The first report of South American edrioasteroids and the paleoecology and ontogeny of rhenopyrgid echinoderms

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Sumrall, C.D., Heredia, S., Rodríguez, C.M., and Mestre, A.I. 2013. The first report of South American edrioasteroids and the paleoecology and ontogeny of rhenopyrgid echinoderms. *Acta Palaeontologica Polonica* 58 (4): 763–776.

A new species of rhenopyrgid edrioasteroid *Rhenopyrgus piojoensis* sp. nov. is described form the Silurian (Lower Ludlow) Los Espejos Formation in the Precordillera of Argentina. This species is the first reported edrioasteroid from South America. Rhenopyrgids are widely distributed in Ordovician through Devonian deposits of most continents. Numerous juvenile specimens show that the general bodyplan is organized early in ontogeny and that the pedenculate zone lengthens with age. Phylogenetic analysis shows that rhenopyrgids are more closely related to edrioasterid edrioasteroids such as edrioblastoids and cyathocystids than to pyrgocystid isorophids.

Key words: Echinodermata, Edrioasteroidea, Rhenopyrgidae, ontogeny, paleoecology, Silurian, South America.

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Received 20 July 2011, accepted 30 January 2012, available online 10 February 2012.

Introduction

Edrioasteroids are a clade of Paleozoic echinoderms that range from the Early Cambrian through Early Permian (Sumrall 2009). Although they are known from most continents, the vast majority of taxa have been reported from North America (e.g., Bell 1976; Guensburg and Sprinkle 1994; Sumrall 2001, 2010) and western Europe (e.g., Bather 1915; Smith 1983) with relatively few reports from Africa (Chauvel 1966, 1978; Klug et al. 2008; Sumrall and Zamora 2011, in press), and Australia (Holloway and Jell 1983; Smith and Jell 1990). Only two species are documented from Asia—the Lower Permian *Neoisorophusella maslennikovi* Sumrall, 2009 and *Kailidiscus chinensis* Zhao, Sumrall, Parsley, and Peng, 2010 from the Middle Cambrian Kaili Biota. Presently, no edrioasteroids have been described from either Antarctica or South America. Here we present a report on the first known South American edrioasteroid *Rhenopyrgus piojoensis* sp. nov. from the Los Espejos Formation (Silurian, lower Ludlow). This edrioasteroid belongs to an enigmatic group called rhenopyrgids that are uncommon, but widely distributed from the early Ordovician through the Middle Devonian (Holloway and Jell 1983).

Rhenopyrgids are unusual edrioasteroids bearing a small, highly domed oral surface, an extremely long and flexible pedunculate zone, and a small, multiplated sac-like holdfast termed a coriaceous sac. However, the morphology and evolutionary history of the group has been hampered by poor preservation, a lack of systematic treatment, and confusion between rhenopyrgids and pyrgocystids. This confusion results from several factors associated with their plating and taphonomy. The type species of *Pyrgocystis* Bather, 1915 as well as many other pyrgocystid species, bear spines over much of the oral surface (Fig. 1B) (Bather 1915; Bell 1982; Holloway and Jell 1983; Guensburg and Sprinkle 1994; Sumrall and Zamora in press). This precluded a thorough understanding of oral surface plating in pyrgocystids until the work of Guensburg and Sprinkle (1994). There it was shown that except for some unusual ambulacral features, the thecae of pyrgocystids were strikingly isorophid-like (Guensburg and Sprinkle 1994). This was later confirmed by Sumrall and Zamora (2011) from thecal interiors showing the oral frame plates and floor plate system. Because the oral surface is commonly obscured, the most strikingly obvious feature of pyrgocystids is the well-developed pedunculate zone formed from numerous irregular circlets of highly imbricate plates (Fig. 1B). Unfortunately, this feature is similar in gross morphology to the typically well-preserved pedunculate zone of rhenopyrgids (Fig. 1). Rhenopyrgids, however, are constructed very differently from isorophids. Integrated interradial plates that dominate the oral surface of rhenopyrgids, are demonstrably absent in iso-

http://dx.doi.org/10.4202/app.2011.0108

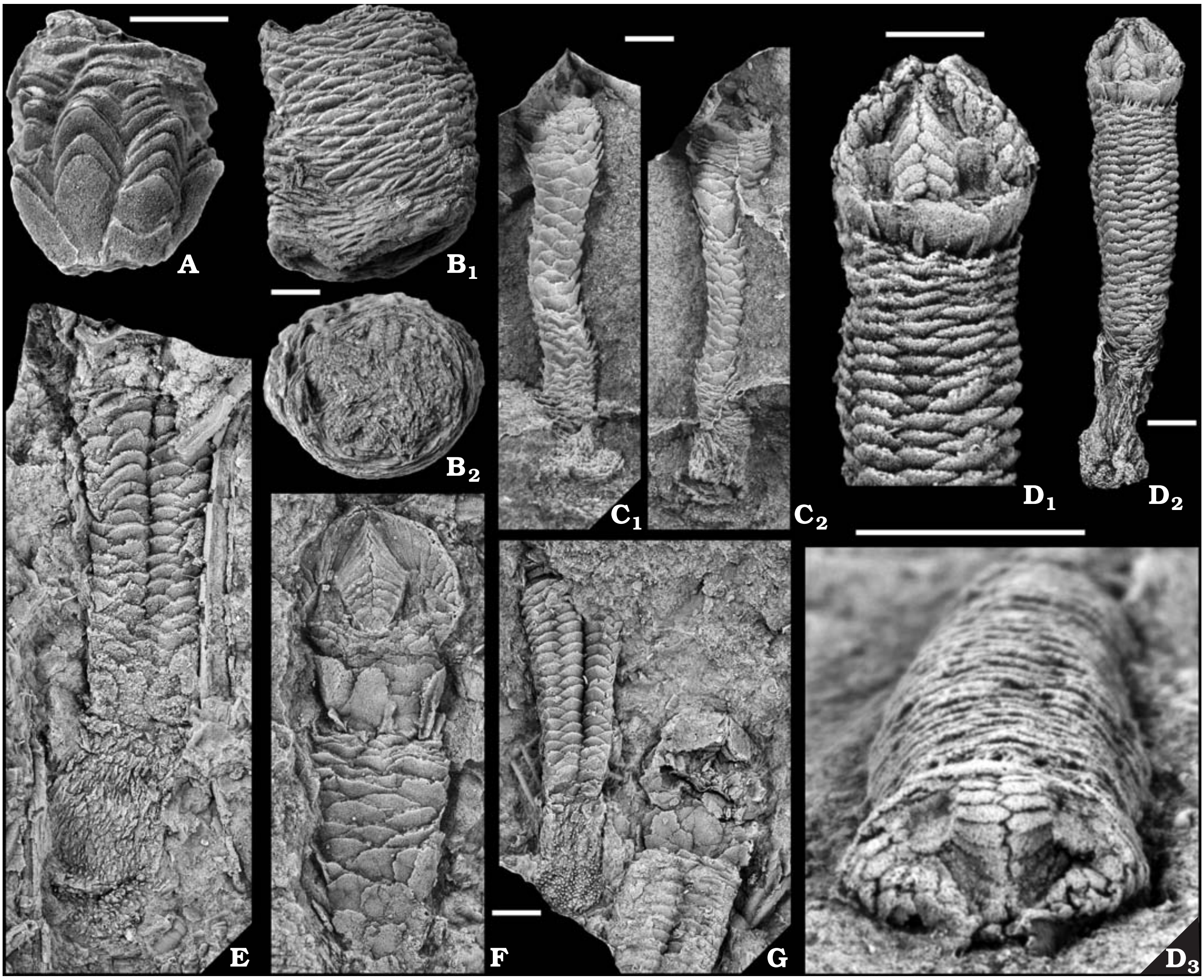

Fig. 1. Rhenopyrgids and *Pyrgocystis* showing the superficial similarity in the construction of the theca. **A**. Paratype NHM-E-16237 of *Rhenopyrgus*? *ansticei* (Bather, 1915) in lateral view; Wenlock Shale, Silurian, UK. **B**. Holotype NHM-E-16232 of *Pyrgocystis sardesoni* Bather, 1915; Decorah Shale (Ordovician) Minnesota, USA. Oral view showing the oral surface covered with small spines (B_1) and lateral view showing the extensive, disorganized pedunculate zone (B_2). **C**. NHM-E-62753 *Rhenopyrgus*? *procera* (Aurivillius, 1892); Silurian, UK. Part (C_1) and counterpart (C_2) showing the well-developed pedunculate of this complete specimen. Note that the oral surface is extremely poorly preserved. **D**. Holotype NHM-E-23470 of *Pyrgocystis grayae* (Bather, 1915); Drummuck Series, Ordovician, Scotland. Lateral summit detail (D_1), lateral A ambulacral (D_2) and summit (D_3) views. **E**, **F**, **G**. *Rhenopyrgus whitei* Holloway and Jell, 1983, Humevale Formation, Silurian, Australia. **E**. Lateral view of distal pedunculate zone of paratype NMV P-67681. **F**. Lateral summit view of holotype NMV P-67680a. **G**. Lateral view of paratype NMV P-67682 showing both proximal and distal portions of the theca. Scale bars 2.5 mm.

rophids. Rhenopyrgid floor plates are biserial, bear podial pores, and are exposed externally in the distal portions of the ambulacra, whereas they are uniserial, lack pores and are fully internal in isorophids. Lastly, the rhenopyrgid oral surface is bounded by a suboral collar, and the holdfast is in the form of a coriaceous sac both of which are unlike the isorophid condition (Fig. 1). These features served to unite rhenopyrgids with edrioasterid edrioasteroids (Smith and Jell 1990; Guensburg and Sprinkle 1994).

New rhenopyrgid material from the Silurian of Argentina adds significantly to our understanding of morphology and ontogeny of these unusual edrioasteroids. Although other concentrations of rhenopyrgids have been described (e.g., Klug et al. 2008) only a few specimens were articulated and those poorly preserved. Here we report on a mass occurrence of some 130 more or less completely articulated specimens. Preservation is in the form of natural molds in fine siltstone channel fill sediments, apparently at the base of a bed. Molds were cast with latex to make positive imprints of specimens. Specimens range in size from a thecal height of 6 to 32 mm showing, for the first time, many features of the ontogeny and growth of the pedunculate zone that were previously unknown.

Institutional abbreviations.—NHM-E, Natural History Museum collection, London, UK; NMV, Museum Victoria collection, Victoria, Australia; PIL, INSUGEO-Instituto Miguel Lillo Collection, Tucumán, Argentina.

Other abbreviations.—CI, consistency index; RC, rescaled retention index; RI, retention index.

Phylogenetic placement of rhynopyrgids

The phylogenetic placement of rhenopyrgids has been problematic. They were first described by Aurivillius (1892) as cirripeds. Bather (1915) redescribed the species of Aurivillius (1892) as edrioasteroids in the genus *Pyrgocystis* Bather, 1915. Bather (1915) detailed the morphology of the pyrgocystid *Pyrgocystis sardensoni* Bather, 1915 (Fig. 1B) and compared its morphology to that of fragmentary specimens of the Silurian rhenopyrgid *Pyrgocystis ansticei* Bather, 1915 (Fig. 1A) and the highly turreted, well-preserved rhenopyrgid *Pyrgocystis grayae* Bather, 1915 (Fig 1D) from the Upper Ordovician of Girvan, UK. *Pyrgocystis sardensoni* from the Late Ordovician Galena Group at St. Paul (MI, USA), was described as having a spine covered oral surface and a short pedunculate zone whereas *P. grayae* bore a more domed oral surface, a longer pedunculate zone, and lacked spines on the oral surface. The comparison was made difficult by strongly different taphonomy: typical polar thecal collapse is seen in *P. sardensoni* whereas *P. grayae* collapsed laterally, flattening the extended theca. However, because both had an extendable pedunculate zone they were thought to be congeneric (Bather 1915).

Recent work on pyrgocystids (Holloway and Jell 1983; Guensburg and Sprinkle 1994; Sumrall and Zamora 2011, in press) has forged a new understanding of pyrgocystids that confirms pyrgocystids and rhenopyrgids are only distantly related. Pyrgocystids have long been an enigmatic group of edrioasteroids known from Early Ordovician through Middle Devonian faunas worldwide. This clade includes a number of genera of mostly small, highly turreted edrioasteroids with a small oral surface and an exaggerated pedunculate zone. However the gross overall similarly of pyrgocystids to isorophids suggests that these groups are very closely related (Sumrall and Zamora 2011).

Previous reports suggested that pyrgocystid ambulacral systems lacked ambulacral floor plates, but bore a derived set of plates, termed hood plates, which articulate to the ambulacral cover plates (Guensburg and Sprinkle 1994). This condition would suggest that pyrgocystids are distantly related to other edrioasteroids. Recently described material from the Lower and Upper Ordovician of Morocco preserves several species of pyrgocystids as high quality natural molds with some specimens preserving both part and counterpart (Sumrall and Zamora 2011, in press). Latex casts of these specimens reveal several important anatomical features previously unknown in pyrgocystids. Unlike previous reports, ambulacral floor plates are present as a distally imbricating uniseries bearing the food groove to which hood plates articulate. Furthermore, pyrgocystids have a peripheral rim system that is identical in detail to isorophid edrioasteroids, the hydropore and gonopore are located in the proximal right CD interambulacrum, and the cover plates bear passageways, but lack intrathecal extensions. These features strongly suggest lebetodiscinid isorophid affinities supported by phylogenetic analysis (Sumrall and Zamora 2011).

Rhynopyrgids are only now becoming well understood. Papers by Ruedemann (1925), Gekker (1939) and Regnéll (1945) described several rhenopyrgids from the Upper Silurian of New York, USA (George C. McIntosh [personal comunication 2010] believes the specimens of Ruedemann [1925] were reported from the wrong unit and they are in fact Eifelian), the Middle Ordovician of the St. Petersburg district Russia, and Lower and Middle Silurian of Gotland, Sweden respectively. Although new taxa were described, little advancement was made in morphologic understanding because the oral surfaces were poorly preserved or remained unknown. Dehm (1961) recognized the distinctiveness of rhenopyrgids from pyrgocystids and erected the subgenus *Rhenopyrgus* Dehm, 1961 to accommodate *Pyrgocystis* (*Rhenopyrgus*) *coronaeformis* Rievers, 1961 from the Hunsrück Slate of Germany. Holloway and Jell (1983) detailed *Rhenopyrgus whitei* Holloway and Jell, 1983 from the Early Devonian of Victoria, Australia and further recognized the distinctiveness of rhenopyrgids by erecting a new family, Rhenopyrgidae, left unassigned to order. Smith and Jell (1990) allied rhenopyrgids with edrioblastoids whereas Guensburg and Sprinkle (1994) allied them to cyathocystids.

New material described here and a reinvestigation of *Pyrgocystis grayae* and *Rhenopyrgus whitei* allows for a new interpretation of morphologies that confirm the distant relation suggested by Holloway and Jell (1983), Smith (1990) and Guensburg and Sprinkle (1994). The presence of integrated interradial plates sensu Zhao et al. (2010) outer floor plates, and podial pores in the ambulacra suggest edrioasterid affinities. The large cover plates in a single biseries, well developed pedunculate zone, and collar of differentiated plates at its proximal extremity suggest similar structures now known in edrioasterids (Bell 1979; Guensburg and Sprinkle 1994; Sumrall and Deline 2009).

To better understand the placement of rhynopyrgids within Edrioasteroidea, a phylogenetic analysis was conducted including seven ingroup taxa that span edrioasteroid diversity. Within this group were included the cyathocystid *Cyathotheca* Jaekel, 1927 the pyrgocystid *Argodiscus* Prokop, 1965, and the edrioblastoid *Lampteroblastus* Guensburg and Sprinkle, 1994. These taxa have been interpreted in earlier papers as potential stem lineages from which rhenopyrgids arose (Dehm 1961; Smith and Jell 1990; Guensburg and Sprinkle 1994). For the analysis, 16 discrete characters were coded for the ingroup taxa and the Cambrian edrioasteroid *Kailidiscus*

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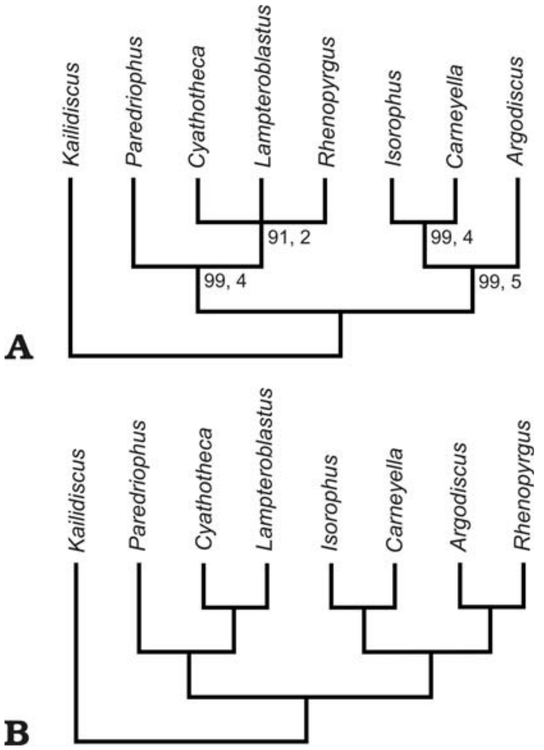

Fig. 2. Trees showing the phylogenetic position of rhenopyrgids with respect to other edrioasteroid clades. **A**. Strict consensus of the two, equally most parsimonious trees of 18 evolutionary steps. Numbers at nodes are the bootstrap and decay index for these nodes. **B**. Single most parsimonious tree of 26 steps recovered when the search was constrained to retain only those trees that placed *Rhenopyrgus* Dehm, 1961 as sister taxon to the pyrgocystid *Argodiscus* Prokop, 1965. Note that except for the placement of *Rhenopyrgus*, the trees are congruent.

Zhao, Sumrall, Parsley, and Peng, 2010 was used as outgroup to polarize the matrix (Appendix 1, Table 1). The matrix was analyzed using Paup* (Swoford 2002) using an exhaustive search algorithm. Tree support was determined using bootstrap analysis and decay index (Felsenstein 1985; Bremer 1988).

The analysis recovered two most parsimonious trees with length of 18 steps, CI = 0.94, RI = 0.96, RC = 0.91. Two main clades were recovered—an edrioasterid clade including cyathocystids, rhenopyrgids, and edrioblastoids, and an isorophid clade including pyrgocystids. Bootstrap and decay index support for these clades are high, having bootstrap support of 98–99% and decay indices support of 4–5 steps (Fig. 2A). Lower, but still high support was found for the clade including rhenopyrgids, cyathocystids, and edrioblastoids with bootstrap support of 91% and a decay index of 2 steps (Fig. 2A).

Table 1. Character matrix for the phylogenetic analysis. Character states are listed in Appendix 1.

Kailidiscus	0	0	0	?	0	0	0	1	0	0	1	0	0	0	0	0
Paredriophus	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0
Cyathotheca	0	1	1	?	?	?	?	0	0	?	0	?	?	2	1	1
Isorophus	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0	0
Carneyella	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0	0
Rhenopyrgus	0	0	1	0	?	?	1	0	0	?	0	0	?	2	1	1
Argodiscus	1	0	0	0	1	1	0	1	0	1	1	0	1	0	0	0
Lampteroblastus	0	?	1	?	?	?	?	0	0	0	?	?	?	2	1	1

To test whether rhynopyrgids are closely related to pyrgocystids, a second analysis was conducted that constrained topologies to those that retain rhynopyrgid *Rhenopyrgus* as sister taxon to the pyrgocystid *Argodiscus*. This analysis recovered one most parsimonious tree of length 26, CI = 0.65, RI = 0.67, RC = 0.44 (Fig. 2B). This tree is 41% longer than the most parsimonious arrangement of the taxa in the unconstrained analysis. Except for the placement of *Rhenopyrgus*, the trees are congruent.

Although the exact ordering of taxa within Edrioasterida cannot be determined from this analysis, likely because of large amounts of missing data in cyathocystids and edrioblastoids, these taxa are here concluded to form a clade. Guensburg and Sprinkle (1994) suggested that rhynopyrgids were closer to cyathocystids than to edrioblastoids, however, their matrix included no character support for this conclusion. Edrioasterida is diagnosed by the loss of inner floor plates, the nature of the holdfast structure, the aboral collar, and pedunculate zone. Rhenopyrgids, cyathocystids, and edrioblastoids are united by the lack of interambulacral plates, the pseudo five fold symmetry of the ambulacral system sensu Sumrall and Wray (2007) and the turreted thecal shape. These groups differ from one another primarily in the form of the pedunculate zone—organized flexible stalk in rhenopyrgids, fused cup in cyathocystids, and an elongate stem in edrioblastoids.

Geological setting

The Precordillera of Western Argentina is an important region for studying South American Silurian rocks sharing faunal affinities within the Malvinokaffric Realm (Sánchez et al. 1991). Silurian deposits in the Central Precordillera, are included in the Tucunuco Group (Cuerda 1969), which is divided into two units: the lower La Chilca Formation, and the upper Los Espejos Formation, both defined by Cuerda (1969). The Los Espejos Formation (Fig. 3) is composed of marine siliciclastic strata, primarily green sandstones and green siltstones, and varies in thickness from 25 m to 510 m (Cuerda 1969; Benedetto et al. 1992; Astini and Piovano 1992). These strata were deposited on a middle-distal but shallow platform and include intercalated storm deposits. Syn-sedimentary deformation structures are frequent, mainly in the middle and upper part of the formation (Astini and Maretto 1996; Peralta 1990). Brachiopods, trilobites, grapto-

Fig. 3. Stratigraphic column (**A**) for the Loma de los Piojos locality (**B**) of the Los Espejos Formation (modified from Rodríguez et al. 2010). Specimens of *Rhenopyrgus piojoensis* sp. nov. were collected near the top of the succession.

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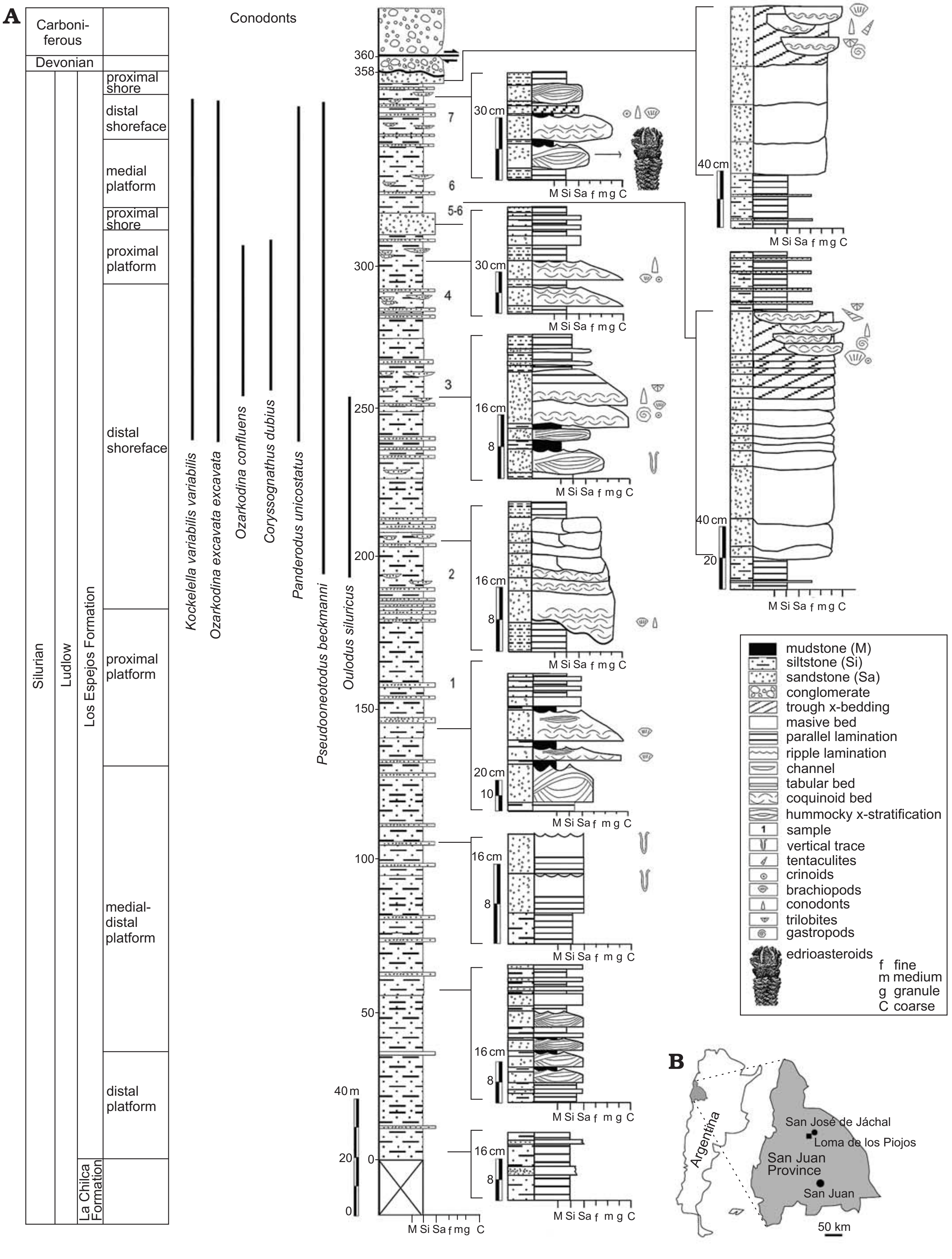
A
Carboniferous
Devonian
Silurian
Ludlow
Los Espejos Formation
La Chilca Formation
proximal shore
distal shoreface
medial platform
proximal shore
proximal platform
distal shoreface
proximal platform
medial-distal platform
distal platform
Conodonts
Kockelella variabilis variabilis
Ozarkodina excavata excavata
Ozarkodina confluens
Coryssognathus dubius
Panderodus unicostatus
Pseudooneotodus beckmanni
Oulodus siluricus
360
358
300
250
200
150
100
50
0
40 m
20
0
7
6
5-6
4
3
2
1
30 cm
30 cm
16 cm
8
16 cm
8
20 cm
10
16 cm
8
16 cm
8
16 cm
8
40 cm
40 cm
20
M Si Sa f m g C
mudstone (M)
siltstone (Si)
sandstone (Sa)
conglomerate
trough x-bedding
masive bed
parallel lamination
ripple lamination
channel
tabular bed
coquinoid bed
hummocky x-stratification
1 sample
vertical trace
tentaculites
crinoids
brachiopods
conodonts
trilobites
gastropods
edrioasteroids
f fine
m medium
g granule
C coarse
B
Argentina
San José de Jáchal
Loma de los Piojos
San Juan Province
San Juan
50 km

lites, tentaculites, crinoids, corals, eurypterids, nautiloids, gastropods, achritarchs, conodonts, and trace fossils are common (Cuerda 1969; Baldis and Aceñolaza 1978; Baldis et al. 1984; Aceñolaza and Peralta 1985; Brussa and Toro 1989; Ciguel and Peralta 1990; Sánchez et al. 1991; Sumrall et al. 2008). The Los Espejos Formation appears to paraconformably overlie the La Chilca Formation, whose upper sandstone beds yielded Llandoverian brachiopods and conodonts (Lehnert et al. 1999). It is overlain in apparent paraconformity by the Lower Devonian shale beds of the Talacasto Formation.

Albanesi et al. (2006) recorded the *Kockelella v. variabilis* Conodont Zone from the Los Espejos Formation at the Sierra de Talacasto section suggesting an early Ludlow age for these deposits. Heredia et al. (2007) suggested the same biozone for the Los Espejos Formation at the Cerro del Fuerte locality. Comparison of conodont populations recorded at different sections of the Los Espejos Formation showed differences in the conodont species distribution. This distribution, with concomitant differences in lithofacies, were used to define conodont biofacies characterizing different environments in the shallow, clastic platform of the Precordilleran during the early Ludlow (Rodríguez et al. 2010).

Silurian stratigraphy at Loma de los Piojos section

The Loma de Los Piojos locality (LPJ) is a classic Silurian section in the Precordillera. This section is located near the town of San José de Jáchal (Fig. 3) at 30°17'56.72"S, 68°45' 42.01"W. At this section, several units are exposed including the La Silla, San Juan, La Chilca, Los Espejos and Talacasto formations ranging from Upper Cambrian through Lower Devonian.

The clastic lithostratigraphy of the Los Espejos Formation shows a regressive–transgressive cycle (Fig. 3) with no evidence of significant breaks in sedimentation. The lower portion of the section represents a coarsening upward package, from the base of a transgressional sequence through the development of typical distal platform facies. The upper portion of the section is interpretable as middle platform deposits that are much shallower, with development of shoaling facies. The uppermost part of the section suggests medial-distal platform facies with several storm events and is shallowest at the very top (samples LPJ 6 to 9).

The Loma de Los Piojos succession includes beds interpretable as shoaling bar and bioclastic channels (Fig. 3). These bioclastic beds are composed of brachiopods, trilobites, graptolites, corals, and tentaculites, with the faunal content varying throughout the section. Channels lower in the section are filled with brachiopods, crinoids, graptolites, trilobites, and conodonts (sample LPJ 2 to 4; Fig. 3), with the highest faunal diversity in bioclastic bed LPJ 3. Fauna in the thick channel sandstones of the channel-bar facies are rich in brachiopod shells and conodonts (sample LPJ 5 to 6; Fig. 3). These channels are thinner towards the top of the section and have a fauna limited to brachiopods and conodonts (sample 7; Fig. 3). Several ophiuroids and many specimens of edrioasteroids were recovered from the thick channel fill sandstone bed at the upper part of the measured section but this unit lacked other taxa (Fig. 3).

Conodonts

In the section, carbonate coquinas yield conodonts especially in the middle through upper portion of the section. The conodont fauna (Fig. 4) consists of *Kockelella variabilis variabilis* Walliser, 1957, *Ozarkodina excavata excavata* Branson and Mehl, 1933, *Ozarkodina confluens* (Branson and Mehl, 1933), *Ozarkodina* sp., *Panderodus unicostatus* (Branson and Mehl, 1933), *Corysognathus dubius* (Rhodes, 1953), *Oulodus siluricus* (Branson and Mehl, 1933), and *Pseudooneotodus beckmanni* (Bischoff and Sannemann, 1958) (Rodríguez 2008). The preservation of conodonts is good and the surface of the elements is limpid (Fig. 4). Conodont elements show Color Alteration Index CAI 3 at the Loma de Los Piojos section.

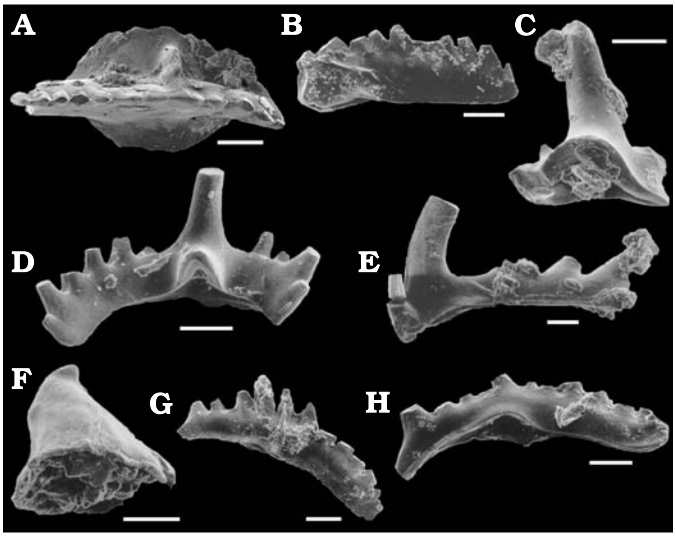

Fig. 4. Scanning electron micrographs of conodont elements documenting the Silurian (lower Ludlow) age of the Los Espejos Formation. All figured elements were collected from the Los Espejos Formation of the Precordillera. **A**, **D**. *Kockelella variabilis variabilis* Walliser, 1957. **A**. P element, upper view, sample 7, CML-C 3067 (1). **D**. S element, posterior view, sample 3, CML-C 3058 (2). **B**, **H**. *Ozarkodina excavata excavata* (Branson and Mehl, 1933). **B**. Pb element, lateral view, sample 3, CML-C 3057 (6). **H**. S element, lateral view, sample3, CML-C 3057 (7). **C**. *Corysognathus dubius* (Rhodes, 1953); Pb element, posterior lateral view, sample 3, CML-C 3055 (4). **E**. *Oulodus siluricus* (Branson and Mehl, 1933); Pb element, lateral view, sample 3, CML-C 3052 (4). **F**. *Pseudooneotodus beckmanni* (Bischoff and Sannemann, 1958); lateral view, samples 3, CML-C 3054 (5). **G**. *Ozarkodina confluens* (Branson and Mehl, 1933); Pb element, lateral view, sample 3, CML-C 3071 (1). Scale bars 0.1 mm.

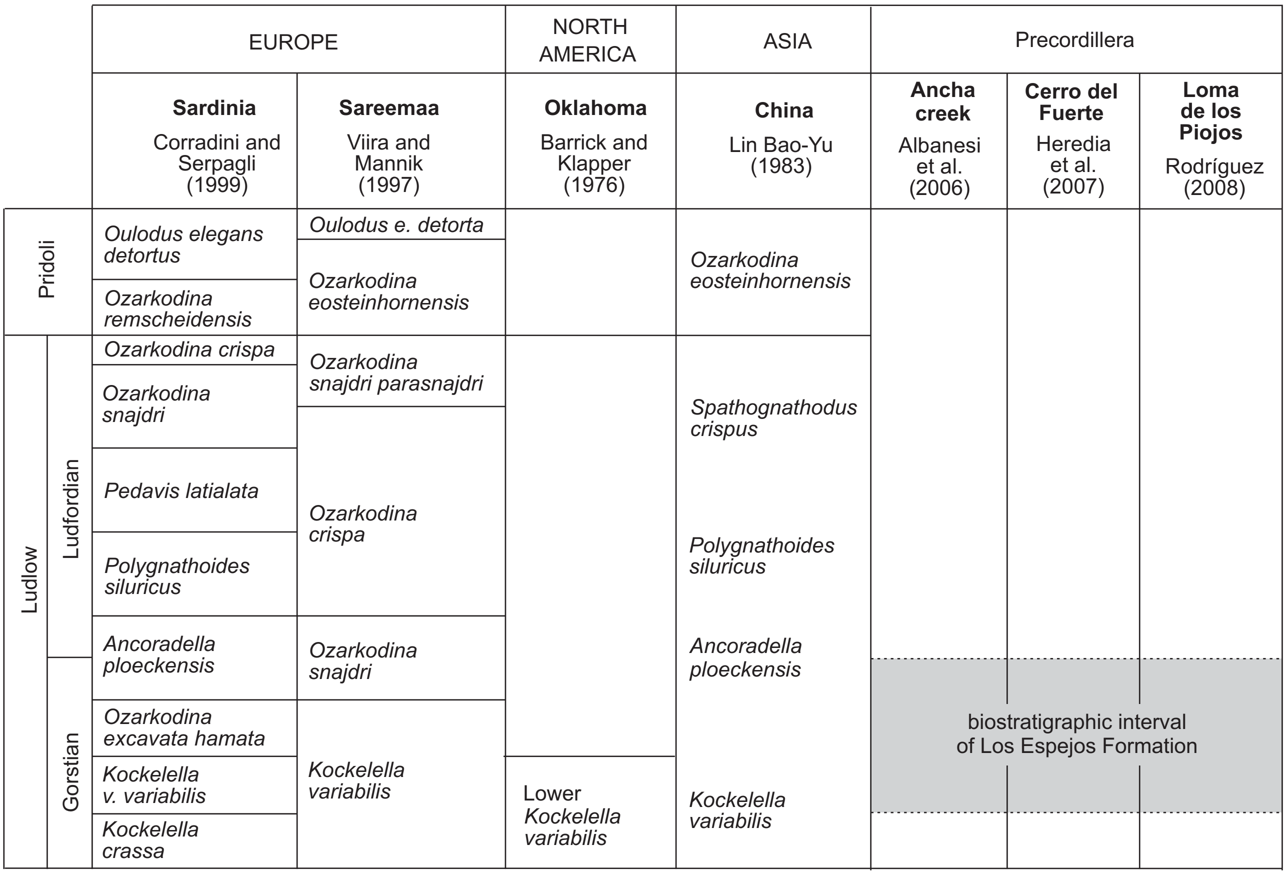

Fig. 5. Comparison of Ludlow conodont zones between Europe, North America, Asia, and the Precordillera.

Conodont biostratigraphy

The *Kockelella v. variabilis* Biozone was reintroduced by Corradini and Serpagli (1999) as an interval zone, whose lower limit is represented by the last occurrence of *Kockelella crassa* Walliser, 1964 and the upper limit by the first occurrence of *Ozarkodina excavata hamata* Branson and Mehl, 1933. *Kockelella variabilis variabilis* Walliser, 1957 is a guide fossil for the lower Ludlow in Europe, North America, and China (Fig. 5). *Kockelella v. variabilis* appears from the upper part of *Kockelella crassa* Biozone to top of the *Ancoradella ploeckensis* Biozone, with a few records from Gotland (Jeppsson et al. 2006) reaching the *Polygnathoides siluricus* Biozone. However, the occurrence of *Coryssognathus dubius* (Rhodes, 1953) in several samples from the Loma de Los Piojos section suggests a younger age for this unit (Lennart Jeppsson, personal communication 2010). Thus, the top of the *K. v. variabilis* Biozone/base of the *Ancoradella ploeckensis* Biozone is considered as the most probable age for these deposits (Fig. 5).

Conodont biostratigraphy suggests the presence of a significant unconformity between the uppermost Los Espejos Formation, which correlates with the lower Ludlow Series, and the overlying lower Talacasto Formation, which correlates with the lower Devonian Lochkovian Stage. New data document this hiatus in the Precordillera, correlative with the upper Ludlow and Pridoli Series, in contrast to the conclusions of Benedetto et al. (1992), Rubinstein (1995), Peralta et al. (2003), and Albanesi et al. (2006) who considered the Talacasto Formation to be stratigraphically continuous with the underlying Los Espejos Formation. As proposed by Rodríguez et al. (2010), the presence and numerical relations of certain guide conodonts and conodont populations seem to reflect ecological conditions that would have affected conodont species distribution.

Edrioasteroids

Taphonomy.—Eighty-six specimens of the rhenopyrgid edrioasteroid *Rhenopyrgus piojoensis* sp. nov. were found on a single slab. Twenty-nine other specimens were associated with this slab but could not be reattached. A single small specimen was found at approximately the same level about 25 m away. All specimens appear to be preserved at the base of a small channel fill similar to many of the sand units in this section, but the rock was out of place and this cannot be directly confirmed.

All specimens described here are preserved as natural molds on bedding planes of fine sandstone. Moldic preservation of rhenopyrgids is fairly common, i.e., Bather (1915), and Holloway and Jell (1983), as well as new undescribed material from the Early Ordovician of Morocco (Colin D. Sumrall and Joseph Botting unpublished data). To study and describe the specimens, latex casts of the molds were prepared so that specimens could be examined in positive relief. No internal anatomy except for the ambulacral tunnels was preserved. External details were fairly well preserved, but limited by the fine-grained sandstone in which the specimens were entombed.

Specimens are invariably preserved as external molds of only half of each specimen entombed in the fine sandstone slab. The other half presumably was preserved in the adjacent shale bed that weathered away revealing the specimens. All of the specimens are fully articulated, but missing portions of theca are common because of weathering, or slight obliquity of specimens relative to the slab surface (Fig. 6). A few of the smallest specimens are preserved fully inflated (Fig. 6D, G), whereas most of the larger specimens are laterally compressed perpendicular to the slab surface reflecting sediment compaction (Fig. 6F, S, U, W). The holotype (PIL 14656-H) is exceptional with the oral surface fully positioned into the slab and the pedunculate zone nearly fully inflated (Fig. 6O_1, O_2).

Taphonomically, rhenopyrgids have a poorly articulated oral surface that readily disassociated upon death as compared to the pedunculate zone, which is generally well preserved. In specimens of *Rhenopyrgus piojoensis* sp. nov., all specimens were fully articulated including the oral surface. Unfortunately, the somewhat coarse nature of the preservation precludes many of the details of the cover plate system and thecal openings from view, but most of the gross morphological features are clear. In all cases the oral surface is domed and somewhat conical, with high ambulacral cover plates and somewhat depressed integrated interradial plates.

Below the oral surface, the sub oral construction is plated with several series of highly imbricate plates that increase in size distally to form a differentiated suboral collar. Nearly all specimens show the plates of the suboral constriction expanded, but some specimens are slightly more extended than others. A few specimens show a gap in the plating of the suboral construction and suboral collar suggesting the placement of the periproctal opening (Fig. 6R, O_2, Z). In the holotype this gap is identified as the CD interambulacrum based on the 2-1-2 ambulacral symmetry (Fig. 5O_1, O_2), although coarse preservation precluded a detailed understanding of this structure. This might be the same structure referred to questionably as the anal structure by Holloway and Jell (1983).

The durable rhenopyrgid pedunculate zone, well known from other species (Fig. 1), has been described by several authors in isolation from the oral surface and holdfast structure (Bather 1915; Ruedmann 1925; Gekker 1939; Regnéll 1945). In gross morphology, these isolated pedunculate zones can easily be confused with pyrgocystids (Bather 1915; Klug et al. 2008 in part) or as parts of other echinoderms (Prokop and Petr 2003; Lefebvre et al. 2012). Except for a few early forms including an undescribed Ordovician taxon from Prague (Lefebvre et al. 2012) and Morocco Colin D. Sumrall and Joseph Botting unpublished data) rhynopyrgid pedunculate zones are highly organized. Such pedunculate zones are proportionately very long and plated with alternating circlets of four plates resulting in eight plate columns running the length of the theca. In specimens of *Rhenopyrgus piojoensis* there is little variation in degree of extension of pedunculate zones, but many preserved specimens are slightly to very curved suggesting at least some degree of flexibility (Fig. 6U, V).

The holdfast structure, typically called a coriaceous sac, is well preserved on a number of specimens of *Rhenopyrgus piojoensis* although generally not at the resolution of individual plates (Fig. 3G, P, Q, X). It appears as a slight constriction beneath the organized pedunculate zone where plate size sharply decreases and plates become disorganized. Several specimens show a star shaped pattern in cross section with apparently eight lobes (Fig. 3G, Q, X) but it is unclear if these lobes are in line or offset from the columns of peduncular plates. In most cases, the coriaceous sac is well preserved and inflated suggesting it is a fairly robust feature of the theca.

Because numerous specimens were preserved on a single bed it is possible to determine if the edrioasteroid specimens exhibit current alignment. An arbitrary north arrow was as-

Fig. 6. Images of specimens of *Rhenopyrgus piojoensis* sp. nov., Silurian (lower Ludlow) Los Espejos Formation, Argentina. All specimens are whitened latex casts of moldic specimens in lateral view. **A**. Smallest complete paratype PIL-14649-J showing relatively short pedunculate zone. **B**. Paratype PIL-14644-F. **C**. Paratype PIL-14649-G. **D**. Paratypes PIL-14177-D, left and PIL-14177-C right. **E**. Incomplete theca of paratype PIL-14645-G. **F**. Proximal half of paratype PIL-14656-A. **G**. Paratype PIL-14653-A showing somewhat retracted suboral constriction and octolobate coriaceous sac. **H**. Small paratype PIL-14177-G and oral surface of large paratype PIL-14177-J. **I**. Proximal half of paratype PIL-14649-T. **J**. Proximal half of paratype PIL-14655-I showing the oral plates and cover plates. **K**. Paratype PIL-14655-G. **L**. Paratype PIL-14649-S showing flattened coriaceous sac. **M**. Paratype PIL-14645-E showing oral plates and cover plates. **N**. Paratypes PIL-14872-A, left and PIL-14872-B right. Note the plating of the suboral constriction in these specimens. **O**. Holotype PIL-14656-H. Summit view showing five ambulacra and poorly preserved anal area (O_1). Nearly complete and very well preserved theca in lateral view (O_2); compare to Fig. 8. **P**. Incomplete theca of paratype PIL-14872-G showing the small plates of the coriaceous sac. **Q**. Incomplete theca of paratype PIL 14644-I showing the octalobate coriaceous sac. **R**. Paratype PIL-14656-B showing the notch in the suboral collar where the anus is positioned. **S**. Very large and incomplete paratype PIL-14655-F. **T**. Paratype PIL-14649-R showing the cover plates. **U**. Paratypes PIL-14174-G, left and PIL-14174-F right. **V**. Complete theca of paratype PIL-14652-A. **W**. Paratype PIL-14655-B. **X**. Paratype PIL-14648-A showing expanded suboral constriction, long pedunclate zone, and octolobate coriaceous sac. **Y**. Paratype PIL-14656-F. **Z**. Paratype PIL-14872-H showing notch in the suboral collar marking the position of the anus. **AA**. Paratype PIL-14656-J. **BB**. Paratype PIL-14656-I.

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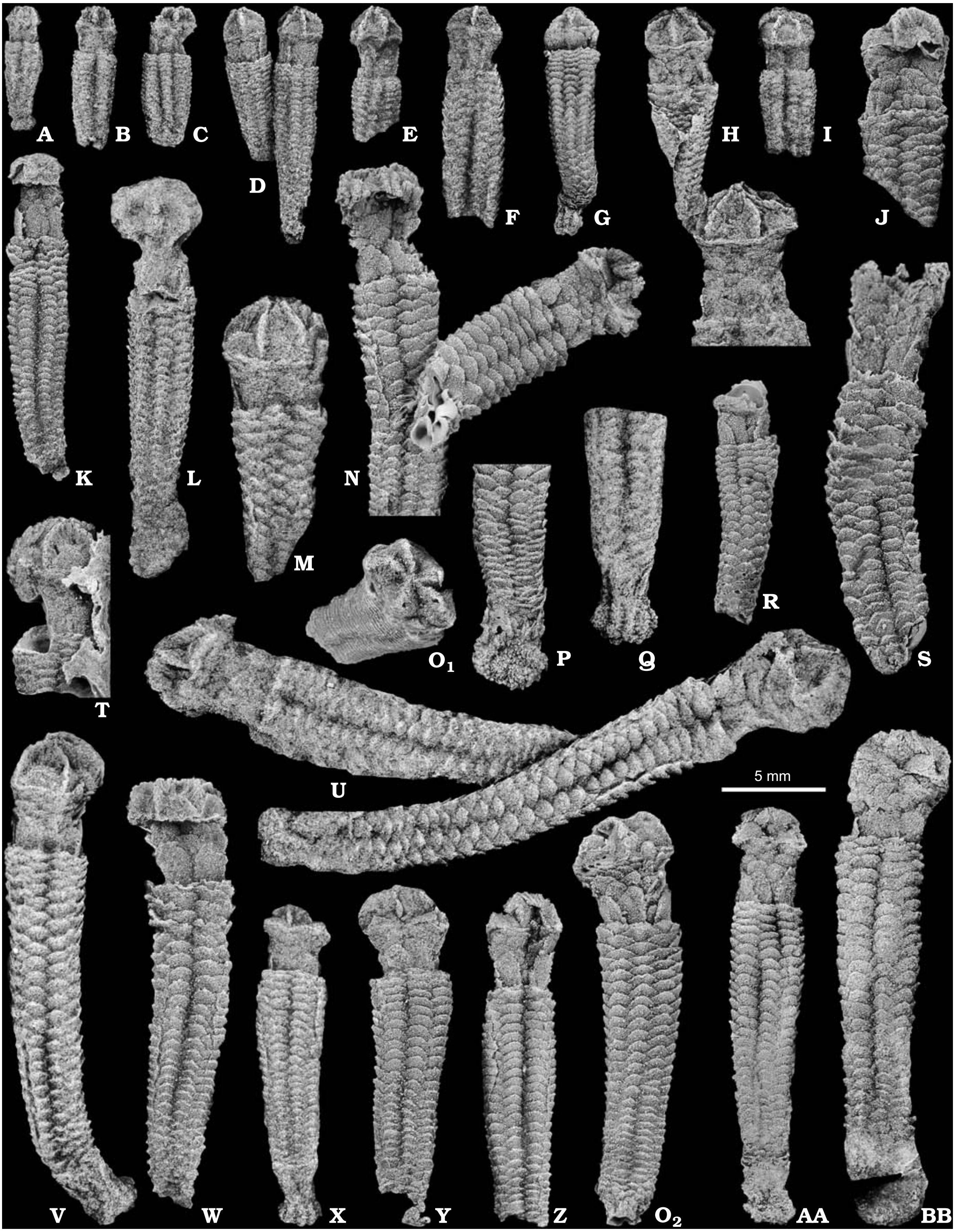
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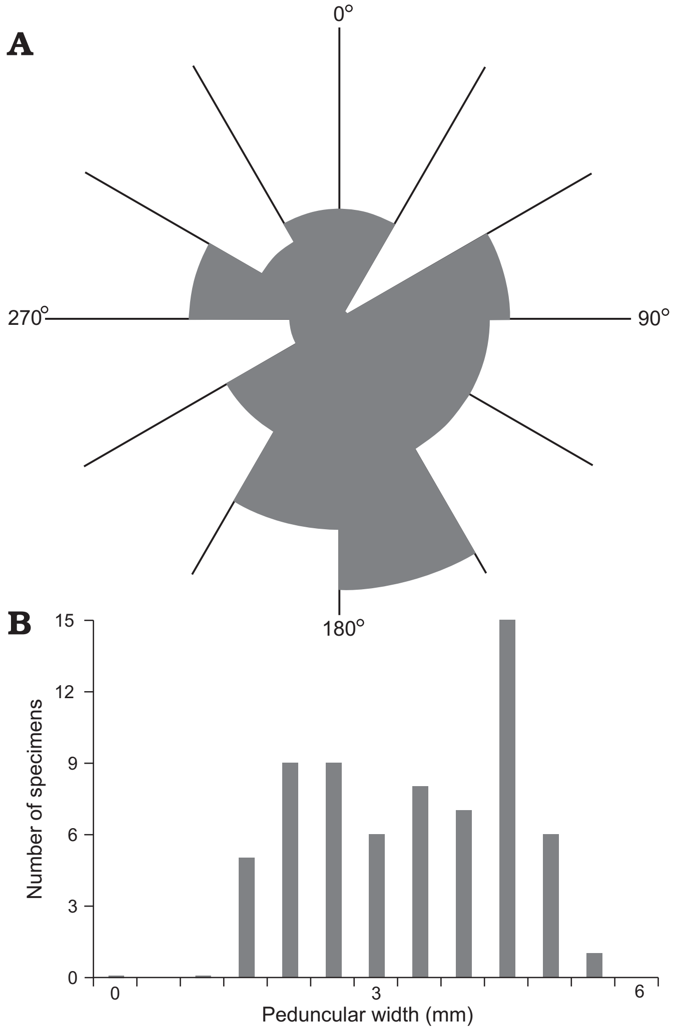

Fig. 7. Size and orientation of rhenopyrgids. **A**. Rose diagram showing the orientation of theca on slab surface. Vector is measured as the angle between a randomly assigned "north" arrow and the projection of the oral surface of the extended theca. **B**. Width of the proximal portion of the pedunculate zone. Note the normal distribution of thecal size.

signed to the surface, and an azimuth relative to this arbitrary north arrow was measured for 86 specimens recovered from the single contiguous surface. The data show an average direction of 160.5° compared to this arbitrary north (Fig. 7A). Data were analyzed using a Rayleigh test with the null hypothesis being that the distribution is not unidirectional. The data show an $r = 0.223$, $s = 1.247$ rejecting the null hypothesis $p = 0.013$ indicating that the orientations are significantly unidirectional. This result is consistent with the interpretation that specimens experienced transport and were current aligned during deposition in the supposed channel.

The highly elongate thecae are not as strongly aligned as one might expect given their shape. Furthermore, there is little difference in shape on the proximal and distal ends of the theca that might suggest unidirectional as opposed to bidirectional thecal orientations on the surface. A better explanation than shape of the theca may be differences in the orientations of plates of the pedunculate zone. The highly imbricate nature of these plates suggest that fluid flow from distal to proximal might have been less turbulent than from proximal to distal and consequently resulted in a preferred alignment of theca with the oral surface pointing downstream. This could be tested with flume experiments, but such research is beyond the scope of this project.

Ontogeny.—The population contains specimens that range in height from 6 mm to 32 mm but most specimens cannot be measured for complete height because of incomplete preservation. Measurements of the diameter of the proximal pedunculate zone show that the population is normally distributed for size (Fig. 7B). This distribution should be viewed with caution as larger specimens are more likely to be compacted perhaps exaggerating the width of the theca.

The ontogeny of rhenopyrgids remains poorly constrained. New specimens of *Rhenopyrgus piojoensis* sp. nov. show some details previously unknown in the clade. The smallest specimen with a thecal height of 6 mm shows that at this size the pedunculate is already well formed, bearing apparently eight columns of peduncular plates (Fig. 6A). The pedunculate zone, however, is proportionally shorter for theca height than that seen on more mature specimens. Preservation is poor on the smallest specimens so the exact number of peduncular plates cannot be counted, but it appears that fewer circlets of plates are present. Even at this small size the suboral constriction and coriaceous sac are well developed.

With increasing size the theca elongates with the pedunculate zone showing positive allometry (Fig. 5G, U). There is some variation in the tightness of the plating of the pedunculate zone likely because of differences in expansion and contraction exhibited by the various specimens (Fig. 5U, AA). Even more pronounced is the variation in the expression of the suboral constriction that may be retracted (Fig. 5G) or greatly extended, Fig. 5S). In general, with maturity the oral surface becomes proportionately larger and more rounded (Fig. 5D, G, U, AA).

Paleobiogeography.—Rhenopyrgids are a geographically widespread and temporally long-lived group of edrioasteroids. The oldest reports of rhenopyrgids include an undescribed species from the Early Ordovician (Arenig) Fezouata Formation from Morocco, and Middle and Upper Ordovician occurrences in Russia and Great Britain (Bather 1915; Gekker 1939). By the Silurian rhenopyrgids were widely distributed including the Middle Silurian of USA, the lower and Middle Silurian of Sweden, and *Rhenopyrgus piojoensis* sp. nov. from Argentina (Regnéll 1945; George A. McIntosh, personal communication 2008). This pattern continues into the Devonian where occurrences are documented in the Lower and Middle Devonian of Germany, and Australia (Rievers 1961; Holloway and Jell 1983; Grigo 2000), and the Middle Devonian of Morocco (Klug et al. 2008), and USA (George A. McIntosh, personal communication 2008). This long history makes rhenopyrgids the longest lived and most widely geographically distributed of the four main clades of edrioasterid edrioasteroids.

Systematic paleontology

Phyllum Echinodermata De Brugière, 1791 (ex Klein, 1734)

Class Edrioasteroidea Billings, 1858

Order Edrioasterida Bell, 1976

Discussion.—Edrioasterida sensu Guensburg and Sprinkle (1994) is greatly expanded compared to the original meaning found in Bell (1976). Based on a new phylogenetic analysis we follow Guensburg and Sprinkle (1994) by including Rhenopyrgidae Holloway and Jell, 1983 in Edrioasterida Bell, 1976 along with Cyathocystidae Bather, 1899 and Astrocystitidae Bassler, 1935 (edrioblastoids).

Suborder Edrioblastoidina Fay, 1962

Family Rhenopyrgidae Holloway and Jell, 1983

Diagnosis (emended).—Pyrgate edrioasteroids with relatively small oral surface bearing five, short, straight ambulacra; interambulacra plated with single integrated interradial plate bearing podial pores; outer floor plates present along edge of ambulacra distally, cover plates tall and biserial; aboral collar present proximal to pedunculate zone; very long pedunculate zone composed of numerous highly imbricate plates; holdfast in form of coriaceous sac of small unorganized platelets.

Discussion.—The phylogenetic analysis presented here, as well as that presented by Guensburg and Sprinkle (1994), did not uniquely recover rhenopyrgids and cyathocystids as sister taxa. For this reason, we do not include them within Cyathocystidae Bather, 1899, but leave them assigned at family level within Edrioblastoidina Fay, 1962. Rhenopyrgids are a very well defined clade of edrioasterids that have a very wide geographic and stratigraphic range. Their fragile oral surface is rarely preserved which has precluded a thorough systematic treatment. Because of their fragile nature, many poorly documented rhenopyrgids were originally described as cirripeds, phylum Arthropoda (Aurivillius 1892).

Genus *Rhenopyrgus* Dehm, 1961

Type species: *Pyrgocystis* (*Rhenopyrgus*) *coronaeformis* Rievers, 1961; Hunsrück Slate, Lower Devonian (Emsian) of Germany.

Species included.—*Rhenopyrgus* includes *R. coronaeformis* Rievers, 1961, *R. piojoensis* sp. nov., *R. whitei* Holloway and Jell, 1983, and *Rhenopyrgus flos* Klug, Krüger, Korn, Rücklin, Schemm-Gregory, DeBaets, and Mapes, 2008.

Diagnosis (emended).—Rhynopyrgid with elongate zone of highly imbricate plates between oral surface and collar; suboral constriction of imbricate plates formed between oral surface and suboral collar; pedunculate zone organized into alternate circlets of 4 plates aligned into 8 columns.

Discussion.—*Rhenopyrgus grayae* (Bather, 1915) is very similar to species assigned to *Rhenopyrgus* Dehm, 1961 but differs in a distal breakdown of the highly organized nature of the plates of the peduncular columns, and a lack of a suboral constriction. This species likely warrants a new generic assignment. Several other species of rhenopyrgids have been named that might belong to *Rhenopyrgus*, but incomplete preservation precludes generic assignment. These include *Pyrgocystis gracilis* Gekker, 1939, *P. pulkovi* Gekker, 1939, *P. sulcata* (Aurivillius, 1892), *P. procera* (Aurivillius, 1892), *P. varia* (Aurivillius, 1892), *P. cylindrica* (Aurivillius, 1892), and *P. ansticei* Bather, 1915; see Bather (1915), Gekker (1939), and Regnéll (1945) for review of these taxa.

Geographic and stratigraphic range.—Middle Silurian (Wenlockian) to Lower Devonian (Emsian) of Germany, Argentina, Australia, Morocco, and USA.

Rhenopyrgus piojoensis sp. nov.

Figs. 6, 8.

Etymology: Named for the Loma de los Piojos locality of the Los Espejos Formation, Argentina.

Type material: Holotype: PIL 14656 H. Paratypes: PIL 14174 A–K, 14175 A–G, 14176 A, 14177 A–J, 14643 A–B, 14644 A–I, 14645 A–H, 14647 A–E, 14648 A–B, 14649 A–Y, 14650 A–G, 14652 A, 14653 A, 14654 A, 14655 A–H, 14656 A–K, and 14872 A–H; reposited at the INSUGEO Instituto Miguel Lillo Collection.

Type locality: The Loma de Los Piojos locality located near the town of San José de Jáchal, Argentina; 68°45’42.01”W, 30°17’56.72”S.

Type horizon: The Los Espejos Formation, Silurian (lower Ludlow)

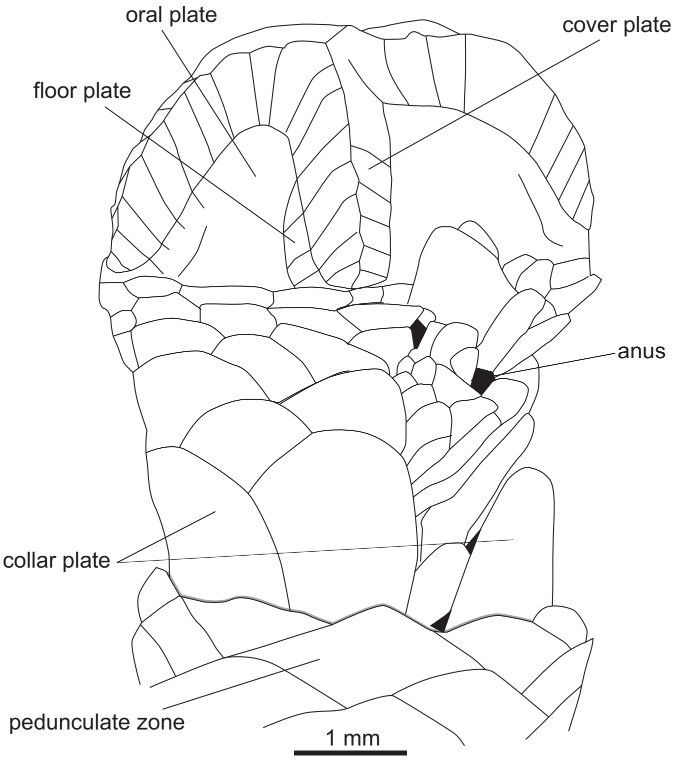

Fig. 8. Lateral CD ambulacral view of holotype PIL 14656-H of *Rhenopyrgus piojoensis* sp. nov., Silurian (lower Ludlow), Los Espejos Formation, Argentina, showing the notch in the collar plates and the small irregular plates leading to the perirpoctal area. Note that floor plates are exposed in the distal ambulacra and the anal pyramid lies along the edge of the integrated interradial plate at the top of the periproctal notch.

http://dx.doi.org/10.4202/app.2011.0108

interpreted as the threshold of the *Kockelella variabilis variabilis*/*Ancoradella ploeckensis* conodont biozones.

Material.—Only type material was examined.

Diagnosis.—A *Rhenopyrgus* with a highly arched, conical oral surface; well-developed suboral constriction, and well-rounded squamose peduncular plates; coriaceous sac octolobate.

Description.—Theca small to medium size, with strongly turreted shape, divided proximally to distally into oral surface, suboral constriction zone, suboral collar, pedunculate zone, and coriaceous sac (Fig. 6); oral surface, highly domed, nearly hemispherical, bearing five highly elevated ambulacra dividing five small interambulacral areas; ambulacra straight, arranged into slight 2-1-2 symmetry (Fig. 6O_1, primary oral plates long and thin, apparently arranged into slight 2-1-2, shared ambulacra absent; distal ambulacra covered by series of high, thin, biserial cover plates with slight zig-zag perradial suture (Figs. 6H, T, 8); proximally, cover plates articulate to integrated interradial plates, distally articulate to exposed floor plates (Figs. 6T, 8); floor plates poorly documented because of preservation, abut integrated interradial plate proximally, extend biserially along edge of ambulacrum distally with a ratio of one floor plate to cover plate; perhaps five plates exposed on each side in largest specimens (Fig. 8), some views show presence of pores between adjacent floor plates and along edge of integrated interradial plates; central area of interambulacra with single integrated interradial plate that articulates along oral surface ambitus with plates of suboral constriction zone (Figs. 6T, 7); suboral constriction zone plated with about five to six irregularly plated circlets of plates that decrease in size proximally (Figs. 6S, O_2, BB, 8); two proximal-most circlets highly laterally elongate, nearly adjacent sutures, stacked atop one another with three per interarea, articulate along ambitus to floor plates and integrated interradial plates (Fig. 8); more distal plate circlets highly proximally imbricate, showing high degree of variation in overlap suggesting great flexibility; distal most circlet forms collar of highly differentiated plates that imbricated over other circlets (Figs. 6N, W, BB, 8); collar plates alternately overlap but show no obvious alignment to columns of peduncular plates; collar plates not associated by radially elongate platelets; gap in collar plates on CD side of theca indicated position of periproct; plating of periproct poorly constrained but appears near proximal portion of gap and marked by numerous small platelets (Figs. 6Z, O_2, 8); pedunculate zone highly organized into alternating circlets of four, highly proximally imbricating plates (Fig. 6); plates from alternate circlets align into straight longitudinal columns of approximately 32–35 plates such that eight peduncular ridges are present; slightly disrupted specimens suggest four plates from each circlet meet beneath more distal circlet to form ring with fairly large lumen; plates squamose proximally with broadly rounded outline becoming more angular distally; distal pedunculate zone grades rapidly into coriaceous sac attachment structure (Fig. 6P, Q); coriaceous sac plated with several hundred small globular platelets that are generally uniform across bottom of structure (Fig. 6P), several specimens show eight lobes to base of structure (Fig. 6G, Q, X); hydropore and gonopore unknown.

Discussion.—*Rhenopyrgus piojoensis* sp. nov. differs from other species of *Rhenopyrgus* bearing a highly arched, conical oral surface with a well-developed suboral constriction. The well-rounded squamose peduncular plates differ from the shape of these plates in other *Rhenopyrgus* species. Radially elongate platelets along the outer margin of the suboral collar are present in both *R. grayae* (Bather, 1915) and *R. whitei* Holloway and Jell, 1983 but lacking in *R. piojoensis*. Although the coriaceous sac is rarely well-preserved, in all other *Rhenopyrgus* species it appears to be nearly circular rather than octolobate.

Geographic and stratigraphic range.—Upper Silurian (Ludlovian), upper Los Espejos Formation, Loma de los Piojos locality near San José de Jáchal, San Juan, Argentina.

Acknowledgements

Many people assisted in the completion of this study. Andrew B. Smith (Natural History Museum, London, UK) and David Holloway (Duke University, Durham, NC, USA) provided access to specimens used in this study. Two reviewers Alexander Glass (Duke University) and Jan Bohatý (Universität zu Köln, Köln, Germany) provided careful reviews that greatly improved this manuscript. Guillermo Aceñolaza (NSUGEO-Instituto Miguel Lillo) provided collections care for the specimens. Funding was provided by NSF-EAR 0745918.

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Appendix 1

List of characters used in the phylogenetic analysis.

1. Integrated interradial plates present (0), absent (1).
2. Outer floor plates present (0), absent (1).
3. Inner floor plates present (0), absent (1).
4. One cover plate per floor plate (0), more than one (1).
5. Interambulacral plates tessellate (0), squamose (1).
6. Interambulacral plates adjacent (0), imbricate (1).
7. Holdfast formed as peripheral rim (0), or polyplated mass (1).
8. Pedunculate zone offset from theca (0), contiguous with theca (1).
9. Pedunculate zone well expressed (0), poorly expressed (1).
10. Hydropore orals absent (0), present (1).
11. Proximally pedunculate zone borders on collar of plates (0), does not (1).
12. Podial pores between floor plates (0), no podial pores (1).
13. Interambulacral plates added randomly (0), along edge of ambulacra only (1).
14. Theca discoidal (0), globular (1), turreted (2).
15. Ambulacra with well-developed 2-1-2 symmetry (0), pseudo five fold symmetry (1).
16. Interambulacral plates present (0), absent (1).