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Discovery of Ordovician scolecodonts from Peru, with a review of Palaeozoic jawed polychaete records from South America

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ABSTRACT

The fossil record of jaw-bearing polychaetes from South America is scarce, and only a few occurrences of Ordovician scolecodonts have been reported so far. Here, we document a monospecific jawed polychaete assemblage from the Darriwilian *Lenodus crassus* conodont zone of the San José Formation in the eastern Cordillera of Peru. The single species, *Protarabellites luztejadae* sp. nov., represents the oldest record of the family Ramphoprionidae worldwide and may point to the biogeographic origin of this group in Gondwana. The reconstructed jaw apparatus of *P. luztejadae* bears primitive characters such as the slightly enclosed myocoele, distinguishing it from the younger members of the family and providing insights into the evolutionary relationships with other labidognath families. The described assemblage is the first record of Ordovician scolecodonts from Peru, as well as from the northern part of the Central Andean Basin, and one of very few cases from where apparatus-based classification has been applied. However, the Palaeozoic scolecodonts in South America appear to be more common than generally thought. A review of poorly known regional literature shows that scolecodonts have been mentioned in various sites from Ordovician, Silurian, Devonian, and Carboniferous–Permian strata of Argentina, Bolivia, Brazil, Colombia, Peru, and Uruguay. This highlights the potential for future scolecodont studies in South America.

KEYWORDS **Scolecodonts. Jawed polychaetes. Middle Ordovician. Gondwana. Peru.**

INTRODUCTION

The diversification of polychaetes in the Ordovician is primarily based on the record of their jaws, the scolecodonts. These organic-walled microfossils are often abundant in shallow-marine deposits starting from the Darriwilian (Eriksson *et al.*, 2013; Hints and Eriksson, 2007), but the currently available data on Ordovician scolecodonts is strongly skewed towards the Late Ordovician, with only a few reports covering the Middle Ordovician. Moreover, some regions, such as Baltoscandia and the North American Midcontinent region, are far better studied than many parts of Gondwana and peri-Gondwana (Eriksson *et al.*, 2013). This has limited our understanding of the early diversification and biogeography of jaw-bearing polychaete worms globally.

Only a few records of Palaeozoic scolecodonts are known from South America, which was part of Gondwana. The papers by Lange (1947, 1949, 1950) were the only reports from this region for a long time and, importantly, established the modern concept of an apparatus-based classification concept as opposed to “form taxonomy” (Eriksson *et al.*, 2000, 2011). Later, Ordovician and Permo-Carboniferous scolecodonts were also reported from Argentina and Brazil, but the number of publications has remained low. The only previous records of Palaeozoic scolecodonts from Peru were some poorly preserved elements from the Silurian Lampa Formation of the Altiplano (Gray in Laubacher *et al.*, 1982, p. 1142), as well as some indeterminate specimens in an upper Famennian (Upper Devonian) palynological sample from the Cabanillas Group of central Peru (Wood, 2010, p. 138).

The present paper describes a low-diversity assemblage of scolecodonts from the Middle Ordovician of Peru. This South American assemblage adds to the scarce Early and Middle Ordovician taxa so far described in the Precordillera and Subandean Ranges of Argentina (Eriksson *et al.*, 2002; Hints *et al.*, 2017; Ottone and Holfeltz, 1992; Ottone *et al.*, 1992, 1999, among others). The collection presented in this study is of interest not only because it constitutes the oldest record of scolecodonts in Peru and the first Ordovician scolecodonts described outside Argentina, but also because it corresponds to a new species that reveals novel evolutionary aspects and palaeobiogeography of the family Ramphoprionidae.

GEOLOGICAL SETTING AND STRATIGRAPHY

The studied area is located in the eastern Cordillera of Peru, within the northern segment of the Central Andean Basin (Fig. 1A), specifically in the lower Palaeozoic outcrops of the southeastern flank of the Pichari–Cielo Punku antiform, which has a metamorphic Neoproterozoic core (Fig. 1B). The area lies along the northeastern bank of the Apurímac River valley, in the Kimbiri district, in the western part of the La Convención province of southern Peru (Cusco Department), approximately 80 km northeast of the city of Ayacucho.

The local Ordovician succession is primarily represented by the San José Formation, which unconformably overlies

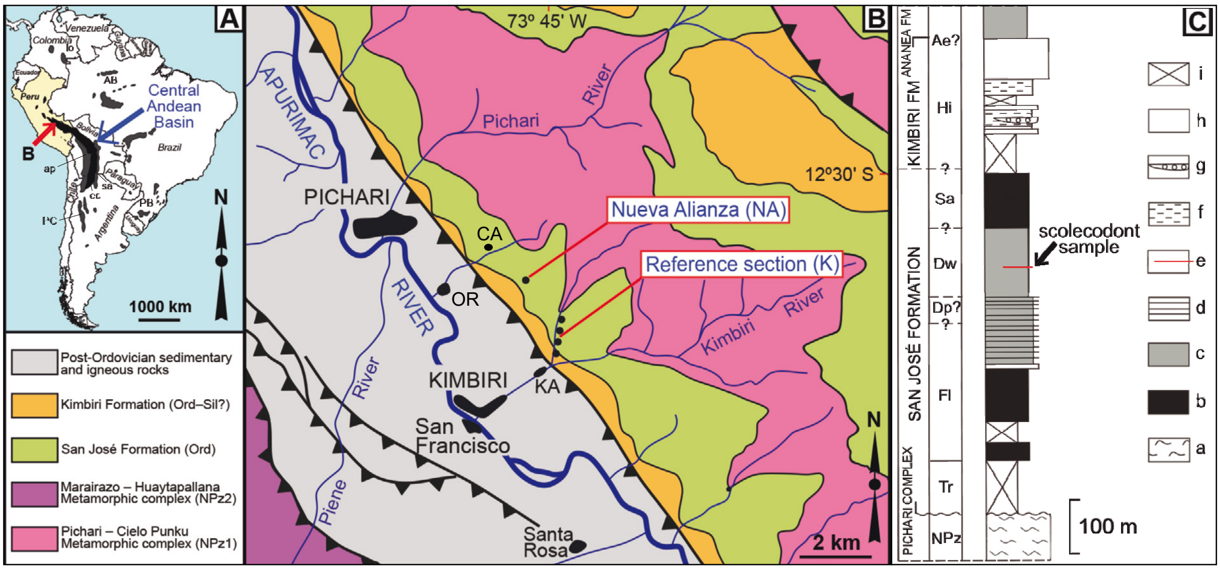

FIGURE 1. A) Sketch map showing the distribution of Lower Palaeozoic sedimentary basins in South America (in black and dark grey), and the position (red arrow) of the studied area in the northern part of the Central Andean Basin. Abbreviations: AB= Amazonian Basin; PB= Paraná Basin; PC: Precordillera Basin; ap= altiplano-Puna (in dark grey); ec= eastern cordillera; sa= subandean range (in dark grey); lo= llanos orientales and Macarena range, Colombia. B) Geological map of the fossil locality in the Apurímac River valley, which yielded Ordovician scolecodonts (NA, Nueva Alianza) and is located close to the Kimbiri Alto Ordovician reference section (K= Kashiroveni stream). Base map modified from Gómez Cahuaya *et al.* (2021) and Valencia Muñoz *et al.* (2021). C) Simplified stratigraphic section from K, made along the Kashiroveni stream. The arrow indicates the approximate position of the limestone horizon at the Nueva Alianza locality, based on correlation inferred from shared lithologies and macrofossils (brachiopods, trilobites, graptolites, molluscs, and ostracods). Abbreviations: CA= Catarata; KA= Kimbiri Alto; O= Oroya; FM= Formation; NPz= Neoproterozoic; Tr= Tremadocian; Fl= Floian; Dp= Dapingian; Dw= Darriwilian; Sa= Sandbian, Hi= Hirnantian; Ae= Aeronian. Lithological symbols: a= metamorphic rocks; b= black shale; c= argillaceous shale; d= siltstone/sandstone alternation; e= thin limestone horizon; f= glaciomarine diamictite; g= conglomerate; h= sandstone; i= covered interval.

the basal metamorphic complex of Pichari-Cielo Punku. The formation consists mainly of fossiliferous shales and siltstones, up to 700 m thick, occasionally interbedded with sandstones, several noduliferous beds, and very scarce thin limestone lenses. The San José Formation terminates with an unconformity related to eustatic changes and is overlain by glaciomarine diamictites, followed by the massive quartzites of the Kimbiri Formation (Colmenar *et al.*, 2024; Gutiérrez-Marco *et al.*, 2019b).

The lower part of the San José Formation has yielded Tremadocian to earliest Floian graptolites (Gutiérrez-Marco *et al.*, 2019a). In the middle and upper parts of the formation, the record of shelly faunas and graptolites documents the presence of Floian, Darriwilian, and lower Sandbian strata. So far, Dapingian strata have not been palaeontologically characterised among the beds containing Floian and Darriwilian fossils.

The most complete, continuous, and fossiliferous section of the San José Formation is the Kimbiri Alto section (K in Fig. 1B), located along a path that follows the left bank of the Kashiroveni stream. This succession (Fig. 1C) serves as the reference framework for projecting the various fossiliferous points represented in nearby localities and also for correlating the numerous partial sections recorded along the slopes of dirt roads, often temporary, in terrain belonging to the dense high-altitude Amazonian rainforest. These sections are subject to rapid coverage by lush tropical vegetation, and their slopes are frequently affected by small landslides.

In the case of the partial section along the dirt road between the locality of Catarata and the Nueva Alianza hamlet (NA in Fig. 1B), it was sampled by one of us (JCG-M) in 2018 with the aim of re-examining and dating a thin limestone level indicated by the petrological sample GR52A-19-098 in the Geological Map of Peru at a 1: 50,000 scale (see supplementary information in Valencia Muñoz *et al.*, 2021). The horizon was relocated, and a partial column of the San José Formation was recorded, comprising approximately 80 m of weathered Darriwilian shales, from which two levels with brachiopods have been recognised (Colmenar *et al.*, 2024, fig. 2). Towards the upper part of the Nueva Alianza section (NA in Fig. 1B), two closely spaced lenticular levels of grey bioclastic limestone are intercalated, each with a maximum thickness of about 10 cm (Fig. 2A): the lower one being a brachiopod coquina and the upper one extraordinarily rich in ostracods, which belong to a single smooth-surfaced species (Fig. 2B). The DMS (Degree, Minutes, Seconds) geographical coordinates of this outcrop are 12°33’07.1”S, 73°45’48.6”W.

Although only the data on brachiopods have been published, the correlation between the upper half of the Nueva Alianza section and the thick, massive package of Darriwilian shales in the Kimbiri Alto reference section is likely. These originally bluish to green highly fossiliferous shales appear deeply weathered to reddish and salmon hues in the upper part of the Nueva Alianza section, but contain identical graptolites, trilobites, and brachiopods. Among the latter, the record of *Ahtiella coloradoensis* (BENEDETTO, 1998), *Apurimella santiagoi* COLMENAR, CHACALTANA AND GUTIÉRREZ-MARCO, 2024 and *Phragmorthis henrylunae* COLMENAR, CHACALTANA AND GUTIÉRREZ-MARCO, 2024 provides direct correlation, at least, with horizons K-15 to K-17 of the reference section of the Kashiroveni stream (see Colmenar *et al.*, 2024, fig. 2).

In addition to the fossils mentioned above, conodonts were recovered for the first time from both limestone samples at Nueva Alianza. The most abundant and diverse conodont assemblage derives from the upper (“ostracod”) limestone, which is approximately coeval with certain Darriwilian assemblages described by Carlorosi *et al.* (2013) from other regions of the eastern Cordillera of Peru, thereby supporting a consistent regional biostratigraphical framework. The new conodont record from the Nueva Alianza locality includes, among others, the following species: *Baltoniodus medius* (DZIK, 1976), *Condorodus* sp., *Drepanodus arcuatus* PANDER, 1856, *Drepanoistodus costatus* (ABAIMOVA, 1971), *Erraticodon hexianensis* AN AND DING, 1985, *Lenodus* (= *Yangtzeplacognathus*) *crassus* (CHEN AND ZHANG IN DING *et al.*, 1993), *Lenodus variabilis* (SERGEEVA, 1963), *Periodon macrodentatus* (GRAVES AND ELLISON, 1941) and *Phragmodus undatus* BRANSON AND MEHL, 1933. This assemblage allows the recognition of the *Lenodus crassus* zone. According to modern biochronological schemes, this zone is of early to early middle Darriwilian age (Bergström and Wang, 1998). Considering that the first middle Darriwilian graptolites were recorded approximately 15 m upsection, the results are consistent with those of Colmenar *et al.* (2024), who tentatively assigned the levels, correlated with those studied here, to the early Darriwilian (Dw1).

The *Lenodus crassus* zone has been recognized previously from Baltica (Löfgren, 2000; Nielsen *et al.*, 2023; Stouge and Nielsen, 2003), South China (Bergström and Wang, 1998; Ding *et al.*, 1993; Zhang, 1997, 1998a, b) and the Argentine Precordillera (Heredia and Mestre, 2013; Heredia *et al.*, 2005; Mestre and Heredia, 2013, 2017). The new Middle Ordovician conodont assemblage recorded at the studied section correlate globally with this biozone.

MATERIAL AND METHODS

The scolecodonts that are the subject of the present study were recovered from two limestone samples

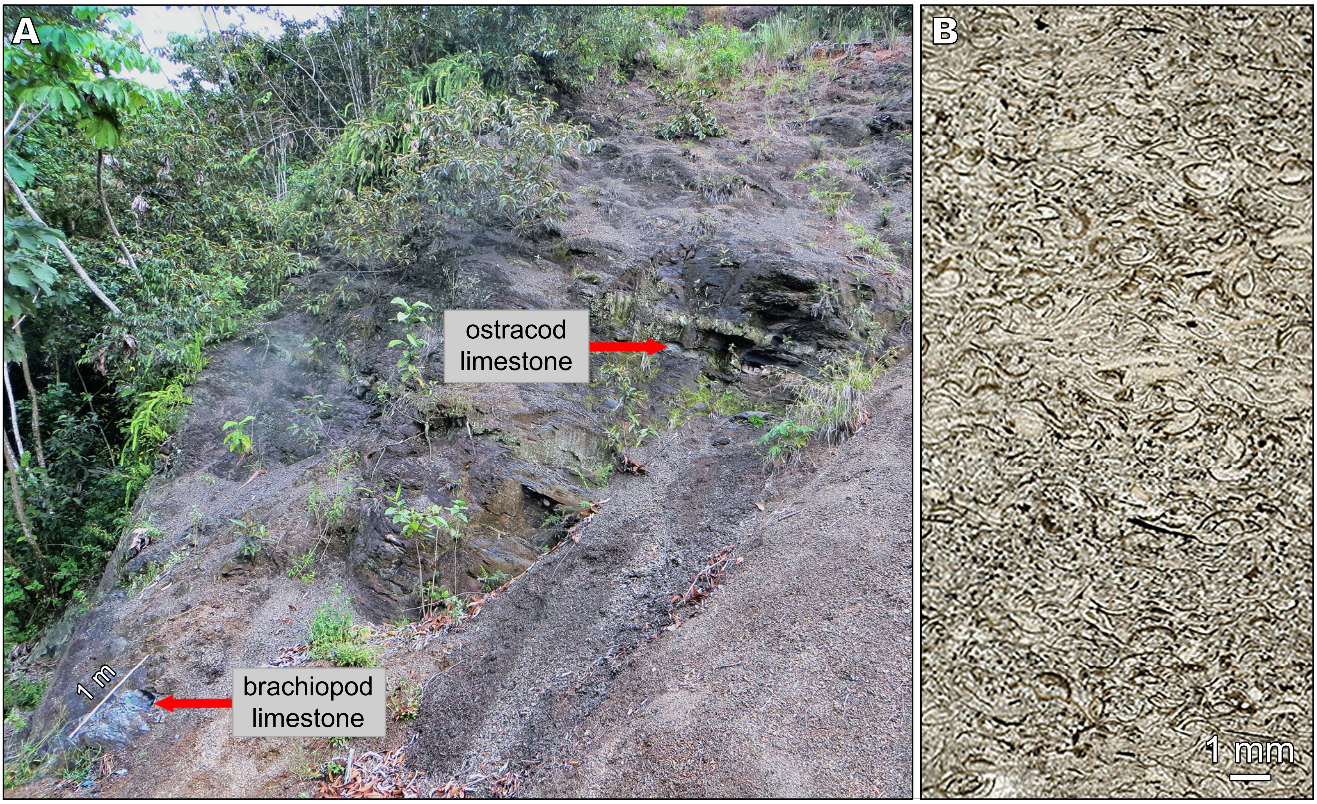

FIGURE 2. A) Field photograph of a detail of the Nueva Alianza section in November 2018, showing the limestone lens rich in ostracods, which provides Darriwilian conodonts and the scolecodont collection studied here. The sampled limestone is intercalated within a sequence of massive argillaceous shale, 0.25 m below a thin lenticular sandstone bed and 5.2 m above a calcareous brachiopod coquina rich in *Ahtiella coloradoensis* (Benedetto, 1998) and rare trilobites (sample NA-4c in Colmenar *et al.*, 2024). B) Microphotograph of the scolecodont-bearing limestone in transverse section (top facing up, natural light), showing a mass of densely packed valves of disarticulated smooth ostracods.

processed in the laboratory for conodont analysis, collected from the Nueva Alianza section ("ostracod limestone" and "brachiopod limestone" in Fig. 2A). Standard weak formic acid processing techniques were used, following Stone (1987). The recovered residues were studied under a stereo microscope, where conodonts, scolecodonts, ostracods, and gastropods were hand-picked. The "ostracod limestone" sample (Fig. 2) contained an abundant and better-preserved microfossil assemblage than the lower sample, providing material for taxonomic study. The lower "brachiopod limestone" sample recorded an association of identical scolecodonts and conodonts, verified through less abundant elements.

The state of preservation of conodonts is excellent, illustrating their complete morphology with processes and denticles. The Conodont Colour Alteration Index (CAI) is 4–4.5 on the scale of Epstein *et al.* (1977), suggesting burial temperatures above 200°C.

The preservation of the scolecodonts is relatively poor. They are shiny black, in some cases exhibiting a bright iridescence, and most specimens show cracking or are fragmentary. From the 800 g of processed sample corresponding to the "ostracod" limestone, 150 scolecodonts were recovered. A selection of specimens was mounted on a stub, coated with a gold-palladium (Au/Pd) alloy and subsequently photographed with a Scanning Electron Microscope FEG-SEM Tescan Mira 3GMU at the Czech Geological Survey in Prague (Czech Republic; Fig. 3).

The apparatus-based classification and descriptive terminology of polychaete jaws follow Kielan-Jaworowska (1966), Szaniawski (1996) and Eriksson (1997).

Institutional abbreviations. All material including the figured specimens is housed in the Palaeontological collection of the Instituto Geológico, Minero y Metalúrgico (INGEMMET: Geological, Mining and Metallurgical Institute) of Peru, in Lima (code CPI), under the accession numbers CPI-10208 to CPI-10228.

SYSTEMATIC PALAEONTOLOGY

Class: Polychaeta GRUBE, 1850

Order: Eunicida Dales, 1963
Family: Ramphoprionidae Kielan-Jaworowska, 1966

GENUS ***Protarabellites*** Stauffer, 1933

Type species. *Protarabellites humilis* Stauffer, 1933, from the lower part of the Decorah Shale (Upper Ordovician, Mohawkian) of Minneapolis, Minnesota, by original designation.

Protarabellites luztejadae sp. nov.
(Figures 3; 4)
LSID. urn:lsid:zoobank.org:act:0715905C-3D77-43EF-910F-7AA8EB150515

Type material. Holotype CPI 10208, Left MI (Fig. 3A). Paratype specimens include 6 left MI maxillae and 10 right MI maxillae (CPI-10209 to CPI-10228). All are housed in the Palaeontological Collection, INGEMMET, in Lima, Peru.

Type locality. Nueva Alianza section, SW flank of the Pichari–Cielo Punku Anticline in the eastern bank of the Apurímac River valley, Kimbiri district, Peru (12°33'07.1"S, 73°45'48.6"W).

Type horizon. Thin "ostracod limestone" bed within shales of the upper half of the San José Formation, lower Darriwilian, *Lenodus crassus* conodont zone.

Derivation of name. After the Peruvian micropalaeontologist Luz Tejada Medina, from the Instituto Geológico, Minero y Metalúrgico (INGEMMET/Geological Survey, Lima), in recognition of her studies and the support she provided us, as the person responsible for the Palaeontology department, for the development of fieldwork in her country during this study.

Diagnosis. First maxilla (MI) with slightly enclosed myocoele and dentary occupying almost the entire jaw length. The anterior part of the dentary is bent outwards, with 3–4 anteriormost denticles protruding at a 90-degree angle above the dentary. Right MI sub-triangular, wide outer face situated at mid-length, with almost 90° bight angle, pointed ramus. Left MI more or less rectangular, wide and abruptly truncated posterior termination, sub-rounded, denticulated anterior termination, prominent inner wing occupying posterior third of jaw length. Second maxilla (MII) is sickle-shaped, with the dentary occupying nearly the entire jaw length.

Description. Left MI is narrow, rectangular, with slightly enclosed myocoele. The length ranges between 990–1360 μm, and the width between 300–480 μm, *i.e.* the length is three times longer than wide (Fig. 5). The outer face has an extension in the middle of the jaw. The inner wing occupies almost half the jaw length; its widest part is situated anteriorly, where it terminates more or less smoothly. The posterior margin is fragile, protruding toward the dentary (inner margin) and sharply ended on both ends. The dentary occupies almost the entire jaw length (the undenticulated ridge is insignificant), with a prominent fang followed by two more prominent denticles; all these three denticles are bent outwards. The dentary is on a prominent ridge, equipped with 22 to 25 denticles. On ventral side, the myocoele opening is slightly closed, the cover extends to 0.25–0.30 of jaw length.

Right MI is slender, with length ranging between 660–1610 μm; and width between 250–580 μm, *i.e.* length is approximately 2.7 times longer than wide (Fig. 5). The dentary occupies almost all jaw length, with 16 to 17 denticles and a prominent fang. The subtriangular denticles are blunt and quite sturdy, growing in size toward the middle part of the dentary. Bight forms 0.4 to 0.45 of the jaw length. The inner wing of the right MI is prominent, occupying more than half of the maxilla length. The ramus is pointed and of a triangular shape. The bight is not smoothly bent, but it has a narrow connection between the outer margin and the triangular end of the ramus. Ventral side: the myocoele opening is slightly closed, the cover extends to 0.2–0.25 of jaw length; only the anteriormost part (the hook) is covered.

Left MII is sickle-shaped and fairly slender jaw, with a thin, pointed, postero-sinistrally extending ramus. The ramus is very narrow. The dentary is equipped with 10–11 blunt denticles.

Other jaws of *Protarabellites luztejadae* are unknown at present. Supposedly, the right MII is a mirror image of the left MII; the basal plate is most likely rectangular, reminiscent of the basal plate of other species of *Protarabellites*.

Comparison. By the outline of the posterior maxillae, *P. luztejadae* sp. nov. is most similar to *Pararamphoprion*? (=*Protarabellites*) *matusevichi* Hints, 1998 from the Upper Ordovician of Severnaya Zemlya, Russian Arctic. Both species have comparable shape of the first maxillae, with slight differences in the ramus of the right MI, which is more rounded in *P.*? *matusevichi*, and its left MI has a more prominent extension in the outer margin. The inner wing of the left MI of *P. luztejadae* has subtriangular rather than subrectangular shape, it is shorter and wider, and has the widest point positioned more posteriorly. Another difference is the cover of the myocoele opening, which corresponds to 0.2–0.31 of jaw length in the new species compared to the 0.23–0.33 in *P. matusevichi*.

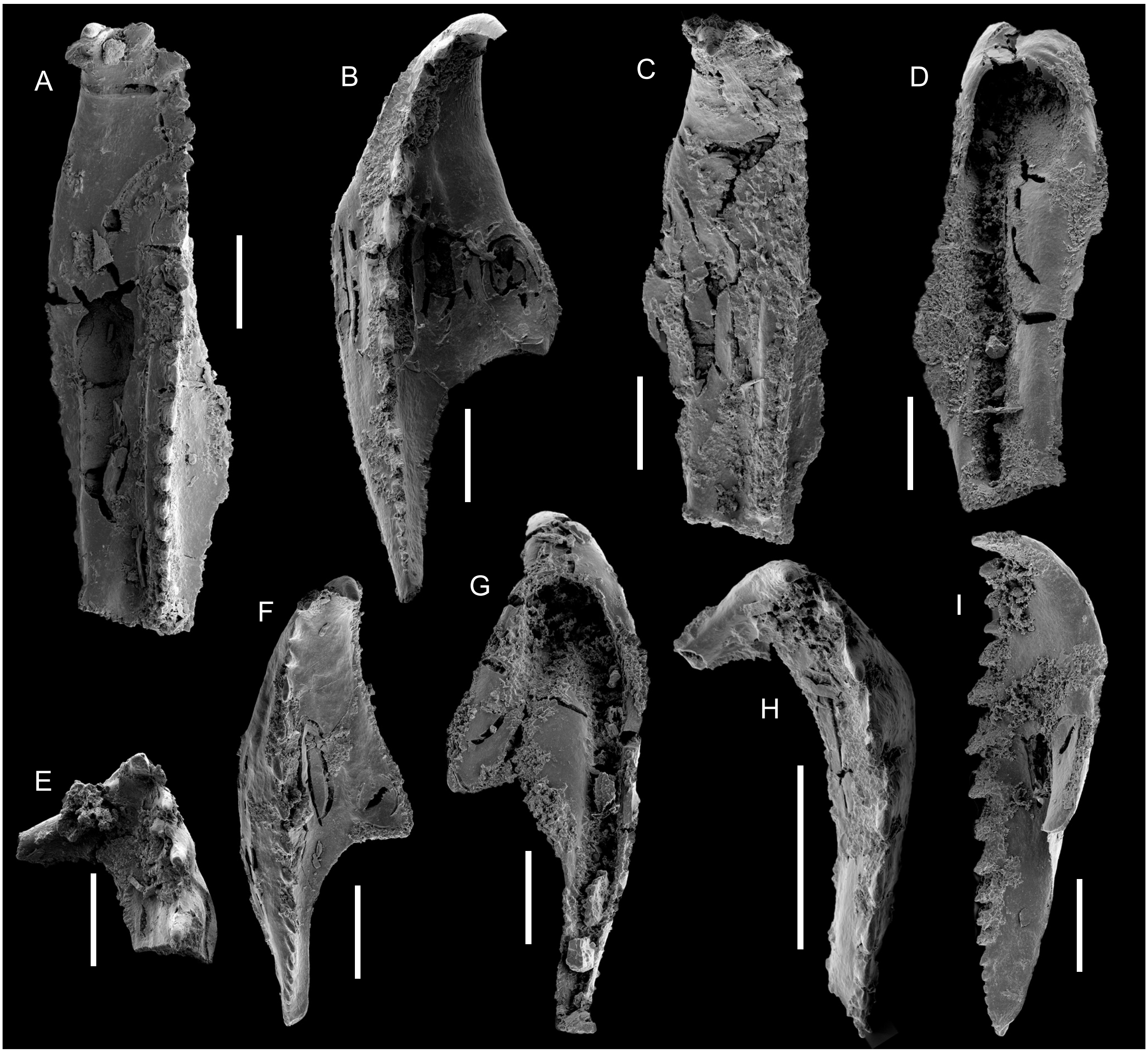

FIGURE 3. SEM images of *Protarabellites luztejadae* sp. nov. All from sample NA-4 (ostracod limestone), Nueva Alianza section, Kimbiri District, southern Peru. Early Darriwilian (Middle Ordovician) *Lenodus crassus* conodont zone. A) Left MI in dorsal view, holotype CPI-10208. B) Right MI in dorsal view, paratype CPI-10209. C) Left MI in dorsal view, paratype CPI-10210. D) Left MI in ventral view, paratype CPI-10211 (note that the jaw is broken in the anterior part and the cover appears therefore shorter than it was). E) Fragment of left MII in dorsal view, paratype CPI-10212. F) Right MI in dorsal view, paratype CPI-10213. G) Right MI in ventral view, paratype CPI-10214. H) Left MII in dorsal view, paratype CPI-10215. I) Right MI in lateral view, paratype CPI-10216. Scale bars represent 200 μm.

Protarabellites luztejadae is also similar to *Ramphoprion* (= *Protarabellites*) *urbaneki* KIELAN-JAWOROWSKA, 1966 (*e.g.* Hints, 1998, figs. 15M-O). However, differences include a less differentiated dentary in posterior maxillae, differently shaped inner margin in the right MI, and the generally more open myocoele in *P. luztejadae*. Another relatively close form to the Peruvian species is *P. staufferi* ERIKSSON, 2001, a common Silurian taxon (Eriksson, 2001), which appeared in the late Mid Ordovician (OH, unpublished collection from the eastern Baltic region). The first maxillae of *P. luztejadae* are narrower and have a slenderer appearance. The ramus in right MI of *P. luztejadae* is more pointed and straight in comparison to *P. staufferi*, and the myocoele opening extends only to half of the maxilla in *P. staufferi*. Species from the Late Ordovician of Laurentia, *Protarabellites* sp. and *P.* cf. *ineptus* ELLER, 1942, also resemble the Peruvian species; however, the Laurentian forms have wider left

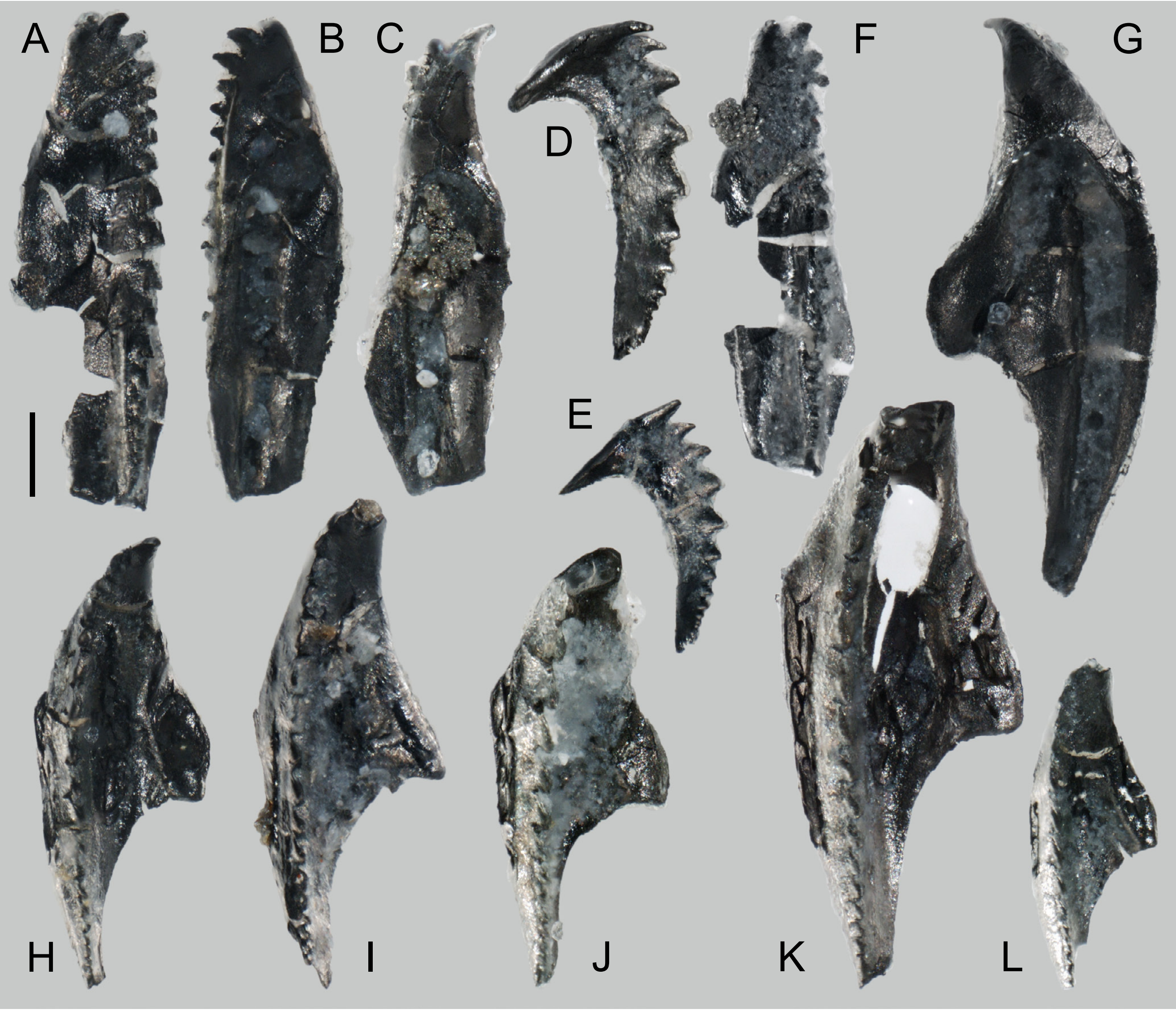

FIGURE 4. Light microscopy photographs of *Protarabellites luztejadae* sp. nov. A) Left MI, in dorsal view, CPI-10217. B) Left MI, in ventral view, CPI-10218. C) Left MI, in ventral view, CPI-10219. D) Left MII in dorsal view, CPI-10220. E) Left MII in dorsal view, CPI-10221. F) Left MI, in dorsal view, CPI-10222. G) Right MI, in ventral view, CPI-10223. H) Right MI, in dorsal view, CPI-10224. I) Right MI, in dorsal view, CPI-10225. J) Right MI, in dorsal view, CPI-10226. K) Right MI, in dorsal view, CPI-10227. L) Right MI, in dorsal view, CPI-10228.

MI, and right MIs have shorter bight, the right MII seems more strikingly different from the Peruvian species by a rounded anterior part and a more dorso-laterally extended ramus. The ventral side of the maxillae was not depicted (Eriksson and Bergman, 2003). In general, the second maxillae of *P. luztejadae* seem to be closer to those of *Ramphoprion* KIELAN-JAWOROWSKA, 1962 rather than to other *Protarabellites* species.

Remarks. An important character of the family Ramphoprionidae is the partially enclosed myocoele. The longitudinal extent of the myocoele opening varies from 0.4 to 0.6 in *Ramphoprion*, from 0.5 to 0.7 in *Protarabellites* STAUFFER, 1933 (0.65 in *P. rectangularis* ERIKSSON, 2001, 0.7 in *P. staufferi*, around 0.55 in *P. triangularis* ERIKSSON, 2001), around 0.5 in *Megaramphoprion* ERIKSSON, 2001. On the other hand, the ramphoprionid genus *Spitiprion* TONAROVÁ, HINTS AND SUTTNER, 2024 has a myocoele opening corresponding to only 0.4 of the jaw length, being more closed than in other ramphoprionids described so far. The slightly enclosed myocoele of *Protarabellites luztejadae* can be considered an ancestral, more primitive feature (Eriksson, 2001, p. 1010). Alternatively, it may infer close relation to the family Polychaetaspidae, which have more open myocoele and have been regarded as the likely ancestor of ramphoprionids (Eriksson, 2001). The open myocoele is typical for other endemic Middle Ordovician species from South America, *Andiprion paxtonae* HINTS,

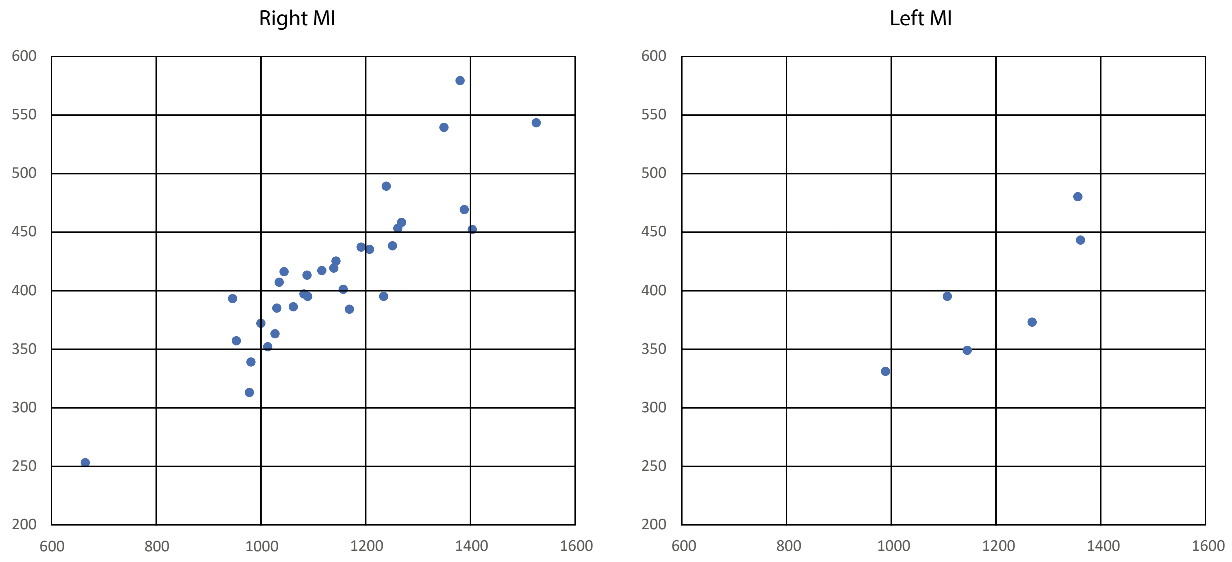

FIGURE 5. Length/width (in µm) measurement data for the posterior maxillae of *Protarabellites luztejadae* sp. nov.

Tonarová and Eriksson, 2017 that belongs to an unknown family. The bight of the right MI of the new species is longer than in other ramphoprionid species (compared with *P. rectangularis* 0.25, *P. staufferi* 0.3, *P. triangularis* 0.22), which is also more typical for the polychaetaspids.

A REVIEW OF PALAEOZOIC SCOLECODONTS FROM SOUTH AMERICA

To illustrate the importance of the present collection, we have done a thorough review of the literature on scolecodonts from South America. The majority of reports are bare mentions of their occurrence in samples collected for acritarchs, chitinozoans, conodonts, prasinophytes or other marine microfossils, often without an illustration of the specimens. The regional publication record is highly scattered and partly difficult to access; therefore, we find it helpful to review the South American scolecodont records through the entire Palaeozoic. The review shows that scolecodonts are more widespread in South America than generally thought. However, the majority of reports need a restudy according to the up-to-date taxonomic approach. None of the published records resembles the specimens from our study. There are no other reports from the Ordovician Peru, and only a few papers on Darriwilian jawed polychaetes of South America in general.

The Ordovician record

In Ordovician rocks, the most frequent record of scolecodonts comes from the dissolution of limestone samples for conodont extraction, as observed in previously published Argentine material, as well as in the specimens obtained in the present study.

Ordovician scolecodonts from Argentina prevail among South American studies. Ottone and Holfeltz (1992) published a short report on early late Dapingian or early Darriwilian scolecodonts from the Gualcamayo Formation of the Precordillera of San Juan Province. These authors illustrated and described eight different forms, assigned to the single-element-based genera *Anisocerasites* Eller, 1955, *Arabellites* Hinde, 1879, *Leodicites* Eller, 1940, *Nereidavus* Grinell, 1877, *Nereigenys* Jansonius and Craig, 1971 and *Staurocephalites* Hinde, 1879. According to modern taxonomy, a single paulinitid maxilla referred to as *Arabellites* sp. (Ottone and Holfeltz, 1992, p. 86, fig. 1.4) can be determined based on the illustrations, other specimens are anterior teeth and fragmented jaws. Ottone *et al.* (1992, pl. 5, fig. 2) illustrated a specimen collected from the upper part of the Acoite Formation of the Los Colorados Creek section, Jujuy Province (eastern Cordillera, Argentina), which is now considered as Floian in age (Carlorosi and Heredia, 2013; Toro and Maletz, 2007).

Kroeck *et al.* (2020, p. 423) mentioned the occurrence of scolecodonts from the Pluspetrol Paisa-1 well, located in the central part of the Colombian Llanos Orientales Basin. At a depth of between 1505 and 1536 m, rare scolecodonts were associated with acritarchs, pointing to a middle Floian age.

Eriksson *et al.* (2002) reported a few Dapingian polychaete jaws from the upper part of the San Juan

Formation of Talacasto section, San Juan Province, Argentine Precordillera. Among these, they identified a polychaetaspid tentatively assigned to the genus *Oenonites* HINDE, 1879, in addition to fragments probably belonging to apparatuses of placognath or possibly ctenognath type.

Hints *et al.* (2017) described early Dapingian scolecodonts found at the transition beds between the Zanjón and Labrado formations of the Capillas section, Sierras Subandinas, Central Andean Basin of North-western Argentina, providing insights into the evolution of advanced polychaete jaw apparatus architecture. They described a monospecific assemblage of *Andiprion paxtonae* HINTS, TONAROVÁ AND ERIKSSON, 2017, which belongs to an unknown family. It shows mixed characteristics of several families, including Polychaeturidae, Polychaetaspidae, Ramphoprionidae, but also Conjungaspidae (genus *Kadriorgaspis* HINTS AND NÕLVAK, 2006).

The first report on South American Late Ordovician scolecodonts was by Ottone *et al.* (1999, p. 226), who mentioned their occurrence as minor components in palynological assemblages from the upper calcareous member (Sandbian) of the Los Azules Formation in the Central Precordillera of San Juan Province. In the eastern Precordillera of San Juan Province, Gómez *et al.* (2024b, fig. 11Q–R) illustrated two unidentifiable specimens obtained from the Sandbian–Katian La Pola Formation. Another report from Argentina was by de la Puente and Rubinstein (2013, p. 233), who found scolecodonts in the Katian and Hirnantian samples of the Las Vacas Formation from the Los Piojos River area, Precordillera Basin; and de la Puente *et al.* (2020, p. 394), who mentioned the occurrence of scolecodonts in the uppermost Ordovician-lowermost Silurian of the uppermost part of the Upper Member of Salar del Rincón Formation, Puna region.

The Hirnantian scolecodonts from South America were mentioned from the Iapó Formation of the Paraná Basin of Brazil (Arouca *et al.*, 2023; Zabini *et al.*, 2024) and the lower beds (*Metabolograptus persculptus* graptolite Biozone) of the La Chilca Formation, San Juan Precordillera of Argentina (Gómez *et al.*, 2024a); however, without illustrations or any taxonomic details. Rubinstein *et al.* (2023, p. 501) mentioned the occurrence of ?Late Ordovician scolecodonts from a borehole in the Llanos Basin of Colombia, located to the northeast of the Macarena Range. However, the age of the assemblage can also be early Silurian.

The Silurian record

The scarce data on Silurian scolecodonts originate from the Argentine Precordillera, the Central Andean Basin of Bolivia and Peru, and the Paraná Basin in Brazil. In the San Juan Province, Precordillera, scolecodonts have been found in two formations. Pöthe de Baldis (1997, pl. 5, fig. 9) illustrated a single unidentified scolecodont of Rhuddanian age from the Don Braulio Formation. Lopez *et al.* (2020, fig. 5k) reported another scolecodont observed on a bedding plane from the La Chilca Formation, initially considered of Rhuddanian age. However, Lopez and Kaufmann (2023, fig. 5D) re-examined this second specimen and determined it was from a younger, Telychian-age layer. The depicted specimen belongs to paulinitids.

In the Central Andean Basin, Laubacher *et al.* (1982) reported the occurrence of rare and unidentifiable scolecodonts in palynological samples from the Altiplano, within a wide age range (Llandovery to Ludlow) in the Lampa (Peru) and Zapla (Bolivia) formations. Subsequently, Zimmermann *et al.* (2015) recorded two different scolecodonts, without providing specific identification, in the Llandovery (Cancañiri Formation) of the Bolivian Altiplano.

In the Paraná Basin of Brazil, some records of Llandovery scolecodonts are also known, cited by Mizusaki *et al.* (2002) and Arouca *et al.* (2023). These consist of unidentified forms recovered from the Vila Maria Formation, one of which was illustrated by Mizusaki *et al.* (2002, fig. 4k).

The Devonian record

The best-known Devonian scolecodonts are those from the Paraná Basin of Brazil. The oldest assemblage from the Ponta Grossa Formation was originally described by Lange (1947, 1949, 1950) and subsequently reviewed by Eriksson *et al.* (2011). It represents a monospecific but high-abundance paulinitid polychaete fauna with endemic *Paulinites paranaensis* LANGE, 1947. Lange (1950) also described *P. caniuensis*, but Eriksson *et al.* (2011) considered it an intraspecific variety of the former species. The maxillae were preserved as isolated elements together with complete and articulated jaw apparatuses lying on bedding planes, in the style of many Fossil-Lagerstätten. The Ponta Grossa Formation was initially considered as uppermost Emsian (upper Lower Devonian), but is now assigned to the upper Pragian to lower or middle Emsian (García Muro *et al.*, 2020, 2022; Grahn *et al.*, 2013). Other mentions of scolecodonts slightly younger than those from the Ponta Grossa Formation are found in the lower part of the overlying São Domingos Formation, upper Emsian (Grahn *et al.*, 2002; Matsumura *et al.*, 2024; Zabini *et al.*, 2012).

In areas close to Brazil, Devonian strata yielding scarce scolecodonts were mentioned in the Chacoparaná Basin of Uruguay, in upper Pragian–lower Emsian palynological samples within the El Cordobés Formation and basal La Paloma Formation (Daners *et al.*, 2018a, b; Rubinstein *et al.*, 2018, fig. 12.4).

In the Subandean Ranges of Argentina and the subsurface of the Tarija Basin, various authors have reported the presence of scolecodonts in palynological samples spanning the Middle–Upper Devonian transition (upper Emsian–lower Frasnian range). These originated from boreholes in the Los Monos Formation (Tarija Basin, Salta Province) and, to a lesser extent, in the underlying Huamapampa Formation. Ottone (1996) identified and illustrated the genera *Leodicites*, *Nereigenys*, *Staurocephalites*, and one cited in open nomenclature. The affinity of illustrated specimens is not apparent, they may belong to paulinitids and mochtyellids. Subsequently, Noetinger and di Pasquo (2011, Tarija Basin, fig. V.u), Noetinger *et al.* (2018, Arasayal section, pl. 4, figs. 9–11), and García Muro *et al.* (2025, Tarija Basin) have cited and illustrated several specimens, but without providing any identification.

In the northern part of the Central Andean Basin, Wood (2010) only referred to the record of rare scolecodonts in the Upper Devonian (?upper Famennian) Cabanillas Group of central Peru. Somewhat older Late Devonian specimens from the Cumaná Formation (Ambo Group) were reported in the Lake Titicaca area of the Bolivian Altiplano (refs. in Díaz-Martínez *et al.*, 1999).

The Carboniferous and Permian record

A significant part of the references to Carboniferous and Permian scolecodonts from South America corresponds to marine levels located in the Gondwanan basins of Argentina, Bolivia and Brazil, partly linked to the great late Palaeozoic glaciation and mostly corresponding to the Gzhelian-late Artinskian time interval.

Mississippian scolecodonts are only known from the Malimán Formation of the Río Blanco Basin, Precordillera of San Juan in western Argentina, but the record is limited to four specimens, possibly reworked from older strata (Amenábar *et al.*, 2007, figs. 1.1–1.4). The specimens are indeterminable, probably belonging to mochtyellidae. Another reported occurrence of scolecodonts in an unnamed Mississippian unit was documented by Dueñas and Césari (2006, pl. 3, fig. 4) in a deep borehole (SM-4 well) from the Colombian Llanos Orientales Basin, east of Macarena Range, assumed to be autochthonous. The illustrated specimen was refigured by Dueñas-Jiménez *et al.* (2020, fig. 7) as part of a Carboniferous assemblage of trilete spores and acritarchs. However, reworked acritarch species were mixed within the interval (Dueñas and Césari, 2006, p. 39) and, according to di Pasquo (2022, p. 303–304), some of these marine taxa, including the scolecodonts, may be reworked elements from Devonian strata.

The earliest records of Pennsylvanian to middle Cisuralian scolecodonts in the central-western basins of Argentina derive from the marine levels of the Santa Máxima and El Imperial formations. Ottone (1988) described twelve different forms in two sections of the Santa Máxima Formation of Northwest of Mendoza, including the new species *Ungulites curvidentatus* (Nereidae), *Nereigenys mendozaensis* (Lumbriconereidae) and *Menogenys curvus* (Leodicidae), as well as representatives of the genera *Leodicites*, *Paleoenonites* ELLER, 1942, *Staurocephalites*, *Marlenites* TAUGOURDEAU, 1971, and *Schistomeringos* JUMARS, 1974. Unfortunately, the majority of figured specimens are anterior or broken maxillae that cannot be assigned to apparatus-based taxa. García (1991) described scolecodonts from the El Imperial Formation in the San Rafael Basin, also in Mendoza province. Her study reported seventeen distinct forms, mostly assigned under open nomenclature to the genera *Anisocerasites*, *Marlenites*, *Menogenys* JANSONIUS AND CRAIG, 1971, *Nereigenys*, *Oenonites*, and *Staurocephalites*. The presence of mochtyellids and paulinitids can be confirmed with certainty.

Scarce scolecodonts are recorded, and in some cases illustrated, within palynological assemblages from the Copacabana Group in central and northwestern Bolivia. Some originate from Pennsylvanian levels, such as the specimen illustrated by di Pasquo (2009, pl. 5, figs. 1, 7) from the Pando X-1 well in the Madre de Dios river valley. However, most belong to the Cisuralian, including material of *Staurocephalites* sp. identified by Ottone *et al.* (1999) in the middle course of the Beni River, or the two undetermined specimens mentioned by di Pasquo and Grader (2012) from Apillapampa, Cochabamba; as well as the specimens from the same locality illustrated by di Pasquo *et al.* (2022, p. 10, figs. 11–13), identified as *Menogenys* sp. and form A (undetermined).

In the southern part of the Tarija Basin, spanning northern Argentina and southern Bolivia (Subandean Range), di Pasquo (2022, pl. 14, figs. 3, 5) and di Pasquo *et al.* (2024, pl. 14, figs. 3 and 5 – as *Leodicites* sp.) illustrated two Pennsylvanian scolecodonts, probably reworked from Devonian strata. The illustrated jaws resemble the second maxillae of kielanoprionids.

Other Argentine basins with records of scolecodonts include the Precordillera of San Juan, where Cisterna *et al.* (2011, figs. 4.11 and 12) illustrated specimens of *Kielanoprion* sp. and *Marlenites* sp., found in uppermost Pennsylvanian rocks from the Rincón Blanco syncline, La Rioja province. In the Claromecó Basin of east-central

Argentina, Di Nardo *et al.* (2024, pl. 5, fig. 11) also reported an unidentified specimen from the Sauce Grande Formation, which spans the Carboniferous–Permian boundary.

Pennsylvanian scolecodonts from Brazil are abundantly represented in 28 horizons within the upper Monte Alegre and lower Itaituba formations of the Amazonas Basin. Moutinho *et al.* (2016, figs. 8 and 9) illustrated nineteen elements belonging to the orders Eunicida and Phyllodocida, which are very well preserved but have yet to be taxonomically studied.

The last major South American basin with late Palaeozoic scolecodonts is the Paraná Basin, located mainly in Brazil. In the southern part of the basin (state of Rio Grande do Sul) is where Pinto (1947) made the first mention of scolecodonts in the Itararé Group. Later, Pinto (1949, 1955) identified *Ildraites* sp. and *Eunicites* sp. A complete description of the scolecodonts recorded from the Budó locality was presented by Pinto and Purper (1974), who reported the new species *Ildraites langei*, *Arabellites santosi*, *Nereidavus beetlae* and *Nereidavus moreirai*. The depicted specimens indisputably belong to paulinitids (genera *Langeites* KIELAN-JAWOROWSKA, 1966, and *Kettnerites* ŽEBERA, 1935) and probably atraktoprionids sensu the current taxonomy. Finally, a correlative stratigraphical unit yielding scolecodonts within the same Paraná Basin, was discovered in the northern part of the state of Santa Catarina (Mouro, 2017; Ricetti and Weinschütz, 2011; Ricetti *et al.*, 2012, 2015), where the so-called Lontras Shale Lagerstätte has been recorded (Boardman *et al.*, 2024; Mouro, 2017; Mouro *et al.*, 2020; Saldanha *et al.*, 2023). It involves organic-rich shales placed at the top of the Campo Mourão Formation of the Itararé Group, recording the exceptional preservation of certain marine and terrestrial biotas around the Pennsylvanian–Cisuralian boundary. Among the scolecodonts, paulinitids and polychaetaspids have been recorded, and rare articulated jaw apparatuses identified. Some of these are preserved within carbonate concretions, where, according to the interpretation of Ricetti and Weinschütz (2011), Ricetti *et al.* (2015), and Mouro (2017), possible polychaete bodies may also have fossilised, appearing as carbonaceous films. However, in the only published photograph of one of these specimens, associated with a minute scolecodont cluster in a nodule (Mouro *et al.*, 2021, p. 214, fig. 4A, B), nothing convincingly distinguishable can be seen that matches the description in the explanation as "a possible polychaete body, with segmented cylindrical structures (somites) and setae".

DISCUSSION

Due to their endurance and common presence in the fossil record, scolecodonts provide important data on the phylogeny of eunicidan polychaetes. Paxton (2009) explored the homologies of jaw elements and functional aspects of the jaw apparatus to clarify the traits of eunicid phylogeny. Six distinct architectural types of maxillary apparatuses were identified based on their arrangement, number, and shape of elements (Paxton, 2009): Labidognatha (pincer-jaw) and Prionognatha (saw-jaw), Ctenognatha (comb-jaw), Placognatha (plate-jaw), Eulabidognatha (with reduced right MI), and Symmetrognatha (symmetric). These types do not represent clades, but rather grades of evolution. However, due to the limited number of papers addressing Early and Middle Ordovician scolecodonts, we largely lack supporting evidence regarding the emergence of different groups. For instance, it remains poorly understood when and how asymmetry arose, as well as how the more complex labidognath/eulabidognath and prionognath-type apparatus architectures evolved. These types of apparatuses persisted throughout the rest of the Phanerozoic and are the most common buccal armatures observed in extant Eunicida (Paxton, 2009).

In the Lower Ordovician, the simple "primitive" placognath maxillae usually dominate the assemblages. Underhay and Williams (1995) described scolecodonts from the Tremadocian and Floian of Newfoundland and found mainly simple lateral teeth of placognath maxillae that may belong to *Vistulella* KIELAN-JAWOROWSKA, 1961, and some probable polychaetaspids. Hints and Nõlvak (2006) recorded the oldest scolecodonts on Baltica from the Tremadocian siliciclastic section from Tallinn, Estonia. They described two new genera and species, *Kadriorgaspis kaisae* and "*Xanioprion*" *viivei,* accompanied by undeterminable anterior teeth of placognath taxa.

Somewhat more is known about the Middle Ordovician scolecodonts. For instance, on Baltica, the typical labidognath forms appear in the early Middle Ordovician (Volkhov Regional Stage). Eriksson *et al.* (2016) discovered a Darriwilian assemblage from southern Sweden (Kunda Regional Stage), dominated by tiny, simple, sawblade-like maxillae of mochtyellids, xanioprionids and tetraprionids, and a single maxilla of *Oenonites*, with labidognath-type of apparatus. In the Kunda Regional Stage in NW Estonia the assemblage showed more diversity, with the proportion of "advanced" labidognath forms and placognaths with compound maxillae being much higher. Starting from the upper Darriwilian (Lasnamägi Regional Stage), the majority of genera common in younger Ordovician strata were already present, and ramphoprionids were common and diverse (Hints, 2000).

There were several views on the possible phylogeny of labidognath families (Paxton, 2009; Paxton and Eriksson, 2012; Szaniawski, 1996). Hints and Nõlvak (2006) suggested that conjungaspids may have given rise to the earliest labidognaths, to which they are not only morphologically similar, but they are the oldest known forms possessing carriers. This view was shared by Paxton (2009), who considered early conjungaspids (*Kadriorgaspis*) to be ancestral to the asymmetrical labidognaths/eulabidognaths, prionognaths, and symmetrognaths. The hypothetical step from the symmetrical *Kadriorgaspis* to an asymmetrical jaw apparatus such as that in polychaetaspids has, however, remained unsupported by fossil evidence until the discovery of the genus *Andiprion* Hints, Tonarová and Eriksson, 2017, which represents this evolutionary step, as it is morphologically intermediate between *Kadriorgaspis* and the earliest taxa with typical labidognath apparatuses (Hints *et al.*, 2017). The new Peruvian ramphoprionid species *P. luztejadae* bears characteristics transitional between *Andiprion* and the younger representative of *Protarabellites* (Fig. 6).

The polychaete family Ramphoprionidae was established as monotypic by Kielan-Jaworowska (1966) to include *Ramphoprion* Kielan-Jaworowska, 1962. The latter study was based on morphological analysis of well-preserved jaw apparatuses from the Baltic erratic boulders with an imprecise stratigraphical position. The author revised the previously described single-element-based genera and placed them in this family based on natural taxonomy. According to the original concept, ramphoprionids emerged in the Middle or Late Ordovician (Kielan-Jaworowska, 1962, 1966). Edgar (1984) suggested assigning the genera *Polychaetaspis* Kozłowski, 1956 (=*Oenonites* Hinde, 1879 *sensu* Eriksson, 1997), *Kozlowskiprion* Kielan-Jaworowska, 1966, *Polychaetura* Kozłowski, 1956 (younger synonym of *Pteropelta* Eisenack, 1939), and *Ramphoprion* Kielan-Jaworowska, 1962 to the family Polychaetaspidae. However, Edgar (1984) did not supply strong arguments for his proposal, omitting rather significant diagnostic features of ramphoprionids.

Eriksson (2001) revised the family Ramphoprionidae and suggested its emergence in the Middle Ordovician. This is also confirmed by our unpublished collections from the eastern Baltic region, where the oldest ramphoprionids appear in the Aseri Regional Stage, middle Darriwilian. Ramphoprionids were also common in the Silurian (Eriksson, 2001), with several genera and species crossing the Ordovician–Silurian boundary. The youngest occurrence of the family so far comes from the Eifelian of the Prague Basin (Tonarová, unpublished data). Eriksson (2001) proposed four valid genera for ramphoprionids: *Protarabellites* Stauffer, 1933; *Ramphoprion* Kielan-Jaworowska, 1962; "*Pararamphoprion*" Männil and Zaslavskaya, 1985; and *Megaramphoprion* Eriksson, 2001. The genera *Ramphoprion* and *Protarabellites* are the most common. Tonarová *et al.* (2024) described another new ramphoprionid genus and species, *Spitiprion khannai* Tonarová, Suttner and Hints, 2024, from the Late Ordovician of India (with assumed palaeolatitude ~25–30°S). This species is endemic to the region. Eriksson (2002) summarised data on Silurian and to some extent also Ordovician ramphoprionids. At his time, there were no reports on the family from the Gondwana region, therefore it seemed that they inhabited only regions close to the equator. Later, Tonarová *et al.* (2012, 2019, 2023, 2025) confirmed their presence from the late Ordovician to Ludfordian of the Prague Basin, which drifted from 50 to 25 degrees south during the Silurian (Tasáryová *et al.*, 2014). Probable ramphoprionids were also recovered from Saudi Arabia (Hints *et al.*, 2015), which was located further

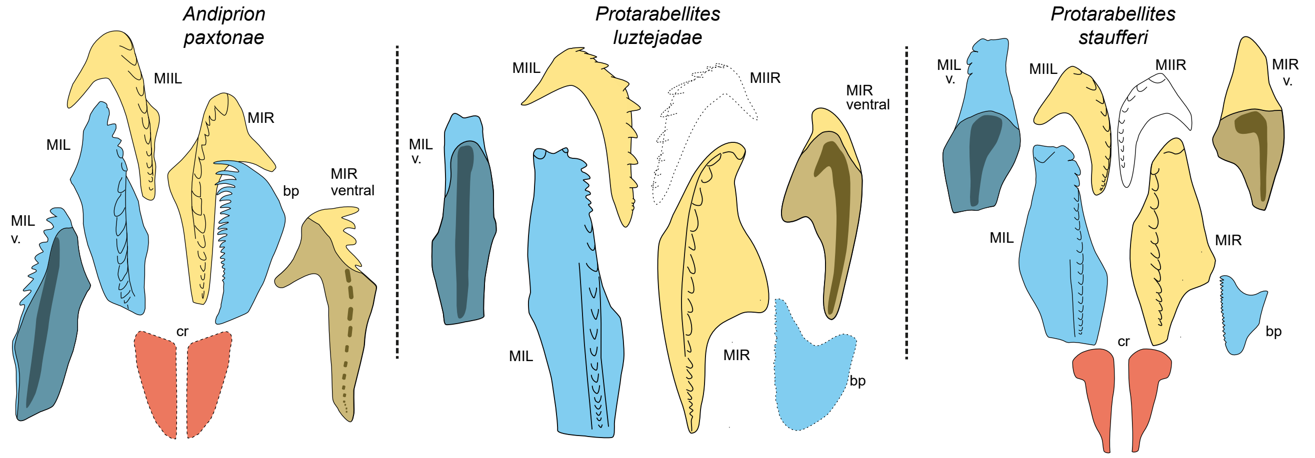

FIGURE 6. Comparison of jaw apparatuses of *Andiprion paxtonae* (family unknown; depicted after Hints *et al.*, 2017), *Protarabellites luztejadae* sp. nov. (Ramphoprionidae) and *Protarabellites staufferi* (Ramphoprionidae; depicted after Eriksson, 2001). Left and right first maxillae are also depicted from the ventral side (facing the myocoele opening, a diagnostic character for the new species). The maxillae with the dashed line are not known and they are only tentatively reconstructed according to better-known related species. MIL= first left maxilla, MIR= first right maxilla, MIIL= second left maxilla, MIIR= second right maxilla, bp= basal plate, cr= carriers, v= ventral view.

south, farther from the equator. This is supported by the present study from the Central Andean Basin, confirming the presence of ramphoprionids in higher latitudes (Cocks and Torsvik, 2021).

Regarding the phylogeny, ramphoprionids exhibit characters considered both primitive (denticulation in first maxillae) and advanced (enclosed to strongly enclosed myocoeles). Therefore, they were assumed to be more advanced than, *e.g.* the polychaetaspids, a group with similar jaw apparatus architecture. However, polychaetaspids have a slightly longer (documented) stratigraphic range (cf. Kielan-Jaworowska, 1966; Szaniawski, 1996). The more primitive characters, notably the nearly open myocoele of *P. luztejadae* bring a new view on the group, suggesting that ramphoprionids may have originated from a common ancestor with polychaetaspids and not descending from them.

In general, even Early Ordovician scolecodont assemblages are typically composed of multiple taxa. The hereby presented monospecific association with a single ramphoprionid species *P. luztejadae* may indicate specific or stressed environmental conditions. On the other hand, monospecific or low diversity assemblages are also known. Hints *et al.* (2017) described a monospecific assemblage from the lower Middle Ordovician of Argentina. In the younger strata, for instance, in the Lower Devonian of Brazil, Eriksson *et al.* (2011) found a monospecific jawed polychaete assemblage that belongs to the Malvinoxhosan fauna.

CONCLUSION

We report the first Ordovician scolecodonts from the San José Formation in Peru and describe a new species of ramphoprionids, representing the family's oldest record so far. The early Darriwilian *Protarabellites luztejadae* sp. nov. exhibits primitive characters such as the lightly enclosed myocoele, distinguishing it from the younger members of the Ramphoprionidae. This suggests that ramphoprionids and polychaetaspids may have derived from a common ancestor that may be related to the enigmatic *Andiprion* reported from the Middle Ordovician of Argentina. Possibly, ramphoprionids emerged from Gondwana and spread to other regions by the mid-Darriwilian.

The early Darriwilian age of *Protarabellites luztejadae* sp. nov. is well constrained by conodonts of the *Lenodus crassus* Zone, recorded from the same limestone samples that define the type locality and type horizon of the new species.

A review of previous findings of Palaeozoic scolecodonts from South America showed that jaw-bearing polychaetes were more widespread in various subregions and time intervals than generally thought. Thus, South America holds significant potential for future scolecodont studies to fill the current knowledge gaps in the stratigraphic and palaeobiogeographic distribution of fossil polychaetes.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural act it contains, have been registered in ZooBank: urn:lsid:zoobank.org:act:0715905C-3D77-43EF-910F-7AA8EB150515.

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