

Machaeridians from the Middle and Upper Ordovician of the Argentine Precordillera

G. ORTEGA^{1,2*}, G. L. ALBANESI^{1,2} and F. J. ZEBALLO¹

¹Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, 5000, Argentina

²CONICET

The machaeridians are marine Palaeozoic annelids, which developed a dorsal skeleton composed of calcite sclerites, achieving a world-wide distribution from the Early Ordovician to the Middle Permian. The absence of records from this group is notable in Argentina in spite of intense studies of Palaeozoic rocks. This fact can be explained by biases in sampling or because of preservation problems. Machaeridian sclerites of the families Plumulitidae and Turrilepadidae collected in Middle and Upper Ordovician rocks from the San Juan Precordillera, Argentina, are described here for the first time. *Plumulites* sp. is recorded in early Darriwilian strata from the Gualcamayo Formation exposed in the western flank of the Cerro La Chilca locality, and from the Las Aguaditas Formation in the Quebrada de Las Aguaditas section. Plumulitid and turrilepadid sclerites are described from the upper member of the Los Azules Formation (late Sandbian) in the Cerro Viejo de Huaco area. The material of the Los Azules Formation is the first record of turrilepadids in Sandbian rocks, which are scarce in Ordovician successions. The referred strata bear pelagic, benthic and nektobenthic faunal assemblages, constituting a similar taphocoenosis preserved in shales and calcareous silty shales related to transgressive events. The record of machaeridians expands our knowledge of the Ordovician biotas from Argentina and provides new information on the palaeobiogeographical distribution of this Palaeozoic annelid group. Copyright © 2012 John Wiley & Sons, Ltd.

Received 19 October 2011; accepted 11 July 2012

KEY WORDS machaeridians; Annelida; palaeoecology; Argentine Precordillera; Middle–Upper Ordovician

1. INTRODUCTION

The machaeridians are worm-like marine animals that dwelt in the Palaeozoic seas. They have a dorsal skeleton (scleritome), made up of calcitic plates (sclerites), arranged in longitudinal series. These organisms were common constituents in the marine biotas from the Early Ordovician to the Middle Permian (Cooper and Grant, 1972; Hoare *et al.*, 1996). Although they remained as enigmatic fossils for over a century, despite being abundant and ubiquitous forms in the Palaeozoic biotas, a specimen with preserved soft parts, discovered recently, allowed them to be referred to the Phylum Annelida (Vinther *et al.*, 2008).

The first record of machaeridian sclerites was reported by de Koninck (1857, 1860) who assigned them to the polyplacophoran remains, *Chiton wrightianus*, from the Much Wenlock Limestone of the Lower Silurian of Dudley, England. The material described by de Koninck actually corresponds to the genus *Turrilepas* Woodward (1865).

New genera were erected in later years: *Plumulites* Barrande (1872) and *Lepidocoleus* Faber (1886) from Bohemia and Ohio, respectively. The monograph published by Withers (1926) sorted out many taxonomic problems and gave the class name, Machaeridia, to the group. Machaeridians have been referred to as polyplacophorans, cirripedes, echinoderms, and annelids over the years (see Adrain, 1992; Vinther and Briggs, 2009, and references therein).

The presence of parapodia and chaetae in an articulated specimen of the plumulitid, *Plumulites bengtsoni* Vinther, Van Roy and Briggs, 2008 of the late Tremadocian of Morocco established the annelid affinity of machaeridians, but its place within the phylum remains unresolved (Vinther *et al.*, 2008; Vinther and Briggs, 2009).

The absence of records from this group is noteworthy in Argentina, in spite of intense studies of Palaeozoic rocks. This fact can be explained by biases in the sampling or because of preservation problems. The discovery of machaeridians in the Los Azules Formation (Cerro Viejo de Huaco section) and Gualcamayo Formation (Cerro La Chilca section), San Juan Precordillera, represents the first records of machaeridians in Argentina. By the end of the 1980s one of the authors (GO) collected sclerites from the upper member of the Los Azules Formation, which were referred to as *Turrilepas* sp.

*Correspondence to: G. Ortega, Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Avda. Vélez Sarsfield 299 1° Piso, C.C. 1598, Córdoba, 5000, Argentina. E-mail: gortega@arnet.com.ar

by Ortega (2010). These specimens were collected from calcareous siltstones bearing an abundant graptolite and conodont fauna (*Climacograptus bicornis* and *Amorphognathus tvaerensis* zones, respectively) from the late Sandbian, associated with trilobites, brachiopods, echinoderms, sponges, gastropods, and palynomorphs.

The succession of shales and siltstones overlying the San Juan Formation in the Cerro La Chilca section, are referred to the Gualcamayo Formation, which bear a profuse graptolite fauna assigned to the *Levisograptus austrodentatus*-*L. dentatus* Zone, conodonts from the *Lenodus variabilis* Zone, and trilobites and brachiopods from the early Darriwilian. The sclerites of machaeridians from this section, frequently fragmentary, correspond to plumulitids (Benedetto, 2010; Ortega, 2010).

In addition, a new collection of plumulitids (under study) resembling the Cerro La Chilca material was recently recovered from the lower member of the Las Aguaditas Formation (lower Darriwilian) exposed in the Cordón de Los Blanquitos, southwest of Jáchal city, which correlates with the Gualcamayo Formation at Cerro La Chilca (Figure 1).

2. GEOLOGIC SETTING

The first work on the Cerro La Chica geology is that of Stappenbeck (1910), who interpreted the deposits exposed in the area as marine Silurian rocks. Later, Cuerda (1965) studied the Silurian sequence. Blasco and Ramos (1976) published on the lower Sandbian deposits (*Nemagraptus gracilis* Zone), and Furque (1983) recognized the presence of the Ordovician San Juan and Los Azules formations. New data were published by Peralta (1993, 1998) and Cuerda *et al.* (1998), completing the knowledge of the Lower Palaeozoic siliciclastic deposits from the area, which are developed over the carbonate platform, including the Gualcamayo Formation (Middle Ordovician) up to the Punta Negra Formation (Lower–Middle Devonian). The succession is unconformably covered by the basal diamictites of the Carboniferous Guandacol Formation (Figure 1).

The sequence analyzed in the present study is exposed in the western slope of the Cerro La Chilca, c. 18 km west of Tucunuco. It corresponds to a lower Darriwilian succession, c. 4.5 m in thickness, of grey to black calcareous siltstones and shales with interbedded mudstones. This succession was assigned to the Gualcamayo Formation by Astini and Benedetto (1992), who considered it as the beginning of a depositional cycle related to a transgressive event that flooded the carbonate platform. Strata of late Darriwilian age are not present in the Cerro La Chilca area, where a succession of black shales with subordinate thin mudstones of early Sandbian age is unconformably overlain by the Gualcamayo Formation. This unit bearing the *Nemagraptus*

gracilis fauna was referred to the Los Azules Formation by Cuerda and Furque (1985) and Cuerda (1986), which was accepted by Peralta (1998) and Peralta *et al.* (2003). K-bentonite levels are present through the upper part of the San Juan Limestone and the Gualcamayo Formation, as can be recognized in many localities of the Precordillera.

The Gualcamayo Formation bears a rich graptolite fauna that is composed of *Tetragraptus bigsbyi* (Hall), *Pseudophyllograptus* sp., *Pseudobryograptus* sp., *Xiphograptus lofuensis* (Lee), *Holmograptus bovis* Williams and Stevens, *Acrograptus* sp., *Parisograptus caduceus* (Salter), *Arienigraptus zhejiangensis* (Yu and Fang), *Paraglossograptus tentaculatus* (Hall), *Levisograptus austrodentatus* (Harris and Keble), *L. dentatus?* (Brongniart), *L. sinicus* (Mu and Lee), *L. primus* (Legg) (Cuerda, 1986; Ortega in Peralta *et al.*, 2003) of early Darriwilian age. This formation conformably overlies the San Juan Formation that yielded a conodont fauna possibly belonging to the *Lenodus variabilis* Zone, with typical species from this zone in the Precordillera such as *Histiodela sinuosa* (see also Keller, 1999, who referred the Gualcamayo Formation to the *Eoplacognathus suecicus* Zone, although a revision of the biostratigraphy for this unit is under consideration).

A rich trilobite association is present in the studied rocks, which is dominated by *Mendolaspis salagastensis* Rusconi, while *Geragnostus* sp., *Neptunagnostella superba* Shergold, *Porterfieldia* sp., *Nileus depressus argentinensis* Tortello and Peralta, *Carolinites latus* Tortello and Peralta, *Carolinites* aff. *pardensis* Legg, and *Macrogrammus pengi* Edgecombe, Chatterton, Vaccari and Waisfeld are also recorded (Tortello and Peralta, 2004), an assemblage that corresponds to the *Kainisiniella cuyana* Zone (Baldis and Pöthe de Baldis, 1995; Tortello and Peralta, 2004). The presence of conodonts, sponges, articulate and chitinophosphatic brachiopods and machaeridians has been mentioned for this unit in diverse contributions (e.g. Carrera, 1997; Keller, 1999; Benedetto, 2010; Ortega, 2010). In the western flank of the Cerro Viejo de Huaco crops out the Los Azules Formation (Harrington and Leanza, 1957), which comprises black shales intercalated with carbonate siltstones, with scarce mudstones and breccias in the upper part. The Los Azules creek, which is the classical locality of this formation, is located c. 7 km southwest of La Ciénaga Village, between the towns of Huaco and Jáchal, to the north of San Juan Province. This sequence, with a maximum thickness of c. 318 m, conformably overlies the limestones of the San Juan Formation, and is unconformably covered by glacial deposits of the Carboniferous Guandacol Formation (Furque, 1979; Ortega, 1987).

The stratigraphic succession was originally described by Borrello and Gareca (1951), who pointed out the presence of *Nemagraptus gracilis* (Hall) in the uppermost part.

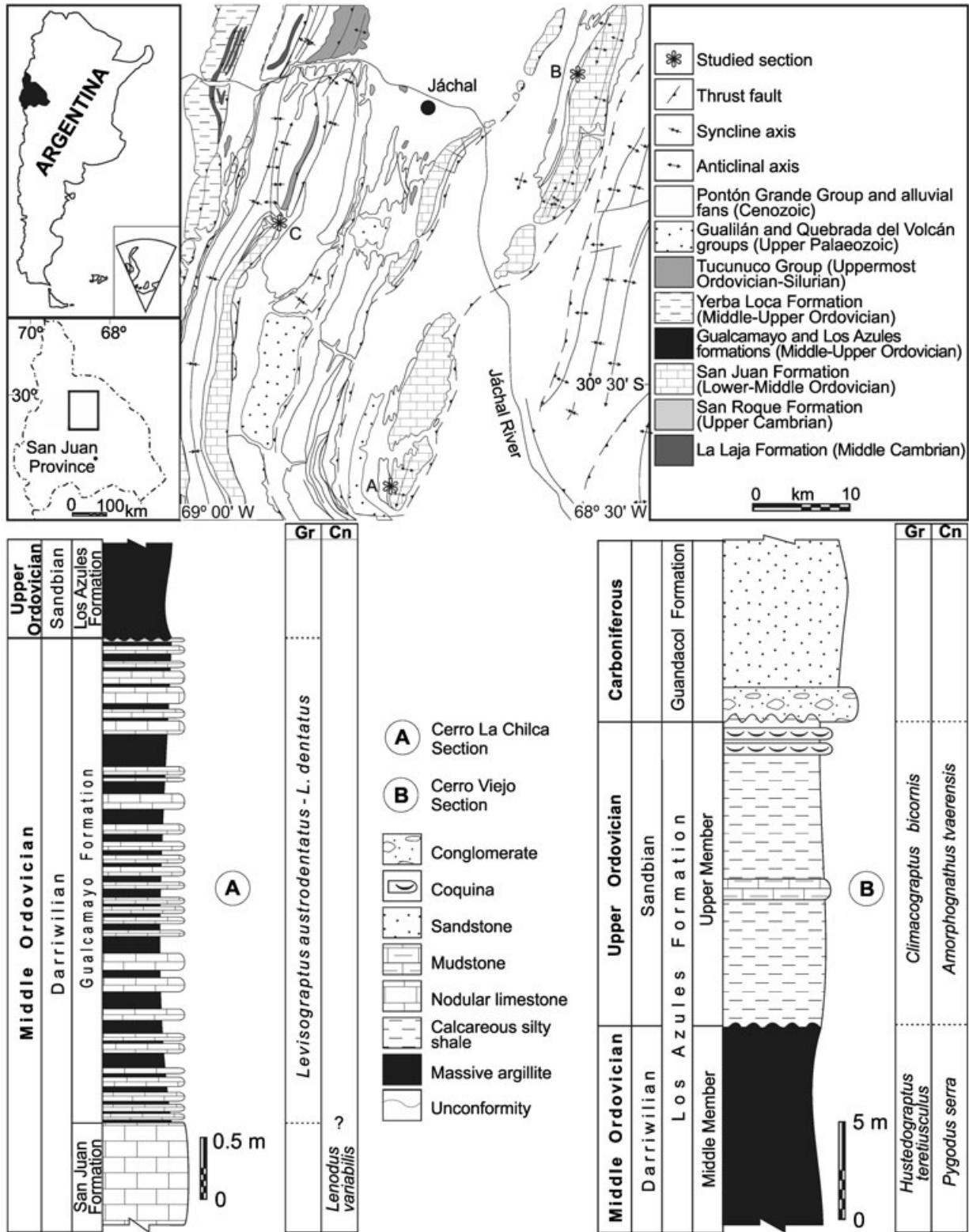


Figure 1. Geological map of the northern San Juan Precordillera, Argentina, with the stratigraphic columns of the studied localities: A, Cerro La Chilca; B, Cerro Viejo de Huaco; and C, Quebrada de Las Aguaditas.

Furque (1979) and Cuerda and Furque (1975) described the geology of the study area, identifying the graptolite fauna. The formation was divided informally into three members (lower, middle and upper) and referred to the Darriwilian and upper Sandbian, according to the graptolite and conodont records (Ortega, 1987, 1995). Palynomorph associations are mainly composed of acritarchs and chitinozoans, which were reported by Ottone *et al.* (1999, 2001).

The upper member of the Los Azules Formation is c. 17 m thick in the eponymous creek. It is made up of calcareous silty shales with scarce mudstones, isolated encrinitic levels, and calcareous coquinas and breccias, the latter better represented to the south of the mentioned creek. It unconformably lies on the middle member of the Los Azules Formation. The upper member bears an important fauna of graptolites corresponding to the *Climacograptus bicornis* Zone and conodonts of the *Amorphognathus tvaerensis* Zone from the late Sandbian (Ortega and Albanesi, 1998; Kaufmann, 2008). The graptolite association comprises *Nemagraptus gracilis* (Hall), *Reteograptus geinitzianus* Hall, *Glossograptus ciliatus* Emmons, *Cryptograptus tricornis* (Carruthers), *Dicellograptus divaricatus* (Hall), *Dicranograptus* cf. *D. spinifer* Lapworth, *Climacograptus bicornis* (Hall), *Archiclimacograptus modestus* (Ruedemann), *Pseudoclimacograptus scharenbergi* Lapworth, and dendroid remains (*Dictyonema* sp., *Aspidograptus* sp., *Callograptus* sp., and *Ptilograptus* sp.) among others (Ortega, 1987; Ortega and Albanesi, 1998; Kaufmann, 2008; Figure 1). The record of synrhabdosomes in the uppermost levels of the member was reported by Kaufmann (2008) and Ortega *et al.* (2009).

The conodont fauna, dominated by *Amorphognathus tvaerensis* Bergström, includes *Phragmodus undatus* Branson and Mehl, *Drepanoistodus suberectus* (Branson and Mehl), *Baltoniodus variabilis* (Bergström), *Panderodus gracilis* (Branson and Mehl), *Scabbardella altipes* (Henningsmoen), *Protopanderodus varicostatus* (Sweet and Bergström), *Periodon aculeatus* Hadding, *Erismodus* sp. and *Plectodina* sp. (Albanesi and Ortega, 1998; Kaufmann, 2008).

The trilobites *Guandacolithus furquei* Harrington and Leanza and *Triarthrus jachalensis* (Harrington and Leanza) are abundant throughout the upper member. Fossil remains of articulate and chitinophosphatic brachiopods, bryozoans and crinoids are common in the coquinas of the upper member. Recently, Carrera and Ortega (2009) described a complete specimen of a hexactinellid sponge (*Cyathophycus extendis* Carrera and Ortega) and gastropods, and Ortega (2010) identified turrilapadid sclerites from this member herein described.

3. MATERIAL

The machaeridian material comes from the Los Azules Formation that crops out in the western flank of the Cerro

Viejo, at Huaco Anticline; and the Gualcamayo Formation, on the western flank of the Cerro La Chilca, Central Precordillera of San Juan (Figure 1). Sclerites of turrilapadids and plumulitids were collected throughout the calcareous siltstones of the upper member of the Los Azules Formation. They are associated with disarticulated remains of the trilobites *Triarthrus jachalensis* and *Guandacolithus furquei*, chitinophosphatic brachiopods, sponge spicules, conodonts and graptolites. The fossil assemblage corresponds to the *Climacograptus bicornis* and *Amorphognathus tvaerensis* zones, of late Sandbian age. Smaller sclerites referred to as *Plumulites* sp. were recorded in calcareous siltstones of the Gualcamayo Formation at Cerro La Chilca. Associated fossils are the trilobites *Mendolaspis salagastensis* and *Carolinites* spp., acrotretid brachiopods, and graptolites, which are the most frequent forms in these strata. This assemblage suggests the *Levisograptus austrodentatus*–*L. dentatus* Zone of early Darriwilian age.

4. SYSTEMATIC PALAEOLOGY

Recently, machaeridians were assigned to an unresolved group of annelids according to the presence of parapodia and chaetae in one exceptionally preserved specimen of *Plumulites bengtsoni* Vinther, Van Roy and Briggs 2008, from upper Tremadocian strata of Morocco. Its epifaunal mode of life is considered primitive for machaeridians (Vinther *et al.*, 2008; Vinther and Briggs, 2009). Calcitic sclerites with inner and outer layers formed by epithelial deposition (Bengtson, 1978) with distinctive rugae patterns are present in all machaeridians, which are regarded as a monophyletic group (Adrain, 1992). The presence of this calcareous exoskeleton is unique within the annelids.

In the present paper we follow the criteria of Herringshaw and Raine (2007) who considered the Class Machaeridia Withers 1926 as a clade containing the families Turrilapadidae Clarke, 1896, Lepidocoleidae Clarke, 1896, and Plumulitidae Jell, 1979, all of them present in the Early Ordovician. The three families can be distinguished according to the scleritome arrangement (Jell, 1979) but, contrary to Jell's opinion, turrilapadids were not able to close their scleritome (Adrain, 1992; Högström, 1997). Turrilapadids and plumulitids have the earliest records of the group; specimens of both families were reported in Tremadocian strata from Asia, Scotland and Morocco (Kobayashi and Hamada, 1976; Herringshaw and Raine, 2007; Vinther *et al.*, 2008). Both families are tetraseriate machaeridians containing two rows of overlapping inner and outer sclerites and tagmatization of the anterior region where outer sclerites are not present (Adrain *et al.*, 1991; Vinther and Rudkin, 2010). Lepidocoleids have two rows of sclerites, except in a few species, which retain the presumed primitive state with four rows.

The machaeridian collection from the Cerro Viejo is composed of peculiar inner sclerites of turrilepadids and a few outer sclerites of plumulitids. The scarcity of outer machaeridian sclerites can not be explained, although it can certainly respond to a particular type of sorting. Specimens found in the Cerro La Chilca correspond to single inner and outer sclerites of Plumulitidae.

The material studied here was described following the terminology of Adrain *et al.* (1991), Adrain (1992) and Högström (1997). The collections are housed in the Museo de Paleontología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, under the repository code CORD-PZ.

Phylum ANNELIDA Lamarck, 1809
Class MACHAERIDIA Withers, 1926
Family PLUMULITIDAE Jell, 1979
Genus PLUMULITES Barrande, 1872

Plumulites sp.
(Figure 2j, k, l, n)

Material and locality. Tens of fragmentary sclerites, mostly minute, partially exposed, and preserved on outer surfaces, which were collected from the Gualcamayo Formation on the western flank of the Cerro La Chilca. Illustrated material corresponds to CORD-PZ 22401 1–2, 22423, 22449.

Description. The collection yields single isolated sclerites with smooth rugae. The edges of the sclerites are broken or blurred and in most cases prevents an assessment of their real shape and dimensions. Inner sclerites exceeding 3 mm in length with medial non-accreting margin slightly shorter than the lateral non-accreting margin. They show slightly closer spaced rugae in the apical region (18 rugae in 1 mm) more widely spaced close to the accreting margin (8–8.5 rugae in 1 mm) with more than 30 rugae present in one incomplete mature sclerite. Inflections I_1 – I_3 present with I_1 90° – 115° and I_3 wider. A deep and narrow furrow roughly coincides with I_2 . Longitudinal fold apparently non expressed. There are two incomplete modified outer sclerites (Figure 2l, n) with the umbo displaced away from apex showing concentric rugae, about 6 in 1 mm. Inflections i_1 – i_3 present with i_1 $c. 90^\circ$ and i_3 shallower. Like in the inner sclerites a deep furrow coincides with the i_2 but it is slightly curved. In both, inner and outer sclerites, it separates a wider medial part and a narrower lateral area. Marginal and apical spines are not observed.

Remarks. In spite of the presence of inner and outer sclerites, most of the collected material is composed of fragmented or very small sclerites, which makes the diagnosis difficult. Modified outer sclerites with easily

spaced rugae, could have occupied the anterior part of the scleritome according to features present in some plumulitids, e.g. *Plumulites richorum* Jell, 1979 and *P. canadensis* Woodward, 1889 (see Vinther and Rudkin, 2010). The presence of a distinctive deep and narrow furrow separating the sclerites in two different areas seems to be an important character to classify the material when more complete specimens are found.

Plumulitidae gen. et sp. indet.
(Figure 2g, m)

Material and locality. Three incomplete outer sclerites preserved in outer surfaces, recorded in the upper member of the Los Azules Formation, in the Amarilla and Árbol Seco creeks, on the western flank of Cerro Viejo de Huaco (CORD-PZ 13544, 13549, 13974).

Description and discussion. Minute sclerites more than 4 mm in length, with poorly preserved margins. The apical region is not clear. Conspicuous rugae more widely spaced close to the accreting margin, with steeper faces toward the apical region. Inflections i_1 – i_3 present with i_1 wide and i_3 more stretched. A curved deep and narrow furrow runs away from the i_2 or slightly displaced to the lateral non-accreting margin. The shape of these outer sclerites resembles those of the genus *Plumulites*. Nevertheless, the specimens have been referred to the family Plumulitidae because of the absence of more complete and better preserved material.

Family TURRILEPADIDAE Clarke, 1896
Turrilepadidae gen. et sp. indet.
(Figure 2a–f, h, i, o?)

Material and locality. Most of the material corresponds to disarticulated inner sclerites, sometimes fragmented, preserved in the outer surface and collected from the upper member of the Los Azules Formation at Los Azules and Amarilla creeks (CORD-PZ 13974, 14255, 14257, 14268, 14266, 14267).

Description. Large and flat sclerites with prominent rugae, edges frequently blurred or broken, and unequal non-accreting margins. The shorter margin contains a closer density of rugae. Marginal and apical spines are not observed. Two different sclerites are present in the studied material. Most common sclerites have a pointed apex containing the umbo (unmodified sclerites) with three pronounced inflections in the apical region, but near the 13 or 14 rugae the inflection I_2 becomes straighter and appear five inflections, usually weakly visible. The I_1 is sharper with $c. 90^\circ$ in the apical part and $c. 100^\circ$ to the accreting margin. The density of rugae is closer in the apical portion (9–10 rugae in 1 mm) than in the accreting

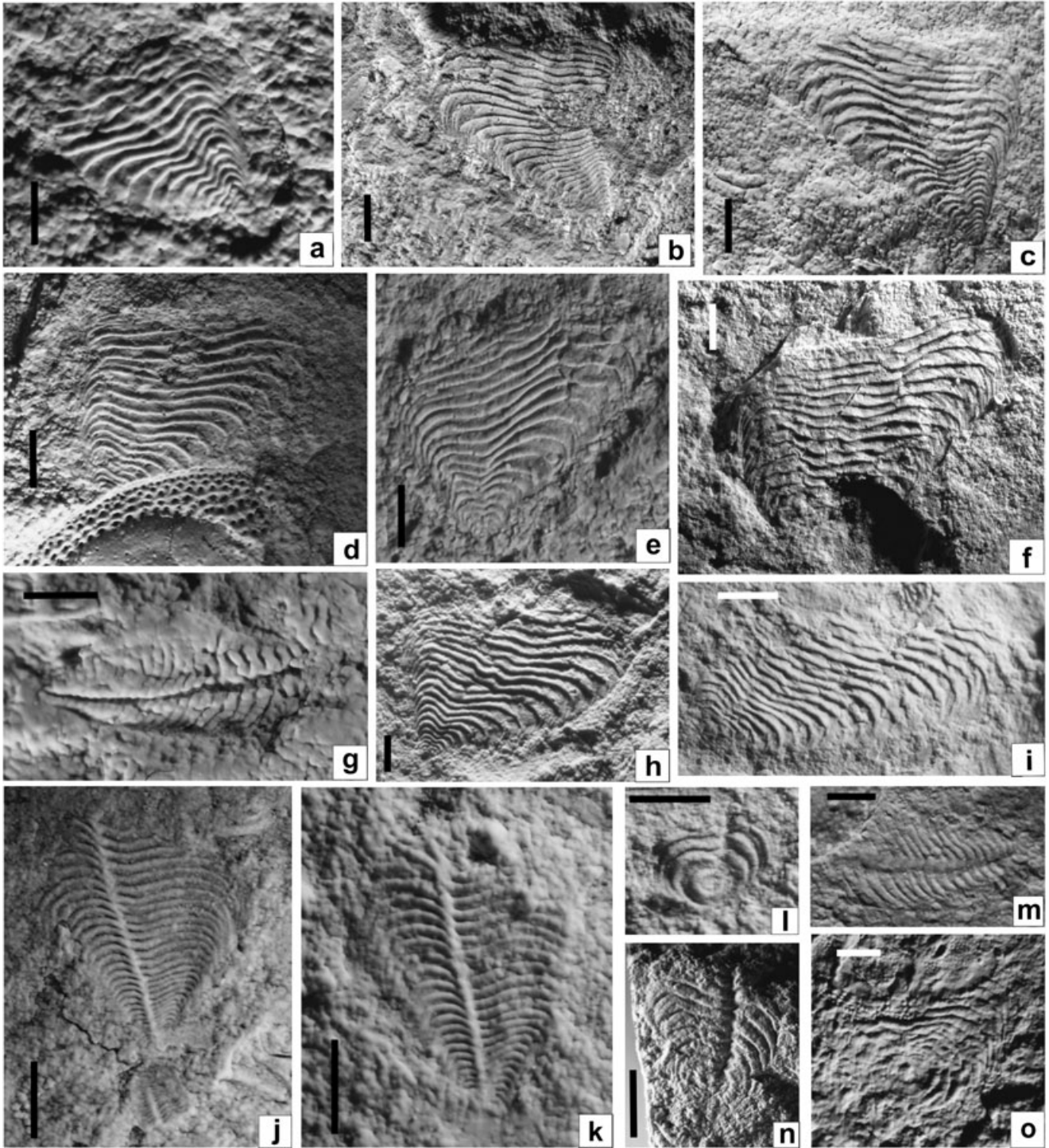


Figure 2. Machaeridian sclerites from the Middle and Upper Ordovician of the San Juan Precordillera, Argentina. (a–f, h, i, o?): *Turrilepadidae* gen. et sp. indet., upper member, Los Azules Formation, Cerro Viejo de Huaco: (a) inner left sclerite, CORD-PZ 14255-1; (b) counterpart of a broken inner right sclerite with shallow inflections, CORD-PZ 14264; (c) inner left sclerite, CORD-PZ 14267-1; (d) inner right sclerite, CORD-PZ 14267-2; (e) inner right sclerite, CORD-PZ 14266-1; (f) inner right sclerite with apical region broken CORD-PZ 14266-2. (h) Inner right sclerite, CORD-PZ 14258; (i) modified inner right sclerite, CORD-PZ 13974. (o) Incomplete apical region of a modified sclerite, provisionally included as *turrilepadid*; CORD-PZ 14255-2. (g, m) *Plumulitidae* gen et sp. indet., upper member, Los Azules Formation, Cerro Viejo de Huaco: (g) outer right sclerite, CORD-PZ 13549; (m) outer left sclerite, CORD-PZ 13974; (j–l, n) *Plumulites* sp., Gualcamayo Formation, Cerro La Chilca: (j) counterpart of an inner left sclerite, CORD-PZ 22423; (k) counterpart of an inner left sclerite, CORD-PZ 22449; (l) apical region with concentric rugae of an outer right sclerite showing a deep furrow, CORD-PZ 22401-1; (n) apical region of a modified outer right sclerite, CORD-PZ22401-2. Scale-bar: 1 mm.

margin (4–5 rugae in 1 mm), and they are closer spaced in the medial non-accreting margin. Occasionally, incomplete sclerites with concentric rugae around the umbo (modified sclerites) are present and display a more rounded shape (Figure 2i). These specimens are the largest of the collection, presenting more than 6.5 mm in length and showing shallow inflections. The total number of rugae is unknown, but there are more than 27 in one modified sclerite. The rugae faces lie more reclined to the accreting margin and are steepest to the apical part. Some sclerites with disturbed growth occur occasionally in most collections (Figure 2h).

Discussion. The presence of robust rugae and five inflections allow us to refer these sclerites to *Turrilepadidae*. For the most part, the studied material includes robust sclerites without longitudinal fold, and unequal non-accreting margins, which do not precisely match with the inner sclerites of turrilepadids. However, the presence of five inflections in the accreting part of these sclerites suggests that they occupied an internal position within the scleritome. The absence of a longitudinal fold in these sclerites could be explained by flattening during diagenesis, although other fossils from the same strata, such as trilobites, do not show this effect. The longitudinal fold of these specimens could be weak, and consequently obliterated during taphonomic processes.

Turrilepadidae gen. et sp. indet. described by Herringshaw and Raine (2007) is based on a singular sclerite with five inflections and edges like those of an inner sclerite without a longitudinal fold, which was referred to by those authors as an outer sclerite. This is the most ancient turrilepadid known, recorded in middle Tremadocian strata of Scotland. The only record of the genus *Turrilepas* in the Ordovician corresponds to *Turrilepas* sp. from the late Katian of central Sweden (Högström *et al.*, 2009). Sclerites collected in the upper member of the Los Azules Formation at San Juan Precordillera referred to here as *Turrilepadidae* gen. et sp. indet. represent the first record of turrilepadids in the late Sandbian.

The poor knowledge of genera other than *Turrilepas* included in the Family *Turrilepadidae* by Adrain *et al.* (1991), i.e. *Deltacoleus* Withers, 1926, *Clarkeolepis* Elias, 1958, *Spinacoleus* Schallreuter, 1985, and *Mojczalepas* Dzik, 1986, does not allow a precise comparison with our material. The presence of a conspicuous rugae pattern with three inflections in the apical region and five inflections to the accreting margin in the Argentine material suggests that it could correspond to a new taxon.

5. PALAEOECOLOGY

The machaeridians have a frequent cosmopolitan record in the Palaeozoic biotas, although they are rare forms in Argentina.

A few records have been documented from Ordovician strata in the Central Precordillera of San Juan (Benedetto, 2010; Ortega, 2010). Recently, a collection of plumulitids was recovered from the Darriwilian lower member of the Las Aguaditas Formation at Cordón de Los Blanquitos (Figure 1). This material is similar to that described for the Cerro La Chilca (collection under study). The presence of other annelids is represented by scarce records of jaw elements from scolecodonts in Middle Ordovician strata of the San Juan and Gualcamayo formations (Ottone and Holfeltz, 1992; Eriksson *et al.*, 2002), Argentine Precordillera. Scolecodonts are also present in Sandbian strata of the Los Azules Formation, as well as from the Sierra de la Invernada Formation (Middle–Upper Ordovician) of the San Juan Precordillera (Ortega, unpublished data).

The upper member of the Los Azules Formation is a carbonate siliciclastic unit that was interpreted as a deep-water outer platform dominated by pelagic faunas (Ortega, 1987; Kaufmann, 2008). Incomplete and sporadic remains of dendroid graptolites were recovered in the member, suggesting that they might have been transported from a nearby platform. The trilobites *Guandacolithus furquei* and *Triarthrus jachalensis* are also common, the latter species indicating a deep-water assemblage similar to the Olenid biofacies of Fortey (1975) (see Edgecombe *et al.*, 2005). The conodont assemblage yielded from calcirudites of the uppermost strata of the Los Azules Formation, is also dominated by pelagic species (Albanesi and Ortega, 1998; Kaufmann, 2008).

A few benthic fossils are present in these calcareous silty shales. Sponge spicules (*Cyathophycus extendis*) are distributed throughout the member, and scarce complete specimens were described by Carrera and Ortega (2009). These authors interpreted *C. extendis* as belonging to an association from a deep-water, low-oxygen environment. Root-tuft attachment of other species of this genus might suggest a soft substrate for anchoring (Botting, 2004). Sclerites of turrilepadids and plumulitids are especially abundant in the middle part of the member. The coquinas of the uppermost part of the unit bear crinoids, bryozoans, articulate brachiopods, gastropods, and trilobite remains, indicating transport from a nearby platform.

In the calcareous-pelitic succession of the Gualcamayo Formation at Cerro La Chilca, the fauna is dominated by a rich assemblage of epipelagic graptolites (Cuerda, 1986; Peralta *et al.*, 2003; unpublished collections). Baldi (1978), Baldi and Beresi (1981), and Tortello and Peralta (2004) documented an important association of benthic and epipelagic trilobites that consist of metagnostids, shumardiids, olenids, illaenids, nileids, raphiophorids, telephinids, and cheirurids. The benthic faunal assemblage comprises brachiopods (lingulids, acrotretids and rhynchonelliforms) and machaeridian sclerites assigned to plumulitids (Benedetto, 2010; Ortega, 2010). The bearer stratigraphic interval corresponds to an outer carbonate platform or ramp (Astini, 1994; Cañas, 1999) with deep-water

environmental conditions and soft substrate (Tortello and Peralta, 2004). A raphiophorid biofacies (*sensu* Fortey and Owens, 1978) was suggested according to the dominant character of *Mendolaspis salagastensis* in the trilobite assemblage (Tortello and Peralta, 2004).

Machaeridians are present in diverse facies indicating that they inhabited from shallow-marine environments to deep-water outer platforms (Högström, 2000). Turrilepadids and plumulitids from the upper member (upper Sandbian) of the Los Azules Formation at Cerro Viejo de Huaco, and plumulitids of the Gualcamayo Formation (lower Darriwilian) at Cerro La Chilca are present in a similar taphocoenosis, with pelagic, benthic, and nektobenthic organisms preserved in calcareous siltstones and shaly successions.

Turrilepadid and lepidocoleid machaeridians would have been burrower organisms (Dzik, 1986; Hints *et al.*, 2004; Vinther and Briggs, 2009). Conversely, the plumulitids, which had a dorsoventrally flattened body covered by a dorsal scleritome and well-developed parapodia, were apparently epibenthic wandering organisms, following recent interpretations (Vinther *et al.*, 2008; Vinther and Briggs, 2009).

The record of machaeridians in the studied sections are associated to transgressive events, and their absence in other units with significant benthic faunas thoroughly studied (e.g. diverse limestone facies of the San Juan Formation, lower member of the Gualcamayo Formation in other parts of the Precordillera) is remarkable.

The presence of machaeridians in the Middle and Upper Ordovician strata of the Argentine Precordillera provides new information on the palaeobiogeographical distribution of this group, previously unknown in the Palaeozoic successions of Argentina.

6. CONCLUSIONS

- Machaeridian sclerites of plumulitids and turrilepadids are described for the first time in Middle and Upper Ordovician successions of the Argentine Precordillera, and represent the first record of these fossil annelids in Argentina.
- Inner and outer sclerites of *Plumulites* sp. are recorded in early Darriwilian strata of the Gualcamayo Formation from the Cerro La Chilca section.
- Sclerites of plumulitids and turrilepadids are documented for the upper member of the Los Azules Formation (late Sandbian) on the western flank of Cerro Viejo de Huaco.
- Turrilepadidae gen. et sp. indet. from the uppermost part of the Los Azules Formation represents the first mention of the family for the Sandbian Stage.
- The finding of machaeridians in Argentina expands our knowledge of the palaeobiogeography of these Palaeozoic annelids.
- The studied fossils, although different in age, correspond to similar taphocoenosis assemblages formed under comparable environmental conditions, which were related to transgressive events.

ACKNOWLEDGEMENTS

We gratefully thank CONICET (PIP 2010–2012) for the financial support and the Universidad Nacional de Córdoba, Argentina, where this research project was accomplished. This paper is a contribution to IGCP Project 591. We acknowledge the reviewers A. Högström and J. Vinther who provided a reasoned discussion of the original manuscript which helped to improve the final version.

REFERENCES

- Adrain, J.M.** 1992. Machaeridian classification. *Alcheringa* **16**, 15–32.
- Adrain, J.M., Chatterton, B.D.E., Cocks, L.R.M.** 1991. A new species of Machaeridian from the Silurian of Podolia, USSR, with a review of the Turrilepadidae. *Palaeontology* **34**, 637–651.
- Albanesi, G.L., Ortega, G.** 1998. Conodont and Graptolite faunas from the Las Plantas Formation and equivalent units (Caradoc) in the Argentine Precordillera. *Seventh International Conodont Symposium Held in Europe: Bologna-Modena Abstracts*, 1–2.
- Astini, R.A.** 1994. Análisis secuencial y paleoambientes de las pelitas negras (aloformación Gualcamayo) que suprayacen a las secuencias carbonáticas eo-ordovícicas en la Precordillera argentina. *Revista de la Asociación Geológica Argentina* **49**, 71–84.
- Astini, R.A., Benedetto, J.L.** 1992. El Ashgilliano tardío (Hirnantiano) del cerro La Chilca, Precordillera de San Juan, Argentina. *Ameghiniana* **29**, 249–264.
- Baldis, B.A.** 1978. Ensayo de análisis paleoecológicos con trilobites ordovícicos argentinos. *Ameghiniana* **15**, 3–14.
- Baldis, B.A., Beresi, M.S.** 1981. Biofacies de culminación del ciclo deposicional calcáreo del Arenigiano en el oeste de Argentina. *II Congreso Latinoamericano de Paleontología y Bioestratigrafía*, Porto Alegre; 1, 11–18.
- Baldis, B.A., Pöthe de Baldis, E.D.** 1995. Trilobites ordovícicos de la Formación Las Aguaditas (San Juan, Argentina), y consideraciones estratigráficas. *Boletín de la Academia Nacional de Ciencias*, Córdoba, Argentina **60**, 409–448.
- Barrande, J.** 1872. *Système Silurien du Centre de la Bohême. 1ère partie. Recherches paléontologiques. Supplement au vol. 1.* Prague, Paris.
- Benedetto, J.L.** 2010. Placas de macaeridios (Annelida) en pelitas negras del Ordovícico Medio de la Precordillera de San Juan, Argentina. *10º Congreso Argentino de Paleontología y Bioestratigrafía y 7º Congreso Latinoamericano de Paleontología: La Plata; Resúmenes*, **137**.
- Bengtson, S.** 1978. The Machaeridia—a square peg in a pentagonal hole. *Thalassia Jugoslavica* **12**, 1–10.
- Blasco, G., Ramos, V.A.** 1976. Graptolitos caradocianos de la Formación Yerba Loca y del cerro La Chilca, Departamento Jáchal, Provincia de San Juan. *Ameghiniana* **13**, 312–329.
- Borrello, A.V., Gareca, P.G.** 1951. Sobre la presencia de “*Nemagraptus gracilis*” (Hall) en el Ordovícico del norte de San Juan. *Revista de la Asociación Geológica Argentina* **6**, 187–193.

- Botting, J.P. 2004.** An exceptional Caradoc sponge fauna from the Llanfawr Quarries, central Wales, and phylogenetic implications. *Journal of Systematic Palaeontology* **2**, 31–63.
- Cañas, F.L. 1999.** Facies and sequences of the Late Cambrian–Early Ordovician carbonates of the Argentine Precordillera: a stratigraphic comparison with Laurentian platforms. In: *Laurentia-Gondwana connections before Pangea*, Ramos, V.A., Keppie, J.D. (eds). Geological Society of America, Special Paper **336**, 43–62.
- Carrera, M.G. 1997.** Significado paleoambiental de los poríferos y briozoos de la Formación San Juan (Ordovícico), Precordillera argentina. *Ameghiniana* **34**, 179–199.
- Carrera, M.G., Ortega, G. 2009.** The hexactinellid sponge *Cyathophycus* from the Upper Ordovician of the Argentine Precordillera. *Ameghiniana* **46**, 449–459.
- Clarke, J.M. 1896.** The structure of certain Palaeozoic barnacles. *American Geology* **18**, 137–143.
- Cooper, G.A., Grant, R.E. 1972.** Permian brachiopods of West Texas, I. *Smithsonian Contributions of Paleobiology* **14**, 1–231.
- Cuerda, A. 1965.** *Monograptus leintwardinensis* var. *incipiens* Wood, en el Silúrico de la Precordillera. *Ameghiniana* **4**, 171–177.
- Cuerda, A.J. 1986.** Graptolitos del techo de la Formación San Juan, Precordillera de San Juan. 4° Congreso Argentino de Paleontología y Bioestratigrafía: Mendoza; **1**, 49–57.
- Cuerda, A., Furque, G. 1975.** Nuevos datos sobre la paleobiogeografía de la Formación Gualcamayo, Ordovícico de la Precordillera. 1° Congreso Argentino de Paleontología y Bioestratigrafía: Tucumán; **1**, 49–58.
- Cuerda, A., Furque, G. 1985.** Graptolitos del techo de la Formación San Juan, Precordillera de San Juan. *Actas Primeras Jornadas sobre Geología de Precordillera*, San Juan, Serie A, Monografías y Reuniones **2**, 113–118.
- Cuerda, A.J., Caballé, M., Cingolani, C., Alfaro, M. 1998.** Ordovician (Caradoc) dendroids and their stratigraphic relationships, northeastern Argentine Precordillera. In: *Proceedings of the Sixth International Graptolite Conference of the GWG (IPA) and the SW Iberia Field Meeting 1998 of the International Subcommittee on Silurian Stratigraphy (ICS–IUGS)*, Gutiérrez-Marco, J.C., Rábano, I. (eds). Instituto Tecnológico Geominero de España, Madrid, Temas Geológico-Mineros **23**, 164–169.
- Dzik, J. 1986.** Turrilepadidae and other Machaeridia. In: *Problematic fossil taxa*, Hoffman, A., Nitecki, M.H. (eds.). Clarendon Press: Oxford, 1–267.
- Edgecombe, G.D., Chatterton, B.D.E., Vaccari, N.E., Waisfeld, B.G. 2005.** Triarthrinid trilobites (Olenidae) from the Middle and Upper Ordovician, Precordillera Argentina. *Journal of Paleontology* **79**, 89–109.
- Elias, M.K. 1958.** Late Mississippian fauna from the Redoak Hollow Formation of southern Oklahoma, part 4, Gastropoda, Scaphopoda, Cephalopoda, Ostracoda, Thoracica, and Problematica. *Journal of Paleontology* **32**, 1–57.
- Eriksson, M., Albanesi, G.L., Hünicken, M.A. 2002.** Early Middle Ordovician scolecodonts from the Argentine Precordillera: the oldest known polychaete jaws of South America. *Ameghiniana* **39**, 427–432.
- Faber, C.L. 1886.** Remarks on some fossils of the Cincinnati Group. *Journal of the Cincinnati Society for Natural History* **9**, 14–20.
- Fortey, R.A. 1975.** Early Ordovician trilobite communities. *Fossils and Strata* **4**, 331–352.
- Fortey, R.A., Owens, R.M. 1978.** Early Ordovician (Arenig) stratigraphy and faunas of the Carmarthen district, south-west Wales. *Bulletin of the British Museum (Natural History), Geology* **30**, 225–294.
- Furque, G. 1979.** Descripción geológica de la Hoja 18c, Jáchal, Provincia de San Juan. *Boletín Servicio Geológico Nacional* **164**, 1–85.
- Furque, G. 1983.** Descripción geológica de la Hoja 19c, Ciénaga de Gualilán. Servicio Geológico Nacional: Buenos Aires; Boletín **193**, 1–111.
- Harrington, H.J., Leanza, A.F. 1957.** *Ordovician trilobites of Argentina*. Department of Geology, University of Kansas Press: Lawrence.
- Herringshaw, L.G., Raine, R.J. 2007.** The earliest turrilepadid: a machaeridian from the Lower Ordovician of the Northwest Highlands. *Scottish Journal of Geology* **43**, 97–100.
- Hints, O., Eriksson, M., Högström, A.E.S., Kraft, P., Lehnert, O. 2004.** Worms, wormlike and sclerite bearing taxa. In: *The Great Ordovician Biodiversification Event*, Webby, B., Droser, M.L., Paris, F., Percival, I. (eds.). Columbia University Press: New York, 223–230.
- Hoare, R.D., Mapes, R.H., Yancey, T.E., Nestell, M.K. 1996.** Late Paleozoic turrilepadid machaeridians from North America. *Acta Palaeontologica Polonica* **41**, 127–145.
- Högström, A.E.S. 1997.** Machaeridians from the Upper Wenlock (Silurian) of Gotland. *Palaeontology* **40**, 817–831.
- Högström, A.E.S. 2000.** Aspects of machaeridian ecology. *Geological Society of America*, Abstract with Programs, **32**, 370.
- Högström, A.E.S., Ebbestad, J.O.R., Suzuki, Y. 2009.** Armoured annelids and molluscs from the Upper Ordovician Boda Limestone, central Sweden. *GFF* **131**, 245–252.
- Jell, P.A. 1979.** *Plumulites* and the machaeridian problem. *Alcheringa* **3**, 253–259.
- Kaufmann, C. 2008.** *Graptolitos y conodontes del Sandbiano tardío (Ordovícico Superior) de la Formación Los Azules, Cerro Viejo de Huaco, Precordillera de San Juan*. Trabajo Final, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, 1–276.
- Keller, M. 1999.** Precordillera. sedimentary and plate tectonic history of a Laurentian crustal fragment in South America. *Geological Society of America, Special Paper* **341**, 1–131.
- Kobayashi, T., Hamada, T. 1976.** Occurrences of the machaeridia in Japan and Malaysia. *Proceedings of the Japan Academy* **52**, 371–374.
- Koninck, L. de. 1857.** Sur deux nouvelles espèces siluriennes appartenant au genre *Chiton*. *Bulletin de l'Académie des Sciences de Belgique* **3**, 190–199.
- Koninck, L. de. 1860.** Observations on two new species of *Chiton* from the Upper Silurian “Wenlock Limestone” of Dudley (translated by W. H. Baily, F. G. S.). *Annals and Magazine of Natural History* **3**, 91–98.
- Lamarck, J. B. de. 1809.** *Philosophie zoologique; ou, Exposition des considérations relatives à l'histoire naturelle des animaux; à la diversité de leur organisation et des facultés qu'ils in obtiennent; aux causes physiques qui maintiennent en eux la vie et donnent lieu aux mouvemens qu'ils exécutent; enfin, è celles qui produisent, les unes le sentiment, et les autres l'intelligence de ceux qui en sont doués*. Dentu, Paris, Volume 1, 1–428, Volume 2, 1–475.
- Ortega, G. 1987.** *Las graptofaunas y los conodontes de la Formación Los Azules, Cerro Viejo, zona de Huaco, Departamento Jáchal, San Juan*. Ph. D. Thesis, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, 1–210.
- Ortega, G. 1995.** Graptolite zones of the Los Azules Formation (Middle Ordovician) from Precordillera, western Argentina. 5° *International Graptolite Conference, Graptolite Working Group, International Palaeontological Association, Graptolite News* (Long Beach, California) **8**, 57–59.
- Ortega, G. 2010.** Primeros registros de Machaeridias (Annelida) en el Ordovícico Medio y Superior de Argentina. 10° *Congreso Argentino de Paleontología y Bioestratigrafía y 7° Congreso Latinoamericano de Paleontología: La Plata; Resúmenes*, 1–52.
- Ortega, G., Albanesi, G.L. 1998.** The record of *Nemagraptus gracilis* Biozone in the Argentine Precordillera. In: *Proceedings of the Sixth International Graptolite Conference of the GWG (IPA) and the SW Iberia Field Meeting 1998 of the International Subcommittee on Silurian Stratigraphy (ICS–IUGS)*, Gutiérrez-Marco, J.C., Rábano, I. (eds). Instituto Tecnológico Geominero de España, Madrid, Temas Geológico-Mineros **23**, 231–235.
- Ortega, G., Kaufmann, C., Albanesi, G.L. 2009.** Faunas del Sandbiano tardío (Ordovícico Tardío) en la Formación Los Azules, cerro Viejo de Huaco, Precordillera de San Juan. *Reunión Anual de Comunicaciones de la Asociación Paleontológica Argentina*: Buenos Aires; Resúmenes, 1–59.
- Ottone, E.O., Holfeltz, G. 1992.** Hallazgo de escolecodontes en la Formación Gualcamayo, Llanvirimiano inferior, Argentina. *XI Simposio Argentino de Paleobotánica y Palinología, Asociación Paleontológica Argentina*, Publicación Especial N° 2, 85–88.
- Ottone, E.G., Albanesi, G.L., Ortega, G., Holfeltz, G.D. 1999.** Palynomorphs, conodonts and associated graptolites from the Ordovician Los Azules Formation, Central Precordillera, Argentina. *Micropaleontology* **45**, 225–250.
- Ottone, E.G., Holfeltz, G.D., Albanesi, G.L., Ortega, G. 2001.** Chitinozoans from the Ordovician Los Azules Formation, Central Precordillera, Argentina. *Micropaleontology* **47**, 97–110.

- Peralta, S.H. 1993.** Estratigrafía y consideraciones paleoambientales de los depósitos marino-clásticos eopaleozoicos de la Precordillera Oriental de San Juan. *12° Congreso Geológico Argentino y 2° Congreso de Exploración de Hidrocarburos* **1**, 128–137.
- Peralta, S.H. 1998.** Graptolites of the *Nemagraptus gracilis* Zone in the black shale sequences of the San Juan Precordillera, Argentina: its biostratigraphic and paleoenvironmental significance. In: *Proceedings of the Sixth International Graptolite Conference of the GWG (IPA) and the SW Iberia Field Meeting 1998 of the International Subcommission on Silurian Stratigraphy (ICS–IUGS)*, Gutiérrez-Marco, J.C., Rábano, I. (eds). Instituto Tecnológico Geominero de España, Madrid, *Temas Geológico-Mineros* **23**, 244–247.
- Peralta, S.H., Albanesi, G.L., Ortega, G. (eds.) 2003.** Ordovician and Silurian of the Precordillera, San Juan Province, Argentina. *Field Trip Guide, 9th ISOS, 7th & FMSSS*, Instituto Superior de Correlación Geológica (INSUGEO), Tucumán, *Miscelánea* **10**, 7–149.
- Schallreuter, R. 1985.** Mikrofossilien aus Geschieben IV. *Machaeridier. Der Geschiebesammler* **18**, 157–171.
- Stappenbeck, R. 1910.** La Precordillera de San Juan y Mendoza. *Anales del Ministerio de Agricultura, Sección Geología, Mineralogía y Minería* **4**, 1–187.
- Tortello, M.F., Peralta, S.H. 2004.** Trilobites del miembro inferior de la Formación Gualcamayo (Llanvirniano temprano) en el cerro La Chilca, Precordillera de San Juan, Argentina. *Boletín Geológico y Minero* **115**, 665–682.
- Vinther, J., Briggs, D.E.G. 2009.** Machaeridian locomotion. *Lethaia* **42**, 357–364.
- Vinther, J., Rudkin, D. 2010.** The first articulated specimen of *Plumulites canadensis* (Woodward, 1889) from the Upper Ordovician of Ontario, with a review of the anterior region of Plumulitidae (Annelida: Machaeridia). *Palaeontology* **53**, 327–334.
- Vinther, J., Van Roy, P., Briggs, D.E.G. 2008.** Machaeridians are Palaeozoic armoured annelids. *Nature* **451**, 185–188.
- Withers, T.H. 1926.** *Catalogue of the Machaeridia (Turrilepas and its Allies)* of the Department of Geology. *British Museum (Natural History), London* xv + 1–99.
- Woodward, H. 1865.** On the discovery of a new genus of Cirripedia in the Wenlock Limestone and Shale of Dudley. *Quarterly Journal of the Geological Society of London* **21**, 486–489.
- Woodward, H. 1889.** On the Discovery of *Turrilepas* in the Utica Formation (Ordovician) of Ottawa, Canada. *Geological Magazine* **6**, 271–275.