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First evidence of Lower–?Middle Ordovician (Floian–?Dapingian) brachiopods from the Peruvian Altiplano and their paleogeographical significance

Jorge Colmenar[1] ⬤ and Eben Blake Hodgin[2]

[1]Centro de Geociências, Universidade de Coimbra, Coimbra 3000-272, Portugal <jorgecolmenarlallena@gmail.com>
[2]Department of Earth and Planetary Sciences, Harvard University, Cambridge, MA 02138, USA hodgin@fas.harvard.edu

Abstract.—The lower strata of the Umachiri Formation from the Altiplano of southeast Peru have yielded a brachiopod-dominated assemblage, containing representatives of the brachiopod superfamilies Polytoechioidea, Orthoidea, and Porambonitoidea, as well as subsidiary trilobite and echinoderm remains. Two new polytoechioid genera and species, *Enriquetoechia umachiriensis* new genus new species and *Altiplanotoechia hodgini* n. gen. n. sp. Colmenar in Colmenar and Hodgin, 2020, and one new species, *Pomatotrema laubacheri* n. sp., are described. The presence of *Pomatotrema* in the Peruvian Altiplano represents the occurrence at highest paleolatitude of this genus, normally restricted to low-latitude successions from Laurentia and South China. Other polytoechioids belonging to *Tritoechia* (*Tritoechia*) and *Tritoechia* (*Parvitritoechia*) also occur. Identified species of orthoids from the genera *Paralenorthis*, *Mollesella*, and *Panderina*? occur in the Peruvian Cordillera Oriental and in the Argentinian Famatina Range. The only porambonitoid represented is closely related to *Rugostrophia latireticulata* Neuman, 1976 from New World Island, interpreted as peri-Laurentian. These brachiopod occurrences indicate a strong biogeographic affinity of the Peruvian Altiplano with the Famatina and western Puna regions, suggesting that the brachiopod faunas of the Peruvian Altiplano, Famatina, and western Puna belonged to a well-differentiated biogeographical subprovince during the Early–Middle Ordovician on the margin of southwestern Gondwana. Links with peri-Laurentian and other low-latitude terranes could be explained by island hopping and/or continuous island arcs, which might facilitate brachiopod larvae dispersal from the Peruvian Altiplano to those terranes across the Iapetus Ocean. Brachiopods from the lower part of the Umachiri Formation indicate a Floian–?Dapingian age, becoming the oldest Ordovician fossils of the Peruvian Altiplano.

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Introduction

The paleobiogeography of the Central Andes during the Ordovician has been extensively investigated using benthic fossil groups such as brachiopods from Argentina (Benedetto et al., 2009 and references therein), Chile (Benedetto et al., 2008), Bolivia (Havlíček and Branisa, 1980; Benedetto, 2013), and Peru (Hughes et al., 1980; Gutiérrez-Marco and Villas, 2007; Villas et al., 2015); trilobites from Argentina (Tortello and Esteban, 2003; Waisfeld and Vaccari, 2003 and references therein), Bolivia (Přibyl and Vaněk, 1980), and Peru (Hughes et al., 1980; Gutiérrez-Marco et al., 2015); bivalves and rostroconch mollusks from Argentina (Sánchez, 2003, 2008, and references therein) and Bolivia (Babin and Branisa, 1987; Sánchez and Babin, 2005); sponges from Argentina (Carrera and Rigby, 1999; Carrera, 2003); and ostracods from Argentina (Salas, 2002a, b; Williams et al., 2003).

The Tremadocian–Floian brachiopod assemblages of the Cordillera Oriental, including its Argentinian, Bolivian, and Peruvian segments, show high endemism during this time, sharing only one genus with the western Puna Region of Argentina (*Lipanorthis* Benedetto in Benedetto and Carrasco, 2002),

suggesting proximity but a certain degree of isolation between these two regions. The faunal affinity in the Cordillera Oriental indicates a strong peri-Gondwanan influence (from both high and low latitudes) as demonstrated by the occurrence of Kvania Havlíček, 1994, *Gondwanorthis* Benedetto and Muñoz, 2017, *Euorthisina* Havlíček, 1950, and *Tarfaya* Havlíček, 1971. Celtic genera (*Astraborthis* Williams, 1974 and *Monorthis* Bates, 1968) are also present in the assemblages of the Cordillera Oriental, implying direct links with Avalonia during Tremadocian and Floian times.

The Argentinian western Puna and Famatina Lower Ordovician assemblages have several taxa in common such as the genera *Hesperonomia* Ulrich and Cooper, 1936, *Tritoechia* Ulrich and Cooper, 1936, and *Rugostrophia* Neuman, 1971 and the species *Monorthis transversa* Benedetto, 2003 and even share endemic genera such as *Pinatotoechia* Benedetto, 2001 and *Trigonostrophia* Benedetto, 2003. Faunal evidence is consistent with the existence of a continuous Puna–Famatinian arc likely connecting with Avalonia (Benedetto, 1998; Ramos, 2018) and retroarc foreland basin (Astini and Dávila, 2004) extending between these two regions along the proto-Andean margin of Gondwana (Benedetto, 1998). Despite the

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strong endemicity of the Puna–Famatinian brachiopod assemblages, certain faunal exchange with other regions occurred during that time as suggested by associations of several Celtic and low-latitude genera (*Schizambon* Walcott, 1884, *Rugostrophia, Ffynnonia* Neuman and Bates, 1978, and *Hesperonomia* Ulrich and Cooper, 1936), minor representatives of high-latitude peri-Gondwana (*Incorthis* Havlíček and Branisa, 1980), and abundant cosmopolitan genera. The Celtic signature of the Puna–Famatinian assemblages was also supported by multivariate analysis (Benedetto, 2004; Benedetto et al., 2009). Faunal exchange among the Central Andean Basin (comprising the Altiplano/Puna, the Cordillera Oriental, and the Subandean Ranges), the Famatina Basin, and the Cuyania Terrane (Precordillera) likely started during the late Floian–Dapingian, slightly before the estimated time for docking of the Cuyania Terrane against Gondwana (Benedetto, 2004; Lavié and Benedetto, 2016, 2019). At that time, the separation of this terrane from the main continent could have been small enough to facilitate fluid faunal exchange (Benedetto, 2004; Lavié and Benedetto, 2016, 2019).

As stated in the preceding, the faunal affinities of the Early Ordovician brachiopod assemblages of the Argentinian segment of the Central Andes are well known. However, the biogeographic relations of the Peruvian Altiplano, which is the northern continuation of the Bolivian Altiplano and Argentinian western Puna, have remained obscured until now. The assemblages of the Umachiri Formation described in this paper contain the only Early–?Middle Ordovician fossils known in the Peruvian Altiplano and, thus, could potentially shed light on the paleogeography of this region and its biogeographic affinity with other terranes of the southwestern margin of Gondwana during the Early–Middle Ordovician.

Geographical and geological setting

The Andean Altiplano (= high plains morphotectonic region) extends from western Bolivia to southern Peru, comprising base elevation ranging from 3,600 to 4,500 m (Fig. 1). Geologically, it is a structural block with a distinct tectonostratigraphic history from the Eastern and Western Cordilleras of the Central Andes (Carlotto, 2013). The basement of the Altiplano is interpreted as the Arequipa Terrane (for extent and boundaries of this terrane, see Ramos, 2008). The partial detachment of this terrane from the Amazonian Craton led to the development of a large retroarc basin of Ordovician to Devonian strata known as the Central Andean Basin (Sempere, 1995; Bahlburg et al., 2006; Ramos, 2018).

Upper Ordovician siliciclastic rocks have been identified near Lake Titicaca, an area known as the Calapuja Formation (Laubacher, 1974, 1977, 1978; Laubacher et al., 1982). This unit has yielded abundant brachiopods, trilobites, gastropods, bivalves, echinoderms, bryozoans, cornulitids, cnidarians, and sponge spicules, suggesting a Sandbian age for these strata (Laubacher, 1977; Villas et al., 2015; Gutiérrez-Marco et al., 2016; Vinn and Gutiérrez-Marco, 2016; Ebbestad and Gutiérrez-Marco, 2019). Previously, outcrops identified as the Calapuja Formation north of Ayaviri have been tentatively correlated with the Sandia and San Gabán formations of the Peruvian

Cordillera Oriental (Díaz-Martínez et al., 2001). Older strata crop out 15 km to the west of Ayaviri, near Umachiri village, in a succession that has been referred to as the Serie Umachiri (Flores and Rodríguez, 1999; Carlotto et al., 2004; Ibarra et al., 2004), also known as the Umachiri beds (Bahlburg et al., 2006, 2011). These beds are currently being redefined as the Umachiri Formation, and it comprises approximately 2,400 m of conglomerate, sandstone, greywacke, siltstone, and rare limestone (Fig. 2). Preliminary results suggest a correlation of this unit with the Lower to Middle Ordovician Verónica and San José formations of southern Peru.

Materials and methods

The material for this study was collected by one of us (EBH) during field campaigns in 2017 and 2018. Five fossiliferous horizons were identified in the Umachiri Formation (Figs. 1, 2). Four horizons (localities 1–4) are situated 100–150 m from the base of the formation, yielding a brachiopod-dominated assemblage with scattered trilobite sclerites and a single columnal plate of pelmatozoan echinoderms; another fossiliferous horizon is located at about 1,700 m (locality 5), yielding poorly preserved graptolites (identified by Cerrón and Chacaltana, 2002). All fossil remains are preserved as internal and external molds. Brachiopods occur in localities 1–4 and will be described herein. Fossils have been prepared using mechanical methods in the labs of the Universidad Complutense of Madrid. Latex casts of the specimens were subsequently prepared for replicating the internal and external features. Fossils and latex casts were whitened using magnesium oxide smoke for photography and studied under binocular microscopes.

Repository and institutional abbreviation.—Original specimens are deposited in the paleontological collection (prefixed CPI) of the Instituto Geológico, Minero y Metalúrgico (INGEMMET) in Lima, Peru.

Systematic paleontology

(by J. Colmenar)

The use of open nomenclature follows Bengtson (1988), and the synonymy lists follow recommendations by Matthews (1973).

Phylum Brachiopoda Duméril, 1806
Subphylum Rhynchonelliformea Williams et al., 1996
Class Strophomenata Williams et al., 1996
Order Billingsellida Schuchert, 1893
Suborder Billingsellidina Öpik, 1934
Superfamily Polytoechioidea Öpik, 1934
Family Polytoechiidae Öpik, 1934
Genus *Enriquetoechia* new genus

Type species.—*Enriquetoechia umachiriensis* n. gen. n. sp., from the lower part of the Umachiri Formation, Peruvian Altiplano, Floian–?Dapingian (Lower–Middle Ordovician).
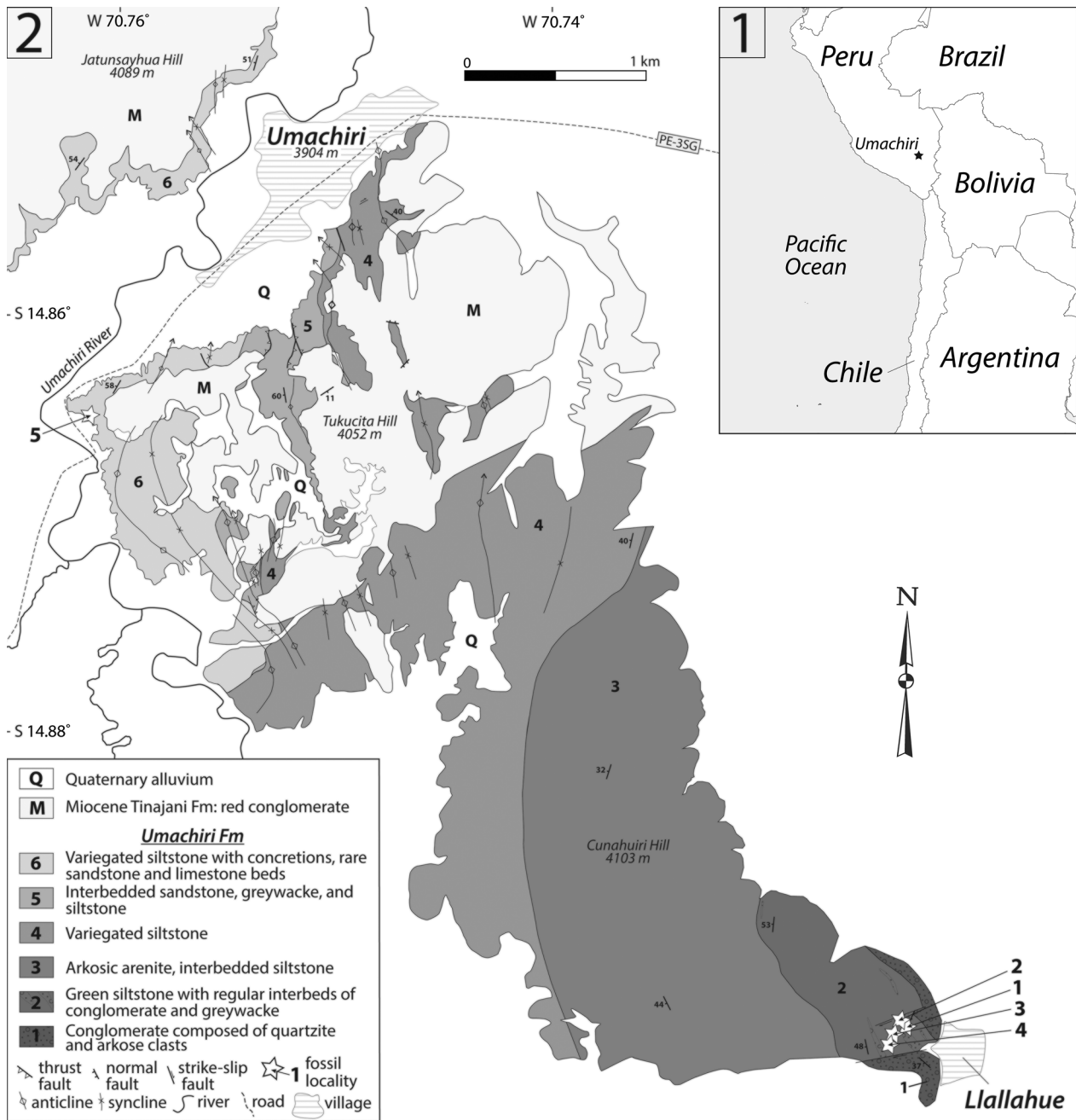
Diagnosis.—As for the species by monotypy.

Figure 1. (**1**) Geographical location of Umachiri village. (**2**) Detailed geological map of the study area. Numbered white stars indicate fossiliferous horizons and localities: 1, samples B1799 and B1806; 2, samples K1708 and B1807; 3, sample B1808; 4, sample B1798; 5, graptolite locality from Cerrón and Chacaltana (2002, 2003).

Occurrence.—Lower part of the Umachiri Formation at locality 2, Floian–?Dapingian (Lower–Middle Ordovician).

Etymology.—After Enrique Villas, brachiopod researcher, who described the first Ordovician brachiopod species of Peru.

Remarks.—Phylogeny of Order Billingsellida has been recently revised by Topper et al. (2013) suggesting that polytoechioids are derived billingselloids, distinct from the clitambonitoids that are a sister group.

There have been extensive discussions about which are the key taxonomical characters for discriminating among the Billingsellida. Wright and Rubel (1996) suggested the use of structures related with their vital functions as key features for superfamily discrimination within this order. These criteria were followed subsequently by several authors (Rubel and Wright in Williams et al., 2000; Popov et al., 2001; Vinn, 2001; Topper et al., 2013, among others). Of special significance are the spondylium/pseudospondylium and related structures and the structures covering the delthyrium and notothyrium.
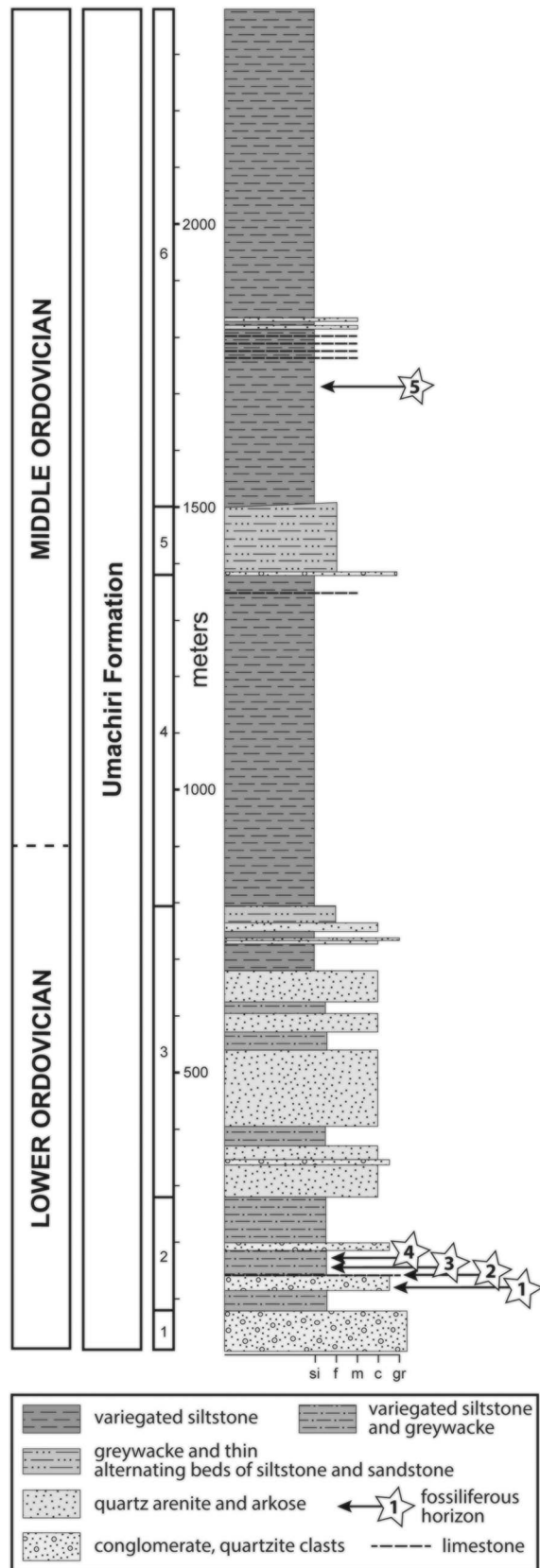
Figure 2. Composite stratigraphy of the Umachiri Formation at Umachiri. Numbered white stars indicate fossiliferous intervals: 1, samples B1799 and B1806; 2, samples K1708 and B1807; 3, sample B1808; 4, sample B1798; 5, graptolite sample from Cerrón and Chacaltana (2002, 2003). si = silt; f = fine sand; m = medium sand; c = coarse sand; gr = gravel.

The delthyrium in the clitambonitine varies from open to partially covered by chilidial plates to completely covered by either a deltidium or a pseudodeltidium. However, the distinction between deltidium and pseudodeltidium is problematic since details, unfortunately, are not preserved in all genera (Wright and Rubel, 1996). The notothyrium in the Billingsellida varies from totally open to partially covered by chilidial plates to completely covered by the chilidium. The cladistic analysis performed by Topper et al. (2013) suggested that the combined presence of a well-developed pseudodeltidium and chilidial plates/chilidium are distinct features shared by most billingselloids and polytoechioids, while clitambonitoids are characterized by having a deltidium.

The spondylium has been described as a spoon-like elevated platform formed by dental plates that coalesce to a varying degree, supported by a median septum, accommodating the ventral muscle field (Williams et al., 2000). However, Vinn and Rubel (2000), studying this structure in several juvenile specimens of genera ascribed to the suborder Clitambonitidina, noted that the spondylium does not derive from the convergence of dental plates but develops from the free plate in early ontogenetic stages. In the clitambonitidine brachiopods, three kinds of spondylium are common: spondylium simplex, which is solely supported by the median ridge; spondylium triplex, which is freestanding and supported in early stages only by the median ridge and afterward additionally by auxiliary lateral ridges growing on both sides of the median ridge, on the undersurface of the spondylium that may or may not reach the valve floor; and pseudospondylium, a structure that mimics the spondylium but is developed instead by discrete, parallel dental plates that reach the valve floor early in the ontogeny, being the muscle field resting, between them, on the valve floor at that time. During the ontogeny, the muscle field is raised by shell thickening, forming a sessile spondylium. In some cases, this raised muscle field is undercut anterolaterally, in lesser or higher degree, becoming even free anteriorly and supported medially and laterally by dental plates simulating the spondylium triplex, as occurs in some genera assigned to the superfamily Polytoechioidea such as *Polytoechia* Hall and Clarke, 1892, *Antigonambonites* Öpik, 1934, and *Raunites* Öpik, 1939 (Wright and Rubel, 1996; Vinn and Rubel, 2000; Topper et al., 2013; Benedetto, 2016). Wright and Rubel (1996, p. 62) also stated that "the opposite is also true: a well-developed spondylium triplex, with its lateral septa reaching the valve floor, strongly simulates a pseudospondylium." Finally, the spondylium simplex characterizes all clitambonitoids excepting the gonambonitids, which develop a spondylium triplex, whereas the presence of a pseudospondylium distinguishes the polytoechioids.

Thus, observations of the well-developed convex pseudodeltidium, the chilidial plates, and the pseudospondylium mimicking the spondylium triplex all suggest including the Peruvian material within the Polytoechioidea. Two families of polytoechioids are recognized: Polytoechiidae and Tritoechiidae. The former is characterized by having a free pseudospondylium, supported medially by a median ridge and laterally by dental plates resembling the spondylium triplex of gonambonitids (Vinn and Rubel, 2000). However, the tritoechiids differ by displaying the ventral muscle field resting directly on the valve floor or raised by shell thickening on a pseudospondylium not undercut

anteriorly (sessile). Thus, this material may be ascribed to the Polytoechiidae. Among the genera included in this family, the Peruvian taxon strongly resembles *Antigonambonites* by having a free-anteriorly pseudospondylium, with a small, transverse ridge separating posteriorly each socket in the dorsal valve, and radial grooves in the ventral interarea at both sides of the convex pseudodeltidium, which limit the external dental lamella with the interarea; it differs in lacking ventral and dorsal peripheral rims and a more raised pseudospondylium. *Antigonambonites* is considered in the Treatise (Williams et al., 2000) to be a gonambonitid, but since this genus has a pseudospondylium and not a spondylium triplex, as many authors suggested (Vinn and Rubel, 2000; Popov et al., 2001; Vinn, 2001), it is now considered a polytoechiid (Topper et al., 2013). In my opinion, another gonambonitid, *Jaanussonites* Neuman, 1976, also has a pseudospondylium, with the muscle field resting directly on the valve floor in early growth stages and becoming free and elevated anteriorly. In addition, this genus displays chilidial plates and radially arranged dorsal muscle scars, which are typical characters of the polytoechioids. This genus has not been included in the cladistic analysis of Topper et al. (2013), but it seems necessary to consider it a polytoechiid from now on. The Peruvian material strongly resembles *Jaanussonites* in its pseudospondylium with the lateral ridges/teeth growing toward the valve floor merging with two vascular ridges posteriorly, by having a convex pseudodeltidium, the same arrangement and shape of dorsal muscle field, and bisected sockets in the dorsal valve; it clearly differs from this genus by its multicostellate ornament without spines in the intercostal spaces and aditicules in the costellae and by lacking peripheral rims in both valves. The Peruvian taxon also strongly recalls *Polytoechia* but differs from it by its bigger size, ornamentation, more elongate outline, wider interarea, undifferentiated ventral adductor scars, and not deeply concave spondylium. Given all these differences, we propose a new genus, *Enriquetoechia*, to include the Peruvian material.

Enriquetoechia umachiriensis new species
Figure 3

Holotype.—Internal and external mold of a ventral valve (CPI–9913) (Fig. 3.1–3.6) from the lower part of the Umachiri Formation at locality 2, Floian–?Dapingian (Lower–Middle Ordovician).

Paratypes.—Internal and external mold of a dorsal valve (CPI–9923) (Fig. 3.7–3.12); internal mold of a ventral valve (CPI–9944); internal mold of a fragmented dorsal valve (CPI–9953); internal and external mold of a dorsal valve (CPI–9958).

Diagnosis.—Polytoechioid of large size, biconvex, multicostellate with well-developed concentric irregular fila giving a zig-zag aspect to the ribs when eroded; pseudodeltidium convex; pseudospondylium formed very early in the ontogeny, elevated on the valve floor, supported posterolaterally by the two dental plates arising below the deltidiodont teeth, which grow toward the valve floor, fusing with two of the radially arranged ovarian vascular ridges and supported medially by a strong, high median ridge reaching its

anterior edge and continuous anteriorly, decreasing in height until mid-valve length, where it disappears; ventral and dorsal peripheral rims absent; notothyrial platform small, restricted to the notothyrial cavity, elevated on the valve floor, strongly undercut in its frontal edge, continuous anteriorly in a median ridge; cardinal process ridge-like, swollen anteroventrally; chilidial plates leaving the notothyrium partially open medially; dorsal transmuscle septa and adductor scars radially arranged.

Occurrence.—Lower part of the Umachiri Formation at locality 2, Floian–?Dapingian (Lower–Middle Ordovician).

Description.—Shells of large size, up to 25 mm wide and 28 mm long; longitudinal profile equally biconvex; elongate in outline; cardinal extremities with obtuse angles; maximum shell width located slightly anteriorly of hinge line; rectimarginate anterior commissure.

Ventral valve about 110% as long as wide and 12% as deep as long; convex umbonal region, subplanar anteriorly. Ventral interarea slightly curved, apsacline, about 12% as long as valve length, with radial grooves marking the boundaries of the interarea with the dental lamella; deltidodont teeth strong, medially grooved; delthyrium covered by convex pseudodeltidium; pedicle foramen not visible. Dorsal valve about 85% as long as wide and 11% as deep as long; maximum depth near the umbo. Dorsal interarea planar, anacline, about 9% as long as valve length, with growth lines subparallel to hinge line; notothyrium partially covered by chilidial plates, diverging anteriorly, forming an angle of about 90°.

Radial ornament multicostellate with 12 ribs per 5 mm at 15 mm anteromedially from umbo, all of them with rounded tops; costellae arise by intercalation at different growth stages; intercostal spaces as wide as ribs. Concentric ornament consisting of well-developed concentric irregular fila, when intersecting with the ribs generating a zig-zag pattern, more visible when the shell is abraded; strongly marked growth lines become more frequent anteriorly.

Ventral interior with a pseudospondylium formed very early in the ontogeny, as long as the interarea, elevated on the valve floor, supported posterolaterally by the dental plates, reaching the anterior edge of the spondylium, arising below the deltidiodont teeth, which grow toward the valve floor fusing with two of the radially arranged vascular ridges; spondylium also supported medially by a strong, high median ridge reaching its anterior edge and continuous anteriorly, decreasing in height until mid-valve length, where it disappears; ovarian vascular ridges radially arranged, evenly spaced, as long as median ridge, counting six at each side of this structure; subperipheral rim absent; mantle canal system pinnate; shell substance unknown.

Dorsal valve with short, anchor-shaped, highly elevated notothyrial platform, undercut in its frontal edge and restricted to the notothyrial cavity, it continues anteriorly into a high and thin median septum about 30% as long as valve; cardinal process ridge-like, swollen anteroventrally; dental sockets transversely elongated, bisected posteriorly by a transverse thin ridge originated in the interarea; sockets bounded anteriorly by strong socket ridges forming an angle of about 23°
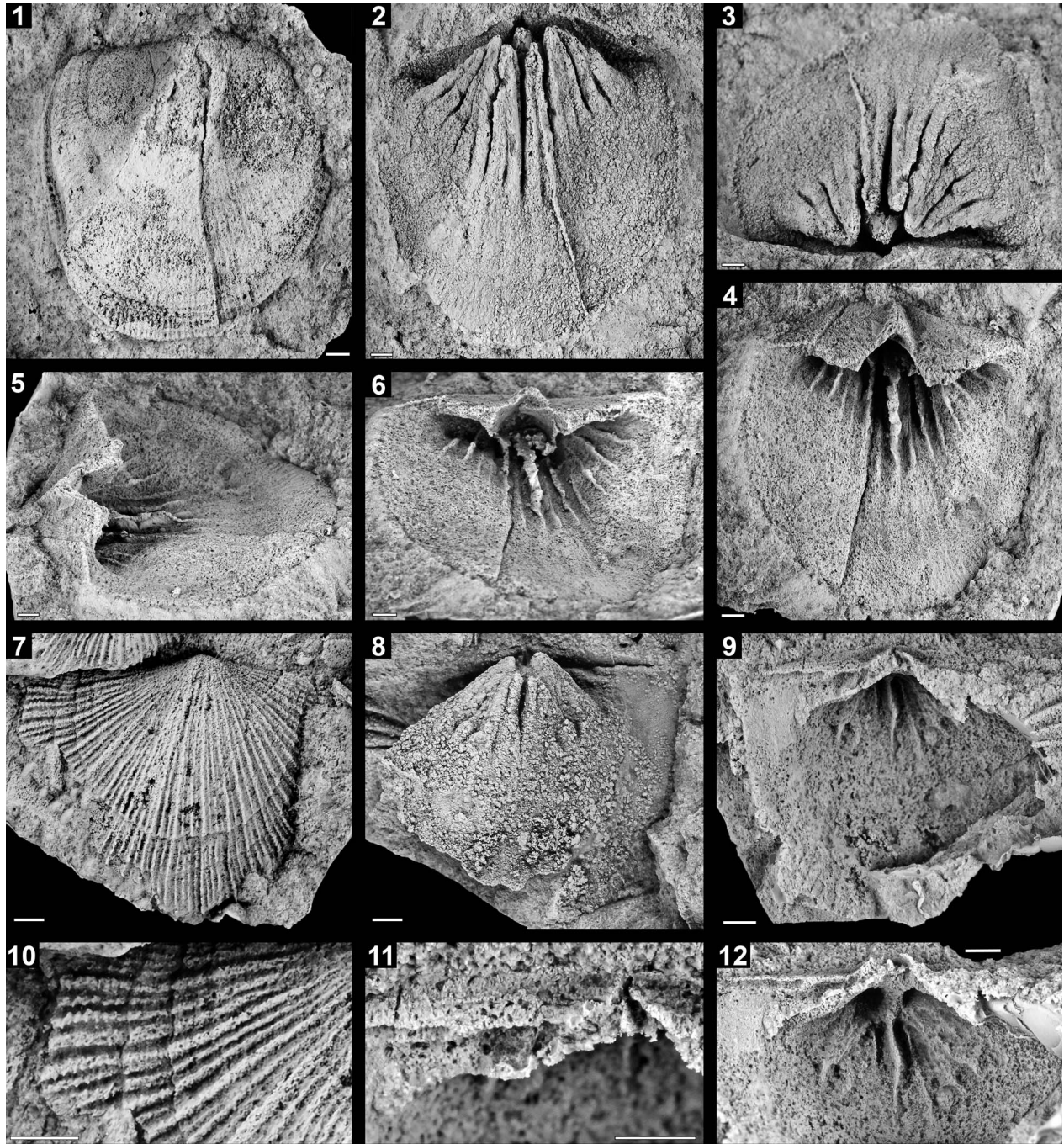
Figure 3. The polytoechioid brachiopod *Enriquetoechia umachiriensis* Colmenar n. gen. n. sp. from the Umachiri Formation at locality 2. (**1–6**) Holotype, external and internal molds of a ventral valve (CPI–9913); (**1**) latex cast of exterior, (**2, 3**) internal mold in (**2**) upper and (**3**) posterior views; (**4–6**) latex cast of interior in (**4**) ventral, (**5**) lateral oblique, and (**6**) anterior oblique views. (**7–12**) Paratype, external and internal molds of a dorsal valve (CPI–9923); (**7**) latex cast of exterior, (**8**) internal mold, (**9**) latex cast of interior, (**10**) detail of external ornamentation, (**11**) magnification of the cardinalia and dorsal interarea, (**12**) anterior oblique view of dorsal interior showing the adductor scars, median ridge, and median septum. Scale bars = 2 mm.

with hinge line; dorsal muscle field large, radially arranged, extending anteriorly slightly beyond median septum; adductor scars with rounded, strongly impressed anterior ends; peripheral rim absent; mantle canal system and shell substance unknown.

Etymology.—After the Umachiri Inlier of the Peruvian Altiplano, where this species occurs.

Remarks.—*Enriquetoechia umachiriensis* is the only species included so far within genus *Enriquetoechia*. See preceding remarks of *Enriquetoechia* n. gen.

Genus *Altiplanotoechia* new genus

Type species.—*Altiplanotoechia hodgini* n. gen. n. sp. Colmenar in Colmenar and Hodgin, 2020, from the lower part

of the Umachiri Formation, Floian–?Dapingian (Lower–Middle Ordovician).

Other species.—*Billingsella dice* Walcott, 1905, from loose boulders at St. Albans, Vermont, USA, likely belonging to the Luke Hill Formation (Lower Ordovician) of the Philipsburg sequence; *Antigonambonites* sp. (in Neuman, 1976, pl. 4, fig. 24) from the Dapingian–lower Darriwilian Calcareous Tuff at Virgin Arm in the New World Island, Newfoundland; *Jaanussonites*? sp. (in Benedetto, 2001, fig. 2V, W) from the upper Floian–lower Dapingian Aguada de la Perdiz Formation of the western Puna region of northwest Argentina.

Diagnosis.—Ventribiconvex shells with hemipyramidal ventral valves and unisulcate commissure; ventral interior with sessile pseudospondylium during early stages, becoming slightly free, undercut anteriorly and supported laterally and medially by septa; radially arranged vascular septa usually present; dorsal interior with ridge-like cardinal process located in a small, triangular notothyrial platform, deeply undercut in its frontal edge, continuous anteriorly into a thin, long median ridge; dorsal adductor scars radially arranged.

Etymology.—After the Altiplano (= high plains) morphotectonic region of Peru where the Umachiri Formation crops out.

Remarks.—The presence of a pseudospondylium in the Peruvian material clearly relates it with the Polytoechioidea. Currently, two families are recognized within the Polytoechioidea: Tritoechiidae and Polytoechiidae (Popov et al., 2001, 2007; Topper et al., 2013; Benedetto, 2016). In the former, the entire ventral muscle field rests directly on the floor of the delthyrial cavity or is raised on a pseudospondylium, not undercut anteriorly. By contrast, in the Polytoechiidae, the pseudospondylium is free anteriorly and supported medially and laterally by septa resembling the spondylium triplex of gonambonitids (Vinn and Rubel, 2000). The Peruvian material displays mixed characters between the Polytoechiidae and Tritoechiidae. The Peruvian taxon shows similar pseudospondylium development to the polytoechiid *Pinatotoechia*, which displays a sessile pseudospondylium until adult stages when it becomes slightly undercut and free anteriorly, but clearly it differs from that genus in its ornamentation consisting of hollow tubular spines developed on the ribs. It also resembles the genera *Polytoechia* Hall and Clarke, 1892 and *Tritoechia* Ulrich and Cooper, 1936. Hall and Clarke (1892, p. 240) described the pseudospondylium of *Polytoechia* as "supported by a stout median septum, and two smaller lateral septa […], the former of these extends for the entire length of the plate, while the latter is free from the accessory septa near its anterior edge. The umbonal cavity of the valve is thus divided into five chambers […]", which means that those three septa are discrete from early ontogenetic stages. *Tritoechia*, however, exhibits a sessile pseudospondylium that can be elevated onto the valve floor in higher or lesser extent by secondary shell thickening, leaving only three chambers in the umbonal cavity. Some gerontic specimens of few *Tritoechia* species, such as the type species

Tritoechia typica (Schuchert and Cooper, 1932) and *T. curvirostris* Sando, 1957, develop obscure ridges at the anterior margins of the ventral muscle field, which tend to elevate the muscular platform slightly above the floor of the valve (see Ulrich and Cooper, 1938, pl. 33B, fig. 19 and Sando, 1957, pl. 14, fig. 3). The pseudospondylium of the Peruvian material is similar to the sessile spondylium of *Tritoechia* only in young stages, but it differs from *Tritoechia* since in the Peruvian specimens this structure becomes free, strongly undercut anteriorly, and supported laterally and medially by septa, in a similar way to *Polytoechia*, but only in adult stages. It also differs from *Tritoechia* in lacking radial lines in the interarea, which is another diagnostic character of that genus. Another character that differentiates this material from *Polytoechia* is the anterior commissure, unisulcate in the Peruvian specimens and uniplicate in *Polytoechia*. The Peruvian material also resembles *Antigonambonites* by having a sessile pseudospondylium becoming slightly raised anteriorly in gerontic specimens but differs from this genus in having a more convex ventral valve and a more raised pseudospondylium from early stages and in lacking a peripheral rim.

Material with pseudospondylium development similar to the material described here can be found in the literature, e.g., *Tritoechia dice* (Walcott, 1905) (see Ulrich and Cooper, 1938, pl. 31B) from the Floian Luke Hill Formation of Canada, *Antigonambonites* sp. (in Neuman, 1976, pl. 4, fig 24) from the Dapingian–lower Darriwilian Calcareous Tuff at Virgin Arm in Newfoundland, *Jaanussonites*? sp. (in Benedetto, 2001, fig. 2V, W) from the upper Floian–lower Dapingian Aguada de la Perdiz Formation of the western Puna region of northwest Argentina, and *Pomatotrema jiangsuense* Wang and Xu (1966, pl. II, figs. 4–7) from the Floian–lower Darriwilian part of the Lunshan Formation at Tangshan, Nanjing. However, the latter clearly differ from the Peruvian material by having peripheral rims, which is a character only displayed by *Pomatotrema* within the Polytoechioidea. The mixed characters of the Chinese species suggest that it may belong to a new genus yet to be described. Dorsal valves attributable to this new genus display typical polytoechioid features such as chilidial plates, ridge-like cardinal process, small notothyrial platform continuous anteriorly in a median septum, widely divergent socket ridges, and radially arranged dorsal adductor scars. However, the dorsal valves studied here show a dorsal sulcus. This character is unique within the polytoechioids, given that the only folded genera in the superfamily are *Polytoechia* and *Martellia* Wirth, 1936, but both genera are uniplicate and not unisulcate as the Peruvian shells.

From the previous discussion, we propose here the establishment of a new genus, *Altiplanotoechia*, to embrace all the species with questionable generic determination mentioned in the preceding (except *P. jiangsuense*), with similar pseudospondylium development and without spinose ornamentation. The family assignment of the new genus is more complicated since it shares characteristics of both Polytoechiidae and Tritoechiidae, but we tentatively place it here within the Polytoechiidae until further investigations have been made in the suprageneric taxonomy of this superfamily.

Altiplanotoechia hodgini new species
Figure 4.1–4.13

Holotype.—Internal and external mold of a ventral valve (CPI–9929) (Fig. 4.6–4.10) from the lower part of Umachiri Formation at locality 2, Floian–?Dapingian (Lower–?Middle Ordovician).

Paratypes.—Internal and external mold of a ventral valve (CPI–9921) (Fig. 4.1–4.5); internal and external mold of a dorsal valve (CPI–9930) (Fig. 4.11–4.13).

Diagnosis.—*Altiplanotoechia* species with hemipyramidal ventral valve, slightly unisulcate commissure and small notothyrial platform, extremely undercut in its frontal edge, highly elevated on the valve floor, and continuous anteriorly in a long and thin median ridge.

Occurrence.—Lower part of Umachiri Formation at locality 2, Floian–?Dapingian (Lower–?Middle Ordovician).

Description.—Shells of medium size up to 18 mm wide and 14 mm long; longitudinal profile ventribiconvex; subcircular in outline; cardinal extremities acute in early growth stages, right to obtuse in adult stages; maximum shell width approximately at mid-valve length; slightly unisulcate anterior commissure.

Ventral valve hemipyramidal, about 104% as long as wide and 50% as deep as long; maximum convexity at umbonal region. Ventral interarea slightly curved, apsacline, about 52% as long as valve length, with strong, triangular deltiodont teeth; delthyrium covered by strongly convex pseudodeltidium apically perforated by a large, ovate pedicle foramen.

Dorsal valve about 92% as long as wide and 22% as deep as long; maximum depth near the umbo; dorsal interarea planar, anacline, about 8% as long as valve length; notothyrium almost totally covered by chilidial plates, which nearly touch the posterior part of the cardinal process, diverging anteriorly forming an angle of about 99°.

Radial ornament multicostellate with 18 ribs per 5 mm at anterior commissure, all of them with rounded tops; costellae arise by branching at different growth stages; intercostal spaces narrower than ribs. Concentric ornament consisting of weakly marked fila and strong growth lines becoming more frequent anteriorly; in abraded parts of the shell, the intersection of costellae and fila is more visible (Fig 4.11).

Ventral interior with strong dental plates arising from the teeth and growing toward valve floor forming a pseudospondylium elevated on the valve floor by shell thickening, sessile during early stages, becoming free, undercut anteriorly and supported laterally and medially by septa in adult stages, medium septum extending anteriorly almost until the commissure; ventral muscle field elongate, with diductor scars separated from adductor scars by strong, subparallel ridges, adductor scars deeply impressed in the pseudospondylium; ovarian vascular ridges radially arranged, shorter than median ridge; mantle canal system pinnate; shell substance unknown.

Dorsal interior with ridge-like cardinal process, slightly thickened anteriorly, located on a small notothyrial platform, extremely undercut in its frontal edge, highly elevated on the valve floor, and continuous anteriorly in a long and thin median ridge reaching less than half of the valve length; divergent socket ridges forming an angle of about 28° with hinge line; sockets big, triangular in outline, fairly deep; adductor scars radially arranged, poorly impressed; shell substance and mantle canal system unknown.

Etymology.—After Eben Blake Hodgin (Harvard University), who found the Umachiri Formation fossil localities.

Remarks.—Some of the taxa included within this new genus are in open nomenclature; however, they will be included here for comparison with the Peruvian species. *Altiplanotoechia hodgini* is here proposed as type species since the type material of *Tritoechia dice* (Walcott, 1905) comes from loose boulders of uncertain origin within the Philipsburg sequence of St. Albans, Vermont, northeastern USA. *A. hodgini* differs from *Tritoechia dice* by having a more subcircular outline, slightly unisulcate anterior commissure, a more convex ventral valve, deeper impressed adductor scars, and longer ventral median and vascular septa. *Antigonambonites* sp. (in Neuman, 1976) differs from the new species in having a much shorter ventral median septum and a more convex dorsal valve with dorsal muscle scars strongly impressed anteriorly. Only one poorly preserved ventral interior of *Jaanussonites*? sp. (in Benedetto, 2001, fig. 2V, W) is known. It displays internal characters very similar to those in *A. hodgini*, e.g., the deeply impressed ventral adductor scars and length of median and vascular septa. Additional and better-preserved material of the Argentinian taxon could perhaps confirm its synonymy with *A. hodgini*.

Family Tritoechiidae Ulrich and Cooper, 1936
Genus *Pomatotrema* Ulrich and Cooper in Schuchert and Cooper, 1932

Type species.—*Pomatotrema murale* Ulrich and Cooper in Schuchert and Cooper, 1932 from the West Spring Creek Formation, Arbuckle Group, Oklahoma, Dapingian–lower Darriwilian (Middle Ordovician).

Other species.—*Pomatotrema semiconvexum* (Poulsen, 1927) (Nunatami Formation, northwest Greenland, Dapingian–lower Darriwilian), *P. magnum* Ulrich and Cooper, 1938 (Arbuckle Limestone, Oklahoma, Dapingian–lower Darriwilian), *P. oklahomense* Ulrich and Cooper, 1936 (West Spring Creek Formation, Oklahoma, Dapingian–lower Darriwilian), *P. transversum* Ulrich and Cooper, 1936 (West Spring Creek Formation, Oklahoma, Dapingian–lower Darriwilian), *P. inconspicuum* Williams and Curry, 1985 (Tourmakeady Limestone, Ireland, Dapingian–lower Darriwilian), *Pomatotrema* sp. (upper Fenxiang Formation., China, Tremadocian–lower Floian, Lower Ordovician).

Pomatotrema laubacheri new species
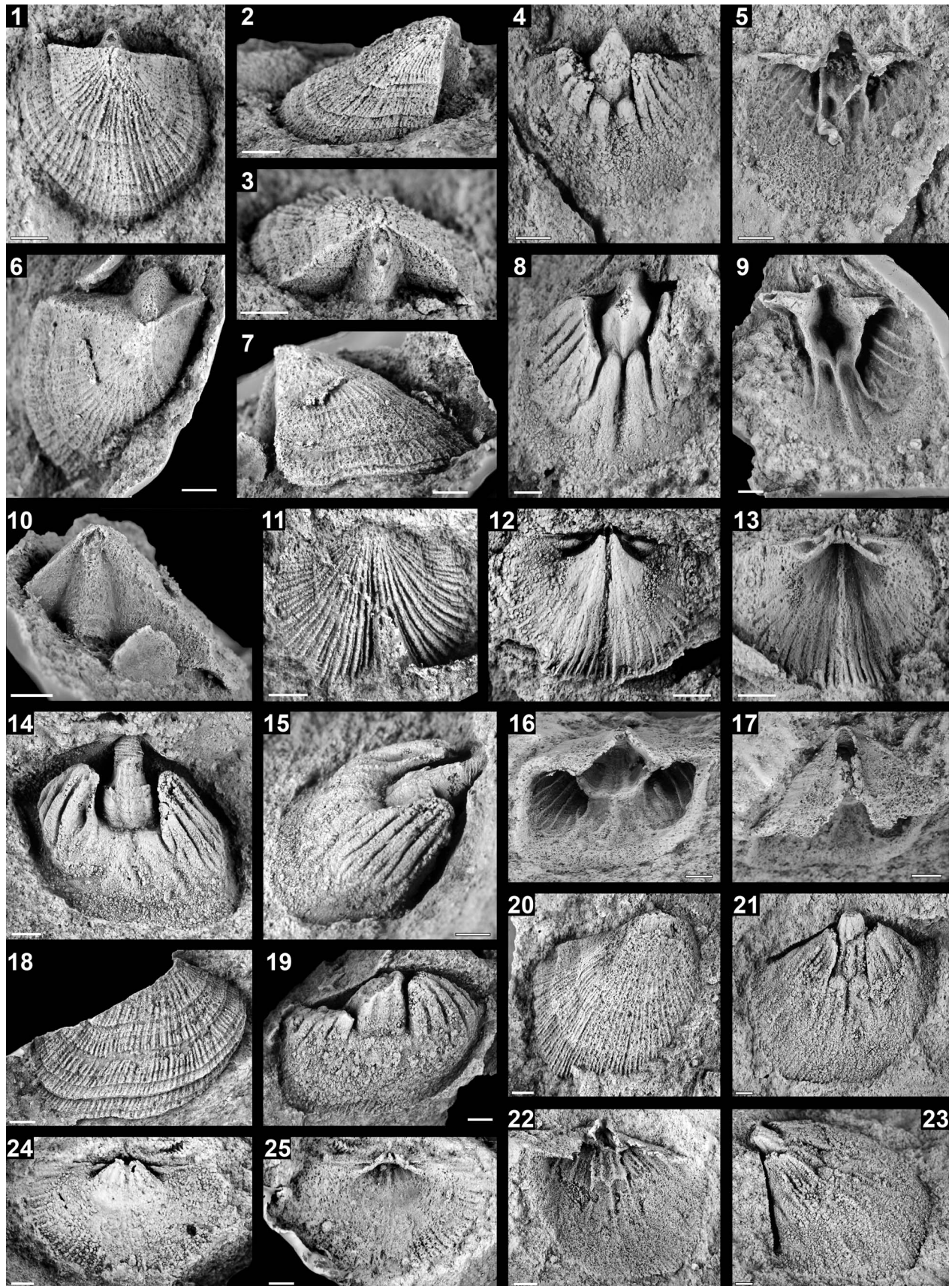Figure 4.14–4.19

Figure 4. Polytoechioid brachiopods from the Umachiri Formation. (**1–13**) *Altiplanotoechia hodgini* n. gen. n. sp. Colmenar in Colmenar and Hodgin, 2020 (**1–5**) Paratype, external and internal molds of a ventral valve (CPI–9921); (**1–3**) latex cast of exterior in (**1**) upper, (**2**) lateral, and (**3**) posterior oblique views; (**4**) internal mold and (**5**) latex cast of interior. (**6–10**) Paratype, external and internal molds of a ventral valve (CPI–9929); (**6, 7, 10**) latex cast of exterior in (**6**) upper, (**7**) lateral, and (**10**) posterior views; (**8**) internal mold and (**9**) latex cast of interior. (**11–13**) Paratype, external and internal molds of a dorsal valve (CPI–9930); (**11**) latex cast of exterior, (**12**) internal mold and (**13**) latex cast of interior. (**14–19**) *Pomatotrema laubacheri* Colmenar n. sp. (**14–17**) Holotype, internal mold of a ventral valve (CPI–9916); (**14, 15**) internal mold in (**14**) upper and (**15**) lateral oblique views; (**16, 17**) latex cast of interior in (**16**) upper and (**17**) posterior oblique views; (**18, 19**) paratype, external and internal molds of a ventral valve (CPI–9914); (**18**) latex cast of exterior and (**19**) internal mold. (**20–23**) *Tritoechia* (*Tritoechia*) sp. (**20–23**) External and internal molds of a ventral valve (CPI–9915); (**20**) latex cast of exterior, (**21–23**) internal mold in (**21**) upper and (**23**) lateral oblique views, (**22**) latex cast of interior. (**24, 25**) Polytoechioidea indet., dorsal valve (CPI–9932); (**24**) internal mold and (**25**) latex cast of interior. Scale bars = 2 mm.

Holotype.—Internal mold of a ventral valve (CPI–9916) (Fig. 4.14–4.17) from the lower part of the Umachiri Formation at locality 2, Floian–?Dapingian (Lower–Middle Ordovician).

Paratype.—Internal and external mold of a ventral valve (CPI–9914) (Fig. 4.18, 4.19).

Diagnosis.—*Pomatotrema* species with hemipyramidal ventral valve, extremely high interarea, and ventral muscle scars raised on the valve floor by shell thickening.

Occurrence.—Lower part of the Umachiri Formation at locality 2, Floian–?Dapingian (Lower–Middle Ordovician).

Description.—Hemipyramidal ventral valves of medium size, up to 15 mm wide and 13 mm long; transversely oval in outline; cardinal extremities rectangular; maximum shell width located at hinge line; rectimarginate anterior commissure.

Ventral valve about 86% as long as wide and 50% as deep as long; maximum convexity at umbonal region. Ventral interarea slightly curved, apsacline, about 50% as long as valve length, with horizontal, subparallel growth lines; deltidiodont teeth strong; delthyrium covered by convex pseudodeltidium, longer than wide, apically perforated by a big, oval pedicle foramen.

Radial ornament multicostellate with 14 ribs per 5 mm at anterior commissure, all of them with rounded tops; costella arise by branching at different growth stages; intercostal spaces narrower than ribs. Concentric ornament consisting of strongly marked growth lines becoming more frequent and lamellose anteriorly.

Ventral interior with strong dental plates, slightly convergent toward valve floor forming a pseudospondylium and bounding laterally the muscle field that is resting on the thickened valve floor; ventral muscle field strongly impressed, diductor scars about 30% shorter than adductor scars, diductor scars elongated, subparallel, undercutting the pseudospondylium posteriorly, adductor scars lanceolate, separated from each other by a narrow, weak ridge and from the diductor scars by strong ridges; strongly marked pedicle callist present in the posterior part of the delthyrial cavity; radially arranged ovarian vascular ridges present posterolaterally; mantle canal system pinnate.

Etymology.—After Gérard Laubacher, French geologist, who devised the first stratigraphic scheme for the Altiplano and the first Ordovician fossil findings in the region.

Remarks.—The curved pseudodeltidium, apically perforated, and the sessile pseudospondylium, formed by the dental plates

extending toward the valve floor, justify the inclusion of this material within the family Tritoechiidae. The presence of a peripheral rim and the absence of radial lines in the interarea are diagnostic characters of *Pomatotrema* Ulrich and Cooper in Schuchert and Cooper, 1932. Only two ventral internal molds and an associated external mold are available. However, the ventral muscle field raised on the valve floor by shell thickening allows differentiation from all species included in this genus. Among all described species, *P. laubacheri* is morphologically closest to the genotype *P. murale* Ulrich and Cooper in Schuchert and Cooper, 1932 by showing strong radial ovarian vascular ridges and strong dental plates, converging toward the valve floor, bounding laterally the ventral muscle field, but *P. laubacheri* clearly differs from the type species in having a more convex ventral valve and higher ventral interarea and lacking the median ridge in the ventral valve.

Genus *Tritoechia* Ulrich and Cooper, 1936
Subgenus *Tritoechia* (*Tritoechia*) Ulrich and Cooper, 1936

Type species.—*Deltatreta typica* Schuchert and Cooper, 1932 from the Arbuckle Limestone of Oklahoma, USA, Dapingian–lower Darriwilian (Middle Ordovician).

Tritoechia (*Tritoechia*) sp.
Figure 4.20–4.23

Occurrence.—Lower part of the Umachiri Formation at locality 2, Floian–?Dapingian (Lower–Middle Ordovician).

Description.—Ventral valve of medium size about 20 mm wide and 19 mm long; subquadrate in outline; cardinal extremities rounded with obtuse angles; maximum shell width slightly anterior to hinge line; anterior commissure rectimarginate.

Ventral valve hemipyramidal, about 95% as long as wide and 60% as deep as long; maximum depth near the umbo; ventral interarea planar, apsacline; delthyrium covered by a convex pseudodeltidium.

Radial ornament multicostellate with 11 ribs per 5 mm at 10 mm anteromedianly, all of them with rounded tops; costellae arise by branching at different growth stages; intercostal spaces as wide as ribs.

Ventral interior with thin dental plates, almost subparallel, slightly convergent toward valve floor forming a sessile pseudospondylium and bounding laterally the muscle field, which is resting on the thickened valve floor; dental plates extending anteriorly beyond muscle field scars as low, narrow ridges; ventral muscle field elongated, about twice as long as wide,

muscle scars strongly impressed, each diductor as wide as both adductor scars altogether, diductor scars separated from the adductors by strong, subparallel ridges, low and thin median ridge growing anteriorly from the adductor scars until approximately two-thirds of valve length; radially arranged ovarian vascular ridges present posterolaterally; mantle canal system pinnate.

Materials.—One ventral interior and exterior (CPI–9915) (Fig. 4.20–4.23).

Remarks.—The curved pseudodeltidium and the sessile pseudospondylium formed by the dental plates extending toward the valve floor justify the inclusion of this material within the family Tritoechiidae. The extremely convex ventral valve, the non-undercut anteriorly ventral muscle field, and the median ridge extending in front of ventral muscle field are characters typically displayed by *Tritoechia*. More than 40 species have been included in this genus. Among the species with hemipyramidal ventral valve, the Peruvian species resembles *T. delicatula* Ulrich and Cooper, 1936 from the Tremadocian Kindblade Formation of Oklahoma in having narrow, almost subparallel ventral muscle scars with subparallel ridges separating diductor from adductor scars. However, the Peruvian species differs from *T. delicatula* in being almost double the size of the largest specimen attributed to that species and by having a much narrower median ridge. The Peruvian species also resembles the type species *T. typica* (Schuchert and Cooper, 1932) from the same formation in having the dental plates extending anteriorly beyond the muscle field as low ridges. However, the Peruvian material clearly differs from *T. typica* in lacking the aditicules/hollow costellae characteristic of the type species and by having a subparallel muscle field, anteriorly widely divergent in *T. typica*. The dental plates extending anteriorly beyond the elongated muscle field as low ridges is a character also shared with *Tritoechia* sp. from the upper member of the Suri Formation from the Famatina Range of northwest Argentina (Benedetto, 2003), but the Peruvian species differs from the Argentinian species in having a slightly thicker ornamentation and having ridges separating diductor from adductor scars. Despite showing differences from all published *Tritoechia* species, it is preferable not to define a new species until additional and more abundant material of this taxon is available.

Subgenus *Tritoechia* (*Parvitritoechia)* Benedetto, 2003

Type   species.—*Tritoechia   (Parvitritoechia)   preandina* Benedetto, 2003 (in Benedetto et al., 2003) from the lower part of the San Juan Formation, Precordillera, Argentina, upper Tremadocian–lower Floian (Lower Ordovician).

Tritoechia (*Parvitritoechia*) sp.
Figure 5.1–5.4

Occurrence.—Lower part of the Umachiri Formation at locality 2, Floian–?Dapingian (Lower–Middle Ordovician).

Description.—Dorsal valve of medium size up to 17 mm wide and 10 mm long; transversely oval in outline; cardinal extremities rounded with obtuse angles; maximum shell width located slightly before mid-valve length; slightly unisulcate anterior commissure.

Dorsal valve about 60% as long as wide and 11% as deep as long; maximum depth near the umbo; dorsal interarea planar, anacline, about 11% as long as valve length; notothyrium partially covered by chilidial plates, diverging anteriorly forming an angle of about 93°.

Radial ornament unequally parvicostellate with up to 12 prominent costae and up to six costellae arising by intercalation; some of the costellae become more marked near the anterior margin. Both costae and costellae with rounded tops. The only dorsal exterior available shows evidence of shell damage reflected as discontinuities in shell ornament (Fig. 5.1).

Dorsal interior with ridge-like cardinal process, located in a small notothyrial platform, undercut in its frontal edge, elevated on the valve floor, and continuous anteriorly in a short and thin median ridge restricted to notothyrial cavity; widely divergent socket ridges forming an angle of about 13° with hinge line; sockets triangular in outline, fairly shallow; dorsal muscle field not impressed; shell substance and mantle canal system unknowns.

Materials.—One dorsal interior and exterior (CPI–9920) (Fig. 5.1–5.4).

Remarks.—This material is assigned to Polytoechioidea on the basis of its typical cardinalia. The only genera in this superfamily with unequally parvicostellate ornament are *Acanthotoechia* Williams and Curry, 1985, *Raunites* Öpik, 1939, and *Tritoechia* (*Parvitritoechia)* Benedetto, 2003. The Peruvian material clearly differs from *Acanthotoechia* by not having rows of spines peripherally and by lacking peripheral rims in the interior. The Peruvian material differs from *Raunites* in lacking concentric fila and in having thicker ribs, rounded cardinal angles, better-marked and fewer costae over the disc, smaller, more elevated notothyrial platform, and thinner median ridge. Benedetto (in Benedetto et al., 2003) described *Tritoechia* (*Parvitritoechia*) to encompass all *Tritoechia* species with clearly unequal parvicostellate ornament. The Peruvian material perfectly fits within the diagnosis of this subgenus, so we propose to include our material within *Tritoechia* (*Parvitritoechia*). This material differs from the type species *T.* (*Parvitritoechia*) *preandina* from the lower part of the San Juan Formation of the Precordillera in having rounded cardinal extremities, a smaller size, a non-thickened anteriorly cardinal process, and a thinner median ridge. It differs from *T.* (*P.*) *pyramidalis* (Bates, 1968) from the Treiorwerth Formation of Anglesey in having much thinner ribs and lacking growth lines. The Peruvian material is morphologically closer to the material assigned to this genus from the volcaniclastic rocks of the Aguada de la Perdiz Formation of the Argentinian western Puna, *Tritoechia* sp. A and *Tritoechia* sp. B (Benedetto, 2001), later reassigned to *T.* (*Parvitritoechia*) by Benedetto (2003). The material from the western Puna also displays rounded cardinal extremities, a similar number of costae, and costellae between them, but
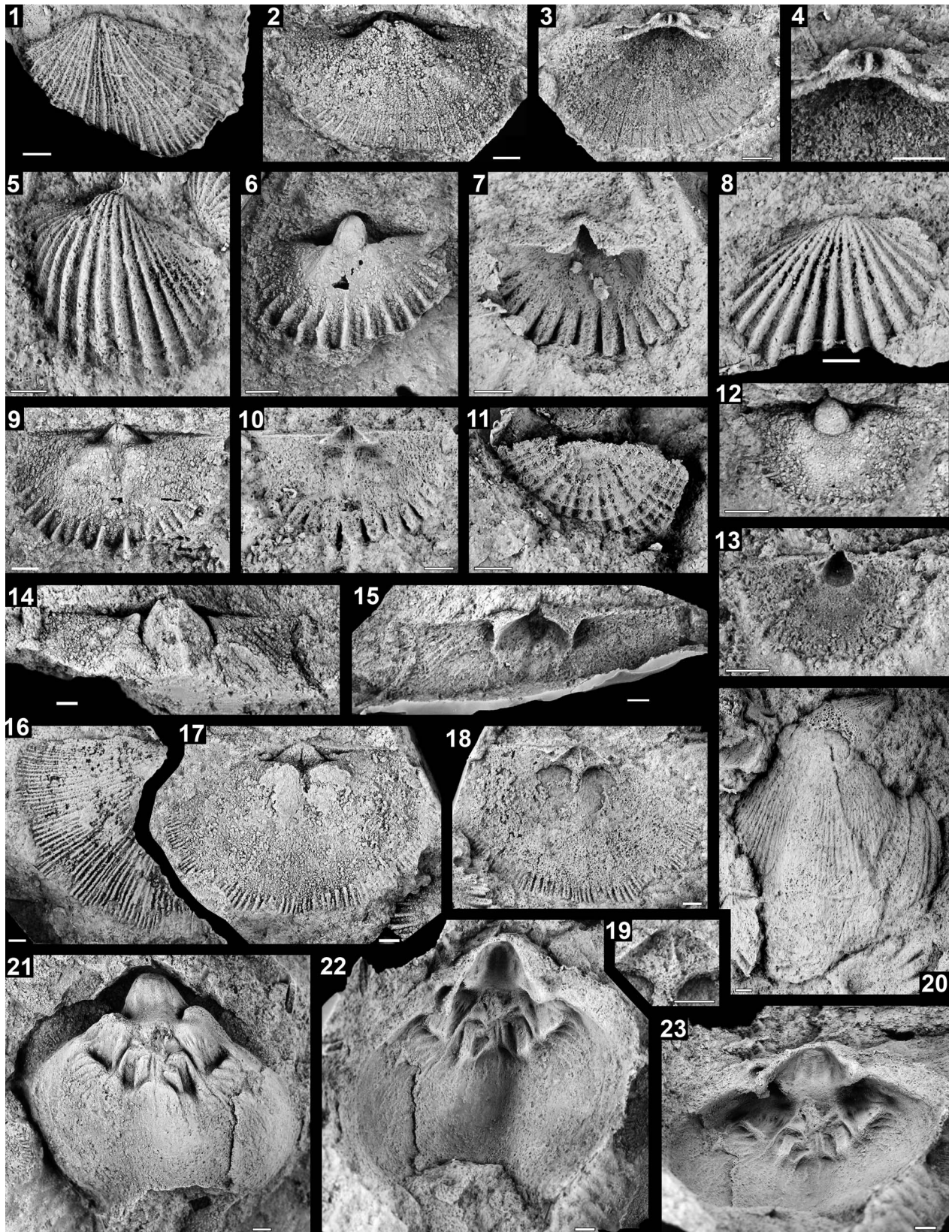
differs from the Peruvian material in having a low median septum dividing the dorsal muscle field. Even though the material from the Umachiri Formation shows differences with all the known species of *T.* (*Parvitritoechia*), it is too scarce and fragmentary to define a new species.

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Polytoechioidea indet.
Figure 4.24, 4.25

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Occurrence.—Lower part of the Umachiri Formation at locality 2, Floian–?Dapingian (Lower–Middle Ordovician).

Materials.—One dorsal interior (CPI–9932) (Fig. 4.24–4.25).

Remarks.—The dorsal valve available can clearly be ascribed to the Polytoechioidea on the basis of its cardinalia. However, it does not seem to correspond to any of the taxa belonging to that superfamily described in this paper in either external or internal features. *Pomatotrema laubacheri* and *Tritoechia* sp. lack dorsal valves in the collection, so this dorsal valve could potentially belong to any of those taxa. However, the absence of a peripheral rim precludes its attribution to *Pomatotrema,* and the subcircular outline does not match *Tritoechia* species described in the preceding. So it is plausible to think that other polytoechioids might be present in the Umachiri associations.

<div align="center">

Order Orthida Schuchert and Cooper, 1932
Suborder Orthidina Schuchert and Cooper, 1932
Superfamily Orthoidea Woodward, 1852
Family Orthidae Woodward, 1852
Genus *Paralenorthis* Havlíček and Branisa, 1980

</div>

Type species.—*Paralenorthis immitatrix* Havlíček and Branisa, 1980; Floian (Lower Ordovician) siltstones at San Lucas, Bolivia.

<div align="center">

Paralenorthis cf. *P. carlottoi* Villas in Gutiérrez-Marco and Villas, 2007
Figure 5.5–5.10

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cf. 2007 *Paraleonorthis carlottoi* Villas in Gutiérrez-Marco and
    Villas, p. 555, fig. 6A–6M$_2$.

Holotype.—External mold of a ventral valve (MGM 5973X−1) from the Horizon A of the San José Formation, Cordillera Oriental, Peru; upper Floian (uppermost Lower Ordovician).

Diagnosis.—*Paralenorthis* species with rectangular cardinal angles, costate and capillate, with 18–20 costae in adult dorsal

valves, only two median costae occupying median sulcus, ventral muscle field 26%–33% as long as valve, notothyrial platform restricted to notothyrial cavity and 14%–22% as long as valve, blade-like divergent brachiophores, and low median ridge.

Occurrence.—Lower part of the Umachiri Formation at localities 1, 2, and 4, Floian–?Dapingian (Lower–Middle Ordovician).

Materials.—Thirty-one specimens; figured: CPI–9917, 9922, 9927, 9928 (Fig. 5.5–5.10); non-figured: CPI–9931, 9933–9943, 9945–9952, 9954–9957, 9959–9961.

Remarks.—The material from the Umachiri Formation strongly resembles, both externally and internally, *Paralenorthis carlottoi* Villas (in Gutiérrez-Marco and Villas, 2007) from the middle–upper Floian San José Formation of the Peruvian Cordillera Oriental. The material studied here commonly displays rectangular cardinal angles, about 18 costae in adult dorsal valves, with only two median costae in the median sulcus, a ventral muscle field about 32% as long as valve, a notothyrial platform about 18% as long as valve, continuous anteriorly in a low median ridge. These values are within the variability range of the species *P. carlottoi*. However, this material displays differences in the dorsal muscle field, showing wider posterior adductor scars than the species described by Villas (in Gutiérrez-Marco and Villas, 2007). Given this difference displayed by the population of the Umachiri Formation, it is assigned here only tentatively to this species.

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Family Hesperonomiidae Ulrich and Cooper, 1936
Genus *Mollesella* Benedetto, 2003

</div>

Type species.—*Mollesella planiventralis* Benedetto, 2003 from the uppermost Floian–lower Dapingian Molles Formation, Famatina, northwest Argentina.

<div align="center">

Mollesella cf. *M. planidorsalis* Benedetto, 2003
Figure 5.14–5.19

</div>

cf. 2003 *Mollesella planidorsalis* Benedetto, p. 233, fig. 11.13–
    11.28.

Holotype.—Internal mold of a ventral valve (CEGH-UNC 19649) from the Molles Formation, Famatina Range, Argentina; middle Floian-Dapingian (Lower–Middle Ordovician).

Diagnosis.—Medium-sized to large shells with planar ventral valve and moderately convex sulcate dorsal valve.

Ornamentation finely multicostellate. Ventral valve with triangular muscle field and proximal half of vascula media subparallel. Notothyrial platform strongly raised, continued anteriorly as high, rounded median ridge bearing simple, anteriorly thickened cardinal process, which becomes bulbous and prominent in full-grown specimens.

Occurrence.—Lower part of the Umachiri Formation at locality 2, Floian–?Dapingian (Lower–Middle Ordovician).

Materials.—One dorsal interior and exterior (CPI–9924) (Fig. 5.16–5.19) and one fragmentary ventral interior (CPI–9925) (Fig. 5.14, 5.15).

Remarks.—The finely costellate ornament, the open delthyrium, the triangular and relatively short ventral muscle field impressed directly on the valve floor, the short dorsal interarea, the simple cardinal process, and the quadripartite dorsal muscle field allow assigning this material to the family Hesperonomiidae. The dental plates laterally and anterolaterally bounding the ventral muscle field, the cardinal process becoming bulbous anteriorly, the absence of chilidial plates, the relatively raised notothyrial platform, and the posterolateral, radially arranged ovarian vascular ridges warrant its inclusion within the monospecific genus *Mollesella* Benedetto, 2003 from the Famatina Range of northwest Argentina. The Peruvian material shows some differences from *M. planiventralis*, such as having wider notothyrial platform and median ridge. Since these features seem to vary within the Argentinian species and given that the Peruvian material is fragmentary and poorly preserved, we decided to assign it tentatively to that species.

Family Productorthidae Schuchert and Cooper, 1931
Subfamily Productorthinae Schuchert and Cooper, 1931
Genus *Panderina* Schuchert and Cooper, 1931

Type species.—*Productus abscissus* Pander, 1830 from the Leetse Formation of northwest Russia, Dapingian (Middle Ordovician).

Panderina? sp.
Figure 5.11–5.13

Occurrence.—Lower part of the Umachiri Formation at locality 2, Floian–?Dapingian (Lower–Middle Ordovician).

Materials.—One ventral interior (CPI–9911) (Fig. 5.12–5.13) and one dorsal exterior (CPI–9926) (Fig. 5.11).

Remarks.—Short and thick dental plates continued as a ridge around the front margin of the oval, small, ventral muscle field, forming a pseudospondylium, closely resembling the genus *Panderina* Schuchert and Cooper, 1931. However, in this genus the pseudospondylium usually continues anteriorly into a median ridge, absent in the Peruvian material. Benedetto (2003) described a new species, *Panderina*? *ambigua* from the Argentinian Famatina Range with similar features in the ventral valve. He also noted that this species showed mixed characters from other productorthid genera,

making the generic classification problematic. Mixed characters include the strongly lamellose ornament in the whole shell surface, shared with the material described here. We agree with Benedetto (2003) that the generic assignment of the Argentinian species is doubtful, and we consider our material congeneric. Further investigation must be done to clarify the generic classification of the Argentinian and Peruvian taxa. Due to small differences in the ventral muscle field outline and the lack of dorsal interiors in the Peruvian collection, it is preferable to leave this material in open nomenclature.

Order Pentamerida Schuchert and Cooper, 1931
Suborder Syntrophiidina Ulrich and Cooper, 1936
Superfamily Porambonitoidea Davidson, 1853
Family Tetralobulidae Ulrich and Cooper, 1936
Subfamily Punctolirinae Andreeva, 1982
Genus *Rugostrophia* Neuman, 1971

Type species.—*Rugostrophia sylvestris* Neuman, 1971 from the Lower Birch Island Member of the Turnbull Mountain Formation. (Dapingian–lower Darriwilian) at Newfoundland, Canada.

Rugostrophia cf. *R. latireticulata* Neuman, 1976
Figure 5.20–5.23

cf. 1976 *Rugostrophia latireticulata* Neuman, p. 41, pl. 7, figs. 1–8.

Holotype.—Dorsal valve, internal mold, and counterpart external mold (GSC 35085) from the 'calcareous tuff' at Virgin Arm, New World Island, Newfoundland; lower Dapingian–lower Darriwilian (Middle Ordovician).

Diagnosis.—Large, transversely elliptical *Rugostrophia* having a coarse reticulate ornament, the costellae more widely spaced than the concentric laminae.

Occurrence.—Lower part of the Umachiri Formation at locality 2, Floian–?Dapingian (Lower–Middle Ordovician).

Materials.—One dorsal external (CPI–9918) (Fig. 5.20) and internal (CPI–9912) (Fig. 5.21–5.23) molds.

Remarks.—The only ventral interior available is identical to *R. latireticulata* Neuman, 1976 (pl. 7, fig.7) from the Dapingian–lower Darriwilian of New World Island. Neuman (1976) stated that differences between *R. sylvestris* and *R. latireticulata* lie essentially in the ornamentation. The Peruvian material differs from *Rugostrophia* sp. from the Dapingian–lower Darriwilian Treiorwerth Formation (Neuman and Bates, 1978, pl. 67, figs. 15–18) in displaying flattened posterolateral extremities. In addition, it clearly differs from the Argentinian *Rugostrophia* species, *R. protoandina* Benedetto, 2003 and *Rugostrophia* sp. in having a much deeper notothyrial cavity and strongly raised anterior ends of adductor scars. Since no exteriors are available in the Peruvian collection that enable differentiating between the Canadian

species, it is preferable to assign this material tentatively to *R. latireticulata.*

Paleobiogeographical remarks

Most of the brachiopod taxa occurring in the Umachiri Formation belong to the superfamilies Orthoidea and Polytoechioidea with the exception of a porambonitoid. Among the orthoids, the most abundant genus is *Paralenorthis*. Even though it is a cosmopolitan genus, the species occurring in the Umachiri Formation strongly resembles *Paralenorthis carlottoi* Villas (in Gutiérrez-Marco and Villas, 2007) from the middle–upper Floian rocks of the San José Formation in the Carcel Puncco Canyon (Inambari River) section of the Peruvian Cordillera Oriental. Another orthoid brachiopod at Umachiri is very similar to the type species of *Mollesella* Benedetto, 2003, previously known only in the uppermost Floian–lower Dapingian rocks of the Molles Formation from the Famatina Range of northwest Argentina (Benedetto, 2003). The similarity of the Peruvian assemblage with those of the Famatina Range is also strengthened by the co-occurrence of specimens referable to the brachiopod genus *Panderina*. Although this genus is typical from Baltica and China, Benedetto (2003) described a new species from the upper volcaniclastic member (Loma del Kilómetro Mb) of the Suri Formation that he tentatively ascribed to *Panderina. Panderina*? *ambigua* Benedetto, 2003 shows mixed characteristics from other productorthid genera, making the generic classification problematic. The material from the Umachiri Formation shows some of the same mixed characteristics, suggesting that the species are strongly related. All these occurrences highlight the resemblance of the Peruvian assemblage to those of the Argentinian Famatina Range.

The brachiopod-dominated assemblage described here contains numerous polytoechioids. One of them, *Enriquetoechia*, is endemic to the Peruvian Altiplano. The other new genus described here, *Altiplanotoechia*, is likely present in the Argentinian western Puna, the Ganderia and Monian composite (including Anglesey) terranes (both likely located west of Avalonia forming an island arc at intermediate latitudes between Gondwana and Laurentia), and the Dashwoods (New World Island) and Moretown (St. Albans, Vermont) terranes (both likely located near Laurentia) (see Domeier, 2016 and Liljeroth et al., 2017, for estimated position of these island arcs during the Cambrian–Ordovician times). *Pomatotrema* is a genus previously known only in the Laurentian realm and South China. Benedetto (1987) described two species of this genus from material of the San Juan Formation of the Precordillera; however, they were subsequently reassigned to *Martellia* (Popov et al., 2001). The occurrence of *Pomatotrema* in the Peruvian Altiplano represents the highest paleolatitudinal occurrence of this genus so far and indicates connections of this region with the Laurentian realm and South China during Floian times. The links with Laurentia, the peri-Laurentian terranes, and other low-latitude terranes during the Floian–Dapingian are strengthened by the presence of *Tritoechia* (*Tritoechia*), with several species described from localities of the Dashwoods Terrane, Laurentia, Siberia, Kazakhstan, and Tasmania (Schuchert and Cooper, 1932; Ulrich and Cooper, 1936, 1938; Sando, 1957; Neuman, 1976; Laurie, 1980; Popov et al., 2001; Hansen

and Harper, 2003). Species of *Tritoechia* (*Tritoechia*) have also been described from the Argentinian Precordillera, western Puna, and Famatina regions, as well as in the Ganderia Terrane. The subgenus *Tritoechia* (*Parvitritoechia*) is known from the Dapingian–lower Darriwilian assemblages of the Treiorwerth Formation of the Midland Valley–Mayo Terrane (Williams and Curry, 1985), located in peri-Laurentian settings, from the San Juan Formation of the Precordillera (Benedetto, 2003), and from the Aguada de la Perdiz Formation of the Argentinian western Puna (Benedetto, 2001). The Peruvian material assigned to *Tritoechia* (*Parvitritoechia*) seems morphologically related to the species described from the upper Floian–lower Dapingian Aguada de la Perdiz Formation of the Argentinian western Puna.

The productorthid present in the Umachiri Formation, assigned here to the brachiopod genus *Rugostrophia*, strongly resembles *Rugostrophia latireticulata* Neuman, 1976 from the 'calcareous tuff' at Virgin Arm, New World Island, Newfoundland. This genus normally occurs in localities belonging to the Ganderia (e.g., Maine, New Brunswick) and Monian composite (Anglesey) terranes, located at intermediate latitudes between Gondwana and Laurentia, and on the Dashwoods Terrane (New World Island), located close to Laurentia, during early Dapingian–early Darriwilian times (Neuman, 1976; Neuman and Bates, 1978). However, species assigned to this genus also occur in the substantially older (uppermost Floian–lower Dapingian) volcaniclastic rocks of the Aguada de la Perdiz Formation of the Argentinian western Puna (Benedetto, 2001, 2003) as well as in the Darriwilian part of the San Juan Formation of the Precordillera (Herrera and Benedetto, 1991).

All these occurrences highlight the strong biogeographic affinity of the Peruvian Altiplano during the Early–?Middle Ordovician with the Famatina and western Puna regions of northwest Argentina. The brachiopod fauna of the Peruvian Altiplano could be integrated, together with their homologues from Famatina and western Puna, into a well-differentiated biogeographical subprovince (in the sense of Servais et al., 2013) during the Early–Middle Ordovician within the South American margin of Gondwana.

As discussed in the preceding, the Peruvian assemblage studied here also shows clear links with several terranes, of probable Gondwanan origin (Murphy et al., 1999; Zagorevski et al., 2015; Reusch et al., 2018), located at intermediate (Ganderia and Monian composite terranes) and low (Moretown, Dashwoods, and Midland Valley–Mayo terranes) latitudes between Gondwana and Laurentia (see Johnson et al., 1991 and Cutts et al., 2011 for paleogeographic position of Dashwoods Terrane) during Floian-Dapingian times. Villas et al. (2015) proposed the existence during Sandbian times (early Late Ordovician) of intermediate islands in the Rheic Ocean between the Peruvian Altiplano and Avalonia, permitting dispersal following the Southern Westerlies currents (Pohl et al., 2016) and island hopping of brachiopod species with low dispersal potential (short larval period) to overcome the presumably large distances between those terranes. Several of these islands/terranes (known as Ganderian terranes) likely detached from Gondwana and drifted toward Laurentia and Baltica during the late Cambrian–Early Ordovician, triggering the opening of the Rheic Ocean (van Staal et al., 1996; Ayuso and Schulz, 2003;

Ayuso et al., 2003; Schulz and Ayuso, 2003; Wilson, 2003; Valverde-Vaquero et al., 2006; Zagorevski et al., 2007, 2010; Dennis et al., 2020). It is also important to consider that these islands were likely connected to continuous, emergent arcs that may have been oblique, consuming oceanic crust and migrating physically across the greater Iapetus realm (see Domeier, 2016, for estimated position of these island arcs during the Cambrian–Ordovician times). These tectonic processes and the resultant island arcs would have facilitated faunal migration from Gondwana to Laurentia (Nowlan et al., 1997; Fortey and Cocks, 2003; Harper et al., 2009). The same method of faunal migration is proposed here, during Floian to Dapingian times, facilitating faunal exchange between the Peruvian Altiplano and the Ganderia and Monian Composite terranes. In addition, Ganderian and Monian composite terranes could have acted as intermediate island arcs allowing subsequent faunal swapping of Gondwanan and Celtic faunas with peri-Gondwanan and peri-Laurentian terranes (Moretown, Dashwoods, and Midland Valley–Mayo terranes). These island arcs collided with Laurentia in the Taconic Orogeny and may have closed the main tract of the Iapetus Ocean in the Floian (Macdonald et al., 2014, 2017; Karabinos et al., 2017), much earlier than previous estimates (i.e., Late Ordovician, van Staal et al., 2012 and references therein). After their docking with Laurentia, faunal transfer with the Scoto-Appalachian Province might have been facilitated (Neuman, 1984; Neuman and Harper, 1992; Harper et al., 1996; Liljeroth et al., 2017). The faunal dispersal mechanisms discussed in the preceding may also explain the slight diachronism existing among the Peruvian, Celtic, and peri-Laurentian faunas, with younger occurrences in the latter.

Age of the fossil assemblages

Given the similarities of the Peruvian brachiopods recorded from the lower strata of the Umachiri Formation, especially with the volcaniclastic uppermost Loma del Kilómetro Mb of the Suri Formation and the Molles Formation of the Central Famatina Range and with those of the volcaniclastic Aguada de la Perdiz Formation from the western Puna of northwest Argentina, a similar Floian to ?middle Dapingian (475–468 Ma) age range has been inferred. The age of correlated strata is constrained by the occurrence of conodonts of the *Prioniodus elegans*, *Oepikodus evae*, and '*Baltoniodus navis*' zones in the Famatinian strata (Albanesi and Vaccari, 1994; Lehnert et al., 1997; Albanesi and Astini, 2000) and by associated trilobite and graptolite occurrences in equivalent western Puna strata (Koukharsky et al., 1996; Monteros et al., 1996; Brussa et al., 2003; Toro et al., 2015).

The youngest identifiable fossils in the Umachiri Formation are graptolites from the upper part of the Umachiri Formation at locality 5 (Figs. 1, 2), previously reported by Cerrón and Chacaltana (2002). The preservation of these graptolites is poor, but preliminary data suggest a Middle–?Upper Ordovician age for this horizon (J.C. Gutiérrez-Marco, personal communication, 2020).

Acknowledgments

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