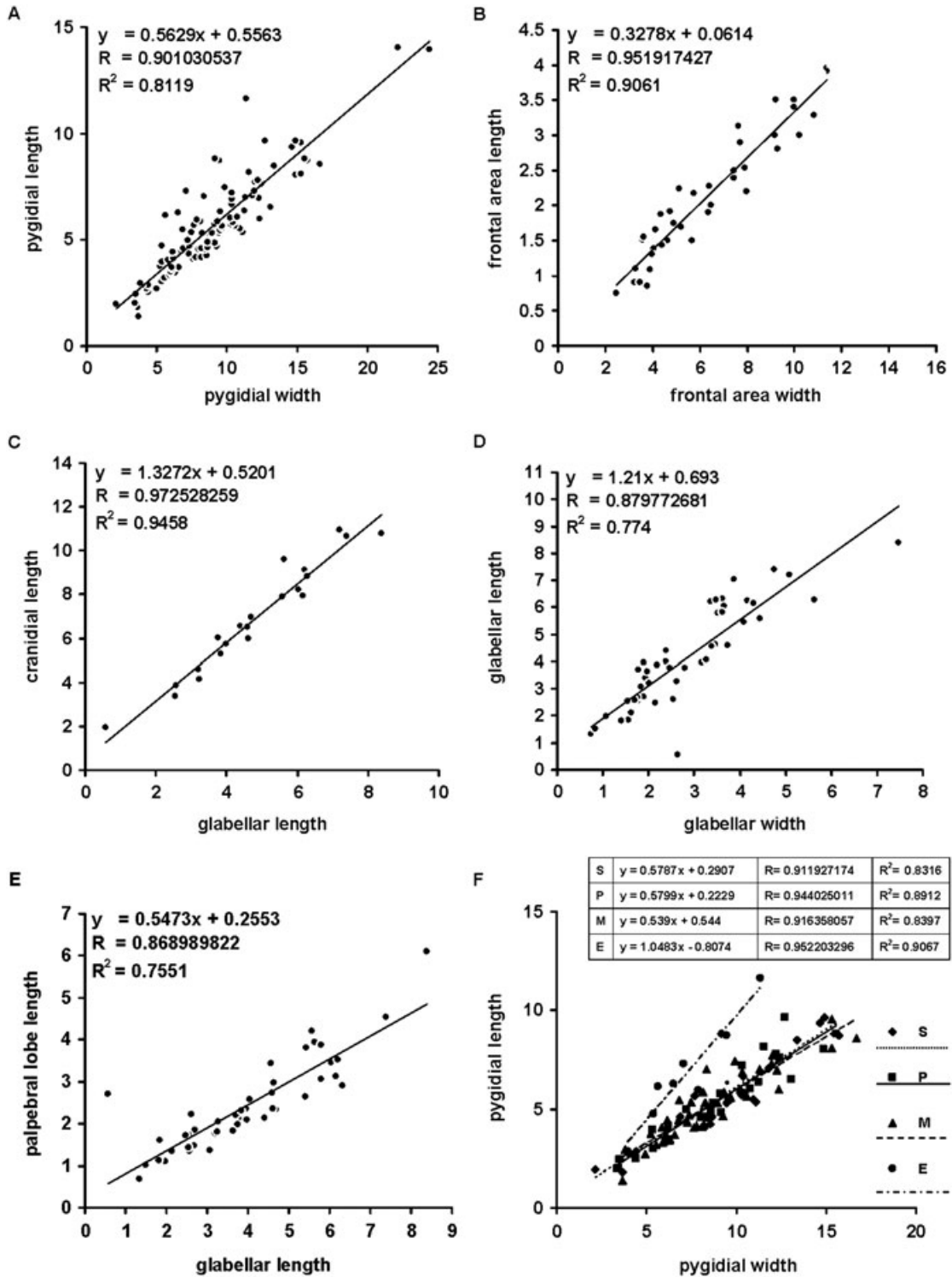
Figure 2. Bivariate plots of perpendicular cephalic and pygidial measurements (i.e. transverse and sagittal dimensions), with slope (*y*), Pearson correlation coefficient (R) and coefficient of determination (R^2) values. (A) Pygidial length versus pygidial width. (B) Frontal area length versus width. (C) Glabellar length versus cranidial length. (D) Glabellar length versus width. (E) Palpebral lobe length versus glabellar length. (F) Pygidial length versus pygidial width for each morphotype. S = pygidial morphotype 1 (sub-ellipsoidal to semi-circular outline without median indentation; P = pygidial morphotype 2 (sub-pentagonal outline with shallow median indentation; M = pygidial morphotype 3 (semi-circular to sub-pentagonal outline with deep median indentation; E = spinose pygidium of *Kochaspis coosensis* (used for comparison).

　　　　　　　　　　　　　　　　　　　Geol. J. **48**: 126–141 (2013)
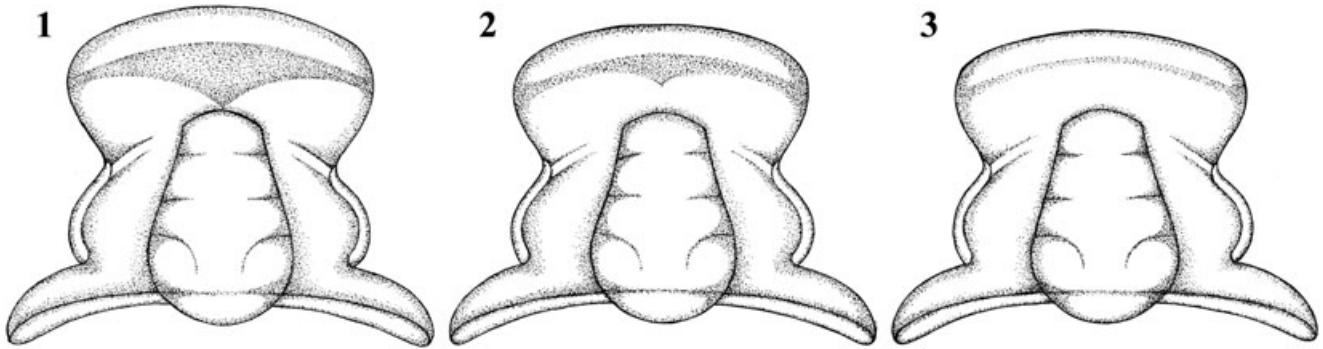
Figure 3. Reconstructions of cranidial morphotypes of *Blainia gregaria*.
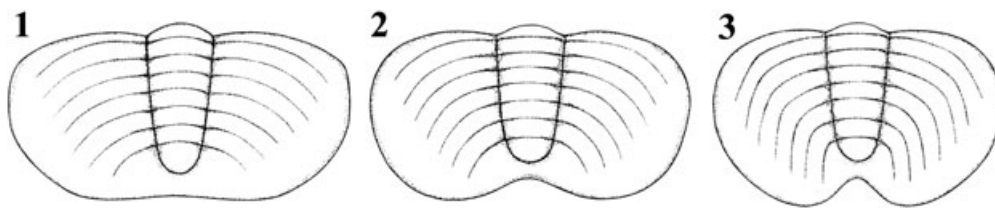
Figure 4. Reconstructions of pygidial morphotypes of *Blainia gregaria*.

regression line but also with a high degree of correlation ($R = 0.95$ and $R^2 = 0.91$).

This range of variability is also exhibited by other species attributed to *Blainia* and *Glyphaspis* including those not placed here in synonymy with *B. gregaria*. Cranidium type 1 with the median depression is exhibited by *G. dearbornensis* Deiss, 1939 (pl. 16, fig. 22). Cranidium type 2 with a relatively well impressed anterior border furrow occurs in: *G. perconcava* Poulsen, 1927 (pl. 17, fig. 3), *G. cowanensis* Resser, 1938 (pl. 8, fig. 39), *G. tetonensis* Resser, 1937 (Melzak and Westrop, 1994, pl. 3, fig. 2, pl. 4, figs 1–3; as *Americare tetonensis*—Lochman and Hu, 1960, pl. 100, figs 43–45, 49), *Blainia buttsi* Rasetti, 1965 (pl. 120, figs 1, 4, 5), *B. gregaria* (Schwimmer, 1989, figs 3.10, 3.12), and *G.* sp. 2 (Melzak and Westrop, 1994, pl. 2, fig. 10). Cranidium type 3 with a shallow anterior border furrow is seen in: *Amecephalina curticei* Resser, 1938 (pl. 8, fig. 59), *A. coosensis* Resser, 1938 (pl. 8, fig. 58), *G. robusta* Deiss, 1939 (pl. 16, fig. 12), *G. storeyi* Deiss, 1939 (pl. 16, fig. 35), *G. kwaguntensis* Resser, 1945 (pl. 26, figs 2, 3), *G. parkensis* Rasetti, 1951 (pl. 34, figs 5, 6), *G.* cf. *G. capella* (Walcott, 1916 (Schwimmer, 1989, fig. 3.13), and *G.* sp. 1 Melzak and Westrop, 1994 (pl. l4, fig. 12). On the other hand, specimens attributed to *G. tetonensis* by Melzak and Westrop (1994) show less variation in the length of the preglabellar field.

Pygidium type 1 with no or just a minimal median indentation of the posterior border is exhibited by: *G. perconcava* Poulsen, 1927 (pl. 17, fig. 4), *G.* cf. *G. concava* [sic] (Miller,

1936, pl. 8, fig. 17), *G.* sp. (Miller, 1936, pl. 8, fig. 39), *G. cowanensis* (Resser, 1938, pl. 8, fig. 39), *G. levis* Deiss, 1939, pl. 16, fig. 11), *G. paucisulcata* Deiss, 1939 (pl. 16, figs 15, 16), *G. ahornensis* Deiss, 1939 (pl. 16, fig. 18), *G. delicata* Deiss, 1939 (pl. 16, fig. 23), *G. similis* Deiss, 1939 (pl. 16, fig. 26), *G.* cf. *similis* (Deiss, 1939, pl. 16, fig. 25), *G. vulsa* Resser, 1945 (pl. 22, fig. 12), *G. tecta* Resser, 1945 (pl. 22, fig. 15), *G. kwaguntensis* (Resser, 1945, pl. 25, fig. 13, pl. 26, figs 3, 4), *G. parkensis* (Rasetti, 1951, pl. 34, figs 6, 7), *B. buttsi* (Rasetti, 1965, pl. 120, figs 6, 10), *G.* cf. *parkensis* (Hu, 1971, pl. 11, figs 26–28, 30), *G. tetonensis* (Melzak and Westrop, 1994, pl. 4, figs 6, 7, 10; as *Americare tetonensis*— Lochman and Hu, 1960, pl. 100, figs 48, 52, 53, 56), *Asaphiscus gregarius* (Schwimmer, 1989, fig. 3.10), and *G. capella* and *G.* cf. *G. capella* (Schwimmer, 1989, figs 3.17–3.19). Pygidium type 2 with a shallow median indentation of the posterior border is exhibited by: a second specimen of *G. cowanensis* (Resser, 1938, pl. 8, fig. 40) and *B. buttsi* (Rasetti, 1965, pl. 120, fig. 9), *A. curticei* (Resser, 1938, pl. 8, fig. 60), *G. indenta* (Deiss, 1939, pl. 16, fig. 7), and *G.*? cf. *G.*? *curticei* (Melzak and Westrop, 1994, pl. 5, figs 1, 2). Pygidium type 3 with a deep median indentation is seen in *G. dearbornensis* (Deiss, 1939, pl. 16, fig. 23).

Variation in outline of pygidia lacking the median indentation, assigned to *Iohomia sickia* (Hu, 1971, pl. 12, figs 17, 18, 20, 22), was ascribed to sexual dimorphism. This speculation cannot be evaluated for the material in La Laja Formation.

5. BIOGEOGRAPHIC DISTRIBUTION

The species included in the proposed synonymy for *Blainia gregaria* have a widespread distribution in Laurentia (see *Occurrences* below; Figure 5A). As in the Precordillera, they occur primarily in thin-bedded, slightly argillaceous limestones deposited in the inner parts of the broad carbonate platform that mantled the periphery and much of the interior of the craton. Other species assigned to *Blainia* (and *Glyphaspis*) not considered synonymous with *B. gregaria* exhibit a similar distribution. The presence of this apparently endemic, benthic polymeroid species in the Precordillera is further evidence for the close faunal link between Cuyania and Laurentia in that the two were within larval dispersal range. This has been explained as due to the rifting of Cuyania from (present-day southeastern) Laurentia (e.g. Thomas and Astini, 2003) or to larval interchange via currents with the sector of Gondwana that eventually became emplaced onto west-central Argentina (Aceñolaza *et al.*, 2002; Finney, 2007). The fact that Laurentian Cambrian polymeroids are highly endemic, even compared to other also more or less equatorial cratons, argues that the Precordillera was geographically close to Laurentia, but does not by itself resolve which tectonic model is preferable (Figure 5B).

6. SYSTEMATIC DESCRIPTION

As used here 'glabella' does not include the occipital ring. Specimens referred to are housed in the paleontological collections of the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA-PI prefix) and Peabody Museum of Natural History of Yale University (YPM prefix).

Order PTYCHOPARIIDA Swinnerton, 1915
Family Uncertain
Genus *Blainia* Walcott, 1916

Diagnosis. A genus of uncertain familial assignment with cephalon semi-circular in outline, gently convex. Glabella sub-quadrate to sub-conical in outline; lateral glabellar furrows weakly impressed to almost effaced. Preglabellar field gently convex to gently concave, equally divided by shallow anterior border furrow (if present), in length half as long to almost as long as glabella. Fixed cheek gently convex, equal in width to half that of glabella; palpebral lobe half to slightly less than half glabellar length. Free cheek with genal spine of medium length. Rostral plate wide, rectangular in outline;
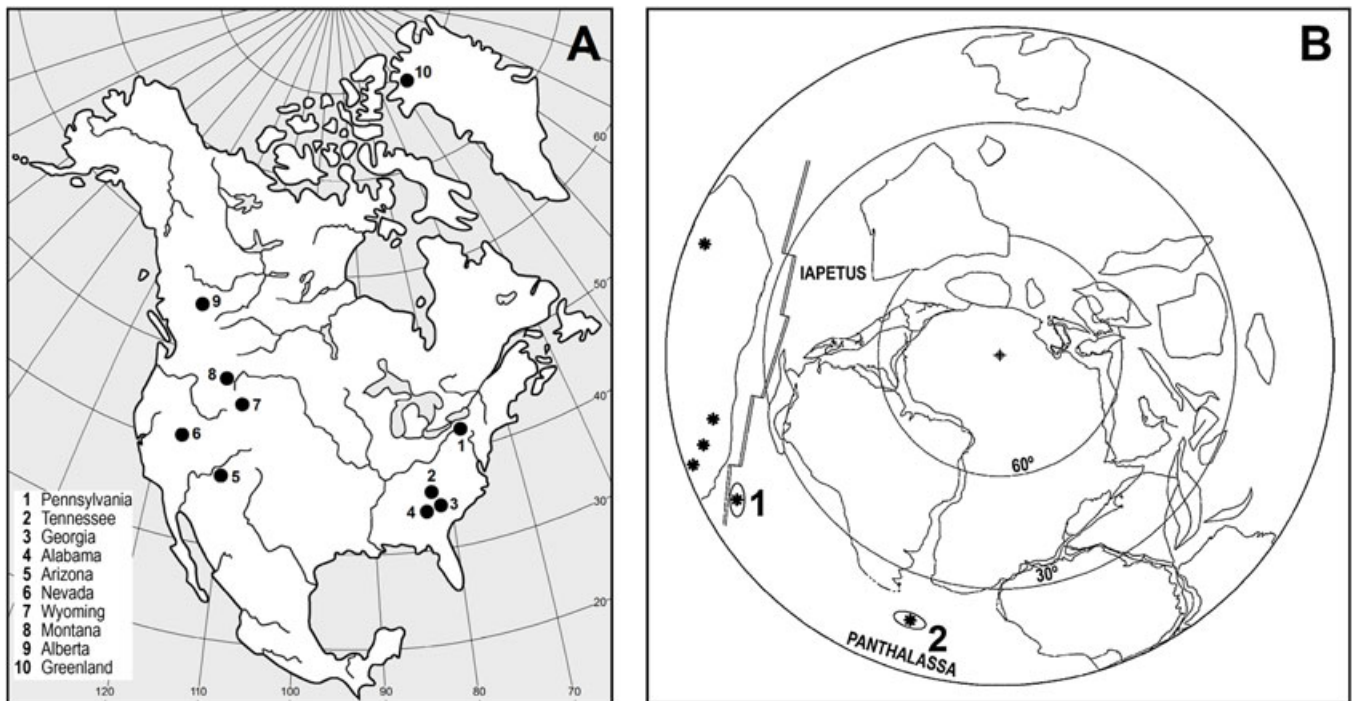

Figure 5. Biogeographic distribution of *Blainia gregaria*. (**A**) Actual distribution in North America. (**B**) Reconstruction of continental positions in Middle Cambrian time (south polar view modified from Cocks and Torsvik, 2002) showing locations of *B. gregaria* (asterisks) and hypothetical positions of Cuyania relative to (present-day eastern) Laurentia. (1) Cuyania close to Laurentia but separated by a narrow rift basin (e.g. Thomas and Astini, 2003). (2) Cuyania part of Gondwana (Finney, 2007).

hypostome natant, ovate in outline with thin, convex marginal rim. Thorax with 9 or 10 segments. Pygidium semi-circular to sub-trapezoidal to ellipsoidal in outline, gently convex, in width two-thirds to equal to that of cephalon. Axis parallel-sided to slightly tapered, bearing 4–8 axial rings plus terminal piece. Pleural field gently convex, in width 1.5–3 times that of axis, crossed by well impressed pleural furrows, straight until curving posteriorly across wide, flat to gently concave posterior border. Posterior margin with or without a shallow to moderately deep median indentation.

Type species. *Asaphiscus* (*Blainia*) *gregarius* Walcott, 1916 from the Conasauga Formation of Alabama (by original designation).

Discussion. *Blainia* was originally named as a subgenus of *Asaphiscus* Meek, 1873 (Walcott, 1916, p. 393), but elevated to generic status by Resser (1935, p. 17). The type species of *Asaphiscus*, *A. wheeleri* Meek, 1873, has a relatively deep anterior border furrow but effaced lateral glabellar furrows, and lacks genal spines; its pygidium is large and semi-circular in outline, and has shallow posterior border and pleural furrows (e.g. Palmer, 1954, pl. 16, fig. 7).

We regard *Glyphaspis* Poulsen, 1927 [not Resser, 1935 as stated in Resser, 1937, p. 12] (type species *Asaphiscus*? *capella* Walcott, 1916 from the Wolsey Shale, Montana) as a subjective junior synonym of *Blainia*. Schwimmer's (1989) claim that *B. gregaria* lacks a genal spine is in error (Walcott, 1916, pl. 62, figs 1a, 1e, 1i; Schwimmer, 1989, fig. 3.12), and the cranidia exhibit little, if any, differences. Indeed, Rasetti (1965) noted the similarity between species assigned to *Blainia* and *Glyphaspis* and the need to revise the content of the two genera. *Americare* Lochman and Hu, 1960 (type species *G. tetonensis* Resser, 1937 [not Miller, 1936, as stated in Lochman and Hu, 1960, p. 828]) is considered a junior synonym of *Glyphapsis* (Melzak and Westrop, 1994, p. 979), and hence of *Blainia*.

Nine species of *Blainia* have been erected: *B. gregaria*, *B. paula* Walcott, 1916 (=*Blountia paula*—Pratt, 1992, p. 66), *B. glaber* Walcott, 1916 (=*Asaphiscus glaber*—Rasetti, 1965), *B. elongatus* Walcott, 1916, *B. centerensis* Resser, 1935, *B. tennesseensis* Resser, 1938, *B.*? *halli* Resser, 1938, *B.*? *kincaidensis* Resser, 1938 and *B. buttsi* Rasetti, 1965.

A large number of species have been assigned to *Glyphaspis*: *G. capella* (Walcott, 1916), *G. camma* (Walcott, 1916), *G. calenus* (Walcott, 1916), *G. brevisulcata* Deiss, 1939, *G. indenta* Deiss, 1939, *G. levis* Deiss, 1939, *G. robusta* Deiss, 1939, *G. paucisulcata* Deiss, 1939, *G. ahornensis* Deiss, 1939, *G. dearbornensis* Deiss, 1939, *G. delicata* Deiss, 1939, *G. similis* Deiss, 1939 and *G. storeyi* Deiss, 1939 from western Montana, as well as *G.*? *montanensis*

(Whitfield, 1876) (see Resser, 1937, p. 35) from central Montana; *G. vulsa* Resser, 1945, *G. tecta* Resser, 1945 and *G. kwaguntensis* Resser, 1945 from the Muav Limestone of northern Arizona; *G. parkensis* Rasetti, 1951 from the Stephen Formation of southeastern British Columbia; *G. tetonensis* Resser, 1937 from the Death Canyon Limestone and Park Shale, northwestern Wyoming (and also the Pika Formation, southwestern Alberta—Melzak and Westrop, 1994); *G. gracilis* Resser, 1938, *G. nitida* Resser, 1938 and *G. cowanensis* Resser, 1938 from the Conasauga Shale of northern Alabama and Georgia; *G. nevadensis* Resser, 1937 and *G. concavus* Sundberg, 1994 [=*G. concava* Sundberg, 1994 *nom. correct.*] from the Swasey, Trailer and Pole Canyon limestones, Utah and Nevada; and *G. perconcava* Poulsen, 1927 from the Cape Wood Formation of northwestern Greenland and questionably also from the Gros Ventre Formation of Wyoming. Most of these species were based on limited material and thus most cannot be fully evaluated. Based on the variation present in individual collections, where available, it is likely that most are synonyms and this is how we treat them herein. On the other hand, *G. nitida* and *G. gracilis* have small pygidia and do not conform to *Glyphaspis* (or *Blainia*).

Melzak and Westrop (1994) transferred to *Glyphaspis*? five species assigned by Resser (1938) to *Amecephalina* Poulsen, 1927 (type species *A. mirabilis* Poulsen, 1927 from the Cape Wood Formation, northwestern Greenland). These are: *A. convexa* Walcott, 1911, *A. coosensis* Resser, 1938, *A. curticei* Resser, 1938, *A. bella* Resser, 1938 and *A. poulseni* Resser, 1938. Following our synonymy they can be assigned now to *Blainia*, except for the last species because it is based on two cranidia without a pygidium so that its affinity is uncertain. *Amecephalina mirabilis* has a smaller, transverse pygidium in which the pleural furrows are straight (Poulsen, 1927, pl. 16, fig. 44). The two species of *Blairella* (Rasetti, 1965), *B. crassimarginta* Rasetti, 1965 and *B. triangularis* Rasetti, 1965 from the Pleasant Hill Formation of Pennsylvania may belong to *Blainia*, but they are also only known from cranidia.

Resser (1935, p. 35) assigned *Crepicephalus* (*Loganellus*) *montanensis* Whitfield, 1876 from central Montana to *Glyphaspis*? and considered that the holotype and only specimen to be too poor to be more certain. Examination of this specimen (YPM 3127) shows that it has convex, relatively narrow fixed cheeks and a short anterior border, and therefore does not belong to *Glyphaspis*. Study of the bedrock geology suggests it was collected from the Pilgrim Formation, which is Sunwaptan in age, younger than the plexus of taxa under discussion.

Blainia gregaria Walcott, 1916
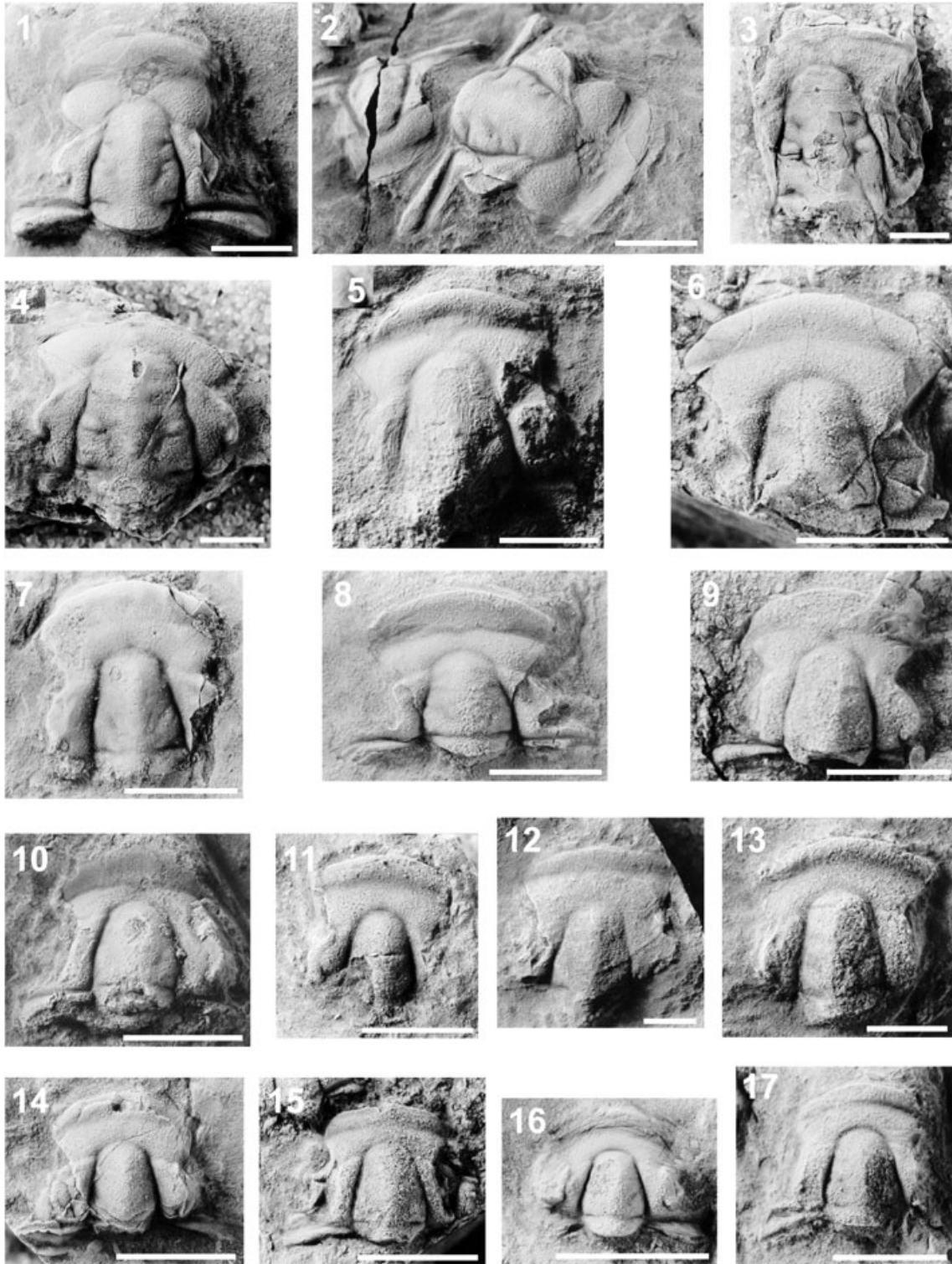Figures 6.1–6.17, 7.1–7.15, 8.1–8.5

Figure 6. (1–17) *Blainia gregaria* (Walcott, 1916). Cranidia. (1, 2) IANIGLA-PI 284, quebrada de Zonda. (3) IANIGLA-PI 386, quebrada de Zonda. (4) IANIGLA-PI 385, quebrada de Zonda. (5) IANIGLA-PI 359, quebrada de Zonda. (6) IANIGLA-PI 306, quebrada de Zonda. (7) IANIGLA-PI 268 quebrada de Zonda. (8) IANIGLA-PI 375, quebrada de Zonda. (9) IANIGLA-PI 358, quebrada de Zonda. (10) IANIGLA-PI 382, quebrada de Zonda. (11) IANIGLA-PI 1867, cerro Tres Marías. (12) IANIGLA-PI 1844, cerro Tres Marías. (13) IANIGLA-PI 1871a, cerro Tres Marías. (14) IANIGLA-PI 307, quebrada de Zonda. (15) IANIGLA-PI 312, quebrada de Zonda. (16) IANIGLA-PI 318, quebrada de Zonda. (17) IANIGLA-PI 315, quebrada de Zonda. Scale bars = 5 mm. Cranidial morphotype 1 is represented by Figures 6.1–6.5; cranidial morphotype 2 is represented by Figures 6.8–6.10; and cranidial morphotype 3 is represented by Figures 6.6, 6.7, 6.11–6.17.
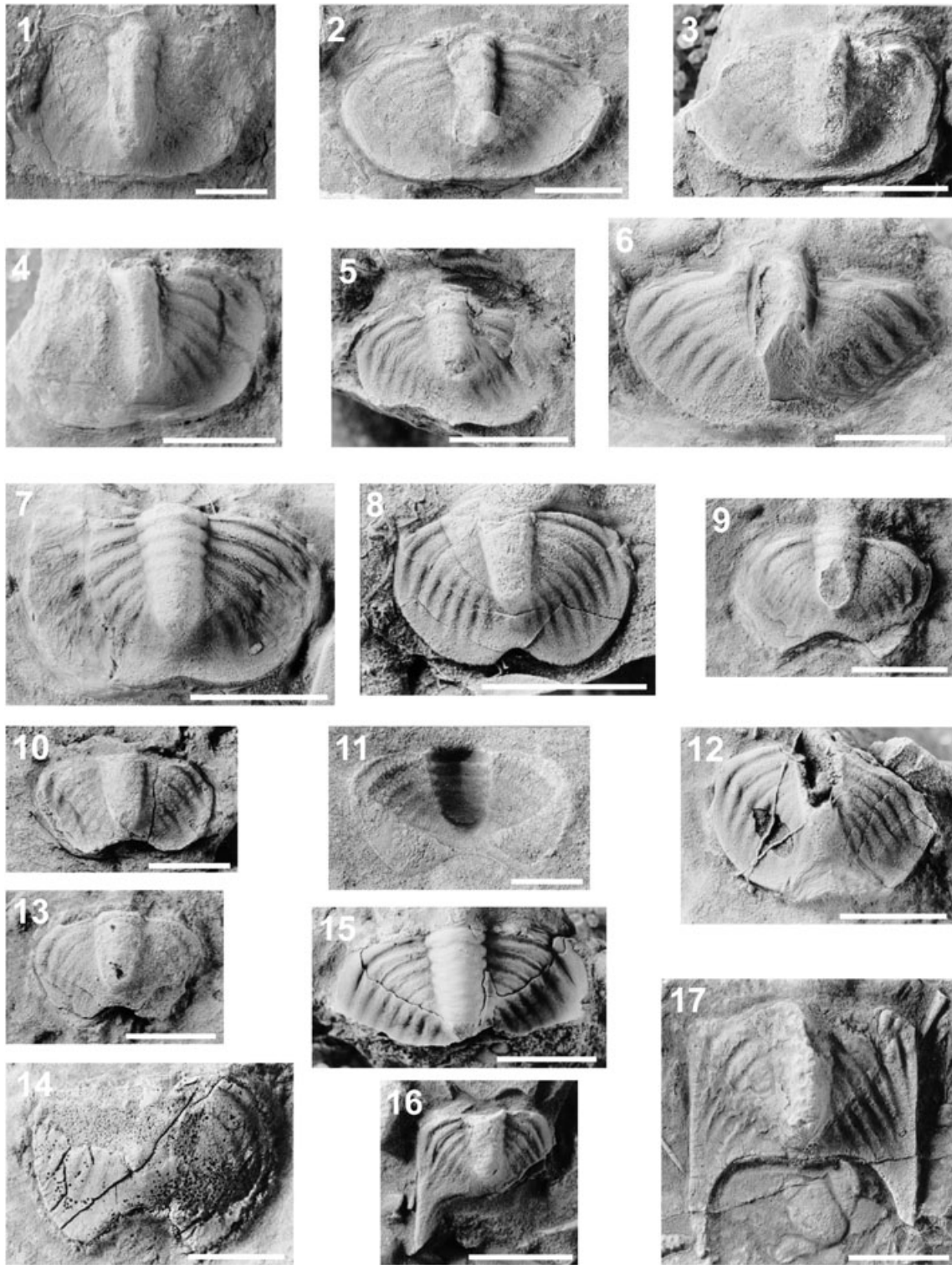
Figure 7. (1–15) *Blainia gregaria* (Walcott, 1916). Pygidia. (1) IANIGLA-PI 1870, cerro Tres Marías. (2) IANIGLA-PI 1869, cerro Tres Marías. (3) IANI-GLA-PI 1864, cerro Tres Marías. (4) IANIGLA-PI 1868, cerro Tres Marías. (5) IANIGLA-PI 381, quebrada de Zonda. (6) IANIGLA-PI 387, quebrada de Zonda. (7) IANIGLA-PI 384, quebrada de Zonda. (8) IANIGLA-PI 383, quebrada de Zonda. (9) IANIGLA-PI 1876, cerro Tres Marías. (10) IANIGLA-PI 1874, cerro Tres Marías. (11) IANIGLA-PI 1875, cerro Tres Marías. (12) IANIGLA-PI 380, quebrada de Zonda. (13) IANIGLA-PI 1871b, cerro Tres Marías. (14) IANIGLA-PI 1873, cerro Tres Marías. (15) IANIGLA-PI1872, cerro Tres Marías. (16) and (17) *Kochaspis coosensis* (Resser, 1938). Pygidia. (16) IANI-GLA-PI 1853, cerro Tres Marías. (17) IANIGLA-PI 1848, cerro Tres Marías. Scale bars = 5 mm. Pygidial morphotype 1 is represented by Figures 7.1–7.5; pygidial morphotype 2 is represented by Figures 7.6, 7.7; and pygidial morphotype 3 is represented by Figures 7.8–7.14.
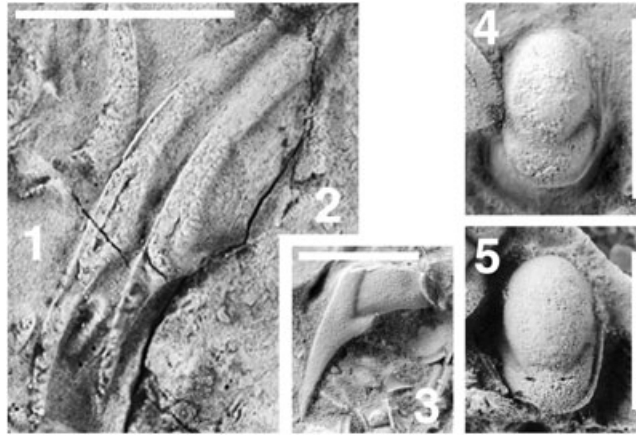
Figure 8. (1–5) *Blainia gregaria* (Walcott, 1916). (1–3) Free cheeks. (1) IANIGLA-PI 1339a. (2) IANIGLA-PI 1339b. (3) IANIGLA-PI 372, 4, 5. Hypostomes. (4) IANIGLA-PI 324, (5) IANIGLA-PI 360. All cerro Tres Marías. Scale bars = 5 mm.

1916　　*Asaphiscus*? sp. undet. 2, Walcott, p. 391, pl. 63, figs 3, 3a.
1916　　*Asaphiscus* (*Blainia*) *elongatus* Walcott (part), p. 393, pl. 63, figs 5, 5a [figs. 4 (holotype), 4a = *Elrathia antiquata*—Schwimmer, 1989, p. 490].
1916　　*Asaphiscus* (*Blainia*) *gregarius* Walcott, p. 394, pl. 62, figs 1, 1a–i.
1927　　*Glyphaspis perconcava* C. Poulsen, p. 273, pl. 17, figs 3, 4.
1935　　*Blainia gregaria* Walcott; Resser, p. 17.
1935　　*Blainia centerensis* Resser, p. 17.
1936　　*Glyphaspis* cf. *G. perconcava* Poulsen; Miller, p. 30, pl. 8, fig. 17 (in caption as *G.* cf. *G. concava*).
1936　　*Glyphaspis* sp., Miller, pl. 8, fig. 39 (part).
1937　　*Glyphaspis tetonensis* Resser, p. 13.
1938　　*Blainia gregaria* Walcott; Resser, p. 62, pl. 9, fig. 7.
1938　　*Blainia tennesseensis* Resser, p. 63, pl. 8, figs 52, 53.
?1938　*Amecephalina curticei* Resser, p. 58, pl. 8, figs 59, 60.
1938　　*Amecephalina bella* Resser, p. 58, pl. 9, fig. 5.
1938　　*Glyphaspis cowanensis* Resser, p. 80, pl. 8, figs 39, 40.
?1939　*Glyphaspis ahornensis* Deiss, p. 94, pl. 16, figs 18, 19.
1939　　*Glyphaspis dearbornensis* Deiss, p. 94, pl. 16, figs 20–23.
1939　　*Glyphaspis indenta* Deiss, p. 95, pl. 16, fig. 7.
?1939　*Glyphaspis levis* Deiss, p. 95, pl. 16, fig. 11.
1939　　*Glyphaspis similis* Deiss, p. 97, pl. 16, figs 26, 27.
1939　　*Glyphaspis* cf. *similis* Deiss, p. 97, pl. 16, fig. 25.
1945　　*Glyphaspis vulsa* Resser, p. 198, pl. 22, figs 12–14.
?1945　*Glyphaspis tecta* Resser, p. 198, pl. 22, fig. 15.
1945　　*Glyphaspis kwaguntensis* Resser, p. 199, pl. 25, figs 12, 13, pl. 26, figs 2–4.
1960　　*Americare tetonensis* (Resser); Lochman and Hu, p. 828, pl. 100, figs 42–57.
1964　　*Glyphaspis parkensis* Rasetti; Poulsen, p. 51, pl. 3, figs 8, 9.
1964　　*Glyphaspis perconcava* C. Poulsen; V. Poulsen, p. 51.
1965　　*Blainia buttsi* Rasetti, p. 1012, pl. 120, figs 1–10.
1989　　*Asaphiscus gregarius* (Walcott) (part); Schwimmer, p. 490, figs 3.10, 3.12 (not 3.6, 3.7, 3.15, 3.16 = *Asaphiscus* sp.; not 3.11 = ?*Blountia paula*—Pratt 1992, p. 66).
1994　　*Glyphaspis tetonensis* Resser; Melzak and Westrop, p. 979, pl. 3, figs 1–12, pl. 4, figs 1–10.
1994　　*Glyphaspis*? cf. *G.*? *curticei* (Resser); Melzak and Westrop, p. 982, pl. 5, figs 1, 3, 6.
1994　　*Glyphaspis* sp. 2, Melzak and Westrop, p. 982, pl. 2, figs 10, 11.

Diagnosis. A species of *Blainia* with moderately long frontal area, in length half to two-thirds that of glabella, divided subequally into preglabellar field and anterior border by shallow anterior border furrow. Palpebral lobe in length about half that of glabella. Pygidium semi-circular to sub-trapezoidal to ellipsoidal in outline, in width two-thirds that of cephalon; posterior margin with or without median indentation.

Lectotype. A complete exoskeleton (Walcott, 1916, pl. 62, fig. 1e) designated by Resser (1938, p. 62).

Material. Hundreds of holaspid cranidia and pygidia; assorted free cheeks, rostral plates, hypostomes, meraspid cranidia and pygidia, protaspides, and a partial thorax.

Description. Cephalon semi-circular in outline and moderately convex. Axial furrow well impressed, outlining conical glabella, straight-sided but in some specimens slightly constricted opposite the S2 furrows; anterior lobe rounded to slightly pointed medially. Three pairs (4 in some larger specimens) of lateral glabellar furrows weakly impressed, S1 curving strongly posteriorly, S2 curving gently posteriorly, and S3 transverse. Occipital furrow transverse, shallowing slightly medially; occipital ring lacking axial node. Frontal area moderately long, about two-thirds the length of the glabella (not including occipital ring), equally to subequally divided by shallow, relatively long anterior border furrow into gently convex preglabellar field and flat to slightly convex anterior border; anterior border furrow often exhibits variably expressed, shallow posterior median deflection. Anterior facial suture divergent at an angle of about 30°, but exhibiting a range from 20° to 35°. Fixed cheek relatively narrow, one-third the width of glabella, gently upsloping, crossed by moderately well defined, obliquely oriented, straight palpebral ridge. Palpebral lobe in length half that of glabella, located opposite glabellar midpoint. Posterior border well impressed.

Free cheek with flat to slightly convex lateral border separated from genal field by shallow lateral border furrow; genal spine round in cross-section, in length about one-third the length from its tip to the anterior facial suture (see also Walcott, 1916, pl. 62, figs 1a, 1b, 1e; Schwimmer, 1989, fig. 3.12; Melzak and Westrop, 1994, pl. 3, fig. 7, pl. 4, fig. 5).

Rostral plate rectangular in outline and elongate, bearing lateral notches (Melzak and Westrop, 1994, pl. 3, figs 6, 8). Hypostome natant, ovoid in outline. Posterior lobe one-third as long as anterior lobe, separated by shallow middle furrow. Anterior wings narrow; lateral border and border furrow narrow, uniform around posterior margin (see also Walcott, 1916, pl. 62, fig. 1c; Melzak and Westrop, 1994, pl. 3, figs 10, 11, pl. 4, fig. 8).

Thoracic segments 9 or 10 in number; pleural furrows well impressed; pleural spines short (Schwimmer, 1989, figs 3.10, 3.12).

Pygidium large, in width two-thirds that of cephalon, semi-circular to sub-elliptical to sub-pentagonal in outline. Axis nearly parallel-sided, strongly convex, crossed by 4–8 axial ring furrows; terminal piece rounded to slightly conical, nearly reaching posterior margin. Pleural field gently convex, merging into flat border lacking posterior border furrow, crossed by six or seven well impressed, narrow pleural furrows with variably distinct interpleural furrows in anterior portion. Anterior margin variably curving posteriorly; lateral margin gently curved. Posterior margin transverse to having a variably pronounced median indentation.

External surface smooth to indistinctly granulate.

Discussion. *Blainia gregaria*, as *Asaphiscus* (*Blainia*) *gregarius*, was distinguished from *A. wheeleri* on the basis of pygidial shape, in that the pygidium of the former was said to be narrower and the pleural furrows extend to its margin (Walcott, 1916, p. 393). In essentially monofacial deposits of La Laja Formation, cranidia and pygidia of this species vary considerably, leading to the extensive synonymy and morphometric analysis presented herein. For example, the degree of divergence of the anterior facial suture is seen to be quite variable, which was also recognized by Schwimmer (1989). The depth of the anterior border furrow is variable, and the preglabellar field ranges in length from slightly less than to slightly more than the length of the anterior border. For this reason, we do not agree with Melzak and Westrop's (1994) acceptance of small variations in preglabellar field length as diagnostic of *Glyphaspis* species. This furrow outlines a faint plectrum in some compressed specimens, a feature also present in material from Wyoming (Lochman and Hu, 1960, pl. 100, fig. 54).

Resser (1935) distinguished *B. centerensis* from *B. gregaria* on the difference of having ten instead of nine thoracic segments. We share Rasetti's (1965) opinion that this could also be ascribed to intraspecific variation.

The nearly complete exoskeleton of *Amecephalina bella* Resser, 1938 (pl. 9, fig. 5) appears to be identical to those of *A. gregaria*. Melzak and Westrop (1994, p. 982) noted that *A. curticei* Resser, 1938 belongs to *Glyphaspis*, and therefore to *Blainia*. The co-type pygidium of *A. curticei* is virtually identical to that of *B. gregaria*, but the co-type cranidium has a palpebral lobe that is one-third as long as the glabella, whereas in *B. gregaria* the palpebral lobe is typically about half as long as the glabella. Although some intraspecific variation in palpebral lobe length is exhibited in collections of *B. gregaria* and species considered synonymous herein, without more material it is uncertain if *B. curticei* can be sustained. However, the specimens attributed to *G.*? cf. *G.*? *curticei* by Melzak and Westrop (1994) appear to fit well within *B. gregaria*. *Glyphaspis* sp. 1 of Melzak and Westrop (1994) is known from cranidia with narrower fixed cheeks and shallower furrows than *B. gregaria* and it could be a variant of *B. gregaria*.

We observe a gradation between pygidia that are semi-circular to sub-trapezoidal to ellipsoidal in outline and those that have a transverse posterior border to those with a slight to moderately deep median indentation. Pygidial pleural furrows are also variably impressed (e.g. Melzak and Westrop, 1994, pl. 4, figs 6, 7, 10).

Asaphiscus? *capella* Walcott, 1916 (pl. 59, figs 2, 2a–c; =*G. capella*—Poulsen, 1927, p. 273; Schwimmer, 1989, fig. 3.19), *A. calanus* Walcott, 1916 (pl. 61, figs 8, 8a), *A. calenus* (Walcott, 1916, pl. 60, figs 1, 1a–c; =*G. calenus*—Resser, 1935, p. 34), *A. camma* Walcott, 1916 (pl. 60, figs 2, 2a–c; =*G. camma*—Resser, 1935, p. 34), *Anomocare convexa* (Walcott, 1911) (pl. 17, figs 2, 2a–d; =*Amecephalina convexa*—Resser, 1938), *A. coosensis* Resser, 1938 (pl. 8, fig. 58), *G. robusta* Deiss, 1939 (pl. 16, figs 12–14), *G. storeyi* Deiss, 1939 (pl. 16, figs 35–37), *G. parkensis* Rasetti, 1951 (pl. 34, figs 6, 7), *G.* cf. *G. capella* of Schwimmer (1989; figs 3.13, 3.14, 3.17, 3.18), *G. concava* Sundberg, 1994 (figs 64.1–64.4) and *G.* cf. *G. concava* (Sundberg 1994, figs 65.1, 65.2) have cranidia similar in general to that of *B. gregaria*, but pygidia have much wider pleural fields—more than twice the width of the axis which is more markedly tapering—and a long, flat posterior border. No cranidia have been described for *G. brevisulcata* Deiss, 1939 (pl. 16, fig. 5), *G. delicata* Deiss, 1939 (pl. 16, fig. 24), *G. paucisulcata* Deiss, 1939 (pl. 16, figs 15–17) but their pygidia are also wide. Their relationships are unclear but they may belong to *Blainia*. The so-called 'female' specimens referred to as *Iohomia sickia* Hu, 1971 (pl. 12, figs 17, 20) may belong to *Glyphaspis* (Melzak and Westrop, 1994, p. 979) and hence to *Blainia*.

Distribution. Upper Soldano, Rivadavia and lower Juan Pobre members, Laja Formation; Conasauga Formation, northeastern

Alabama–northwestern Georgia; Pleasant Hill Formation, central Pennsylvania; Muav Limestone, northern Arizona; Steamboat Limestone, west-central Montana; Gros Ventre Formation, western Wyoming; Pika Formation, southwestern Alberta; Cape Wood Formation, northwestern Greenland.

7. CONCLUSIONS

The ptychoparioid trilobite *Blainia gregaria* Walcott, 1916 is recognized for the first time in the Precordillera of western Argentina. It occurs in large numbers in slightly argillaceous limestones of the upper part of the middle Cambrian (Series 3) La Laja Formation, which were deposited in the interior of the broad, west-facing carbonate platform that forms the core of this terrane, known as Cuyania. Visual inspection combined with morphometrics shows that this trilobite exhibits an unusually large degree of intraspecific variation, expressed by small cranidial differences, but especially in the shape of the pygidium. An intergradation is seen between specimens possessing a deep median indentation of the posterior border with those in which the posterior border is transverse. This variation permits the synonymy of *Glyphaspis* Poulsen, 1927 with *Blainia* Walcott, 1916 and the synonymy of some 30 species with *B. gregaria*. The biogeographic distribution of *B. gregaria*, as defined here, shows that it was endemic to Laurentia, but its occurrence in the Precordillera is indicative of the close faunal links with that continent during the Cambrian.

ACKNOWLEDGEMENTS

REFERENCES

Aceñolaza, F.G., **Miller, H.**, **Toselli, A.J. 2002**. Proterozoic–Early Paleozoic evolution in western South America—a discussion. *Tectonophysics* **354**, 121–137.

Baldis, B.A., **Bordonaro, O.L. 1981**. Evolución de facies carbonáticas en la cuenca cámbrica de la Precordillera de San Juan. *8º Congreso Geológico Argentino, Actas* **2**, 385–397.

Bordonaro, O.L. 1980. El Cámbrico en la quebrada de Zonda, Provincia de San Juan. *Revista de la Asociación Geológica Argentina* **35**, 26–40.

Bordonaro, O. 2003. Review of the Cambrian stratigraphy of the Argentine Precordillera. *Geologica Acta* **1**, 11–21.

Bordonaro, O.L., **Pratt, B.R. 2008**. Middle Cambrian trilobites of La Laja Formation, western Argentina. In: *Advances in Trilobite Research*, Rábano, I., Gozalo, R., García Bellido, D. (eds). Cuadernos del Museo Geominero, Instituto Geológico y Minero de España **9**, 55.

Bordonaro, O.L., **Banchig, A.L.**, **Pratt, B.R.**, **Raviolo, M.M. 2008**. Trilobite-based biostratigraphic model (biofacies and biozonation) for the Middle Cambrian carbonate platform of the Argentine Precordillera. *Geologica Acta* **6**, 115–129.

Borrello, A.V. 1962. Caliza La Laja (Cámbrico Medio de San Juan). *Notas del Comité de Investigaciones Científicas de Buenos Aires* **2**, 3–8.

Chirivella Martorell, J.B., **Gozalo, R.**, **Liñán, E. 2003**. Estudio taxonómico y biométrico de *Badulesia tenera* (Hartt *in* Dawson, 1868), Trilobita, Caesaraugustiense (Cámbrico Medio) de las Cadenas Ibéricas (NE de España). *Revista Española de Paleontología* **18**, 83–101.

Cocks, L.R.M., **Torsvik, T.H. 2002**. Earth geography from 500 to 400 million years ago: a fauna and palaeomagnetic review. *Journal of the Geological Society of London* **159**, 631–644.

Deiss, C. 1939. Cambrian stratigraphy and trilobites of northwestern Montana. *Geological Society of America, Special Paper* **18**, 1–135.

Dies, M.E., **Gozalo, R. 2004**. Agnostida (Trilobita) de la Formación Valdemiedes (Leoniense: Cámbrico Medio basal) de las Cadenas Ibéricas (NE de España). *Boletín Geológico y Minero* **115**, 683–698.

Finney, S.C. 2007. The parautochthonous Gondwanan origin of the Cuyania (greater Precordillera) terrane of Argentina: a re-evaluation of evidence used to support an allochthonous Laurentian origin. *Geologica Acta* **5**, 127–158.

Gomez, F.J., **Ogle, N.**, **Astini, R.A.**, **Kalin, R.M. 2007**. Paleoenvironmental and carbon–oxygen isotope record of Middle Cambrian carbonates (La Laja Formation) in the Argentine Precordillera. *Journal of Sedimentary Research* **77**, 826–842.

Hammer, O., **Harper, D.A.T. 2006**. *Paleontological Data Analysis*. Blackwell Publishing: Oxford, 1–351.

Hu, C.-H. 1971. Ontogeny and sexual dimorphism of Lower Paleozoic Trilobita. *Palaeontographica Americana* **7**(44), 1–153.

Hughes, N.C. 1994a. Morphological plasticity and genetic flexibility in a Cambrian trilobite. *Geology* **19**, 913–916.

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

Hughes, N.C., **Jell, P.A. 1992**. A statistical/computer-graphic technique for assessing variation in tectonically deformed fossils and its application to Cambrian trilobites from Kashmir. *Lethaia* **25**, 317–330.

Keller, M. 1999. Argentine Precordillera: sedimentary and plate tectonic history of a Laurentian crustal fragment in South America. *Geological Society of America, Special Paper* **341**, 1–131.

Labandeira, C.C., **Hughes, N.C. 1994**. Biometry of the Late Cambrian trilobite genus *Dikelocephalus* and its implications for trilobite systematics. *Journal of Paleontology* **68**, 492–517.

Lochman, C., **Hu, C.H. 1960**. Upper Cambrian faunas from the northwest Wind River Mountains, Wyoming. Part 1. *Journal of Paleontology* **34**, 793–834.

Meek, F.B. 1873. Preliminary palaeontology report, consisting of list and descriptions of fossils, with remarks on the age of the rocks in which they are found. *Annual Report of the United States Geological Survey of Territories* **6**, 429–518.

Melzak, A, **Westrop, S.R. 1994**. Mid-Cambrian (Marjuman) trilobites from the Pika Formation, southern Canadian Rocky Mountains, Alberta. *Canadian Journal of Earth Sciences* **31**, 969–985.

Miller, B.M. 1936. Cambrian trilobites from northwestern Wyoming. *Journal of Paleontology* **10**, 23–34.

Palmer, A.R. 1954. An appraisal of the Great Basin Middle Cambrian trilobites described before 1900. *U.S. Geological Survey Professional Paper* **264-D**, 55–86, pls 13–17.

Poulsen, C. 1927. The Cambrian, Ozarkian and Canadian faunas of northwest Greenland. *Meddelelser om Grønland* **70**, 237–343.

Poulsen, V. 1964. Contribution to the Lower and Middle Cambrian paleontology and stratigraphy of Northwest Greenland. *Meddelelser om Grønland* **164**, 1–105.

Pratt, B.R. 1992. Trilobites of the Marjuman and Steptoean stages (Upper Cambrian), Rabitkettle Formation, Southern Mackenzie Mountains, northwest Canada. *Paleontographica Canadiana* **9**, 1–179.

Pratt, B.R., **Bordonaro, O.L. 2007**. Tsunamis in a stormy sea: Middle Cambrian inner shelf limestones of western Argentina. *Journal of Sedimentary Research* **77**, 256–262.

Rasetti, F. 1951. Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains. *Smithsonian Miscellaneous Collections* **116**(5), 1–277.

Rasetti, F. 1965. Middle Cambrian trilobites from the Pleasant Hill Formation in central Pennsylvania. *Journal of Paleontology* **39**, 1007–1014.

Resser, C.E. 1935. Nomenclature of some Cambrian trilobites. *Smithsonian Miscellaneous Collections* **93**(5), 1–46.

Resser, C.E. 1937. Third contribution to nomenclature of Cambrian fossils. *Smithsonian Miscellaneous Collections* **95**(22), 1–29.

Resser, C.E. 1938. Cambrian system (restricted) of the Southern Appalachians. *Geological Society of America, Special Paper* **15**, 1–140.

Resser, C.E. 1945. Cambrian fossils of the Grand Canyon. In: *Cambrian History of the Grand Canyon*, McKee, E.D., Resser, C.E. (eds). Carnegie Institution: Washington, 169–220, pls 16–27.

Schwimmer, D.R. 1989. Taxonomy and biostratigraphic significance of some Middle Cambrian trilobites from the Conasauga Formation in western Georgia. *Journal of Paleontology* **63**, 484–494.

Sundberg, F.A. 1994. Corynexochida and Ptychopariida (Trilobita, Arthropoda) of the *Ehmaniella* Biozone (Middle Cambrian), Utah and Nevada. *Natural History Museum of Los Angeles County, Contributions in Science* **446**, 1–137.

Swinnerton, H.H. 1915. Suggestions for a revised classification of trilobites. *Geological Magazine* **n.ser. 2**, 407–496, 538–545.

Thomas, W.A., **Astini, R.A. 2003**. Ordovician accretion of the Argentine Precordillera terrane to Gondwana: a review. *Journal of South American Earth Sciences* **16**, 67–79.

Walcott, C.D. 1911. Cambrian geology and paleontology. II, no. 4. Cambrian faunas of China. *Smithsonian Miscellaneous Collections* **57**, 69–108.

Walcott, C.D. 1916. Cambrian geology and paleontology. III, no. 5. Cambrian trilobites. *Smithsonian Miscellaneous Collections* **64**, 303–456.

Whitfield, R.P. 1876. Descriptions of new species of fossils. In: *Report of a Reconnaissance from Carroll, Montana Territory, on the Upper Missouri, to the Yellowstone National Park, and Return, Made in the Summer of 1875*, Ludlow, W. (ed.). War Department: Washington, 139–145, pls 1, 2.