South American Ordovician phyllocarids (Crustacea, Malacostraca)

PATRICK R. RACHEBOEUF, SYLVIE CRASQUIN & †EDSEL BRUSSA

A detailed morphological analysis of exoskeleton remains of the South American Ordovician phyllocarid crustaceans leads to the recognition of a previously unexpected biodiversity from the Tremadocian up to the Katian. As a result, the genus *Caryocaris*, as up to now understood, clearly appears to be a comprehensive genus. Taxonomically significant characters are listed and discussed. Two new caryocaridid genera are described: *Janviericaris* gen. nov., and *Ivocaris* gen. nov. The diagnosis of the Family Caryocarididae is emended accordingly. In addition to the previous description of *Caryocaris acuta* Bulman, 1931 from Peru, *C. bodenbenderi* Aceñolaza & Esteban, 1996 and *C. delicata* Racheboeuf, Vannier & Ortega, 2000 from Argentina, seven phyllocarid species belonging to five genera are identified from the Tremadocian up to the Sandbian of Argentina and Bolivia. New caryocaridid representatives are *Caryocaris acoitensis* sp. nov., *Ivocaris saltitensis* sp. nov., *Janviericaris formosa* sp. nov. and *J. jujuyensis* sp. nov.; three other Sandbian and lower Katian forms are provisionally left in open nomenclature as *Caryocaris* sp. A to C. Ceratiocaridids are represented by the Upper Ordovician genus *Pumilocaris* Racheboeuf, Vannier & Ortega, 2000, with *Pumilocaris granulosa* Racheboeuf, Vannier & Ortega, 2000 and *Pumilocaris acuta* (Bulman, 1931). The familial assignment of the late Tremadocian-Floian genus *Rolfecaris* gen. nov., represented by *Rolfecaris lethiersi* sp. nov. and *R. parchaensis* sp. nov., to the Family Ceratiocarididae still remains uncertain. Caryocaridid phyllocarids have been revealed to be a significantly potential tool for both Ordovician biostratigraphy and palaeobiogeography. • Key words: Phyllocarida, crustaceans, biodiversity, biostratigraphy, paleobiogeography, Ordovician, South America.

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Field work undertaken since the 2000s, mainly through the Argentina-France scientific programme of cooperation 'Faunes paléozoïques de l'Ouest de l'Argentine' of ECOS-Sud (Action A99U03, 2000–2002) allowed completion of the Ordovician phyllocarid inventory in South America. Previous data from Argentina (Racheboeuf *et al*. 2000) have been completed by field work in Argentina (2000, 2001) and in Bolivia (2001, 2002). The aim of the present paper is to give an overview of the Ordovician phyllocarid biodiversity in South America and to clarify their stratigraphic range with respect to the graptolite zonation.

The first occurrence of a South American Ordovician phyllocarid crustacean was discovered by Bulman (1931) who described *Caryocaris acuta* from supposed Caradoc age strata in Peru. Rusconi (1950) described the genus *Mendocaris* (type species *M. australis*, OD) from the Cambrian of western Argentina, the holotype of which (by monotypy) is preserved in the collection of the Museo de Ciencias Naturales de Mendoza (MCNAM) under No. 7556. The specimen was poorly described and not illustrated (as already mentioned by Rolfe *in* Treatise 1969, p. R326). Revision of the type specimen by one of us (E.B.) confirms that it cannot be formally assigned to any crustacean nor to any other zoological group. Hence the genus name *Mendocaris* has to be considered a nomen dubium until the discovery of new specimens. More recently, Aceñolaza & Esteban (1996) described *Caryocaris bodenbenderi* from the Tremadoc beds of northern Argentina and southern Bolivia, later Racheboeuf *et al*. (2000) described *Caryocaris delicata* from Llanvirn strata, and

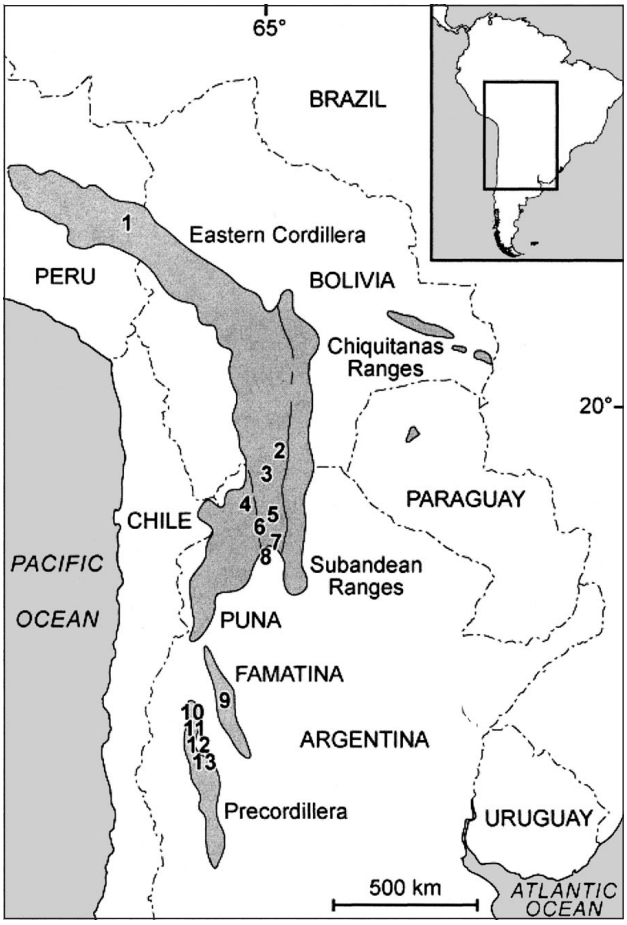

Figure 1. Geographic location of localities from Argentina, Bolivia and Peru listed and sampled in this paper. Peru: 1 – Huichiyuni. Bolivia: 2 – Quebrada de Chapiuno, 3 – Cieneguillas section. Argentina: 4 – Muñayoc Creek, 5 – Los Colorados section, 6 – Mina Natasia section, 7 – Agua Blanca Creek, 8 – Parcha-Incamayo Creek, 9 – Portezuelo de la Alumbrera Creek, 10 – Zonja Honda Creek, 11 – Los Saltitos Creek, 12 – Potrerillos hill, 13 – Los Azules Creek.

Pumilocaris granulosa from early Caradoc beds, both from the Argentine Precordillera.

Between 1931 and 2000 numerous South American Ordovician phyllocarid remains have been reported and listed – but rarely illustrated – mainly in open nomenclature as *Caryocaris* sp., from many localities of Argentina and Bolivia by Harrington & Leanza (1957), Ahlfeld & Branisa (1960), Branisa (1965), Aceñolaza (1966), Mendez (1973), Aceñolaza *et al*. (1976), Súarez-Soruco (1976), Hughes (1980), Ramos (1984), Ortega (1987), Manca (1991), Hannibal & Feldmann (1996), Racheboeuf *et al*. (2000) and Legrand-Smith & Hannibal (2000). Other caryocaridid occurences have been published, such as that of *Caryocaris* sp. from the upper Llanvirnian beds of the San José Formation of Peru, *i.e.* in an older level that the *Caryocaris acuta* of Bulman (Laubacher 1974). Ordovician phyllocarids also occur in the Darriwilian El Higado Formation of the Andean Cordillera Central of Colombia (Gutiérrez-Marco *et al*. 2006, p. 624), and *Caryocaris* sp. was listed from Arenigian levels of the southwestern Llanos of Colombia (Trumpy 1943, p. 1289; Turner 1960; Harrington & Kay 1951, p. 656). Two recent overviews of Ordovician phyllocarids, partly dealing with South America faunas, have been recently published by Vannier *et al*. (2003) and Racheboeuf (2004). All known citations of South American Ordovician phyllocarids drawn from the literature are listed in Table 1 below.

Palaeontological collections

Specimens from Argentina described and illustrated here are housed in the collections of the Universidad Nacional de Córdoba (UNC, No. CORD PZ), the collections of the Instituto Miguel Lillo of the Universidad de Tucumán (No. PIL) and the Universidad de Mendoza (No. UM). Materials from Peru are housed in the Naturhistoriska Riksmuseum of Stockholm (Sweden) (No. Ar) and those from Bolivia are housed in the Museo de Historia Natural Alcide d'Orbigny in Cochabamba (No. MNHNC).

Localities and stratigraphy

Ordovician phyllocarid remains have been cited, and/or found and collected in the four main sedimentary basins of the Andean belt: 1) the Central Andean Basin, located in northern Argentina, extending into Bolivia, Chile and Peru, 2) the Famatina Basin, 3) the Precordillera Basin (Fig. 1) and 4) the Central Cordillera of Colombia. We follow criteria by Astini (2003) regarding the Puna, the Cordillera Oriental ('Eastern Cordillera') and the Sierras Subandinas ('Subandean Ranges') within the Northwest Basin although this region corresponds to the southern extent of the Central Andean Basin.

Puna

The Puna region belongs to the Eastern Eruptive Belt (Faja Eruptiva Oriental) and the phyllocarid *Janviericaris jujuyensis* gen. et sp. nov. has been collected in three distinct horizons of the Muñayoc section in the west of the Quichagua and Cochinoca Ranges. The fossiliferous black shales belong to the Muñayoc-Cochinoca-Escaya volcanosedimentary Complex. The sections are difficult to measure because of intense folding. The results of facies analysis reveal that the volcano-sedimentary succession record and the upward progression from mudstone-dominated deposits, have to be attributed to deposition under storm and wave influenced processes (Martínez *et al*. 1999, Coira & Pérez 2002). Vertical sequences include a range of types from Bouma turbidites-like beds to heterolithics lithofacies dominated by

Table 1. Citations of South American Ordovician phyllocarid taxa drawn from the literature, from 1931 to 2006. Asterisk indicates type species.

Genera and species	Authors	Range	Country
Family Caryocarididae			
Caryocaris	Salter, 1863		
acuta	Bulman, 1931	Caradoc	Peru
acuta	Camacho, 1975	Ordovician	Argentina
acuta	Súarez-Soruco, 1976	Llanvirn	Bolivia
acuta	Legrand-Smith & Hannibal, 1996	?Arenig	Bolivia
acuta	Racheboeuf, 2004	?Caradoc	Peru
bodenbenderi	Aceñolaza & Esteban, 1996	Tremadoc	Argentina
bodenbenderi	Racheboeuf *et al*., 2000	Tremadoc	Argentina
bodenbenderi	Racheboeuf, 2004	Tremadoc	Argentina
delicata	Racheboeuf *et al*., 2000	Llanvirn	Argentina
delicata	Racheboeuf, 2004	Darriwilian	Argentina
sp.	Trumpy, 1943	Arenig	Colombia
sp.	Harrington & Kay, 1951	Arenig	Colombia
sp.	Harrington & Leanza, 1957	Arenig	Argentina
sp.	Ahlfeld & Branisa, 1960	Arenig	Bolivia
sp.	Turner, 1960	Arenig	Colombia
sp.	Branisa, 1965	Arenig	Bolivia
sp.	Aceñolaza, 1966	Arenig	Argentina
sp.	Ramos, 1970	L-M. Arenig	Argentina
sp.	Mendez, 1973	Arenig	Argentina
sp.	Laubacher, 1974	L. Lanvirn	Peru
sp.	Súarez-Soruco, 1976	Trem./Arenig	Bolivia
sp.	Aceñolaza *et al.*, 1976	Arenig	Argentina
sp.	Hughes, 1980	Trem./Arenig	Bolivia
sp.	Ramos, 1984	Arenig–Llanvirn	Argentina
sp.	Ortega, 1987	Llanvirn	Argentina
sp.	Manca, 1991	Tremadoc	Argentina
sp.	Aceñolaza & Esteban, 1996	Trem.– Llandeil.	Arg.-Boliv.-Peru
sp.	Hannibal & Feldmann, 1996	Arenig/Llanvirn	Bolivia
sp.	Legrand-Smith & Hannibal, 2000	Arenig	Bolivia
sp.	Gutiérrez-Marco *et al*. 2006	Darriwilian	Colombia
sp. 1	Racheboeuf *et al*., 2000	L. Arenig	Argentina
sp. 1	Racheboeuf, 2004	L. Arenig	Argentina
sp. 2	Racheboeuf *et al*., 2000	Caradoc	Argentina
sp. 2	Racheboeuf, 2004	Mohawkian	Argentina
sp. 3	Racheboeuf, 2004	L. Darriwilian	Argentina
Family Ceratiocarididae			
Ceratiocaris sp.	Branisa, 1965	Arenig	S Bolivia
Pumilocaris	Racheboeuf *et al*., 2000		
*granulosa**	Racheboeuf *et al*., 2000	Caradoc	Argentina
granulosa	Racheboeuf, 2004	Mohawkian	Argentina
?sp.	Racheboeuf *et al*., 2000	L. Arenig	Argentina
?sp.	Racheboeuf, 2004	L. Arenig	Argentina
Archaeostraca indet.			
Phyllocarid undet.	Racheboeuf *et al*., 2000	L. Arenig	Argentina
Phyllocarid gen. et sp. nov.	Racheboeuf, 2004	L. Arenig	Argentina
'Pre-epipodites'	Levy, 1971	Arenig	Argentina
Questionable Phyllocarida			
Mendocaris	Rusconi, 1950		
australis	Rusconi, 1950	Cambrian	Argentina

swell-wave generated ripple cross-lamination. The stacking pattern of the graptolitic sequence, overlapping synsedimentary silicic volcanism, is indicative of increasing accommodation space and restricted sediment supply during a relative sea level rise. The graptolites found in the rhythmites suggest a late early/middle Arenig age.

Eastern Cordillera

In the thick sections of the Eastern Cordillera region, the phyllocarids are contained in the Acoite and Parcha Formations. The former and the Santa Rosita Formation comprise the Santa Victoria Group. The Acoite Formation is composed of alternating dominantly sandy and shaly packages. The Acoite Formation records *Tetragraptus phyllograptoides* to *Didymograptellus bifidus* Zones (Toro 1999). Astini (2003) recognized in this unit a transition from oxygen deficient laminated black shales to increasingly bioturbated green shales punctuated by graded sandy beds with rippled tops that could involve long term environmental changes. This transition is developed between the early to mid Arenig (uppermost *B. deflexus* Zone to lowermost *D. bifidus* Zone).

Phyllocarids from the Parcha Formation in the region of the Incamayo Creek are late Tremadocian. The Parcha Formation overlies unconformably the middle Tremadoc Saladillo Formation. It is composed of laminated sandstones and greenish-grey shales with interbedded calcareous lenses indicating a shallow marine environment represented by platforms alternating with transgressive systems. Recent studies in the area (Ortega & Albanesi 2002, Waisfeld *et al*. 2006) have modified the age of the upper levels of this unit, formerly related to the early Arenig. These studies included graptolites, conodonts, trilobites and palynomorphs. The phyllocarid ?*Rolfecaris parchaensis* sp. nov. has been collected all along the unit and its range corresponds to the *Araenograptus murrayi* and *Hunnegraptus copiosus* Zones (late Tremadoc).

Phyllocarids from the south of Bolivia were found in the Chapiuno section, along the Isacayachi-Culpina road, 61.9 km NW of Tarija. The graptolite assemblages permit us to confirm the *Azygograptus lapworthi* Zone equivalent to the *Pseudophyllograptus angustifolius* Zone of Baltoscandia.

Famatina

The Famatina Basin is located between the northern extent of the Precordillera and the Cordillera Frontal to the west and the Sierras Pampeanas region to the east. The Ordovician sections in Famatina are more than 3200 m thick and include (Astini 2003): latest Cambrian to Tremadoc carbonates and siliciclastic rocks, Arenig volcano-sedimentary deposits and Middle Ordovician siliciclastics.

Phyllocarid remains have been collected from three lithostratigraphic units. The oldest one, according to Aceñolaza & Esteban (1996), is the Tremadocian Volcancito Formation which provided the authors with the species *Caryocaris bodenbenderi*. However the stratigraphical statement of the Volcancito Fm. was modified (Esteban 2002) and the entire section of the Portezuelo de La Alumbrera, type locality of *C. bodenbenderi*, belongs to the Bordo Atravesado Formation which also yields late Tremadocian conodonts, graptolites, and trilobites (Albanesi *et al*. 2005). In its type section, the Portezuelo de La Alumbrera section, the lower and middle thirds of the Bordo Atravesado Fm. yield five distinct phyllocarid bearing horizons (Esteban 1996, 1999, 2002; Tortello & Esteban 1995, 2003; Albanesi *et al*. 2005, among others). The depositional environment was interpreted by Astini (2003) as relatively deep-water with a well-stratified water column throughout in which fine-grained settling took place in anoxic bottom conditions.

The La Alumbrera Formation of the Famatina Range (Arenigian) yields *Caryocaris* sp. (Aceñolaza *et al*. 1976, pl. 2, figs 2, 6, 7). Phyllocarid remains also occur in the *Tetragraptus akzharensis* biozone (early Arenigian / basal Floian) of the Portezuelo de las Minitas Formation (Aceñolaza & Gutiérrez-Marco 2000, p. 20).

Argentine Precordillera

The Argentine Precordillera (Baldis *et al*. 1984) is almost 1000 km length and includes vast regions of La Rioja, San Juan, Mendoza and La Pampa provinces. Astini (1992) divided the Precordillera into western and eastern tectofacies to understand more clearly the lower Paleozoic rock distribution in the Precordillera. The eastern domain is represented by Cambrian-Ordovician carbonates, black shales and clastic facies overlying and the western domain is represented by a thick clastic wedge, including bouldery units and mafic rocks. The studied phyllocarids come from four formations of the eastern tectofacies *sensu* Astini, namely the Gualcamayo/Los Azules, Las Plantas and Trapiche formations.

In 1984 Ramos summarized the previously published occurrences of *Caryocaris* sp. in the Argentine Precordillera, most of them being Arenigian. Manca (1991) described *Caryocaris* sp. from the lower Tremadocian Santa Rosita Formation of the Jujuy Province, before the publication of the first monograph dedicated to the Ordovician South American phyllocarids (Racheboeuf *et al*. 2000).

Ivocaris delicata (Racheboeuf, Vannier & Ortega 2000) is one of the most widely distributed phyllocarids along the Los Azules Formation. The outcrops of the Los Azules Formation are exposed along the western flank or the Cerro Viejo anticline, east of Jáchal. This unit has a maximum thickness of 318 meters and is made up mainly of black shale, partly calcareous and partly silicified. The Los Azules Formation was informally divided into three members: lower, middle and upper (Ortega 1987). The lower member is represented by silicified black shales and K-bentonite levels which conformably overlie the San Juan Limestone. Recent analysis of the biostratigraphy, based on graptolites, assigned the lower member to the *Undulograptus dentatus* and *Holmograptus lentus* Zones (Darriwilian, Da2/?Da3) (Ortega & Rickards 2003, Brussa *et al*. 2003b). The middle member includes thin dark sandstones in its basal part and gray laminated siltstones above. The graptolite assemblages of the middle member belong to the *Pterograptus elegans* and *Hustedograptus teretiusculus* Zones (Darriwilian, Da4a and Dab) (Ortega 1987, Brussa *et al*. 2003). A stratigraphic gap is present between the middle and the upper members of the Los Azules Formation. The graptolites of the upper member were assigned to the *Climacograptus bicornis* Zone of the late Sandbian.

The change from the San Juan Formation limestones into graptolite-rich, deep-water black shales of the Gualcamayo Formation and the partly equivalent Los Azules

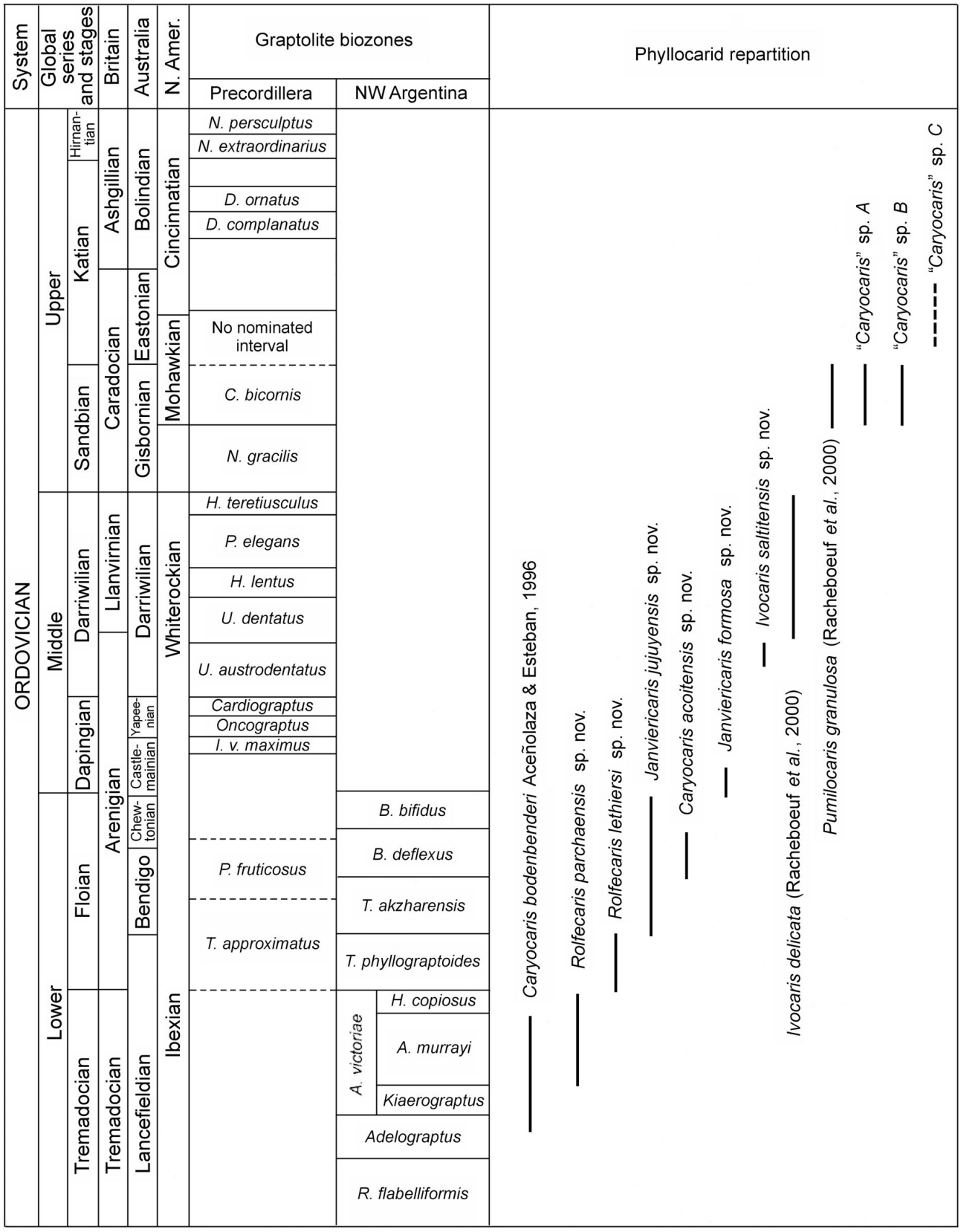

Figure 2. Biostratigraphy and graptolite zonation of the South American Ordovician and vertical range of the phyllocarid taxa from Argentina and Bolivia described in this paper.

Formation (Astini 1994, 2003; Brussa *et al.* 2003b; Ortega & Rickards 2003) is diachronous across the basin. In localities such as Cerro Viejo and Los Saltitos Creek the change is locally expressed as a sharp boundary. Phyllocarids come from both sections. The Gualcamayo Formation in Los Saltitos Creek is 12 m thick and comprises the Middle Member of this unit (*sensu* Astini 1994). The *Undulograptus austrodentatus* Zone (*Undulograptus sinicus* Zone) (Darriwilian/Da1) was recognized in these levels (Brussa & Astini 1996, Brussa & Flores in press), associated with specimens of *Ivocaris saltitensis* sp. nov.

Phyllocarids are also present in the Trapiche Group, the siliciclastic succession deposited above the Gualcamayo Formation. The Trapiche Group is composed of the Las Vacas Formation (330 m) and the Trapiche Formation (more than 800 m). The Las Vacas Formation is a conglomeratic unit with varying facies. Several wedges of fine-grained graptolite-rich silty shales with lenses of fossiliferous limestones (former Las Plantas Formation) are present within this coarse grained interval, reflecting relatively warm climates (Astini 2003). *Pumilocaris granulosa* Racheboeuf, Vannier & Ortega, 2000 is reported from equivalent levels in Cerro Potrerillo. The overlying Trapiche Formation is largely rhythmic with similar proportions of graded sandy beds embedded within black, silty shales and distinctive intercalations of amalgamated thick, sandy, lenticular units and limestone-clast dominated megabeds (Astini 1994, 2003). Only one specimen related to '*Caryocaris'* sp. was reported from this unit in the Quebrada Zanja Honda Creek in the northern Precordillera.

Environmental setting and preservation

According to the literature, Ordovician representatives of the Subclass Phyllocarida mainly belong to the Family Caryocarididae and are, as a whole, considered to have been cosmopolitan members of the active epipelagic zooplankton (Vannier *et al*. 2003). Caryocaridid phyllocarids are mostly found associated with graptolites, in the graptolitic shale facies communities of the pelagic realm and the open-shelf environment, the Benthic Assemblage 6 of Boucot's (1975) classification. They were probably active swimmers (Vannier *et al*. 1997) living near the mesopelagic-epipelagic boundaries (Vannier *et al*. 2003), or in the uppermost part of the water column, in the upper photic zone, most probably associated with carpets of floating algal thalli (Chlupáč 2003).

The recent discovery of caryocaridids in the Upper Ordovician Soom Shale Lagerstätte of South Africa (Whittle *et al*. 2007) sheds new light on the family and to their environment. Firstly, the description of *Caryocaris cedarbergensis* Whittle *et al*. extends the distribution of the family up to the Ashgill, *i.e.*, 10My more than previously established. Secondly, from an environmental point of view, the species is associated with many nektic and nektobenthic organisms, without any graptolite. Whittle *et al*. (2007) concluded that *Caryocaris* was "...a cool-adapted, stenothermic, mesopelagic group during the Early-Middle Ordovician [according to the wide distribution of the genus] and inhabited an epipelagic cold-water shelf environment during the Late Ordovician" (Whittle *et al*. 2007, p. 395). Such an hypothetical environmental shift from mesopelagic to epipelagic and from cool- to cold-water setting, through Ordovician times, can only be considered if we agree that caryocaridids belong to a single genus, namely *Caryocaris*, which is not the case, *Caryocaris* being considered to be a comprehensive genus.

Commonly abundant in the Ordovician black shale graptolitic facies, phyllocarid remains are unfortunately often poorly preserved. Their preservation is directly related to the small-sized, thin, flimsy nature and poorly mineralized composition of the exoskeleton. The flimsy nature of the exoskeleton is indirectly expressed by the scarcity of complete, articulated specimens, as well as by the coiling of carapaces, a post-mortem natural alteration tendency of the exoskeleton (Ekström 1937, Churkin 1966, Chlupáč 1970, Racheboeuf *et al*. 2000). The coiling of the carapace might have occured on the sea floor or, more probably, during their post-mortem fall to the sea floor. Preservation of caryocaridids might also have been affected by their excessive abundance, when carapaces and other exoskeletal parts are accumulated by currents on bedding planes. Poor preservation may also often result from diagenetic and metamorphic processes, or tectonics. The former induced flattening, alteration and/or destruction of the carapace, including mineralization processes, while the latter implied flattening, distortion, stretching etc. No example of coiling could be observed among archaeostracan remains assigned to the Family Ceratiocarididae, but it is to be noted that: 1) they are much less abundant than caryocaridids; 2) this fact may reflect a thicker, more mineralized cuticle, associated with a distinct mode of life, or both associated conditions.

Thousands of isolated elements of caryocaridid exoskeleton have been collected from the South American Ordovician sequence but most of them are very poorly preserved and, in some cases, up to about 200 isolated carapace valves and/or furcal rami have been counted on a single black shale bedding plane about 50 cm by 50 cm square. No complete exoskeleton has been found, the most complete specimens being articulated fragments of the abdomen. Only specimens retained in most competent levels, and those preserved in lenses and/or in early diagenetic concretions as in the Ordovician of Bohemia (Chlupáč 1970) and in South America (this paper) are sufficiently well preserved to allow complete detailed descriptions. In

addition, the low number of well preserved specimens preclude any biometric analysis as was carried out on the carapaces of the Bohemian material of *Caryocaris wrighti* and *C. subula* by Chlupáč (1970) for example. Measurements are given below for the best preserved carapaces only and for furcal rami, when reliable.

Taxonomically significant characters in caryocaridids

The anatomy of archaeostracan Crustacea is known from a few, exceptionally well-preserved specimens such as *Nahecaris stuertzi* Jaeckel, 1921 from the Lower Devonian Hunsrück Lagerstätte of Germany, *Ceratiocaris papilio* Salter, 1859, from the Silurian of Scotland (Rolfe 1962) and *Ceratiocaris papilio* and *C. macroura* from the Silurian of Ontario, Canada (Collette & Rudkin in press). Other complete exoskeletons, although yet undescribed, are known from the Middle Ordovician Black Shales of Oklahoma (Hannibal & Feldmann 1997), but such specimens remain exceptional. The only available information upon the segmentation of the pereion of caryocaridids was given by Hannibal & Feldmann (1996) who figured a carapace of *Caryocaris* sp. from southern Bolivia showing indications of segmentation and the mandible in situ. However that interpretation is not fully convincing and remains questionable pending further observations.

The exoskeleton of caryocaridids (Fig. 3) resembles Recent phyllocarids such as *Nebalia* or *Nebaliopsis*. However, the bauplan of modern phyllocarids with its 5-8-7 segmentation pattern (5 head segments, 8 thoracic segments, 7 abdominal segments + telson) remains poorly known in caryocaridids, as in most archaeostracan phyllocarids, although it is globally accepted in the literature. Moreover, taxonomically significant characters in modern phyllocarids mainly relie upon features such as: the segmentation of antennule and antenna, morphology and structure of the eye stalk, morphology of thoracopods, *etc.* (see Rolfe 1969, pp. R312–314), *i.e.* characters which are only exceptionally preserved in fossil specimens. This fact implies that the taxonomy of Paleozoic phyllocarids, among which are the caryocaridids, relies mainly upon morphologic characters of exoskeletal elements (carapace, abdominal somites, tail piece).

Representatives of the genus *Caryocaris* share a relatively small-sized carapace (less than 50 mm long; commonly about 20 to 30 mm) and all are characterized by a thin, bivalved, elongated carapace. Both valves were most probably articulated along the dorsal hingeline by transverse muscles and ligaments, without any articulatory process. The carapace is devoid of rostral and median dorsal plates, in contrast with most other

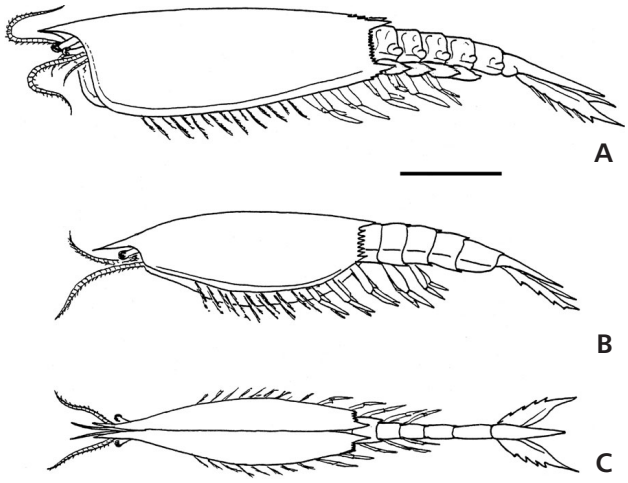

Figure 3. Tentative reconstructions of the complete exoskeleton of caryocaridids. • A – *Janviericaris formosa* gen. et sp. nov., in lateral view. • B, C – *Caryocaris acoitensis* sp. nov., in lateral and dorsal views, respectively. Scale bar is about 10 mm.

Archaeostraca (Rolfe 1969, Vannier *et al.* 1997). Most species of *Caryocaris* exhibit a variably developed anterior horn, which is an anterior expansion of each carapace valve. The relative development of the anterior horn led to the distinction of the subgenera *C.* (*Caryocaris*) with a short horn, and *C.* (*Rhinopterocaris*) with a long horn (Chlupáč 1970). However, the variable morphology and development of that character makes it unreliable, even at the subgenus level and led to the suggestion that the latter subgenus is a junior synonym of the former (Racheboeuf *et al.* 2000, Chlupáč 2003). If we consider *Caryocaris zhejiangensis* Shen, 1986, the curvature of the anterior horn may result from deformation. Ventrally, the carapace of caryocaridids exhibits a narrow, flattened ventral border which is limited by a shallow furrow. The inner side of the carapace bears a well defined doublure as could be established from well preserved specimens from southern Bolivia (Fig. 4).

The carapace of caryocaridids usually exhibits a variably spinose posterior margin. If the posterodorsal spine is usually present, the posteroventral one may be variably developed, reduced or lacking. The posterior margin is commonly straight, or variably sinuous and nearly vertical. In some cases it may be obliquely oriented, especially when the posteroventral spine is shortened, as in *Caryocaris subula* Chlupáč, 1970 and even more so when the posteroventral spine is absent as in *C. delicata* Racheboeuf *et al.* 2000. The posterior parts of the ventral and dorsal margins may bear (both or neither) a variable number of short, posteriorly directed, spinose expansions named here 'pre-posteroventral' and 'pre-posterodorsal' spines, respectively (see Fig. 4). An exception is *C. cedarbergensis* which has a smooth posterior margin and ventral border extending backward to almost the short posterodorsal

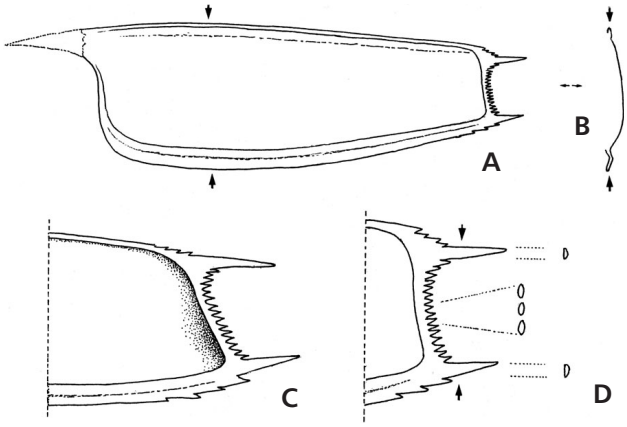

Figure 4. *Janviericaris formosa* sp. nov. Reconstructed inner side of a right valve showing the outline of the inner border (A) with the corresponding cross section (B); arrows indicate the location of the cross section. • C – hypothetical anteroventral view of the inner posterior part of the carapace. • D – enlarged view of the posterior margin of the carapace with cross sections of spines; note the elliptical section of the small posterior spines and the sub-semicircular cross section of posteroventral and posterodorsal spines. Pre-posteroventral and pre-posterodorsal spines are well developed.

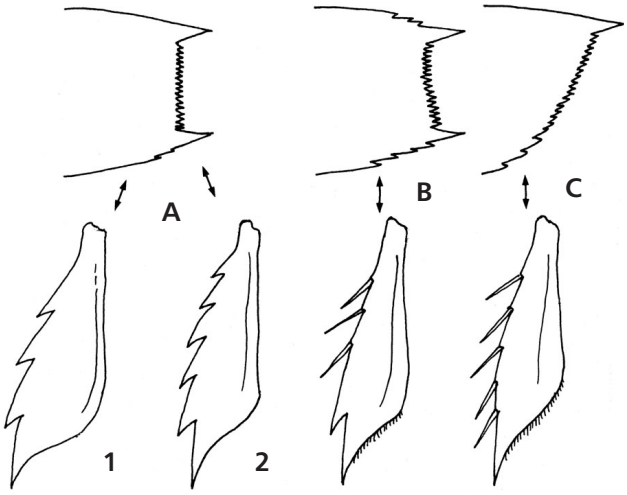

Figure 5. Compared morphology and outline of the posterior margin of the carapace (above), and of the corresponding furcal rami (below) for the three caryocaridid genera discussed in this paper. • A – *Caryocaris* Salter, 1863 (A1 – *C. bodenbenderi*, A2 – *C. acoitensis*). • B – *Janviericaris* gen. nov. • C – *Ivocaris* gen. nov.

spine. The discovery of almost three-dimensionally, well preserved, caryocaridid specimens in early diagenetic concretions and lenses of southern Bolivia (Chapiuno section, north-west of Tarija), completes our knowledge of exoskeleton morphology. A doublure was previously known to strengthen the ventral margin of the carapace (Vannier *et al*. 1997, 2003); the preservation of the newly collected Bolivian specimens allows study of the precise development of the doublure, especially in the posterior part of the carapace.

When developed, posterodorsal and posteroventral spines are not only leaf-like expansions of the dorsal and ventral margins. They are hollow with a markedly convex external side and a flat inner side, giving them a typical subsemicircular cross section. Secondary spinules, developed between these two spines, along the posterior margin of the carapace, are also three-dimensionally preserved and exhibit a subelliptical cross section. The hollow nature of spines and spinules is attested by the sediment infilling. As a consequence, the posterior part of the carapace was also underlined by a doublure, like the dorsal and ventral margins (Fig. 4).

The pleon is still poorly known. Complete exoskeletons are rare and abdominal elements (pleonites) of the exoskeleton are most often found as isolated segments, or still connected together and/or connected to the tail piece. As can be understood from the completely preserved specimens, five of the seven pleonites are exposed beyond the posterior margin of the carapace. In this way the reconstruction of the complete exoskeleton is somewhat different (Fig. 3) from that proposed earlier (Vannier *et al*. 2003, fig. 2A, B, p. 176). All pleonites are about the same length and they become less elevated and narrower posteriorly. The last, pretelson pleonite, is sometimes more weakly elongated than the preceding ones. According to the species, each pleonite may bear short dorsal posterodorsal spines and their flanks may exhibit a lateral longitudinal carina, as in *Caryocaris*. In *Caryocaris acoitensis* sp. nov., pleonites lack posterodorsal spines and the short lateral carina ends in a small posterior rounded tubercle.

The tailpiece includes the telson and a pair of furcal rami. The telson is typically triangular in outline, with weakly convex lateral margins and a pointed posterior end. It is weakly concavoconvex in cross section, its ventral side being flat to weakly concave. Furcal rami are most often elongated, typically leaf-like or, more precisely, flame-like in outline, with a pointed extremity (Fig. 5), the only exception being *Caryocaris stewarti* Jell, 1980 which exhibits widened, subtriangular furcal rami. These flattened natatorial organs, are articulated below the head of the telson, with a small, rounded articulatory process. Their inner margin is almost straight in its anterior half, becoming variably convex backwards, then concave to join the posterior acute extremity. When well-preserved, the posterior, concave part of the inner margin of furcal rami commonly bears a row of very small spinules. The outer margin of the rami is weakly to markedly convex. In *Caryocaris*, it bears a variable number (usually 3 to 6) of flattened, triangular, spine-like expansions (Fig. 5A1, 2); in other forms, such as *Janviericaris* gen. nov. only the most posterior triangular expansion is still present and the others are replaced by small articulated spinules (Fig. 5B), anterior lateral spine-like expansions; in *Ivocaris* gen. nov. all lateral ex-

pansions are replaced by small articulated spinules (Fig. 5C); based on such observations, the assignment of the species *C. stewarti* Jell, 1980 to the genus *Caryocaris* seems questionable.

Phyllocarid carapaces yielded from black shales can be only superficially appreciated or evaluated in size and outline, because of diagenetic and/or tectonic processes. Although the anterior margin of the carapace appears to be possibly significant from a taxonomic point of view [relative development of an anterior horn or not; see *Caryocaris* (*Rhinopterocaris*) Chlupáč, 1970; curvature of the anteroventral part of the carapace, *etc*.], the most reliable feature on the carapace seems to be the morphology and ornamentation of its posterior margin: 1) smooth or spinose ventro- and dorsoposterior margins; 2) presence or absence, and relative development of ventro- and dorsoposterior spines; 3) number and relative development of secondary spines (spinules) along the posterior margin of the carapace between the posterior spine(s), and 4) outline and orientation of the posterior margin of the carapace (vertical, oblique, straight or sinuous, *etc*.).

As complete exoskeletons, with abdominal segments and tail piece still connected are rarely preserved, other reliable characters and features are connected with the tail-piece, *i.e.*, the telson and furcal rami. In *Caryocaris,* the telson most often looks like a triangular, transversally concavoconvex, pointed element of the exoskeleton, with or without longitudinal lateral ridges or furrows. Due to diagenetic compaction and/or tectonic distorsion, its concavoconvex lateral profile, its length-width ratio is of no value, excepted when three-dimensionally preserved in early diagenetic concretions. Furcal rami are considered here, together with the posterior margin of the carapace, to be highly significant at the genus and species taxonomic level. Due to their flattened, leaf-like morphology, furcal rami can only be affected by tectonic distorsion which would only affect their length-width ratio. Tectonics would not affect the presence (or the lack) of leaf-like spinose expansions on their lateral outer margin, as well as that of articulated spines, or that of small spinules on their inner, convex, posterior margin. Regarding furcal rami we consider the following characters to be taxonomically significant: 1) the morphology and outline; 2) the presence (and number) or absence of spine-like expansions along the outer margin; 3) the presence or absence of long and narrow, acute, articulated (or non-articulated) spines; 4) the presence of setae along the posterior margin. However, the length ratio between the telson and the two flat furcal rami may be relevant. On the base of such considerations, we consider here that the Family Caryocarididae as it was originally proposed by Racheboeuf *et al*. (2000), can no longer be assigned to the Suborder Ceratiocaridina.

Systematic palaeontology

Class Malacostraca Latreille, 1806
Subclass Phyllocarida Packard, 1879
Order Achaeostraca Claus, 1888
Family Caryocarididae Racheboeuf, Vannier & Ortega, 2000
[non Caryocaridae Chapman, 1903].

Diagnosis. – Small to medium-sized, elongated, bivalved carapace covering thoracic and anterior abdominal pleonites, lacking prominent nodes and ridges, devoid of rostral and median dorsal plates; anterior horn variably developed; posterior margin straight, oblique or sinuous usually spinose, with variably developed posterodorsal and posteroventral spines; posteroventral spine sometimes reduced or absent; abdominal pleonites short with pretelson somite about the same length; tail piece with triangular telson and a pair of furcal rami.

Genera assigned. – *Caryocaris* Salter, 1863; *Janviericaris* gen. nov.; *Ivocaris* gen. nov.

Remarks. – The family Caryocaridae (sic) was firstly proposed by Chapman (1903, p. 113) but this author did not give any diagnosis of the new family which included the genera *Caryocaris*, *Saccocaris* Salter, 1873, and the new genus *Rhinopterocaris*. Rolfe (1969, p. R315) considered the family Caryocaridae Chapman, 1903, as a junior synonym of the family Ceratiocarididae Salter, 1860 in which he placed *Caryocaris* together with the genera *Ceratiocaris* M'Coy, 1849 (?Early Ordovician to ?Late Permian), *Gonatocaris* Gürich, 1929 (Late Silurian) and *Heroldina* Broili, 1931 (Lower Devonian) (Rolfe 1969, p. R315–317). The exoskeleton of *Caryocaris* exhibits such a range of peculiar characters that it can no longer be assigned to the family Ceratiocarididae Salter, 1860. Hence the family Caryocarididae was proposed by Racheboeuf *et al*. (2000) to accomodate the single genus *Caryocaris,* the genus *Rhinopterocaris* Chapman, 1903 being considered to be a synonym of *Caryocaris* (Racheboeuf *et al.* 2000) and *Saccocaris* questionably belonging to the phyllocarids (Rolfe 1969, p. R327). According to the diversity of morphological characters related to time, as expressed in this paper, it clearly appears that the genus *Caryocaris*, as up to now accepted, is a comprehensive taxon. Such an idea was recently supported by Chlupáč (2003). The diagnosis of the family Caryocarididae is accordingly emended above to accomodate the two new genera together with *Caryocaris*.

Genus *Caryocaris* Salter, 1863

Type species. – *Caryocaris wrightii* Salter, 1863.

Junior synonyms. – *Caryocaris* (*Rhinopterocaris*) Chlupáč, 1970; *Dawsonia* Nicholson, 1873 (*pars*; see Page *et al*. in press).

Emended diagnosis. – Caryocaridids with posterior margin of carapace valve almost subvertical, straight, with well-developed posterodorsal and posteroventral spines and with a row of variably developed tiny spines; variable number of subtriangular, flattened, spine-like expansions along the outer lateral margin of leaf-like furcal rami.

Species assigned. – *Caryocaris wrightii* Salter, 1863 (type species); *Caryocaris wrighti* Salter, 1863, *sensu* Chlupáč 1970; *Caryocaris wrighti sensu* Rushton & Williams 1996; *Caryocaris acuminata* (Nicholson, 1873); *Caryocaris bodenbenderi* Aceñolaza & Esteban, 1996; *Caryocaris acoitensis* sp. nov.

The species *C. stewarti* Jell, 1980 is provisionally left within the genus *Caryocaris*.

Geographic distribution. – England, Ireland, Belgium, Germany, Czech Republic, Canada, United States, Argentina, Bolivia, Colombia, Peru.

Stratigraphic range. – Tremadocian–Floian (lower Arenig).

Remarks. – The type species of *Caryocaris*, *C. wrightii*, was initially described from a single carapace from the Arenig strata of the Skiddaw Group of England (Salter 1863, p. 139). The tail piece remained unknown until Chlupáč (1970) described specimens from the Darriwilian Šárka and Dobrotivá formations of Bohemia which he assigned to Salter's species. More recently Rushton & Williams (1996) described the tail piece of *C. wrightii* from the Hope Beck and Kirkstile formations of the Skiddaw Group, in the supposed type area of England and from the Oaklands Fm. of Ireland and compared their material with the Bohemian specimens of *C. wrightii* described and reconstructed by Chlupáč (1970). However, two points needs to be emphasized and discussed:

– According to Rushton & Williams (1996), it clearly appears that both the British and Irish furcal rami bear outer lateral, spine-like flattened expansions ('spinules' of the authors), but whilst the oldest British specimen (*varicosus* Biozone) bears 5 expansions, the youngest specimens (*gibberulus* and *hirundo* Biozones) bear only 3 expansions (op. cit., p. 108). The question is: 1) do the two morphotypes really belong to the same species?; 2) if not, does the type species *C. wrightii* bear 5 or 3 lateral spine-like expansions?

– Rushton & Williams (1996) noted (p. 108) that the Bohemian specimens assigned by Chlupáč to *C. wrightii* show "... only one distinct spinule [= spine-like flattened expansion] towards the rear end of the outer lateral margin, in front of which ... 3–4 tiny notches, suggestive of the presence of further minute spinules". However, the authors did not discuss the significance of these characters. Original specimens of *C. wrighti – sensu* Chlupáč 1963 – have been carefully observed by Dr. P. Budil (Geological Survey, Prague) who is greatly acknowledged here. According to photos it is unclear whether the 'tiny notches' correspond to the articulatory processes of very small moveable spines and in this respect they cannot be compared with lateral spine-like expansions, or to the bases of very minute, elongate spines almost parallel to the outer margin of the furcal rami. Thus they can no longer be compared with lateral spine-like expansions either. Taxonomically, this last character means that, in our opinion, the Bohemian specimens can no longer be assigned to the species *C. wrightii* Salter, 1863, nor to the genus *Caryocaris*. Bohemian specimens (tail pieces and furcal rami) of *C. wrighti* figured by Chlupáč are probably more closely allied with *C. subula* Chlupáč, 1963. Chlupáč wrote (1970, p. 58) that both species occur together in the Llanvirnian beds of the Šárka Fm. Moreover the specimen ICh 781 of *C. wrighti* figured by Chlupáč on plate 1, fig. 9, exhibits a posterior margin of the carapace which looks different from the posterior margin of valves illustrated on plate 2. The first specimen would probably (?) be better assigned to *Ivocaris* gen. nov., while specimens figured on plate 2 resemble *Janviericaris* gen. nov.

Within the family Caryocarididae we consider the genus *Caryocaris* to be characterized by the presence of lateral, subtriangular, spine-like flattened expansions along the outer lateral margin of elongated, leaf-like furcal rami and the diagnosis of the genus *Caryocaris* is emended accordingly. In other respects here we follow Chlupáč's remarks (2003, p. 107) about the feminine gender of the Greek word *karys* (= shrimp) implying species name endings in '*-a*' instead of '*-us*' (Article 34 of the ICZN).

Caryocaris bodenbenderi Aceñolaza & Esteban, 1996

Figure 6A–C

1996 *Caryocaris bodenbenderi*; Aceñolaza & Esteban, p. 283.
2000 *Caryocaris bodenbenderi.* – Racheboeuf, Vannier & Ortega, pp. 318, 326.
2004 *Caryocaris bodenbenderi.* – Racheboeuf, pp. 258, 260.

Type locality. – Quebrada del Portezuelo de la Alumbrera (Cuesta de Miranda), Provincia de La Rioja, Argentina.

Material and occurrence. – Eight specimens No. PIL 14182 (holotype) and PIL 14183 to 14189 (paratypes) originally designated by the authors, from the late Tremado-

cian deposits of the Bordo Atravesado Formation, Sierra de Famatina.

Remarks. – As previously established, the phyllocarid remains upon which the species *C. bodenbenderi* was defined, are furcal rami and not carapaces (Racheboeuf *et al*. 2000, pp. 318, 326). The original material is redescribed below.

Description. – Carapace unknown. Length of furcal rami between about 5 mm and 10.3 mm long (measurements from the 5 more complete specimens); corresponding length : width ratio between 2.37 and 3.50, but most specimens are broken in their proximal part, or weakly distorted. The holotype, which is the largest and more complete specimen, is 10.26 mm long and 2.93 mm wide, with a L : W ratio of 3.50. The maximum width of the ramus is located in the posterior third of the total length. The outer margin of the furcal ramus is moderately to markedly, regularly convex. It bears two to three relatively large, triangular, flattened and posteriorly directed spine-like outgrowths. The anterior spine-like outgrowth is often much smaller than posterior ones and sometimes scarcely perceptible, probably due to preservation. The inner margin is almost straight or weakly concave in its anterior half, becoming strongly convex up to the inner base of the terminal spine. The pointed, terminal spine is relatively large and stout. The distal inner margin shows no spinules or setae. A shallow longitudinal furrow originating from the condyle, reaches the inner margin of the terminal spine.

Discussion. – Due to the misinterpretation of furcal rami as carapaces, as previously stated (Racheboeuf *et al*. 2000), the authors compared *C. bodenbenderi* with several taxa exhibiting a well-developed anterior horn. However, regarding the characters of the furcal rami, *C. bodenbenderi* can only be compared with species that exhibit several spine-like, flattened, outgrowths along the outer margin, such as *C. wrighti* Salter, 1863, *sensu* Rushton & Williams (1996), and other species of *Caryocaris sensu stricto*.

The furcal rami of *C. bodenbenderi* differ markedly from those of *C. wrightii* Salter (the type species) and other species of the genus *Caryocaris* by a less elongate outline, with a strongly convex, almost geniculate interior margin and a convex outer margin bearing two to three spine-like outgrowths instead of five. The terminal spine is also stouterand better differentiated in *C. bodenbenderi*.

***Caryocaris acoitensis* sp. nov.**
Figures 3B, C, 6D–H

2000 *Caryocaris* sp. 1; Racheboeuf, Vannier & Ortega, p. 328.
2004 *Caryocaris* sp. 1. – Racheboeuf, p. 260.

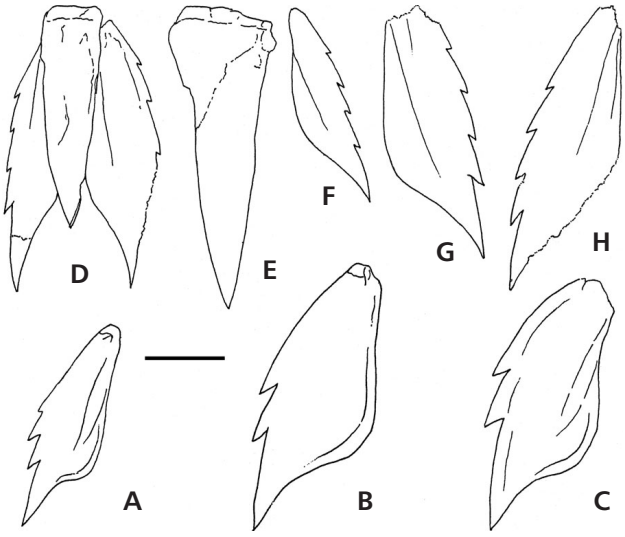

Figure 6. Camera lucida drawings. Furcal rami, all × 8. • A–C – *Caryocaris bodenbenderi* Aceñolaza & Esteban, 1996. Locality Quebrada del Portezuelo de la Alumbrera, Provincia de La Rioja, Bordo Atravesado Formation, Tremadoc. A – holotype, No. PIL 14182. B – No. PIL 14188. C – No. PIL 14189. • D–H – *Caryocaris acoitensis* sp. nov. Mina Natasia section, locality 2, Acoite Formation, Arenig. D – tail piece, holotype, No. 23319. E – isolated telson, No. 23323. F–H – furcal rami, No. 23320 to 23.322 respectively. Scale bar = 2 mm.

Holotype. – Tail piece No. 23319, telson with the two furcal rami still connected (Fig. 6D).

Etymology. – From the Acoite Fm., the stratum typicum.

Type locality. – Section along the trackway between road 52 and Mina Natasia, locality 2, sampled in 2000, about 1 km S of road 52; coordinates S 23°42´ 13˝, W 65°42´ 23˝.

Material and occurrence. – A complete tail piece, an isolated telson and ten isolated furcal rami, among which five well–preserved specimens (No. 23319 to 23323). Argentina, Eastern Cordillera, Acoite Formation, level possibly equivalent to the *Baltograptus deflexus* Zone (upper Be2 to Be4), middle to late Floian.

Diagnosis. – Species characterized by relatively wide furcal rami with a markedly but regularly convex outer margin with four flattened spine-like outgrowths; inner margin markedly convex at three quarters of the furca length from the anterior extremity.

Description. – Telson subtriangular, elongated in outline, with posterolateral margins weakly convex, ending in stout posterior spine. The largest telson (Fig. 6E) is 7.5 mm long with a corresponding width of 2.75 mm, *i.e.* a length : width ratio of 2.72. Telson head with a weak, transverse furrow terminating laterally at the anterior margin of the rounded articulatory process. The largest

furcal ramus is 7.4 mm long with a corresponding width of 2.5 mm. The length : width ratio of the furcal rami is about 3 (between 3 and 3.17; 4 measurements). The outer margin is regularly convex and bears four flattened, regularly spaced, spine-like outgrowths the size of which weakly increases posteriorly. Inner margin almost straight in its anterior half, becoming markedly convex, then bending outwards to delineate the wide and curved terminal spine. Each furcal ramus bears a weak longitudinal furrow almost parallel to its longitudinal axis. No setae could be observed along the inner posterior margin of the available material.

Discussion. – At first sight , the furcal rami of *C. acoitensis* sp. nov. resemble that of *C. bodenbenderi* Aceñolaza & Esteban, 1996, but they can be easily distinguished by their more elongated outline, *i.e.*, a higher length : width ratio between 3.5 and 4, instead of 2.37 to 3.5 in *C. bodenbenderi*. In *C. acoitensis* sp. nov. the inner margin of the furcal rami is much less convex, less arcuated than in *C. bodenbenderi* and the spine-like expansions number four along the outer margin, instead of two to three and all expansions are about the same size. The furcal rami of *C. acoitensis* sp. nov. differ from *C. wrightii* as illustrated by Rushton & Williams (1996, Fig. 2) by both the better differentiated and relatively longer terminal spine and the outline of the spine-like outgrowths which are more triangularand more prominent along the outer margin. Considering the number of spine-like outgrowths, specimens of *C. wrightii* from the *varicosus* Zone exhibit five 'spinules' while those from the *gibberulus–hirundo* Biozones bear 3 spinules. *C. acoitensis* sp. nov. from the *deflexus* zone bears four spine-like outgrowths.

Genus *Janvieicaris* gen. nov.

Type species. – *Janvieicaris formosa* sp. nov.

Etymology. – To honour Dr. Philippe Janvier, MNHN, Paris, for his work on South American Paleozoic vertebrates.

Diagnosis. – Caryocaridids with an almost vertical anterior margin below the short anterior horn; subvertical, sinuous spinose posterior margin of the carapace; well-developed posterodorsal and posteroventral spines; pre-posteroventral and pre-posterodorsal spines usually developed; furcal rami with a unique spine-like expansion and small articulated anterior spines.

Comparison. – *Janvieicaris* gen. nov. differs primarily from *Caryocaris* by the variably sinuous posterior spinose margin of the carapace. Moreover, the posterior end of the dorsal line, just before the posterodorsal spine, is usually arcuated, more or less convex dorsally, with several preposterodorsal spine-like expansions. The outer margin of the furcal rami bears a unique, posterior, flattened spine-like expansion and anteriorly small articulated spines inserted on notches, instead of three to five spine-like expansions.

Species assigned. – *Janvieicaris formosa* sp. nov. (type species); *J. jujuyensis* sp. nov.; ?*Caryocaris monodon* Gurley, 1896; *C. curvilata* Gurley, 1896.

Geographic distribution. – Southern Bolivia and northwestern Argentina; North America.

Stratigraphic range. – Floian–Darriwilian.

Janvieicaris formosa sp. nov.

Figures 3A, 4, 5B, 7, 8

1965 *Caryocaris* sp. – Branisa, p. 12.
1965 *Ceratiocaris* sp. – Branisa, pp. 76, 227, 228, pl. 6, fig. 6.
2000 *Caryocaris*. – Legrand, Smith & Hannibal, pp. 12, 13.
2003 *Caryocaris* sp. 3. – Vannier *et al*., fig. 6 (pars).
2004 *Caryocaris* sp. 1. – Racheboeuf, fig. 25.1 (pars).

Etymology. – From the Latin *formosus, -a*: fine, beautiful, elegant.

Holotype. – Right valve of the carapace, MNHNC13330 (Fig. 8A–C).

Type locality. – Quebrada Chapiuno section, along the road Iscayachi-Culpina, 61.9 km NW of Tarija and about 14 km N of Estancia Puesto, coordinates S 21°16´ 32˝, W 65°10´ 57˝, Department of Tarija, Province of Méndez, southern Bolivia. *Azygograptus lapworthi* Zone, equivalent to the *Pseudophyllograptus angustifolius* Zone of Baltoscandia, equivalent to the Castlemainian Ca1 of Australia, middle Arenig, Dapingian.

Material and occurrence. – 76 more or less complete carapaces, 5 tail pieces, 2 telsons and 13 furcal rami have been collected from two silty lenses with cone in cone structures, at the top of the Ordovician sequence, about 60 meters below the Ordovician/Cretaceous unconformity. Pircancha/Cieneguillas formations, *Azygograptus lapworthi* Zone, Arenig (Third Stage). *B. formosa* sp. nov. also occurs in northernmost Argentina, in levels 4 to 11 of the Muñayoc section, W of Abra Pampa, Jujuy Province. Level 4 might be considered to be an equivalent of the Ch1 (Chewtonian), while levels 9 and 11 can be assigned to the Ch2 (they may possibly reach the Ca1 – Castlemanian) of Australia, middle Arenig (late Floian–early Dapingian).

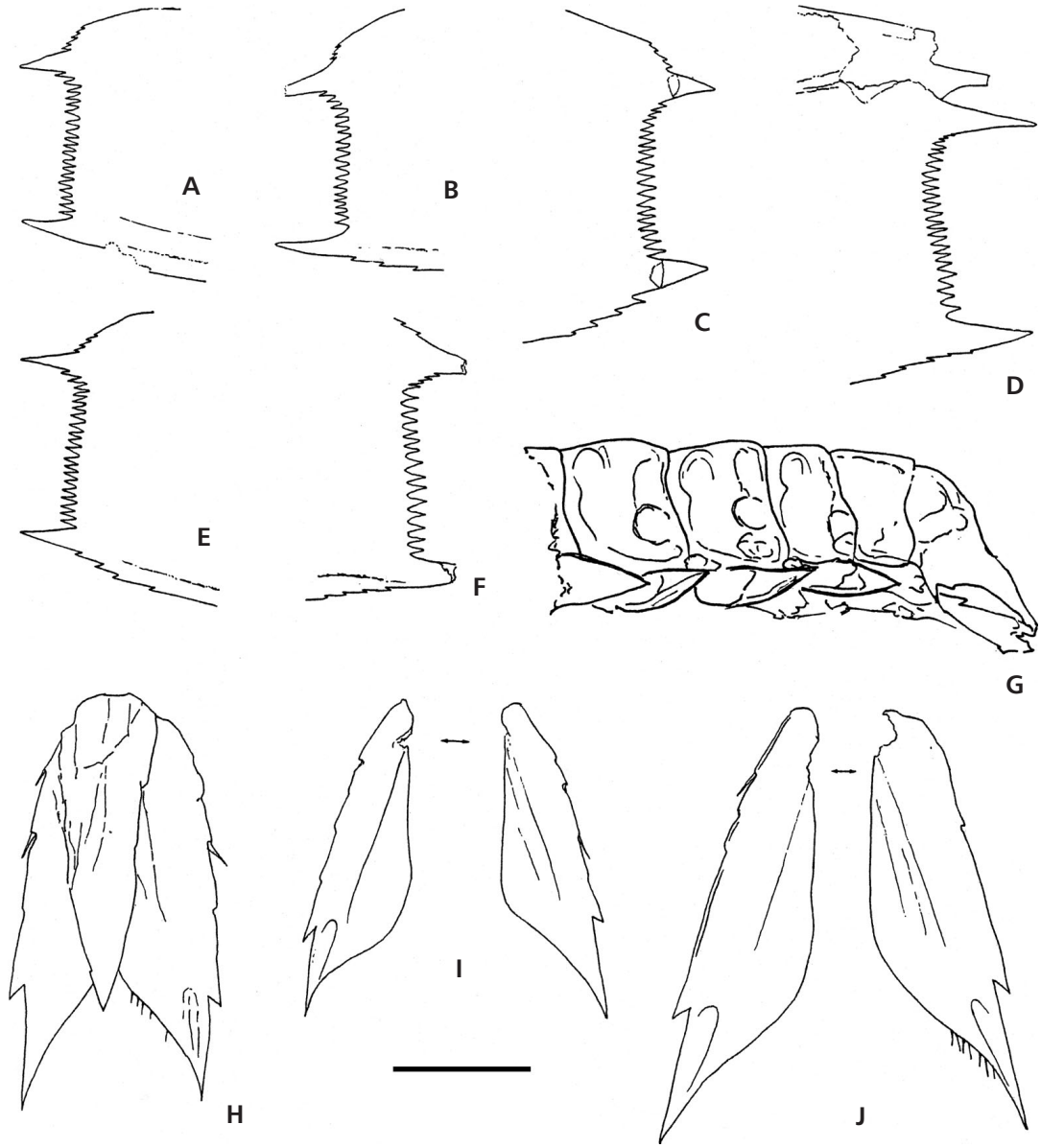

Figure 7. *Janviericaris formosa* sp. nov. Camera lucida drawings of specimens from the Chapiuno section, type locality, NW of Tarija, Southern Bolivia. • A–F – posterior part of several valves of the carapace showing the sinuous spinose margin; A – MNHNC 13334, B – MNHNC 13339, C – MNHNC 13340, D – MNHNC 13332, E – MNHNC 13341, F – MNHNC 13343. • G – five abdominal somites still connected with the tail piece, in lateral view, MNHNC 13342. • H – tail piece, MNHNC 13335. • I, J – upper and lower sides of two isolated furcal rami MNHNC 13338 (I), and MNHNC 13344 (J). Scale bar = 5 mm.

16 specimens (holotype and paratypes) are numbered MNHC 13330–13345.

Diagnosis. – Species of *Janviericaris* with markedly sinuous posterior margin of carapace; well-developed posterodorsal and posteroventral spines and pre-posterodorsal and pre-posteroventral short spines; 18 to 26 long, relatively stout posterior spinules, numbering 6 to 9 per mm.

Description. – Carapace: Maximum observed length about 28.0 mm for a corresponding height of 10.0 mm. Carapace length : height ratio (L : H) between 2.63 and 2.97 for 8 carapaces between 12.5 mm and 28 mm long. However the species may reach a larger size, as in level 11 of the Muñayoc section where weakly tectonically distorted carapaces of 40 mm long are not uncommon. None of the available specimens have their anterior horn preserved, the anterodorsal part of the carapace always being irregularly broken (Figs 4A, 8D). However the broken line suggests a stout, relatively short horn. Dorsal line gently and evenly arched. Anteroventral margin markedly convex, with a very narrow but well developed marginal rim. Narrow ventral

border (approx. 0.6 mm to 0.7 mm wide), subtriangular in cross section, dorsally limited by a well impressed ridge running parallel to the whole ventral margin which is evenly and regularly arched. Posterior part of the ventral margin bearing 4 to 6 small, short, and posteriorly directed, pre-posteroventral spine-like expansions. Posterior part of the dorsal margin weakly convex, bearing 4 to 5 very short, posteriorly directed, pre-posterodorsal spine-like expansions. Posterodorsal and posteroventral spines strongly developed, of the same size, up to 2.5 mm to 3.0 mm long, semicircular in cross section (Fig. 4D). Their outer side is regularly and markedly convex, while their inner side is flat. Posterior margin of the carapace weakly oblique and sinuous between the two posterior spines and bearing 18 to 26 posteriorly directed spinules. Spinules subelliptical in cross section, decreasing in width and length towards the posterodorsal spine. Length of spinules between 0.8 mm and 1.0 mm.

Ornamentation of the carapace: Except for the bottom of the longitudinal dorsal and ventral furrows and the top of the ridges, as well as the dorsal and ventral margins, which are smooth, the carapace surface is extremely finely granulose (Fig. 8) and devoid of any other kind of ornamentation.

Abdominal somites: Some are preserved still in connection with the tail pieces, while others have been observed as isolated elements. Specimen No. 13342 (Fig. 7G) exhibits five pleonites in connection with the tail piece. The total length of the five somites equals 5.2 mm along their dorsal side, indicative of a mean length close to 1.0 mm per somite. Their height is about 2.5 mm but this is of little use as the abdomen is markedly flattened and compressed laterally.

Tail piece: Telson subtriangular, elongate, with straight lateral margins becoming very weakly convex near posterior extremity which ends in a very tiny, acute, short spine. Cross section concavoconvex. Dorsal side devoid of any ridge and/or furrow. Maximum observed length about 9.0 mm for a corresponding width of 2.4 mm near its proximal end; L : W ratio between 3.2 and 3.77 for five specimens. Furcal rami relatively elongated. Observed length between 4.65 mm and 11.0 mm; corresponding width between 1.25 mm and 2.8 mm for 14 specimens. L : W ratio varying between 3.5 and 4.05. Maximum width located at about mid length. Outer lateral margin very weakly and evenly convex, with a unique, relatively small-sized, spine-like triangular expansion; base of the spine located between one quarter and one third of the total length from the long, narrow, spinose posterior extremity.

Anterior to the spine-like expansion, three very small spines are regularly spaced, inserted and articulated on notches. Inner margin almost straight in its proximal part, becoming regularly convex at about mid length, then becoming concave terminating in a well differentiated terminal spine. Distal inner margin, between maximum width and terminal spine, fringed by numerous short setae. Each furcal ramus exhibiting a well differentiated longitudinal, submedian furrow originating anteriorly at the inner side of the articulatory process and ending at about two-thirds of the total length. A very discrete furrow, markedly arched in its antior part, running from almost the base of the spine-like expansion to the axis of the terminal posterior spine.

Comparison. – Among previously described species, *J. formosa* sp. nov. can only be compared with *Caryocaris curvilata* Gurley, 1896. The outline and morphology of the posterior part of the carapace of the North American species is very similar to that of *J. formosa* sp. nov. with pre-posterodorsal and pre-posteroventral short spines and a sinuous posterior margin. However, Gurley's species exhibits 13 to 15 posterior spinules between the two posterior spines, instead of 18 to 26 in *J. formosa* sp. nov. (Churkin 1966, Rolfe unpublished). These characters make the species *curvilata* a probable representative of *Janviericaris* gen. nov. According to Churkin (1966) *C. curvilata* is known from Alaska, Great Basin (USA) and Canada in beds of probable upper Floian–lower Dapingian age (*Didymograptus hirundo* or *D. bifidus* zones).

***Janviericaris jujuyensis* sp. nov.**
Figures 9A–L, 10A–ZD

Etymology. – From the Jujuy Province of northern Argentina.

Holotype. – Specimen No. 23295, posterior margin of both valves of a carapace (Fig. 9E).

Type locality. – Los Colorados section, Acoite Fm., W-NW of Purmamarca, Jujuy Province, northern Argentina.

Material and occurrence. – This species is undoubtedly the most common, found in the northern part of the Argentine Precordillera, but it occurs mainly as isolated furcal rami. Levels of the Acoite Formation which provided us with phyllocarids are assigned to the *Tetragraptus akzharensis* Zone (locality La Luna) of the Floian, lower Arenig (Be1-Be2, Bendigonian of Australasia), up to the *Didymograptus bifidus* Zone, of middle Arenig age (Ch1, Chewtonian of Australasia). The species occurs in the Los Colorados section (No. 23266 to 23288), as in Agua Blanca-La Luna section (No. 23240–23243). In the Mina Natasia section, the species is common in the graptolitic shales from the first outcrop along the road, up to the mine entrance, about 1,500 m to the South (No. 23289 to 23318).

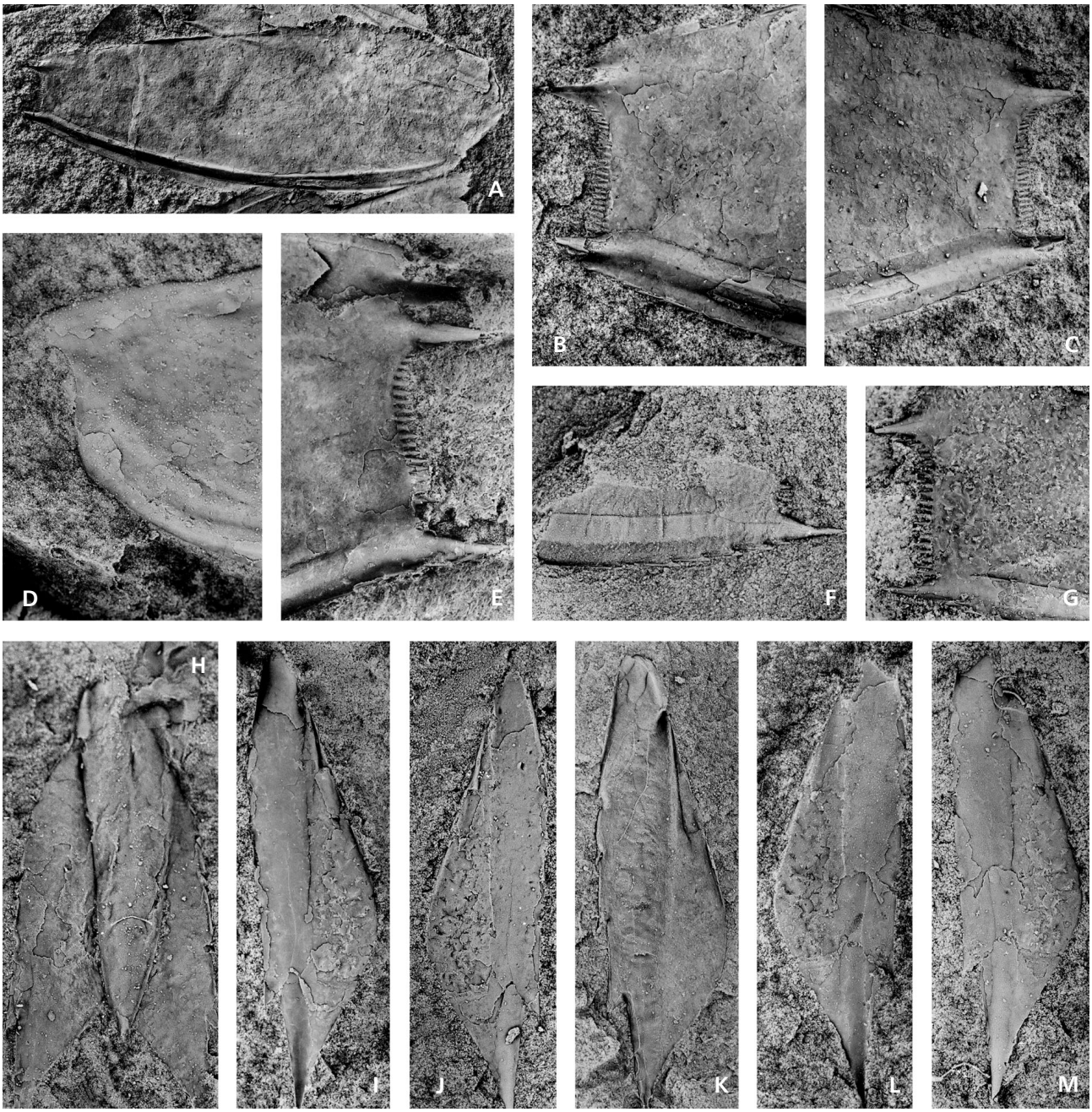

Figure 8. *Janviericaris formosa* sp. nov. Chapiuno section, type locality, NW of Tarija, Southern Bolivia. • A–C – right valve of the carapace, natural mould (A), holotype MNHNC 13330, × 3, and enlarged views of the posterior part of the carapace showing the sinuous spinose margin on the natural mould (B) and on the latex cast (C), × 10. • D – anterior part of a left valve, MNHNC 13331, showing the subvertical sinuous anterior margin and the base of the anterior horn, × 10. • E – posterior part of a left valve, MNHNC 13332, showing the sinuous spinose margin on the natural mould, × 10. • F – incomplete posterior part of carapace MNHNC 13333, latex cast, showing the well preserved posterior ventral spines, the posteroventral spine, and a part of the sinuous spinose margin, × 10. • G – posterior part of carapace MNHNC 13334, showing the sinuous spinose margin on the natural mould, × 10. • H – latex cast of a tail piece MNHNC 13335 showing the telson and the two furcal rami in connection, × 10. • I, J – left furcal ramus MNHNC 13336, natural mould and latex cast, × 10. • K – left furcal ramus MNHNC 13337, natural mould, × 10. • L, M – right furcal ramus MNHNC 13338, natural mould and latex cast, × 10. Compare with the camera lucida drawings of Fig. 7.

The section was sampled in 2000, then in 2001; except for the first outcrop which yields no graptolites, the section is tentatively assigned to the *Baltograptus deflexus* Zone, *i.e.* Floian, upper lower Arenig (equivalent to the Be3-Be4, Bendigomian of Australasia). The species is also known from the Quebrada Saladillo locality (Sierra de Famatina) in beds of the Suri Fm assigned to the *Baltograptus deflexus* Zone, late Floian. It also occurs in three levels of the

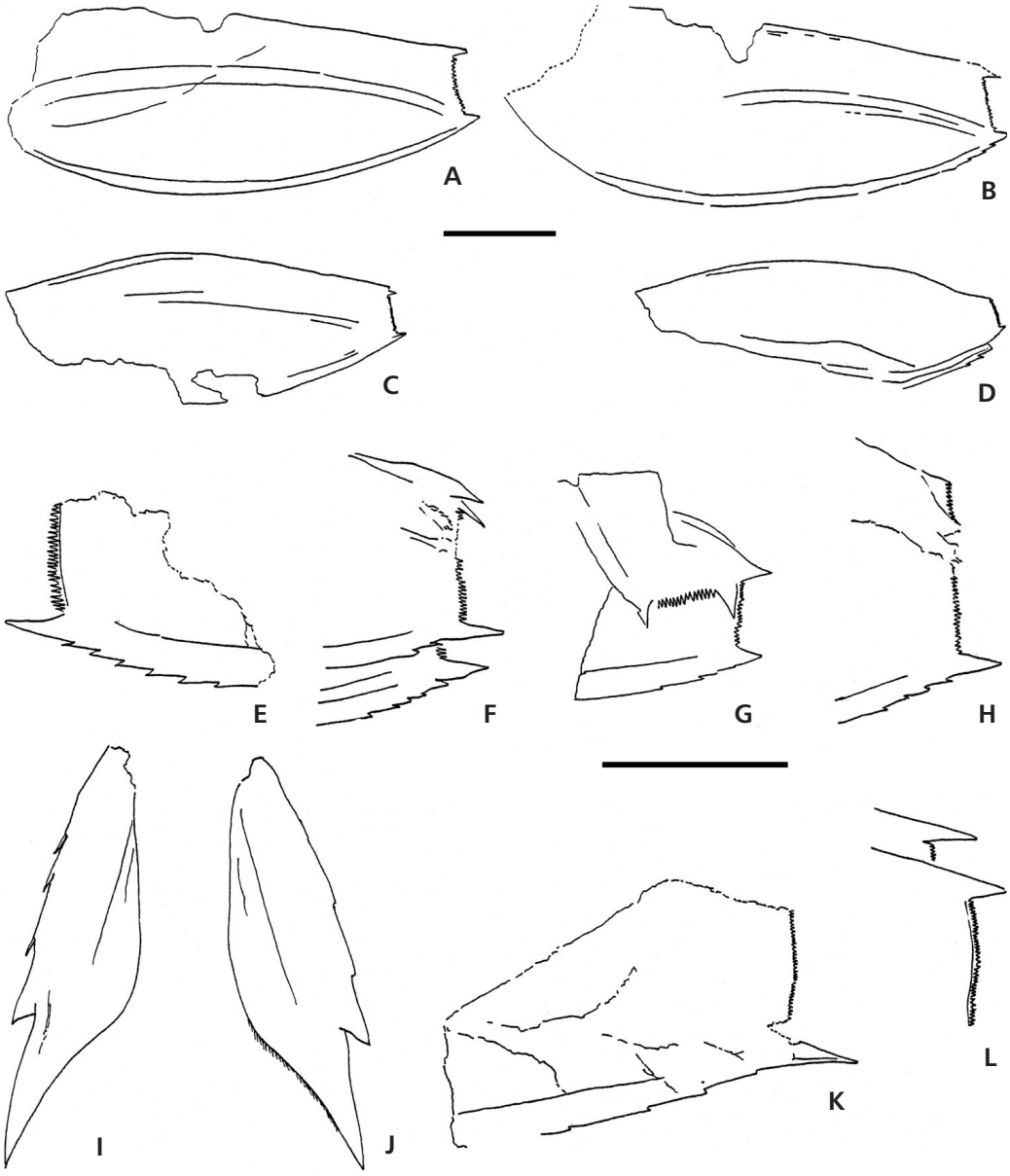

Figure 9. *Janviericaris jujuyensis* sp. nov. • A, B – left valves from Los Colorados, No. 23271 and 23272 respectively. • C–G – left valves and posterior parts of fragmentary valves from Mina Natasia (localities 3 and 4), No. 23295, 23301, 23267 and 23302, respectively. • H–L – Agua Blanca section, No. 23316, 23242, 23243 and 23240, respectively. Scale bar = 5 mm.

Muñayoc section in the Puna area, in late early to middle Arenig levels. In South Bolivia, *B. jujuyensis* is common both in silts with concretions and fine-grained sansdstone around Cieneguillas, between the coordinates S 21° 22´ 01˝, W 65° 03´ 66˝, and S 21° 21´ 53˝, W 65° 03´ 04˝. These outcrops of the Cieneguillas Fm. are late Floian–early Dapingian in age.

Diagnosis. – Species of *Janviericaris* with weakly sinuous posterior margin of carapace and without pre-posterodorsal spines; very small, short spinules numbering 13 to 20 per mm.

Description. – Carapace: Maximum observed length about 15 mm for a corresponding (estimated) height of 5 mm. Only specimen No. 23308 (Fig. 9C) has its anterior margin preserved; it is angular, pointed, but shows no development of a differentiated horn. Dorsal line gently and evenly arched. Anteroventral margin markedly convex, with a very narrow but well developed marginal rim. Narrow ventral border (approx. 0.6 mm to 0.7 mm wide), subtriangular in cross section, dorsally limited by a well impressed ridge running parallel to the whole ventral margin which is evenly, and regularly arched. Posteroventral part of the ventral margin bearing 4 to 6 small, short and posteriorly

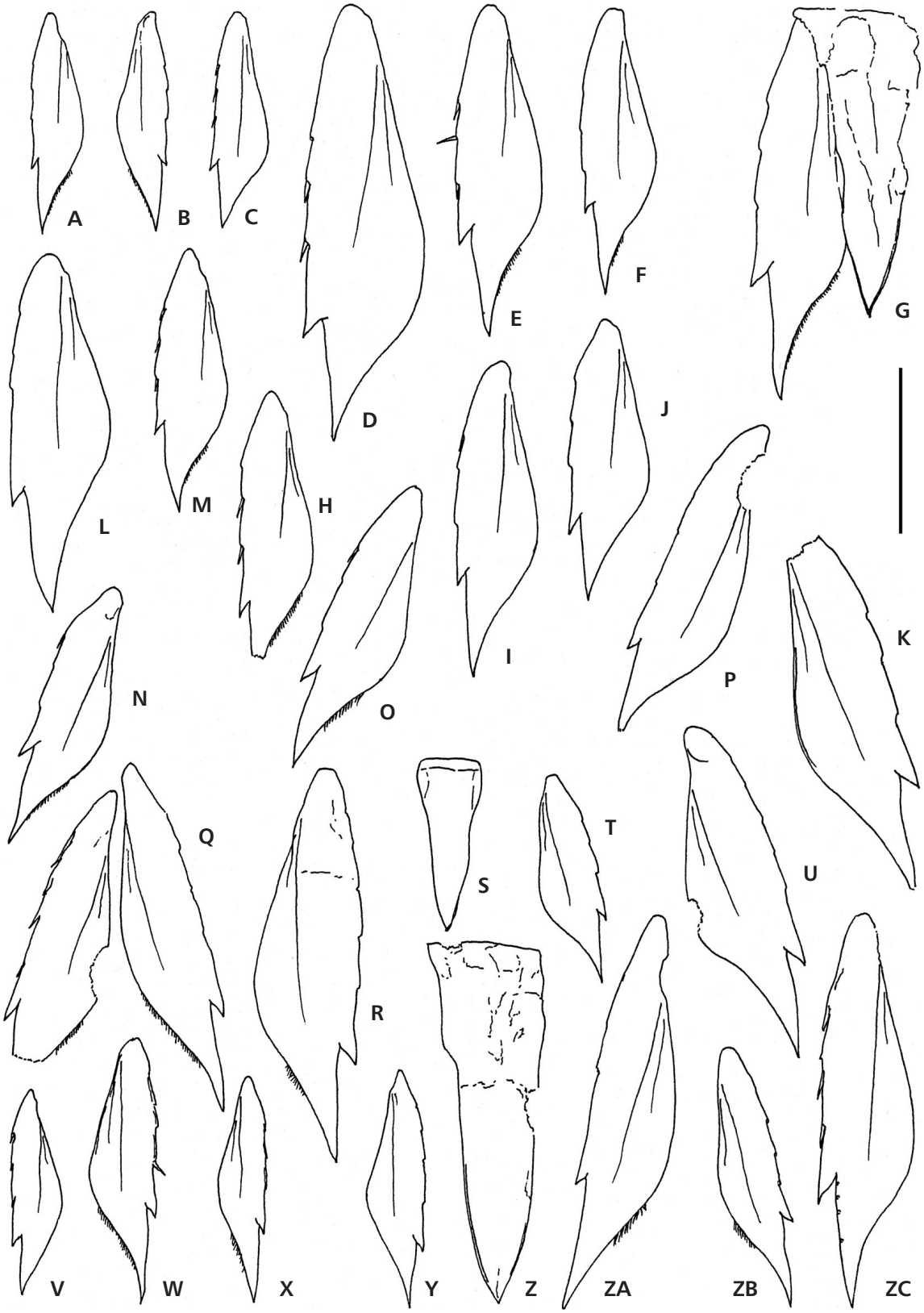

Figure 10. *Janviericaris jujuyensis* sp. nov. furcal rami, telsons and tailpieces from Los Colorados (A–K), La Luna (L–O), and Mina Natasia (localities 3–4) (P-ZC) sections. • A–F – No. 23274–23279, 23285, and 23286–23288, respectively. • L–O – No. 23280, 23281, 23283, and 23284, respectively. • Q–ZC – No. 23311, 23312, 23300, 23298 , 23305, 23316–23318, 23314, 23313, 23315, 23299 and 23297. Scale bar = 5 mm.

directed, pre-posteroventral spine-like expansions. Ventral margin of the posteroventral spine is a continuation of the ventral margin of the carapace. Posterodorsal and posteroventral spines markedly developed, 2.0 mm to 3.0 mm long, the posteroventral one being often slightly longer and thicker than the posterodorsal one. Pre-posterodorsal spines not observed or missing (?). Posterior margin of the carapace sinuous, very weakly convex ventrally, becoming weakly concave dorsally, bearing 18 to 26 posteriorly directed spinules. Spinules decreasing in size slightly towards the dorsal spine. Length of spinules between 0.8 mm and 1.0 mm.

Ornamentation of the carapace: Except for the longitudinal dorsal and ventral furrows and the top of ridges, as well as the dorsal and ventral margins, which are smooth, the carapace surface is extremely finely granulose and devoid of any other kind of ornamentation.

Abdomen and abdominal somites unknown.

Tail piece: Telson subtriangular, moderately elongate, with lateral margins weakly concave in their anterior part, just after the telson head. Their lateral margins become weakly convex towards the posterior end. Only three available telsons, but one (Fig. 10.G), was found isolated. The dorsal side shows no evidence of any longitudinal ridge or furrow, nor any ornamentation. The length : width (L : W) ratio varies from 2.70 to 3.16 for 3 telsons 5.4 mm to 11.4 mm long. Furcal rami elongated. Observed length between 6.4 mm and 14.4 mm for 36 specimens; corresponding width between 1.6 mm and 3.8 mm. L : W ratio varying between 3.52 and 4.56. Maximum width located around the posterior third of the length. Outer margin weakly convex with a unique spine-like expansion, and three to four narrow, acute articulated spines. Inner margin almost straight proximally, becoming convex posteriorly, then variably and moderately concave until joining the terminal spine. Inner convex margin fringed by numerous, short setae. Well differentiated, straight to weakly sinuous submedian longitudinal furrow.

Comparison.– J. jujuyensis sp. nov. is assigned to *Janviericaris* gen. nov. on the basis of the carapace outline, with a short anterior horn, a markedly straigthened anterior margin, and a weakly sinuous posterior margin, with long, stout posteroventral and posterodorsal spines. The posterior end of the dorsal margin lacks the row of pre-posterodorsal, well developed spine-like expansions, however furcal rami are similar to those of the type-species, with a unique, posterior, spine-like expansion, and three small, articulated spines. *J. jujuyensis* sp. nov. differs from *J. formosa* sp. nov. by its much shorter anterior horn, and by a less markedly sinuous posterior margin with much more numerous, smaller and shorter spinules, numbering 13 to 20 per mm instead of 6 to 9 per mm in *J. formosa* sp. nov.

Genus *Ivocaris* gen. nov.

Type species. – *Caryocaris delicata* Racheboeuf, Vannier & Ortega, 2000.

Etymology. – To honour the late Dr. Ivo Chlupáč for his extensive work on Paleozoic Bohemian arthropods.

Diagnosis. – Caryocaridids with an oblique, spinose posterior margin to the carapace; posterodorsal and posteroventral spines present, or posteroventral spine reduced, or absent; furcal rami without any spine-like triangular expansion, but with a variable number of very small articulated spines along the outer margin.

Discussion. – *Ivocaris* gen. nov. differs from *Caryocaris* Salter, by its oblique, sinuous and spinose posterior margin, with reduced or absent posteroventral spine; outer margin of furcal rami with a variable number of small, articulated spines inserted on notches without any flattened spine-like expansion.

Species assigned. – *Caryocaris delicata* Racheboeuf, Vannier & Ortega, 2000 (type species); *Ivocaris saltitensis* sp. nov.

Geographic distribution. – Argentine Precordillera; ?Czech Republic.

Stratigraphic range. – Darriwilian (Uppermost Arenig–Llanvirn).

Comparison. – *Ivocaris* gen. nov. differs from both *Caryocaris* and *Janviericaris* gen. nov. by the oblique posterior margin of the valves, with or without posteroventral spine, as well as by the lack of any flattened spine-like expansion on the outer margin of the furcal rami.

The species *Caryocaris* (*Rhinopterocaris*) *subula* Chlupáč, 1970 from the Dobrotivá Formation of the Czech Republic, is very similar in every aspect of its morphology to the species assigned here to the new genus *Ivocaris* and especially *I. saltitensis* sp. nov. Detailed and careful complementary investigations of the furcal rami of the original specimens of *C. subula* described and illustrated by I. Chlupáč (1970) have been made by Petr Budil (Czech Geological Survey). As a result, the outer margin of the furcal rami of *C. subula* bears small, acute, straight, relatively long and narrow cylindrical spines which always exhibit the same attitude, *i.e.* almost parallel to the outer ramus margin, instead of articulated spines as in *I. delicata,* and *I. saltitensis* sp. nov. Hence Chlupáč's species *subula* cannot be assigned to *Ivocaris* gen. nov.

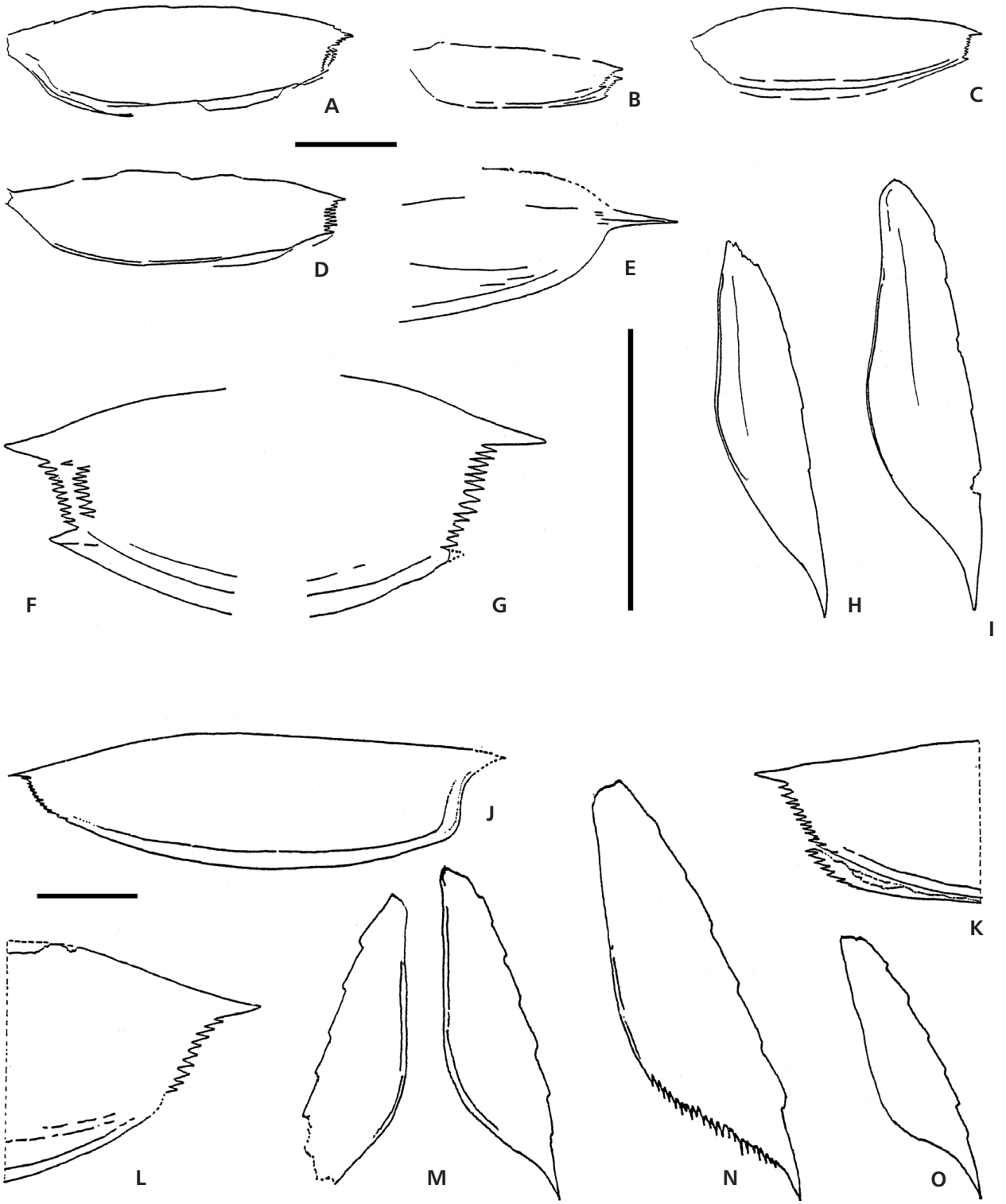

Figure 11. A–I – *Ivocaris saltitensis* sp. nov. from the lower part of the Los Saltitos section (type locality). • A–D – carapace outline of specimens 23334–23336 and 23339, respectively. • E – anterior horn of specimen CEGH-UNC 16244. • F, G – posterior margin of specimens 23329 and 23330 showing the oblique posterior margin and the posterodorsal and posteroventral spines, the latter being broken on specimen 23329 (Fig. 7). • H – isolated furcal ramus, 23332. I – isolated fursal ramus, 23331. Scale bar 5 mm. • J–O – *Ivocaris delicata* Racheboeuf, Vannier & Ortega, 2000. J – holotype, right valve of the carapace, CORD PZ 13073. K – posterior margins of both valves of an almost complete carapace, CORD PZ 11546. L – posterior margin of left valve CORD PZ 13073. M – furcal rami of presumably the same tail piece, CORD PZ 14159. N – large isolated furcal ramus with setae preserved along inner margin, CORD PZ 13256. O – isolated furcal ramus, CORD PZ 13211. Scale bar = 5 mm.

***Ivocaris delicata* (Racheboeuf, Vannier & Ortega, 2000) comb. nov.**
Figure 11J–O

2000 *Caryocaris delicatus* Racheboeuf, Vannier & Ortega, p. 323.
2004 *Caryocaris delicatus.* – Racheboeuf, pp. 258, 260.

Type locality. – Los Azules Creek, Cerro Viejo Range, Huaco, Argentine Precordillera.

Material and occurrence. – Nineteen variably preserved carapaces, 3 tail pieces and 10 furcal rami from the lower member (*Undulograptus dentatus* Zone) and middle member (*Pterograptus elegans* and *Hustedograptus teretiusculus* Zones) of the Los Azules Formation, Darriwilian. Specimens housed in the Museo de Paleontología de Córdoba (No. CORD PZ 12292, 12681, 12846, 12860, 13073, 13211, 13253, 13256, 14150, and 14159).

Description. – See Racheboeuf *et al*. 2000, pp. 323–327.

Discussion. – The species was initially described from the lower and middle members of the Los Azules Fm. (Argentine Precordillera), in beds belonging to the *Undulograptus dentatus* Zone of early Darriwilian age (lower member) and in beds belonging to the *Pterograptus elegans* and *Hustedograptus teretiusculus* Zones of middle to upper Darriwilian age (middle member).

Comparison. – The species *delicata* remains up to now unique among caryocaridids by its lack of a posteroventral spine associated with an oblique posterior margin. It differs from *Caryocaris subula* Chlupáč, 1970, by a longer-sized carapace (length is about 24 mm, *i.e.* twice the length of the carapace of *C. subula*), by the lack of the posteroventral spine of the carapace, by curved and less spinose posterior carapace margin and by articulated small spines along the outer margin of furcal rami instead of 'ordinary' spines.

***Ivocaris saltitensis* sp. nov.**
Figure 11A–I

Etymology. – From the type locality Los Saltitos.

Holotype. – Specimen No. 23336, left valve of the carapace (Fig. 11.C).

Type locality. – Quebrada Los Saltitos, SW Guandacol, La Rioja Province, Northern Argentine Precordillera.

Material and occurrence. – Ten carapaces and three isolated furcal rami from the type locality. Lowermost part of the Gualcamayo Formation (between 0.10 m and 4.80 m above the base); No. CEGH-UNC 16221, 16244; No. 23329 to 23339. Upper part of the *Undulograptus austrodentatus* Zone (*U. sinicus* Subzone), uppermost Arenig-Llanvirn (equivalent to the Dariwillian Da1).

Diagnosis. – Species of *Ivocaris* with moderately convex anteroventral margin and present, although reduced, posteroventral spine; oblique posterior margin bearing 10 to 12 spinules; furcal rami markedly elongated with 4 to 5 articulated spines.

Description. – Carapace markedly elongated. Length between 14.5 mm and 17.5 mm for the three best preserved specimens; corresponding height varying from 4.3 mm to 5 mm; length – height ratio (L : H) between 3.3 and 3.6. Dorsal margin regularly and moderately convex; ventral margin similarly arched. Anterior horn long (about 3.5 mm) and narrow. Anteroventral margin regularly arched and moderately convex. Narrow ventral border (approx. 0.5 mm wide). Both posterodorsal and posteroventral spines present, the latter being shorter, between half and three-quarters the length of the former which is about 1.2 mm long in specimen 23.329. No pre-posteroventral spine-like expansions. The posterior margin of the carapace is oblique, and its overall outline makes an angle of about 70° with a theoretical, straight and horizontal dorsal line. Ten to twelve short triangular spinules (about 0.3 mm long) are inserted along the posterior margin (Fig. 11F, G).

Abdomen and abdominal somites unknown.

Tail piece: telson unknown. Furcal rami markedly elongated; the lengths of two well preserved specimens are 7 mm and 8 mm with corresponding widths of 1.6 mm and 1.8 mm, respectively. Maximum width at mid length. Length : width ratio between 4.26 and 4.3. Outer margin with 4 to 5 notches suggesting 4 to 5 articulated spines. No setae observed. Longitudinal furrow weakly sinuous, close to the longitunal median axis of each furcal ramus.

Discussion. – The new species is assigned to the genus *Ivocaris* on the basis of the markedly oblique posterior margin of the carapace and on the morphology of the furcal rami which are identical to those described for *C. delicata*. However, the carapace of *C. saltitensis* sp. nov. differs mainly in its posterior margin which exhibits a posteroventral spine, although shorter than the posterodorsal spine, which is always lacking in *C. delicata*. According to the development of the anterior horn (as deduced from specimen CEGH 16244) and to the presence of a posteroventral spine, *C. saltitensis* sp. nov. resembles *C.* (*Rhinopterocaris*) *subula* Chlupáč, 1970 from the Šárka and Dobrotivá formations (Darriwilian) of the Barrandian area, but the new species can be distinguished by a relatively shorter anterior horn and a more developed posteroventral spine. The

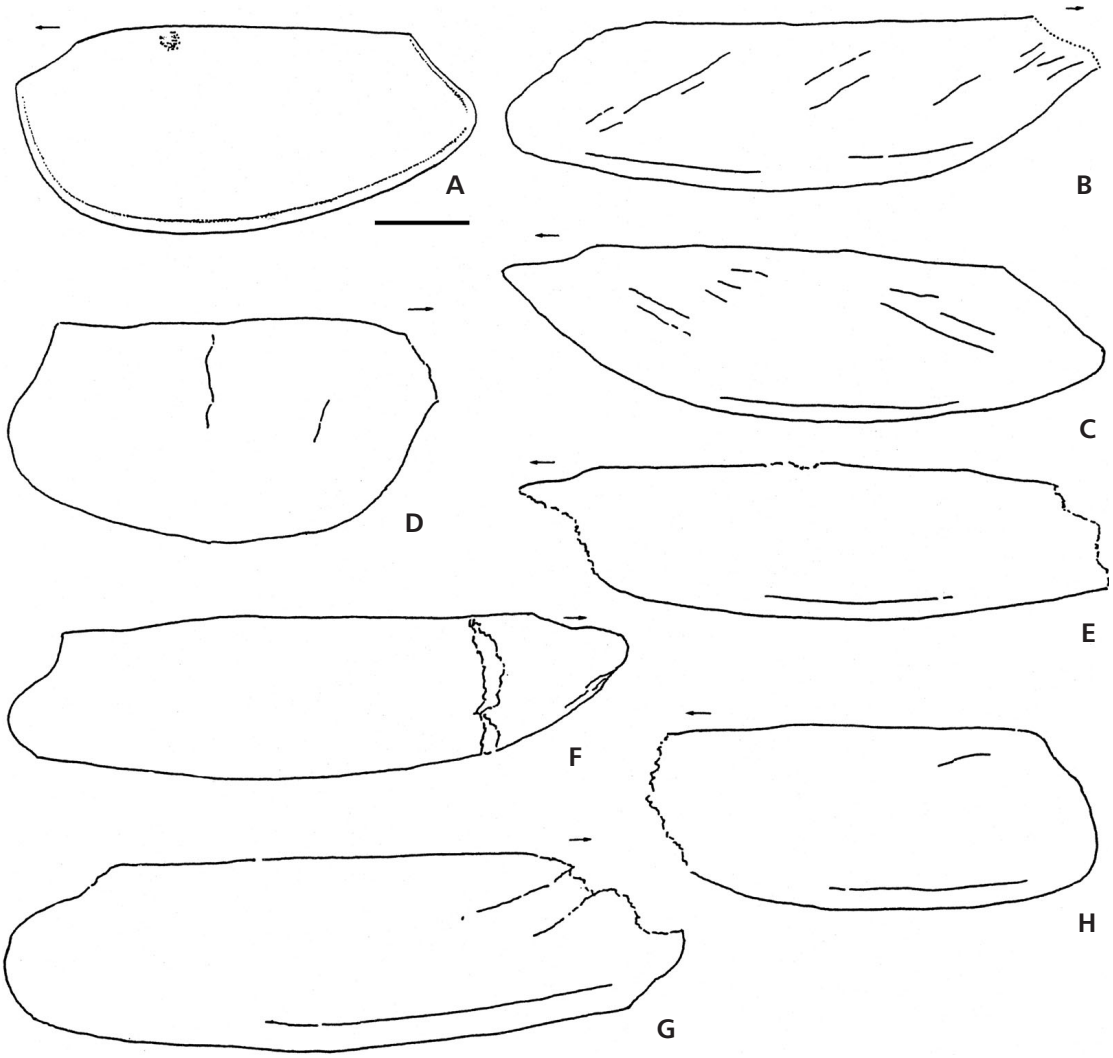

Figure 12. Genus *Pumilocaris*. Camera lucida drawings of carapaces. • A – *Pumilocaris granulosa* Racheboeuf, Vannier & Ortega, 2000, late Sandbian (early Caradoc) of the Argentine Precordillera, reconstruction drawn from the holotype CORD PZ 19371. • B–H – *Pumilocaris acuta* (Bulman, 1931), Caradoc of Huichiyuni, Peru, original specimens of Bulman housed in the Riksmuseum in Stockholm. B, C – both sides of a right valve, specimens Ar 42450 and 42454 (specimen 427 from Bulman 1931, text-fig. 41, upper) respectively. D – right valve, Ar 42451 (specimen 107 of Bulman 1931, textfig. 41, lower). E – right valve, Ar 42452. F – left valve, Ar 42459. G – right valve, Ar 42467. H – left valve, Ar 42453. Arrows indicate the anterior side. Scale bar = 2 mm.

posterior margin of *I. saltitensis* sp. nov. bears 10 to 12 spinules instead of about 20 in *I. delicata*, and about 15 in *C. (R.) subula*.

Family Ceratiocarididae Salter, 1860

Genus *Pumilocaris* Racheboeuf, Vannier & Ortega, 2000

Type species. – *Pumilocaris granulosus* Racheboeuf, Vannier & Ortega, 2000.

Emended diagnosis. – Ceratiocaridid with subovate carapace, rounded posteroventral margin, and oblique, concave posterodorsal margin; no spines nor spinules; anterior margin markedly convex, with an anterodorsal concave margin suggestive of a (?)frontal incision or of a rostral plate; variably developed ventral border; valve surface finely granulose.

Species assigned. – *Pumilocaris granulosus* Racheboeuf, Vannier & Ortega, 2000 (type species); *Caryocaris acuta* Bulman, 1931.

Geographic distribution. – South America (Argentina, Peru).

Stratigraphic range. – Caradocian.

***Pumilocaris granulosa* Racheboeuf, Vannier & Ortega, 2000**
Figure 12A

2000 *Pumilocaris granulosus* Racheboeuf, Vannier & Ortega, p. 328.
2004 *Pumilocaris granulosus.* – Racheboeuf; p. 260, fig. 25.1.

Etymology, diagnosis and description. – See Racheboeuf *et al*. 2000.

Remarks. – Pumilocaris granulosa is restricted to the early Caradoc beds of the Las Plantas Formation (Argentine Precordillera, western side of the Cerro Potrerillo section NE of Jachal, San Juan Province), where it is associated with *Climacograptus bicornis*, *Nemagraptus gracilis* and *Orthograptus* ssp. assigned to the *C. bicornis* Zone (see Racheboeuf *et al*. 2000), early Caradocian.

***Pumilocaris acuta* (Bulman, 1931) comb. nov.**
Figure 12B–G

1931 *Caryocaris acuta* Bulman, p. 84, text-fig. 41, pl. 11, fig. 7.
2004 ?*Pumilocaris acuta.* – Racheboeuf, p. 260, fig. 25.1.

Discussion. – The species *acuta* was originally described from the Huichiyuni section of Peru, North of Lake Titicaca. Specimens Ar 42461 and 42462 are associated with graptolites which can be assigned to *Dicranograptus* cf. *nicholsoni* and specimen Ar 42466 is associated with *Dicranograptus* sp. These graptolites suggest a late Darriwilian to Sandbian age.

Although poorly preserved and tectonically distorted Bulman's specimens from the Peruvian locality Huichiyuni are assigned to the genus *Pumilocaris*, mainly with regard to the posterior region of the carapace which is devoid of any spinose ornamentation and which exhibits the characteristic convex outline becoming concave when reaching the dorsal margin. Despite distorsion, *Pumilocaris acuta* differs clearly from the type species *P. granulosa* by its larger size, its more rounded posterior margin and wider ventral border. The anterodorsal node and the granulose ornamentation described in the type species could not be observed in *P. acuta*.

Dimension of the carapaces (in mm).

Specimen Ar No.	Length	Height
42450	12.0	3.5
42451	8.5	4.5
42452	12.5	3.2
42456	8.5	2.6
42459	?12	3.1
42467	13.5	3.8

Genus *Rolfecaris* gen. nov.

Type species. – Rolfecaris lethiersi sp. nov.

Etymology. – To honour Dr. W.D. Ian Rolfe for his extensive work on phyllocarids.

Diagnosis. – Carapace elongate, subovate in outline, with straight hinge line, covering thoracic and abdominal somites; no median dorsal plate, nor rostral plate; anterior and posterior margins rounded, markedly arched dorsally to join hinge line; well differentiated and flat ventral border; carapace ornamented with thin, sinuous and irregular, non anastomosing longitudinal striae; tail piece with an elongate, rodlike telson, subtriangular in cross section, longitudinally grooved and bearing numerous articulated spinules; furca rodlike, devoid of spinules, subcylindrical in cross section and about the same length as the telson.

Discussion. – The new genus is here only tentatively and provisionally assigned to the Family Ceratiocarididae as diagnosed in the Treatise (Rolfe 1969). Such a family assignment relies upon the overall outline and characters of the carapace, the absence of a median dorsal plate and on the morphology of the tail piece with a long, narrow, rodlike, spinule bearing telson and long, rodlike furca. However, *Rolfecaris* strongly differs from *Ceratiocaris* in the oval outline of the carapace which is apparently devoid of anterior horn or rostral plate (?), and in the fact that the carapace covers thoracic and all abdominal somites, as evidenced by nearly complete specimens of the type species. The outline of the carapace resembles *Heroldina* Broili, 1931 from the Lower Devonian of Germany, but *Heroldina* bears a large rostral plate and exhibits a well developed abdomen and its tail piece is devoid of rodlike furca (Rolfe 1969, p. R317). The ornamentation of the carapace of *Rolfecaris* with thin, sinuous longitudinal striae, is very similar to that of the ceratiocaridids and it resembles that of the Silurian genus *Gonatocaris* (Rolfe 1969, p. R316). No hinge nodes nor tubercles could be observed on the available material.

Species. – Rolfecaris lethiersi sp. nov. (type species); *Rolfecaris parchaensis* sp. nov.

Geographic distribution. – Northwestern Argentina.

Stratigraphic range. – Parcha and Acoite formations, late Tremadocian to early Floian.

***Rolfecaris lethiersi* sp. nov.**
Figures 13, 14

2004 gen. et sp. nov. (*pars*), Racheboeuf, p. 260, fig. 25.1.

Etymology. – To honour Dr. F. Lethiers for his extensive work on Devonian ostracodes.

Holotype. – Incomplete left valve of the carapace with proximal part of the tail piece still attached, No. 23259, Fig. 14A.

Type locality. – Agua Blanca section, about 30 km WNW of Purmamarca (Provincia de Jujuy); coordinates S 23° 40´ 48˝, W 65° 42´ 43˝.

Material and occurrence. – A total of 21 specimens (11 carapaces, of which six still with connected telson; four more or less complete tail pieces and six isolated telsons) collected by Dra Blanca Toro (Mendoza) from the Acoite Formation. An isolated telson (No. 23326) was collected in the section along the trackway between road 52 and Mina Natasia, sample 4, in front of the entrance of the mine; coordinates S 23° 42´ 13", W 65° 42´ 23". Acoite Formation, *Tetragraptus phyllograptoides* to *T. akzharensis* Zones, early Floian. All specimens are housed in the collection of the La Pampa University (Santa Rosa) under numbers 23244 to 23264, and 23326.

Diagnosis. – As for the genus.

Description. – Small, elongate, subovate carapace; maximum length observed ca. 19.0 mm for a corresponding height of 8.7 mm; length/height ratio varying between 2.0 and 2.2 for seven more or less complete carapaces. Hingeline present as deduced both from the "butterfly" position of some specimens (23235) and isolated valves of others. Dorsal margin of the valves straight for most of its length, with a markedly arched anterodorsal extremity and a less convex posterodorsal one. Anterior and posterior margins of the carapace probably rounded and regularly convex. Ventral margin moderately and regularly convex, with a flat, relatively wide (0.6 mm to 1.1 mm) ventral border. Valve surface covered with thin, sinuous, non anastomosing, spaced and irregular longitudinal striae. Dorsally, striae relatively short, almost straight and parallel to the dorsal margin; ventrally, striae becoming longer, more spaced ventrally and curved, following the curvature of the ventral furrow.

Ventral margin with very thin, dense, sinuous and oblique striae.

Telson head relatively stout and rounded, subtriangular, concavoconvex in cross section. In dorsal view the telson is subtriangular in outline, with weakly concave lateral margins. The width of the telson diminishes progressively from its proximal part to the anterior third of its total length. Each lateral side of the telson bears a row of very small pits corresponding to the attachment of very small spinules. Spinules appear to be distributed from the posterior extremity of the telson head almost to the extremity of the telson. The density of spinules varies from 6 to 8 per 2 mm. Furca long and narrow, rodlike, subcylindrical in cross section, without spinules or setae. In specimen 23252, the length of the left furca equals about that of the telson (about 10 mm), with a diameter of 0.2 mm.

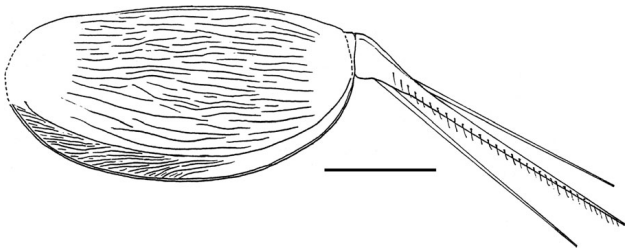

Figure 13. *Rolfecaris lethiersi* gen. et sp. nov. Tentative reconstruction of the complete exoskeleton, mostly after specimens illustrated in Fig. 14. Note that stylets are straight; it is not clear whether the curvature of the stylets observed on specimens No. 23251 and 23252 results from distorsion or not. Scale bar = 5 mm.

Dimensions (in mm).

			Carapace	
Specimen No.	H	L	H'	L/H
23244	7.8	?16.5	1.1	2.11
23245	8.7	?19	0.7	2.18
23256	6.7	?	0.6	–
23258	2.6	?5.7	0.4	2.19
23259 (holotype)	6.9	14.0	1.0	2.02
23263	?	?	0.9	–
23264	6.5	?	0.6	–

		Telson	Furca
Specimen No.	L	W	d
23248	7.5(+)	–	–
23249	7.5(+)	–	–
23250	9.0	–	–
2325	10.0(+)	1.7	0.2
23253	?5.5	0.6	0.1
23254	13.0	–	–

***Rolfecaris parchaensis* sp. nov.**
Figure 16

2000 ?*Pumilocaris* sp. – Racheboeuf *et al.*, p. 331, fig. 11.
2000 Undetermined phyllocarid. – Racheboeuf *et al.*, p. 331, fig. 12.
2004 gen et sp. nov. (*pars*), Racheboeuf, p. 260, fig. 25.1.

Etymology. – From the stratum typicum, the Parcha Formation.

Holotype. – Left valve of the carapace, No. 23231, Fig. 16A.

Type locality. – Incamayo creek, about 3 km N of Incahuasi, Argentine Eastern cordillera (Salta Province).

Material and locality. – A total of 11 specimens (eight isolated valves and three incomplete tail pieces) from the type locality, collected by Gladys Ortega (No. CORD PZ 18924, 18962, 19075 of the Córdoba University collection) and by Beatriz Waisfeld (No. 23231 to 23238 of the La Pampa University collection) from Huaico Hondo; both localities belong to the Parcha Formation and comprise the *Aranaeograptus murrayi* and *Hunnegraptus copiosus* Zones (late Tremadoc).

Description. – Small, elongate, subovate carapace; maximum length observed is *ca* 9.0 mm for a corresponding height of 3.8 mm; length/height ratio varying between 2.0 and 2.36 for nine more or less complete carapaces. Dorsal hinge present as deduced both from the "butterfly" position of some specimens (23235) and isolated parts of the carapace. Dorsal line weakly sinuous, with an accentuated curved anterodorsal part and an almost rectilinear posterodorsal part. Anterior and posterior margins of the carapace probably rounded and regularly convex. Ventral margin moderately and regularly convex, with a narrow (0.12 mm to 0.18 mm high) ventral border.

Discussion. – This small species can only be assigned to the new genus *Rolfecaris*. Carapace outline, as well as length-height ratio are very close to *R. lethiersi*, but it differs in its much narrower, almost linear ventral border; this is particularly evident when comparing ?*R. parchaensis* with juvenile specimens of *R. lethiersi* (see Figs 14 and 16). ?*R. parchaensis* also differs by the apparent lack of lateral spinules on the telson.

Dimensions (in mm). –

Specimen No.	H	L	Carapace H'	L/H ratio
23231 (holotype)	3.43	7.5	0.15	2.18
23232	2.31	–	0.3	–
23234	3.18	7.06	–	2.22
23235	3.06	7.18	0.18	2.34
23236	3.12	6.25	–	2.00
23237	3.31	7.25	0.12	2.19
23238a	3.31	6.87	0.12	2.07
23238b	3.43	7.18	–	2.09
18924	3.8	9.0	–	2.36

Undetermined phyllocarids

Despite the efforts we made during field work, several levels, and/or localities, of the South American Ordovician succession provided us with only scarce and poorly preserved phyllocarid remains. Carapaces were often spirally coiled, distorted and preserved in coarse-grained deposits. These forms which cannot be figured here can only be questionably assigned to the Family Caryocarididae and they are mentioned here in Fig. 2 as '*Caryocaris*' sp. A, sp. B, and sp. C. All these specimens are from upper Ordovician levels.

'*Caryocaris*' sp. A

Locality and age. – Quebrada Los Azules, upper member of the Los Azules Formation, at 2.20 m and 8.40 m below the top of the formation, late Sandbian age.

Material. – Six isolated valves and fragments of carapaces (No. 23348–23353).

'*Caryocaris*' sp. B

2000 ?*Caryocaris* sp. 2; Racheboeuf, Vannier & Ortega, p. 328.

Locality and age. – Western side section of the Cerro Potrerillo, NE of Jachal, San Juan Province, Northern Argentina, Miembro Las Plantas, Las Vacas Formation, *Climacograptus bicornis* Zone, late Sandbian age.

Material. – Four very poorly preserved carapaces (No. 23354–23357).

'*Caryocaris*' sp. C

Locality and age. – Quebrada Zanja Honda, Cerro Negro, Trapiche Formation, early Katian age.

Material. – A unique poorly preserved carapace (No. 23328).

Ordovician phyllocarid taxonomic diversity

The diversity and vertical range of South American Ordovician phyllocarid taxa were previously dealt with in three recent publications (Racheboeuf *et al*. 2000, Vannier *et al*. 2003, Racheboeuf 2004), and all known data drawn from the literature are summarized in Table 1 here. Table 2 gives

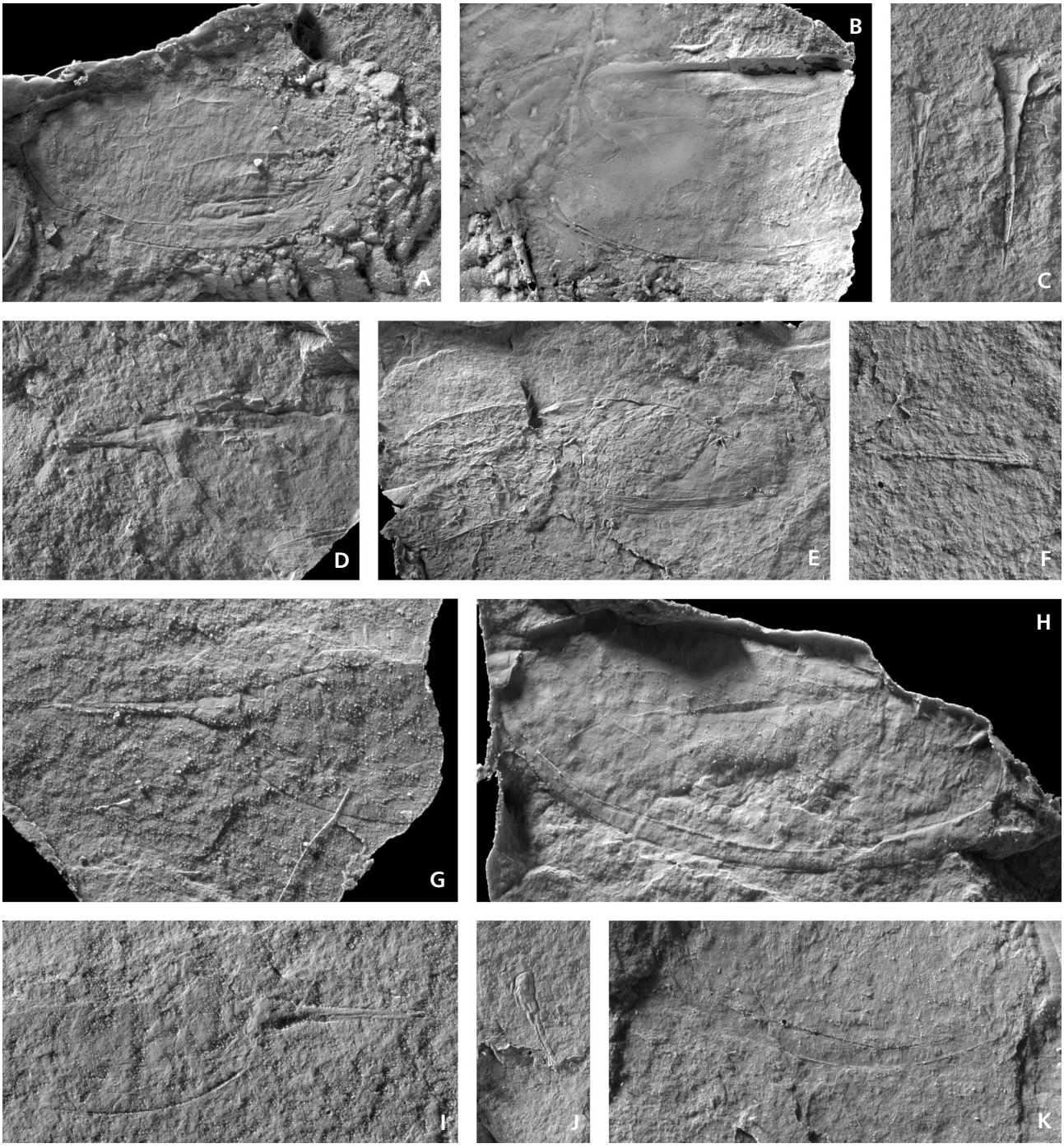

Figure 14. *Rolfecaris lethiersi* gen. et sp. nov. Agua Blanca section (type locality) sample 7 of Blanca Toro. All figures are latex casts. All specimens × 5. • A – incomplete left valve of the carapace with proximal part of the tail piece still attached, holotype No. 23259. • B – incomplete right valve, No. 23346. • C – two isolated telson, No. 23258. • D – posterior part of an incomplete right valve with telson still articulated, No. 23257. • E – right valve, No. 23240. • F – isolated telson, No. 23254. • G – posterior part of an incomplete right valve with telson still articulated, No. 23262. • H – large right ventral valve, No. 23255. • I – posterior part of a left valve with articulated telson, No. 23261. • J – small isolated telson, No. 23260. • K – ventral margin of an incomplete right valve, No. 23264.

a list of all Ordovician phyllocarid taxa described throughout the world, including those described in this paper.

Following the Treatise (Rolfe 1969), Ordovician representatives of the subclass Phyllocarida belong to two orders, namely Hymenostraca Rolfe, 1969 (?Early Cambrian, Middle Cambrian-Middle Ordovician) and Archaeostraca Claus, 1888 (Early Ordovician–Late Triassic). Representatives of the Order Hymenostraca are as a

whole characterized by a carapace devoid of a hinge line and by three pairs of caudal spines, both characters which clearly distinguish hymenostracans from archaeostracans. Hymenostracans still remain poorly known and their phyletic relationships are still questionable (Rolfe 1969, p. 314). Nevertheless, none of the phyllocarid specimens found in South America could actually be assigned to the Order Hymenostraca and that order will not be discussed below, although some species initially described under the genus name *Hymenocaris* could now be more accurately assigned to *Caryocaris* (see below).

According to the Treatise (Rolfe 1969) five archaeostracan genera (*Caryocaris* Salter, 1863; *Ceratiocaris* McCoy, 1849; *Nothozoe* Barrande, 1872; *Saccocaris* Salter, 1863, and *Trigonocarys* Barrois, 1891) have been described from – or are known to occur in – Ordovician strata throughout the world. The last three genera are assigned to uncertain order and family (Rolfe 1969, p. 323). The genus *Rhinopterocaris* Chapman, 1903, is considered to be a junior synonym of *Caryocaris*, whereas *Lamprocaris* Želízko, 1919 is considered to be a *nomen nullum* (Rolfe 1969, p. R316, Chlupáč 1970), whilst *Dawsonia* Nicholson, 1873 is no more considered to be a phyllocarid genus (Page, in press).

Chlupáč (1970) described the Bohemian genus *Mytocaris* under 'subordo et familia incerta' and considered *Rhinopterocaris* Chapman, 1903, to be a subgenus of *Caryocaris*. Bassett & Berg-Madsen (1993) assigned the Ordovician genus *Protocimex* Moberg, 1892 from Sweden (initially described as an insect wing) to the Phyllocarida. They stated that *Protocimex* has to be considered as a *nomen dubium*, though they regarded *Protocimex* to be a probable junior synonym of *Caryocaris* (Bassett & Berg-Madsen 1993, p. 144). More recently Racheboeuf *et al*. (2000) rejected *Trigonocarys* from the phyllocarids and proposed the family Caryocarididae for the genus *Caryocaris* only; they considered *Rhinopterocaris* to be a junior synonym of *Caryocaris* and they described the genus *Pumilocaris* from the Late Ordovician of Argentina, which they assigned to the family Ceratiocarididae.

As a consequence, most Ordovician representatives of Archaeostraca presently belong to either the Family Caryocarididae, or the Family Ceratiocarididae, with exception of the genera *Nothozoe*, *Saccocaris* and *Mytocaris* which still remain of uncertain affinities among phyllocarids as explained above.

Among the Family Caryocarididae, the new concept of the genus *Caryocaris* developed in the present paper leads to the description of two new caryocaridid genera on the basis of selected morphological characters (see the taxonomic discussion below), namely *Janviericaris* gen. nov., and *Ivocaris* gen. nov. The Family Caryocarididae now includes three genera namely *Caryocaris* Salter, 1863, *Ivocaris* gen. nov. and *Janviericaris* gen. nov.

South American representatives of the Family Ceratiocarididae are *Pumilocaris* Racheboeuf *et al*. 2000, and *Rolfecaris* gen. nov. Despite several references in the literature (for example Branisa 1965), no representative of the genus *Ceratiocaris* could up to now be identified among specimens in collections or among newly collected material. References to *Ceratiocaris* most probably correspond to large, poorly preserved caryocaridid specimens. Therefore South American Ordovician occurrences of *Ceratiocaris* remain speculative or uncertain (Rolfe 1969, p. 315).

Although undoubtedly far from complete, the worldwide generic diversity of Ordovician phyllocarid crustaceans actually includes five genera belonging to two families (Caryocarididae and Ceratiocarididae). Other taxa have been illustrated without description, such as the two probably new archaeostracans (among which a possible ceratiocaridid) from the Middle Ordovician of Oklahoma (North America) (Hannibal & Feldmann 1997).

According to the literature, 28 species names (among which several probable synonyms) and one subspecies have been described under the genus name *Caryocaris* between 1863 and 2000 (Table 2). They range from the Tremadocian to the Hirnantian with the recent description of *Caryocaris cedarbergensis* Whittle *et al*. (2007) from South Africa. The distribution of taxa cited and/or figured in the literature as *Caryocaris* sp. was given in Vannier *et al*. (2003) and it is not taken into account here. Among the species that can be actually considered to belong to *Caryocaris* (see Table 2), fifteen species have been defined on carapaces only; four other species have been described based on furcal rami only; five other species are known both by their carapace and tail piece, while 2 species have been described from complete exoskeletons. Each of the two new caryocaridid genera proposed here, namely *Janviericaris* gen. nov. and *Ivocaris* gen. nov. includes two species, as in the two ceratiocaridid genera, *Pumilocaris* and *Rolfecaris* gen. nov.

Conclusion

This paper provides the first accurate tentative inventory and description of the Ordovician phyllocarid fauna from South America. It includes nine species belonging to five genera from the Tremadocian–Sandbian time interval, while the upper Sandbian and the lower Katian provided us with three other forms still in open nomenclature. Such a diversity has no equivalent in the world at the moment and it does not include the 21 forms of *Caryocaris* sp. found in the literature and which have not been revised or studied. This South American diversity is undoubtedly directly related to the development of the graptolitic black

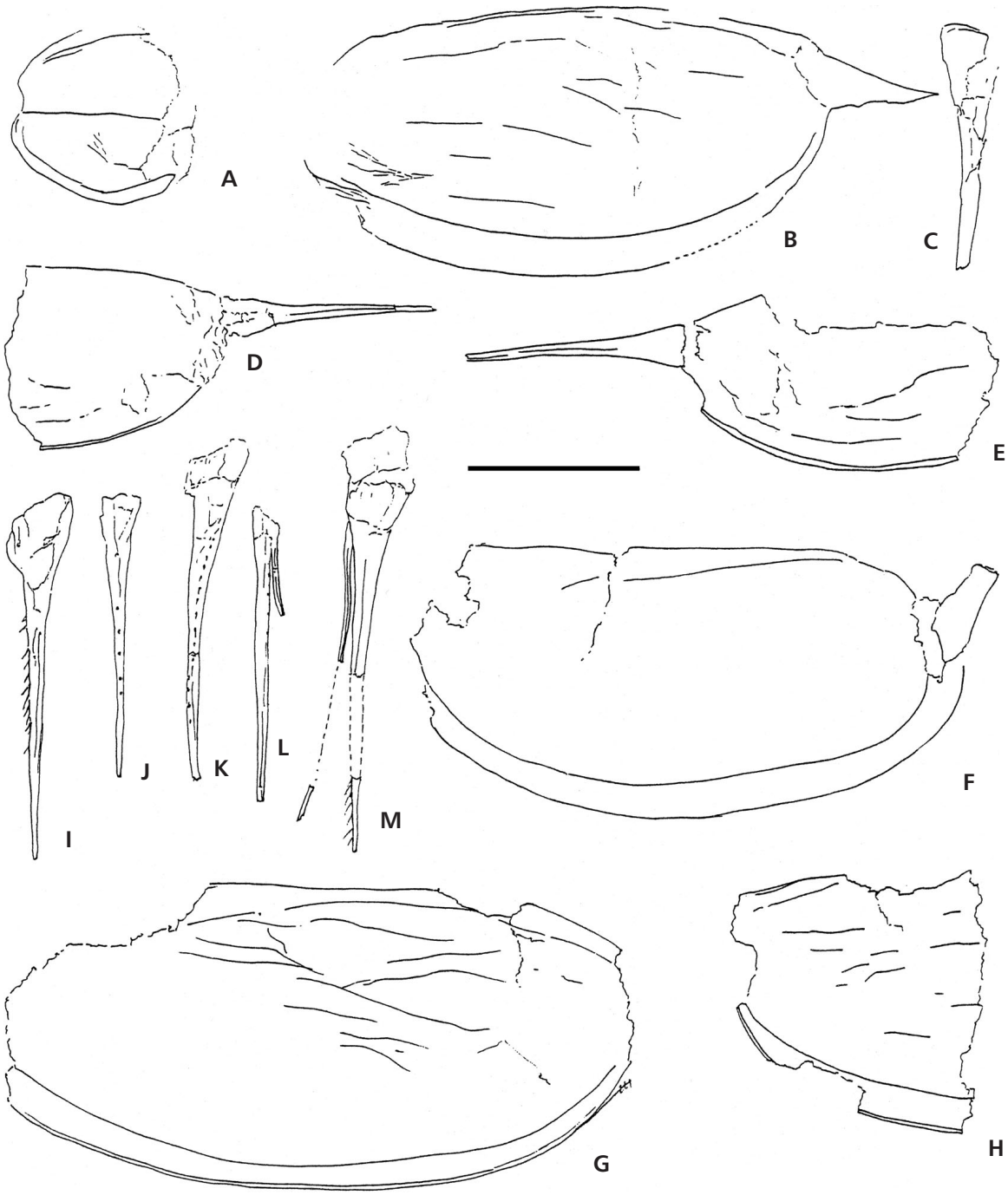

Figure 15. *Rolfecaris lethiersi* gen. et sp. nov. Camera lucida drawings of carapaces and tail pieces. All specimens from the Agua Blanca section (type locality) sample 7 of Blanca Toro, except Fig. 15I from Mina Natasia section. Acoite Formation, *Tetragraptus approximatus* to *T. akzharensis* Zones, early Floian (early Arenig). Scale bar = 5 mm. • A – juvenile specimen with valves still articulated, No. 23258. • B – almost complete left valve with proximal part of telson, No. 23259. • C – isolated telson, No. 23260. • D – posterior half of a left valve, with telson, No. 23262. • E – posteroventral part of a right valve with telson, No. 23261. • F – left valve, with well preserved ventral border, and proximal part of telson, No. 23244. • G – incomplete, large left valve with partly preserved ornament, No. 23245. • H – anterior part of a left valve, No. 23263. • I – isolated telson in dorsal view with longitudinal furrows, and the right row of lateral spinules, No. 23326. • J, K – two isolated telson showing the lateral row of spinules, No. 23249 and 23250, respectively. • L – poorly preserved tail piece, with the proximal part of a stylet still connected, No. 23251. • M – tail piece in ventral view, still connected to the last abdominal somite; note the length of the right stylet and the presence of lateral spinules up to the extremity of the telson, No. 23252.

Table 2. List of Ordovician phyllocarid taxa drawn from the literature. The column 'M' (Material) gives the nature of the original specimens upon which the corresponding taxa were described: CS – complete specimens; C – carapace; C+TP – carapace and tail piece; C+A – carapace and abdominal segments; F – isolated furcal rami. Asterisk indicates type species.

Genera and species	Author	Range	Country	M
Family Caryocarididae				
Caryocaris Salter, 1863				
acoitensis sp. nov.	this paper	Floian	Bolivia	F+TP
acuminata	(Nicholson, 1873)	Ordovician	Canada	F
angusta	Chapman, 1903	Arenigian	Australia	C
barrandei	Želízko, 1919	Llandeilo	Bohemia	C
bensoni	(Chapman, 1934)	L. Ordovician	New Zealand	CS
bodenbenderi	Aceñolaza & Esteban, 1996	Tremadocian	Argentina	F
bulmani	(Chapman, 1934)	L. Ordovician	New Zealand	C
cedarbergensis	Whittle *et al*., 2007	Hirnantian	South Africa	C
curvilata	Gurley, 1896	L. Ordovician	Canada	C
kilbridensis	Woodward, 1912	Arenigian	UK	C
lepadoides	(Chapman, 1934)	L. Ordovician	New Zealand	CS
maccoyi	(Etheridge, 1892)	Arenigian	Australia	C
maccoyi var. *tumida*	(Chapman, 1934)	L. Ordovician	New Zealand	C
magna	Ruedemann, 1935	L. Ordovician	Oklahoma	C
marrii	Hicks, 1876	Arenigian	UK	C
minima	Chapman, 1934	L. Ordovician	New Zealand	C
monodon	(Gurley, 1896)	Arenigian	Canada	F
oblonga	Gurley, 1896	Arenig/Llanvirn	Canada	C
oklahomensis	Ruedemann, 1935	L. Ordovician	Oklahoma	CS + A
raymondi	Ruedemann, 1934	M. Ordovician	Tennessee	C+TP
salteri	(McCoy, 1861)	L. Ordovician	Australia	TP
scanica	Möberg & Segerberg, 1906	Tremadocian	Sweden	C
silicula	Bassler, 1919	Ordovician	Maryland	C
silurica	Ruedemann, 1934	L. Ordovician	Alaska	CS+C
stewarti	Jell, 1980	Lancefieldian	Australia	C+TP
subula	Chlupáč, 1970	Llanvirnian	Bohemia	C+TP
tridens	(Gurley, 1896)	Arenigian	Canada	F
*wrightii**	Salter, 1863	Arenigian	UK	C
zhejiangensis	Shen, 1986	L. Ordovician	SE China	C+TP
Janviericaris gen. nov.	this paper			
*formosa** sp. nov.	this paper	Floian–L. Daping.	Bolivia	C+TP
jujuyensis sp. nov.	this paper	Floian	Argent. + Bolivia	C+TP
Ivocaris gen. nov.	this paper			
*delicata**	(Racheboeuf *et al*., 2000)	Darriwilian	Argentina	C+ TP
saltitensis sp. nov.	this paper	L. Darriwilian	Argentina	C+TP
Family Ceratiocarididae				
Pumilocaris Racheboeuf *et al.*, 2000				
acuta	(Bulman, 1931)	Darr.–Sandbian	Peru	C
*granulosa**	Racheboeuf *et al*., 2000	U. Sandbian	Argentina	C
Rolfecaris gen. nov.	this paper			
*lethiersi** sp. nov.	this paper	L. Floian	Argentina	CS
parchaensis sp. nov.	this paper	U. Tremadocian	Argentina	C+TP
Ordovician taxa of uncertain order and family and of uncertain systematic assignment				
Mendocaris Rusconi, 1950				
*australis**	Rusconi, 1950	Cambrian	Argentina	? C
Mytocaris Chlupáč, 1970				
*klouceki**	Chlupáč, 1970	Arenig	Bohemia	C+A
Nothozoe Barrande, 1872				
*pollens**	Barrande, 1872	M. Ordovician	Bohemia	C
barrandei	Chlupáč, 1970	Caradoc	Bohemia	C+TP
Protocimex Möberg, 1892				
*silurica**	Möberg, 1892	Arenig/Llanvirn	Sweden	C
Saccocaris Salter, 1873				
*major**	Salter, 1873	L. Ordovician	UK	C

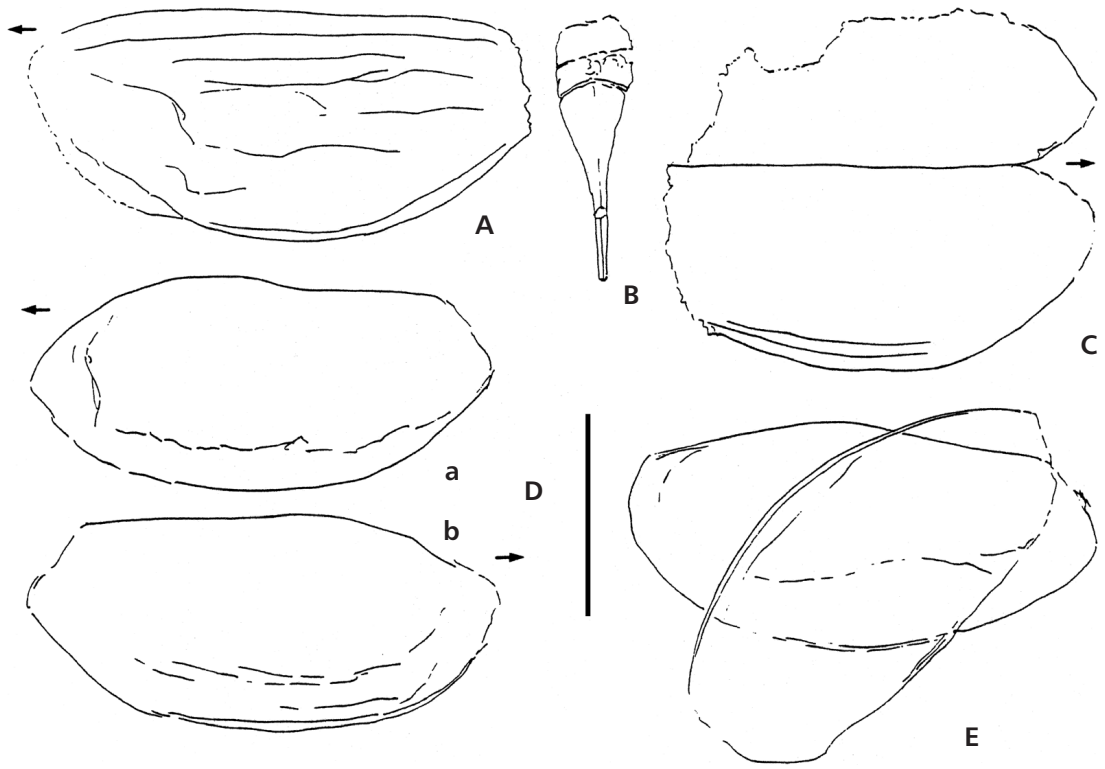

Figure 16. *Rolfecaris parchaensis* sp. nov. Camera lucida drawings of five carapaces and one tail piece. All specimens from the locality Guaico Hondo. Parcha Formation, *Araenograptus murrayi* and *Hunnegraptus copiosus* Zones (late Tremadoc). • A – left valve, holotype, No. 23231. • B – incomplete tail piece (telson) in dorsal view, still connected to the two last abdominal somites, No. 23233. • C – incomplete, still articulated carapace, No. 23235. • D – the two valves, right (Da) and left (Db) of a single carapace, No. 23234, and 23237, respectively. • E – right and left valves of a single (?) carapace, No. 23238. Scale bar = 3 mm.

shale facies from the Tremadocian to the middle Katian, as it also results from the effects of currents, temperature of water, *etc*. More acurate taxonomic studies are needed, especially regarding old, poorly described species. Most of the species previously assigned to the genus *Caryocaris* and listed in Table 2 are in need of immediate further thorough revision for their taxonomic identity, their assignment, their age, their geographic distribution as well as their vertical range. Several taxa are probably junior synonyms. Such work would lead to a more precise stratigraphic range for each taxon and will undoubtedly make Ordovician phyllocarids and among them representatives of the Family Caryocarididae, a more reliable, helpful tool, for both biostratigraphic and palaeobiogeographic considerations during the Ordovician. Evolutionary tendencies within the Family Caryocarididae will be dealt with in another paper (Racheboeuf & Crasquin, in press). An exhaustive, detailed, worldwide revision of all Ordovician phyllocarid remains in collections, using new, actualized biostratigraphical data, associated with complementary field sampling when necessary, would be indispensable to evaluate the evident potential biostratigraphical and biogeographical value of Ordovician phyllocarids.

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References

ACEÑOLAZA, F.G. 1966. *Geología estratigráfica de la región de la sierra de Cajas, Departamento Humahuaca, provincia de Jujuy*. 143 pp. Unpublished doctoral thesis, Universidad Nacional de Córdoba.

ACEÑOLAZA, F.G. & ESTEBAN, S. 1996. Filocáridos (Crustacea) en el Tremadociano del Sistema de Famatina, Provincia de La Rioja, Argentina. *Memorias del XII Congreso Geológico de Bolivia, Tarija 28*, 1–288.

ACEÑOLAZA, F.G., GORUSTOVICH, S. & SOLIS, J. 1976. El Ordovícico del río La Alumbrera, Departamento Tinogasta, Provincia de Catamarca. *Ameghiniana 13*, 269–288.

ACEÑOLAZA, F.G. & GUTIÉRREZ-MARCO, J.C. 2000. Graptolitos de la Formación Portezuelo de las Minitas (Ordóvicico Inferior) del Sistema de Famatina, La Rioja, Argentina. *Boletín de la Academia Nacional de Ciencias, Córdoba 64*, 17–26.

AHLFELD, F. & BRANISA, L. 1960. Geología de Bolivia. *Revista del Museo de La Plata, N.S. 3(19)*, 5–370.

ALBANESI, G., ESTEBAN, S.B. & BARNES, C.R. 1999. Conodontes del intervalo del límite Cámbrico-Ordovícico en la Formación Volcancito, Sistema de Famatina, Argentina. *Temas Geológico-Mineros ITGE 26(52)*, 1–526.

ALBANESI, G., ESTEBAN, S.B., ORTEGA, G., HÜNICKEN, M. & BARNES, C.R. 2005. Bioestratigrafía y ambientes sedimentarios de las formaciones Volcancito y Bordo Atravesado (Cámbrico Superior-Ordóvicico Inferior), Sistema de Famatina, provincia de La Rioja. *Associación Geológica Argentina, Serie D, Publicación Especial 8*, 41–64.

ALBANESI, G. & ORTEGA, G. 2002. Advances on conodont-graptolite biostratigraphy of the Ordovician System of Argentina, 143–165. *In* ACEÑOLAZA, F.G. (ed.) *Aspects of the Ordovician System in Argentina. Serie de Correlación Geológica 16*.

ASTINI, R. 1992. Tectofacies ordovícicas y evolución de la cuenca eopaleozoica de la Precordillera Argentina. *Estudios Geológicos 48*, 315–327.

ASTINI, R. 1994. Análisis secuencial y paleoambientes de las pelitas negras (aloformación Gualcamayo) que suprayacen a las sucesiones carbonáticas eo-ordovícicas en la Precordillera argentina. *Revista de la Asociación Geológica Argentina 49*, 71–84.

ASTINI, R. 2001. Nuia y Girvanella a través de la transición cambro-ordovícica (Formación Volcancito) en el Famatina: significado paleoambiental, paleoclimático y paleogeográfico. *Ameghiniana 38*, 243–255.

ASTINI, R. 2003. The Ordovician Proto-Andean Basins, 75–90. *In* BENEDETTO, J.L. (ed.) Ordovician Fossils of Argentina. *Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba*.

BALDIS, B.A., BERESI, M., BORDONARO, O. & VACA, A. 1984. The Argentine Precordillera as a key to the Andean structure. *Episodes 17*, 14–19.

BARRANDE, J. 1872. *Système silurien du centre de la Bohême, I*. Prague & Paris.

BARROIS, C. 1891. Mémoire sur la faune du grès armoricain. *Annales de la Société géologique du Nord 19*, 134–237.

BASSETT, M.G. & BERG-MADSEN, V.D. 1993. *Protocimex*: a phyllocarid crustacean, not an Ordovician insect. *Journal of Paleontology 67*, 144–147.

BASSLER, R.S. 1919. Report on the Cambrian and Ordovician formations of Maryland. *Maryland Geological Survey, Special Paper*, 1–424, 58 pls.

BOUCOT, A.J. 1975. *Evolution and extinction rate controls*. 427 pp. Elsevier, Amsterdam.

BRANISA, L. 1965. Los fosiles guías de Bolivia. I. Paleozoico. *Boletin del Servicio Geológico de Bolivia 6*, 1–282.

BRUSSA, E. &. ASTINI, R. 1996. La Biozona de *Undulograptus austrodentatus* en la Formación Gualcamayo, quebrada de Los Saltitos, suroeste de Guandacol, Precordillera Argentina. *Reunión Anual de Comunicaciones de la Asociación Paleontológica Argentina, Córdoba. Ameghiniana 34(1),* 116.

BRUSSA, E. & FLORES, L. In press. Darriwilian (Middle Ordovician) and Sanbian (Upper Ordovician) graptolite faunas of the Gualcamayo and Las Vacas Formations, Los Saltitos Creek, San Juan Precordillera, Argentina. *Acta Geologica Sinica*.

BRUSSA, E., MITCHELL, C., ORTEGA, G. & ASTINI, R. 2003b. Middle Ordovician graptolite biostratigraphy from the Los Azules Formaton at Los Gatos Creek, Central Precordillera, Argentina. *Proceedings 7th International Graptolite Conference – Field Meeting Subcommission on Silurian Stratigraphy, Serie de Correlación Geológica 18*, 21–25.

BRUSSA, E., TORO, B.A. & BENEDETTO, J.L. 2003a. Biostratigraphy, 75–90. *In* BENEDETTO, J.L. (ed.) *Ordovician Fossils of Argentina*. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba.

BULMAN, O.M.B. 1931. South American graptolites, wih special reference to the Nordenskiöld Collection. *Arkiv för Zoologi 22A(3)*, 1–111.

CAMACHO, H.H. 1975. *Invertebrados Fósiles. 2nd edition*. 707 pp. Editorial Universitaria de Buenos Aires.

CHAPMAN, F.C. 1903. New or little-known Victorian fossils in the National Museum, Melbourne. *Proceedings of the Royal Society of Victoria 16*, 104–122.

CHAPMAN, F.C. 1934. On some phyllocarids from the Ordovician of Preservation Inlet and Cape Providence, New Zealand. *Transactions of the New Zealand Institute 64*, 105–114.

CHLUPÁČ, I. 1970. Phyllocarid crustaceans of the Bohemian Ordovician. *Sborník geologických věd, Paleontologie 12*, 41–75.

CHLUPÁČ, I. 2003. Phyllocarid crustaceans from the Middle Ordovician Šárka Formation at Praha-Vokovice. *Bulletin of Geosciences 78*, 107–111.

CHURKIN, JR. M. 1966. Morphology and stratigraphic range of the phyllocarid crustacean *Caryocaris* from Alaska and the Great Basin. *Palaeontology 9*, 371–380.

CLAUS, C. 1888. Über den Organismus der Nebaliden und die systematische Stellung der Leptostraken. *Arbeiten aus dem zoologische Institut der Universität Wien und der zoologischen Station in Triest 8*, 1–148.

COIRA, B. & PÉREZ, B. 2002. Peperitic textures of Ordovician dacitic synsedimentary intrutions in Argentina Puna Highland: clues to emplacement conditions. *Journal of Volcanology and Geothermal Research 114*, 165–180. DOI 10.1016/S0377-0273(01)00291-8

COLLETTE, J.H. & RUDKIN, D.M. In press. A new phyllocarid crustacea from the Eramosa Lagerstätte (Silurian – Wenlockian), Ontario, Canada, and a revised interpretation of abdomi-

nal 'scales' in Ceratiocaris 'papilio'. *Transactions of the Royal Society of Edinburgh.*

EKSTRÖM, G. 1937. Upper *Didymograptus* Shale in Scania. *Sveriges Geologiska Undersökning Serie C, Afhandlingar och Uppsatser 403*, 1–53.

ESTEBAN, S.B. 1996. Los primeros trilobites ciclipígidos en el Ordovícico de Argentina (Formación Volcancito, Sistema de Famatina). *Ameghiniana 33*, 57–64.

ESTEBAN, S.B. 1999. Cyclopygid trilobites and associated facies from the Ordovician of the Famatina basin (Northwestern Argentina): Paleogeographic and evolutionary implications. *Acta Universitatis Carolinae, Geologica 43*, 377–379.

ESTEBAN, S.B. 2002. The Early Ordovician in the Sistema de Famatina: stratigraphic and geotectonic framework. *In* ACEÑOLAZA, F.G. (ed.) Aspects of the Ordovician System in Argentina. *Correlación Geológica, Tucumán 16*, 27–40.

ESTEBAN, S. & GUTIÉRREZ-MARCO, J.C. 1997. Graptolitos del Tremadoc del Sistema de Famatina (Argentina). *5° Reunión Internacional del Proyecto 351 PICG 'Paleozoico Inferior del Noroeste de Gondwana'. Abstracts*, 59–63.

ETHERIDGE, R. JR. 1892. A monograph of the Carboniferous and Permo-Carboniferous invertebrata of New South Wales, Part II. Echinodermata, Annelida and Crustacea. *New South Wales Geological Survey, Memoir, Palaeontology 5*, 65–131.

GURLEY, R. R. 1896. North American graptolites: new species and vertical range. *The Journal of Geology 4*, 63–301.

GUTIÉRREZ-MARCO, J.C. & ESTEBAN, S. 2005. Graptolitos del Tremadociense (Ordovícico Inferior) de la Formación Volcancito, Sistema de Famatina (La Rioja, Argentina). *Revista Española de Paleontología 20(11),* 65–118.

GUTIÉRREZ-MARCO, J.C., GÓMEZ, C. & SARMIENTO, G.N. 2006. El Ordovícico dela Cordillera colombiana y su correlación con Perú, 623–626. *In* CARLOTTO, V., CÁRDENAS, J., SOLER, P. & JACAY, J. (eds) *XIII Congreso peruano de Geología. Sociedad Geológica del Perú, Lima, Publicación Especial 7*.

HANNIBAL, J.T., & FELDMANN, R.M. 1996. *Caryocaris* (Crustacea: Phyllocarida) from the Ordovician of the Cordillera Oriental of Souhern Bolivia. *Kirtlandia 49*, 7–11.

HANNIBAL, J.T. & FELDMANN, R.M. 1997. Phyllocarid crustaceans from a Middle Ordovician Black Shale Within the Ames Structure, Northwest Oklahoma. *Oklahoma Geological Survey, Circular, 100*, 370–373.

HARRINGTON, H.J. & KAY, M. 1951. Cambrian and Ordovician faunas of Eastern Colombia. *Journal of Paleontology 25*, 655–668.

HARRINGTON, H.J. & LEANZA, A.F. 1957. Ordovician Trilobites of Argentina. *University of Kansas Press, Special Publication 1*, 1–259.

HICKS, H. 1876. *In* MARR, J.E. Fossiliferous Cambrian shales near Caernarvon. *Quarterly Journal of the Geological Society of London 32*.

HUGHES, C.P. 1980. A brief review of the Ordovician faunas of northern South America. *Actas del Segundo Congreso Argentino de Paleontología y Bioestratigrafía y Primer Congreso Latinoamericano de Paleontología, Buenos Aires (1978)1*, 11–22.

JELL, P.E. 1980. Two arthropods from the Lancefieldian (La 1) of central Victoria. *Alcheringa 4*, 37–46.
DOI 10.1080/03115518008558979

LATREILLE, P.A. 1806. *Genera Crustaceorum et Insectorum secundum ordinem naturalem in familias doisposita, iconibus exemplurisque plurimis explicata.* T. 1, 302 pp., pls 1–16. Paris & Argentorati.

LAUBACHER, G. 1974. Le Paléozoïque inférieur de la Cordillère orientale du sud-est du Pérou. *Cahiers de l'ORSTOM, Série Géologique 6(1)*, 29–40.

LEGRAND-SMITH, A. & HANNIBAL, J.T. 2000. Rock shrimp. *Explorer 41(2)*, 11–13.

LEVY, R. 1971. Noticia sobre el hallazgo de apendices ventrales de trilobites en la Formación Parcha (Salta). *Revista de la Asociación Paleontológica Argentina 8(2)*, 73–76.

MANCA, N. 1991. Organismos planctónicos en el Tremadociano inferior de los alrededores de la Quebrada de Humahuaca, Provincia de Jujuy, Agentina. *Revista del Instituto de Geología y Minería, Jujuy 8*, 141–150.

MARTÍNEZ, M., BRUSSA, E., PÉREZ, B. & COIRA, B. 1999. El Ordovícico de la sierra de Quichagua (Puna nororiental argentina): litofacies volcanosedimentarias y graptofaunas. (Volcanic sedimentary lithofacies and graptolites from the sierra de Quichagua, Ordovician of the Northeastern Puna of Argentina. *XIV Congreso Geológico Argentino, I*, 347–350.

MCCOY, P. 1849. On the classification of some British fossil Crustacea, with notices of new forms in the University of Cambridge. *The Annals and Magazine of Natural History 4*.

MENDEZ, V. 1973. Geología de la comarca de Mina 'Aguilar' y alrededores, Departamento Humahuaca, Provincia de Jujuy. *Revista de la Asociación Geológica de Argentina 28*, 319–330.

MÖBERG, J.C. 1892. Om en Hemipter fran Sveriges Undre Graptolitskiffer. *Geologiska Föreningens i Stockholm Förhandlingar 14*, 121–124.

MÖBERG, J.C. & SEGERBERG, O. 1906. Bidrag till kännedomen om Ceratopygeregionen med sörskild hänsyn till dess utveckling i Fogelsångstrakten. *Meddelande från Lunds Geologiska Faltklubb, new series 2(7)*, 1–113.

NICHOLSON, H.A. 1873. On some fossils from the Quebec Group of Point Lévis, Quebec. *The Annals and Magazine of Natural History 11*, 133–143.

ORTEGA, G. 1987. *Las graptofaunas y los conodontes de la Formación Los Azules, cerro Viejo, zona de Huaco, departamento Jáchal, San Juan*. 210 pp. Unpublished tesis doctoral, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba.

ORTEGA, G. & ALBANESI, G. 2002. Bioestratigrafía de graptolitos y conodontes del Tremadociano tardío de la Cordillera Oriental, Argentina. *15th Congreso Geológico Argentino I*, 542–547.

ORTEGA, G. & RICKARDS, B. 2003. A Darriwilian (Middle Ordovician) graptolite fauna of the Lower Member of the Los Azules Formation, Cerro Viejo, San Juan Precordillera, Argentina. *Proceedings 7th International Graptolite Conference – Field Meeting Subcommission on Silurian Stratigraphy, Serie de Correlación Geológica 18*, 21–25.

PACKARD, A.S. 1879. A monograph of the Phyllopod Crustacea of north America, with remarks on the order phyllocarida. *12th Report of the U.S. Geological Survey Territories 12*, 295–592.

PAGE, A., WILBY, P.R., MELLISH, C., WILLIAMS, M. & ZALASIEWICZ, J.A. In press. *Dawsonia* Nicholson: linguliform

brachiopods, crustacean tail-pieces and a problematicum rather than graptolite ovarian vesicles. *Transactions of the Royal Society of Edinburgh*.

RACHEBOEUF, P.R. 1994. Silurian and Devonian phyllocarid crustaceans from the Massif armoricain, NW France. *Revue de Paléobiologie 13*, 281–305.

RACHEBOEUF, P.R. 2004. Phyllocarid crustaceans, 257–260. *In* WEBBY, B.D., PARIS, F., DROSER, M. & PERCIVAL, I.G. (eds) *The Great Ordovician Biodiversification Event*. Columbia University Press.

RACHEBOEUF, P.R. & CRASQUIN, S. In press. The Ordovician caryocaridid phyllocarids (Crustacea): diversity and evolutionary tendencies. *Neues Jahrbuch für Geologie und Paläontologie*.

RACHEBOEUF, P.R., VANNIER, J. & ORTEGA, G. 2000. Ordovician phyllocarids (Arthropoda; Crustacea) from Argentina. *Paläontologische Zeitschrift 74*, 317–333.

RAMOS, V.A. 1970. *Geología de los primeros contrafuertes de la puna saltojujeña, entre San Antonio de los Cobres y El Moreno, provincias de Salta y Jujuy*. Unpublished doctoral tesis, Universidad de Buenos Aires.

RAMOS, V.A. 1984. Filocáridos (Crustacea) del Ordovícico Argentino. *Actas del III° Congreso Argentino de Paleontología y Bioestratigrafía, Corrientes (1982)*, 29–38.

ROLFE, W.D.I. 1962. Grosser morphology of the Scottish Silurian phyllocarid crustacean Ceratiocaris papilio Salter in Murchison. *Journal of Paleontology 36*, 912–932.

ROLFE, W.D.I. 1969. Phyllocarida, R296–R331. *In* MOORE, R.C. & TEICHERT, C. (eds) *Treatise on Invertebrate Paleontology. Part R. Arthropoda 4(1).* 398 pp. Geological Society of America & University of Kansas Press, Boulder, Colorado & Lawrence, Kansas.

RUEDEMANN, R. 1934. Paleozoic plankton of North America. *Geological Society of America, Memoir 2*, 1–141.

RUEDEMANN, R. 1935. Silurian phyllocarid crustaceans from Oklahoma. *Journal of Paleontology 9*, 447–448.

RUSCONI, C. 1950. Nuevos trilobitas y otros organismos del Cámbrico de Canota. *Revista del Museo de Historia Natural de Mendoza 4*, 85–94.

RUSHTON, A.W.A. & WILLIAMS, M. 1996. The tail-piece of the crustacean *Caryocaris wrightii* from the Arenig rocks of England and Ireland. *Irish Journal of Earth Sciences 15*, 107–111.

SALTER, J.W. 1863. Note on the Skiddaw Slate fossils. *Quarterly Journal of the Geological Society of London 19*, 135–140.

SCOTESE, C.R. & MCKERROW, W.S. 1990. Revised world maps and introduction, 1–21. *In* MCKERROW, W.S. & SCOTESE, C.R. (eds) Palaeozoic Palaeogeography and Biogeography. *Geological Society of London, Memoir 12*, 1–435.

SHEN, Y.-B. 1986. *Caryocaris* from the Lower Ordovician of Jiangshan, Zhejiang. *Kexue Tongbao 31*, 765–769.

STRAELEN, V. VAN & SCHMITZ, G. 1934. Crustacea Phyllocarida (= Archaeostraca). *Fossilium Catalogus, I. Animalia 64*, 1–246.

SÚAREZ-SORUCO, R. 1976. El sistema Ordovícico en Bolivia. *Revista Técnica YPFB 5*, 111–223.

TORO, B. 1999. Graptolitos arenigianos de Santa Victoria, Cordillera Oriental, Argentina. Bioestratigrafía y paleogeografía. *14° Congreso Geológico Argentino I*, 339–342.

TORO, B. & Brussa, E. 2003. Graptolites, 441–505. *In* BENEDETTO, J.L. (ed.) *Ordovician Fossils of Argentina*. Secretaría de Ciencias y Tecnología, Universidad Nacional de Córdoba.

TORTELLO, M.F. & ESTEBAN, S.B. 1995. Un trilobite agnóstido en el Ordovícico de la región de Bordo Atravesasdo (Cuesta de Miranda), Provincia de La Rioja, Argentina. *Actas del VI Congreso Argentino de Paleontología y Bioestratigrafía, Trelew*, 271–275.

TORTELLO, M.F. & ESTEBAN, S.B. 2003. Lower Ordovician stratigraphy and trilobite faunas from the southern Famatina Range, La Rioja, Argentina. *Special Papers in Palaeontology 70*, 213–239.

TRUMPY, D. 1943. Pre-Cretacerous of Colombia. *Bulletin of the Geological Society of America, 54(9)*, 1281–1304.

TURNER, J.C.M. 1960a. Faunas graptolíticas de América del Sur. *Revista de la Associación Geológica Argentina 14*, 5180.

TURNER, J.C.M. 1960b. Estratigrafía del tramo medio de la Sierra del Famatina y adyacencias (La Rioja). *Boletín de la Academia Nacional de Ciencias de Argentina 42*, 77–126.

VANNIER, J., BOISSY, P. & RACHEBOEUF, P.R. 1997. Locomotion in *Nebalia bipes*: a possible model for Palaeozoic phyllocarid crustaceans. *Lethaia 30*, 89–104.

VANNIER, J., RACHEBOEUF, P.R., BRUSSA, E., WILLIAMS, M., RUSHTON, A.W.A., SERVAIS, T. & SIVETER, D.J. 2003. Cosmopolitan arthropod zooplankton in Ordovician seas. *Palaeogeography, Palaeoclimatology, Palaeoecology 195*, 173–191. DOI 10.1016/S0031-0182(03)00307-9

WAISFELD, B., VACCARI, N., TORO, B., RUBINSTEIN, C. & ASTINI, R. 2006. Revisión de la Biozona de Ogygiocaris araiorhachis (Trilobita, Tremadociano tardío) en la región de Pascha-Incamayo, Cordillera Oriental, Argentina. Parte 1: Bioestratigrafía. *Ameghiniana 43(4)*, 717–728.

WHITTLE, R.J., GABBOTT, S.E., ALDRIDGE, R.J. & THERON, J.N. 2007. Taphonomy and palaeocology of a Late Ordovician caryocaridid (Crustacea, Phyllocarida) from the Soom Shale Lagerstätte, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology 251*, 383–397. DOI 10.1016/j.palaeo.2007.04.006

WOODWARD, H. 1912. Note on a new species of *Caryocaris* (*C. kilbridensis*) from the Arenig rocks of the Kilbride Peninsula. *Quarterly Journal of the Geological Society of London 68*, 99–101.

ŽELÍZKO, J.V. 1919. Nálezy phyllocaridů ve spodním siluru západočeském. *Rozpravy České akademie věd a umění, Třída II (matematicko-přírodovědná) 27,* 32.