

THE AULACOPLEURID TRILOBITE *MAUROTARION* ALBERTI, 1969, IN THE SILURIAN-DEVONIAN OF ARGENTINA: SYSTEMATIC, PHYLOGENETIC AND PALEOBIOGEOGRAPHIC SIGNIFICANCE

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ABSTRACT—Five new species of *Maurotarion* Alberti, 1969 from the Silurian Lipeón Formation and Lower Devonian Talacasto Formation of Argentina are recognized. The comparisons with Bolivian and South African species support a Malvinokaffric clade based on librigenal synapomorphies, here erected as *Maurotarion* (*Malvinotarion*) new subgenus. The Malvinokaffric origin of the family would not be a migration from lower paleolatitudes but an Early Silurian stock of rare cosmopolitan ancestors which underwent a great Devonian radiation. Two lineages can be recognized within Malvinokaffric *Maurotarion*. The Silurian-Pragian *dereimsi* lineage is a plesiomorphic one resembling Silurian representatives and involves *M.* (*Malvinotarion*) *dereimsi*, *M.* (*Malvinotarion*) *talacastoense* new species, *M.* (*Malvinotarion*?) new species A, *M.* (*Malvinotarion*?) new species B, *M.* (*Malvinotarion*) sp., and eventually *M.* (*Malvinotarion*?) cf. *dereimsi*. The *isaacsoni* lineage ranges from the Lower Pragian to Eifelian exhibiting a defined morphologic trend in the librigena. This lineage comprises *M.* (*Malvinotarion*) *isaacsoni*, *M.* (*Malvinotarion*) sp. A from South Africa, *M.* (*Malvinotarion*) *gaucho* new species, *M.* (*Malvinotarion*) *haudei* new species and *M.* (*Malvinotarion*) *legrandi*. A Lochkovian diversification probably took place yet an adequate assessment remains difficult. In contrast, a great evolutionary burst is recognized during the Emsian and is related to Pragian-Emsian global relative sea level curves which are coincident with those proposed from Bolivian and Argentinian basins.

INTRODUCTION

OUTSIDE THE Malvinokaffric Realm aulacopleurids trilobites are widespread, common and diverse elements with a long (Ordovician-Carboniferous) stratigraphic range. Nevertheless, their Malvinokaffric record includes only two genera almost exclusively restricted to the Devonian: *Malimanaspis* Baldis and Longobucco, 1977 and *Maurotarion* Alberti, 1969, and are therefore considered of low abundance and diversity (Adrain and Edgecombe, 1996).

Due to this particularity and to the absence of good illustrations and detailed studies, these trilobites have received little attention and apart from a preliminary communication of the present investigations (Rustán, 2008), there are no specific works after the review by Adrain and Edgecombe (1996). Principal discussions about these faunas include their origin, evolutionary events, paleobiogeographic significance, and biostratigraphic implications (Eldredge and Ormiston, 1979; Eldredge and Braniša, 1980; Lieberman, 1993; Adrain and Edgecombe, 1996; Racheboeuf et al., 1998; Edgecombe and Fortey, 2000).

Lower-Middle Devonian information about *Maurotarion* from Bolivia has been fundamental to these topics and has suggested a monophyletic radiation that involves five formally named species, separated in two informal groups. The origin of this clade has been explained by means of two independent migration events of cosmopolitan groups from low paleolatitudes (Adrain and Edgecombe, 1996). However, new evidence from eastern Bolivia confirms the presence of *Maurotarion* in South America by the latest Silurian, questioning the nature and age of these events (Edgecombe and Fortey, 2000). A sixth Emsian species from the Bokkeveld group of South Africa completes the list of known Malvinokaffric *Maurotarion* species up to the present.

In this scenario the contributions from Argentina are relevant, yet apart from the mention of “*Otharion*” (textual

in the Lower Devonian of the Talacasto Formation (Cuerda and Baldis, 1971), the only aulacopleurid described from this country was the Middle-Upper Devonian *Malimanaspis sarudianskii* Baldis and Longobucco, 1977 from the Chigua Formation in Western Argentine Precordillera.

Silurian (Llandovery-Wenlock) data from northwest Argentina, together with new Lower Devonian (Lochkovian-Lower Emsian) *Maurotarion* species from central-west Argentina are treated in the present work. Systematic aspects are fully discussed and alternative phylogenetic, evolutionary and paleobiogeographic proposals are also discussed. Eustatic patterns are considered in relation to the recognized evolutionary and paleobiogeographic patterns.

GEOLOGICAL SETTING

The Silurian record studied here corresponds to the Lipeón Formation (Turner, 1960; Antelo, 1978) which is largely exposed in the Provinces of Salta and Jujuy, northwestern Argentina, mainly involving the geologic provinces of Eastern Cordillera and Subandean Ranges (Fig. 1.1). The Lipeón Formation is composed of shelf sequences (Andreis et al., 1982) of shales and micaceous fine-grained sandstones, with variable thickness up to ca. 700 m at the Zapla Range, southeast of San Salvador de Jujuy. This unit conformably overlies the latest Ordovician-earliest Silurian? diamictites of the Zapla Formation (Antelo, 1978) and is transitional with the sandstones of the latest Silurian-earliest Devonian Arroyo Colorado Formation (Padula et al., 1967). In the Zapla Ranges, the lower member of the Lipeón Formation (“yellowish sandstones” member) is ca. 220 m thick of yellow brown fine to medium micaceous wackes with iron staining; the middle member (“light clayed sandstones” member) is ca. 300 m thick, composed of light brown to grey siltstones and mudstones principally; and the sandy upper member (“transitional member”) is ca. 100 m thick, having been considered

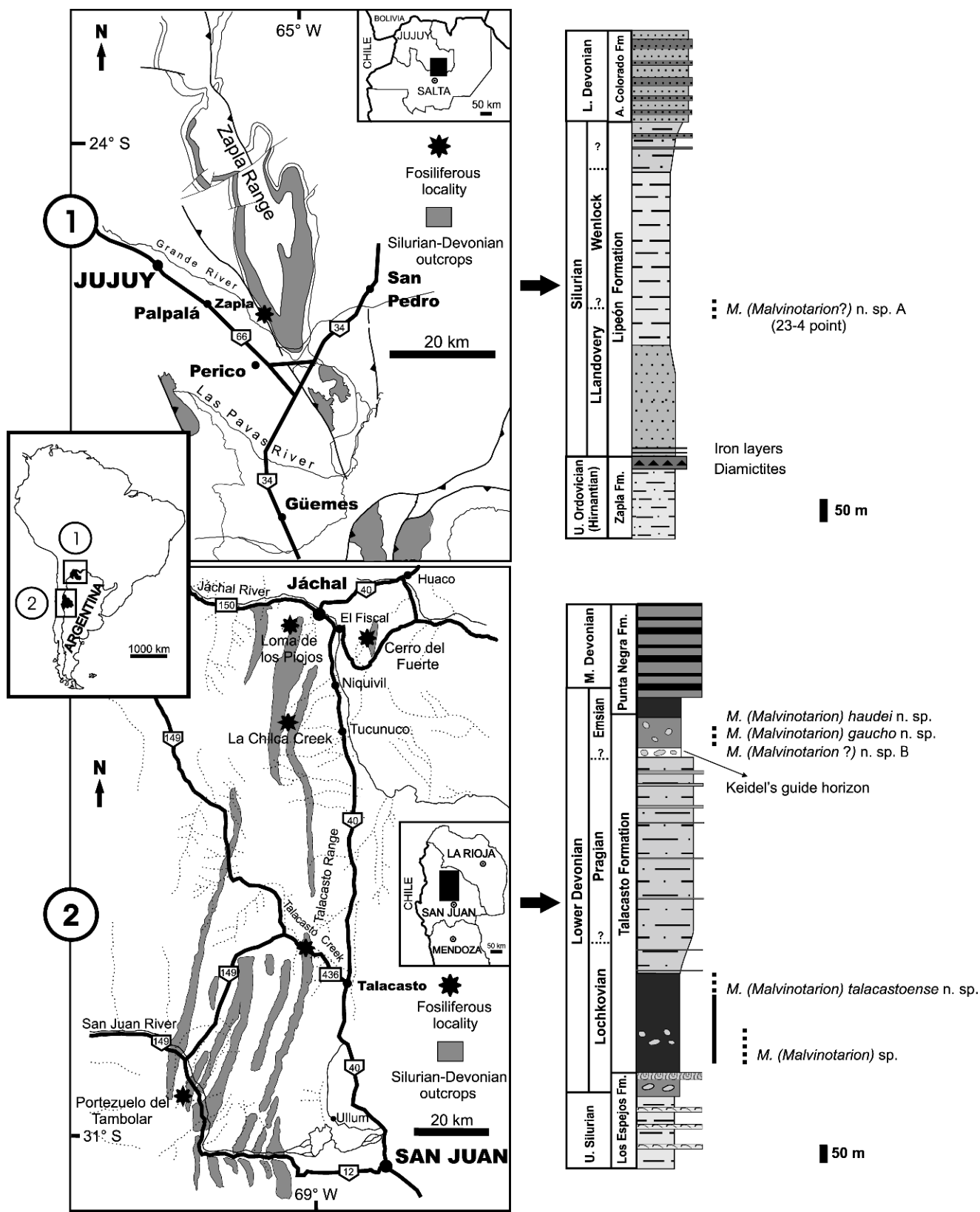


FIGURE 1—Location map of the studied areas, with detail of fossiliferous localities and schematic stratigraphic columns with reference of fossil occurrences. 1, Silurian-Devonian outcrops of the Lipeón and Arroyo Colorado Formations in northwest Argentina, Subandean Ranges, Jujuy Province (modified from Rickards et al., 2002; Benedetto, 1991); 2, Silurian-Devonian outcrops of the Los Espejos and Talacasto Formations in central west Argentina, Argentine Precordillera, San Juan Province. See the section on geological setting in the text for a characterization of each stratigraphic column.

the base of the Arroyo Colorado Formation (Andreis et al., 1982), in some cases (Fig. 1.1 column). These stratigraphic units belong to an Argentinian extension of the Tarija Basin from Bolivia, also known as “Northwestern Basin of Argentina,” which corresponds to the southernmost part of the Central Andean Basin. An Early Llandovery-Pridolian? stratigraphic age has been considered for the Lipeón Formation on the basis of its trilobites (Baldis et al., 1976; Waisfeld and Sánchez, 1993), bivalves (Sánchez, 1989; Sánchez, 1991), brachiopods (Benedetto, 1991; Benedetto and Toro, 1996), graptolites (Toro, 1995; Rickards et al., 2002; Rubinstein and Toro, 2006) and chitinozoans (Grahn and Gutiérrez, 2001; Rubinstein and Toro, 2006).

Lower Devonian rocks studied correspond to the Talacasto Formation (Lower Lochkovian-Lower Emsian) which is widespread and very well exposed in the Central Argentine Precordillera, in San Juan Province, central-west Argentina (Fig. 1.2). The Talacasto Formation (Padula et al., 1967) is composed of a marine sequence of intensely bioturbated greenish-gray mudstones with intercalated beds of sandstone. A composite stratigraphic column typically displays dark muddy levels basally, passing toward the top to sandy levels, and in the uppermost levels fine with fossiliferous concretions (Fig. 1.2 column). The Talacasto Formation reaches 1,000 m in the northern part of the basin where it is thickest. According to Astini (1991) this unit corresponds to a muddy shelf depositional system developed during a high stand. It overlies the mainly Silurian shelf system of Los Espejos Formation. The age of the Talacasto Formation was established basing on its rich brachiopod fauna. Herrera (1991, 1993, 1995) and Racheboeuf and Herrera (1994) assigned the basal part of this unit to the Lower (but not lowermost) Lochkovian. The stratigraphic record of the Silurian-Devonian boundary in Central Precordillera is poor due to a stratigraphic discontinuity spanning the boundary between Los Espejos and Talacasto Formations. Only at the Cerro del Fuerte section has the brachiopod fauna permitted the recognition of the earliest Lochkovian; although not at the base of the Talacasto Formation, but at the top of the underlying Los Espejos Formation (Benedetto et al., 1992). Hence, even in this complete section, the basal boundary of the Talacasto Formation is not earliest Lochkovian in age. The deltaic system (Astini, 1990) of the upper Lower-lower Upper Devonian Punta Negra Formation overlies the Talacasto Formation.

The uppermost levels of the Talacasto Formation at its type locality (Talachasto Creek) were referred to the lowermost Emsian by Herrera (1991, 1993). However, they have recently been reassigned a latest Pragian age (Herrera and Bustos, 2001, p. 369). This is important because the levels at the top correspond to the distinctive horizon (Fig. 1.2) of Keidel (1921) and Astini (1991), named as a stratigraphic marker which is laterally continuous for more than 100 km to the north, including the Loma de los Piojos section. This light marker bed is interpreted as originating by stratigraphic condensation (Astini, 1991) and allows reliable lateral correlation. The strata overlying it, which are mainly recorded in the thicker northernmost sections of the basin, are considered Lower Emsian in age.

This layer can be correlated with a similar stratigraphic one (seismic “marker” 4 of the SG VII base) from the base of the Emsian in Bolivia (Albariño et al., 2003, p. 53) which has been related to a sudden rise of the relative sea level after a strong eustatic fall displayed during the Pragian (Albariño et al., 2003; Álvarez et al., 2003). Thus, the eustatic arrangement

inferred from Bolivia becomes coincident with that of the Argentine Precordillera (Astini, 1991; Ferrero, 2006) and globally (Johnson et al., 1985; Haq and Schutter, 2008). These South American stratigraphic patterns are still difficult to relate to other similar earliest Emsian recognized, for example, the major transgression associated with the Zlíčov event (Chlupáč, 1994).

MATERIALS

The Silurian material studied comes from the access route to the 9 de Octubre iron mine at Zapla, about 27 km to the southeast of San Salvador de Jujuy city, Jujuy Province (Fig. 1.1)

The Devonian material studied derives from classical sections of the Talacasto Formation, in San Juan Province, as follows: Talacasto Creek, the type section, that runs in an E-SW trend 60 km N-NW of San Juan city; La Chilca Creek section, located approximately 16 km to the west of Tucunuco town; Loma de los Piojos section, located 6 km to the Southwest of Jáchal city, about 170 km N-NW of San Juan city; Cerro del Fuerte section, near El Fiscal town, located nearly 10 km to the Southeast of Jáchal city (Fig. 1.2). Illustrated specimens herein are housed in the paleontological repository of the Centro de Investigaciones Paleobiológicas (CIPAL), at Universidad Nacional de Córdoba, Córdoba, Argentina, numbered with the prefix CEGH-UNC.

SYSTEMATIC PALEONTOLOGY

In order to facilitate the systematic comparisons, the morphological descriptions will be based on the criterion followed by Adrain and Edgecombe (1996) in their review of Malvinokaffric aulacopleurids. Open nomenclature follows Bengston (1988).

- Superfamily AULACOPLEUROIDEA Angelin, 1854
- Family AULACOPLEURIDAE Angelin, 1854
- Subfamily OTARIONINAE Richter and Richter, 1926
- Genus MAUROTARION Alberti, 1969
- Subgenus MALVINOTARION new subgenus

Type species.—*Maurotarion isaacsoni* Adrain and Edgecombe, 1996, (uppermost Lochkovian?) Lower Pragian-Lower Emsian, Gamonedá Formation, Subandean Ranges, Bolivia.

Diagnosis.—*Maurotarion* with librigena very wide (tr.), flat lateral border, long (exsag.) posterior border, wide (tr.) and flattened genal spine with very broad (tr.) base, posterior librigenal border furrow starting as a fine and shallow incision behind the eye, continuing along a ridge of posterior section of facial suture, becoming wide and deeper distally, terminating in a small depression almost in front of genal angle.

Etymology.—After Malvinokaffric Realm, the Devonian paleobiogeographic area of the records.

Included species.—*Maurotarion dereimsi* (Kozłowski, 1923); *Maurotarion isaacsoni* Adrain and Edgecombe, 1996; *Maurotarion* sp. A Adrain and Edgecombe, 1996; *Maurotarion racheboeufi* Adrain and Edgecombe, 1996; *Maurotarion legrandi* Adrain and Edgecombe, 1996; *Maurotarion talacastoense* n. sp., *Maurotarion gaucho* n. sp. and *Maurotarion haudei* n. sp. Tentatively: *Maurotarion* n. sp. A, and *Maurotarion* n. sp. B.

Discussion.—Apart from the synapomorphies enumerated in the subgeneric diagnosis, general features could include a reduction of the ornamentation, wide glabellae with rather straight anterior side, absence of large thoracic spines on the sixth or seventh segments, a constant number of fourteen thoracic segments and relatively small pygidia. As previously mentioned, the evidence indicates that all Malvinokaffric

Maurotarion species form a natural group, which is considered a subgenus. The knowledge of the Silurian forms is still insufficient to discriminate clearly new species or to decide with certainty if they belong to the new subgenus. Therefore they are only tentatively referred to *M. (Malvinotarion)* n. subgen. (i.e., in open nomenclature) until better evidence becomes available.

Maurotarion periergum (Haas, 1969) from the Pragian of central Nevada had been included as sister species to the Malvinokaffric *Maurotarion* clade (Adrain and Edgecombe, 1996; Adrain, 2009) since it particularly resembles members of the *dereimsi* group put forward by these authors. However, it differs from Malvinokaffric forms in having thirteen thoracic segments, remarkable tuberculation and granulation dorsally, a strongly inflated lateral border ornamented with subparallel lines, and a narrower genal spine trending to be subcylindrical in section. These features, together with the presence of Silurian ancestors in South American basins, suggest that the *Malvinotarion*-like features of *M. periergum* could be convergent. The alternative, a migration of this species from the South to the North seems to be improbable due to the very low relative sea level proposed globally for the Pragian (Johnson, 1985; Haq and Schutter, 2008), particularly for the Great Basin (Morrow and Sandberg, 2008), and for Andean South America (Astini, 1991; Álvarez et al., 2003). The issue is currently under consideration in light of new evidence from the Talacasto Formation.

This new subgenus, exclusive from South America and South Africa, strongly supports the maintenance of the Malvinokaffric Realm as a paleobiogeographic area of endemism during Early Devonian, in agreement with evidence from other trilobite groups (i.e., calmoniids).

MAUROTARION (MALVINOTARION)

TALACASTOENSE new species

Figure 2.1–2.17

Diagnosis.—*M. (Malvinotarion)* n. subgen. with short (sag.) and wide (tr.) cephalon; anterior margin describing subtly an open inverted “V”-like contour; subtle caeca on preglabellar and librigenal field; subquadrate glabella, weakly inflated and with strong antero-lateral constriction; fine postero-lateral ridge on librigenal field; inflated librigenal posterior border with distinctive very broad (exsag.) expansion near genal angle; small occipital node near posterior margin on the occipital ring.

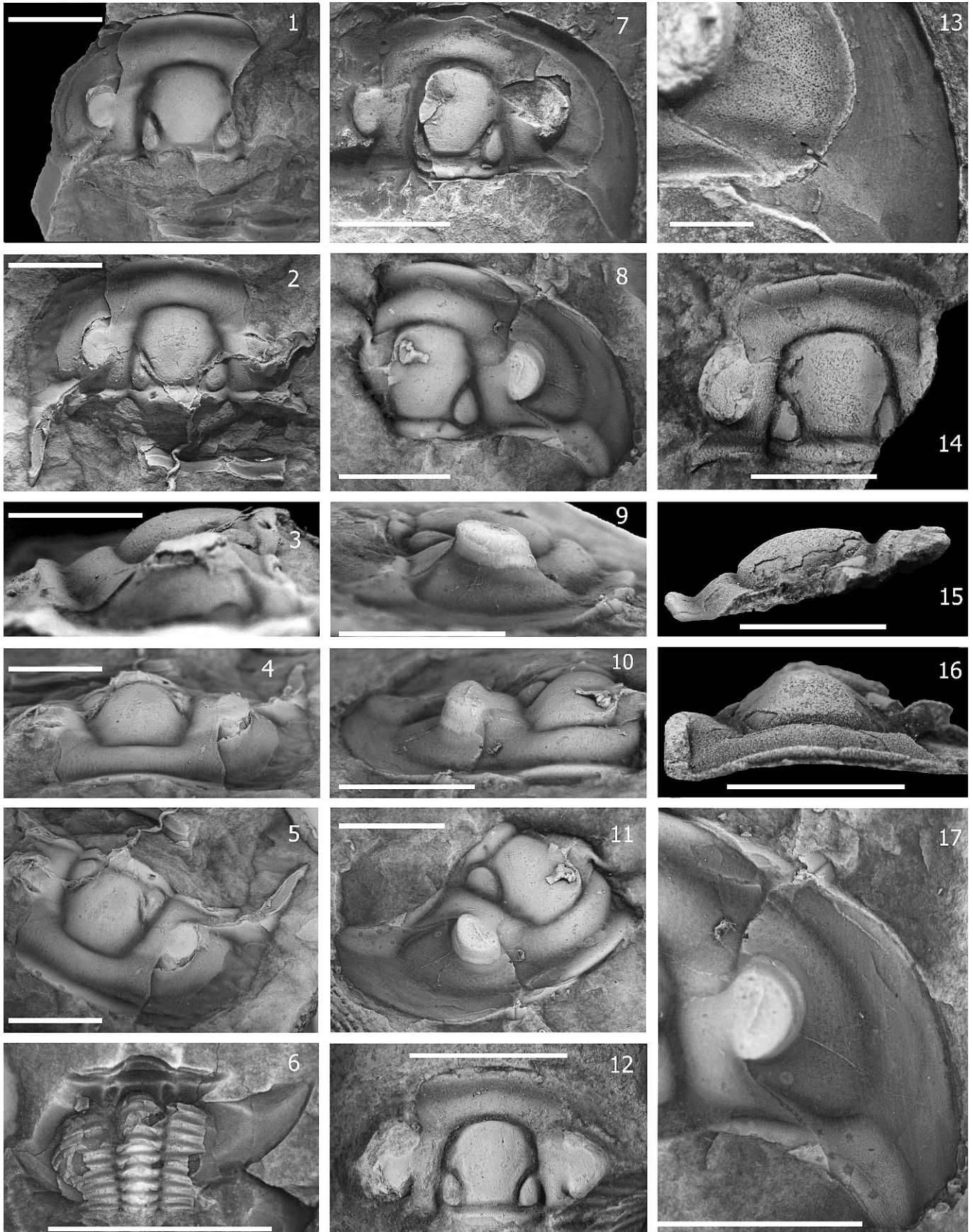
Etymology.—After the Talacasto Formation, the classic Lower Devonian unit from the Argentine Precordillera bearing beautiful trilobites.

Types.—The Holotype CEGH-UNC 12.734 (Fig. 2.7–2.11, 2.13, 2.17) is a cranidium with incomplete right librigena attached. Paratype CEGH-UNC 7.085 (Fig. 2.1–2.5) is an almost complete cranidium, showing the incomplete left librigena with broken genal spine. All material comes from La Cantera point at Talacasto Creek, preserved in greenish-grey to dark grey mudstones dated as Early (but not earliest) Lochkovian (Herrera, 1991, 1993; Racheboeuf and Herrera, 1994; Herrera, 1995). Paratype CEGH-UNC 23.986 specimen (Fig. 2.14–2.16) is an almost complete cranidium, from younger sandy levels nearly 20 m above of those described.

Other material examined.—CEGH-UNC 7.101 (Fig. 2.6) and CEGH-UNC 23.985 (Fig. 2.12) are juvenile Early Lochkovian specimens from La Cantera point at Talacasto Creek.

Occurrence.—Lochkovian (not lowermost).

Description.—Cephalon lacking any tuberculate sculpture, with length (sag.) 70–80 percent width (tr.) across palpebral lobes; anterior margin drawing an open inverted “V,” nearly straight in its exsagittal portions, most strongly curved in its mid-sagittal section; anterior border nearly flat (without appreciable inflation) and directed upward, only subtly longer sagittally than exsagittally in dorsal view, gently convex dorsally with a maximum inflation sagittally in frontal view; anterior border furrow long (sag.) and shallow, with a minimum depth sagittally and other near anterior section of facial suture, having no strong definition of inverted “V”; preglabellar field long sagittally, more than anterior border, gently convex in general with a very small area of stronger convexity posteriorly and sagittally in front of preglabellar furrow, gentle and evenly sloped forward and laterally, with subtle caecal ornamentation principally near anterior section of facial suture; glabella subquadrate, scarcely inflated, with length (sag., including occipital ring) more than 95 percent maximum width across L1, with dorsally even and gentle convexity in sagittal profile but more curved sagittally in transverse profile; preglabellar furrow weakly convex forward, shallow and narrow exsagittally, deeper sagittally; axial furrows, weakly convex to nearly straight, converging slightly anteriorly, broad and shallow, with a long (sag.) and evident antero-lateral constriction in front to S2, at junction of eye ridges; LO (occipital ring) slightly shorter (sag.) than anterior border, shortening behind L1, approximately as tall as posterior part of glabella in sagittal profile, with gentle slope forward at the top, small occipital node located sagittally almost on posterior margin; L1 medium-sized, width 25 percent that of glabella length (exsag.) around 40 percent that of glabella (sag., including occipital ring), acute anterior side, not outstanding the glabellar contour either laterally or upward; L2 somewhat faint but visible next to eye ridge; L3 not clearly distinguishable; SO short (sag., exsag.) and shallow, deeper behind L1; S1 slightly curved, shallower and narrower posteriorly, S2 strongly impressed (for the genus); S3 distinguishable as a faint slot-like depression in relation to anterior part of antero-lateral constriction of glabella; faint eye ridge, running anteromedially toward the most pronounced part of glabellar constriction; interocular fixigena wide (tr.) and sloped; palpebral lobe long (more than L1), wide (tr.), nearly kidney shaped, describing more than one half circle in dorsal view and with faint pit-like median depression; posterior border furrow approximately straight, long (exsag.), shallowing at junction with axial furrows; posterior border with narrow (tr.) part proximal to fulcrum, then gently broader and longer (exsag.), with gently backward curved distal part. Librigenal field wide, with width (tr.) measured at minimum point near front of eye about 50 percent length (exsag.), gentle and evenly sloped, showing subtle caecal sculpture dorsally, postero-lateral ridge (Fig. 2.13, 2.17) and dense upstanding, pustule-like structures ventrally (Fig. 2.13); eye large and tall (reaching or exceeding the glabellar height) and with a ring-like eye socle; lateral margin nearly straight in its anterior section as continuation of the anterior margin direction, distinctive anterolateral section of maximum curvature and expansion, then posteriorly inflected in its postero-lateral section becoming only scarcely curved laterally; lateral border very wide (tr.), more than librigenal field, flattened, sub-horizontally oriented, broadening posteriorly to reach a maximum near genal angle; lateral border furrow wide and shallow (tr.), shallowest posteriorly, trending to effacement near librigenal posterior border furrow; librigenal posterior border furrow beginning as a shallow incision along strong



sutural ridge behind eye, running subparallelly to the posterior section of facial suture, deeper and broadening distally until it bends forward just in front of genal angle, where becomes a shallow slot-like depression near genal angle, then continuing as a shallow furrow along dorsal aspect of genal spine; librigenal posterior border exceedingly broad and inflated, with maximum inflation near genal angle where it reaches the median area of genal spine base; genal spine with very broad base, flat, showing an apparent rapid thinning distally, incorporating the broad and expanded distal part of lateral and posterior borders, exhibiting subtle and thin sculptural lines running subparallel over the posterior border margin; the tip could not be observed; doublure considerably narrow anteriorly, broadening laterally and backward, with a maximum width (tr.) at genal spine base, characterized by an evident set of terrace lines which run subparallel to anterior and lateral margins, diverging on marginal ventral aspect of genal spine base.

Thorax known only from the internal mould of juvenile specimen CEGH-UNC 7.101 (Fig. 2.6). Rostral plate, hypostome and pygidium unknown.

Discussion.—*M. (Malvinotarion) talacastoense* n. sp. strongly resembles *M. (Malvinotarion) dereimsi* Adrain and Edgecombe, 1996, particularly in its cranial characters. Both species share the presence of a subquadrate, weakly inflated glabella with distinct antero-lateral constriction in front of S2; S2 and S3 strongly impressed (for the genus) and a lack of any tuberculate sculpture on the dorsal surface of the cephalon. Other similarities include the anterior border with only very subtle sagittal lengthening and directed upward; very weakly defined inverted “V” shape of anterior border furrow (for the genus); preglabellar field weakly inflated; L1 clearly contained inside of general outline of glabella; occipital ring not taller than posterior part of glabella and lateral border furrow distinguishable, shallowing at genal angle. The main differences lie in the wider (tr.) shape of the cephalon, librigenal margin with maximum anterolateral expansion; posterior librigenal border extremely broad near genal angle and definition of occipital node in *M. (Malvinotarion) talacastoense* n. sp. This species also differs from *M. (Malvinotarion) dereimsi* in the better defined small convex area on the preglabellar field, subtle caecal lines on preglabellar and librigenal fields, and posterolateral ridge on the librigenal field. However, taking all the characters into account *M. (Malvinotarion) talacastoense* n. sp. can be considered sister taxon of *M. (Malvinotarion) dereimsi*.

Maurotarion (Malvinotarion) dereimsi is known from the lowest Pragian lower Member of the Icla Formation from Chuquisaca, Bolivia, and was initially considered the most ancient migrant of the *Maurotarion* Malvinokaffric clade (Adrain and Edgecombe, 1996). Later, additional materials from the El Carmen Formation, Santa Cruz, Bolivia reported as *M. cf. dereimsi* (Edgecombe and Fortey, 2000), suggested a Silurian record for the species. These materials, represented

only by cranidia, may not belong to *M. (Malvinotarion) dereimsi*, considering that the librigena of *M. (Malvinotarion) talacastoense* n. sp. bears unexpected diagnostic specific characters. Indeed, the new material described herein indicates that without librigenae, it is very difficult to evaluate species-level identity in the new subgenus. Consequently, the form from the El Carmen Formation is presently treated as a different taxon most closely related with *M. (Malvinotarion) dereimsi* until further evidence is at hand. The presence of *M. (Malvinotarion) talacastoense* n. sp. in Argentina is significant because it fills the Lochkovian gap of *Maurotarion* existent in Bolivia.

It must be mentioned that two very small specimens suggest an allometric growth in *M. (Malvinotarion) talacastoense* n. sp. The differences in relative proportions can be observed in the cephalon width (tr.) and palpebral lobe length (exsag.), which in small specimens, are especially developed relative to glabellar measurements. Both smallest specimens come from the same levels of La Cantera point at Talacasto creek section where the only *Maurotarion* recorded is *M. (Malvinotarion) talacastoense* n. sp. The specimen CEGH-UNC 7.101 (Fig. 2.6) is an articulated individual showing enrollment; a wide (tr.) cephalon (7.2 mm) is about five times the distance between the external (lateral) sides of L1 (1.5 mm). This ratio has not been previously observed in any larger specimens. For example the holotype (specimen CEGH-UNC 7.085) is 16.34 mm in cephalic width (tr.), representing no more than three times the distance between external sides of L1 (5.4 mm). Likewise, the other small specimen CEGH-UNC 23.985 (Fig. 2.12) is a cranidium only 5.4 mm in sagittal length, with a huge palpebral lobe of subtriangular shape in dorsal view, which almost reaches the sagittal length of the glabella including occipital ring (66 percent). This situation does not occur in the holotype which has a kidney-shaped palpebral lobe only about 35 percent the length of the glabella including the occipital ring (Fig. 2.8).

MAUROTARION (MALVINOTARION) GAUCHO new species
Figures 3.1–3.16, 7.2

Diagnosis.—*M. (Malvinotarion)* n. subgen. with anterior margin bowed with subtle median maximum of curvature; anterior border furrow projecting forward subtly (sag.); strongly sloped frontal area in continuation with anterior glabellar profile in lateral view; very shallow preglabellar furrow; short anterior border (sag.), elongated and moderately inflated (for Malvinokaffric *Maurotarion* species) subtrapezoidal glabella; narrow marginal inflation in anterior and lateral borders; moderately broad flattened genal spine, reaching tenth thoracic segment; small spine-like median nodes on occipital and axial rings.

Etymology.—After gaucho (an Argentinian native cowboy), present in the Argentine Precordillera (the Argentinian Far West). Gaucho is an Argentinian word, herein not latinized.

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FIGURE 2—1–17, *Maurotarion (Malvinotarion) talacastoense* n. sp.; 7–11, 13, 17, holotype, CEGH-UNC 12.734; 7, dorsal view of cephalon internal mould; 8, dorsal view of external mould (latex replica); 9, lateral view showing eye socle and weakly inflated glabella; 10, anterior view, note the relatively tall eye; 11, dorsoanterolateral view; 13, detail of cephalic internal mould showing posterolateral ridge on librigenal field, terrace lines of the lateral doublure, and dense pitting resulting from ventral impression of upstanding pustule-like structures; 17, detail of cephalon external mould showing caeca on preglabellar and librigenal fields, posterolateral ridge on librigenal field, posterior librigenal furrow broader and deepest distally and broad and inflated posterior librigenal border. 1–5, paratype, CEGH-UNC 7.085: 1, dorsal view of internal mould; 2, dorsal view of external mould (latex replica); 3, lateral view; 4, anterior view; 5, dorsoanterolateral view. 14–16, paratype, CEGH-UNC 23.986: 14, dorsal view of cranidium; 15, lateral view; 16, anterior view. 6, CEGH-UNC 7.101; juvenile showing enrolled thorax internal mould and proportionally wide cephalon; 12, CEGH-UNC 23.985; small cranidium showing large palpebral lobes. All from the lower part of the Talacasto Formation, at Talacasto Creek section, Lochkovian, San Juan Province. Scale bar: 5 mm.

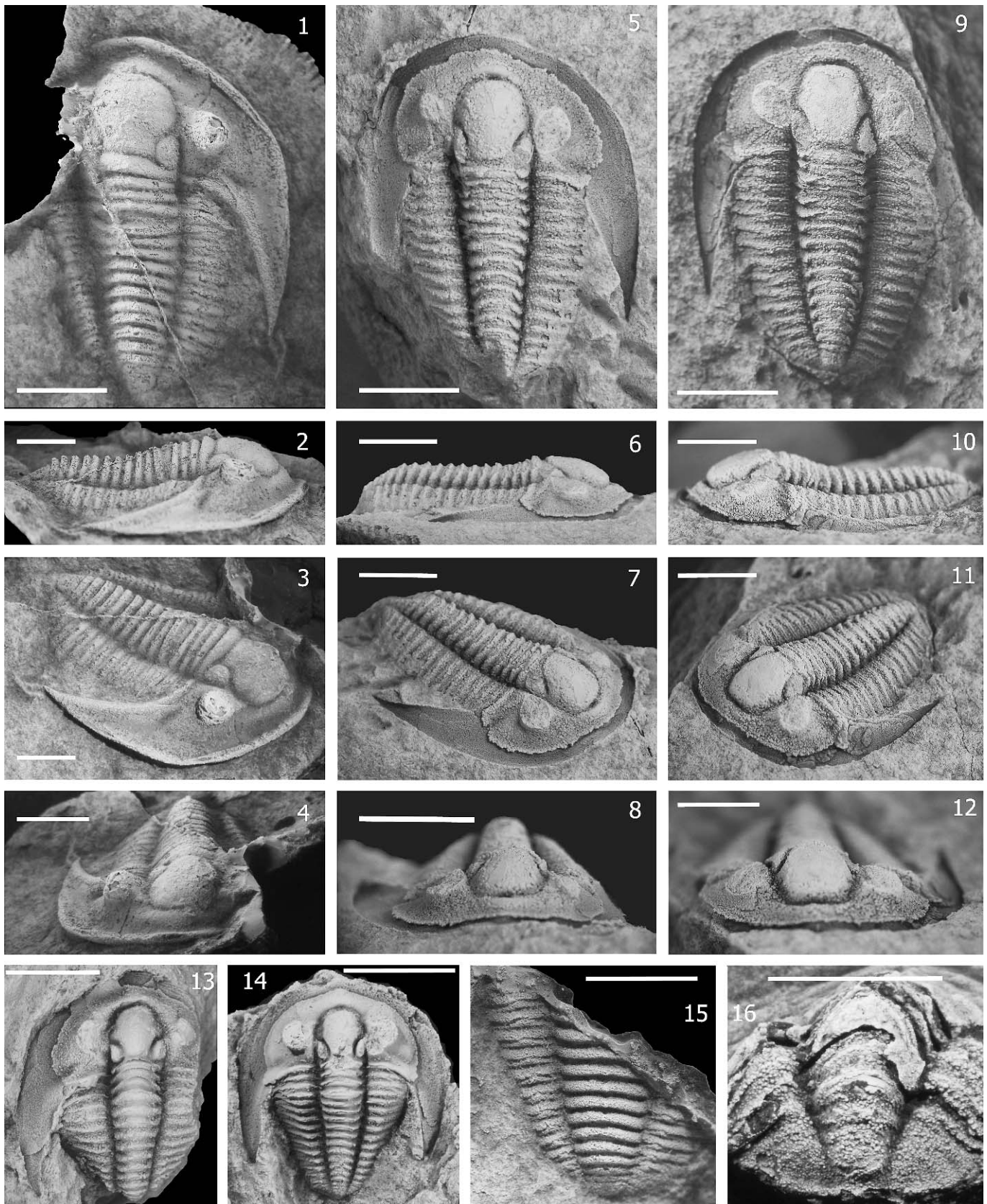


FIGURE 3—1–16, *Maurotarion* (*Malvinotarion*) *gauchio* n. sp.: 1–4, holotype, CEGH-UNC 23.950: 1, dorsal view of external mould, latex replica showing narrow (tr.) thoracic lobes and nodes on axial rings; 2, lateral view; 3, dorsoanterolateral view; 4, anterior view; 5–8, paratype, CEGH-UNC 23.952: 5, dorsal view of internal mould; 6, lateral view; 7, dorsoanterolateral view; 8, anterior view; 9–12, paratype, CEGH-UNC 23.951: 9, dorsal view of internal mould; 10, lateral view; 11, dorsoanterolateral view; 12, anterior view; 13, CEGH-UNC 23.990; juvenile with proportionally small glabella; 14, CEGH-UNC 23.954; smallest juvenile showing wide cephalon, bracket-like anterior border furrow, large palpebral lobes, and proportionally small glabella; 15, CEGH-UNC 23.960; detail of nodes on axial rings, latex replica of external mould; 16, CEGH-UNC 23.965; detail of pygidium, internal mould. All from the upper part of the Talacasto Formation at Loma de los Pijos section, Early Emsian, San Juan Province. Scale bar: 5 mm.

Types.—The holotype CEGH-UNC 23.950 (Fig. 3.1–3.4) is an almost complete articulated specimen, preserved in greenish-grey bioturbated sandstones. Paratypes CEGH-UNC 23.951 (Fig. 3.9–3.12), and CEGH-UNC 23.952 (Fig. 3.5–3.8), are articulated internal moulds covered by a thin siliceous granular layer.

Other material examined.—Specimens CEGH-UNC 23.953, CEGH-UNC 23.954 (Fig. 3.14), and CEGH-UNC 23.990 (Fig. 3.13) are juveniles. Specimens CEGH-UNC 23.955, and CEGH-UNC 23.956 are articulated and exhibit scarce deformation. Additional partial or distorted material: CEGH-UNC 23.957–81, CEGH-UNC 23.984. All materials come from more fossiliferous lenses within sandy levels of the upper part of the Talacasto Formation, above Keidel's light horizon (Early Emsian) at Loma de los Piojos section (see Fig. 1.2). The specimens were collected by Dr. R. Haude.

Occurrence.—Early Emsian.

Description.—Cranidium with length (sag.) 70–75 percent width (tr.) across palpebral lobes, width (tr.) across maximum divergence of anterior sections of facial sutures 85 percent width across palpebral lobes; strongly sloped frontal area in continuation with anterior glabellar profile in lateral view (Fig. 3.2); anterior margin curved, with a sagittal maximum of curvature; anterior border short (sag.), subtly longer sagittally than exsagittally and directed forward, with narrow marginal inflation; anterior border furrow with more angular median section corresponding to a corner of inverted "V" shape in larger specimens, clearer and resulting in a bracket-like line in smaller ones (Fig. 3.13–3.14); preglabellar field relatively short, but longer than anterior border sagittally, sloped, weakly convex in sagittal profile, with a small most convex area posteriorly and medially in front of preglabellar furrow; glabella elongated (for Malvinokaffric *Maurotarion* species), subtrapezoidal, considerably inflated, with length (sag., including occipital ring) approximately equal (more than 95 percent) of maximum width across L1, with gently convex dorsal surface; preglabellar furrow slightly convex, very shallow and narrow, with small slot-like apodemal fossula sagittally distinguishable on internal moulds (Fig. 3.5, 3.7–8); axial furrows nearly straight to weakly convex, evenly convergent anteriorly; LO (occipital ring) short (sag., exsag.) shortening slightly behind L1, barely taller than posterior part of glabella in sagittal profile, convex at the top with small occipital node located posteriorly; L1 medium-size, width 25 percent that of glabella, length (exsag.) around 40 percent that of glabella (sag., including occipital ring), contained dorsal and laterally inside of glabellar outline; L2 evident (for the genus), considerably extended laterally, L3 faint; SO short (sag., exsag.) and shallow, shorter and deeper behind L1; S1 curved, inflecting abruptly outward anteriorly, where is broader and deepest; S2 strongly impressed for the genus; S3 faint; eye ridge running anteromedially; interocular fixigena rather narrow (tr.) and sloped; palpebral lobe medium-size and sub-rounded; posterior border furrow slightly curved, posterolaterally directed, considerably short (exsag.) and shallow, narrower and shallowing to become effaced at junction of posterior section of facial suture; posterior border narrow (tr.) proximally then gently curved, broader and longer (exsag.) distally. Librigenal field relatively narrow, with width (tr.) measured at minimum point near front of eye around 33 percent length (exsag.), gentle and evenly sloped; eye big and tall (more than glabella in smaller specimens), subrounded to somewhat kidney-shaped, with eye socle developed; margin of librigena curved, mostly in its anterolateral section; lateral border very broad (tr.), almost as wide as the librigenal field,

broadening posteriorly, with marginal inflation; lateral border furrow wide (tr.), trending to be effaced; posterior border furrow wide (exsag.) and shallow, exhibiting a shallow depression near junction with lateral border; posterior section of facial suture laterally limited by a ridge and a furrow inside librigena, broadening and deepest posterolaterally until the shallow depression at junction of posterior and lateral border furrows; genal spine flat, moderately broad and with broad base, long, reaching the tenth thoracic segment, tapering in a flattened tip; doublure considerably narrow in appearance anteriorly, broadening laterally and backward slightly, without evident terrace lines.

Rostral plate and hypostome, unknown.

Thorax of 14 segments, axial lobe relatively narrow; pleural lobe measured at fourth segment of specimen CEGH-UNC 23.951 with width (tr.) around 85 percent that of axial lobe, increasing to more than 90 percent by posteriormost few segments; segments considerably short (sag., exsag.); axial furrows approximately straight, converging progressively backward; fulcrum located at 55 percent width (tr.) of pleural lobe anteriorly, reaching nearly the axial furrow most posteriorly; axial ring with length (sag.) approximately 15 percent width (tr.); axial ring with small median spiny node posteriorly located (Fig. 3.1, 3.15), separated from the articulating half ring by apparently deep articulating furrow; articulating half ring apparently as long as axial ring (sag.) or slightly longer; axial furrow deep and narrow (tr.), shallowing and narrowing posteriorly; pleural furrow apparently in contact with axial furrow adaxially, then running slightly sinuously abaxially; posterior pleural band about twice as long (exsag.) as anterior band proximal to fulcrum; with sub-triangular articular boss developed on anterior band at fulcrum; articulating facet with slightly lobate or truncated posterior edge; pleural tips subquadrate or barely rounded; small apodeme positioned ventrally at posterior edge of axial ring at junction with axial furrow on all segments.

Pygidium (Fig. 3.16) very small, short (sag.) and wide (tr.); length (sag. excluding articulating half ring) 30 percent maximum width (tr.); wide axis, with anterior width near 30 percent pygidial width; axial furrows gently converging posteriorly and meeting posteromedially, leaving a narrow posterior field; seemingly first two axial rings prominent, posterior-most rings faint or not developed; ending rapidly in a sloped sagittal profile; pleural field well developed with interpleural furrows (apparently corresponding to segment one and two) more evident than interpleural ones, becoming increasingly indistinguishable backward.

Discussion.—This species is discussed after the particular discussions of the similar *M. (Malvinotarion) haudei* n. sp. (see below).

In comparison to later ontogenetic stages, small specimens of this species exhibit allometric growth. They have a proportionally shorter (sag.) and wider (tr.) cephalon, where the anterior border furrow better draws an inverted "V" line with a stronger outstanding median section. Nonetheless distinctive features in juveniles are larger and proportionally longer genal spine, proportionally bigger (exsag.) palpebral lobe, smaller glabella, and a thorax with more rapid narrowing. In other respects, the remaining characters (i.e., elongated glabella, broad, flat and long genal spine, very convex and relatively narrow thoracic axial lobe, etc.) are consistent between small and large specimens.

Some specimens were measured in order to show this allometric trend. The holotype CEGH-UNC 23.950 (Fig. 3.1) is the biggest undistorted specimen, around 22 mm in total

length. This measure represents approximately 1.3 times the cephalic width (17 mm), which is no more than three (2.7) times the distance between the more external sides of L1 (6.28 mm). The length (sag.) of the glabella including the occipital ring is almost three (2.77) times the length (exsag.) of the palpebral lobe.

The smallest specimen CEGH-UNC 23.954 (Fig. 3.14), is as long as wide. It is 11 mm in maximum length (sag.), signifying 1.1 times the cephalic width (tr.) of 10 mm. This represents more than four (4.2) times the distance between the more external sides of L1 (2.36 mm). The length (sag.) of the glabella including the occipital ring (2.9 mm) is less than two (1.9) times the length (exsag.) of the palpebral lobe (1.54 mm).

The specimen CEGH-UNC 23.990 (Fig. 3.13) is medium sized, approximately 14 mm in length (sag.), almost 1.3 times the maximum cephalic width (tr.) of 11 mm, which is no more than four (3.79) times the distance between the external sides of L1 (2.9 mm). The length of the glabella including the occipital ring (3.1 mm) is 2.21 times the length (exsag.) of the palpebral lobe (1.4 mm).

Different features of small specimens in relation to larger ones have already been discussed above with *M. (Malvinotarion) talacastoense* n. sp., and interpreted as allometric growth. A similar explanation is suitable for this case, instead of recognition of a different taxon.

Described juvenile specimens resemble the adult holaspis of *M. (Malvinotarion) legrandi* Adrain and Edgecombe, 1996, particularly in the shape and proportions of the cephalon (see especially the illustrated specimen in Přibyl and Vaněk, 1981, pl. 1, fig. 12; and Pek and Vaněk, 1991, pl. 3, fig. 2). These similarities suggest a paedomorphosis phyletic relation between these species, which is consistent with the younger (Late Emsian-Late Eifelian) stratigraphic rank of *M. (Malvinotarion) legrandi* (Fig. 6).

MAUROTARION (MALVINOTARION) HAUDEI new species
Figure 4.1–4.10

Diagnosis.—*M. (Malvinotarion)* n. subgen. with wide (tr.) cephalon; very wide (tr.) subquadrate glabella with scarcely convex dorsal aspect; medium to large L1 with subrounded anterior side; lateral border with extreme lateral expansion; lateral border furrow almost completely effaced; exceedingly broad genal spine base; flat and very wide (tr.) genal spine, reaching at least tenth thoracic segment; wide (tr.) and weakly convex axial and pleural thoracic lobes (relatively depressed thorax); smooth axial rings.

Etymology.—After Dr. Reimund Haude, brilliant collector, who found wonderful levels with trilobites at the Loma de los Piojos section.

Types.—The holotype CEGH-UNC 23.982 (Fig. 4.1–4.5) lacks the anterolateral portion of the cephalon and genal spines distal parts, being an almost complete articulated specimen, preserved as external mould in greenish-grey bioturbated sandstones. Paratype, CEGH-UNC 23.983 (Fig. 4.6–4.10), the same observations. Materials come from the same levels yielding *M. (Malvinotarion) gaucho* n. sp. and were also collected by R. Haude (see above).

Occurrence.—Early Emsian.

Description.—Cranidium with length (sag.) 55 percent width (tr.) across palpebral lobes, width (tr.) across maximum divergence of anterior sections of facial sutures 66 percent (approximate) width across palpebral lobes; cephalic margin with outstanding open inverted “V” outline, conferred by a great frontal outstanding curvature between subtly more concave portions anterolaterally; anterior border short

(sag.), longer sagittally than exsagittally and directed forward; anterior border furrow very shallow; preglabellar field short, shorter than anterior border sagittally, strongly sloped forward, weakly convex in sagittal profile; glabella very wide, subquadrate, with length (sag., including occipital ring) 80 percent maximum width across L1, with scarcely convex dorsal surface; preglabellar furrow weakly convex anteriorly, shallow and narrow; axial furrows weakly convex, evenly convergent anteriorly; LO (occipital ring) rather short (sag., exsag.), shortening slightly behind L1, barely taller than posterior part of glabella in sagittal profile, nearly flat at the top, apparently with a very small occipital node located posteriorly; L1 medium to large, width near 25 percent that of glabella, length (exsag.) nearly 45 percent that of glabella (sag., including occipital ring), without outstanding dorsal nor laterally from general glabellar outline, with subrounded anterior side; L2 somewhat faint; L3 apparently effaced; SO short (sag., exsag.) and shallow, shortest and deepest behind L1; S1 strongly curved, bending abruptly outward anteriorly; S2 somewhat faint; S3 apparently effaced; eye ridge apparently inconspicuous; interocular fixigena narrow and sloped; palpebral lobe medium to large and rounded; posterior border furrow slightly curved, posterolaterally directed, considerably short (exsag.) and shallow, narrowing and shallowing distally, to become effaced at junction of posterior section of facial suture; posterior border proximally narrow (tr.) then gently curved and longer (exsag.) distally. Librigenal field relatively narrow, with width (tr.) measured at minimum point near front of eye 35 percent (approximate) length (exsag.), scarcely and evenly sloped; eye medium sized, as tall as glabella, subrounded; margin of librigena strongly curved, mostly in its anterolateral section; lateral border with extreme posterolateral expansion, broadening posteriorly becoming broader (tr.) than librigenal field; lateral border furrow approximately effaced; posterior librigenal border furrow running as a fine and shallow line posterolaterally, then becoming wider (exsag.) and deeper, giving rise to a depression near genal angle; genal spine flat, broad and with very broad base, very long, reaching the tenth thoracic segment, tapering in a flat tip; double unavailable.

Rostral plate and hypostome, unknown.

Thorax of 14 segments, without any ornamentation; axial lobe wider (tr.) than pleural lobe measured at fourth segment; pleural lobe measured at fourth segment, with width (tr.) 60 percent (approximate) that of axial lobe anteriorly, increasing to 70 percent (approximate) by posteriormost few segments; segments considerably short (sag., exsag.); fulcrum located at almost 70 percent width (tr.) of pleural lobe anteriorly, reaching the axial furrow posteriorly; axial ring with length (sag.) 13–14 percent width (tr.); axial ring with straight edges and flat, smooth surface; axial furrow shallow and narrow (tr.), shallowing and narrowing posteriorly; pleural furrow contacting the axial furrow adaxially, then running posterolaterally, longer (exsag.) and deeper at fulcrum; posterior pleural band about twice as long (exsag.) as anterior band proximal to fulcrum; with little subtriangular articular boss developed on anterior band at fulcrum; articulating facet apparently with slightly lobate or truncated posterior edge; pleural tips subquadrate or barely rounded in appearance; small apodeme positioned at posterior edge of axial furrow on all segments.

Pygidium small, relatively short (sag.) and wide (tr.); wide anterior part of axis; axial furrows gently converging posteriorly and meeting posteromedially; first two segments very well defined, posterior ones not defined; axial rings

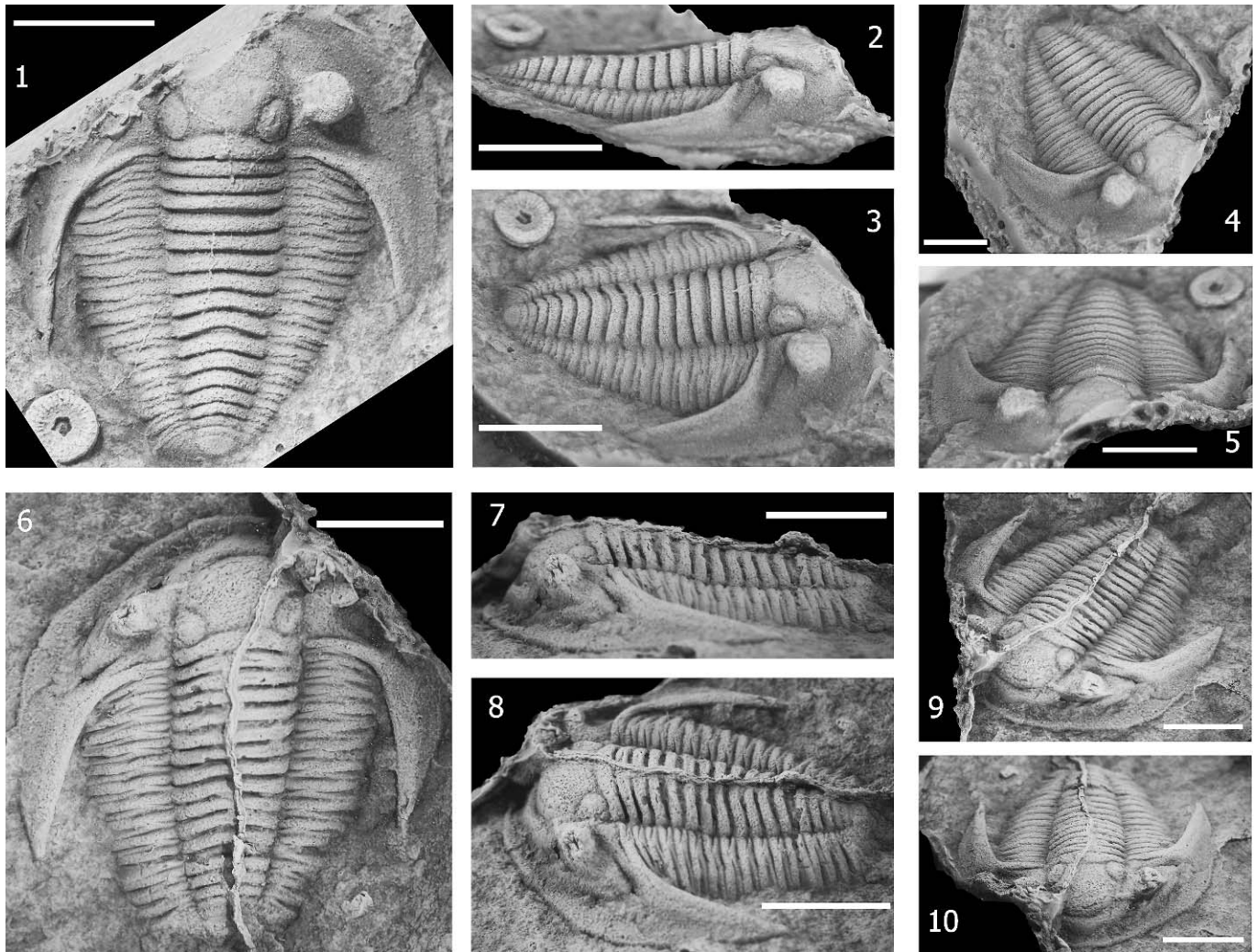


FIGURE 4—1–10, *Maurotarion (Malvinotarion) haudei* n. sp.; 1–5, holotype, CEGH-UNC 23.982, external mould (latex replica): 1, dorsal view, note the wide glabella and smooth axial rings; 2, lateral view; 3, dorsolateral view; 4, dorsoanterolateral view, showing effacement of the lateral border furrow; 5, anterior view, showing the relatively depressed thorax; 6–10, paratype, CEGH-UNC 23.983, external mould (latex replica): 6, dorsal view of external latex mould; 7, lateral view, note the pronounced slope of preglabellar field; 8, dorsolateral view; 9, dorsoanterolateral view showing wide and depressed thorax; 10, anterior view, note the extreme lateral expansion of librigenal border. All from the upper part of the Talacasto Formation, at Loma de los Piojos section, Early Emsian, San Juan Province. Scale bar: 5 mm.

convex forward in dorsal view; posterior and lateral field could not be adequately appreciated. Pleural field with interpleural furrows (apparently corresponding to segments one and two) more evident than interpleural ones.

Discussion.—*Maurotarion (Malvinotarion) haudei* n. sp. and the co-occurring *M. (Malvinotarion) gauchio* n. sp. are considered sister taxa. They share a short and sloped preglabellar field; glabella with moderate inflation and scarcely convex dorsal surface; lateral border furrow strongly trending to effacement; long, flat and broad genal spines with very broad base and elongated subtriangular shape; narrow (tr.) segments adaxial to fulcrum in the pleural lobe; and very similar small pygidia. Differences lie principally in the curved anterior margin without bell-like contour in *M. (Malvinotarion) gauchio* n. sp., which has a shorter (sag., exsag.) anterior border; more elongated glabella; librigena with narrower (tr.) lateral border; narrower (tr.) genal spine and genal spine base; narrower thorax with more convex and narrower thoracic lobes, and small spiny tubercles on the axial rings. Although juveniles of *M. (Malvinotarion) gauchio* n. sp. are similar to the mature holaspis of *M. (Malvinotarion) haudei* n. sp. (compare

Fig. 3.13–14 and Fig. 4), the insufficient ontogenetic information from this species prevent further interpretations of heterochrony.

Maurotarion (Malvinotarion) gauchio n. sp. and *M. (Malvinotarion) haudei* n. sp. are closely related to *M. (Malvinotarion) isaacsoni* Adrain and Edgecombe, 1996, from Pragian-Emsian of Gamonedá Formation, Subandean Ranges of Bolivia, and to *M. (Malvinotarion) sp. A* Adrain and Edgecombe, 1996, from the Bokkeveld Group of South Africa, no older than Late Emsian.

Maurotarion (Malvinotarion) gauchio n. sp. differs from *M. (Malvinotarion) isaacsoni* in a narrower (tr.) cephalon, anterior margin more curved, shorter (sag.) anterior border, anterior border furrow without a strongly defined inverted “V,” longer (sag.), and narrower (tr.) glabella with flattened dorsal surface, narrower (tr.) lateral border, longer and narrower genal spine, and narrower genal spine base.

Maurotarion (Malvinotarion) haudei n. sp. differs from *M. (Malvinotarion) isaacsoni* mainly in its wider (tr.) cephalon, which has a bell-like anterior margin contour, shorter anterior border and preglabellar field, less evident inverted “V”

contour, wider (tr.) glabella with flattened dorsal surface, broader and more laterally expanded lateral border, much broader genal spine base, wider and longer genal spine, and wider (tr.) thorax that is somewhat more depressed, without tubercles on axial rings.

Maurotarion (*Malvinotarion*) sp A from South Africa resembles *M. (Malvinotarion) isaacsoni*, *M. (Malvinotarion) gaucho* n. sp. and *M. (Malvinotarion) haudei* n. sp. in its (although extremely short) subtriangular genal spines, broad genal spine bases, effaced lateral border furrow and narrower section adaxial to the fulcrum on thoracic segments. Differences consist of shorter anterior border furrow, anterior border and preglabellar field, barely inclined, weakly inflated glabella, and shorter genal spine.

Evidently, the compared species are related and the phylogenetic implications will be fully explored in the general discussions.

MAUROTARION (*MALVINOTARION*?) new species A
Figure 5.1–5.5

Materials, occurrence and stratigraphic position.—The only assigned material is CEGH-UNC 23.949, an almost complete cranidium poorly preserved in micaceous clayed light fine sandstones with bioturbations. It comes from the 23–4 point of the Lipeón Formation, corresponding to an approximately 30 m thick, more fossiliferous segment located about 320 m above the base (see Sánchez, 1989, fig. 2). This point, placed in the lower part of the middle member, most probably corresponds to Late Llandovery–Early Wenlock levels according to trilobites (Waisfeld and Sánchez, 1993, p. 79) and chitinozoan evidence (Grahn and Gutiérrez, 2001, p. 37). However, a more ancient (Llandovery) age seems to be indicated by graptolites (Rickards et al., 2002, p. 346).

Discussion.—Following Adrain and Edgecombe (1996), the assignment to *Maurotarion* is on the basis of the anterior section of facial suture less laterally extended than the palpebral lobe in appearance, anterior border sagittally more lengthened, and anterior border furrow describing (although slightly) an inverted “V” shape. The assignment to the new subgenus *Malvinotarion* is tentative (in open nomenclature) because no librigenae are known, and it is indicated by the “?” in the same way as other similar cases along the text for which no librigenal data are available. This form most closely resembles *M. (Malvinotarion?)* cf. *dereimsi*, from the El Carmen Formation (eastern Bolivia). Similarities are given by a subquadrate and weak to moderately inflated glabella (in spite of the fact that the most dorsal glabellar surface is eroded in the Lipeón specimen), with rather straight anterior side, anterior border with only very subtle sagittal lengthening, very weakly defined inverted “V” shape of preglabellar furrow (for the genus), and a similar shaped profile. Proportions between sagittal length of the preglabellar field and anterior border, and degree of glabellar furrow impressions seem to differ. Despite of the poor preservation of the specimen of *M. (Malvinotarion?)* n. sp. A, it seems to have scattered tubercles and granulated sculpture on the preglabellar field, which would be a major difference with respect to comparable species. Resemblances and differences with *M. (Malvinotarion) dereimsi* Adrain and Edgecombe, 1996, are obviously the same in general terms, yet a more inflated glabella and a less defined glabellar constriction seem to separate the Lipeón and El Carmen forms from *M. (Malvinotarion) dereimsi*. Nevertheless, as pointed out, without librigenal features it is not possible to decide with certainty whether the El Carmen Formation form is effectively a new species more closely

related to the Lipeón species than to *M. (Malvinotarion) dereimsi*. This new record from the Lipeón Formation is decisive in considering the origin of the aulacopleurids in western Gondwana basins, particularly in the Malvinokaffric Realm, and will be treated in the general discussions.

MAUROTARION (*MALVINOTARION*?) new species B
Figure 5.6–5.10

Materials, occurrence and stratigraphic position.—The single specimen CEGH-UNC 10.497 consists of a part and counterpart of a nearly complete cranidium, preserved in a greenish-gray micaceous concretion, from the uppermost part of the Talacasto Formation at Cerro La Chilca section. These levels are considered lowermost Emsian, according to brachiopod and stratigraphic position (Herrera, 1993; Vaccari et al., 1994; Herrera and Bustos, 2001).

Discussion.—This specimen is, in appearance, closely related to *M. (Malvinotarion?)* n. sp. A, *M. (Malvinotarion) dereimsi*, *M. (Malvinotarion?)* cf. *dereimsi* from the El Carmen Formation, and *M. (Malvinotarion) talacastoense* n. sp. Similarities lie principally in the glabella, which is subquadrate, weak to moderately inflated, with antero-lateral constriction, S2 strongly impressed and relatively large L1. However, it differs in the anterior part of the cranidium which is in general lengthened, scarcely sloped in sagittal profile and directed forward, with preglabellar field approximately as long as anterior border (sag., exsag.), and anterior margin more curved. This last situation is identical to *M. (Malvinotarion) dereimsi*'s, which exhibits no caeca as well. Differences from *M. (Malvinotarion) talacastoense* n. sp. lie in the absence of caecal ornamentation and anterior margin with a less-opened inverted “V” contour. The lack of librigenal morphologies prevents further comparisons. Despite the fact that this specimen reasonably represents a new species, the nomenclature is left open due to the scarcity of the available material.

MAUROTARION (*MALVINOTARION*) sp.
Figure 5.11–5.15

Materials, occurrence and stratigraphic position.—The single specimen is CEGH-UNC 7.086, part and counterpart of a nearly complete cephalon with a few thoracic segments, preserved in greenish-gray mudstones. The specimen comes from Lochkovian levels of the Talacasto Formation at Portezuelo del Tambolar section, collected by Dr. Z. Herrera.

Discussion.—In spite of the crushed frontal area, the assignment to *Maurotarion* seems reliable, because of a recognizable inverted “V” anterior border furrow and librigenal features agreeing with the diagnosis of *M. (Malvinotarion)* n. subgen. This specimen could represent a new taxon on grounds of its very wide (tr.) interocular fixigena and palpebral lobe, tall occipital ring dorsally convex and acute, extremely wide (tr.) glabella with large L2 and L1, and very well impressed S2. This form most closely resembles *M. (Malvinotarion) dereimsi*, *M. (Malvinotarion?)* cf. *dereimsi* and *M. (Malvinotarion) talacastoense* n. sp. Similarities lie principally in the glabella, which is subquadrate, moderately inflated, and with antero-lateral constriction. Resemblances are particularly strong with *M. (Malvinotarion) talacastoense* n. sp., because of subtle librigenal caeca, strong antero-lateral glabellar constriction and very broad (tr.) librigena and genal spine base. However, the nomenclature is left open due to the single available specimen and its degree of deformation, which render the recognition of a new taxon unreliable.

M. (Malvinotarion) sp. together with *M. (Malvinotarion) talacastoense* n. sp., are the most ancient representatives of the

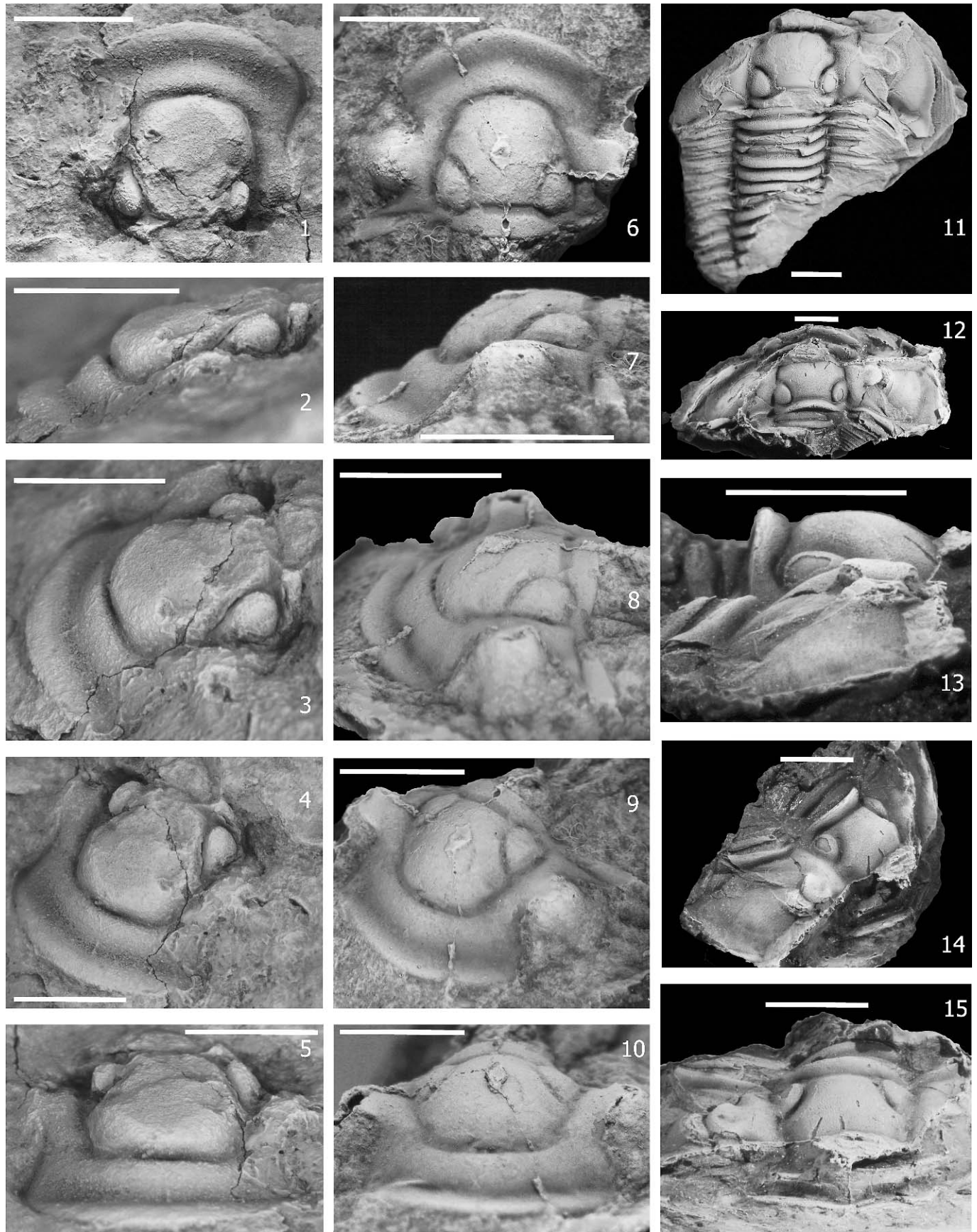


FIGURE 5—1–5, *Maurotarion* (*Malvinotarion*?) n. sp. A, CEGH-UNC 23.949, lower part of middle “light clayed” member of the Lipeón Formation, Llandoverly-Wenlock, access to the 9 de Octubre mine section, Zapla Ranges, Jujuy Province; 6–10, *Maurotarion* (*Malvinotarion*?) n. sp. B, CEGH-UNC 10.497, external mould (latex replica), upper part of the Talacasto Formation at La Chilca section, Early Emsian, San Juan Province; 11–15, *Maurotarion* (*Malvinotarion*) sp., CEGH-UNC 7.086: 11; internal mould, 12–15 external mould (latex replica); lower part of the Talacasto Formation at Portezuelo del Tambolar section, Lochkovian, San Juan Province. Scale bar: 5 mm.

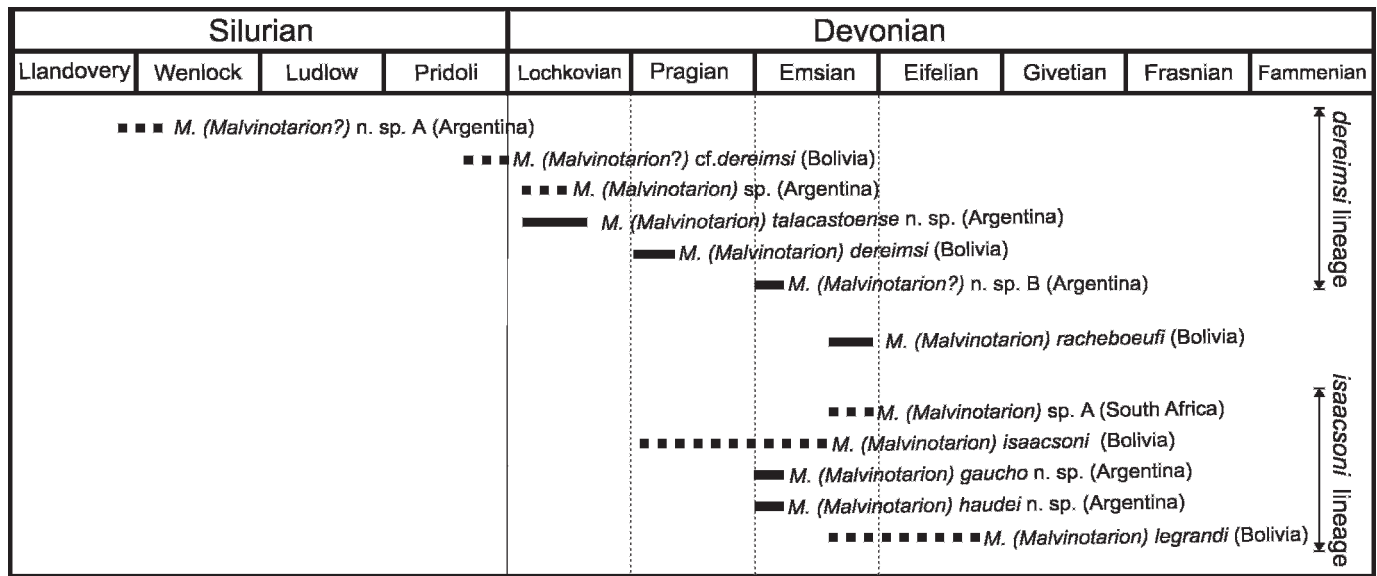


FIGURE 6—Stratigraphic ranges of Malvinokaffric aulacopleurids (stratigraphic scheme from Adrain and Edgecombe, 1996, with slight modifications according to Grahn, 2002 and 2005). Solid lines represent confirmed ranges; dashed lines represent most probably ranges following from imprecise occurrences. A Devonian radiation can be observed. Note the consistency between stratigraphic data and phylogenetic relationships discussed in the text and Figs. 7 and 8. Several first stratigraphic appearances during Emsian suggest an evolutionary burst for this period.

genus in the Malvinokaffric Devonian, and fill the Lochkovian gap of *Maurotarion* in Bolivia.

CONCLUSIONS

Paleobiogeographic aspects.—The origin of Malvinokaffric aulacopleurids had been initially supposed to be derived from cosmopolitan groups already present during the Silurian (Eldredge and Ormiston, 1979). However, since Silurian records were unknown, Adrain and Edgecombe (1996) proposed migration waves during Lower Devonian, one for the earliest Pragian and other for the Emsian, as an explanation. Later, the latest Silurian (Pridolian) record from the El Carmen Formation suggested no migrations, making necessary a reconsideration of the issue (Edgecombe and Fortey, 2000). In this study, *Maurotarion* (*Malvinotarion?*) n. sp. A from the Lipeón Formation represents an unquestionably pre-Devonian (Early Silurian) aulacopleurid record in western Gondwana. As a consequence, aulacopleurids must be reliably considered cosmopolitan trilobites since Silurian times, from which originated the Malvinokaffric Devonian forms. Thus, no migration assumptions are necessary to explain the Devonian origin of the group in western Gondwana basins, a finding in agreement with the paleobiogeographic proposals of Eldredge and Ormiston (1979). The Silurian absence previously postulated for aulacopleurids in these basins (particularly in Bolivia and Northwestern Argentina) can be considered an artifact largely due to their low abundance and insufficient sampling. A similar problem could complicate the Silurian-Devonian record in intracratonic areas from South America (i.e., principally Brazilian basins) where, surprisingly, no aulacopleurids are known. This may also be the case in the Argentine Precordillera basin where the complete absence of aulacopleurids during the Silurian, together with their sudden occurrence by the Early Devonian, seem to indicate an earliest Devonian migration from other Malvinokaffric basins; while in contrast, coeval Silurian dispersals are indicated by cosmopolitan brachiopods (Benedetto et al., 1992; Sánchez and Benedetto, 1996) and trilobites (Waisfeld et al., 1988; Waisfeld and Sánchez, 1993;

Edgecombe et al., 1994b; Edgecombe and Ramsköld, 1994). Unfortunately, librigenal data of the most ancient representatives (Silurian Lipeón and El Carmen specimens) are unknown, hindering further phylo-geographic precisions on the origin of synapomorphic (*Malvinotarion*-type) features of the Devonian species.

Phylogenetic and evolutionary aspects.—The Argentinian *Maurotarion* recognized in the present work total five new species, three of which are formally named. This represents a group as diverse as all remaining previously known Malvinokaffric species (Adrain and Edgecombe, 1996), making a total of ten of them known up to the present.

Among the Malvinokaffric *Maurotarion* species previously known, Adrain and Edgecombe informally recognized (1996) two groups: the “*dereimsi* group” and another unnamed group. The “*dereimsi* group” included: *M. (Malvinotarion) dereimsi*, *M. (Malvinotarion) racheboeufi* and *M. (Malvinotarion) legrandi*, related on the basis of their lateral border furrow shallowing in front of the genal angle, posterior border furrow bending backward distally to run along dorsal aspect of genal spine, and only subtle sagittal lengthening of the anterior border. The second unnamed group, included *M. (Malvinotarion) isaacsoni* and *M. (Malvinotarion) n. sp. A* from South Africa, is characterized by a librigena with the lateral border furrow almost completely effaced, the lateral border extremely broad, short and subtriangular genal spines with exceedingly broad bases, and a thorax with a very narrow section of the pleural lobe adaxial to the fulcrum. In light of the data treated herein, that grouping appears justified with slight modifications, and two major groups can be recognized: the *dereimsi* lineage and the *isaacsoni* lineage (Figs. 6, 8).

The *dereimsi* lineage involves the Devonian species *M. (Malvinotarion) dereimsi* and closely related species, this is: *M. (Malvinotarion) talacastoense* n. sp., *M. (Malvinotarion) sp.*, *M. (Malvinotarion?) n. sp. B*, and eventually *M. (Malvinotarion?) cf. dereimsi* from the El Carmen Formation. The position of the Early Silurian *M. (Maurotarion) n. sp. A* from the Lipeón Formation could be interpreted as basal within the *dereimsi* group, according its discussed characters

(Fig. 8). But, alternatively it could be considered basal for the whole *M. (Malvinotarion)* clade taking into account that it is the most ancient aulacopleurid known for the Malvinokaffric Realm, and it could bear scattered tubercles as a basal condition.

The *dereimsi* lineage is considered to have evolved from Silurian to latest Pragian or earliest Emsian times (Figs. 1.1, 6, 8). It is characterized by weakly inflated subquadrate glabellae with an antero-lateral constriction, lack of any sculpture apart from subtle caeca, preglabellar field not abruptly inclined, and relatively well impressed (but delicately in comparison to some non Malvinokaffric congeners) lateral border furrow. This group of species seems to be a plesiomorphic one because it does not display (at least in the cranidium) any evident evolutionary trend, retaining in Devonian species the general characters of Silurian representatives. Librigenal characters of this group are so poorly known to state conclusive internal relationships. In fact, when compared with the Lochkovian *M. (Malvinotarion) talacastoense* n. sp. and *M. (Malvinotarion)* n. sp., only the derivated tube-like genal spine tip of the younger (Early Pragian) *M. (Malvinotarion) dereimsi* indicates polarity. Therefore, and in spite of the successive stratigraphic ranges of each species (Fig. 6), we only tentatively consider this group as a lineage. To be conservative, it is graphically represented with unresolved and putative internal relationships in members without known librigenae (Fig. 8). The *isaacsoni* lineage relates *M. (Malvinotarion) isaacsoni*, *M. (Malvinotarion)* sp. A from South Africa, *M. (Malvinotarion) gaucho* n. sp., *M. (Malvinotarion) haudei* n. sp. and *M. (Malvinotarion) legrandi*, evolving during Pragian-Eifelian times (Figs. 6, 8). They share moderate to considerably inflated glabellae, lateral border furrow trending to effacement, very broad genal spine and genal spine bases (even for the subgenus), flat genal spines with more or less subtriangular shape and variable length (sometimes very long), and fulcral line closer to the axial furrow than to the margin, in the thorax.

A morphologic trend can be recognized in the *isaacsoni* lineage from *M. (Malvinotarion) isaacsoni* up to *M. (Malvinotarion) legrandi*, passing by intermediate stages in *M. (Malvinotarion) gaucho* n. sp. (Fig. 7). This trend consists of sagittal shortening of the frontal area and increasing of the slope, narrowing of librigenal field, broadening of librigenal border and, above all, a strong lengthening and proportional narrowing of the genal spine. The youngest (Emsian-Eifelian) *M. (Malvinotarion) legrandi* is considered an extreme in the described evolutionary trend. As indicated, a probable paedomorphic relationship with *M. (Malvinotarion) gaucho* n. sp. supports this interpretation. In this way, the tuberculation and wide (tr.) anterior and lateral border furrows of *M. (Malvinotarion) legrandi* could be interpreted as a reversal and autapomorphic features, respectively, although other phylogenetic possibilities cannot be rejected.

Another issue is the relation of *M. (Malvinotarion)* sp. A from South Africa with the *isaacsoni* lineage. Adrain and Edgecombe (1996), already noted the similarities with *M. (Malvinotarion) isaacsoni*, and our data seem not to drastically alter this proposal (Fig. 8). It would be considered a sister taxon of the *isaacsoni* lineage, in a trend toward scarcely inflated glabella and shortening of genal spines (which acquire a typical brief triangular shape). Another possibility implies a basal position in the major trend of genal lengthening as described in the *isaacsoni* lineage, but the Late Emsian age of this species does not suggest this possibility (see Fig. 6).

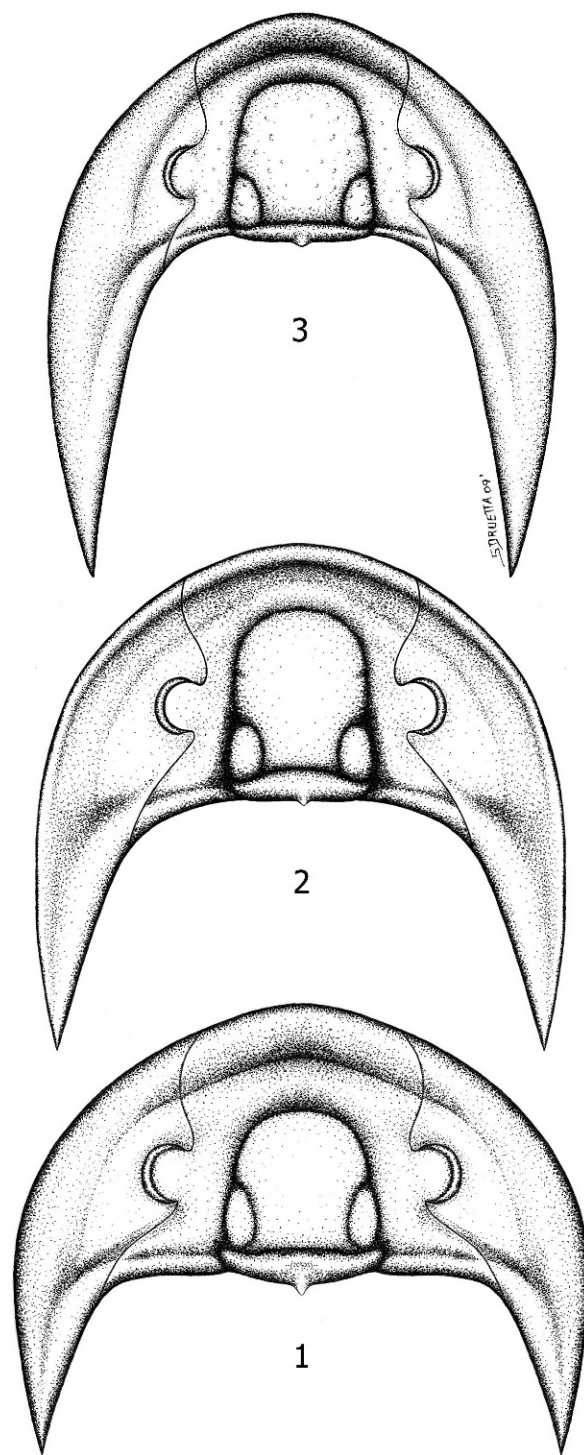


FIGURE 7—Evolutionary trend in the *isaacsoni* lineage. 1, *Maurotarion (Malvinotarion) isaacsoni* Adrain and Edgecombe, 1996, Pragian-Early Emsian from Bolivian Altiplano, long (sag.) frontal area, wide (tr.) genal spines reaching up to seventh thoracic segment, wide (tr.) librigenal field, ($\times 3.2$); 2, *Maurotarion (Malvinotarion) gaucho* n. sp., Early Emsian from western Argentina, shortening of frontal area, narrowing and lengthening of genal spines reaching the tenth thoracic segment, narrowing (tr.) of librigenal field, broadening (tr.) of lateral border, ($\times 4.3$); 3, *Maurotarion (Malvinotarion) legrandi* Adrain and Edgecombe, 1996, Late Emsian-Late Eifelian from Subandean Ranges of Bolivia, shortened frontal area, extremely narrow and very long genal spines, narrow librigenal field and broad lateral border, ($\times 4$). All rescaled to the same glabellar transverse width across L1.

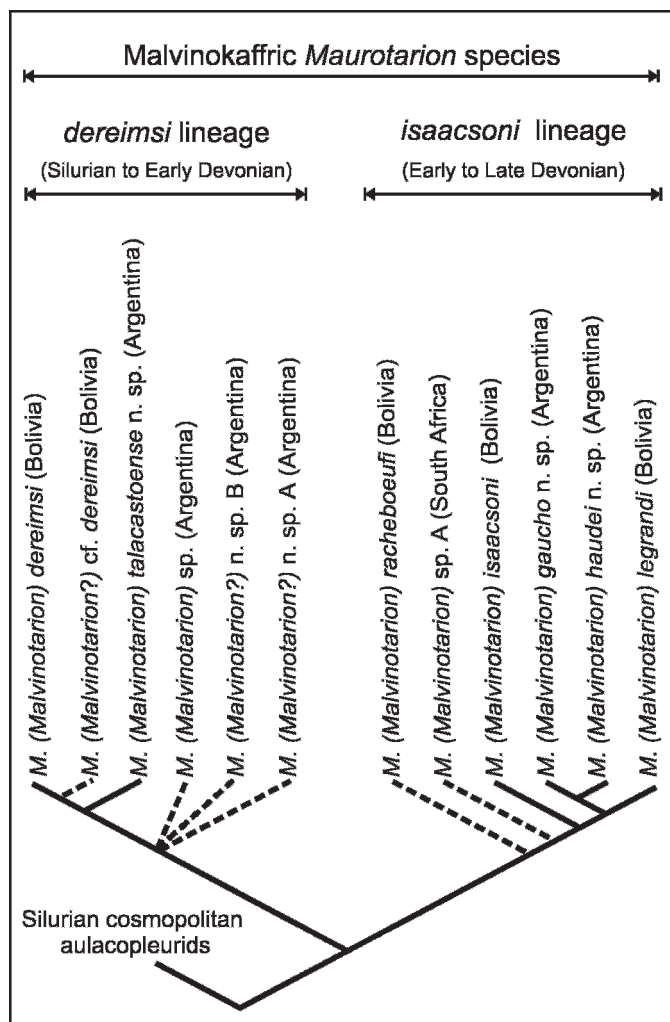


FIGURE 8—Phylogenetic hypothesis of Malvinokaffric *Maurotarion* explored in this work. Solid lines are best supported relationships, dashed lines represent tentative ones (see discussion in the text).

The relationship of the *isaacsoni* lineage with the *dereimsi* lineage remains unclear. An intermediate form could be *M. (Malvinotarion) racheboeufi*, which has an unusual combination of characters: a strongly globose glabella more similar to that of *M. (Malvinotarion) isaacsoni*, and a librigena which has been related by Adrain and Edgecombe (1996) to that of *M. (Malvinotarion) dereimsi*. However, the glabellar inflation degree and cephalon shape most closely resemble the *isaacsoni*-type. At present this is considered putative (Fig. 8), pending a cladistic analysis with more data.

A significant aspect can be recognized in the Malvinokaffric evolutionary history of the genus: a great Devonian diversification (Fig. 6). The sudden occurrence of *M. (Malvinotarion) talacastoense* n. sp., and *M. (Malvinotarion) sp.*, by the Lochkovian, would signal a moderate initial radiation already by lowermost Devonian in coincidence with other trilobite patterns (Abe and Lieberman, 2009). However, the scarce Silurian-Devonian boundary data from Bolivia and Argentina impede further assessment on this evolutionary pattern.

Conversely, a major diversification for the subgenus can be recognized by Emsian times. During this period at least *M. (Malvinotarion?)* n. sp. B, *M. (Malvinotarion) gaucho* n. sp., *M. (Malvinotarion) haudei* n. sp., *M. (Malvinotarion)*

racheboeufi, *M. (Malvinotarion) legrandi* and *M. (Malvinotarion)* sp. A from South Africa have their stratigraphic first appearance (see Fig. 6). As a matter of fact, this represents about 60 percent of species of the subgenus *Malvinotarion* participating in an evolutionary burst. Since the cladistic structure became rapidly very complex, which is indicated by the timing and phylogenetic structure of the *isaacsoni* lineage, a high cladogenetic rate can be inferred for this period, as is typical in radiation patterns (i.e., Eldredge and Cracraft, 1980; Lieberman et al., 1991; Hulbert, 1993; Lieberman, 2001). In addition, the possibility of an evolutionary burst explaining the Emsian occurrence of other trilobites like calmoniid genera allied to the *Bouleia* Group from Bolivia (e.g., *Malvinella*, *Plesiomalvinella*, *Vogesina*, *Palpebrops* and *Metacryphaeus*) was already noted (Edgecombe et al., 1994a). Finally, some considerations about the high level of endemism observed in other groups such as brachiopods (Isaacson, 2007) and bivalves (Dalez Farjat, 2005) during this interval independently support these ideas.

The radiation pattern described could be related with some extrinsic factors such as eustasy. Global eustatic curves display a strong fall of relative sea level during the Lochkovian-Pragian to Emsian, which peaked precisely at the Pragian-Emsian boundary before an earliest Emsian major transgression (Johnson et al., 1985) registered as a condensed stratigraphic interval (Haq and Shutter, 2008). In spite of the tectonic settings of convergent margins proposed for Devonian Andean basins, this eustatic pattern has been recognized in Bolivian and northwest Argentinian basins (Albariño et al., 2003; Álvarez et al., 2003) and particularly in the Argentine Precordillera basin (Astini, 1991; Ferrero, 2006).

Thus, falling sea level encouraging vicariance and concomitant speciation can be posited for pre-Emsian times, particularly during Pragian, and related to the recognized taxic radiation pattern during the Emsian. However, it must be pointed that this Emsian pattern of diversification could be representing an effect of the delay in the record of the first stratigraphic appearance of the involved species with respect of their true moment (mainly Pragian) of origination or divergence (this is, ghost lineages sensu Edgecombe, 1992 and Smith, 1994), in combination with the bias of the fossil record during highstands (Holland, 1995).

The evidence can integrally be considered one more example of correlation between extrinsic factors and evolutionary events which are well understood and recognized in the fossil record in many different taxonomic groups (e.g., Eldredge and Branisa, 1980; Eldredge and Cracraft, 1980; Vbra, 1980; Boucot, 1985; Brooks and McLennan, 1991; Lieberman, 1993; Lieberman and Eldredge, 1996; Lieberman, 2000; Lieberman, 2003; Rode and Lieberman, 2004; Lieberman, 2005; Rode and Lieberman, 2005; Bartholomew and Brett, 2007; Lieberman et al., 2007; Lieberman, 2008; Abe and Lieberman, 2009; etc.).

This approach, as a contribution to the knowledge of the dynamic between biotic and geologic-eustatic events in the Malvinokaffric Devonian, will be significantly improved by a further work performing a more exhaustive cladistic analysis involving more than a single aulacopleurid genus.

The Malvinokaffric Realm, because of its endemic faunas established in isolated tectonics basins, was proposed as a natural model to study the relationships between spatial distribution of taxa, geologic history of a region, and patterns of global eustasy (Lieberman, 1993). Much of the observations of this work are in accordance with that prediction.

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