AMEGHINIANA (Rev. Asoc. Paleontol. Argent.) - 40 (2): 197-203. Buenos Aires, 30-06-2003 ISSN 0002-7014

The genus *Prasopora* (Bryozoa) from the Middle Ordovician of the Argentine Precordillera

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Abstract. Abundant zoaria of the discoidal to mound-shaped genus *Prasopora* are described from the Las Plantas and Las Aguaditas Formations in the Argentine Precordillera. Forty complete zoaria were collected from Middle Ordovician rocks, which include a graptolithic and conodont faunas belonging to the *Nemagraptus gracilis* and *Amorphognathus tvaerensis* biozones respectively. The specimens occur in parautochtonous calcareous breccias (debris flow deposits) and autochthonous laminated mudstones and peloidal calcisiltites. *Prasopora* inhabited the external platform, the upper slope and probably the toe of slope, exhibiting high environmental tolerance. The genus attained a worldwide distribution by the Mid to Late Ordovician. *Prasopora argentina* n. sp. is described and figured and compared with the type species, *P. grayae* Nicholson and Etheridge from Scotland and *P. discula* (Coryell) from North America.

Resumen. EL GÉNERO *PRASOPORA* (BRYOZOA) EN EL ORDOVÍCICO MEDIO DE LA PRECORDILLERA ARGENTINA. Numerosos ejemplares del género *Prasopora* han sido colectados en las Formaciones Las Plantas y Las Aguaditas en la Precordillera Argentina. Cuarenta zoarios completos aparecen asociados a una fauna de graptolitos y conodontes correspondientes a las biozonas de *Nemagraptus gracilis* y *Amorphognathus tvaerensis* respectivamente. El material estudiado se encuentra en depósitos parautóctonos como brechas calcáreas (depósitos gravitacionales) y autóctonos como calcipelitas y mudstones. *Prasopora* habitaría ambientes de plataforma externa, talud superior e inferior, mostrando una alta tolerancia a diferentes condiciones ambientales. El género muestra una distribución mundial en el Ordovícico Medio y Tardío. Se describe e ilustra la nueva especie *Prasopora argentina* que es comparada con la especie tipo *P. grayae* Nicholson y Etheridge de Escocia y *P. discula* (Coryell) de América del Norte.

Key words. *Prasopora.* Bryozoa. Ordovician. Precordillera. Argentina.

Palabras clave. *Prasopora.* Bryozoa. Ordovícico. Precordillera. Argentina.

Introduction

The Ordovician rocks of the Argentine Precordillera (figure 1) are mainly composed of Early Ordovician limestones where sponges and brachiopods are the dominant components, and Middle to Late Ordovician calcareous and siliciclastic rocks where brachiopods, trilobites and bryozoans dominate faunal assemblages (Carrera, 1997; Sánchez *et al.*, 2002). Bryozoans constitute a distinctive feature mostly in the Caradocian units where they show great abundance and diversity. In contrast, only two occurrences of bryozoans have been reported from the Early Ordovician limestones (Carrera, 1995).

Keller *et al.* (1993) and Carrera (1997) reported the presence of several genera of trepostome and cryptostome bryozoans from different Caradocian units, although no taxonomic descriptions were given. One of the most conspicuous form, in these faunas is a free-living discoidal to mound-shaped bryozoan reported as *Prasopora* sp. by Benedetto *et al.* (1991) and Carrera (1997). The aim of this contribution is the taxonomic description of this abundant form that occurs in a wide range of environments in different Early Caradocian units of the Argentine Precordillera. Forty complete zoaria were collected from the equivalent Las Aguaditas and Las Plantas Formations in rocks which include graptolite and conodont faunas belonging to the *Nemagraptus gracilis* and *Amorphognathus tvaerensis* biozones respectively.

The material collected is housed at Córdoba University in the Facultad de Ciencias Exactas Físicas y Naturales, Cátedra de Estratigrafía y Geología Histórica (CEGH-UNC), and the Museo de Paleontología (CORD-PZ).

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Geological setting and paleoenvironment

The bryozoan fauna appears to be mainly concentrated in the Las Aguaditas and Las Plantas Formations. These coeval units belong to the Las

 AMGHB2-0002-7014/03$00.00+.50

Figure 1. Geologic map and location of the studied sections / *Mapa geológico y ubicación de las secciones estudiadas* 1. Las Aguaditas. 2. Potrerillos. 3. Las Plantas.

Plantas alloformation (Astini, 1998) that includes in addition the siliciclastic and also bryozoan-dominated La Cantera Formation (figure 2).

Sedimentation of the Las Plantas alloformation started with the drowning of the underlying carbonate platform (San Juan Limestones). In the Early Llanvirn a rapid eustatic sea-level rise led to the deposition of graptolitic black shales and mudstones representing the lower part of the Las Aguaditas Formation. After a gap, the Caradocian deposits of the Las Aguaditas Formation witnessed the onset deposition of breccias and megabreccias, and slumping phenomena.

The Las Aguaditas and Las Plantas formations consist of platy hemipelagic mudstones, peloidal calcisiltites and rare black shales representing autochthonous facies associations, whereas gravity mass flow deposits with abundant fossil debris dominate both allochthonous and parautochthonous deposits. The most important facies of these deposits include breccias, megabreccias and turbidites. These units are interpreted to represent a carbonate margin to foreslope environment (Astini 1995; Keller *et al.*, 1993).

The discoidal to mound-shaped colonies of *Prasopora* occur in the calcareous breccias (debris flow deposits) or in the autochthonous laminated mudstones and peloidal calcisiltites. The rest of the bryozoan fauna comes from the calcareous breccias with some erect bryozoans appearing in a compensation horizon (Keller *et al.*, 1993) covering several individual breccias.

Prasopora appears to be randomly and variably oriented in the debris flows deposits, while in the autochthonous facies the zoaria seem to be in growth position attached directly to the sea floor or encrusting brachiopod valves. The brachiopods *Campylorthis*, *Tissintia* and *Oepikoides* (Benedetto, 1995) commonly bear these encrustations.

Specimen distribution in different facies suggests that *Prasopora* inhabited the external platform, the upper slope and probably the toe of slope. The free-lying habit allowed *Prasopora* to flourish on different substrates and in various sedimentary regimes. This growth form is common among trepostomes (Wyse Jackson *et al.*, 2002). Large, sheet-like colonies were common on the surface of sediments, they typically began growth on brachiopod shells or other skeletal debris and spread across surrounding sediment. If colonies are detached from their original substrate by physical processes, and not totally covered by sediment, their shape and size allows them to be stable lying freely on the see floor (see McKinney and Jackson, 1989; Taylor, 1999).

Occurrences of *Prasopora* inhabiting different environments include: the "*Prasopora* beds" in the Coburn Limestones of Pennsylvania where colonies form coquinites associated with frequent storm deposits (Cuffey, 1997); rippled surface of calcarenites (Ross, 1970; Cuffey, 1997); deeper water environments such as the Iowa Decorah Shale (in Cuffey 1997); and in typical carbonate platform facies (Mc Kinney, 1971; Karklins, 1984). The high environmental tolerance evident among *Prasopora* species, may have allowed the genus to attain worldwide distribution by the Mid to Late Ordovician.

Systematic paleontology

Order TREPOSTOMATA Ulrich, 1882
Family MONTICULIPORIDAE Nicholson, 1881

Genus ***Prasopora*** Nicholson and Etheridge, 1877

Figure 2. Stratigraphic columns of the studied sections and occurrence of *Prasopora argentina* n. sp. / *Columnas estratigráficas de las secciones estudiadas y ubicación de* Prasopora argentina *n. sp.* SJ: San Juan Formation, G: Gualcamayo Formation, LAF: Las Aguaditas Formation, LV: Las Vacas Formation, LP: Las Plantas Formation.

Type species. *Prasopora grayae* Nicholson and Etheridge, 1877.

Prasopora argentina n. sp.
Figures 3.A-M

Diagnosis. Zoaria discoidal to mound-shaped. Autozooecia subcircular in tangential sections, surrounded by polygonal mesozooecia. Maculae 3 to 4 mm apart, composed of enlarged autozooecia and clusters of mesozooecia. Mean maximum diameter of intermacular autozooecia 0.27 mm, 10 entire autozooecia on average in 1 square millimeter. Mesozooecia maximum diameter ranging from 0.01 to 0.22 mm, mean value 0.11 mm, 17 mesozoecia in 1 square millimeter. Cystiphragms in tangential section generally circular and almost all extending all the way around zooecial tubes. Cystiphragms in longitudinal section generally occurring in doubly, overlapping series, 13 cystiphragms in a millimeter length. Acanthostyles absent or rare and small.

Etymology. For Argentina, where the material was discovered.

Material and occurrence. The holotype (CORD-PZ 8541), a paratype (CORD-PZ 8540) and 21 zoaria (CEGH-UNC 20588-20608, and 13523), are from the Las Plantas Formation (Early Caradocian, *Nemagraptus gracilis* zone), quebrada Las Plantas, quebrada Gualcamayo and quebrada Potrerillos sections, Argentine Precordillera. Eighteen zoaria (CEGH-UNC 20609-20627) are from the Las Aguaditas Formation (Early Caradocian, *Nemagraptus gracilis* zone), quebrada Las Aguaditas section, Argentine Precordillera.

Description. Zoaria discoidal to hemispherical, variable in size, approximately 5-45 mm wide at base, 3-35 mm high on average. Upper surface gently to strongly convex, base planar or slightly concave. Autozooecia subcircular in surface view, surrounded by polygonal mesozoecia. Maculae 3 to 4 mm apart, composed of enlarged autozooecia and clusters of mesozoecia. Zoarial base concentrically wrinkled in external view.

Tangential section. Zooecial apertures generally circular to subcircular, occasionally ovate. Mean maximum diameter of intermacular autozooecia 0.27 mm (table 1), 10 entire zooecia on average in 1 square millimeter. Zooecial walls thin, ranging from 0.01 to 0.02 mm, poorly laminated locally. Mesozooecia subrounded to angular, the later predominating in intermacular areas. Mesozooecial maximum diameter highly variable, ranging from 0.01 to 0.22 mm, with a mean value of 0.11 mm, 17 mesozooecia in 1 square millimeter. Maculae composed of local concentrations of mesozooecia, with a stellate distribution in some cases, and clustered enlarged autozooecia (centers of zooecial budding), mean maximum diameter of macular zooecia 0.44 mm. Cystiphragms generally circular and usually extending all the way around zooecial tubes. Some nested cystiphragms appear in single zooecial apertures. Acanthostyles absent in most of the specimens, only one colony showing small and scarce styles at autozooecial-mesozooecial junctions.

Longitudinal section. Endozone limited to the recumbent portion of zooecia. Zooecia in exozone oriented at right angles to zoarial surface. Autozooecia straight to slightly sinuous, normally separated by mesozooecia. Autozooecial walls highly variable in thickness, approximately 0.01-0.03 mm.

Cystiphragms abundant, strongly overlapping and restricted to the exozone, generally occurring in doubly, overlapping series. An average of 13 cystiphragms occur in a millimeter distance. No isolated cystiphragms occur. All cystiphragms hemispherical, completely recurved to zooecial wall or to the overlapped adjacent cystiphragm.

Basal diaphragms of living chambers abundant, curved, slightly concave distally, oriented at right angles to zooecial axis. Straight diaphragms occurring between double cystiphragms series.

Mesozooecial diaphragms straight, oriented at right angles to walls, an average of 16 diaphragms occurring in a millimeter distance.

No acanthostyles were observed in longitudinal sections.

Figure 3. A-M. ***Prasopora argentina*** n. sp. **A.** Lateral view of a mound shaped specimen designated as the holotype CORD-PZ 8541 x 1 / *vista lateral de un especimen con forma de montículo designado como holotipo.* **B.** Base of the same specimen, x 1 / *base del mismo ejemplar.* **C.** Encrusting form attached to the exterior surface of a brachiopod shell, CEGH-UNC 13523, x 2 / *Forma encostrante sobre el exterior de una valva de braquiópodo.* **D.** Discoidal form lying on a laminated mudstone surface CEGH-UNC 20591, x 2 / *Forma discoidal sobre una calcifangolita laminada*. **E.** General view of the colony in oblique longitudinal section CORD-PZ, 8540, x 8 / *Vista general de una colonia en sección longitudinal oblicua*. **F.** Longitudinal section showing inmature and mature zones with cystiphragms beginning at the junction, CORD-PZ 8540, x 20. / *Sección longitudinal mostrando la zona inmadura y madura con el inicio de los cystrifragmas en la unión de ambas*. **G.** General view of the zoaria in tangential section, with maculum at the centre, CEGH-UNC 20588, x 15 / *Vista general del zoario en sección tangencial con macula en el centro.* **H.** Enlarged tangential section of the intermacular area, same specimen, x 50 / *Sección tangencial ampliada en área intermacular del ejemplar anterior.* **I.** Enlarged tangential section of the macular area of the same specimen, showing mesozooecia and large autozooecia, x 50 / *Sección tangencial ampliada del área macular del mismo ejemplar, mostrando mesozoecios y grandes autozoecios.* **J.** Longitudinal section of the upper part of the zoaria, CORD-PZ 8540, x 20 / *sección longitudinal de la parte superior del zoario.* **K.** Enlarged view of a living chamber showing basal diaphragm and overlapping vertical series of cystiphragms, same specimen, x 50 / *Vista ampliada de la cámara habitación mostrando el diafragma basal y las series verticales de cistifragmas sobrepuestos.* **L.** Detail of the upper part of a living chamber showing thin autozoecial walls, same specimen, x 50 / *Detalle de la parte superior de la cámara habitación mostrando delgadas paredes del autozoecio.* **M.** Autozooecial living chambers and intercalated mesozooecia in the same specimen, x 35 / *Cámara habitación y mesozoecios intercalados del mismo especimen.*

Table 1. Measurements of taxonomic characters of *Prasopora argentina* n. sp. / *Medidas de los caracteres taxonómicos de* Prasopora argentina *n. sp.*

Character	Mean	Range	Standard deviation	Number of measurements	Number of zoaria measured
Autozoecia maximun diameter	0.271	0.20-0.35	0.039	148	9
Autozoecia max diameter in maculae	0.44	0.35-0.60	0.059	44	8
Autozoecia (number per mm2)	10.3	7.8-16.0	1.69	29	9
Mesozoecia maximun diameter	0.11	0.01-0.22	0.055	60	9
Mesozoecia (number per mm2)	17.7	12-25	3.2	28	8
Cystiphragms (number per mm)	13.5	11-16	1.46	38	7
Distance between centers of maculae	3.9	3.5-4.2	0.19	16	4

Remarks

The characters shown by the specimens from the Argentine Precordillera fit well with the emended diagnosis for the genus *Prasopora* given by Ross (1967). The diagnosis includes the presence of cystiphragms in autozooecial tubes as one of the most relevant characters.

Ross (1967), McKinney (1971) and McKinney and Jackson (1989) recognized that the most significant evolutionary trend in *Prasopora* consists of changes in cystiphragms, which initially are strongly overlapping in longitudinal section and extend around three-fourths to four-fifths the circumference of the zooecial tube (cystiphragm type 1 of Ross, 1967). In younger rocks the cystiphragms gradually became more restricted horizontally and more separated vertically, which results in one lineage with completely isolated bulbous cystiphragms (cystiphragms type 3 of Ross, 1967).

Cystiphragms of type 1 are typical of the widely described North American species *P. simulatrix* Ulrich (Sparling, 1964; Brown 1965; Ross, 1967; Bork and Perry, 1968), which although included by Marintsch (1981) in the synonymy of *P. falesi* (James), is considered by other authors to be a distinct species (Karklins, 1984; Cuffey, 1997).

McKinney (1971) and McKinney and Jackson (1989) included at the base of this evolutionary trend the species *P. discula* (Coryell, 1919) in which the cystiphragms are very closely spaced and in many instances completely encircle a reduced central open space within the zooecia. The expression of this character in longitudinal sections is a double series of overlapping cystiphragms within a zooecial tube. These features and comparable zooecial and mesozooecial measurements and arrangement are observed in the type species *P. grayae*, Nicholson and Etheridge (1877) from Scotland and also in the Argentine material.

Although no statistical measurements are given in the primary description of *Prasopora grayae* Nicholson and Ethedridge (1877), characters of *P. grayae* are included as part of a cladistic analysis by Pachut *et al.* (1994) and were also analyzed in a recent study of diaphragm function by Boardman (2001). According to these analysis and material figured autozooecia diameter in *P. grayae* ranges from 0.28 to 0.36 mm with 8 to 13 cystiphragms per mm.

Prasopora argentina n. sp. is closely related to *P. grayae* Nicholson and Etheridge. The shape and arrangement of zooecia and mesozooecia are comparable as well as the number of cystiphrams per mm., and the general lack of acanthostyles. However, maximum diameter of autozooecia and mesozooecia in *P. grayae* is slightly higher than in *P. argentina*. Cystiphragms in tangential sections of *P. grayae* make zooecial apertures strongly V-shaped or cuneiform (Pachut *et al.*, 1994) rather than rounded like those of *P. argentina.*

Prasopora argentina is also related to *P. discula* (Coryell, 1919) from the Middle Ordovician of Tennessee and from the Lower Chickamauga Gp. of Alabama (McKinney, 1971). Both species have similar size of autozooecia and mesozooecia, but *P. discula* differs in having more cystiphragms per unit length of autozooecia, a slightly angular polygonal autozooecial shape, maculae without clusters of mesozooecia and almost half the number of mesozooecia per square millimeter.

The typical cystiphragm arrangement, completely encircling the autozooecial tube diameter and forming overlapping vertical series, is a feature shared by these three species and any one of them could be considered as the base of the *Prassopora* evolutionary trend.

Acknowledgements

The author thank Dr. Nora Sabattini and Dr. Paul Taylor for theirs constructive reviews. Financial support for this work was supplied by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Agencia Nacional de Promoción Científica y Tecnológica (ANPCYT).

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Recibido: 3 de junio de 2002.
Aceptado: 31 de octubre de 2002.

Rectificación al artículo "Corales de la transición siluro-devónica en la Precordillera argentina"

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Esta nota tiene por objeto rectificar una de las conclusiones del trabajo titulado "Corales de la transición siluro-devónica en la Precordillera argentina", aparecido en Ameghiniana 39(4), 479-491 y suscrito por los aquí firmantes.

En dicho trabajo se incluye una muy somera descripción de un fragmento mal conservado atribuible, por los escasos caracteres que pudieron ser estudiados, a la familia Pleurodictyidae. En las conclusiones, se afirma que este hallazgo constituye la primera cita de esta familia en América del Sur pero, tras la publicación del artículo comentado, Y. Plusquellec, especialista en tabulados y buen conocedor de los representantes de la familia Pleurodictyidae, nos ha indicado la presencia conocida de este taxón en otras regiones de América del Sur. Una nueva revisión de la bibliografía nos ha permitido constatar que también existen citas previas en Argentina.

En Bolivia, Kozlowski (1923) cita *Pleurodictyum amazonicum*, una forma descrita por Katzer en 1903. Dicha especie es también citada por Branisa (1965) junto a *Pleurodictyum* cf. *P. styloporum* (Eaton), *Pleurodictyum* sp. y *Pleurodictyum* cf. *P. amazonicum* Katzer. Racheboeuf *et al.* (1993) indican la existencia en varios niveles del Devónico de Bolivia de "*Pleurodictyum*" sp. Más recientemente, Plusquellec *et al.* (1999) han citado *Procteria (Granulidictyum)* sp. (n. sp.?) en el Altiplano boliviano.

También en Bolivia, Knod (1908) cita y figura *P.* cf. *P. problematicum* Goldfuss que, según Y. Plusquellec (comunicación personal) es un pleurodictyido muy dudoso. Salfeld en Hauthal (1911) cita y figura *Pleurodictyon* (sic) Petrii (?) Maurer, que parece tratarse de una forma próxima al género *Petridictyum* (Plusquellec y Jahnke, 1999).

En Venezuela, Benedetto (1984) cita el género *Pleurodictyum* en la Sierra de Perija. Y. Plusquellec (comunicación personal) ha revisado este material en un estudio que permanece inédito, hallando dos formas diferentes atribuibles respectivamente a los taxones *Pleurodictyum* y *Procteria (Granulidictyum)*.

En Argentina, y más concretamente en la sección estudiada en el trabajo aquí rectificado, *Pleurodictyum* sp. ha sido citado por Thomas (1905). Castellaro (1966) recoge esta cita y la de Stappenbeck (1910) en su Guía Paleontológica Argentina. No obstante, la figuración realizada por Thomas (1905) no permite confirmar la asignación realizada.

La presencia en Argentina de *Pleurodictyum*, y más concretamente de *P.* cf. *P. problematicum* Goldfuss, ha sido confirmada por Baldis (1975), quien cita esta forma en tres secciones de la Formación Talacasto próximas a Cerro del Fuerte (Isla del Sauce, Talacasto y Km. 18 de Río Jáchal).

Por tanto, la presencia de representantes de la familia Pleurodictyidae es históricamente conocida en Bolivia, Venezuela y Argentina. Lamentablemente, este conocimiento se reduce, de forma casi exclusiva, a antiguas figuraciones y a citas no siempre originales, sin que se haya publicado ningún estudio detallado de este material. Por este motivo y hasta la fecha, se desconoce tanto la importancia de su presencia como la asignación sistemática concreta de gran parte del material citado.

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