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EARLY MIDDLE ORDOVICIAN SCOLECODONTS FROM NORTH-WESTERN ARGENTINA AND THE EMERGENCE OF LABIDOGNATH POLYCHAETE JAW APPARATUSES

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Abstract: Scolecodonts provide fossil evidence of the evolution and diversification of jaw-bearing polychaetes from the latest Cambrian onwards. However, their record before the Darriwilian (Middle Ordovician) is scarce worldwide, which limits our understanding of key evolutionary events. One such event is the emergence of taxa possessing the asymmetrical labidognath-type jaw apparatus architecture, which became common in the Middle Ordovician and is often dominant throughout the Palaeozoic. Here, we document a small collection of Dapingian scolecodonts from the Capillas section, Sierras Subandinas, north-western Argentina. The isolated elements recovered allowed us to reconstruct the distinctive jaw apparatus, and to introduce a new taxon, *Andiprion paxtonae* gen. et sp. nov. The maxillary apparatus of *Andiprion* is intermediate between the symmetrognath type of the Early Ordovician *Kadriorgaspis* and the labidognath type that is present in polychaetaspids and related taxa. The apparatus architecture of *Andiprion* corresponds best to the labidognath type, but the morphology of the individual jaws suggests that it may be the most primitive representative of this lineage currently known. We propose that *Andiprion*-like forms were ancestral to polychaetaspids, polychaeturids and ramphoprionids. The Capillas collection provides supporting evidence for the evolutionary homology of the 'basal plate' and the left first maxilla. Thus the labidognath-type asymmetry, with an unpaired left maxilla III, developed as a result of gradual reduction in size of the first right jaw ('basal plate') in front of the carriers, instead of loss or fusion of anterior maxillae.

Key words: scolecodonts, Eunicida, polychaete jaw apparatus, evolution, Ordovician, Argentina.

SCOLECODONTS (polychaete jaws) provide fossil evidence of the evolution and diversification of eunicidan polychaetes. These acid-resistant microfossils are known from the latest Cambrian, and became common and diverse in the Darriwilian (Hints *et al.* 2004; Hints & Eriksson 2007; Eriksson *et al.* 2013). However, the Early and early Middle Ordovician record of scolecodonts, and hence that of jaw-bearing polychaetes, is incomplete and only a handful of reports are available worldwide (Underhay & Williams 1995; Cooper *et al.* 2001; Eriksson *et al.* 2002, 2016; Hints & Nõlvak 2006). Currently available data suggest that key events in polychaete evolution took place during the Dapingian or late Early Ordovician, and that this was followed by rapid diversification and an increase in the ecological significance of the group from the Darriwilian onwards (Hints *et al.* 2004; Eriksson *et al.* 2013). This largely coincides with the main phase of the Great Ordovician Biodiversification Event (GOBE; see e.g. Webby *et al.* 2004; Harper 2006; Rasmussen *et al.* 2016). One important, yet poorly documented and understood, step in the evolution of eunicidan polychaetes is the emergence of more complex and functionally advanced labidognath- and prionognath-type jaw apparatuses, and compound jaws with multiple denticulated ridges in placognath taxa (Kielan-Jaworowska 1966; Paxton 2009). Prior to that event the polychaete jaw apparatuses were largely composed of simple, saw-blade-like jaws and single, individual teeth. The labidognath and prionognath jaw apparatus

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architectures emerged to persist through the Palaeozoic. In the present-day oceans polychaetes inhabit various environments and successfully use jaws that are often remarkably similar to those of their early Palaeozoic ancestors (Rouse & Pleijel 2001; Paxton 2009).

In order to understand better the early history of eunicidan polychaetes in a stratigraphical as well as palaeogeographical context, new data from Lower and lower Middle Ordovician strata from different regions are much needed (Hints *et al.* 2004; Eriksson *et al.* 2013). The entire Gondwanan realm is under-represented in fossil polychaete studies, especially compared to Baltica and Laurentia (Eriksson *et al.* 2013; Hints *et al.* 2015). Previous data on Ordovician scolecodonts from South America are limited to two brief reports. Ottone & Holfeltz (1992) described a Llanvirnian assemblage of poorly preserved scolecodonts from the Gualcamayo Formation from San Juan and La Rioja Precordillera, Argentina, and Eriksson *et al.* (2002) reported a few Dapingian specimens from the San Juan province, Argentine Precordillera. These meagre collections merely note the occurrence of a few taxa and thus provide little information on the actual taxonomic composition of the polychaete faunas.

In this paper, we report a small collection of Dapingian scolecodonts from north-western Argentina, characterizing the western margin of Gondwana. The collection contains isolated scolecodonts of a jaw apparatus inferred to be of primitive labidognath type. Morphological criteria and co-occurrence of elements suggest that they all belong to a single new, multi-element-based polychaete genus and species. Albeit small and monospecific, the collection at hand provides new data from a critical stratigraphical level and a poorly documented region. As such it helps by providing new insights into the early evolution of polychaete jaw apparatuses and the temporal as well as biogeographical distribution of Early Palaeozoic eunicidan worms.

GEOLOGICAL SETTING AND STRATIGRAPHY

The Central Andean Basin, located in north-west Argentina and extending into Chile, Bolivia and Peru, is considered to be one of the more outstanding regions in the world for the study of Gondwanan Ordovician sequences, given its vast and continuous exposures that reach a thickness of more than 5000 m and extend over thousands of square kilometres (Astini & Marengo 2006). The Central Andean Basin had a complex evolutionary history during the Early–Middle Palaeozoic. It developed as a foreland basin to the east of the Arequipa–Antofalla Massif, with an active subduction zone to the west, and was dominated by large-scale, transtensional or transpressional conditions from the Late Ordovician to the Triassic (Sempere 1995).

The Central Andean Basin comprises the geological provinces of Puna to the west, Cordillera Oriental in the centre and Sierras Subandinas and Sierras de Santa Bárbara to the east, extending to the subsurface of the Chaco plain (Fig. 1A). This physiographical division is a consequence of tectonic processes, most of which were part of the Cenozoic Andean Cycle (Ramos 2009).

Astini (2008) distinguished three depositional zones in the Ordovician stratigraphy of the basin. The eastern depositional zone corresponds to the eastern part of the

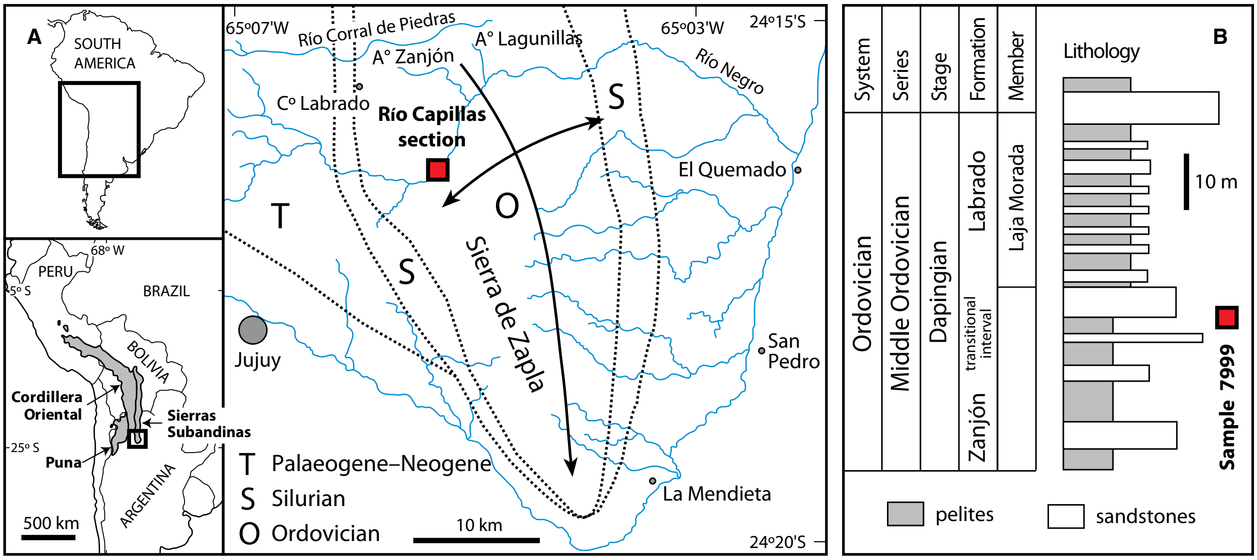

FIG. 1. A, locality maps. B, generalized stratigraphy and sedimentary profile of the Río Capillas section, showing the level of the scolecodont-yielding sample 7999 (after Astini & Marengo 2006). Colour online.

Cordillera Oriental and the Sierras Subandinas, and is characterized by strongly bioturbated deltaic and estuarine units. The Sierras Subandinas, which represent the outermost part of the foreland basin, consist of alternating shallow-marine deltaic systems and estuarine environments which indicate frequent changes in the shoreline, caused by fluctuations in the relative sea level (Astini & Marengo 2006).

The Sierras Subandinas correspond to a typical 'thin-skinned' Andean foreland thrust and fold belt that has been developing since about 12 Ma. The shortening is mainly produced by several major east-vergent thrust sheets, thus yielding an abrupt topographic relief (Astini 2003). The Ordovician outcrops have been recognized only in anticlines, in the innermost part of the thrusts. The Sierra de Zapla anticline, in the Jujuy Province, exhibits the most complete Ordovician succession of the Sierras Subandinas (Astini 2003).

The best and most complete palynologically constrained Ordovician section across the Sierras Subandinas crops out in the southern part of the Sierra de Zapla, along the Río Capillas, exhibiting an approximately 450 m thick, shallow marine and marginal marine succession. This stratigraphy is exposed in both flanks of the Sierra de Zapla anticline. Frequent subaerial exposures and largely marginal marine settings explain the scarcity of invertebrates throughout the section (Rubinstein *et al.* 2011).

The Zanjón Formation is the lowest unit of the exposed stratigraphic section, constituting the core of the Sierra de Zapla anticline. Its base is however unexposed. This unit is characterized by a heterolithic facies association with subordinate storm layers, thin-bedded phosphate-rich micro-conglomerates and lingulate shell beds. Common subaerial exposure features, such as truncated ripple tops and mud cracks, suggest tidal flat environments (Astini & Marengo 2006). The overlying unit, the Labrado Formation, is divided into two members. The lower of these, the Laja Morada Member, records extensive subaerial exposure, with water table fluctuations in the interfluves, which occurred during a lowering of the relative sea level, indicated by subaerial features and a gradual change toward purple–red colours near the top (Rubinstein 2005; Rubinstein *et al.* 2011). The low fossil content of the upper Zanjón and Labrado formations could be a consequence of early oxidation of these stratigraphic units (Rubinstein *et al.* 2011). Organic-walled phytoplankton (acritarchs and chlorophyte algae) and chitinozoans are the only biostratigraphically significant fossils of the upper part of the Zanjón Formation and its transition to the Labrado Formation (Rubinstein 2005; Rubinstein *et al.* 2010; de la Puente & Rubinstein 2013). The chitinozoan *Lagenochitina combazi* Finger, 1982, occurring in these beds, which also include the scolecodont-yielding sample 7999 (Fig. 1B), is a biostratigraphic marker from the Dapingian of China (Chen *et al.* 2009). A Dapingian age is consistent with the organic-walled phytoplankton assemblage recorded from the same level (de la Puente & Rubinstein 2013). The land-derived cryptospore assemblage recorded from sample 7999 is considered to be the earliest fossil evidence of land-plants (Rubinstein *et al.* 2010).

MATERIAL AND METHOD

Scolecodonts and other organic-walled microfossils, notably chitinozoans, were extracted from a single 350 g siltstone sample (No 7999, cf. Rubinstein *et al.* 2010; Fig. 1B) using standard palynological processing. Half of the sample was dissolved with 15% hydrofluoric acid (HF) and the remaining half with 30% HF (see Green 2001 for details) in the laboratories of the Czech Geological Survey. The sample level was selected based on two previously observed scolecodonts in palynological slides from the section. The insoluble residues were washed through a 50-micron sieve, microfossils were picked from the residue under water and stored in plastic containers with glycerine. A select few specimens were examined under a Zeiss EVO MA15 scanning electron microscope; the rest were imaged using a Nikon AZ 100 microscope equipped with a digital camera to avoid drying and breaking small and delicate specimens. Photographs of chitinozoans were taken using a PHILIPS XL 30 scanning electron microscope at the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires. The preservation of the scolecodonts was sufficiently good to allow for (species level) identification, but the shiny black appearance and partly rough surface suggest that they have suffered from elevated palaeotemperatures. Most jaws were partly flattened or otherwise distorted and some were fractured. Altogether the collection consists of 22 maxillae and 1 basal plate. This corresponds to *c.* 60 maxillae per kg of rock, which is comparable to previous records from the Lower and lower Middle Ordovician, but notably less than what is common for Upper Ordovician and Silurian strata (Hints 2000; Eriksson *et al.* 2004; Tonarová *et al.* 2012). All jaws recovered belong to a single species, *Andiprion paxtonae* gen. et sp. nov., described below. Descriptive terminology follows Kielan-Jaworowska (1966), Jansonius & Craig (1971) and Eriksson *et al.* (2004).

Institutional abbreviations. IANIGLA, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Argentina; GIT, Department of Geology, Tallinn University of Technology, Estonia.

SYSTEMATIC PALAEONTOLOGY

Class POLYCHAETA Grube, 1850
Order EUNICIDA Dales, 1963
Family uncertain

Genus ANDIPRION nov.
Figures 2A–T, 3A–I

LSID. urn:lsid:zoobank.org:act:F801E272-95CB-4D21-AAE0-944B6AEA1281

Type and only known species. Andiprion paxtonae gen. et sp. nov.

Derivation of name. Named after the Sierras Subandinas mountain range where the taxon was found, and Greek word *prion*, meaning a saw.

Diagnosis. Jaw apparatus of labidognath type; dentary in posterior maxillae undifferentiated; left MI slender with wide, anterolaterally directed posterior margin, subrectangular outer and inner wings; right MI elongated with long shank and narrow pointed ramus; myocoele opening gaping. Left MII similar to mirror image of right MI. Basal plate large, subtriangular, with short anterolaterally directed posterior margin.

Remarks. The genus is monospecific and for the time being its family-level assignment remains uncertain. It shares some characters with several labidognath families including Polychaeturidae, Polychaetaspidae and Ramphoprionidae (see e.g. Kielan-Jaworowska 1966; Eriksson 2001; Hints & Eriksson 2010). Considering its apparatus architecture and geological age, *Andiprion* may be ancestral to these families. However, *Andiprion* also shows some features in common with *Kadriorgaspis* Hints &

FIG. 2. Light microscopy photographs of scolecodonts. A–T, *Andiprion paxtonae* gen. et sp. nov; all from sample 7999, Dapingian, upper part of the Zanjón Formation or its transition to the Laja Morada Member of the Labrado Formation from the Río Capillas area, Argentina (see Fig. 1). U, *Andiprion*? from sample OM12-4, Uuga cliff, NW Estonia, *Paroistodus originalis* Conodont Zone, Volkhov Regional Stage, Dapingian. Scale bars represent 100 μm (left scale bar A–T; right U). A, left MI in outer-lateral; IANIGLA PI 3097. B, left MI; IANIGLA PI 3098. C, left MI; IANIGLA PI 3099. D, right MI; IANIGLA PI 3100. E, right MI; IANIGLA PI 3101. F, right MI with anterolateral part broken off; IANIGLA PI 3102. G, anterolateral part of right MI; IANIGLA PI 3103. H, right MI; IANIGLA PI 3104. I, right MI; IANIGLA PI 3105. J, right MI; IANIGLA PI 3106. K, left MI; IANIGLA PI 3107. L, left MI in outer-lateral; IANIGLA PI 3108. M, left MI in outer-lateral; IANIGLA PI 3109. N, left MI in outer-lateral; IANIGLA PI 3110. O, right MI; IANIGLA PI 3111. P, left MI; IANIGLA PI 3112. Q, right MII in outer-lateral; IANIGLA PI 3113. R, basal plate; IANIGLA PI 3114. S, right MI in outer-lateral view; IANIGLA PI 3115. T, left MIII in outer-lateral; IANIGLA PI 3116. U, left MI; GIT 775-1. Colour online.

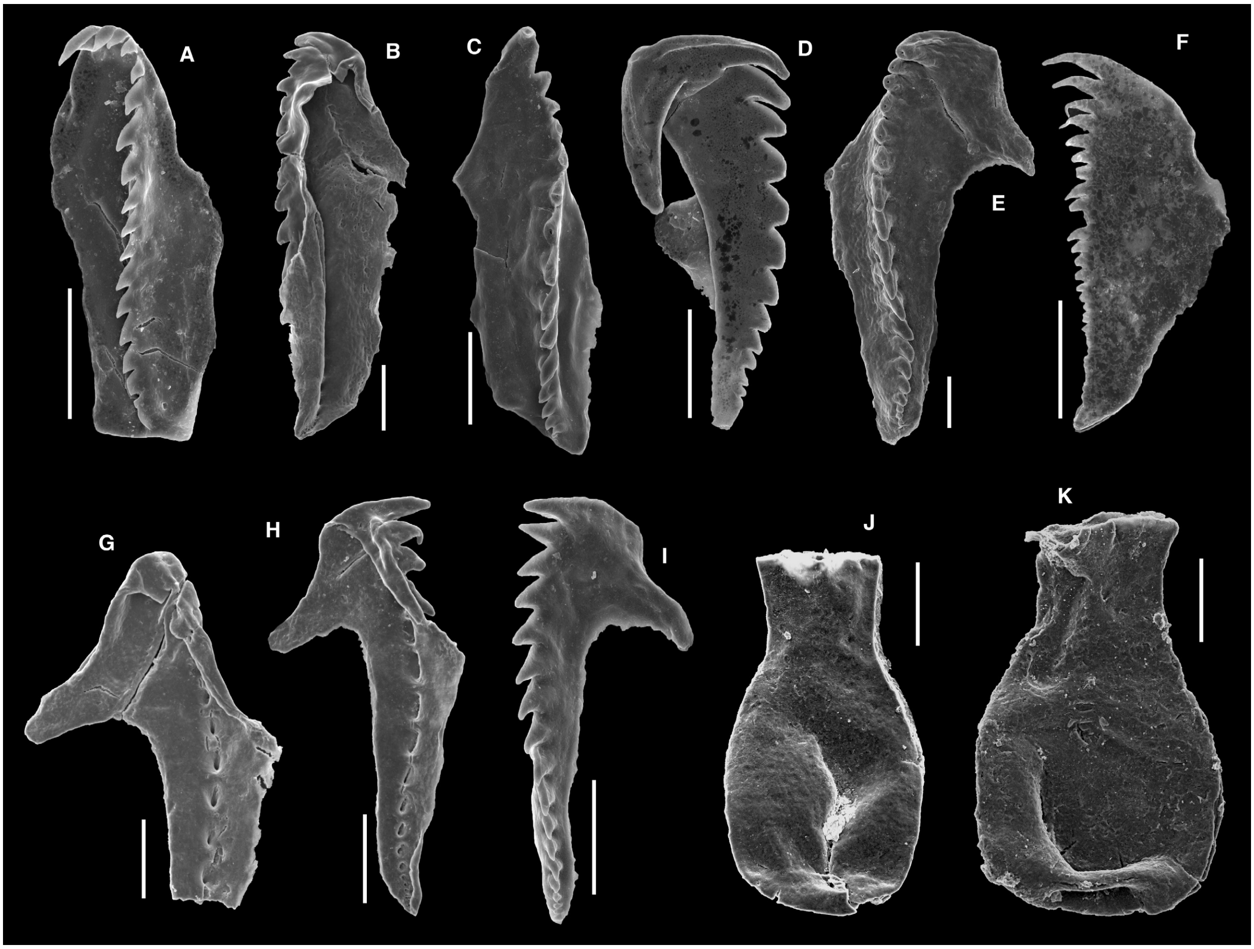

FIG. 3. Scanning electron images. A–I, *Andiprion paxtonae* gen. et sp. nov.; J–K, *Lagenochitina combazi* Finger, 1982; all from sample 7999, Dapingian, upper part of the Zanjón Formation or its transition to the Laja Morada Member of the Labrado Formation from the Río Capillas area, Argentina. All scale bars represent 50 μm. A, left MI; IANIGLA PI 3107 (same as Fig. 2K). B, left MI; IANIGLA PI 3099 in ventral view (same as Fig. 2C). C, left MI; holotype IANIGLA PI 3117. D, left MII; IANIGLA PI 3113 (same as Fig. 2Q). E, right MI; IANIGLA PI 3105 (same as Fig. 2I). F, basal plate; IANIGLA PI 3114 (same as Fig. 2R). G, right MI; IANIGLA PI 3112 (same as Fig. 2P). H, right MI; IANIGLA PI 3111 (same as Fig. 2O). I, right MI; IANIGLA PI 3118. J, vesicle; IANIGLA MPLP 7999-1. K, vesicle; IANIGLA MPLP 7999-2.

Nõlvak, 2006, a genus with a symmetrical jaw apparatus assigned to the family Conjungaspidae (Hints 1999). See further comments in species comparison below.

Occurrence. Dapingian of South America and possibly Baltoscandia.

Andiprion paxtonae sp. nov.
Figures 2A–T, 3A–I, 4B

LSID. urn:lsid:zoobank.org:act:5405291F-01A1-4975-AA33-D41073494C8B

Derivation of name. Named in honour of Dr Hannelore Paxton, an expert on extant polychaetes, who has also used fossil scolecodonts in phylogenetic analyses.

Holotype. Left MI, IANIGLA PI 3117, Figure 3C.

Type locality. Río Capillas section, Sierras Subandinas, northwestern Argentina.

Type horizon. Transition between the Zanjón and Labrado formations, Dapingian, Middle Ordovician.

Material. 10 left MI, 11 right MI, 1 left MII, 1 left MIII, 1 basal plate.

Diagnosis. As for the genus.

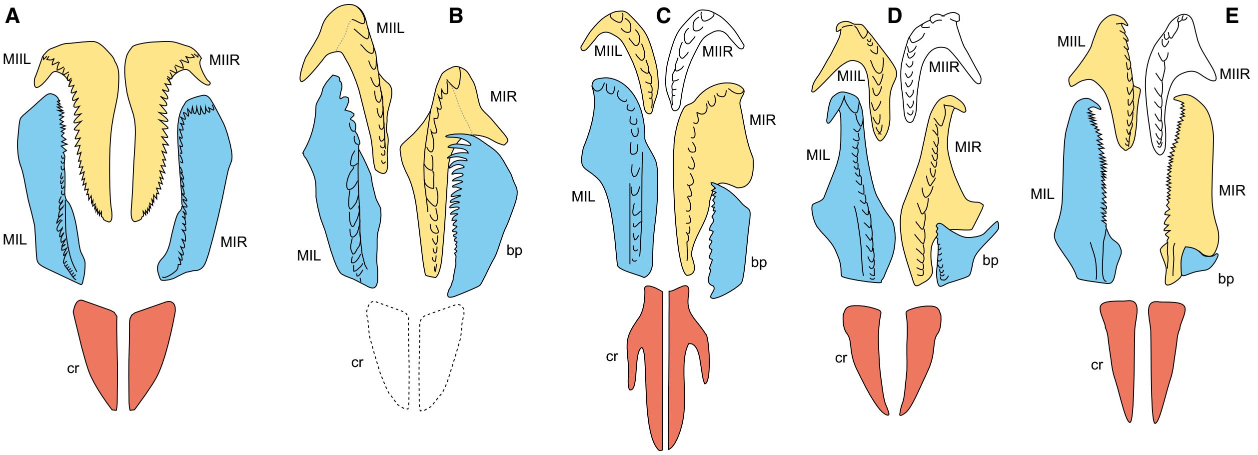

FIG. 4. Apparatus reconstruction of *Andiprion* and comparison with other genera discussed in the main text. A, *Kadriorgaspis*, symmetrognath. B–D, labidognaths; B, *Andipirion*; C, *Pteropelta*; D, *Ramphoprion*. E, *Kettnerites*, eulabidognath. From left to right the images show the oldest symmetrognath apparatus (*Kadriorgaspis*) via the putatively ancestral labidognath *Andiprion* and towards later/typical labidognath/eulabidognath taxa. Note that in A and B some maxillary elements are unknown, possibly not present; in C–E the anterior maxillae and other elements are known, but not illustrated (for reference, see Kielan-Jaworowska 1966; Eriksson *et al.* 2004; Hints & Nõlvak 2006). Apparatus elements are abbreviated as follows: cr, carriers; bp, basal plate; MIL and MIR, left and right first maxillae; MIIL and MIIR, left and right second maxillae. Colour online.

Description. Labidognath-type apparatus consisting of basal plate, left and right MI, and anterior maxillae of which only left MII and MIII are known; carriers most likely present, probably subtriangular; precise size relationships of elements in apparatus unknown.

Right MI. L = 138–405 μm, L/W = 1.7–2.7. Elongated jaw. Anterolateral margin from anterior towards posterior with convex and then concave part, ramus pointed, directed posterolaterally, extending to 0.25–0.4 of jaw length. Anterolateral part of jaw with fang and ramus loosely connected with rest of jaw, commonly showing suture line (Figs 2P, 3E, G); if broken off, anterolateral margin is straight (Fig. 2F). Shank slender, posteriorly rounded. Inner margin straight or slightly concave in anterior third to half of jaw length, then turns sharply at 120–140° angle and runs towards posterior end of jaw. Dentary contains 12–18 denticles, which are often smaller and slenderer in the anterior third of dentary, the largest denticles occur around mid-length decreasing in size posteriorly. In ventral view myocoele opening gaping; cover missing.

Left MI. L = 166–430 μm, L/W = 2.4–4.0 (holotype: L = 230 μm, W = 81 μm, L/W = 2.8). Outer margin runs posterolaterally almost straight or with convex and concave part, then turns and runs straight to meet posterior margin; outer face has maximum width around 0.35–0.5 of jaw length. Posterior margin straight, directed anterolaterally, corresponds to 0.5–0.8 of jaw width. Inner wing subrectangular, *c.* 0.3 of jaw width, occupying 0.4–0.6 of jaw length. Dentary has 13–17 denticles, which are slender in the anterior third and largest and sturdiest around mid-length decreasing in size posteriorly. In ventral view myocoele opening gaping; cover missing.

Basal plate. L = 166 μm, W = 86 μm, L/W = 1.9. Subtriangular jaw, widest at mid-length; posterior margin straight, directed anterolaterally, corresponding to one-third of jaw width; dentary with 20 tightly packed denticles directed laterally, decreasing in size posteriorly; posterior quarter undenticulated.

Left MII. L = 190 μm. Slender jaw with pointed ramus directed posterolaterally and extending to nearly half of jaw length. Similarly to right MI, ramus with first denticle may separate from rest of jaw along suture line (Fig. 3D). Dentary with 12 denticles of which two anterior ones are more slender, largest denticles occur around mid-length, decreasing in size posteriorly, similarly to left and right MI. Inner wing subtriangular, widest at around mid-length.

Left MIII. L = 180 μm. Similar to left MII, but relatively shorter; inner wing occupies *c.* half of jaw length; dentary with 10 posteriorly decreasing denticles not differentiated in shape.

Carriers. Unknown, but the posterior margin of the left and right MI indicates that carriers with a wide anterior margin were present in the apparatus. Probably they were subtriangular in shape, like those recorded in *Kadriorgaspis*.

Variability. Assessing the variability of *A. paxtonae* is complicated as most of the jaws to hand are partly flattened or otherwise deformed and broken. For instance, the length/width ratio and element size therefore vary greatly. However, the type of denticulation and the main outline, especially the shape of the inner and outer wings in both MI, are rather constant. One small left MI (Figs 2K, 3A) is slightly different from the other specimens in having a posterior margin directed more perpendicular to the dentary and an inner wing which is longer and anteriorly wider. However, these minor differences are considered to fall within the intraspecific variability.

Comparison. The individual jaws of *A. paxtonae* show resemblance to those of several different taxa, but the entire apparatus has no closely matching forms. An unpublished Dapingian collection from northern Estonia contains a single left MI (illustrated for comparison in Fig. 2U), which is notably similar to that of *A. paxtonae*, especially the element shown in Figs 2K and 3A. The similar morphology and closely matching age suggest that these two taxa may be congeneric, but further comparison awaits additional material from the Baltic region. The left MI of *A. paxtonae* also shows similarity with the corresponding jaw of polychaeturids in possessing a wide and straight posterior margin, such as in *Pteropelta kielanae* and *P. huberti* (see Hints 1998; Hints & Eriksson 2010) and some ramphoprionids, like species of *Protarabellites* (see e.g. Hints 1998; Eriksson 2001); but other jaws are different. The right MI shares the long shank and narrow ramus with certain polychaetaspids. The basal plate of *A. paxtonae* resembles that of *Conjungaspis minutus* Hints, 1999 in having similar denticulation, but differs in the posterior termination. The left MI, and to some extent also the basal plate, of *A. paxtonae* also resemble those elements of *Kadriorgaspis* Hints & Nõlvak, 2006.

Remarks. The jaw apparatus of *Andiprion* is reconstructed from isolated jaws using both morphological criteria and relative abundance of individual jaws. For instance, the size range, type of denticulation and shape of the anterolateral margin in both left and right MI suggest that these jaws belong to one and the same apparatus and hence a single, multi-element-based species. This is supported by the nearly equal number of corresponding left and right MI recorded in the sample and the lack of feasible alternative apparatus configurations. In addition to posterior maxillae the collection contains a basal plate and a left MII. The basal plate is compatible with the same apparatus architecture as its shape fits well into the bight of the right MI and those elements combined have a posterior margin similar to that of the left MI. Both the basal plate and left MI must fit with the posterior carriers; the plate-like, supporting elements that are symmetrical in all taxa hitherto known. The left MII shares the main outline and denticulation type with that of the right MI, and has also a similarly attached ramus.

Occurrence. Dapingian of Argentina.

DISCUSSION

Jaws have been used to identify evolutionary relationships among extant worms of the Eunicida (Hartman 1944). In the early period of fossil scolecodont research, a single-element-based classification (form taxonomy) was mostly applied, greatly reducing the level of biostratigraphical, palaeobiological and evolutionary information about this group of fossils (see discussion in Kielan-Jaworowska 1968; Szaniawski 1996; Eriksson & Bergman 1998; Eriksson *et al.* 2000). Discussion of the distribution and evolution of extinct jawed polychaetes only became possible after a biologically justified, multi-element-based classification concept (apparatus-based taxonomy) was introduced (Lange 1947; Kozłowski 1956). The major advances in the understanding of fossil polychaete jaw apparatus architecture and its evolution during the Palaeozoic were made by Polish palaeontologists, who collected and described large numbers of fused jaw apparatuses from Baltic Ordovician and Silurian carbonate rocks (Kielan-Jaworowska 1961, 1962, 1966; Szaniawski 1970). Kielan-Jaworowska (1966) discussed homology of individual jaws in different taxa and, for the first time, included fossil taxa in outlining the phylogeny of eunicidan polychaetes. Many of the observations and ideas of Kielan-Jaworowska (1966) have been confirmed or agreed upon in subsequent studies; for instance, that the ancestral jaw apparatus of Eunicida was most likely of symmetrical ctenognath/placognath type (Orensanz 1990; Paxton 2009). However, the early phases in jawed polychaete evolution are far from well understood, and the pre-Darriwilian scolecodont collections known are few and small.

For example, it has remained poorly known when and how asymmetry arose and the more complex labidognath/eulabidognath and prionognath-type apparatus architectures developed (see Kielan-Jaworowska 1966; Paxton 2009, for explanation of different apparatus types). These types of apparatus, accommodating carriers and several pairs of asymmetrical jaws, turned out to be very successful and functionally advanced. They persisted throughout the rest of the Phanerozoic and are the most common buccal armatures in extant Eunicida (Paxton 2009). The present discovery from Argentina helps to shed light on the origin and early evolution of the asymmetric maxillary apparatuses.

Most Early Ordovician scolecodonts hitherto reported are primitive saw-blade-like forms (Underhay & Williams 1995; Williams *et al.* 1999) attributable to ctenognath/placognath groups. Assemblages dominated by such taxa may continue into the Darriwilian as recently shown by Eriksson *et al.* (2016) but generally the Darriwilian and younger faunas contain a relatively high proportion of labidognath/prionognath taxa (Hints & Eriksson 2007; Eriksson *et al.* 2013). No reliable records of labidognath-type apparatuses are known from the Lower Ordovician so far. However, Hints & Nõlvak (2006) described an enigmatic conjungaspid, *Kadriorgaspis*, from the *Paroistodus proteus* Conodont Zone (late Tremadoc to early

Floian) of Estonia. This taxon has a symmetrical jaw apparatus, but is equipped with carriers that were previously known only from the more advanced labidognath/prionognath taxa. Hints & Nõlvak (2006) argued that conjungaspids are not only morphologically similar to, but may have also given rise to the earliest labidognaths since they are so far 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 and prionognaths, as well as to a separate group of advanced taxa with symmetrical jaw apparatuses, the 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 now. We consider the new genus *Andiprion* to represent this evolutionary step as it is morphologically intermediate between *Kadriorgaspis* and the earliest taxa with typical labidognath apparatuses.

Before discussing morphological details, it is necessary to address the question of terminology and homology of elements within different jaw apparatuses. Kielan-Jaworowska (1966) established a complete terminological system for Palaeozoic polychaete jaw apparatus types, based on an assumed homology of elements in placognath, ctenognath, labidognath and prionognath apparatus types. For the posteriormost jaw (but above the carriers) on the right side of labidognath and prionognath maxillary apparatuses, she applied the concept of a basal plate of Lange (1947) and Kozłowski (1956), with the third maxilla on the left side of the apparatus (left MIII) typically unpaired. This naming convention has been followed in subsequent palaeontological studies. Neontologists, on the other hand, denote the 'basal plate' as the right MI (Orensanz 1990; Paxton 2009), which leads to an equal number of maxillae on the two sides of the apparatuses, although the size and morphology of the paired elements may differ considerably. Paxton (2009) and Paxton & Eriksson (2012) discussed the 'basal plate' problem, and showed that when considering the most parsimonious evolutionary pathway, the basal plate concept is unnecessary. However, they argued also that, while the homology of elements in the apparatus should be acknowledged, it is reasonable to retain the established terminology and naming of individual jaws.

Hints & Nõlvak (2006) denoted the first jaws anterior of the carriers in *Kadriorgaspis* as basal and laeobasal plates, and the next paired elements as the first maxillae (MI). This convention was questioned by Paxton (2009) as there is no evidence that the elements connected to carriers are homologous to basal and laeobasal plates of the placognath apparatus type. The great similarity between these jaws of *Kadriorgaspis* and *Andiprion* suggests that they are indeed homologous. In the case of *Kadriorgaspis*, the posterior jaws are of equal size and shape, hence a 'basal plate' concept seems unnecessary and the jaws connected to the carriers in *Kadriorgaspis* could be denoted as the left and right MI. In *Andiprion*, on the other hand, the first left jaw in front of the carriers forms a functional pair with the second right jaw, whereas the first right jaw has decreased in relative size within the apparatus compared to that of *Kadriorgaspis*. Thus *Andiprion* may be considered to be the most primitive form of labidognath type apparatus to which the term 'basal plate' could be reasonably applied (Fig. 4). It is also the genus with the largest basal plate (in relation to the left MI) currently known, further supporting its primitive character.

In terms of homology, however, the present collection fully supports the idea that the 'basal plate' of labidognath and prionognath apparatuses is in fact the first right maxillary piece. As emphasized previously by Kielan-Jaworowska (1966), the general evolutionary pathway of this jaw (bp) concerned gradual decrease in size, to complete fusion with the second jaw (MIR) to form a 'compound maxilla' in several groups, such as the extinct skalenoprionids and extant eunicidans. However, posterior maxillae (MI) with transverse posterior margins were regarded as an advanced character in labidognath and prionognath type jaw apparatuses by Kielan-Jaworowska (1966, p. 47), but the present find indicates that this character was also common in the early stages of labidognath evolution.

The exact phylogenetic position of *Andiprion* between *Kadriorgaspis*-type forms and typical labidognath taxa such as polychaetaspids cannot be resolved because of the limited material available. However, based on the report by Underhay & Williams (1995, fig. 4j) and a single polychaetaspid right MI reported previously from Argentina (Eriksson *et al.* 2002, fig. 3E), it is evident that taxa with a typical labidognath-type apparatus were present in the Dapingian, and overlapped with *Andiprion* in time. Thus, *Andiprion* probably cannot be taken as a direct ancestor, but rather as a representative of a type of jaw apparatus which is ancestral to younger labidognaths. The functional benefit of having asymmetrical elements remains unknown, but possibly it was easier to achieve a stronger grip between the left and right side of the jaw apparatus. The appearance of an asymmetrical maxillary apparatus seems to have approximately coincided in time with the jaws evolving to be thicker and stronger.

In order to explain some discrepancy with genetic analyses Paxton (2009, p. 262) argued that perhaps the carriers could have evolved twice, once in the symmetrognath *Kadriorgaspis* and then in the labidognath Polychaetaspidae. The morphology of *Andiprion* suggests that it is more likely that these taxa belong to one lineage, thus supporting the hypothetical cladogram of Paxton (2009, fig. 9) in which conjungaspids may have given rise to labidognaths and symmetrognaths. As a side remark, the position of the Symmetroprionidae, shown on the symmetrognath lineage by Paxton (2009), may need further consideration, as the number and morphology of its anterior maxillae (if present) and possible associated jaws remain poorly known. It also remains unknown if and how *Kadriorgaspis* evolved from taxa with primitive ctenognath type jaw apparatuses. This question can only be answered if new ctenognath apparatuses from the Tremadocian and perhaps the latest Cambrian become available, and the number and arrangement of the main jaws in such apparatuses is revealed.

The previously reported Early and early Middle Ordovician scolecodont collections (e.g. Underhay & Williams 1995; Eriksson *et al.* 2002; Hints & Nõlvak 2006) are generally characterized by the presence of multiple taxa. Simple ctenognath and placognath jaws often dominate these assemblages. Recently Eriksson *et al.* (2016) reported the discovery of mostly simple, sawblade-like forms from the lower Darriwilian of southern Sweden, and argued that a rapid diversification and abundance increase started within the early Darriwilian, Baltoscandian Kunda time.

The reasons why the present collection contains no taxa other than *Andiprion paxtonae* may simply be due to insufficient sample size. However, it is noteworthy that also later in the Ordovician, many Gondwanan assemblages presently known differed from those of Baltica in having a very low proportion of placognath/ctenognath forms (Hints *et al.* 2015). Monospecific or low diversity assemblages derived from larger collections without sampling bias have also been reported in younger strata, for instance, in the Devonian of Brazil (Eriksson *et al.* 2011).

None of the previously published Dapingian collections seem to contain specimens closely related to *Andiprion*. However, a recently obtained small collection from the Volkhov Regional Stage, *Paroistodus originalis* Conodont Zone, of NW Estonia (OH, unpublished data) deserves mention. That assemblage is of similar low abundance as the Argentinian collection, but is taxonomically more diverse and dominated by simple sawblade-like jaws including *Lunoprionella*, possible tetraprionids and mochtyellids. Additionally, the Estonian material contains a single left MI, which is very similar to, and possibly congeneric with *Andiprion paxtonae*. The specimen illustrated for comparison in Figure 2U differs from *Andiprion* mainly by the larger number and smaller size of its denticles. Initially this jaw had been identified as *Pteropelta*? as it resembles the corresponding jaw of polychaeturids (Hints & Eriksson 2010). It has similar overall shape, wide posterior margin, long inner wing and an almost gaping myocoele opening. Moreover, polychaeturids possess a relatively long basal plate and their anterior maxillae may be developed in the form of fused denticles (Hints & Eriksson 2010, fig. 1U). The latter may represent a primitive character, deriving from a hypothetical ancestral ctenognath-type jaw apparatus. This possible link is supported by the stratigraphic range of polychaeturids; they are among the oldest polychaetes with a labidognath apparatus, appearing in earliest Darriwilian, if not earlier in Baltoscandia (Hints & Eriksson 2010). However, testing the idea that the single left MI from Estonia, *Andiprion* and polychaeturids are closely related awaits further material from Baltoscandia and for the time being the family-level position of *Andiprion* and its possible biogeographical links with Baltica remain open.

CONCLUSIONS

The present collection, albeit small and monospecific, reveals a new polychaete genus and species, *Andiprion paxtonae*, which provides novel insights into the early evolution of polychaete jaw apparatuses and the emergence of asymmetry in the apparatus architecture. It supports the hypothesis that the major diversification phase of eunicidan polychaetes and the appearance of labidognath type jaw apparatuses occurred during the early Middle Ordovician. Moreover, our study encourages future sampling of Argentinian sections to study Ordovician jaw-bearing polychaete worms and fill the regional gap in South America specifically and Gondwana in general.

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