

# Biostratigraphic significance of the latest Cambrian-earliest Ordovician agnostoid trilobites from Northwestern Argentina

M. F. TORTELLO

Departamento Paleozoología Invertebrados, Museo de La Plata  
Paseo del Bosque s/n°, La Plata 1900, Argentina. E-mail: tortello@museo.fcnym.unlp.edu.ar

## ABSTRACT

The biostratigraphic significance of the latest Cambrian-earliest Ordovician trilobite agnostoids from northwestern Argentina is summarized. A characterization of the faunas recognized below and above the Cambrian-Ordovician boundary is presented on the bases of information from sierra de Cajas (Jujuy Province, Eastern Cordillera; Lampazar and Cardonal Formations), río Volcancito (La Rioja Province, Famatina range; Volcancito Formation) and other localities assigned to the *Parabolina frequens argentina* Biozone. In addition, the stratigraphic meaning of each agnostoid species from the *P. frequens argentina* Zone is updated. The uppermost Cambrian is characterized by a distinctive agnostoid assemblage composed of *Lotagnostus* (*Lotagnostus*) sp., *Lotagnostus* (*Semagnostus*) *zuninoi* (HARRINGTON and LEANZA), *Micragnostus vilonii* HARRINGTON and LEANZA, *M. calviformis* HARRINGTON and LEANZA, *Strictagnostus?* *micropeltis* (HARRINGTON and LEANZA), *Pseudorhaptagnostus* (*Machairagnostus*) *tmetus* HARRINGTON and LEANZA, *Pseudorhaptagnostus* (*Machairagnostus*) cf. *tmetus* HARRINGTON and LEANZA, *Pseudorhaptagnostus* (*Machairagnostus*) sp., *Gymnagnostus bolivianus* (HOEK), *Gymnagnostus perinflatus* HARRINGTON and LEANZA, and *Leiagnostus turgidulus* HARRINGTON and LEANZA. This fauna is commonly recorded together with the polymeroid *Beltella ulrichi* (KAYSER), *Onychopyge* HARRINGTON, *Plicatolina scalpta* HARRINGTON and LEANZA, *Parabolina frequens argentina* (KAYSER), *Parabolinella coelatifrons* HARRINGTON and LEANZA, and *Angelina hyeronimi* (KAYSER). Based on this agnostoid-polymeroid fauna, a *Pseudorhaptagnostus* (*Machairagnostus*) - *Gymnagnostus* Assemblage Subzone (lower part of the *P. frequens argentina* Zone) is formally proposed. Agnostoid diversity drastically declines through the Cambrian-Ordovician boundary, probably as a consequence of a regional regressive-transgressive event. In the lowest Tremadoc the agnostoid records are mainly restricted to *Trilobagnostus chiushuensis* (KOBAYASHI) and some forms described under open nomenclature (*Anglagnostus?* sp., *Micragnostus* sp.). The upper part of the *P. frequens argentina* Zone is better defined by polymeroid trilobites. *Jujuyaspis keideli* KOBAYASHI is its most characteristic species.

**KEYWORDS** | Trilobita. Agnostida. Latest Cambrian-earliest Ordovician. Northwestern Argentina. Biostratigraphy.

## INTRODUCTION

Occurrences of agnostoid trilobites are restricted to the Cambrian - Ordovician (late Early Cambrian-Ashgillian). Because of their abundance and rapid evolution, the Middle and early Late Cambrian representatives have great potential for biostratigraphy. Accurate strati-

graphic schemes have been based on those Cambrian species that, being preserved in dark limestones and shales, lived on the outer, ocean-facing margins of carbonate bank complexes and outer detrital environments (e.g., Shergold, 1981; Shergold et al., 1990). In addition, though the agnostoids were less abundant after the Cambrian, several Ordovician taxa seem to have good bio-

stratigraphic and paleobiogeographic potential (e.g., Ahlberg, 1989, 1992; Nielsen, 1997).

Agnostoids are represented in the Upper Cambrian-Tremadoc of the Baltic shield, northern Siberia, and in cold to temperate areas of the margin of Gondwana (“Baltic Province”, see Shergold, 1988). This province is characterized by the cold water “olenid biofacies”, which is associated with dark shales and limestones representing bottom conditions low in oxygen, mainly assignable to outer shelf environments (Fortey, 1975). This facies contains a restricted trilobite fauna which is mainly composed of olenids. The olenid biofacies can be recognised in the uppermost Cambrian-lower Tremadoc in northwestern Argentina, where several formations assigned to the trilobite *Parabolina (Neoparabolina) frequens argentina* Biozone are essentially composed of shales and subordinated sandstones (Harrington and Leanza, 1957).

Although the *Parabolina (Neoparabolina) frequens argentina* Biozone was originally assigned to the early Tremadoc, subsequent analyses demonstrated that its lower part is assignable to the latest Cambrian (e.g. Rushton, 1982: p. 46; Ludvigsen, 1982: p. 150; Aceñolaza, 1983; Salfity et al., 1984). Current interdisciplinary studies aim to determine the position of the Cambrian-Ordovician boundary within the unit, as well as to reconsider the biostratigraphic significance of its abundant trilobite faunas. The importance of this subject was especially pointed out by Nielsen (1997), who stressed the unsettled exact stratigraphic position of several agnostoids in the biozone.

Biostratigraphic significances of the latest Cambrian-earliest Ordovician trilobite agnostoids from northwestern Argentina are summarised here. Based on information from representative localities of Jujuy, Salta (Eastern Cordillera) and La Rioja (Famatina Range), a brief characterization of the faunas recognized below and above the Cambrian-Ordovician boundary is presented. In addition, the stratigraphic meaning of each agnostoid species from the *Parabolina frequens argentina* Biozone is updated. Part of the information condensed here is from an unpublished doctoral thesis by the author, and from Tortello and Aceñolaza (1993), Tortello and Esteban (1997, 1999) and Tortello et al. (1999).

### THE *Parabolina frequens argentina* ZONE AND THE CAMBRIAN-ORDOVICIAN BOUNDARY

Upper Cambrian in Salta and Jujuy was first mentioned by Kayser (1876), who correlated a trilobite fauna composed of “*Agnostus*” *tilcuyensis*, “*Olenus*” *argentinus* and “*Arionellus*” *hyeronimi*, with the *Olenus* beds of northern Europe and Canada. On the other hand, Kayser (1897) assigned to the “Middle Cambrian” a

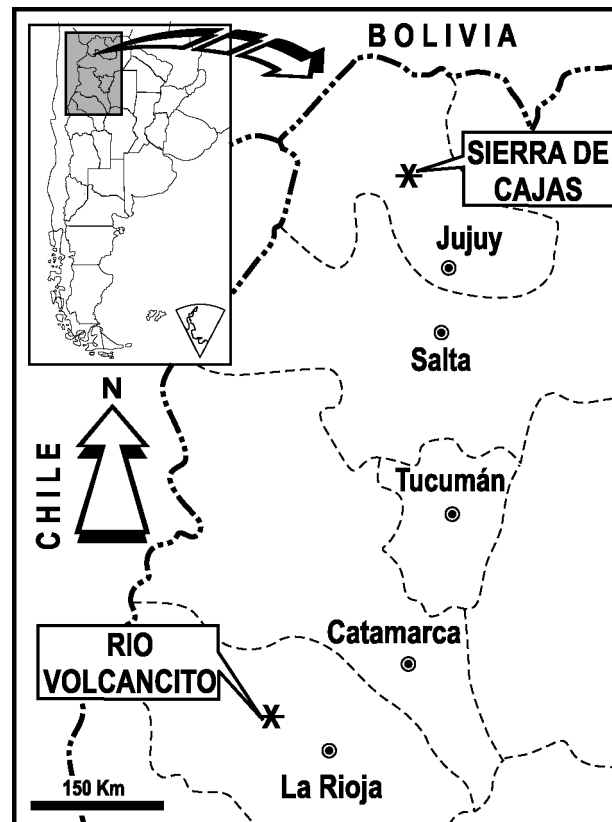


FIGURE 1 | Location map showing sierra de Cajas (Eastern Cordillera) and río Volcancito (Famatina Range) localities.

trilobite fauna (“*Arionellus*” *hyeronimi*, “*Liostracus*” *ulrichi* and “*Agnostus*” *iruyensis*) from Iruya (Salta). Later, Kobayashi (1936, 1937) pointed out the Late Cambrian-earliest Ordovician affinities of the material of southern Bolivia and northern Argentina previously studied by Kayser, Lake and Hoek, and examined new collections obtained by Keidel and Brown (see Kobayashi, 1937).

Harrington and Leanza (1957: pp. 23-26) defined the *Parabolina frequens argentina* Biozone based on the study of numerous trilobites from northwestern Argentina. These authors evaluated the stratigraphic significance of each species of the unit, and pointed out the Tremadocian affinities of many of them. Although such global evaluation originally led to the assignment of the whole biozone to the lower Tremadoc, Harrington and Leanza (1957) clearly indicated the Late Cambrian affinities of several forms (e.g. *Micragnostus tilcuyensis*, “*Micragnostus*” *micropeltis*, *Machairagnostus tmetus*, *Plicatolina scalpta*, *Parabolina kobayashii*).

Subsequent studies pointed out the biostratigraphic significance of certain faunistic variations recognised within the biozone. Benedetto (1977) showed that

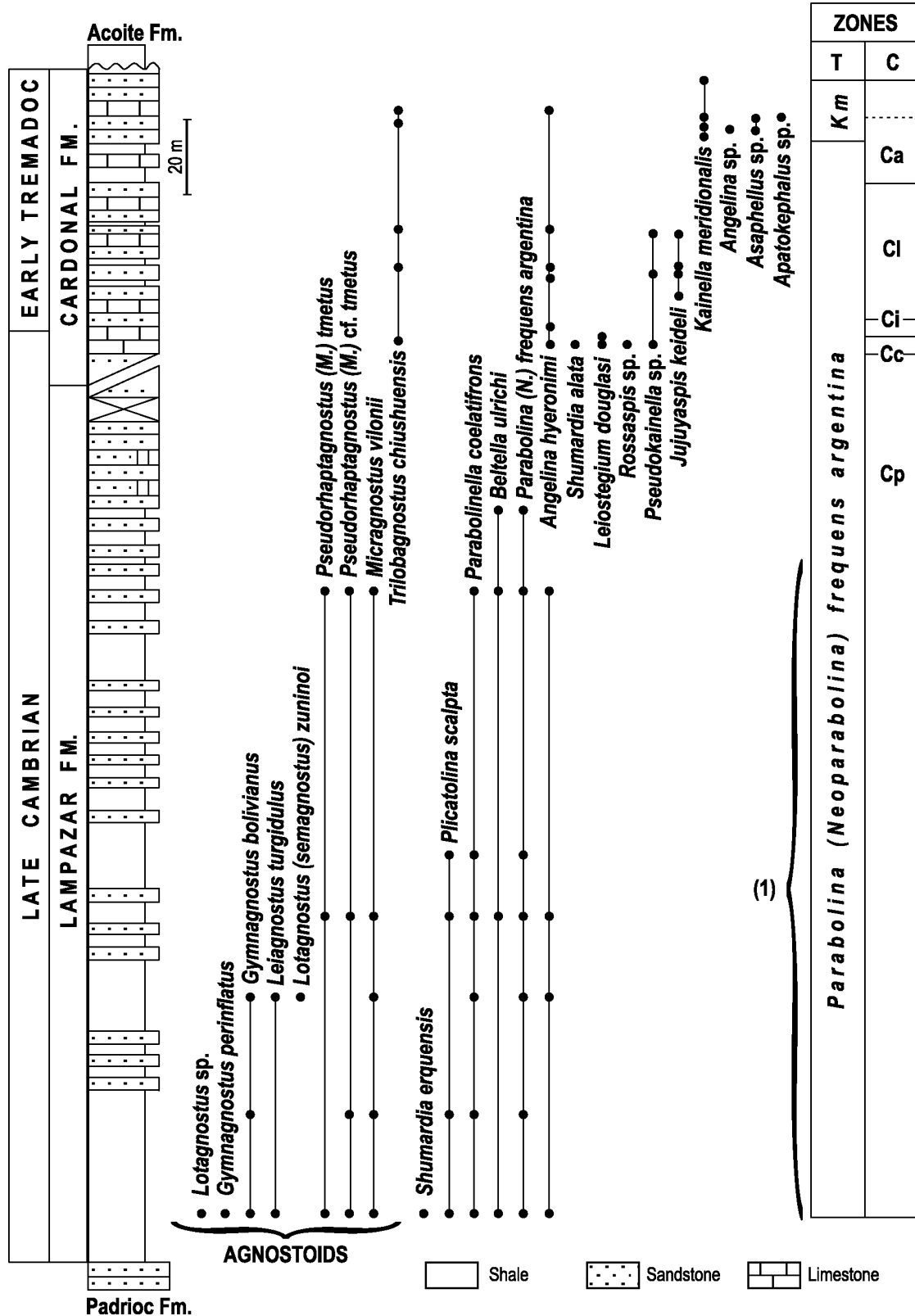


FIGURE 2 | Simplified stratigraphic column and species ranges of trilobites of sierra de Cajas (Quebrada Azul -Lampazar Formation- and Quebrada Amarilla -Cardonal Formation). Adapted from Aceñolaza, 1968; Tortello and Aceñolaza, 1993; Ortega and Rao, 1995; Rao, 1999; Tortello et al., 1999. Notice the indication (1) of the *Pseudorhaptagnostus* (*Machairagnostus*) - *Gymnagnostus* Subzone. T: trilobites; C: conodonts; Km: *Kainella meridionalis*; Cp: *Cordylodus proavus*; Cc: *Cordylodus caboti*; Ci: *Cordylodus intermedius*; Cl: *Cordylodus lindstromi*; Ca: *Cordylodus angulatus*.

*Parabolina frequens argentina* (KAYSER) is generally better represented in the lower part of the unit, whereas *Jujuyaspis keideli* KOBAYASHI characterizes the upper part. On the basis of a global evaluation of the Lower Paleozoic of South America, Aceñolaza (1983) proposed that the Cambrian-Ordovician boundary could be defined at the first appearance of *J. keideli* and *Rhabdinopora flabelliformis* (Graptolithina), meaning that the lower part of the biozone is assignable to the latest Cambrian (see also Salfrity et al., 1984; Moya et al., 1994).

The sierra de Cajas (Eastern Cordillera) and río Volcancito (Famatina Range) have proved to be outstanding localities from the Cambrian-Ordovician transition interval of Argentina (Figs. 1-3). In the sierra de Cajas, an excellent stratigraphic section crops out at the quebrada Azul and quebrada Amarilla, comprising the Lampazar (shales and subordinated sandstones) and Cardonal (sandstones, quartzites, and interbedded shales and limestones) Formations (Aceñolaza, 1968). There, a remarkable conodont biostratigraphic succession, composed of the *Cordylodus proavus*, *C. caboti*, *C. intermedius*, *C. lindstromi* and *C. angulatus* Zones, was described by Rao and Hünicken (1995) and Rao (1999). The Cambrian-Ordovician boundary is at the base of the *C. lindstromi* Zone (Rao, 1999), close to the FAD of *Jujuyaspis keideli*, in the lower part of the Cardonal Formation (upper levels of the Lampazar Formation sensu Rao and Hünicken, 1995; Rao, 1999) (Ortega and Rao, 1995; Tortello et al., 1999). Above these levels, graptolites from the Assemblage Zones 1 (early Tremadoc) and 3 (middle Tremadoc) sensu Erdtmann (1988) have been recorded by Ortega and Rao (1995).

The río Volcancito succession, belonging to the “Lower Member” of the Volcancito Formation (marls, muddy sandstones and shales), bears a succession of conodont zones comparable to those from sierra de Cajas (*Cordylodus proavus*, *C. caboti*, *C. “intermedius”*, *C. lindstromi*, *Iapetognathus* and *Cordylodus angulatus* Zones) (Albanesi et al., 1999; Esteban, 1999). The Cambrian-Ordovician boundary is established at the *Iapetognathus* Zone (Albanesi et al., 1999; Esteban, 1999), a few meters below the first records of *Jujuyaspis keideli* and *Rhabdinopora flabelliformis* (Tortello and Esteban, 1997, 1999; Esteban, 1999, this volume; Esteban et al., 1999).

Other outcrops from the *Parabolina frequens argentina* Biozone of northwestern Argentina provide complementary stratigraphic information. According to data from Harrington and Leanza (1957), the classical section of the río Santa Victoria (Salta, Santa Rosita Formation) encloses the Cambrian-Ordovician transition interval. In addition, other sequences represent intervals assignable either to the late Late Cambrian (e.g. cerro Colorado, Harrington and Leanza, 1957; quebrada de La Huerta, Manca, 1992) or the earliest Tremadoc (e.g. Purmamarca, Aceñolaza, 1996).

## AGNOSTOID FAUNAS OF THE *Parabolina frequens argentina* ZONE

Most of the agnostoid species of the *Parabolina frequens argentina* Zone were described in great detail by Harrington and Leanza (1957). Additional information was provided by Manca (1992), Tortello and Aceñolaza (1993), Moya et al. (1993), Tortello and Esteban (1999), and Tortello et al. (1999). The precise stratigraphic position (above or below the Cambrian-Ordovician boundary) of most of them can be settled in sierra de Cajas and río Volcancito sections (Figs. 2-3). Taking these sections as a reference, it is also possible to discuss the biostratigraphic significance of material described from other localities of the Eastern Cordillera (Fig. 4). On the other hand, the latest Cambrian-earliest Tremadoc agnostoids described from southern Bolivia, as well as some species from Argentina [*Micragnostus tilcuyensis* (KAYSER), “*Ciceragnostus*” *iruyensis* (KAYSER)], are not included in this review.

### Latest Cambrian

The lower part of the *P. frequens argentina* Zone is characterized by a distinctive agnostoid assemblage composed of *Lotagnostus* (*Lotagnostus*) sp., *Lotagnostus* (*Semagnostus*) *zuninoi* (HARRINGTON and LEANZA), *Micragnostus vilonii* HARRINGTON and LEANZA, *M. calviformis* HARRINGTON and LEANZA, *Strictagnostus?* *micropeltis* (HARRINGTON and LEANZA), *Pseudorhaptagnostus* (*Machairagnostus*) *tmetus* HARRINGTON and LEANZA, *Pseudorhaptagnostus* (*Machairagnostus*) cf. *tmetus* HARRINGTON and LEANZA, *Pseudorhaptagnostus* (*Machairagnostus*) sp., *Gymnagnostus bolivianus* (HOEK), *Gymnagnostus perinflatus* HARRINGTON and LEANZA, and *Leiagnostus turgidulus* HARRINGTON and LEANZA. This particular fauna is associated with polymeroids which seem to be restricted to the lower part of the Zone [*Beltella ulrichi* (KAYSER), *Onychopyge*, *Plicatolina scalpta* HARRINGTON and LEANZA] and, also, with olenids which range throughout the whole unit [e.g. *Parabolina frequens argentina* (KAYSER), *Parabolinella coelatifrons* HARRINGTON and LEANZA, *Angelina hyeronimi* (KAYSER)]. Based on this agnostoid-polymeroid fauna, the *Pseudorhaptagnostus* (*Machairagnostus*) - *Gymnagnostus* assemblage Subzone (Lower part of the *P. frequens argentina* Zone, late Late Cambrian) is formally proposed.

This new biostratigraphic unit is based on two stratotypes: the quebrada Azul (sierra de Cajas, Fig. 2), where the subzone ranges throughout the lower 130 m of the Lampazar Formation (Aceñolaza, 1968: p. 211; Tortello and Aceñolaza, 1993: p. 179, Fig. 1); and the río Volcancito section (Fig. 3), comprising the lower 8 m of the “Lower Member” of the Volcancito Formation (Tortello

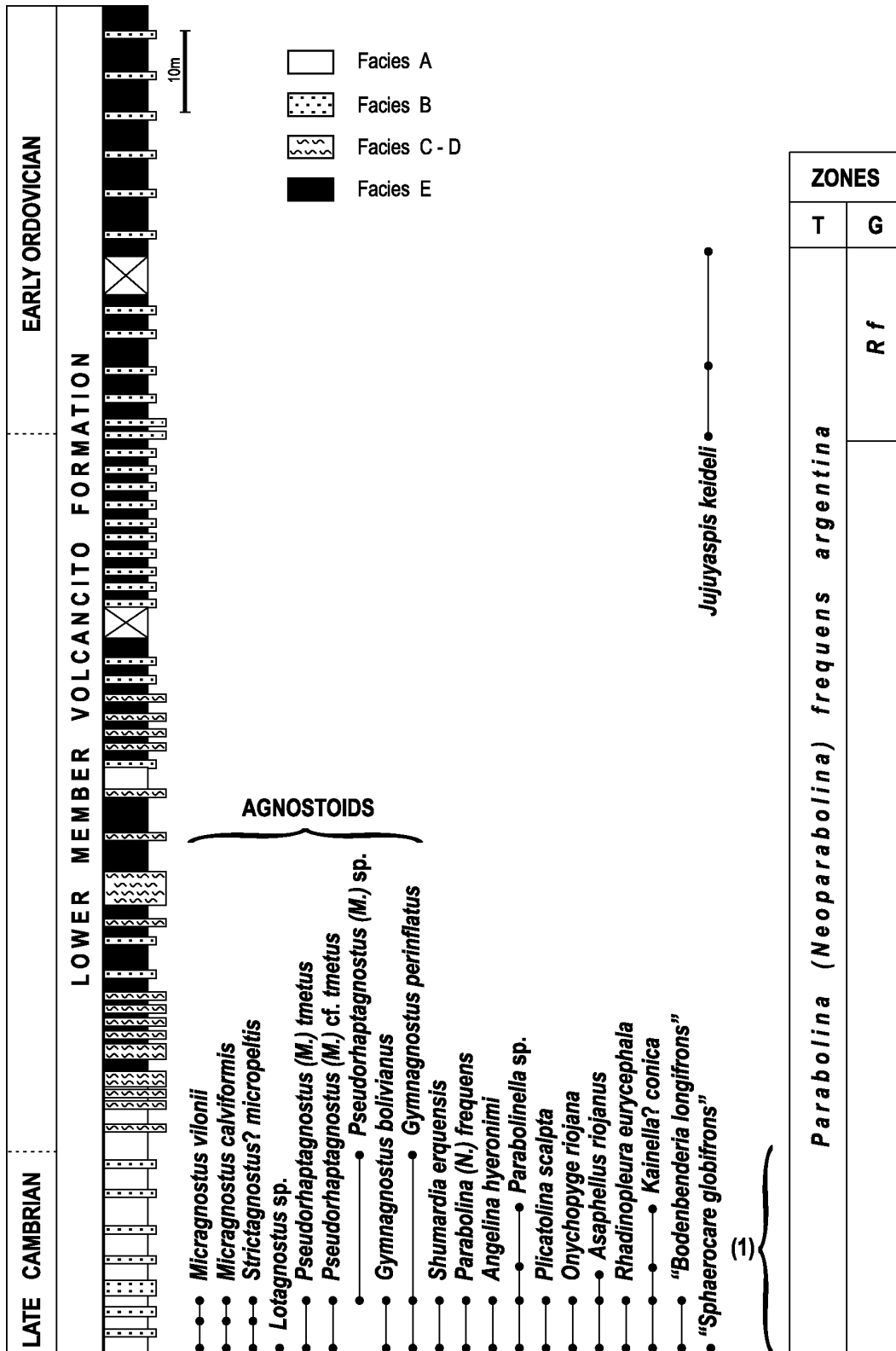


FIGURE 3 | Simplified stratigraphic column and species ranges of trilobites of río Volcancito (río Volcancito section, Lower Member of the Volcancito Formation). Adapted from Esteban, 1999; Tortello and Esteban, 1999; Esteban et al., 1999; Esteban, this volume. Notice the indication (1) of the *Pseudorhaptagnostus (Machairagnostus)* - *Gymnagnostus* Subzone. T: trilobites; G: graptolites; Rf: *Rhabdinopora flabelliformis*; Facies A: thin bedded marls; Facies B: fine grained sandstones; Facies C: massive coarse grained sandstones; Facies D: hummocky cross stratified sandstones and mudstones; Facies E: shales.



and Esteban, 1999: pp. 373-376, fig. 3; Esteban, this volume). The subzone is also well documented at the cerro Colorado locality (Salta; lower levels of the Santa Rosita Formation) (Harrington and Leanza, 1957: pp. 238-239).

**Earliest Ordovician**

Agnostoid diversity drastically declines in the beds very close to the Cambrian-Ordovician boundary in north-western Argentina. *Trilobagnostus chiushuensis* (KOBAYASHI) crosses the boundary in the classical section of sierra de Cajas (Fig. 2; Tortello et al., 1999). Moreover, in the lowest Tremadoc the agnostoid records are mainly restricted to *T. chiushuensis* (Tortello et al., 1999; Tortello and Rao, 2000) and some forms described in open nomenclature (*Anglagnostus?* sp., *Micragnostus* sp.) (Tortello and Aceñolaza, 1999). Definitely, the upper part of the *P. frequens argentina* Zone is better defined by polymeroid trilobites, being *Jujuyaspis keideli keideli* its most characteristic taxon (Aceñolaza, 1983). Following Aceñolaza and Baldis (1987), these levels can be assigned to the “*Jujuyaspis keideli* Subzone”.

**DISCUSSION**

Agnostoids from the *Pseudorhaptagnostus* (*Machairagnostus*) - *Gymnagnostus* Subzone are more diverse than those described from other typical sequences of the Cambrian-Ordovician boundary interval in the Baltic Province (e.g. North Wales, Rushton, 1982; southern Norway, Bruton et al., 1982, 1988; Newfoundland, Fortey et al., 1982; Mexico, Robison and Pantoja-Alor, 1968). Precise international correlation of the unit is difficult because most of its agnostoid species are confined to the Bolivian-Argentinian basin, and many olenid species are rather long-ranging. Nevertheless, the occurrences of different agnostoid taxa indicate a Late Cambrian age.

The widespread subgenus *Lotagnostus* (*Lotagnostus*) has proved to have great biostratigraphic value as a guide for the Late Cambrian. It has been reported from the Upper Cambrian of China, Australia, Kazakhstan, Sweden, North America, Great Britain and Argentina (e.g. Whitehouse, 1936; Jago, 1972; Lu and Lin, 1984; Shergold et al., 1990). Specimens of *Gymnagnostus bolivianus* from Argentina closely resemble those of *Gymnagnostus* from the uppermost Cambrian of Mexico (*Cordylodus proavus* Zone) (Robison and Pantoja-Alor, 1968) and western Newfoundland (*Missisquoia typicalis* Zone) (Fortey et al., 1982). Similarly, *Pseudorhaptagnostus* (*Machairagnostus*) sp. from the Volcancito Formation is most similar to specimens from the Late Cambrian (*Mictosaukia* Zone) of China. *Pseudorhaptagnostus* (*Machairagnostus*) also occurs in the uppermost Cambrian of Korea (Sohn et al., 2000) and the

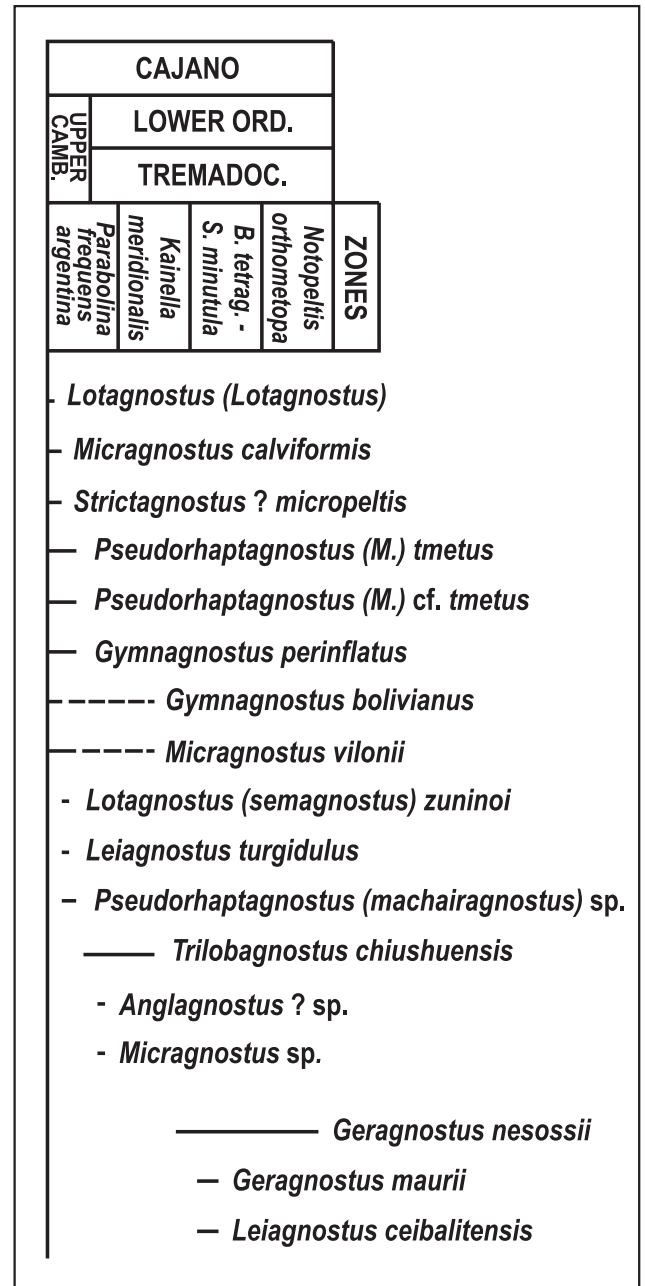


FIGURE 4 | Distribution of the Late Cambrian-early Tremadocian agnostoids from northwestern Argentina. Middle and late Tremadocian species originally assigned to the *P. frequens argentina* Zone are also shown.

lower Tremadoc of Kazakhstan (Nielsen, 1997); and *Strictagnostus* is well known from the uppermost Cambrian of Australia (Shergold, 1975) and the Cambrian-Ordovician transition of North America (Winston and Nicholls, 1967). On the other hand, *Leiagnostus*, *Micragnostus* and *Trilobagnostus* have stratigraphic ranges from the Upper Cambrian to the Lower Ordovician. Since the trilobite fauna from the *Pseudorhaptagnostus* (*Machairagnostus*) -

*Gymnagnostus* Subzone appears associated with, or immediately below conodonts from the *Cordylodus proavus* Zone (Latest Cambrian, see Rao, 1999; Albanesi et al., 1999), it could be equivalent to that from the lower part of the Tiñu Formation (Oaxaca, Mexico; Robison and Pantoja-Alor, 1968).

The proposed subzone seems to be environmentally restricted. Both in Sierra de Cajas and río Volcancito sections, this fauna is better represented in dark shales and limestones which denote a low oxygen environment and presumably cold water facies. According to Nielsen (1997), Cambrian-Early Ordovician representatives of the Agnostidae (e.g. *Lotagnostus*, *Micragnostus*) and *Pseudagnostidae* (e.g. *Pseudorhaptagnostus*) are characteristic of low-oxygen realms.

The faunal impoverishment documented in the upper part of the *Parabolina frequens argentina* Zone could be attributed to the world-wide regressive-transgressive events that characterized the Cambrian-Ordovician transition interval (e.g. Miller, 1995). A regressive event was recorded in sierra de Cajas and río Volcancito below the Cambrian-Ordovician boundary (Rao, 1999; Esteban, 1999; Tortello and Esteban, 1999). *Trilobagnostus chiushuensis* is well represented in the Cardonal Formation (Eastern Cordillera). Following the synonymy proposed by Dean (1989), Sun (1989) and Westrop (1995), this species has a wide geographic distribution (SE and N China, Alaska, Canada, United States, Mexico and Argentina) and a stratigraphic range from the Late Cambrian to the middle Tremadoc (see Tortello et al., 1999). On the other hand, the agnostoids *Micragnostus* sp. and *Anglagnostus?* sp. have been recorded assembled with *Jujuyaspis keideli* KOBAYASHI (Olenidae) at Purmamarca (Jujuy). *Anglagnostus* has been previously described from England, France, Germany and China, and it has a stratigraphic range from the lower Tremadoc to the upper Tremadoc (e.g. Shergold et al., 1990; Nielsen, 1997). The biostratigraphic value of *Jujuyaspis* as a guide for the lowermost Tremadoc has been pointed out by Aceñolaza and Aceñolaza (1992).

## UPDATED BIOSTRATIGRAPHIC POSITION OF THE AGNOSTOID SPECIES

Updated occurrences and biostratigraphic ranges of the agnostoids from the *Parabolina frequens argentina* Biozone (latest Cambrian-Early Ordovician) are summarized below.

*Lotagnostus* (*Lotagnostus*): the occurrences of this subgenus in the basal part of the Volcancito Formation (Tortello and Esteban, 1999: fig. 5A), the Lampazar For-

mation, and the lower portion of the Santa Rosita Formation (quebrada de La Huerta, Eastern Cordillera; Manca, 1992: fig. 2) provide important evidence in support of a Late Cambrian age for the lower part of the *Parabolina frequens argentina* Zone.

*Lotagnostus* (*Semagnostus*) *zuninoi* (HARRINGTON AND LEANZA): Nielsen (1997) designated this taxon as the type species of *L. (Semagnostus)*. Based on Harrington and Leanza (1957: figs. 19, 21:6a-c) and Tortello and Aceñolaza (1993: lám. 1, fig. 12), Nielsen (1997) indicated a ?Late Cambrian-early Tremadoc age for the species. *Lotagnostus* (*S.*) *zuninoi* has been described from sierra de Cajas (Tortello and Aceñolaza, 1993), cerro Colorado (Harrington and Leanza, 1957, loc. S.Iru-3.C) and Santa Victoria (ibidem, loc. S.Vic-1.D) (Eastern Cordillera), being part of an assemblage which, according to the scheme proposed here, is indicative of the Late Cambrian.

*Micragnostus calviformis* HARRINGTON and LEANZA: up to the present, *M. calviformis* has been described only from the basal part of the Volcancito Formation (Late Cambrian) (Harrington and Leanza, 1957: figs. 16, 17: 3a-b; Tortello and Esteban, 1999: figs. 5B-D).

*Micragnostus vilonii* HARRINGTON and LEANZA: this species was described from the uppermost Cambrian of sierra de Cajas (Tortello and Aceñolaza, 1993: lám. 1, figs. 1-4) and río Volcancito (Tortello and Esteban, 1999: figs. 5E-F). In addition, Harrington and Leanza (1957: figs. 12 and 13:7-8) described it from three other localities of the Eastern Cordillera: Santa Victoria (ibidem, loc. S.Vic-1.F, S.Vic-18.VO2), cerro Colorado (ibidem, loc. S.Iru-3.C) and La Caldera (ibidem, loc. S.Cal-2, S.Cal-5). Santa Victoria and cerro Colorado assemblages seem to be assignable, according to the scheme proposed here, to the Late Cambrian. On the other hand, specimens from La Caldera are associated with a typical fauna of the *Kainella meridionalis* Zone (Early Ordovician) (see Harrington and Leanza, 1957).

*Gymnagnostus bolivianus* (HOEK): although the records of this species are confined to the northwestern Argentina-southern Bolivia basins, forms very similar to *G. bolivianus* were described from the uppermost Cambrian of Mexico (Robison and Pantoja-Alor, 1968) and Newfoundland (Fortey et al., 1982). In Argentina, the occurrences with major biostratigraphic control correspond to the uppermost Cambrian of sierra de Cajas (Tortello and Aceñolaza, 1993: lám. 1, figs. 5-6) and río Volcancito (Harrington and Leanza, 1957; Tortello and Esteban, 1999: figs. 5N-O). In addition, Harrington and Leanza (1957: figs. 21:2a-b) described *G. bolivianus* from Santa Victoria (ibidem, loc. S.Vic-1.F, S.Vic-19.A48), Orán (ibi-

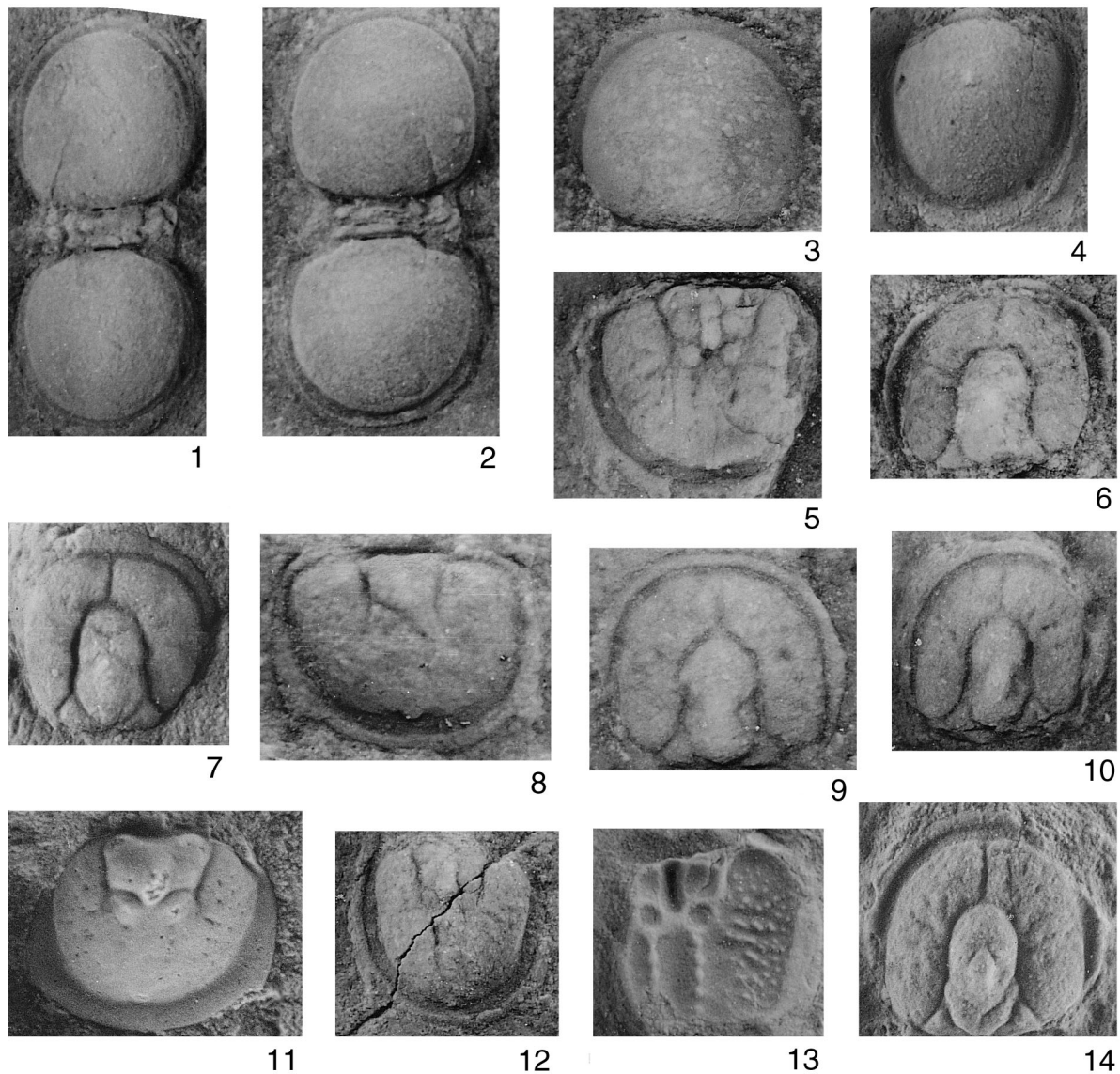


FIGURE 5 | Selected *Gymnagnostus* and *Pseudorhaptagnostus* (*Machairagnostus*) taxa from the uppermost Cambrian [*P. (Machairagnostus)* - *Gymnagnostus* Subzone] of northwestern Argentina. The material is housed in the paleontological collections of Universidad Nacional de Tucumán (PIL) and Museo de La Plata (MLP). 1-3. *Gymnagnostus bolivianus* (HOEK), 1, complete specimen, PIL 13846 (x 6.6), from sierra de Cajas; 2, complete specimen, PIL 13847 (x 6.7), from sierra de Cajas; 3, cephalon, PIL 13926 (x 10.3), from río Volcancito. 4. *Gymnagnostus perinflatus* (HARRINGTON and LEANZA), pygidium, PIL 14081 (x 6.6), from sierra de Cajas. 5-6, 9-10, 12-14. *Pseudorhaptagnostus* (*Machairagnostus*) cf. *tmetus* HARRINGTON and LEANZA, 5, pygidium, PIL 13844 (x 6.3), from sierra de Cajas; 6, cephalon, PIL 11394 (x 7.9), from río Volcancito; 9, cephalon, PIL 13971 (x 13), from sierra de Cajas; 10, cephalon, PIL 13972 (x 7), from sierra de Cajas; 12, pygidium, PIL 13984 (x 5.8), from sierra de Cajas; 13, incomplete pygidium (external mould), PIL 13983 (x 6.7), from sierra de Cajas; 14, cephalon, PIL 13975 (x 6.4), from sierra de Cajas. 7-8. *Pseudorhaptagnostus* (*Machairagnostus*) *tmetus* HARRINGTON and LEANZA, from sierra de Cajas; 7, cephalon, PIL 13967 (x 10); 8, pygidium, PIL 13969 (x 10.4). 11. *Pseudorhaptagnostus* (*Machairagnostus*) sp., pygidium, MLP 28268 (x 8.1), from río Volcancito.

dem, loc. S.Ora-2, S.Ora-5), Nazareno River (ibidem, loc. S.Iru-5.54) and Tilcara (ibidem, loc. J.Til-2) (Eastern Cordillera). Some of the latter localities would be assignable to the Lower Ordovician: in Santa Victoria River and Nazareno River, Harrington and Leanza (1957) cited *G. bolivianus* in association with *Jujuyaspis keideli* and

*Kainella meridionalis*, respectively. According to all these data, the species seems to have a stratigraphic range from the Late Cambrian to the Early Tremadoc.

*Gymnagnostus perinflatus* (HARRINGTON and LEANZA): up to the present, *G. perinflatus* has been described from



the basal parts of the Volcancito and Lampazar Formations (Late Cambrian) (Harrington and Leanza, 1957: fig. 21:3; Tortello and Esteban, 1999: figs. 5P-T; Tortello, unpublished doctoral thesis 1995).

*Strictagnostus? micropeltis* (HARRINGTON and LEANZA): as *Micragnostus calviformis*, this taxon has been described only from the basal part of the Volcancito Formation (Late Cambrian) (Harrington and Leanza, 1957: figs. 13:6 and 15; Tortello and Esteban, 1999: figs. 5G-I). Tortello and Esteban (1999) reassigned the species to *?Strictagnostus* SHERGOLD. As the type species *Strictagnostus chronius* SHERGOLD, from the Chatsworth Limestone at Black Mt. (Queensland, Australia) (Shergold, 1975: text-fig. 21, pl. 13, figs. 1-6), *S.? micropeltis* is Late Cambrian in age.

*Pseudorhaptagnostus (Machairagnostus) tmetus* HARRINGTON and LEANZA: this species was described from several localities of the Eastern Cordillera and Famatina (Harrington and Leanza, 1957: figs. 6 and 7:1-5). The assemblages from Yavi (ibidem, loc. J.Yav-2.L2), Santa Victoria (ibidem, loc. S.Vic-17.VP5, S.Vic-18.VO2) and cerro Colorado (ibidem, loc. S.Iru-2, S.Iru-3) are very similar to those from the uppermost Cambrian of sierra de Cajas (Tortello and Aceñolaza, 1993: p. 179) and río Volcancito (Harrington and Leanza, 1957; Tortello and Esteban, 1999: fig. 5J). Apparently, this species does not range above the Late Cambrian.

*Pseudorhaptagnostus (Machairagnostus) cf. tmetus* HARRINGTON and LEANZA: this taxon is a characteristic element of the lower part of sierra de Cajas and río Volcancito sections (Tortello and Aceñolaza, 1993: lám. 1, figs. 8-11; Tortello and Esteban, 1999: figs. 5K-L) (Late Cambrian). According to Tortello and Esteban (1999: pp. 381-382), *P. (M.) cf. tmetus* is strongly similar to both *P. (M.) tmetus* and *P. (M.) corrugatus*, from southern Bolivia (Suárez Soruco, 1975: pl. 1, fig. 5). Further systematic studies are necessary in order to establish the specific affinities of this taxon.

*Pseudorhaptagnostus (Machairagnostus) sp.*: this taxon was described on the basis of two pygidia collected from the basal part of the Volcancito Formation (uppermost Cambrian) (Tortello and Esteban, 1999: fig. 5M). The specimens closely resemble species from the uppermost Cambrian of N and NE China (Tortello and Esteban, 1999).

*Leiagnostus turgidulus* HARRINGTON and LEANZA: *Leiagnostus turgidulus* was originally erected on the basis of a complete specimen from cerro Colorado (Harrington and Leanza, 1957: p. 76; loc. S.Iru-3.C), three cephalae from río Iturbe (ibidem, loc. J.Hum-6.A8), and a complete specimen from the quebrada de Pingüiyal (southern Mojotoro Range) (ibidem, loc. Cer-1.PG37).

Later, Tortello and Aceñolaza (1993) added material from the lower part of the sierra de Cajas section. Recently, Tortello (1998) has reconsidered the identity and the stratigraphic position of the specimen from quebrada de Pingüiyal (= *Leiagnostus ceibalitensis* TORTELLO, early late Tremadoc), and has regarded unassignable the cephalae from río Iturbe (lower upper Tremadoc, *Shumardia minutula-Bienvillia tetragonalis* Zone). Thus, *Leiagnostus turgidulus* is here considered to be based on material from sierra de Cajas (Tortello and Aceñolaza, 1993: lám. 1, fig. 7) and cerro Colorado (Harrington and Leanza, 1957: fig. 21:1a). In both localities, *L. turgidulus* occurs as part of an assemblage assignable to the Late Cambrian.

*Trilobagnostus chiushuensis* (KOBAYASHI): in Argentina, the Cambrian occurrences of this taxon are restricted to the basal part of the Cardonal Formation in sierra de Cajas (Tortello et al., 1999: figs. 3A-C). Besides, *T. chiushuensis* is better documented in the Tremadoc; it was described from the lower Tremadoc (upper part of the *Parabolina frequens argentina* Zone - *Kainella meridionalis* Zone) of sierra de Cajas (Tortello et al., 1999: figs. 3A-C) and the Angosto de Lampazar (Tortello and Rao, 2000, figs. 3A-C); and from the upper lower Tremadoc (*Kainella meridionalis* Zone) of the cerro Gólgota (Incamayo Creek, Salta) (Rao and Tortello, 1998: figs. 4A-F). A fragmentary cephalon from the Lower Ordovician of the Puna, tentatively assigned to *Geragnostus* sp. aff. *G. intermedius* (Moya et al., 1993: lám. 1, fig. 1), is probably conspecific.

*Anglagnostus? sp.*: this taxon was described on the basis of a few specimens collected from the Purmamarca Shales (Purmamarca, Jujuy Province) (Tortello and Aceñolaza, 1999: figs. 2A-B). The co-occurrence of *Jujuyaspis keideli* supports a basal Tremadoc age.

*Micragnostus sp.*: this taxon was described associated with *Anglagnostus? sp.* at Purmamarca (Tortello and Aceñolaza, 1999: figs. 2C-D) (see above).

## MIDDLE AND LATE TREMADOCIAN AGNOSTOIDS ORIGINALLY ASSIGNED TO THE *P. frequens argentina* ZONE

Some agnostoids originally assigned to the *P. frequens argentina* Zone have proved to be middle and late Tremadoc in age, as follows: *Geragnostus nesossii* HARRINGTON and LEANZA (= *Geragnostus neumanni*, see Tortello, 1996): Harrington and Leanza (1957: figs. 9:1-5, 10) originally described *G. nesossii* based on material from both the headwater region of the quebrada de Lampazar (Saladillo Formation, *Kainella meridionalis* and *Bienvillia tetragonalis-Shumardia minutula* Zones; loc.

S.Ros-12.P14) and the quebrada de Pingüiyal (southern Mojotoro Range, "Pingüiyal shales", loc. S.Cer-1). Subsequently, Tortello (1996) described specimens from the *Notopeltis orthometopa* Zone of the quebrada de Acoite (Santa Victoria region; upper part of the Santa Rosita Formation) and quebradas de Coquena and Chalala (Puramarca area; "Coquena shales"). Harrington and Leanza (1957) assigned the material from the quebrada de Pingüiyal to the *Parabolina frequens argentina* Zone (lower lower Tremadoc). Nevertheless, González (1983; see also Tortello, 1996, 1998) reassigned a part of the "Pingüiyal shales", bearing *Geragnostus nesossii*, *G. maurii* HARRINGTON and LEANZA, *Parabolinella argentinensis* KOBAYASHI, *Bienvillia tetragonalis* (HARRINGTON), *Apatokephalus exiguus* HARRINGTON and LEANZA, and *Iliaenopsis stenorhachis* (HARRINGTON), to the *Bienvillia tetragonalis-Shumardia minutula* Zone (lower upper Tremadoc).

*Geragnostus maurii* HARRINGTON and LEANZA: this species was collected associated with *Geragnostus nesossii* in the quebrada de Pingüiyal (southern Mojotoro Range) (Harrington and Leanza, 1957: figs. 8, 9:6; loc. S.Cer-1), from levels of the "Pingüiyal Shales" reassigned to the lower upper Tremadoc (*Bienvillia tetragonalis-Shumardia minutula* Zone; González, 1983; Tortello, 1996; see *G. nesossii*).

## CONCLUSIONS

The uppermost Cambrian of northwestern Argentina is characterized by a distinctive agnostoid fauna and associated polymeroids. Based on this trilobite assemblage, the lower part of the *Parabolina* (*Neoparabolina*) *frequens argentina* Zone is assigned to the *Pseudorhaptagnostus* (*Machairagnostus*) - *Gymnagnostus* Subzone (late Upper Cambrian).

The proposed stratotypes of the subzone (quebrada Azul, sierra de Cajas; río Volcancito, sierra de Famatina) are suitable references for regional correlation with other sections from Eastern Cordillera of Bolivia and Argentina. Although the described agnostoid species seem to be confined to southwestern Gondwana, the occurrences of *Lotagnostus*, *Pseudorhaptagnostus* (*Machairagnostus*), *Gymnagnostus* and *Strictagnostus* provide a basis for intercontinental correlation.

Agnostoid diversity drastically declines through the Cambrian-Ordovician boundary probably as a consequence of a regional regressive-transgressive event. The upper part of the *P. frequens argentina* Zone is better defined by polymeroid trilobites, being *Jujuyaspis keideli* its most characteristic species (*J. keideli* Subzone).

## ACKNOWLEDGEMENTS

My particular thanks to F. G. Aceñolaza and A. C Riccardi for their valuable comments and advice. Thanks are also due to G. F. Aceñolaza, S. B. Esteban and R. I. Rao for their help and fruitful discussions. M. Campaña produced the line illustrations and S. Castro copied the photographs. Support has been provided by the Instituto Superior de Correlación Geológica (Tucumán) and the Consejo Nacional de Investigaciones Científicas y Técnicas. L. Cabrera and J. H. Shergold improved the manuscript with their constructive suggestions.

## REFERENCES

- Aceñolaza, F.G., 1968. Geología estratigráfica de la región de la Sierra de Cajas, Dpto. Humahuaca (Provincia de Jujuy). *Revista de la Asociación Geológica Argentina*, 23(3), 207-222.
- Aceñolaza, F.G., 1983. The Tremadocian beds and the Cambrian-Ordovician boundary problems in Latin America. In: *Papers for the Symposium on the Cambrian-Ordovician and Ordovician-Silurian Boundaries*, Nanjing Institute of Geology and Palaeontology, Academia Sinica, 88-93.
- Aceñolaza, F.G., Aceñolaza, G.F., 1992. The genus *Jujuyaspis* as a world reference fossil for the Cambrian-Ordovician boundary. In: Webby, B.D., Laurie, J.R. (eds.). *Global Perspectives on Ordovician Geology*, Balkema, Rotterdam, 115-120.
- Aceñolaza, F.G., Baldis, B.A.J., 1987. The Ordovician System of South America. IUGS Publication, 22, 1-68.
- Aceñolaza, G.F., 1996. Bioestratigrafía del límite Cámbrico-Ordovícico y Ordovícico basal en la quebrada de Humahuaca, provincia de Jujuy, República Argentina. Doctoral Thesis. Universidad Nacional de Tucumán. 245 pp.
- Ahlberg, P., 1989. Agnostid trilobites from the Lower Ordovician Komstad Limestone Formation of Killeröd, Scania, Sweden. *Palaeontology*, 32(3), 553-570.
- Ahlberg, P., 1992. Agnostid trilobites from the Lower Ordovician of southern Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 83, 539-570.
- Albanesi, G.L., Esteban, S.B., Barnes, C.R., 1999. Conodontes del intervalo del límite Cámbrico-Ordovícico en la Formación Volcancito, Sistema de Famatina, Argentina. *Temas Geológico-Mineros*, Instituto Tecnológico Geominero de España, 26, 521-526.
- Benedetto, J.L., 1977. Una nueva fauna de trilobites tremadocianos de la Provincia de Jujuy (Sierra de Cajas), Argentina. *Ameghiniana*, 14, 186-214.
- Bruton, D.L., Erdtmann, B.D., Koch, L., 1982. The Naersnes section, Oslo Region, Norway: a candidate for the Cambrian-Ordovician boundary stratotype at the base of the Tremadoc Series. In: Basset, M.G., Dean, W.T. (eds.). *The Cambrian-Ordovician boundary: sections, fossils distributions, and correlations*. National Museum of Wales, Geological Series, 3, 61-69.

- Bruton, D.L., Koch, L., Repetski, J.E., 1988. The Naersnes section, Oslo Region, Norway: trilobite, graptolite and conodont fossils reviewed. *Geological Magazine*, 125(4), 451-455.
- Dean, W.T., 1989. Trilobites from the Survey Peak, Outram and Skoki Formations (Upper Cambrian-Lower Ordovician) at Wilcox Pass, Jasper National Park, Alberta. *Geological Survey of Canada Bulletin*, 389, 1-141.
- Erdtmann, B.D., 1988. The earliest Ordovician nematophorid graptolites: taxonomy and correlation. *Geological Magazine*, 125(4), 327-348.
- Esteban, S.B., 1999. Estratigrafía, geología sedimentaria y paleontología del Ordovícico basal del Sistema de Famatina. Unpublished Ph.D. thesis, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina.
- Esteban, S.B., 2003. Biogenic and physical sedimentary structures in latest Cambrian-earliest Ordovician mudrocks facies (Famatina Range, northwestern Argentina). *Geológica Acta*, 85-94.
- Esteban, S.B., Tortello, M.F., Mángano, M.G., Buatois, L.A., Aceñolaza, F.G., 1999. Bioestratigrafía del Paleozoico Inferior del Sistema de Famatina. In: Bonorino, G., Omarini, R., Viramonte, J. (eds.), *Geología del Noroeste Argentino, Relatorio del XIV Congreso Geológico Argentino*, 217-223.
- Fortey, R.A., 1975. Early Ordovician trilobite communities. *Fossils and Strata*, 4, 331-352.
- Fortey, R.A., Landing, E., Skevington, D., 1982. Cambrian-Ordovician boundary sections in the Cow-Head Group, Western Newfoundland. In: Basset, M.G., Dean, W.T. (eds.). *The Cambrian-Ordovician boundary: sections, fossils distributions, and correlations*. National Museum of Wales, Geological Series, 3, 95-129.
- González, C.E., 1983. Evaluación faunística del Tremadociano del tramo austral de la sierra de Mojotoro, provincia de Salta, República Argentina. Professional Thesis. Universidad Nacional de Salta. 35 pp.
- Harrington, H.J., Leanza, A.F., 1957. Ordovician trilobites of Argentina. Department of Geology, University of Kansas Special Publication, 1, 276 pp.
- Jago, J.B., 1972. The youngest recorded Tasmanian Cambrian trilobites. *Search* 3(5), 173-174.
- Kayser, E., 1876. Über primordiale und untersilurische Fossilien aus der Argentinischen Republik. *Palaeontographica, Supplementum* 3, Lieferung 2, Theil II. In *Actas de la Academia Nacional de Ciencias*, 8, 297-332.
- Kayser, E., 1897. Beiträge zur Kenntnis einiger paläozoischer Faunen Südamerikas. *Zeitschrift der deutschen Geologischen Gesellschaft*, 49, 274-317.
- Kobayashi, T., 1931. Studies on the Stratigraphy and Palaeontology of the Cambro-Ordovician Formation of Hua-Lien-Chai and Niu-Hsin-Tai, south Manchuria. *Japanese Journal of Geology and Geography*, 8 (3), 131-189.
- Kobayashi, T., 1936. On the *Parabolinella* Fauna from Province Jujuy, Argentina with a note on the Olenidae. *Japanese Journal of Geology and Geography*, 13(1-2), 85-102.
- Kobayashi, T., 1937. The Cambro-Ordovician shelly faunas of South America. *Journal of the Faculty of Science, Imperial University of Tokyo, Section 2*, 4(4), 369-522.
- Lu, Y., Lin, H., 1984. Late late Cambrian and earliest Ordovician trilobites of Jiangshan-Changshan Area. In: *Stratigraphy and Palaeontology of Systemic Boundaries in China, Cambrian-Ordovician Boundary*, Anhui Science and Technology Publishing House, 1, 45-143.
- Ludvigsen, R., 1982. The Cambrian-Ordovician boundary in the western District of Mackenzie, Canada. In: Basset, M.G., Dean, W.T. (eds.). *The Cambrian-Ordovician boundary: sections, fossils distributions, and correlations*. National Museum of Wales, Geological Series, 3, 141-153.
- Manca, N., 1992. El género *Lotagnostus* (Trilobita, Agnostida) en la Formación Santa Rosita (Jujuy, Argentina) y su significado cronológico. *Ameghiniana*, 29, 45-48.
- Miller, J.F., 1995. Acid insoluble residues, regressive-transgressive events, and conodont biostratigraphy in the Upper Cambrian and Lower Ordovician of western Utah and Central Texas. *Ordovician Odyssey: Short Papers for the seventh International Symposium on the Ordovician System*, 99-104.
- Moya, M.C., Malanca, S., Hongn, F.D., Bahlburg, H., 1993. El Tremadoc temprano en la Puna occidental argentina. XII Congreso Geológico Argentino y II Congreso de Exploración de Hidrocarburos, Mendoza, *Actas*, 2, 20-30.
- Moya, M.C., Malanca, S., Monteros, J.A., Cuerda, A.J., 1994. Bioestratigrafía del Ordovícico Inferior en la Cordillera Oriental Argentina basada en graptolitos. *Revista Española de Paleontología*, 9(1), 91-104.
- Nielsen, A.T., 1997. A review of Ordovician agnostid genera (Trilobita). *Transactions of the Royal Society of Edinburgh, Earth Sciences*, 87, 463-501.
- Ortega, G., Rao, R.I., 1995. Nuevos hallazgos de graptolitos (Ordovícico Inferior) en la sierra de Cajas, Departamento Humahuaca, Provincia de Jujuy, Argentina. *Boletín de la Academia Nacional de Ciencias*, 60(3-4), 293-316.
- Rao, R.I., 1999. Los conodontes Cambro-Ordovícicos de la sierra de Cajas y del Espinazo del Diablo, Cordillera Oriental, República Argentina. *Revista Española de Micropaleontología*, 31(1), 23-51.
- Rao, R.I., Hünicken, M.A., 1995. Conodont biostratigraphy of the Cambrian-Ordovician boundary in northwestern Argentina. *Ordovician Odyssey: Short Papers for the seventh International Symposium on the Ordovician System*, 125-128.
- Rao, R.I., Tortello, M.F., 1998. Tremadoc conodonts and trilobites from the Cardonal Formation, Incamayo Creek, Salta Province, northwestern Argentina. *Palaeontologia Polonica*, 58, 31-45.
- Robison, R.A., Pantoja-Alor, J., 1968. Tremadocian trilobites from the Nochixtlán region, Oaxaca, Mexico. *Journal of Paleontology*, 42(3), 767-800.
- Rushton, A.W.A., 1982. The biostratigraphy and correlation of the Merioneth-Tremadoc Series boundary in North Wales. In: Basset, M.G., Dean, W.T. (eds.). *The Cambrian-Ordovician boundary: sections, fossils distributions, and correlations*.

- National Museum of Wales, Geological Series, 3, 41-59.
- Salfity, J.A., Malanca, S., Moya, M.C., Monaldi, C.R., Brandán, E.M., 1984. El límite Cámbrico-Ordovícico en el norte de la Argentina. IX Congreso Geológico Argentino, Actas, 1, 568-575.
- Shergold, J.H., 1975. Late Cambrian and Early Ordovician trilobites from the Burke River Structural Belt, Western Queensland, Australia. Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, 153 (2 volumes).
- Shergold, J.H., 1981. Towards a global Late Cambrian agnostid biochronology. II International Symposium on the Cambrian System, Short Paper, 208-214.
- Shergold, J.H., 1988. Review of trilobite biofacies distributions at the Cambrian-Ordovician Boundary. Geological Magazine, 125(4), 363-380.
- Shergold, J.H., Laurie, J.R., Sun, X., 1990. Classification and review of the trilobite Order Agnostida Salter, 1864: an Australian perspective. Bureau of Mineral Resources, Geology and Geophysics Report, 296, 1-93.
- Sohn, J., Kim, D.H., Choi, D.K., 2000. An uppermost Cambrian trilobite fauna from the Yongwol Group, Taebaeksan Basin, Korea. In: Aceñolaza, G.F. and Peralta, S. (eds.), Cambrian from the southern edge, INSUGEO, Miscelánea 6, 135-136.
- Steinmann, G., Hoek, H., 1912. Das Silur und Cambrium des Hochlandes von Bolivia und ihre Fauna. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, 34, 176-252.
- Suárez-Soruco, R., 1975. Nuevos trilobites del Tremadociano inferior del sur de Bolivia. Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos, 4, 129-146.
- Sun, X., 1989. Cambrian agnostids from the North China Platform. Palaeontologia Cathayana, 4, 53-129.
- Tortello, M.F., 1995. El Orden Agnostida (Trilobita, Cámbrico-Ordovícico) en la República Argentina. Unpublished Ph.D. thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina. 295 p.
- Tortello, M.F., 1996. *Geragnostus nesossii* Harrington y Leanza, 1957 (Trilobita, Agnostida) en el Tremadociano superior del noroeste argentino. XII Congreso Geológico Argentino y III Congreso de Exploración de Hidrocarburos, Buenos Aires, Actas, 5, 17-25.
- Tortello, M.F., 1998. Una nueva especie de *Leiagnostus* (Trilobita, Agnostida) en el Tremadociano superior (Ordovícico Inferior) de Salta, Argentina. Ameghiniana, 35(1), 97-99.
- Tortello, M.F., Aceñolaza, G.F., 1993. Trilobites agnóstidos del límite Cámbrico-Ordovícico de la Formación Lampazar, Sierra de Cajas, Provincia de Jujuy, Argentina. Revista Española de Paleontología, 8(2), 177-184.
- Tortello, M.F., Aceñolaza, G.F., 1999. Trilobites agnóstidos del Ordovícico basal en la localidad de Purmamarca, Provincia de Jujuy, Argentina. Temas Geológico-Mineros, Instituto Tecnológico Geominero de España, 26, 585-588.
- Tortello, M.F., Esteban, S.B., 1997. Significado bioestratigráfico de una asociación de trilobites del tramo basal de la Formación Volcancito (Sistema de Famatina, La Rioja, Argentina). Ameghiniana, 34(3), 265-270.
- Tortello, M.F., Esteban, S.B., 1999. La transición Cámbrico-Ordovícico en la Formación Volcancito (sierra de Famatina, La Rioja, Argentina). Ameghiniana, 36(4), 371-387.
- Tortello, M.F., Rábano, I., Rao, R.I., Aceñolaza, F.G., 1999. Los trilobites de la transición Cámbrico-Ordovícico en la quebrada Amarilla (sierra de Cajas, Jujuy, Argentina). Boletín Geológico y Minero (España), 110(5), 555-572.
- Westrop, S.R., 1995. Sunwaptan and Ibexian (Upper Cambrian-Lower Ordovician) trilobites of the Rabbitkettle Formation, Mountain River region, northern Mackenzie Mountains, northwest Canada. Palaeontographica Canadiana, 12, 1-75.
- Whitehouse, F.W., 1936. The Cambrian faunas of Northeastern Australia. Parts 1-2. Memoirs of the Queensland Museum, 11, 59-112.
- Winston, D., Nicholls, H., 1967. Late Cambrian and Early Ordovician Faunas from the Wilberns Formation of Central Texas. Journal of Paleontology, 41(1), 66-96.

Manuscript received October 2001;  
revision accepted May 2002.