

THE TRILOBITE *REEDOPS* (PHACOPIDAE) IN THE LOWER DEVONIAN OF ARGENTINA (MALVINOKAFFRIC REALM)

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ABSTRACT—The trilobite *Reedops* is documented from strata probably corresponding to the middle part of the Talacasto Formation in the Sierra de las Minitas, at the northernmost extent of the Precordillera in La Rioja Province, northwestern Argentina. The specimens resemble the type species of the genus, *R. bronni*, indicating a Pragian (Early Devonian) age for the strata, and suggesting the occurrence at this time of faunal exchange between the Old World Realm, particularly the Bohemian area, and the Malvinokaffric Realm. The taxon represents the first Early Devonian macrofaunal element in the Malvinokaffric Realm with global biostratigraphical significance.

INTRODUCTION

THE PHACOPID trilobite *Reedops* Richter and Richter, 1925 was first recorded from Argentina by Baldis and Peralta (1991) who identified two unnamed species of the genus, referred to as *Reedops* sp. a and *R.* sp. b, from three localities in San Juan Province. The specimens were not illustrated photographically and their present whereabouts are unknown, so the identifications cannot be verified.

Reedops sp. a was said by Baldis and Peralta to come from the middle part of the Talacasto Formation (Lower Devonian; upper Lochkovian to Pragian) in the Las Chacritas River section of the Central Precordillera. Support for this occurrence is provided by the discovery of *Reedops* in strata possibly belonging to the same formation about 200 km to the north in La Rioja Province. The specimens from La Rioja Province, which we document here, belong to a species very similar to the type species, *R. bronni* (Barrande, 1846), considered a Pragian index fossil in the Czech Republic (Chlupáč, 1977).

Reedops sp. b of Baldis and Peralta (1991) was described as having a sculpture of well-developed tubercles on the glabella, similar to that of the very coarsely tuberculate calmonioid genus *Bouleia* Kozłowski, 1923. However, such sculpture is not consistent with an assignment to *Reedops*, which is characterized by a glabellar sculpture of very fine tubercles or coarse granules that are commonly more poorly developed on the posterior part of the composite lobe than on the anterior part. Furthermore, this species was said to occur in the Mogotes Negros Formation (a junior synonym of the Rinconada Formation; upper Silurian) at La Pola Creek in the Sierra de Villicum of the Eastern Precordillera, whereas *Reedops* is not known to range below the Pragian elsewhere in the world. The same species was reported by Baldis and Peralta from the El Molle area where it was said to accompany trilobites described by Baldis (1967). The only species from El Molle described in that publication was *Bainella sanjuanina*, which came from the middle part of the Talacasto Formation (Vaccari et al., 1994). In view of the much younger age of the strata at El Molle than at La Pola Creek, we consider it unlikely that the same species occurs at both localities.

Several other members of the Phacopidae are known from the Silurian and Devonian of Argentina. They include (as identified by the various authors) *Zaplaops zaplaensis* Baldis and Blasco in Baldis et al., 1976, from the Lipeón Formation (Silurian) in Jujuy Province (the genus may be a junior synonym of *Ananaspis* Campbell, 1967); *Paciphacops argentinus* (Thomas, 1905) from the upper part of the Los Espejos

Formation (Ludlow) in San Juan Province (see also Waisfeld et al., 1988; Edgecombe and Ramsköld, 1994); three as yet unnamed species of *Paciphacops* (*Paciphacops*) from the lower part of the Talacasto Formation (Lochkovian) in San Juan and La Rioja provinces (Rustán et al., 2011a, 2011b); and ‘*Phacops*’ *chavelai* Baldis and Longobucco, 1977 from the Pircas Negras and lower Chigua (Chavela Member) formations (Middle Devonian) in San Juan Province.

LOCALITY, STRATIGRAPHY AND AGE

The specimens were collected during geological mapping by T. J. Coughlin and R. J. Holcombe (both at that time with the University of Queensland, Australia) in the Sierra de las Minitas, a series of low mountain ranges about 30 km southwest of the small town of Jagüé in northwestern La Rioja Province (Fig. 1). The stratigraphy and structure of this area are very complex, and updated information can be found in Rustán et al. (2011b). The locality for the *Reedops* specimens is not known precisely but is very close to that from which Rustán et al. (2011b) described a trilobite fauna including *Paciphacops*, the calmonioids *Talacastops* and *Tormesiscus*, and the proetid *Unguliproetus*?. The strata yielding that fauna were assigned by those authors on lithological and faunal grounds to the lower part of the Talacasto Formation, the type area of which is in the Central Precordillera of San Juan Province (Padula et al., 1967; Astini, 1991). In accordance with this interpreted stratigraphic position, a late Lochkovian age has recently been recognized for these levels in the Sierra de las Minitas on the basis of palynological evidence (Rubinstein et al., 2010). The specimens of *Reedops* are likely to have come from a higher stratigraphical horizon of Pragian age based on most known occurrences of the genus in Europe, North Africa and North America, though in Europe it also ranges into the Emsian.

SYSTEMATIC PALEONTOLOGY

Repository.—The specimens are housed in the paleontological collections of the Museo de Ciencias Naturales of the Universidad Nacional de La Rioja, La Rioja, Argentina (PULR).

Family PHACOPIDAE Hawle and Corda, 1847
Subfamily PHACOPINAE Hawle and Corda, 1847
Genus REEDOPS Richter and Richter, 1925
REEDOPS cf. *R. BRONNI* (Barrande, 1846)
Figure 2.1–2.6

Material.—PULR 158, an incomplete cephalon with incomplete and partially enrolled thorax; and PULR 159, an

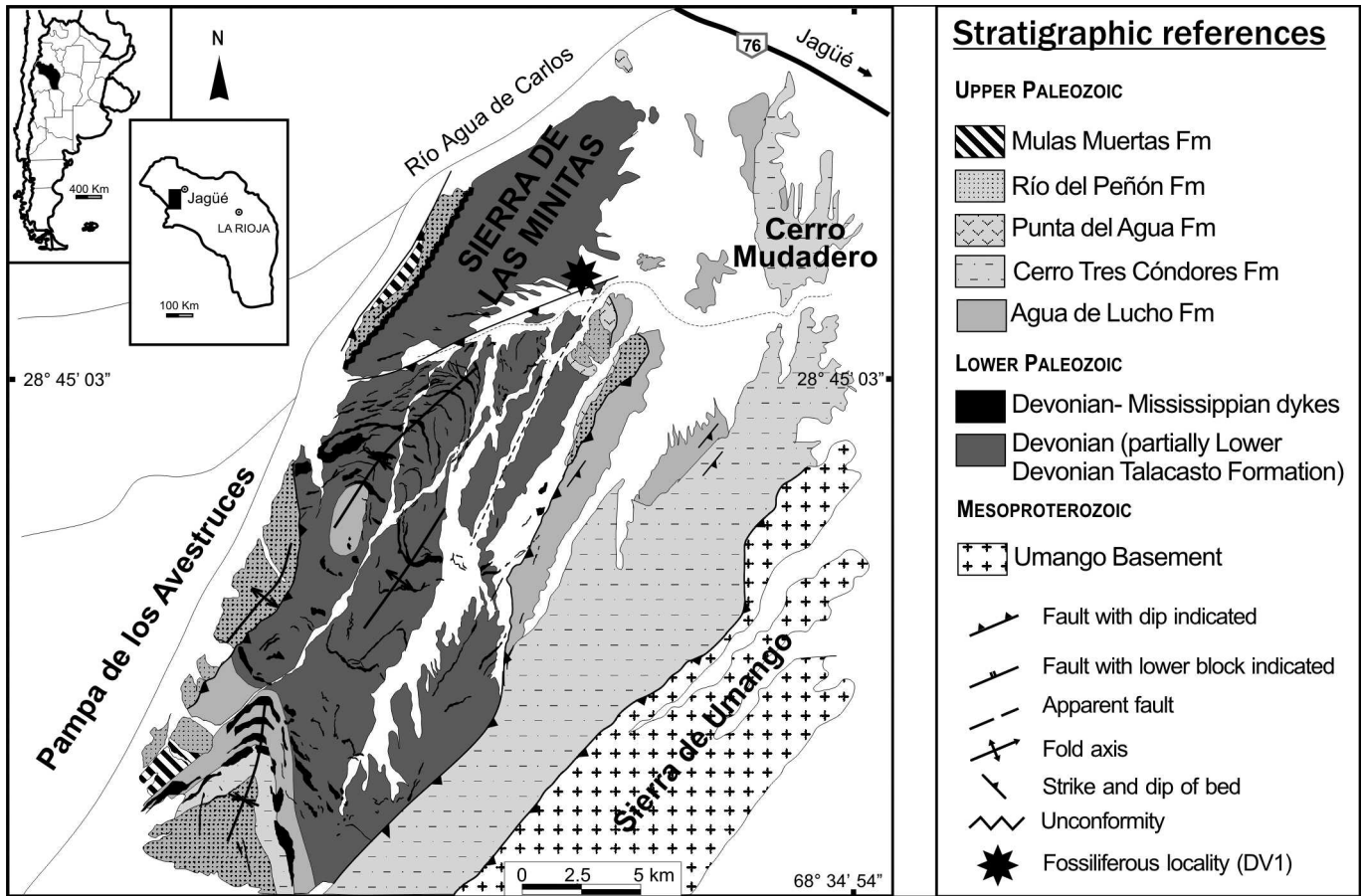


FIGURE 1—Simplified geological map of the Sierra de las Minitas, La Rioja Province, Argentina, showing the approximate locality where the specimens of *Reedops* were collected; the structural and stratigraphical settings of the area are complex. Adapted from Rustán et al. (2011b, fig. 1).

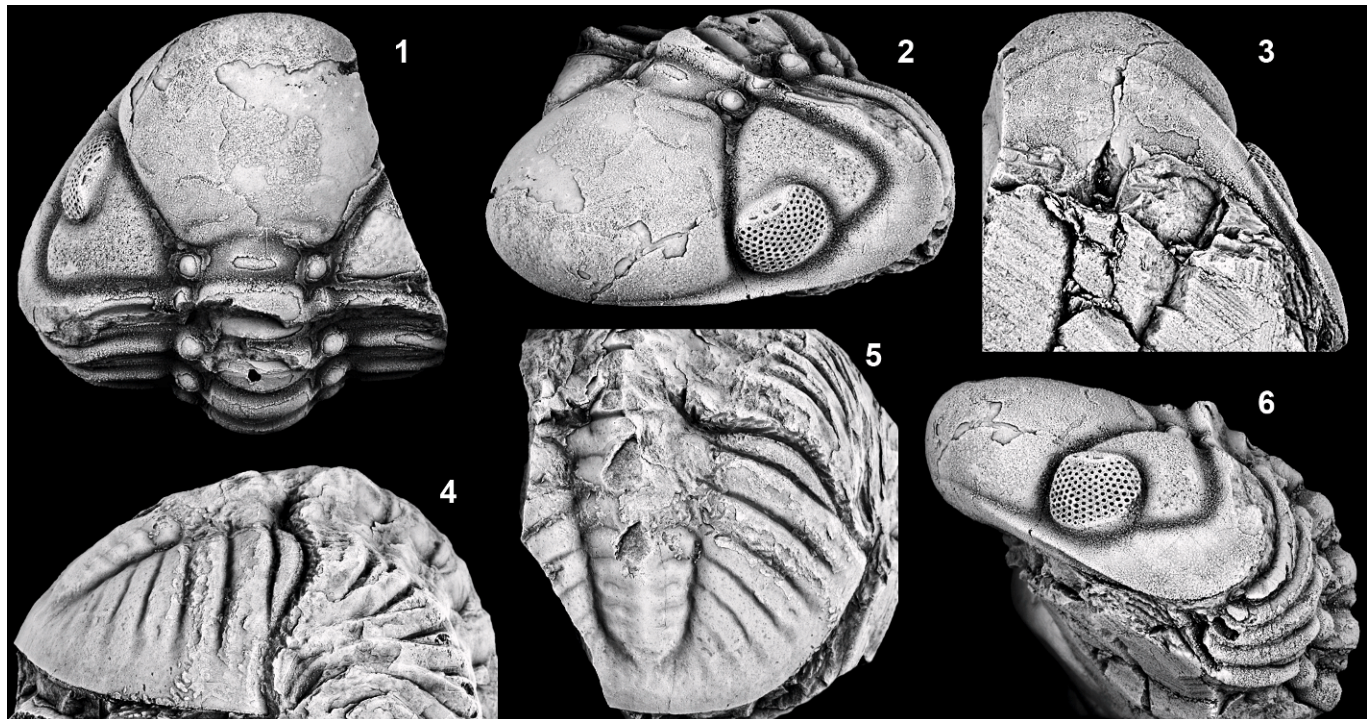


FIGURE 2—*Reedops* cf. *R. bronni* (Barrande, 1846), from strata probably corresponding with middle part of Talacasto Formation (Pragian), Sierra de las Minitas, northwestern La Rioja Province, Argentina. 1–3, incomplete cephalon and partially enrolled thorax, PULR 158, cephalon in dorsal, oblique, ventral and lateral views; 4, 5, incomplete and enrolled exoskeleton, PULR 159, pygidium in lateral and dorsal views; all $\times 2$.

incomplete and enrolled exoskeleton of which virtually nothing remains of the cephalon. The specimens are preserved in nodules in dark grey, sheared mudstone, mostly as internal molds although extensive areas of silicified exoskeleton retaining traces of the sculpture are present on the cephalon of PULR 158.

Discussion.—*Reedops bronni* was comprehensively described and illustrated by Chlupáč, (1977, p. 87, pl. 22, figs. 1–22, pl. 23, figs. 21, 22) based on abundant material from the Prague Basin, and we have also examined casts of some of the specimens illustrated by him. The specimens from Argentina are almost indistinguishable in most aspects of morphology, so a full description is not warranted; however, there are small differences in a number of respects. On the glabella, the anterior branch of S3 diverges a little less strongly forwards, being aligned more nearly parallel to the axial furrow. The preglabellar furrow is a little weaker medially and the lateral border furrow is deeper on the fixigena. The eye extends a little farther back towards the posterior border furrow and contains a greater number of lenses (121 in total), arranged in 17 dorsoventral files with nine lenses in the longest file, whereas in Czech specimens of *bronni*, Chlupáč recorded 14 (less commonly 13, 15 or 16) dorsoventral files of up to seven or eight lenses each, with the total number of lenses no more than about 100 and generally much less. Although the left eye is complete in PULR 158, it is difficult to give a complete lens formula because of irregularities in the arrangement of lenses in the upper part of the visual surface, as is also the case in Czech specimens of *bronni*. In PULR 158 the granulose sculpture is widely distributed on the cephalon, being densely developed on the posterior as well as on the front of the composite lobe, and on the genal field it is interspersed with distinct pits. In Czech specimens of *bronni* granulation is commonly absent or only sparsely developed on the posterior part of the composite lobe and on the genal field (though they are more strongly developed there on rare specimens; see Chlupáč, 1977, pl. 22, figs. 16, 17), and the genal field is not as distinctly pitted. In PULR 159, the inter-ring furrows on the pygidium are deeper laterally than in Czech specimens of *bronni* but are much shallower medially on the anterior half of the axis, and on the posterior half they are effaced medially. Finally, the pygidial pleural furrows, especially the more posterior ones, are a little deeper, and they all extend a little closer to the margin distally.

Chlupáč (1977, p. 90, 91) documented considerable morphological variability in *R. bronni*, particularly in the length/width ratio of the cephalon, the anterior outline of the glabella, the depth of S2 and S3, the size of the eyes and their distance from the posterior border furrow, the number of lenses and their arrangement on the visual surface, the distinctness of the pygidial pleural furrows, and the density and distribution of the cephalic and pygidial sculpture. He related this variability to geographical variation and environmental settings. Similar variability was reported by McKellar and Chatterton (2009) amongst specimens of *R. bronni* from Morocco. In the case of the present specimens from Argentina, some of their morphological features lie outside the range of variability shown by specimens of *R. bronni* from the Prague Basin, notably the cephalic sculpture, the number and arrangement of lenses in the eye and its size, the orientation of the outer branch of S3, and the medial shallowing and effacement of the inter-ring furrows on the pygidium. For this reason, and because the limited amount of available material does not enable us to judge variability, we designate the Argentinean specimens as *R. cf. R. bronni*.

The Argentinean specimens also seem to be similar to two species from the Pragian of North America: *R. amsdeni* Ormiston, 1968 from the Turkey Creek limestone of southern Oklahoma and '*Phacops (Reedops)* n. sp.' of Haas (1969) from the Wenban Limestone of central Nevada. The Turkey Creek limestone, a small and informally named unit that is no longer exposed, was originally regarded as Emsian in age but is now considered more likely to be Pragian (Amsden, 1985, 1988; Oliver, 1992). *Reedops amsdeni* differs from the Argentinean species in having somewhat larger eyes extending closer to the posterior border furrow, a greater number of lenses in the visual surface, a more strongly curved palpebral furrow, possibly denser granulation on the posterior part of the glabella and no conspicuous pitting on the genal field, and pygidial inter-ring furrows that are not effaced medially. The unnamed *Reedops* species from Nevada is known only from a single, incomplete cephalon that is considerably smaller than the single cephalon from Argentina, making comparison between the two difficult. However, in the Nevada species the glabella is more parabolic in outline anteromedially and its maximum width is situated farther back, just behind the midlength of the composite lobe instead of just in front; the eye occupies a greater proportion of the genal field; there are fewer lenses in the dorso-ventral files of the visual surface; the granulation on the posterior part of the glabella is possibly denser and there is no conspicuous pitting on the genal field; and the vincular furrow may be a little deeper medially.

PALEOBIOGEOGRAPHICAL AND BIOSTRATIGRAPHICAL SIGNIFICANCE

Ever since the Malvinokaffric Realm was recognized as a major southern paleobiogeographical province in the Devonian, based largely on the distribution of trilobites (Richter and Richter, 1942), discussion has focused on the evolutionary and geographical origin of its faunas. Hypotheses on the source of Malvinokaffric endemism have involved either ancestral cosmopolitan stocks already present in the Silurian and radiating during the Devonian, or migrations from low paleolatitudes during the Devonian (Eldredge and Ormiston, 1979). In fact, both factors seem to have played a part in a complex historical process that is not yet clearly understood. Some trilobite groups represented in Malvinokaffric faunas, like the calmoniids, are strongly endemic, whereas others such as the aulacopleurids have been shown to have Silurian origins in cosmopolitan stocks (Adrain and Edgecombe, 1996; Rustán and Vaccari, 2010), and yet others like the dalmanitids appear to fit a dispersal model better (Carvalho and Fonseca, 2007; Holloway and Carvalho, 2009, 2010). Postulated extrinsic controls driving these processes include complex paleogeographical settings (Abe and Lieberman, 2009), latitudinal position (Boucot et al., 1969), oceanographic factors such as paleocurrents (Eldredge and Ormiston, 1979; Isaacson, 2007) and variations in sea level (Rustán and Vaccari, 2010). As a result, the signature of strong Malvinokaffric endemism may be 'diluted' by the occurrence of taxa showing clear extra-Malvinokaffric affinities. This external faunal influence, mainly from the Eastern Americas Realm, has supported the proposal of a 'mixed area', particularly in the case of the Devonian faunas of the Argentine Precordillera, based on well-known brachiopod data (Herrera et al., 1998; Isaacson, 2007).

Within this framework, the occurrence of *Reedops* cf. *R. bronni* in Argentina constitutes a very unusual and clear indicator of paleobiogeographical affinities with the Bohemian area of the Old World Realm, as was noted by Baldis and Peralta (1991). Unlike other cosmopolitan phacopids present

in Malvinokaffric faunas, such as *Paciphacops*, *Reedops* is unknown anywhere in strata older than Pragian, so that migration has to be invoked to explain its presence in the middle part of the Talacasto Formation. This interpretation contrasts strongly with previous proposals suggesting low sea levels during the Pragian encouraging vicariance and speciation and restricting dispersals (Rustán and Vaccari, 2010). The presence of *Reedops* in Malvinokaffric basins provides compelling evidence of faunal exchange during the Pragian, suggesting the possibility of reverse migration from the Malvinokaffric areas to lower paleolatitudes at this time, a hypothesis hitherto largely neglected (Adrain and Edgecombe, 1996; Holloway and Carvalho, 2010; Rustán and Vaccari, 2010).

A striking characteristic of Malvinokaffric faunas is the scarcity or absence of biostratigraphical index groups for the Devonian, making stratigraphic correlation between different basins difficult. No graptolites have been reported, only an isolated mention has been made of conodonts (Hünicken et al., 1988), and goniatites are known only from a few localities (Leanza, 1968; Suárez Riglós, 1979; Hünicken et al., 1980; Babin et al., 1991). Hence, Malvinokaffric biostratigraphical schemes were based on some taxa of restricted geographical distribution (mainly brachiopods and trilobites) and have proved to be of only limited usefulness. Although more accurate biostratigraphical schemes utilizing palynological data have been proposed in recent years (e.g., Racheboeuf et al., 1993; Grahn, 2002, 2005; Troth et al., 2011), the lack of macrofaunal elements with global distributions and short stratigraphic ranges continues to be a problem. In this context, *Reedops* cf. *R. bronni* constitutes a new indicator for the Pragian, representing the first Early Devonian macrofaunal element in the Malvinokaffric Realm with global biostratigraphical significance, in a similar way that the homalonotid trilobite *Dipleura dekeyi* (Green, 1832) allows wide correlation in the Middle Devonian of Bolivia (Wolfart, 1968).

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