Reinterpretation of *Malvinoconularia cahuanotensis* (Braniša and Vaněk) from the Devonian Altiplano and Western Andean Cordillera, Bolivia, South America



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Abstract. The holotype of *Malvinoconularia cahuanotensis* (Braniša and Vaněk) (Devonian, Bolivia), the type species of the monospecific genus *Malvinoconularia* Babcock *et al.*, is redescribed and refigured. *M. cahuanotensis* exhibits several gross morphological features that together are uniquely shared with *Reticulaconularia baini* (Babcock and Feldmann). In both taxa, the transverse ribs are nodose, the interspaces bear longitudinal ridges (bars or crests) that are collinear (line up) across the transverse ribs, and the longitudinal centerline (midline) of the faces is marked by a subdued ridge. Additionally, the two species may also be similar in the anatomy and external ornament of the corner sulcus. The slightly undulose geometry of the transverse ribs of *M. cahuanotensis* also is exhibited by certain specimens of *Reticulaconularia*; however, whether this feature is primary or taphonomic in origin is unclear at present. Together, these similarities suggest that the genus *Malvinoconularia* probably is a junior synonym of the genus *Reticulaconularia*.

Resumen. Reinterpretación de Malvinoconularia cahuanotensis (Braniša y Vaněk) del Devónico de Bolivia, America del Sur. El holotipo de Malvinoconularia cahuanotensis (Braniša y Vanek) (Devónico, Bolivia), la especie tipo del género Malvinoconularia Babcock et al., es reinterpretado y refigurado. M. cahuanotensis exhibe varios rasgos morfológicos que en conjunto son compartidos únicamente con Reticulaconularia baini (Babcock y Feldmann). En ambos taxones las costillas transversas son nodosas, los interespacios poseen aristas longitudinales (barras o crestas) que son colineares a las costillas transversas, y las caras presentan una pequeña elevación externa sobre su línea media. Además, estas especies parecen ser similares en la anatomía y ornamentación externa del surco marginal. La geometría suavemente ondulada de las costillas de M. cahuanotensis es también exhibida por ciertos especímenes de Reticulaconularia, aunque aún no es claro si esta característica es primaria o tafonómica en su origen. En conjunto, estas similitudes sugieren que Malvinoconularia es un sinónimo junior de Reticulaconularia.

Key words. Bolivia. Devonian. Conulariids. Cnidaria. Systematics.

Palabras clave. Bolivia. Devónico. Conuláridos. Cnidaria. Sistemática.

Introduction

Devonian strata of Bolivia have long been known for their exceptionally abundant and well preserved invertebrate fossils, particularly in comparison with equivalent strata in other parts of the Malvinokaffric Realm (Sharpe, 1856; Bernard, 1895; Kayser, 1897; Reed, 1904, 1925; Thomas, 1905; Schwarz, 1906; Knod, 1908; Clarke, 1913; Kozlowski, 1913, 1923; Douglas, 1920; Richter and Richter, 1942; Boucot, 1971; Méndez-Alzola and Sprechmann, 1973; Cooper, 1977; Eldredge and Ormiston, 1979; Babcock *et al.*, 1987; Leme, 2002; Rodrigues, 2002; Rodrigues *et al.*, 2003; Leme *et al.*, 2004). The most common fossils in the Bolivian rocks are trilobites,

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rhynchonelliform brachiopods, molluscs, and conulariids (d'Orbigny, 1842; Ulrich, 1892; Kozlowski, 1923; Braniša, 1965; Babcock et al., 1987; Babcock, 1993). Conulariids are very common in the Belén, Icla, and Sicasica formations (figure 1), where they generally occur in hard siliceous concretions (Ulrich, 1892; Kozlowski, 1923; Braniša, 1965; Babcock et al., 1987; Babcock, 1993). In the most recent review of the conulariids of these strata, Babcock et al. (1987) described six species: Conularia albertensis Reed, 1925, C. quichua Ulrich, 1890, (in Steinmann and Doderlein), Paraconularia africana (Sharpe, 1856), P. ulrichana (Clarke, 1913), Reticulaconularia baini (Ulrich, 1892), and Malvinoconularia cahuanotensis (Braniša and Vaněk, 1973). Malvinoconularia cahuanotensis originally was placed in the genus Metaconularia (Braniša and Vaněk, 1973), and was erected on the basis of three specimens, all from the Lower Devonian Belén Formation. Unfortunately, Braniša and Vaněk's holotype and nearly all other

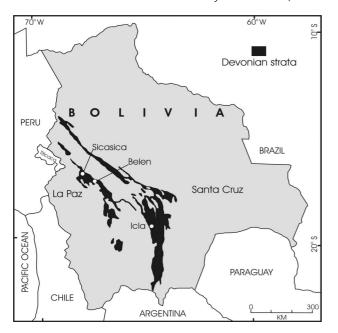


Figure 1. Map showing the distribution of Devonian strata in Bolivia / mapa exhibiendo la distribución de los estratos del Devónico en Bolivia.

specimens, originally reposited in collections of the Yacimientos Petrolíferos Fiscales Bolivianos (YPFB, Santa Cruz de La Sierra, Bolivia), have been lost (José Oliveira and Hugo Barba, YPFB, oral communication, 2003). Only one actual specimen, the holotype of *Malvinoconularia cahuanotensis* (YPFB 5630; Braniša and Vaněk, 1973, Fig. 2.1-4), currently is available for study.

According to Babcock et al. (1987, p. 219), the monospecific genus Malvinoconularia differs from all previously described conulariid genera "by [1] having rods [transverse ribs] that usually abut at the midline, [2] widely spaced rods, [3] large apical angles (37 to 43°), and [4] subtle thickenings of [the] integument which run the length of the exoskeleton and [5] by lacking spines [interspace bars, ridges, or crests]." However, reexamination of the holotype of M. cahuanotensis shows that it exhibits anatomical features that were not noted previously or may have been misinterpreted (Braniša and Vaněk, 1973; Babcock et al., 1987). Furthermore, comparison of this specimen with specimens of Reticulaconularia baini shows that it and other species of Reticulaconularia exhibit most of the characteristics attributed by Babcock et al. (1987) to Malvinoconularia, and that these two taxa share several anatomical features not shared with other conulariids. Based in part on these new observations, presented below, we argue that Malvinoconularia may be a junior synonym of Reticulaconularia.

Materials and methods

The present study is based on direct examination of the holotype of Malvinoconularia cahuanotensis and 78 specimens of *Reticulaconularia baini*, all from Bolivia (see Appendix). Most of the R. baini specimens are from the Icla Formation, though some may be from the Belén Formation of the Altiplano and Western Andean Cordillera. Specimens were examined and photographed using reflected light microscopy. Use of anatomical terminology in this paper generally is consistent with precedents to be found in Sinclair (1940a, 1940b, 1942, 1948, 1952), Moore and Harrington (1956), Bischoff (1978), Van Iten (1991a, 1991b, 1992a, 1992b), Jerre (1993), Van Iten et al. (1996, 2000), Leme (2002), and Leme et al. (2004). Finally, all examined specimens are reposited in collections of the Yacimientos Petrolíferos Fiscales Bolivianos (YPFB), Santa Cruz de La Sierra, Bolivia, and Museo de Historia Natural Alcide d'Orbigny, Cochabamba, Bolivia.

Previous descriptions of Malvinoconularia

Braniša and Vaněk (1973). The original description of *Metaconularia cahuanotensis* reads as follows: "The faces are not uniform in size, with bent edges. The corners are marked by broad shallow furrows, across which the transverse ridges are clearly continuous. These ridges are slightly variable in thickness. The transverse ridges are slightly arched adaperturally, and are offset along the midline. Midline of faces inconstantly marked by faint groove; on inner side (internal mould) enclosed by well-developed septal ridge. The interspaces, because of the close spacing of the transverse ridges, are represented only by shallow grooves. Faces with accessory longitudinal lines in outer surface. Apical angle: about 14°. Transverse ridge spacing: 10-11/5 mm".

Babcock et al. (1987). Based on examination of a single specimen (YPFB 5630), Babcock et al. (1987) erected the new, monospecific genus Malvinoconularia, with type species M. cahuanotensis Braniša and Vaněk (1973). Their description of the genus Malvinoconularia reads as follows (Babcock et al., 1987, p. 219): "Conulariids with rods [transverse ribs] widely spaced; 18 to 24/cm; undulose; fewer than 30% alternate at midline; greater than 70% abut. Apical angles large, approximately 37 to 43°. Nodes present and closely spaced. Adapertural and adapical spines absent. Several narrow, subtle thickenings of integument run longitudinally along the exoskeleton".

Present description

The holotype of Malvinoconularia cahuanotensis

(figure 2.A-D) can be redescribed as follows: Pyramidal theca having four faces that differ in width, with one set of opposing faces (the major faces; Babcock and Feldmann, 1986) approximately 1.3 times as wide as the other set of opposing faces (the minor faces); theca slightly compressed both parallel and perpendicular to its long axis, with several low, broad transverse folds, probably produced by secondary compaction parallel to the longitudinal axis of the theca (figure 2.C), crossing the faces; apical region and apertural margin missing; minimum original length of the theca approximately 4.2 cm. Apical angles of the major and minor faces approximately 51° and 37.5°, respectively. Midline of the faces marked discontinuously by a very low external ridge (figure 2.C). Transverse ribs finely nodose, slightly undulated, confluent at the midlines, widely spaced (figures 2.C, 2.D), with 4 ribs/mm within approximately 10 mm of the former apex and 3-3.5 ribs/mm elsewhere; transverse ribs on the faces chevron-like (figure 2.D); in some places (figure 2.B1), inflected toward the aperture on the shoulders of the corner sulcus; geometry of the transverse ribs in the corner sulcus proper cannot be determined owing to poor preservation of this feature; rib nodes on the faces hemispherical, generally numbering 4/mm. Interspaces locally (near the corners) showing narrow, bar-like longitudinal ridges (interspaces ridges) that line up across the transverse ribs and are more or less parallel to the corners (figure 2.B1-3); interspaces of the two major faces also exhibit four subdued, relatively broad longitudinal ridges that likewise extend across the full width of the interspaces and are collinear (line up) across the transverse ribs (figure 2.A). Corner sulcus relatively deep, possibly angulated (figure 2.B1); edges (shoulders) of the corner sulcus also angulated (figure 2.B1). Schott (apical wall; Babcock and Feldmann, 1986) absent.

Discussion. The present description differs from the descriptions of Braniša and Vaněk (1973) and Babcock et al. (1987) in several ways. One of these concerns the anatomy of the longitudinal centerline, or midline, of the faces (figure 2.C). According to Braniša and Vaněk (1973), the midline is marked by a discontinuous "faint groove" associated with a "well-developed septal ridge". Although it is no longer possible (apparently) to examine the full suite of specimens assigned by Braniša and Vaněk (1973) to Metaconularia cahuanotensis, we found no evidence of a faint groove or internal ridge at or near the midlines of YPFB 5630. Instead, the midlines of at least some of the faces of this specimen appear to be slightly and discontinuously raised (figure 2.C). In many other conulariids (e.g., many species of Conularia and Paraconularia; e.g., Babcock and Feldmann, 1986) having transverse ribs that arch or point toward the aperture on the faces, the summit of the ribs more or less coincides with the midline. In YPFB 5630, the summit of many of the chevron-like transverse ribs is noticeably displaced from the geometrical centerline (figure 2.D). Also, none of the transverse ribs on this specimen is disrupted (offset) at or near the midline (figure 2.D).

A second point of disagreement concerns the anatomy of the interspaces. According to Babcock *et al.* (1987), the interspaces of *Malvinoconularia* lack longitudinal ridges (referred to by these authors as "spines"). However, as shown here in figures 2.B1-3, relatively narrow, bar-like interspace ridges clearly are present in YPFB 5630. [These ridges may correspond to the "accessory longitudinal lines" noted by Braniša and Vaněk (1973)]. Moreover, these ridges line up (are collinear) across the transverse ribs (figure 2.B1-3).

Babcock and Feldmann (1986) also noted the presence of eleven "subtle thickenings" running along the length of each face (Babcock et al., 1987, fig. 6; this paper, figures 2.1, 2.3). Inspection of YPFB 5630 shows that these features probably are not sites of actual thickening, but instead are subtle folds or corrugations that are somewhat similar to the interspace ridges (crests) of other conulariids (e.g., Reticulaconularia). Thus, YPFB 5630 exhibits both bar-like interspace ridges and broader, subtler longitudinal ridges (figure 2.A). While the interspace ridges probably are primary anatomical features, the broad longitudinal ridges may be artifacts of transverse compaction. Owing, unfortunately, to the fact that there is only specimen of Malvinoconularia available for study, we cannot resolve this problem.

A third difference involves the geometry of the transverse ribs within and near the corner sulcus. According to Braniša and Vaněk (1973), the transverse ribs are "clearly continuous" across the corner sulcus. Babcock et al. (1987) did not describe the corner sulcus, and continuity of the ribs across the sulcus is not evident in their published photographs (Babcock et al., 1987, figure 6, p. 220). In YPFB 5630, the corner sulcus is distorted (by compaction) and/or partially obscured by rock matrix, and thus without further preparation (possibly) it cannot be determined whether the transverse ribs are in fact continuous across the sulcus (as is the case in many other conulariids such as Conularia and Metaconularia; e.g., Van Iten et al., 1996). However, on the rounded shoulders (edges) of one of the corner sulcus (figure 2.B1), some of the transverse ribs are inflected (bent) toward the apertural end of the theca. Such bending generally is displayed by conulariids, including Climacoconus, Paraconularia, and Reticulaconularia, whose transverse ribs terminate within the corner sulcus (e.g., Van Iten et al., 1996; Van Iten et al., 2000).

Finally, Babcock and Feldmann (1986) noted that the transverse ribs of *Malvinoconularia* are slightly undulated. Similar undulation of the transverse ribs, though perhaps not as pronounced as in YPFB 5630 (figure 2.D), also is exhibited by certain specimens of *Reticulaconularia* (figure 2.E). Again, however, it is not clear whether these features are primary or are artifacts of preservation (see Simões *et al.*, 2003).

The genus *Reticulaconularia* Babcock and Feldman

According to Babcock *et al.* (1987), *Malvino-conularia cahuanotensis* is most similar to *Reticulaconularia*. The original diagnosis of this genus (Babcock and Feldmann, 1986, p. 447) reads as follows: "Conulariids with rods that are widely spaced, 12-39/cm. 30-80% of rods alternate at midline; 20-70% abut. Apical angles large, 22-59°. Nodes and adapertural spines present and widely spaced; adapical spines not known." At present, *Reticulaconularia* contains three species: *R. penouili* (Clarke, 1907), *R. sussexensis* (Herpers, 1949), and *R. baini* (Babcock *et al.*, 1987).

In a recent study comparing Reticulaconularia with the monospecific genus Changshaconus Zhu, 1985 (Devonian, China), Van Iten et al. (2000) noted five additional characteristics of Reticulaconularia: (1) midline of the faces marked by an external ridge; (2) nodes located at the ends of the interspace furrows (as opposed to the interspace bars or ridges); (3) long axes of the interspace ridges generally line up across the transverse ribs; (4) interspace ridges extend across the full width of the interspaces; (5) interspace ridges inclined at high angles (approximately 70°) to the transverse ribs. Van Iten et al. (2000) argued further that Changshaconus and Reticulaconularia may have been more closely related to each other than either genus was to any other conulariid, and suggested that one or both genus names may have to be abandoned in order to eliminate paraphyly.

Based on the two descriptions previously published and on direct examination of 78 specimens of *R. baini* from the Devonian of Bolivia (Appendix), we summarize the common characteristics of the three species placed by Babcock and Feldmann (1986) in the genus *Reticulaconularia* as follows: Conulariids with four faces; apical angles range from approximately 22° (minor faces) to 59° [major faces; see however Simões *et al.* (2003) for a discussion of the limitations of the use of the apical angles to diagnose conulariid species]. Transverse ribs finely nodose, chevron-like or bell-shaped on the faces, numbering from 39 ribs/mm in the apical region and from 12 to 21 ribs/mm elsewhere; transverse ribs generally

cross the midlines without disruption or offset (figure 2.G); transverse ribs inflected toward the aperture on the shoulders (edges) of the corner sulcus and terminate within the corner sulcus, where the ends of the transverse ribs of one face alternate and interlock with the ends of the transverse ribs of the adjacent face (figure 2.F). Midlines marked by a low external ridge (figure 2.G). Interspaces with interspace ridges (bars or crests) that extend across the full width of the interspaces and are collinear (line up) across the transverse ribs (figure 2.F). Corner sulcus deep, angulated (figure 2.F), with shoulders (edges) also angulated (figure 2.F). Schott not observed.

Comparisons of Reticulaconularia and Malvinoconularia

As noted above in the introduction, Babcock et al. (1987, p. 219) stated that Malvinoconularia differs from all other conulariid genera "by [1] having rods [transverse ribs] that usually abut at the midline, [2] widely spaced rods, [3] large apical angles (37° to 43°), and [4] subtle thickenings of [the] integument which run the length of the exoskeleton and [5] by lacking spines [interspace bars, ridges, or crests]". However, our work shows that characteristics 1-3 also are exhibited by species in the genus Reticulaconularia. Furthermore, some specimens of R. baini also exhibit subdued longitudinal ridges, which may or may not be primary anatomical features, and interspace bars (crests) and troughs are present in Malvinoconularia. Data presented in this and previous studies (Sinclair, 1942; Braniša and Vaněk, 1973; Babcock and Feldmann, 1986; Babcock et al., 1987; Babcock, 1993; Van Iten et al., 2000) show further that Malvinoconularia and Reticulaconularia share the following anatomical similarities: (1) interspaces with interspace ridges (bars or crests) that line up (are collinear) across the transverse ribs; (2) midline of the faces marked by a more or less distinct external ridge; (3) transverse ribs with nodes; (4) transverse ribs commonly chevron-like. Finally, although the anatomy of the transverse ribs in the corner sulcus of *Malvinoconularia* is unclear, the geometry of the ribs on the shoulders of the corner sulcus is consistent with the hypothesis that the sulcus proper is similar to that of Reticulaconularia, in which the transverse ribs terminate and their ends are arranged in alternation.

In short, then, *Malvinoconularia* Babcock *et al.* (1987) exhibits all of the characters regarded by Babcock and Feldmann (1986) as diagnostic of *Reticulaconularia*, and many and possibly all of the characteristics attributed to this genus by Van Iten *et al.* (2000). For this reason, we conclude that *Malvinoconularia cahuanotensis* (Braniša and Vaněk, 1973)

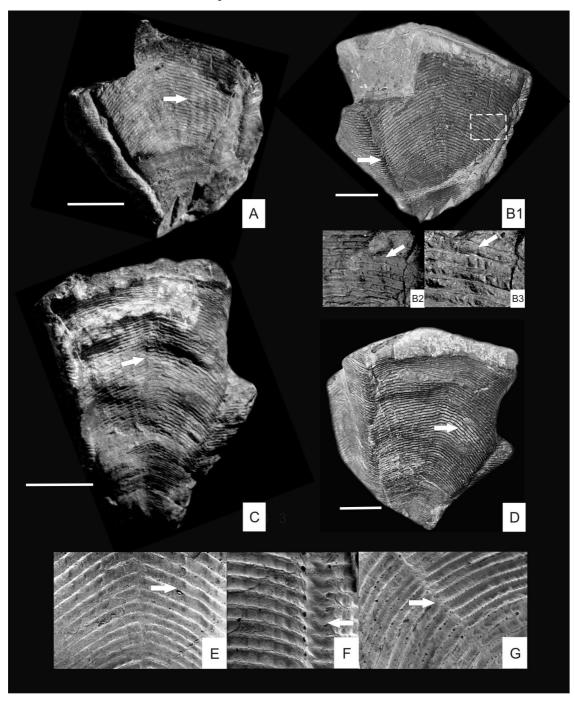


Figure 2. Malvinoconularia cahuanotensis (Braniša and Vanek, 1973) and Reticulaconularia baini (Ulrich, 1892) from the Devonian of Bolivia. A-D, M. cahuanotensis (YPFB 5630). A, General view of the specimen showing the "subtle thickenings" on one of the faces (white arrow) / vista general del especimen presentando "subtle thickenings" (espesamientos longitudinales) en el peridermo (flecha blanca); B1, General view of the same specimen with transverse ribs on the faces inflected toward the aperture on the shoulders of the corner sulcus (white arrow) / vista general del mismo especimen con costillas que se doblan en dirección a la abertura en el surco de las aristas (flecha blanca); B2, Detail of the collinear alignment of the interspace ridges (crests), extending across the full width of the interspaces and lining up across the transverse ribs (white arrow), (x1.6) / detalle del peridermo exhibiendo elevaciones colineares a través del interespacio (crestas) (flecha blanca); B3, Same detail of B2 showing the collinear alignment of the interspace ridges (white arrow), (x2.0) / mismo detalle del B2 exhibiendo elevaciones colineares a través del interespacio (crestas) (flecha blanca); C, Side view of the holotype, a relatively complete specimen showing the subdued longitudinal external ridge at the facial midline (white arrow) / vista del holotipo, presentando una pequeña elevación externa en la línea media (flecha blanca); D, Theca showing the "undulate" transverse ribs (white arrow) / Peridermo exhibiendo costillas "onduladas" (flecha blanca). E-G, R. baini. E, View of the specimen (YPFB 3139) showing the "undulate" transverse ribs (white arrow), (x25.0) / vista del especimen (YPFB 3139) presentando costillas "onduladas" (flecha blanca); F, Same specimen of E, with the transverse ribs inflected toward the aperture on the shoulders of the corner sulcus (white arrow), (x25.0) / mismo especimen del E con costillas que se doblan en dirección a la abertura en el surco de las aristas (flecha blanca); G, Specimen (YPFB 461) with the longitudinal external ridge at the facial midline (white arrow), (x 15.0) / especimen (YPFB 461) con elevación externa en la línea media (flecha blanca). Scale bar = 1 cm / escala = 1 cm.

might be placed in the genus *Reticulaconularia*. Thus, under the rules of priority of the International Code of Zoological Nomenclature (2000), *Malvinoconularia* should be considered a junior synonym of *Reticulaconularia*, and *M. cahuanotensis* a junior synonym of *R. baini*.

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References

- Babcock, L.E. 1993. Exceptionally preserved conulariids from the *Conularienschichten, Fossil- Lagerstätten* in the Devonian of Bolivia. *Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos* 13-14: 77-91.
- Babcock, L.E. and Feldmann, R.M. 1986. Devonian and Mississippian conulariids of North America. Part A. General description and Conularia. Annals of Carnegie Museum 55: 349-410.
- Babcock, L.E., Feldmann, R.M., Wilson, M.T. and Suárez-Riglos, M. 1987. Devonian conulariids of Bolivia. *National Geographic Research* 3: 210-231.
- Bernard, F. 1895. Éléments de paléontologie. Libraire J.B. Bailliere et Fils, Paris, 116 pp.
- Bischoff, G.C.O. 1978. Internal structures of conulariid tests and Circonulariina n. suborder (Cnidaria, Scyphozoa). Senckenbergiana Lethaea 59: 275-327.
- Boucot, A.J. 1971. Malvinokaffric Devonian marine community distribution and implications for Gondwana. *Anais da Academia Brasileira de Ciência, Supl.* 43: 23-49.
- Braniša, L. 1965. Los fósiles guías de Bolivia. I. Paleozoico. *Servicio Geológico de Bolivia, Boletín* 6: 1-282.
- Braniša, L. and Vaněk, J. 1973. Metaconularia cahuanotensis sp. n. from Bolivian Lower Devonian. Vestník Ústredníhoústavu geologického 48: 95-96.
- Clarke, J.M. 1907. Some new Devonic fossils. New York State Museum, Bulletin 107 (Geology 12) (New York State Education Department, Bulletin 401):153-291.
- Clarke, J.M. 1913. Fosseis devonianos do Paraná. *Monografias do serviço geológico e mineralógico do Brasil*, Volume 1, Rio de Janeiro, 353 pp.
- Cooper, P. 1977. Paleolatitudes in the Devonian of Brazil and the Frasnian-Famennian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 21:165-207.
- d'Orbigny, A. 1842. Voyage dans l'Amerique Meridionale, 1826-1833, pt. 4, Paléontogie. Bertrand, Paris.
- Douglas, J.A. 1920. Geological sections through the Andes of Peru and Bolivia: II. From the port of Mollendo to the Inambari River. *Quarterly Journal of the Geological Society of London* 76:1-61.
- Eldredge, N. and Ormiston, L. 1979. Biogeography of Silurian and

- Devonian trilobites of the Malvinokaffric Realm. In: A.J. Boucot and J. Gray (eds.), *Historical Biogeography, plate tectonics and the changing environment*, Oregon State University Press, Corvallis, pp. 147-167.
- Herpers, H. 1949. A new conulariid from the Esopus Formation, Sussex County, New Jersey. In: State of New Jersey Department of Conservation and Economic Development, Miscellaneous Geologic Paper, pp. 3-5.
- International Commission on Zoological Nomenclature 2000. International Code of Zoological Nomenclature. 4° edition, Natural History Museum. London, 306 pp.
- Jerre, F. 1993. Conulariid microfossils from the Silurian lower Visby beds of Gotland, Sweden. *Palaeontology* 36: 403-424.
- Kayser, F.H.E. 1897. Beiträge zur Kenntniss einiger paläozischer Faunen Sud-Amerikas. Deutsche geologische Gesellschaft, Zeitschrift 49: 274-317.
- Knod, R. 1908. Devonische Faunen Boliviens. In: G. Steinmann (ed.), 16° Beiträge zur Geologie und Paläontologie von Sudamerika, Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 25: 493-600
- Kozlowski, R. 1913. Fossiles Devoniens de l'État de Paraná (Brésil). *Annales de Paleontologie* 8: 14-19.
- Kozlowski, R. 1923. Faune Dévonienne de Bolivie. *Annales de Paléontologie* 12: 1-112.
- Leme, J.M. 2002. [Revisão sistemática dos Conulatae Collins et al. 2000, Formação Ponta Grossa, Devoniano (?Lochkoviano-Frasniano), Bacia do Paraná, Brasil: implicações paleobiogeográficas e comentários sobre as relações filogenéticas entre os Conulatae. USP, São Paulo, SP (Dissertação de Mestrado, Instituto de Geociências), 100 pp, Unpublished.].
- Leme, J.M., Rodrigues, S.C., M.G. Simões and Van Iten, H. 2004. Sistemática dos Conulários (Cnidaria) da Formação Ponta Grossa (Devoniano), do Estado do Paraná, Bacia do Paraná, Brasil. Revista Brasileira de Paleontologia 7: 213-222.
- Mendéz-Alzola, R. and Sprechmann, P.G. 1973. Fauna del Devónico Temprano del Uruguay, II. Sobre representantes de Conularia y Mesoconularia (Conulariidae, Conulariinae). Revista de Biología del Uruguay 1: 129-138.
- Moore, R.C. and Harrington, H.J. 1956. Conulata. In: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology: Part F: Coelenterata*, Geological Society of America and University of Kansas, New York and Lawrence, pp. F54-F66.
- Reed, F.R.C. 1904. Mollusca from the Bokkeveld Beds. *South African Museum Annals* 4: 239-274.
- Reed, F.R.C. 1925. Revision of the fauna of the Bokkeveld Beds. South African Museum Annals 22: 27-225.
- Richter, R. and Richter, E. 1942. Die Trilobiten der Weismer-Schichten am Hohen Venn, mit Bemerkunger über die Malvinocaffrisch Provinz. Senckenbergische Naturforscher, Gesellschafte, Ablandlungen 25: 156-179.
- Rodrigues, S.C. 2002. [Tafonomia comparada dos Conulatae Collins, et al. 2000, Formação Ponta Grossa, Devoniano (?Lochkoviano-Frasniano), Bacia do Paraná: implicações paleoeautocológicas e paleoambientais. USP, São Paulo, SP (Dissertação de Mestrado, Instituto de Geociências), 100 pp., Unpublished.].
- Rodrigues, S.C., Simões M.G. and Leme, J.M. 2003. Tafonomia Comparada dos Conulatae (Cnidaria), Formação Ponta Grossa, Bacia do Paraná, Estado do Paraná. *Revista Brasileira de Geociências* 33: 381-390.
- Schwarz, E.H.L. 1906. South African Palaeozoic fossils. *Albany Museum, Records* 1: 347-404.
- Sharpe, D. 1856. Descriptions of Palaeozoic Mollusca from South Africa. *Transactions of the Geological Society of London, ser.* 2: 206-215.
- Simões, M.G., Rodrigues, S.C., Leme, J.M. and Van Iten, H. 2003. Some middle Paleozoic conulariids (Cnidaria) as possible examples of taphonomic artifacts. *Journal of Taphonomy* 1: 165-186.
- Sinclair, G.W. 1940a. The genotype of Conularia. Canadian Field-Naturalist 54: 72-74.
- Sinclair, G.W. 1940b. A discussion of the genus Metaconularia with

- descriptions of new species. Transactions of the Royal Society of Canada 34: 101-121.
- Sinclair, G.W. 1942. The Chazy Conularida and their congeners. *Annals of Carnegie Museum* 29: 219-240.
- Sinclair, G.W. 1948. [The Biology of the Conulariida. Ph.D. thesis. McGill University, Montreal, 442 pp., Unpublished.].
- Sinclair, G.W. 1952. A classification of the Conularida. *Fieldiana Geology* 10: 135-145.
- Steinmann, G. and Doderlein L. 1890. *Elemente der Paläontologie*. Verlag von Wilhelm Engelmann. Leipzig, 848 pp.
- Thomas, I. 1905. Neue Beiträge zur Kenntnis der devonischen Fauna Argentiniens. Deutsche Geologische Gesellschaft, Zeitschrift 57: 233-290.
- Ulrich, A. 1892. Palaeozoische Versteinerungen aus Bolivien. En: G. Steinmann (ed.), Beiträge zur Geologie und Paläontologie von Sudamerika, I. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 8: 5-116.
- Van Iten, H. 1991a. Evolutionary affinities of conulariids. In: A.M. Simonetta and S.C. Morris (eds.), *The early evolution of Metazoa and the significance of problematic fossil taxa*, Cambridge University Press, pp. 145-155.
- Van Iten, H. 1991b. Anatomy, patterns of occurrence, and nature of the conulariid schott. *Palaeontology* 34: 939-954.

- Van Iten, H. 1992a. Morphology and phylogenetic significance of the corners and midlines of the conulariid test. *Palaeontology* 35: 335-358.
- Van Iten, H. 1992b. Microstructure and growth of the conulariid test: implications for conulariid affinities. *Palaeontology* 35: 359-372.
- Van Iten, H., Fitzke, J.A. and Cox, R.S. 1996. Problematical fossil cnidarians from the Upper Ordovician of the north-central USA. *Palaeontology* 39: 037-1064.
- Van Iten, H., Zhi-Kang, Z. and Mao-Yan, Z. 2000. Anatomy and systematic of the Devonian conulariids *Changshaconus Zhu*, 1985 and *Reticulaconularia* Babcock et Feldmann, 1986. *Acta Palaeontologica Sinica* 39: 466-475.
- Zhu Zhi-kang. 1985. New materials of Devonian and Permian conulariids from China. *Acta Palaeontologica Sinica* 24: 528-538 (in Chinese with English abstract).

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Appendix

List of examined material of *Malvinoconularia cahuanotensis* and *Reticulaconularia baini*. Specimens deposited in the paleontological collections of the Yacimientos Petroliferos Fiscales Bolivianos (YPFB), Santa Cruz de La Sierra, Bolivia, and the Museo de Historia Natural Alcide d'Orbigny (MHNC), Cochabamba, Bolivia / *lista del material examinado de* Malvinoconularia cahuanotensis y Reticulaconularia baini. *Especímenes depositados en las colecciones paleontológicas de Yacimientos Petrolíferos Fiscales Bolivianos (YPFB), Santa Cruz de La Sierra, Bolivias y en el Museo de Historia Natural Alcide d'Orbigny (MHNC), Cochabamba, Bolivia.*

| Institution | Species | Formation | Age | Register Number |
|-------------|-------------------------|-----------|----------|-----------------|
| YPFB | Reticulaconularia baini | - | Devonian | 332 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 345 |
| YPFB | Reticulaconularia baini | - | Devonian | 394 |
| YPFB | Reticulaconularia baini | - | Devonian | 458 |
| YPFB | Reticulaconularia baini | - | Devonian | 461 |
| YPFB | Reticulaconularia baini | - | Devonian | 564 |
| YPFB | Reticulaconularia baini | - | Devonian | 635 |
| YPFB | Reticulaconularia baini | - | Devonian | 668 |
| YPFB | Reticulaconularia baini | - | Devonian | 698 |
| YPFB | Reticulaconularia baini | = | Devonian | 713 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 1942 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 1950 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 1952 |
| YPFB | Reticulaconularia baini | - | Devonian | 2370 |
| YPFB | Reticulaconularia baini | - | Devonian | 2371 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3035 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3037 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3075 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3111 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3112 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3113 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3114 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3115 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3116 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3121 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3122 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3123 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3124 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3125 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3126 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3136 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3137 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3138 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3139 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3143 |

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|------|--------------------------------|---------|----------|-------|
| YPFB | Reticulaconularia baini | Icla | Devonian | 3434 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3483 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3488 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3554 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3560 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 3568 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 4292 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 4657 |
| YPFB | Reticulaconularia baini | - | Devonian | 4958 |
| YPFB | Reticulaconularia baini | - | Devonian | 4962 |
| YPFB | Reticulaconularia baini | - | Devonian | 5230 |
| YPFB | Reticulaconularia baini | - | Devonian | 5602 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 5606 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 5611 |
| YPFB | Reticulaconularia baini | Icla | Devonian | 5618 |
| YPFB | Malvinoconularia cahuanotensis | - | Devonian | 5630 |
| YPFB | Reticulaconularia baini | - | Devonian | 5656 |
| YPFB | Reticulaconularia baini | - | Devonian | 5657 |
| YPFB | Reticulaconularia baini | - | Devonian | 5685 |
| YPFB | Reticulaconularia baini | - | Devonian | 5926 |
| YPFB | Reticulaconularia baini | - | Devonian | 5930 |
| MHNC | Reticulaconularia baini | Icla | Devonian | 584 |
| MHNC | Reticulaconularia baini | Icla | Devonian | 587 |
| MHNC | Reticulaconularia baini | Icla | Devonian | 588 |
| MHNC | Reticulaconularia baini | Icla | Devonian | 7406 |
| MHNC | Reticulaconularia baini | Icla | Devonian | 7410 |
| MHNC | Reticulaconularia baini | Icla | Devonian | 7411 |
| MHNC | Reticulaconularia baini | Icla | Devonian | 7412 |
| MHNC | Reticulaconularia baini | Belén ? | Devonian | 7724 |
| MHNC | Reticulaconularia baini | Belén ? | Devonian | 7744 |
| MHNC | Reticulaconularia baini | Belén ? | Devonian | 7745 |
| MHNC | Reticulaconularia baini | - | Devonian | 11482 |
| MHNC | Reticulaconularia baini | - | Devonian | 11505 |
| MHNC | Reticulaconularia baini | - | Devonian | 11505 |
| MHNC | Reticulaconularia baini | - | Devonian | 11506 |
| MHNC | Reticulaconularia baini | - | Devonian | 11508 |
| MHNC | Reticulaconularia baini | - | Devonian | 11510 |
| MHNC | Reticulaconularia baini | - | Devonian | 11511 |
| MHNC | Reticulaconularia baini | - | Devonian | 11512 |
| MHNC | Reticulaconularia baini | - | Devonian | 11514 |
| MHNC | Reticulaconularia baini | - | Devonian | 11515 |
| MHNC | Reticulaconularia baini | Icla | Devonian | 11631 |
| MHNC | Reticulaconularia baini | Icla | Devonian | 11634 |
| MHNC | Reticulaconularia baini | Icla | Devonian | 11635 |
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