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First record of Palaeozoic vertebrates from Peru

Primer registro de vertebrados paleozoicos del Perú

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Abstract: Devonian vertebrates from South America are notably scarce compared with those of other continents. This is particularly evident in Peru, where no palaeozoic vertebrates have been formally reported so far. In this paper, we figure and describe the first Devonian vertebrates remains from Peru recovered in the Puno region. The remains belong to a very unusual group of Emsian to Eifelian stem-chondrichthyan *Pucapampella* and *Zamponiopteron* that characterise the vertebrate fauna of the so-called marine "Malvinokaffric Realm". The remains studied here are represented by three jaw fragments assigned to *Pucapampella*, and three fin plates of *Zamponiopteron*. These records increase the palaeogeographic distribution of this assemblage in the Palaeozoic of Gondwana, but more importantly, our findings highlight the potential of the Peruvian outcrops to contribute to our knowledge of the diversity and distribution of the early vertebrate faunas in the South American continent.

Resumen: Los vertebrados devónicos en América del Sur son notablemente escasos en comparación con otros continentes, siendo esta circunstancia particularmente evidente en Perú, donde hasta el momento no se han descrito formalmente vertebrados devónicos. En el presente trabajo se figuran y describen los primeros restos de vertebrados del Devónico recuperados en la región de Puno. Los restos descritos pertenecientes al inusual grupo de *stem*-condríctios del Emsiense–Eifeliense de la llamada "Región Malvinokaffric", estando representados por fragmentos de mandíbula asignados a *Pucapampella* y fragmentos de aletas de *Zamponiopteron*. Ambos registros constituyen los primeros restos de vertebrados documentados en el país aumentando así su distribución paleogeográfica en el Paleozoico de Gondwana. Finalmente, nuestros hallazgos destacan el potencial de los afloramientos peruanos para contribuir al escaso conocimiento sobre la diversidad y distribución de las faunas de vertebrados tempranos en el continente sudamericano.

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INTRODUCTION

In comparison with other continents, the fossil record of Devonian vertebrates in South America is notably scarce (see an overview in Janvier & Maisey, 2010; Racheboeuf *et al*., 2012; or Olive *et al*., 2019; Botella *et al*., 2020 for more recent findings). This situation is particularly evident in Peru, where no Devonian vertebrates have been formally reported so far. In fact, the only reference to Palaeozoic vertebrates in Peru comes from Maisey *et al*. (2019) that mentioned the existence of a chondrichthyan lower jaw fragment in the collections of the "Museo Paleontológico de Puno". However, the specimen (which lacks a catalogue number in the original publication) was neither described nor figured, and no information about its stratigraphic provenance was available.

Due to the relevance of this finding for the Peruvian palaeontological heritage, one of the authors (LZ) started a systematic work to track the origin of this report, reviewing the collections of the "Museo Puno Paleontológico", as well as other collections with Devonian specimens from the Puno region at the San Agustín National University of Arequipa (Arequipa, Peru). This work has led to the identification of several vertebrate remains and more importantly, to locate the original fossil locality. After a field expedition in 2016, we were able to identify the stratigraphic levels where the specimens most probably come from, and to collect new *in situ* material. Therefore, the aim of this work is to present the first formal description of Palaeozoic (Devonian) vertebrates from Peru, highlighting the potential of the Peruvian outcrops to contribute to the knowledge of the diversity and distribution of early vertebrate faunas in the South American continent.

GEOGRAPHICAL AND GEOLOGICAL SETTINGS

Palaeozoic outcrops in Peru constitute around 10% of the total surface of the country, being represented in the south region mostly by metasediments of Upper Silurian and Middle Devonian ages (Newell, 1949). These strata mainly belong to the Chagrapi Formation, which are equivalent to the Upper Belen and Sica Sica formations from Bolivia (Janvier & Suárez-Riglos, 1986); the Fox Bay Formation from Falkland Islands (Maisey *et al*., 2002); and the Pimenteira Formation from Brazil (Janvier & Melo, 1987,1992). All these Middle Devonian formations from South America have yielded palaeozoic vertebrate remains (Fig. 1).

The new specimens here described come from the surroundings of the Taraco municipality located in the Puno region, southwestern Peru, near to the Titicaca Lake at 4200 m asl (Fig. 1A). The area of study is located at the Imarrucos hill, 5 km south-southwest from the village of Taraco. In this hill, a continuous section of around 450 m of thickness has been described, the Taraco Section (Fig. 1B), belonging to the Chagrapi Formation. Geologically, the section is characterised by a cyclic sequence of grey and dark shales with fine layers of sandstones (fine-grained) which are interpreted as sandy deltaic channels. In more detail, the first 300 m of the section is represented by the lower member of the Chagrapi Formation, composed of cyclic sequences of dark and grey shales with fine grain sandstones and ripples. The rest of the sequence represents the upper member of the Chagrapi Formation, characterised by approximately 150 m of dark shales with abundant organic matter with fine levels of silt and very fine sandstones. Towards the top of the section, sandstones are less abundant and shale intervals with phosphatic nodules become more common. The Chagrapi Formation in the region is interpreted as a marine infralittoral environment with deltaic influence, with some episodes of deepening with associated anoxic conditions (Valdivia *et al*., 2021).

The age of the Taraco Section was determined by Valdivia *et al*. (2021) based on stratigraphical correlation, and palaeontological evidences (invertebrate fauna), giving an Emsian–Eifelian age. The nodular layers containing the vertebrate remains are located in the upper part of the section, belonging to the upper part of the Chagrapi Formation with an Eifelian age (Fig. 1C). These layers are represented by grey shales that contain numerous phosphatic nodules from a few centimetres up to 10 cm in length. The nodules frequently contain an abundant and diverse invertebrate fauna (trilobites, conularids, corals, molluscs and crinoids), and among them, vertebrate remains are also present.

MATERIALS AND METHODS

The six remains here described come from local collections, and just one (LP-UNSA-VP-02; Fig. 2C) was collected by us in a preliminary field campaign. Three specimens are deposited at the Vertebrate Collection of the “Universidad San Agustín de Arequipa” (LP-UNSA-VP-02, LP-UNSA-VP-03, LP-UNSA-VP-04) and

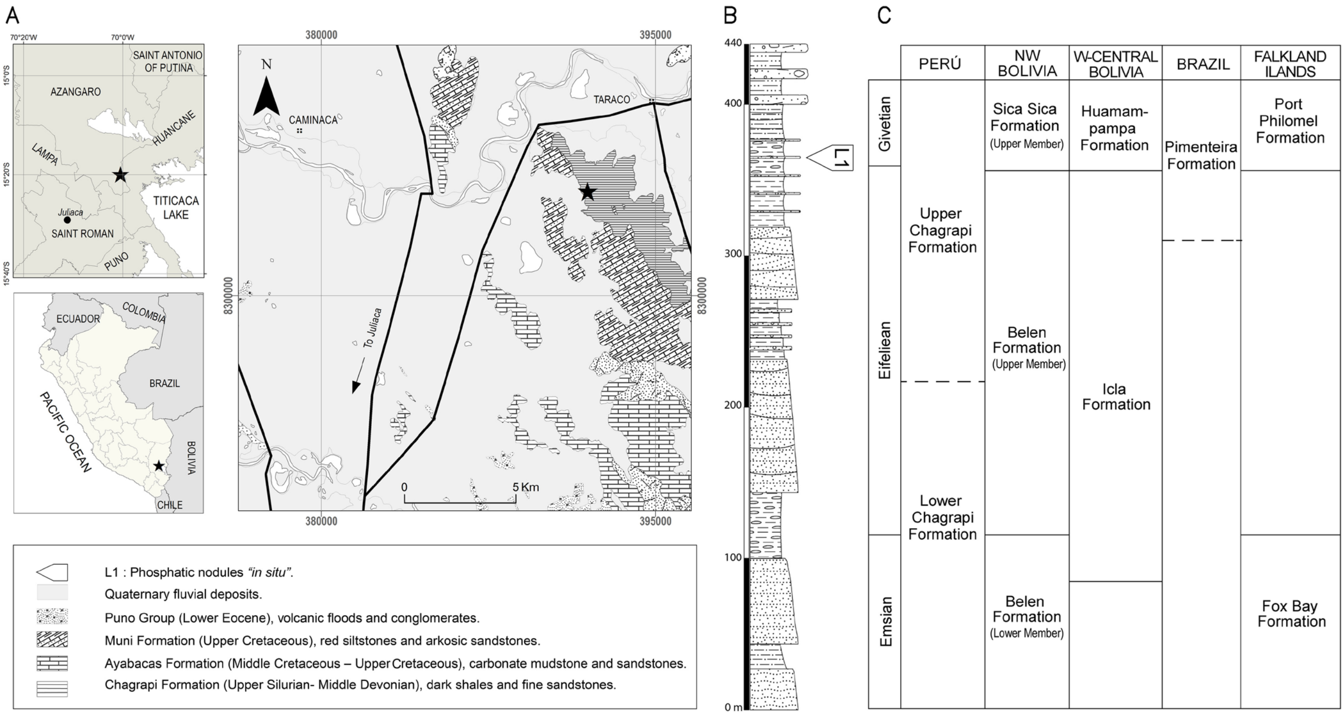

Figure 1. A, Geographical and geological settings of the studied area; **B,** general column of the Taraco Section (Puno, Peru), the arrow shows the levels of phosphatic nodules with chondrichthyan remains; **C,** stratigraphic unit distribution of the main South America vertebrate-bearing formations including Peru (modified from Janvier, 2007).

the other three are housed at "Museo Puno Paleontológico" (MPP01, MPP02, MPP03). All the vertebrate remains were found inside small phosphatic nodules of no more than 4–5 cm in length. Some of the specimens studied (Fig. 2A–2D) were scanned for its taphonomic analysis with the help of a Nikon XTH 225ST X-ray tomography scanner at the XTM Facility of the Palaeobiology Research Group, University of Bristol (UK) with a Tungsten target, a current of 90 μA, a voltage of 180 kV, and exposure time of 708 ms. A total of 3141 projections were obtained equiangularly through 360° of rotation. The ensuing data were reconstructed using VG Studios software, with a final voxel size of 0.0126 mm. Slice data were analysed and manipulated using Avizo Lite 9 (FEI Visualization Sciences Group).

All the specimens were photographed with a camera 70D Canon Reflex with a macro lens of 100 mm (F2/8) at the Faculty of Geology, Geophysics and Mines of the National University of San Agustin of Arequipa (**UNSA**).

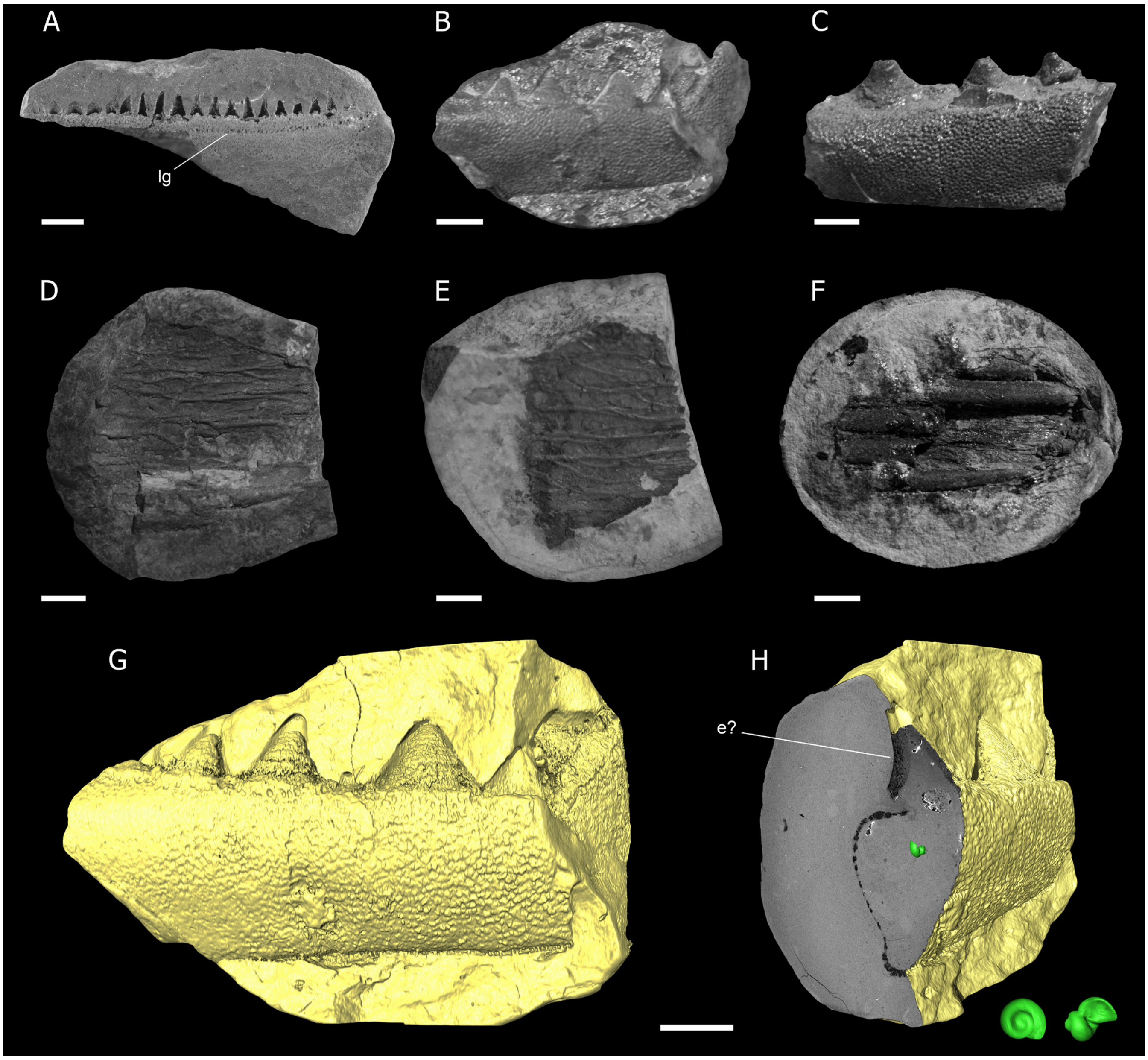

Figure 2. Devonian vertebrate remains from the Taraco Section (Puno, Peru). **A**–**C,** *Pucampella* sp.; **A,** external mould of a Meckel cartilage fragment, (MPP01); **B,** phosphatic nodule with a Meckel cartilage fragment (MPP02); **C,** isolated Meckel cartilage fragment (LP-UNSA-VP-02); **D**–**E,** two mould fragments of *Zamponioteron triangularis* (LP-UNSA-VP-03, MPP03); **F,** *Zamponioteron* sp. preserving some 3D radial canals (LP-UNSA-VP-04) (Janvier & Suarez-Riglos, 1986); **G**–**H,** 3D model of the specimen MPP02 after CT-scan; **H,** virtual thin section of the same specimen showing: complete replacement of the cartilage by sediment; a gastropod; and the differentiated "enameloid cup" of one tooth. **lg,** longitudinal groove; **e?,** enameloid?; scale bars = 0.5 cm.

RESULTS AND DISCUSION

Descriptions of specimens and taxonomic identifications

Although most of the revised and collected concretions from the Taraco area contain invertebrates, amongst them, we were able to identify 6 isolated vertebrate remains (Fig. 2). Three of them represent part of mandibular arches attributed to the chondrichthyan *Pucapampella* (Fig. 2A–2C). The specimen MPP01 (Fig. 2A) is preserved as an external mould of a right lower mandibular arch, probably in lingual view. The Meckelian cartilage is incomplete, displaying a total length of 36 mm and a maximum depth of 5.3 mm. The surface shows clear evidences of tessellated prismatic calcified cartilage with a longitudinal "groove" in the upper part, but no median deep groove is visible. The specimen shows a row of, at least, 18 small triangular teeth, directly attached to the Meckelian cartilage (Fig. 2A). Teeth are conical, although slightly compressed linguo-labially, and similar in size. The maximum diameter of the cusps (at the contact with the cartilage) is around 1.5 mm and the height of the most complete conserved cusp is around 3 mm. The teeth are arranged with very small interdental spaces. The other two specimens (MPP02 and LP-UNSA-VP-02) correspond to fragments of a right Meckel cartilage preserved in three dimensions of around 30 mm in length each (Fig. 2B, 2C). Specimen MPP02, that shows a small part of the proximal part broken and displaced, preserves four robust and low conical teeth, which decrease in size toward the (putative) posterior part of the jaw, meanwhile specimen LP-UNSA-VP-02 preserves just three conical teeth of similar sizes. In both cases, the maximum diameter of the teeth cusp reaches up to 5 mm. The external surfaces of the specimens show the typical prismatic calcification. The depth of the Meckel's cartilage, compared with the teeth sizes, and the lack of the median groove suggest that the preserve portion in these specimens could correspond to the distal part of the Meckelian cartilage, although assignation is difficult due to the fragmentary nature of the remains. The size and overall shape of MPP02 and LP-UNSA-VP-02 is comparable to the 'large-toothed' Meckelian fragments referred to *Pucapampella* sp. in Maisey *et al*. (2019, figs. 5.5, G). However, MPP01 is smaller than other pucapampelid Meckelian cartilages currently known from the Middle Devonian of Bolivia (*i.e*., Janvier & Maisey, 2010, figs. 7B, 8; Maisey *et al*., 2019, figs. 5.5, G). Additionally, MPP01 shows an upper longitudinal thin groove and lacks, in the preserve portion, the typical median groove present in other pucapampellids. Moreover, their teeth seem higher and more "gracile" than the typical more robust and low teeth present in other pucapampellid jaws. The fact that the isolated jaw elements assigned to *Pucapampella* show notable diversity in morphology, size and teeth arrangement has been noted by previous authors, suggesting that the genus could include many more species than the only one formally erected so far (*i.e*., the type species, *Pucapampella rodrigae* Janvier & Suárez-Riglos, 1986). The material from Peru could provide additional information in this sense.

The other three elements (LP-UNSA-VP-03, MPP03, and LP-UNSA-VP-04; Fig. 2D and 2E respectively), are assigned to *Zamponiopteron* pterygial plates (or 'fin plates' *sensu* Janvier & Maisey, 2010). LP-UNSA-VP-03 and MPP03 are preserved as natural moulds showing a dense network of vascular channels. Main vascular channels (up to 7) run parallel to each other in proximal-distal direction and bifurcate at several locations (Fig. 2D, 2E). Specimen LP-UNSA-VP-03 additionally preserves two 3D radial canals in a lateral part of the fin (Fig. 2F). Both specimens, LP-UNSA-VP-03 and MPP03, are incomplete, lacking the most distal part of the fin, however the preserved portion is very similar in morphology to the proximal part of *Zamponiopteron triangularis* (compared with Janvier & Suárez-Riglos, 1986, pl. 5, fig. 2b; Gagnier *et al*., 1989, pl. 5, fig. 2b). On the other hand, LP-UNSA-VP-04 is preserved in three dimensions showing a slightly different morphology. The specimen shows five hollow parallel radial canals (regarded as fused paired fin radials), opened at the proximal edge of the plate (Fig. 2F). Some of the canals seem to be blind in their distal part, suggesting that the fin plate is almost complete, hence representing a different morphology from those previously described as different taxa (Janvier & Suárez-Riglos, 1986).

Taphonomic remarks

Understanding the origin of the phosphatic nodules can be a useful tool for unravelling the palaeonvironmental and taphonomic settings of the outcrop in which the nodules were formed (Zangerl & Richardson, 1963). In our case, the phosphatic nodules from Taraco contain fossils that seem exceptionally well preserved in three dimensions, representing, at least partially, an example of the invertebrate and vertebrate community. The preliminary study of the fossil content shows a faunal community composed by cartilaginous fishes, trilobites and conularids, with a minor proportion of molluscs (orthoceratids, gastropods, bivalves), corals, and echinoderms. We expect, that future palaeoecological analyses of the fossil diversity within the nodules will add valuable information and ultimately provide a clearer picture of the conditions represented by this black shale facies.

Regarding their taphonomical history, apparently, the formation of the nodules seems to have occurred under anoxic conditions early in diagenesis, favouring the formation of the phosphatic nodules. Based on field observations, the host black shales were clearly deformed around the concretions, preserving the fossil remains in three dimensions. In addition, one specimen (Fig. 2B, MP002) shows the anterior part of the mandibular arch broken within the nodule, suggesting that the concretions lithified prior to compaction of the surrounding mud early in the diagenesis.

On the other hand, none of the specimens examined seem to display original microstructure, being the original tissues secondarily replaced, but preserving the characteristic appearance of the Meckelian prismatic cartilage. In order to understand their taphonomical history, four specimens where scanned, two of them (Fig. 2A, 2D) were external moulds, so no histological information was recovered. The other two specimens (Fig. 2B, 2C), represented by Meckel cartilage fragments with some teeth, show how the original tissues have been completely replaced, or just decomposed and refilled (cartilage) by the same material that forms the nodule (Fig. 2H). Interestingly, analysing the tomograms, the outer part of the tooth cusp can be clearly distinguished from the rest of the jaw, suggesting that the tooth could have been covered with a different tissue (*i.e.*, enameloid).

Finally, one significant characteristic of the studied material is its disarticulated nature. Most of the nodules examined seem to have formed around isolated pieces of fossil material rather than aggregations of specimens. The nature of this kind of assemblage has been previously explained in other similar outcrops with phosphatic concretions and vertebrate remains as the result of regurgitation or coprolites (*i.e.*, Poplin, 1986; Murthy *et al*., 2004; Pradel, 2010). However, the destruction of the microstructure of the fossil fragments during phosphatisation makes it difficult to identify the marks on the bone surface related with digestion processes (Fernández-Jalvo & Andrews, 2016). Therefore, further studies are needed, with a better sampling effort, to elucidate the depositional and taphonomic history of the new outcrops here described.

FINAL COMMENTS AND PERSPECTIVES

Pucapampellids (*i.e.*, family Pucapampellidae) are a very unusual group of Emsian to Eifelian stem-chondrichthyan, which lack the characteristic shark-like dental families and mode of tooth replacement (see *e.g.*, Botella, 2006; Botella *et al*., 2009), endemics of the so-called marine “Malvinokaffric Realm” of Boucot (1975, 1990). It currently includes two genera: *Pucapampella* and *Gydoselache* (Maisey *et al*., 2019). The latter is known only from a single specimen collected at the Gydo Formation of South Africa (Maisey & Anderson, 2001). Conversely, *Pucapampella* is known from a plethora of specimens collected from the Belén and the Icla formations in Bolivia (Janvier & Maisey, 2010). Additionally, as said above, a lower jaw fragment in the collection of the Museo Paleontológico of Puno (Peru) was mentioned by Maisey *et al*. (2019). This specimen probably corresponds with specimen MPP01 described here as the other remains belonged to other collections or were found posteriorly.

Zamponiopteron is an enigmatic taxon of still uncertain taxonomic and anatomic affinities. These fossils have been interpreted as paired “fin-plates” of a primitive chondrichthyan (Janvier & Suárez-Riglos, 1986, but see discussion in Janvier & Maisey, 2010). The fact that *Zamponiopteron* and *Pucapampella* occurred in the same localities of the Belén and Icla formations in Bolivia has led some authors to suggest that these remains could represent different anatomical parts of the same taxa (*i.e.*, Janvier & Maisey, 2010; Janvier & Racheboeuf, 2018). The finding of *Zamponiopteron* and *Pucapampella* in co-occurrence also in Chagrapi Formation in Peru could support this view (but see Janvier & Maisey, 2010; Janvier & Racheboeuf, 2018 for discussion).

To sum up, the description of the first vertebrate remains from the Peruvian Palaeozoic represents an important finding that will allow us to increase our knowledge about this unusual assemblage of vertebrates that characterises the well-defined Devonian vertebrate association in South America (Janvier & Maisey, 2010). In addition, the description of several new jaw fragments of *Pucapampella* and fin plates of *Zamponiopteron* extends the limits of the *Pucapampella*-*Zamponiopteron* assemblage (Janvier & Maisey, 2010) to the north, but more importantly, these findings highlight the potential of Peruvian Devonian rocks to contribute to our understanding of the distribution and diversity of the early vertebrates in South America. As stated above, a short preliminary field expedition allowed us to locate the *in situ* fossiliferous levels. Consequently, we expect that new and more extensive field research will provide abundant new fossils material that will be of great significance for elucidating early gnathostome relationships, in particular of these problematic groups, and contribute to resolving the problems of global palaeobiogeography during the Devonian (see Janvier & Maisey, 2010; Olive *et al*., 2019)

Supplementary information. This article has no additional data.

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Competing Interest. We declare no competing interests

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