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Ordovician phyllocarids (Arthropoda; Crustacea) from Argentina

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With 13 figures and 2 tables

Kurzfassung: Neue Phyllocarida werden aus dem Ordovizium (Frühes Arenig bis Unteres Caradoc) der argentinischen Prä- und Ost-Kordilleren beschrieben, namentlich *Caryocaris delicatus* n. sp., *Caryocaris* sp. 1, ?*Caryocaris* sp. 2, *Pumilocaris granulosus* n. gen., n. sp., ?*Pumilocaris* sp. sowie eine unbestimmte Form. Sie alle treten in graptolithen-haltigen Schiefern auf. Die bisher in der Literatur beschriebenen südamerikanischen Phyllocarida werden kritisch besprochen, und *Caryocaris delicatus* n. sp. (Llanvirn) wird mit congenerischen Arten verglichen, die aus dem Ordovizium (Tremadoc - Caradoc) Nordamerikas, Europas, Chinas und Australiens bekannt sind. Die Präsenz von *Caryocaris* in Südamerika ist nun belegt, was die Ansicht bestätigt, daß die Gattung im Unteren Ordovizium weltweit verbreitet war – in bezug auf die mögliche pelagische Lebensweise. Eine neue Definition von *Caryocaris* wird vorgeschlagen und die frühere Unterteilung der Gattung [*C.* (*Caryocaris*) und *C.* (*Rhinopterocaris*)] aufgegeben. Ein Satz von ursprünglichen Merkmalen (z.B. Fehlen einer Rostralplatte, kurze blattförmige Furkaläste, kurzes Telson, extrem dünner Carapax) deutet stark darauf hin, daß *Caryocaris* außerhalb der Ceratiocarididae liegt und die Basis einer neuen taxonomischen Einheit bilden könnte.

Abstract: New phyllocarids are described from the Ordovician (early Arenig to lower Caradoc) of the Precordillera and Eastern Cordillera of Argentina, namely *Caryocaris delicatus* n. sp., *Caryocaris* sp. 1, ?*Caryocaris* sp. 2, *Pumilocaris granulosus* n. gen., n. sp., ?*Pumilocaris* sp. and an undetermined form. They all occur in graptolite-bearing shales. A critical review of the South American phyllocarids formerly described in the literature is made and *Caryocaris delicatus* n. sp. (Llanvirn) is compared with congeneric species known from the Ordovician (Tremadoc-Caradoc) of North America, Europe, China and Australia. The presence of *Caryocaris* in South America is therefore attested, which confirms the view that the genus had a worldwide distribution in the lower Ordovician in relation with a possible pelagic lifestyle. A new definition of *Caryocaris* is proposed and the former subdivision of the genus [*C.* (*Caryocaris*) and *C.* (*Rhinopterocarys*)] abandoned. A set of original characters (e.g. lack of rostral plate, short leaf-like furcal rami, short telson, extremely thin carapace) strongly indicates that *Caryocaris* lies outside the Ceratiocarididae and may form the basis of a new taxonomic unit.

Introduction

Phyllocarids have been reported in numerous Ordovician localities of the South American Continent, especially in Argentina, Bolivia and Peru and, in places, form a significant although largely ignored component of the non-trilobitic arthropod fauna. The entire phyllocarid material discovered so far has been exclusively referred by authors (BULMAN 1931; AHLFELD & BRANISA 1960; ACEÑOLAZA 1966; ACEÑOLAZA et al. 1976; SUAREZ SORUCO 1976; HUGHES 1980; RAMOS 1984; ORTEGA 1987; MANCA 1991; HANNIBAL & FELDMANN 1996; ACEÑOLAZA & ESTEBAN 1996) to the genus *Caryocaris* SALTER 1863 and comprises a majority of poorly documented forms kept under open nomenclature (Tab. 1). Most works published over the last 60 years fail in providing accurate systematic descriptions or illustrations suitable for detailed comparisons with established taxa (e.g. European fauna; CHLUPAC 1970; RUSHTON & WILLIAMS 1996). In South America, *Caryocaris* ranges from the Upper Tremadoc through to the Caradoc. Our interest in the South American phyllocarids was triggered by the recent discovery by one of us (G. ORTEGA) of well-preserved specimens in the Ordovician series of the Eastern Cordillera and the Precordillera of Argentina. The present paper aims to give a detailed description of the new fauna and to reassess the palaeobiodiversity of South American phyllocarids during the Ordovician. In addition, a new definition of the genus *Caryocaris* is proposed and the affinities of *Caryocaris* within the Phyllocarida are discussed.

Ordovician phyllocarids from Argentina: previous work

The occurrences of *Caryocaris* in the Ordovician of Argentina, Bolivia and Peru were critically reviewed by RAMOS (1984), HANNIBAL & FELDMANN (1996), and ACEÑOLAZA & ESTEBAN (1996) and are summarized in

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Tab. 1. Major occurrences of Ordovician phyllocarids in South America. – Taxa described in the present paper indicated in bold. Fm. = Formation; Pr. = Province. 1 = ACEÑOLAZA 1966; 2 = ACEÑOLAZA 1976; 3 = ACEÑOLAZA & ESTEBAN 1996; 4 = AHLFELD & BRANISA 1960; 5 = BULMAN 1931; 6 = CAMACHO 1975; 7 = HANNIBAL & FELDMANN 1996; 8 = HARRINGTON & LEANZA 1957; 9 = LEVY 1971; 10 = MANCA 1991; 11 = MENDEZ 1973; 12 = ORTEGA 1987; 13 = RAMOS 1970; 14 = RAMOS 1984; 15 = this paper; 16 = WEBER, pers. comm.

Taxa	Formation	Age	Locality	Country	Refs
Caryocaris acuta Bulman,1931	unnamed Fm	Caradoc	Huichiyuni	Peru	5, 6
Caryocaris bodenbenderi A. & E., 1996	Volcancito Fm	Tremadoc	Quebrada del Portezuelo de la Alumbrera, La Rioja Pr.	Argentina	3
***Caryocaris delicatus* n. sp.**	Los Azules Fm	early to Late Llanvirn	Quebrada Los Azules, Amarilla de Los Gatos, San Juan Pr.	Argentina	15
***Caryocaris* sp. 1**	Parcha Fm	early Arenig	Angosto de Lampazar area, Salta Pr.	Argentina	15
***?Caryocaris* sp. 2**	Las Plantas Fm	early Caradoc	Cerro Potrerillo (W. side), San Juan Pr.	Argentina	15
***Pumilocaris granulosus* n. gen. n. sp.**	Las Plantas Fm	early Caradoc	Cerro Potrerillo (W. side section), San Juan Pr.	Argentina	15
***?Pumilocaris* sp.**	Parcha Fm	early Arenig	Quebrada de Incamayo, Incahuasi area, Salta Pr.	Argentina	15
Caryocaris sp.	"Toro Ara Group"	Arenig	Rio Toro Area, S of La Quiaca, Jujuy Pr.	Argentina	4, 8
Caryocaris sp.	La Alumbrera Fm	Arenig	Rio La Alumbrera, Catamarca Pr.	Argentina	2, 14
Caryocaris sp.	Acoite Fm	Arenig	Sierra de Cajas, Jujuy Pr.	Argentina	1, 2, 14
Caryocaris sp.	Acoite Fm	Arenig	Sierra de Aguilar, Jujuy Pr.	Argentina	11, 14
Caryocaris sp.	?	? Arenig	Puerta Tastil, Salta Pr.	Argentina	2, 14
Caryocaris sp.	?	upper Arenig-Llanvirn	Rio Gualcamayo, San Juan Pr.	Argentina	14
Caryocaris sp.	Parcha Fm	lower/mid Arenig	Piscuno sur, Salta Pr.	Argentina	9, 13, 14
Caryocaris sp.	Los Azules Fm	Llanvirn	Cerro Viejo (W. side section), San Juan Pr.	Argentina	12
Caryocaris sp.	Santa Rosita Fm	lower Tremadoc	Quebrada de Moya, Jujuy Pr.	Argentina	10
Caryocaris sp.	? Pircancha Fm	? Llanvirn	Quebrada de Chaupi Uno, NW Tarija	Bolivia	7
Caryocaris sp.	Pircancha Fm	Arenig	Quebrada de Chaupi Uno, NW Tarija	Bolivia	16

Tab. 1 along with the occurrence of the new Argentinan phyllocarids described in our paper.

To our knowledge, AHLFELD & BRANISA (1960: 44) were the first authors to note the presence of *Caryocaris* in the 'Arenig' of Northern Argentina. *Caryocaris* sp. from the lower part of the Santa Rosita Formation (Tremadoc; Eastern Cordillera, Jujuy Province; MANCA 1991) is the earliest known occurrence of the genus in Argentina. However, *Caryocaris* is most typically found in graptolite-bearing sediments from the Arenig and is reported by several authors (e.g. ACEÑOLAZA 1966; MENDEZ 1973; ACEÑOLAZA et al. 1976; RAMOS 1984; see Tab. 1) in numerous localities of the Eastern Cordillera (Jujuy Province), the Precordillera (San Juan and La Rioja Provinces) and in the Famatima System (Catamarca Province). Although mistakenly identified as a trilobite remain by RAMOS (1970) and LEVY (1971), *Caryocaris* also occurs in the Arenig of the Salta Provinces. The stratigraphical range of the genus largely extends into the Llanvirn as attested by the biostratigraphical work of ORTEGA (1987) in the Precordillera. In the Los Azules Formation *Caryocaris* distributes throughout at least 3 graptolite zones (*Undulograptus austrodentatus*, *Pterograptus elegans*, and *Hustedograptus teretiusculus*) indicating an Abereiddian to early Llandeilian (sensu FORTEY 1995) age. *Caryocaris bodenbenderi* ACEÑOLAZA & ESTEBAN 1996 is the only species to have been established and comes from the Tremadoc deposits of the Volcancito Formation (La Rioja Province). However, it is worth mentioning here that the holotype of *C. bodenbenderi* figured and reconstructed by ACEÑOLAZA & ESTEBAN (1996) is definitely not a carapace but an isolated right furcal ramus (compare with Fig. 8) bearing an indented inner margin.

The poor and 'unattractive' state of preservation of most Ordovician phyllocarids such as *Caryocaris* (these fossils typically occur as flattened, wrinkled or folded carapaces in dark graptolitic shales; see CHURKIN 1966) is probably largely influenced by the original composition and ultrastructure of the animal exoskeleton. For example, *Caryocaris* from the Llanvirn of Bohemia had a very thin (less than 5 µm), flimsy and probably uncalcified carapace comparable to that of the Recent bathypelagic phyllocarid *Nebaliopsis typica* (VANNIER et al. 1997). Moreover, *Caryocaris* has a very limited number of diagnostic features due to the relatively simple morphology of its carapace and abdominal parts. All these drawbacks apply to the Argentinan material and make it difficult to ascertain whether forms are conspecific or not.

Geological setting and origin of the new material

Argentine Precordillera

General setting

Phyllocarids are most commonly found in the black shales of the Gualcamayo and the Los Azules Formations which overlie the widespread carbonate platform of the San Juan Formation and correspond to a transgressive-diachronic event known to occur in the Precordillera during the middle Arenig to the early Llanvirn. These black shales are middle Arenig to early Llanvirn in age in the northern region of the Precordillera (between Guandacol River and Gualcamayo River sections), and early Llanvirn in the central area (between Cerro Viejo of Huaco and Villicum Range).

The Gualcamayo Formation crops out in several localities of the Precordillera, (1) in the central region (i.e. Guandacol River, Potrerillo and Las Plantas Creeks, Potrerillo-Perico Range) and, (2) in the eastern region (Villicum Range). It is overlain either by the Las Vacas Conglomerate (Llanvirn, possibly late Abereiddian; ex-

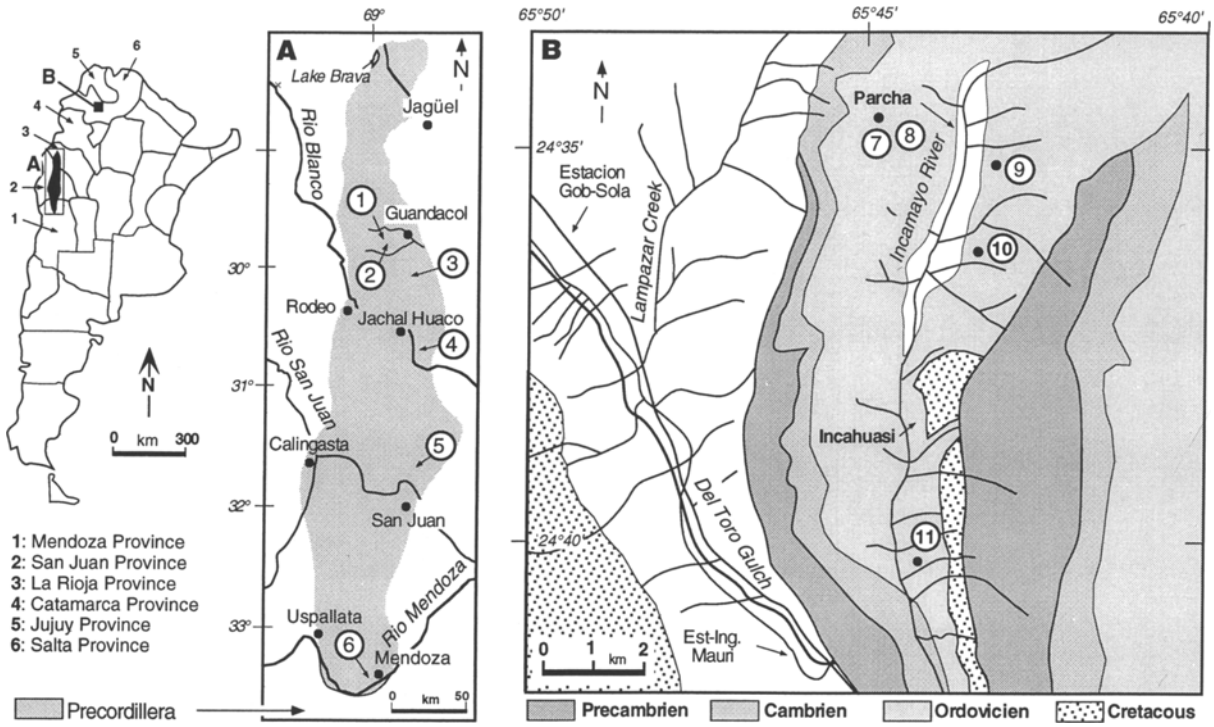

Fig. 1. Phyllocarid localities of the the Precordillera (**A**) and the Eastern Cordillera (**B**). – 1 = Potrerillo Creek and Gualcamayo River; 2 = Guandacol River and Los Sapitos Creek; 3 = Cerro Potrerillo; 4 = Cerro Viejo de Huaco area (Los Azules, Amarilla and Los Gatos Creeks); 5 = Villicum Range; 6 = Empozada and San Isidro Creeks; 7 = Incamayo Creek; 8 = Angosto de Lampazar area (path between Parcha and Abra de Sococha); 9 = La Pedrera Creek; 10 = Barranca Creek; 11 = loc. 3 km S. of Incahuasi.

posures between the Guandacol River and the Potrerillo-Las Plantas Creeks) or, unconformably by the Las Plantas Formation (early Caradoc; e.g. the Potrerillo-Perico Range), a shaly sequence containing limestones in its basal part.

The Los Azules Formation is well-exposed in the Cerro Viejo Range (Central Precordillera, West Huaco; see Fig. 1). The lower and middle members of the Los Azules Formation are partly correlated with the middle and upper parts of the Gualcamayo Formation, whilst its upper member may roughly correspond to the Las Plantas Formation (ORTEGA 1987). It is worth noting the presence of a stratigraphic gap encompassing the major part of the late Llanvirn in the northern part of the Precordillera.

Phyllocarids in the Gualcamayo Formation

Phyllocarid remains are fairly abundant throughout the Gualcamayo Formation but they are often poorly preserved. In the Potrerillo Creek section (Fig. 2), the Gualcamayo Formation overlies conformably the limestones of the San Juan Formation, and it is overlain by the conglomerates of the Las Vacas Formation. In this locality and neighbouring sections, the lower member of the Gualcamayo Formation consists of an alternating sequence of shales (dark mudstones) and limestones which is usually slightly folded. Trilobites and inarticulate brachiopods are present in limestones and form accumulation beds in places. Rare graptolites were found with the shelly fauna in the basal part of the formation. Phyllocarids usually occur in shales with graptolites and inarticulate 'lingulid-like' brachiopods. *Isograptus victoriae maximus*, *Oncograptus* and lower *Undulograptus austrodentatus* Zones indicate the late Arenig. The middle member of the formation (ca. 116 m thick) begins with 5 to 7 m of dark-brown argilites and is followed by thin dark gray siltstones. The upper member is a uniformous succession of siltstones (approx. 24 m) containing olistoliths from the San Juan Formation in its uppermost part. The middle and upper members of the Gualcamayo Formation yielded an abundant and diversified graptolite fauna which belongs to the *Undulograptus austrodentatus* Zone of early Llanvirn age (ORTEGA et al. 1993). Most of the phyllocarid material from the Gualcamayo Formation was collected in the northern part of the Precordillera, between the Guandacol River (La Rioja

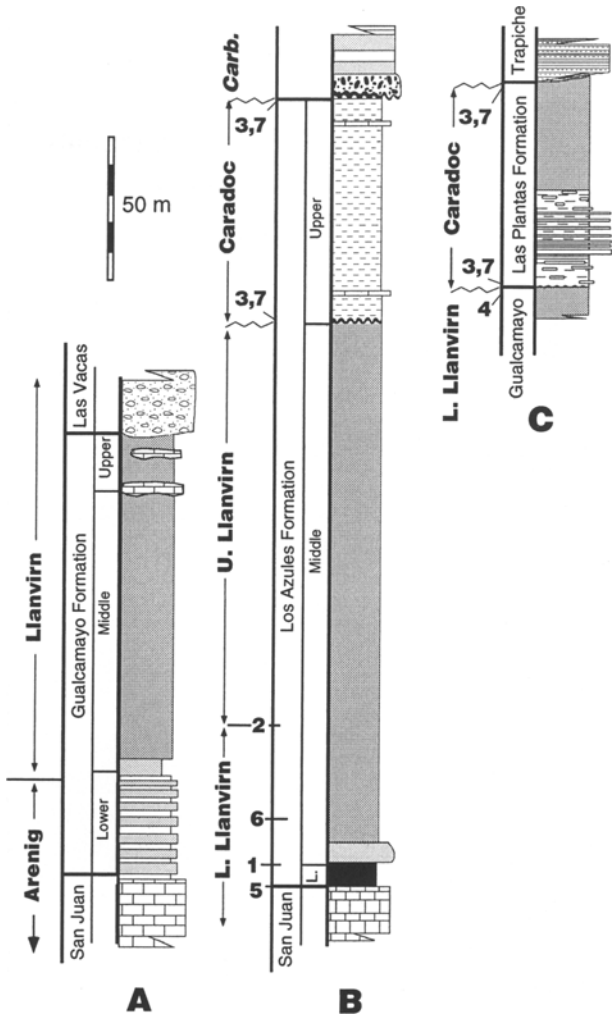

Fig. 2. Lithology and biostratigraphy of the phyllocarid-bearing sediments in the Argentinan Precordillera. – **A:** Gualcamayo Formation at Potrerillo Creek (Fig. 1, loc. 1); **B:** Los Azules Formation at Cerro Viejo de Huaco area (Fig. 1, loc. 4), reconstructed stratigraphic column; **C:** Plantas Formation at Cerro Potrerillo (Fig. 1, loc. 3). Numbers indicate main graptolite (1-4) and conodont (5-7) biostratigraphic markers indicated by numbers: 1 = *P. tentaculus* / *P. elegans* boundary; 2 = *P. elegans* / *H. teretiusculus* boundary; 3 = *N. gracilis*; 4 = *P. elegans*; 5 = *L. variabilis* / *E. suecicus* boundary; 6 = *E. suecicus* / *P. serra* boundary; 7 = *A. tvaerensis*. 'Upper Llanvirn' and 'Lower Llanvirn' are used to designate the upper (Llandeilian) and lower (Abereiddian) part of the Llanvirn sensu FORTEY (1995). – Modified from TORO (1998); ALBANESI et al. (1998, 1999); ORTEGA et al. (1998).

Province) and the Gualcamayo River (San Juan Province, see Fig. 1A). Additional specimens come from the Cerro Potrerillo section, ca. 40 km NE of Jachal, and from the Villicum Range, NE of San Juan.

Phyllocarids in the Los Azules Formation

Numerous phyllocarid remains were also recovered from the Los Azules Formation (Fig. 2) especially in its lower and middle members which are well exposed on the western side of the Cerro Viejo Range (northern part of San Juan Province). The lower member of the Los Azules Formation (about 10 m thick) consists of dark to black shales with intercalated beds of potassic bentonites (HUFF et al. 1995). An abundant graptolite fauna indicating the early Llanvirn (*Undulograptus austrodentatus* Zone) was found in this member (ORTEGA 1987). The middle member of the Los Azules Formation starts with 8 to 10 m of sandstones followed by a thick unit (about 200 m) of dark-grey siltstones. The whole member corresponds to the *Pterograptus elegans* and *Hustedograptus teretiusculus* Zones indicating an early to late Llanvirn (ORTEGA 1987, 1995) age. Other stratigraphic markers such as conodonts (*Eoplacognathus suecicus* and *Pygodus serra* Zones), inarticulate brachiopods (*Obolus* sp.), chitinozoans and acritarchs give a similar age (ORTEGA et al. 1996; OTTONE et al. in press).

Phyllocarids in the Las Plantas Formation

Phyllocarids also occur in the Las Plantas Formation and have been collected from the western side of the Cerro Potrerillo section (Figs. 1, 2). The lower part of the sequence consists of about 85 m of shales/calcareous shales with interbedded limestones and calcareous lenses. It contains graptolites of the *Climacograptus bicornis* Zone (ORTEGA & ALBANESI 1998). The overlying sediments are dark-grey shales with *Climacograptus tridentatus* and *Dicranograptus* sp. Using graptolite biozonation, BENEDETTO et al. (1991) and ALBANESI & ORTEGA (1997) proposed an early Caradoc age for the whole Las Plantas Formation. The Las Plantas Formation overlies paraconformably the Gualcamayo Formation which implies the existence of a stratigraphical gap covering most of the late Llanvirn (Llandeilian). The Las Plantas Formation is interpreted as a lateral equivalent of the upper member of the Los Azules Formation. In the Cerro Potrerillo section, it is tectonically topped by the Trapiche Formation (late Caradoc-Ashgill). Phyllocarid remains occur throughout the Las Plantas Formation except in the basal calcareous horizons (approx. 5 m).

Other phyllocarid occurrences in the Precordillera

Other localities of the Precordillera have yielded phyllocarids (mainly poorly preserved specimens of *Caryocaris*) as for example the Empozada and San Isidro Creeks in the Mendoza Province. The phyllocarids occur within the lower member of the Empozada Formation and are associated with *Tetragraptus approximatus* indicating the lowermost Arenig (BORDONARO & PERALTA 1987).

Eastern Cordillera

The presence of phyllocarids (*Caryocaris*) has long been reported in the northwest of Argentina, especially in the early Arenig strata of the Acoite Formation (Cajas Range,

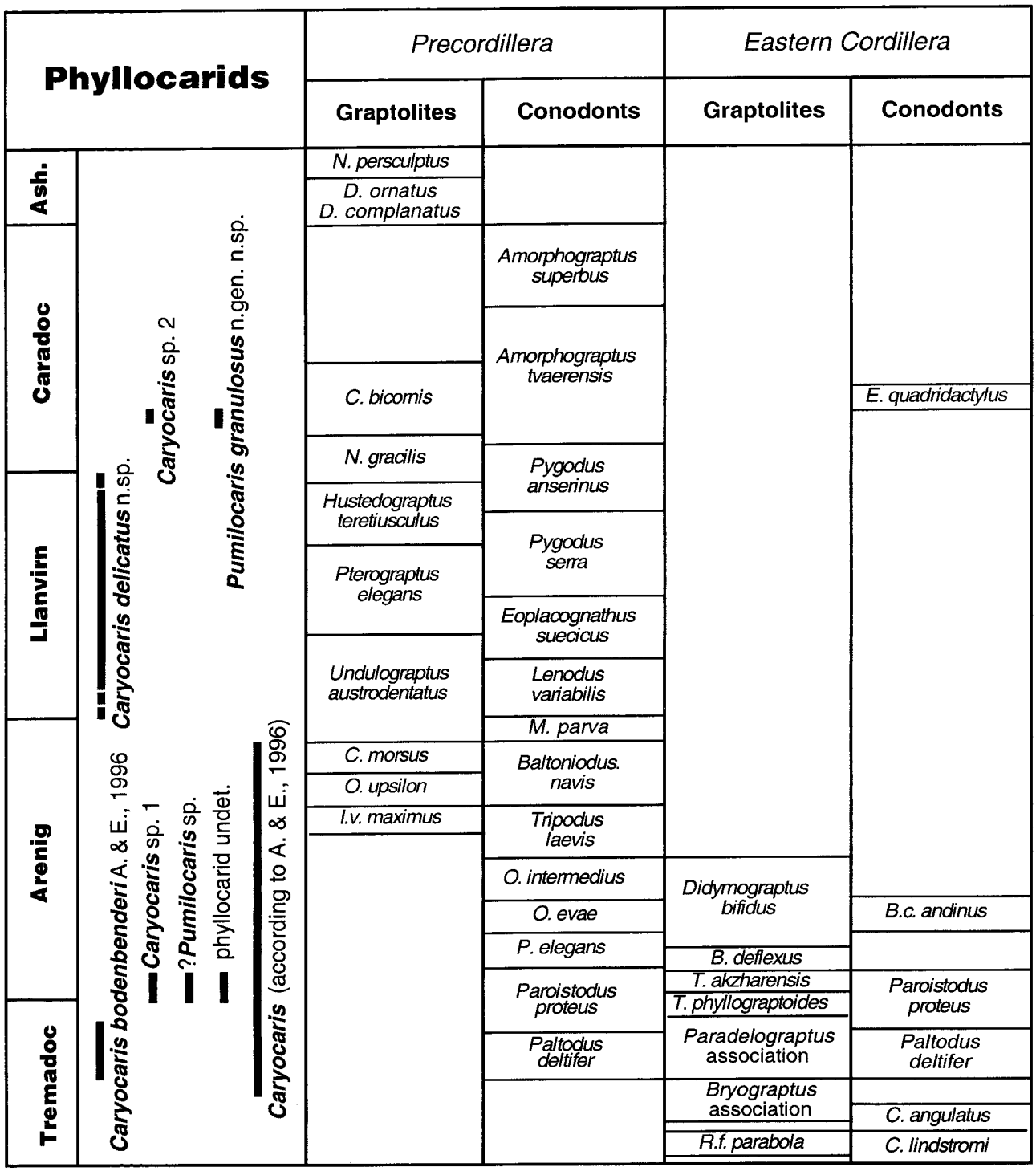

Fig. 3. Vertical distribution of the Ordovician phyllocarids from Argentina based on the present study and from ACEÑOLAZA & ESTEBAN (1996). 'Upper Llanvirn' and 'Lower Llanvirn' are used to designate the upper (Llandeilian) and lower (Abereiddian) part of the Llanvirn sensu FORTEY (1995).

Eastern Cordillera of Jujuy; ACEÑOLAZA et al. 1976) and the Parcha Formation (Eastern part of the Puna region, Salta Province; RAMOS 1970, 1984).

The Parcha Formation exposed in the Incamayo Creek and in the Angosto de Lampazar area ca. 60 km NW of Salta (type locality of the formation; see KEIDEL 1937 and HARRINGTON & LEANZA 1957) yielded a new phyllocarid material (Fig. 1B). In these localities, the Parcha Formation overlies unconformably the late Tremadoc Saladillo Formation and starts with a sequence of white laminated sandstones followed by greenish-grey shales with interbedded calcareous lenses. Above these beds, greenish-grey and yellowish-brown shales with sparse sandy horizons occur. Cone-in-cone structures and siliceous to

weakly calcareous concretions are commonly found in this part of the sequence. Its total thickness is not easy to evaluate due to intense folding and faulting. Graptolite, trilobite and more recently conodont zonations indicate an early Arenig age for the Parcha Formation (HARRINGTON & LEANZA 1957; RAMOS 1970, 1974; ALBANESI et al. 1997; ORTEGA et al. 1998). In the Angosto de Lampazar area, the basal section of the Parcha Formation yielded abundant phyllocarids (e.g. path between Parcha and Abra de Sococha; Fig. 1, loc. 8) and additional materials were also found (1) in the Parcha area (La Pedrera and Barranca Creeks near their confluence with the Incamayo River; Fig. 1, loc. 9, 10) and (2) 3 km south of the Incahuasi, near an eastern tributary of the Incamayo River (Fig. 1, loc. 11). Specimens have been collected from different levels throughout the Parcha Formation.

Phyllocarids are absent from all the calcareous horizons of the studied sections, for example in the upper member of the Los Azules Formation, the lower part of the Las Plantas Formation and more remarkably in the upper part of the San Juan Limestone (Fig. 2) where abundant benthonic organisms occur (sponges, bryozoans, brachiopods, trilobites, gastropods, nautiloids and conodonts) associated with scarce epipelagic and benthonic graptolites. The calcareous shales of the upper member of the Los Azules Formation contain a rich graptolite fauna, scarce shelly fossils, mainly trilobites and brachiopods, but no phyllocarids. Similarly, no phyllocarids were found in the graptolitic calcareous shales and muddy limestones of the lower Las Plantas Formation whereas they were fairly abundant in the intercalated shaly beds. The group is also absent from the limestones and calcarenites of the Parcha Formation. This may indicate a distinctive (outer-shelf ?) depositional setting influenced by the possible pelagic lifestyle of the phyllocarids (VANNIER et al. 1998).

Measurements and terminology follow those used by CHURKIN (1966) and CHLUPAC (1970). Specimens described and illustrated in this paper are housed in the collections of the Museo de Paleontología de Córdoba (CORD PZ), Argentina.

Systematic description

Superclass Crustacea PENNANT 1777
Class Malacostraca LATREILLE 1806
Subclass Phyllocarida PACKARD 1879
Order Archaeostraca CLAUS 1888
Family Caryocarididae n. fam.

Diagnosis: Small elongated, bivalved carapace without rostral and dorsal plates; anterodorsal horn and posterodorsal spine commonly present; short abdominal somites; telson laterally widened, and short; furca laterally expanded, leaflike, with or without articulated spinules along their outer margin.

Genera assigned: *Caryocaris* SALTER 1863.

Junior synonyms: *Caryocaris* (*Caryocaris*) SALTER 1863; *C.* (*Rhinopterocaris*) CHLUPAC 1969.

Discussion: Representatives of the family Caryocarididae differ from those of the family Ceratiocarididae by their smaller, elongate size, and by their very thin, possibly flimsy carapace. The anterior part of each valve of the carapace typically consists of a prominent horn, instead of a rostral plate. The posterior part of the body is reduced to short abdominal somites, all about the same length, whereas typical ceratiocaridids display a markedly elongated pretelson somite. The tail piece of caryocaridids is relatively small, with a laterally widened telson and flattened lateral expansions (leaf-shaped furca). By contrast, ceratiocaridids have an usually long, styliform telson flanked with elongated, cylindrical or flattened, furcal rami.

Caryocaris: definition and affinities

Ordovician phyllocarids are classically referred to the genus *Caryocaris* SALTER 1863. *Caryocaris* occurs worldwide in typical graptolite-bearing outer-shelf sediments dated from the Arenig to the Llanvirn (RUSHTON & WILLIAMS 1996; VANNIER et al. 1998) and is currently represented by about ten species and numerous undetermined forms. The genus was subdivided into two subgenera by CHLUPAC (1970) on the basis of differences in carapace outline, *Caryocaris* (*Caryocaris*) bearing "a sharp anterodorsal extremity of the carapace (without protracted anterior carapace horn)" and *Caryocaris* (*Rhinopterocaris*) bearing an "elongated anterior carapace horn" (CHLUPAC 1970: 44, 54). The comparison of the lateral outlines of 8 different species (Fig. 13) shows that there is no such clear morphological boundary between the two subgenera. With no exception, the anterodorsal extremity of the carapace is pointed and variably expressed as a wedge-like head (Fig. 13A, C, H), a short (Fig. 13D, G) or a very promiment rostrum (Fig. 13B, E). Neither the posterior end of the carapace (anterodorsal spine, posteroventral spinule, minute posterior spinules) nor the tail-piece (leaflike rami) of *Caryocaris* (*Rhinopterocaris*) are fundamentally different from those of *Caryocaris* (*Caryocaris*). *Caryocaris delicatus* n. gen., n. sp. (Fig. 13 C) from Argentina appears as it is an intermediate form between *Rhinopterocaris* (posterior spinule complex) and *Caryocaris* (anterior end). We concur with ROLFE (1969), JELL (1980), and HANNIBAL & FELDMAN (1996: 10) that *Rhinopterocaris* is a junior synonym of *Caryocaris* and find no reason to maintain subgeneric categories. This lead us to propose a new definition of the genus *Caryocaris*.

Genus *Caryocaris* SALTER 1863

Type species: *Caryocaris wrightii* SALTER 1863.

Definition: Elongated carapace with both dorsal and ventral convex margins. No rostral plate. Pointed ante-

rior end expressed as a wedge-like head or a prominent horn-like rostrum. Short anterodorsal spine. Posterior margin straight to oblique typically fringed with a row of minute secondary spinules. Indented posteroventral margin (one to several spinules). Narrow ridge and/or shallow furrow running parallel to ventral margin. Very thin, flimsy, weakly or uncalcified carapace. Short distal abdominal segments followed by a short pointed telson. Leaf-like furcal rami with strong spinules along the outer margin and a row of minute spinules or setae along the inner margin.

Species assigned to *Caryocaris*:
Caryocaris wrightii SALTER 1863 (type species); Arenig-Llanvirn; UK, Ireland, Germany, Bohemia, Norway, Australia;
Caryocaris acuta BULMAN 1931; ? Caradoc; Peru;
Caryocaris curvilata GURLEY 1896; latest Arenig-early Llanvirn; Alaska, Nevada, Idaho, USA;
Caryocaris delicatus n. sp.; early to late Llanvirn; Argentina;
Caryocaris maccoyi CHAPMAN 1903; lower Ordovician; New Zealand;
Caryocaris oblongus GURLEY 1896; lower Ordovician; Canada;
Caryocaris stewarti JELL 1980; middle Tremadoc; Victoria, Australia;
Caryocaris subula CHLUPAC 1970; Llanvirn; Bohemia, Czech Republic;
Caryocaris zhejiangensis SHEN 1986; Arenig; SE China.

Affinities: Although it is classically referred to the family Ceratiocarididae (e.g. ROLFE 1969), *Caryocaris* has a number of original characters (e.g. lack of rostral plate, short leaf-like furcal rami, short telson, extremely thin carapace) which deny this familial assignment. Typical ceratiocaridids such as *Ceratiocaris* and *Heroldina* have long rod-like tail pieces and a long terminal abdominal segment (ROLFE 1969: figs. 136, 139, 144). The representatives of the genus *Caryocaris* clearly constitute an homogeneous group within the Phyllocarida, which most probably lies outside the ceratiocaridids. Our study support this view but a complete revision of *Caryocaris* and allied genera would be needed before we propose a formal new taxonomic unit.

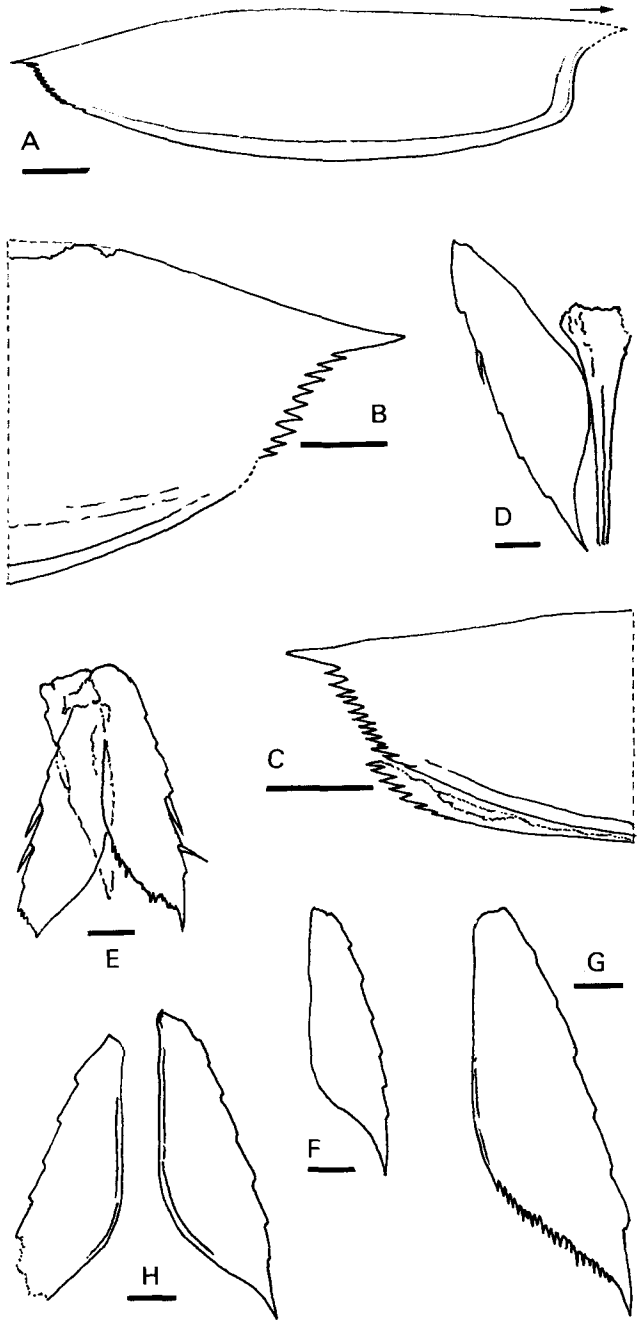

Fig. 4. *Caryocaris delicatus* n. sp. – Early to late Llanvirn, Los Azules Formation, Precordillera, Argentina. Camera lucida drawings of the carapace and tail-pieces. Scale bar = 1 mm for all specimens. – **A:** CORD PZ 13073, holotype, right side of carapace in lateral view (see Fig. 5B); **B:** CORD PZ 13073, posterior margin of left valve; **C:** CORD PZ 11546, posterior margin of an almost complete carapace with the right valve lying on top of the left valve; **D:** CORD PZ 12681, furcal ramus and telson (not connected); **E:** CORD PZ 13253, complete but weakly disarticulated tail-piece, with furcal rami overlying the internal mold of the telson (row of setae and articulated spinules along the margins of both rami preserved); **F:** CORD PZ 13211, isolated furcal ramus; **G:** CORD PZ 13256, large isolated furcal ramus with well-preserved setae along inner margin; **H:** CORD PZ 14159, two furcal rami (presumably the same pair) with a narrow rim along their inner margin.

Caryocaris delicatus n. sp.
Figs. 4, 5, 7, 8B

Derivatio nominis: From delicatus (lat.), elegant, alluding to the fine shape of the carapace and the furcal rami.
Holotype: CORD PZ 13073, right valve.
Type locality: Los Azules Creek, Cerro Viejo Range, Huaco, Precordillera, Argentina (Fig. 1A, loc. 4).
Horizon and age: Los Azules Formation; lower member belonging to the *Undulograptus austrodentatus* Zone of early Llanvirn age, and middle member assigned to the *Pterograptus elegans* and *Hustedograptus teretiusculus* Zones ranging from early to late Llanvirn.

Material: 7 more or less complete carapaces and isolated valves; 12 incompletely preserved or enrolled valves; 3 complete tail-pieces (telson + furcal rami in connection) and

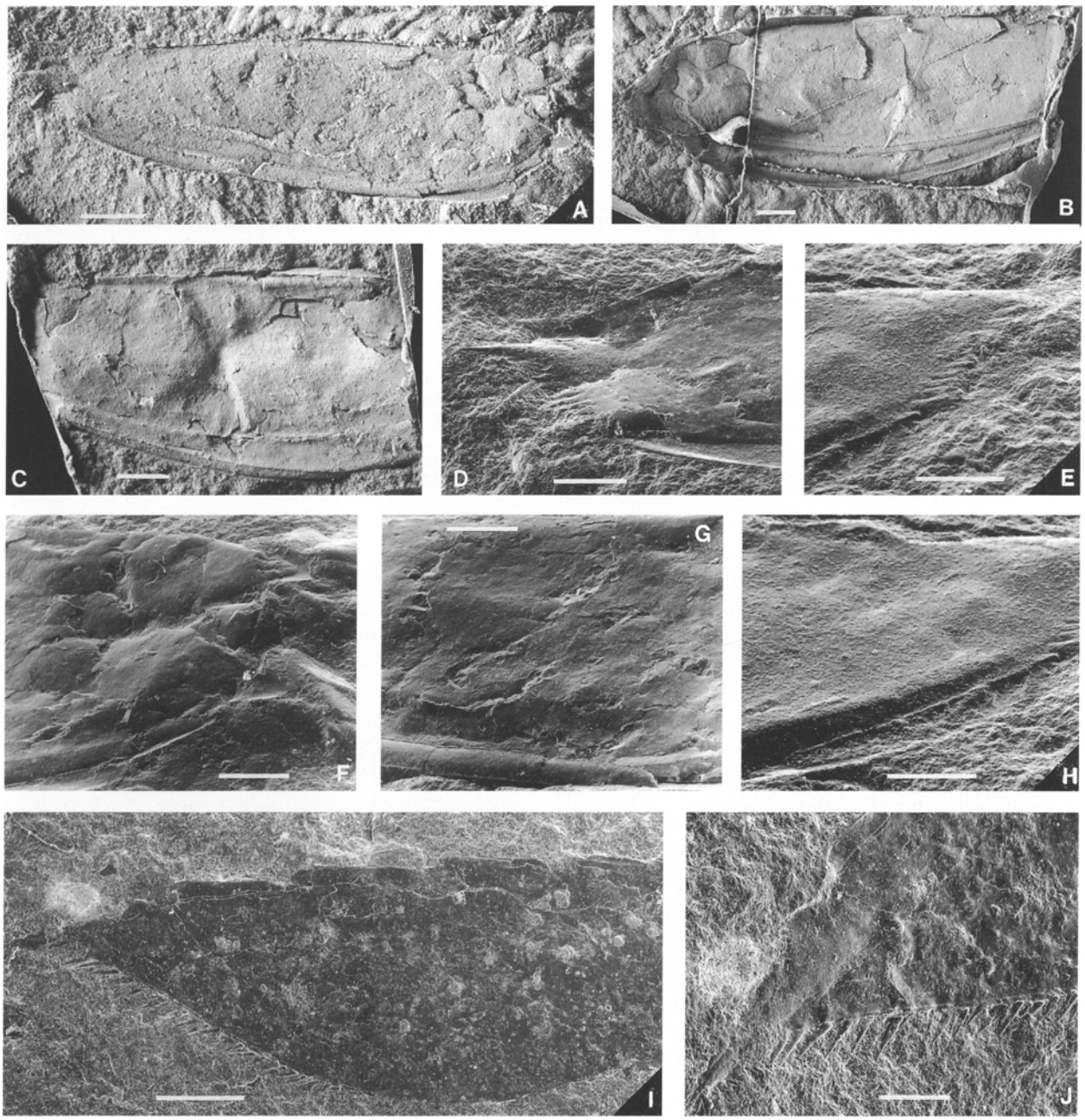

Fig. 5. *Caryocaris delicatus* n. sp. – Early to late Llanvirn, Los Azules Formation, Precordillera, Argentina. All latex casts of external moulds. All SEM micrographs except A-C. Scale bar = 2 mm in A-C, 1 mm in D, F, G, I and 500 µm in E, H, J. – **A, D, F, G:** CORD PZ 13073, holotype, right valve in lateral view, posterior end, anterior end and central part showing marginal features, respectively; **B:** CORD PZ 11582, incomplete left valve, lateral view; **C:** CORD PZ 11584, counterpart of the same incomplete left valve, lateral view; **E, H:** CORD PZ 13073, left valve, tilted view of posterior end and intermediate ventral view showing marginal features; **I, J:** CORD PZ 13256, left furcal ramus, lateral view of the distal part and tilted view showing marginal setae.

10 isolated furcal rami, from the Los Azules Creek (CORD PZ 13073, 13211, 13253, 13256), the Amarilla Creek (CORD PZ 14150, 14159), and the Los Gatos Creek (CORD PZ 12292, 12681, 12846, 12860).

Diagnosis: Carapace ratio L:H ~ 3. Well-developed posterodorsal spine; anterior margin strongly convex becoming almost perpendicular to the dorsal mid-line of the carapace; strong pointed anterodorsal rostrum; posterior margin oblique (approx. 60° with respect to the dorsal line) and fringed with posteriorly directed spinules parallel to each other and pointing in the same direction as the anteroposterior spine; telson narrow, with a longitudinal dorsal carina; furcal rami elongate, leaf-shaped, about 1.5 times longer than the telson, with an acute distal extremity, and bearing stout articulated spinules along their outer margin and minute setae along their distal inner margin.

Description

Carapace: See generic features. Maximum length (in a

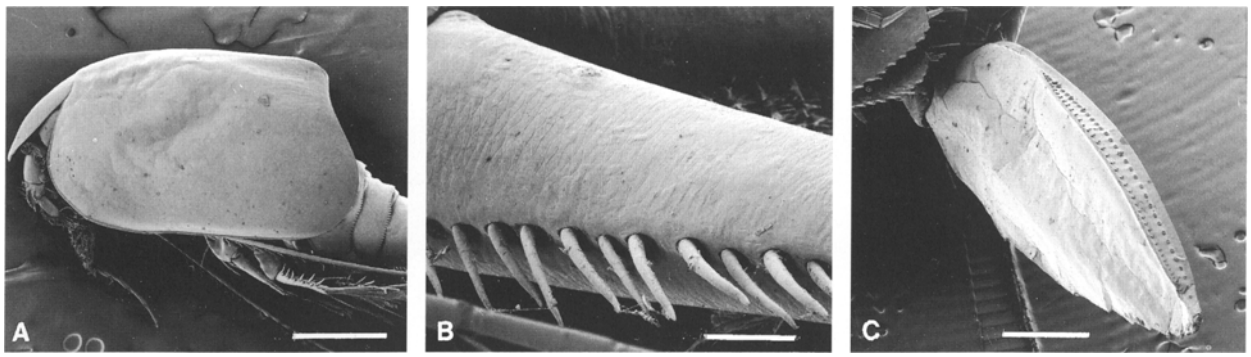

Fig. 6. Tail-piece of Recent phyllocarids for comparison with *Caryocaris*. All SEM micrographs. Scale bar = 1 mm in A, C and 100 µm in B. – **A-B:** *Nebalia bipes* (FABRICIUS 1780) from coastal environments near Roscoff (N. Brittany, France), lateral view of the left side of the carapace and detailed view of the outer margin of the left furcal ramus (note cylindrical shape) showing strong articulated setae. **C:** *Nebaliopsis typica* SARS 1887 from bathypelagic environments (NE Pacific), detailed view of the right furcal ramus (note flattened shape).

valve enrolled along its longitudinal axis): 24 mm. Maximum height (in an incomplete but not enrolled valve): 8 mm. None of our specimens has its anterior rostrum completely preserved. However, the convergence of the dorsal and anterior margins makes no doubt that the rostrum was a strong pointed feature overhanging the almost vertical anterior margin. Dorsal line gently and evenly arched, terminating posteriorly in a well-differentiated posterodorsal spine which is approx. 0.8 mm long. Anteroventral margin with very strong convexity. Narrow border (approx. 0.4 mm wide), dorsally limited by a faint ridge running parallel to the whole ventral margin which is evenly arched. The posterior end of the rim does form a posteroventral spine. Posteroventral margin of the carapace gently convex, bending dorsally to connect with the posterodorsal spine. Its overall oblique outline makes an angle of about 60° with the dorsal line. A series of about twenty spinules all equal in length (about 0.4 mm long) and parallel to each other are inserted along the posterior margin (Fig. 4).

Tail-piece: Neither abdominal segments attached to the tail-pieces (telson + furcal rami) nor complete inviduals (carapace + body segments in connection) were found in our material. However, since only one type of carapace and one type of tail-pieces were recovered from the type locality and neighbouring sampling spots, it makes no doubt that both fossil elements belong to the same species. The tail-piece is relatively large (maximum length 10 mm) almost reaching half the length of the largest valve (24 mm). The telson is 4.6 to 4.9 mm long and may reach 1.3 mm width near its proximal end. Although most of the tail-pieces are dorsoventrally flattened, it seems that the dorsal part of the telson, when seen in transverse section, was rounded in its proximal part to become more subtriangular distally. A faint longitudinal, medio- dorsal ridge is present in CORD PZ 12681-12670 (counterpart) (Fig. 4D) and seems to originate near the proximal third of the telson. The lateral margins of the telson are weakly concave in their proximal section and then straight up and converge to form an arrow-like termination. The furcal rami range between 5.2 and 10 mm long (measurements on 6 well-preserved specimens) and are about 1.5 times longer than the telson. The measurements of two tail-pieces showing the telson and furcal rami in connection are as follows: telson 4.6 and 4.9 mm long, respectively; furcal rami 6.5 and 7.5 mm long; telson 1.45 and 2.6 mm wide at midlength. The length : width ratio ranges between 3.42 and 3.87. The outer margin of the furcal ramus is weakly and evenly convex and bears a series of 6 to 7 spinules (Fig. 4C-G). Each spinule was probably inserted along the furcal margin by means of an articulated feature as suggested by their variable orientation and the fact that some of them are often missing (Fig. 4E). The proximal part of the inner margin is straight and forms a narrow rim (Fig. 4F) whereas the distal part is fringed with numerous spinules, possibly setae (Fig. 4D, E, G) of about 0.3 mm long. Their total number may be up to 21 (i.e. about 6 to 7 per mm). They were probably not articulated thus contrasting with the spinules present along the opposite outer margin. Their absence in some specimens may be due to intraspecific variations such as sexual dimorphism or more likely to preservation.

Remarks: The strong setae which fringe the outer margin of the furcal rami of Recent phyllocarids such as *Nebalia* (Fig. 6B) may be analogous to the articulated spinules of *Caryocaris delicatus* n. sp. Similarly, the flattened rami of the Recent bathypelagic phyllocarid *Nebaliopsis* (Fig. 6C) recalls the leaf-like rami of *Caryocaris delicatus* n. sp. and other congeneric species (Fig. 13).

Comparison: Only two species have been previously described from the Ordovician of South America: (1) *Caryocaris acuta* BULMAN 1931 from the (?)Caradoc of Southern Peru (Tab. 1), and (2) *C. bodenbenderi* ACEÑOLAZA & ESTEBAN 1996, from the Tremadoc of the Argentinan Precordillera (Tab. 1). Neither the photo-

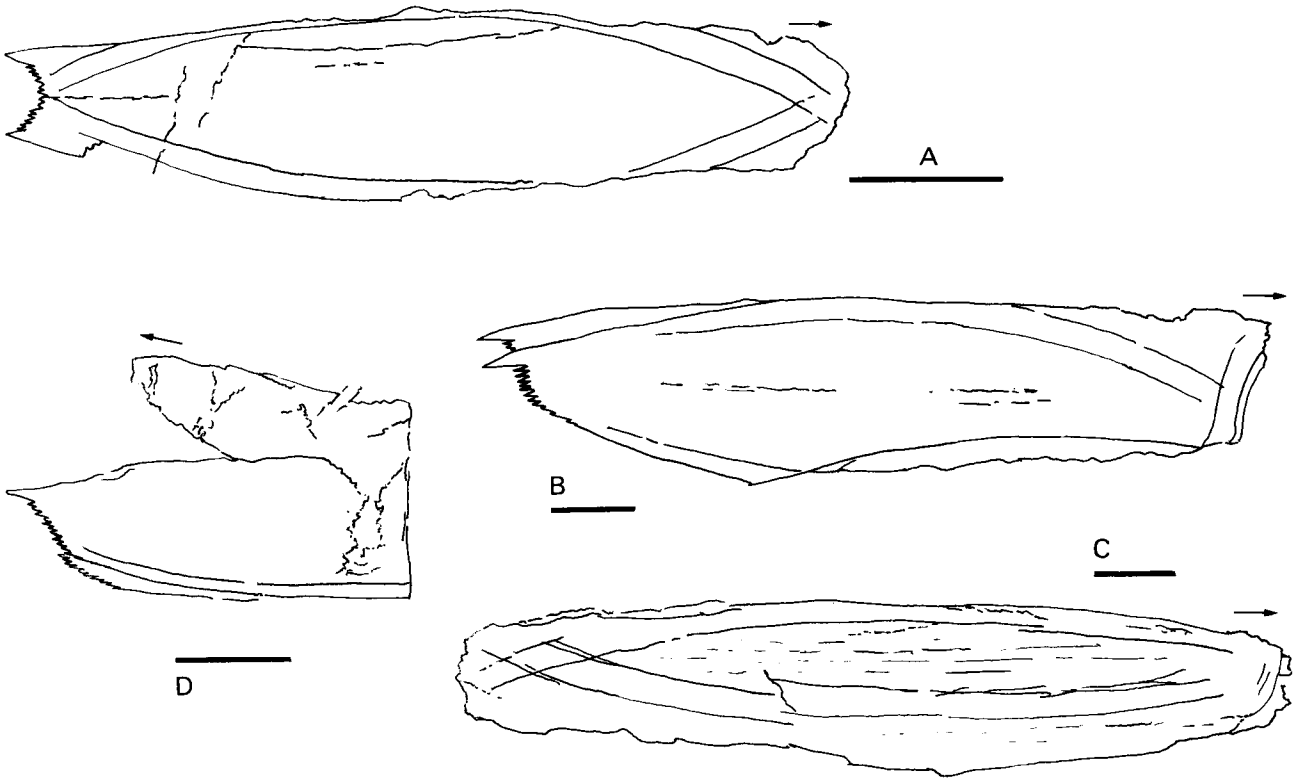

Fig. 7. *Caryocaris delicatus* n. sp. – Early to late Llanvirn, Los Azules Formation, Precordillera, Argentina. Camera lucida drawings showing flattened, possibly originally coiled specimens (see explanation in text). Arrows indicate anterior of carapace. Scale bar = 2 mm for all specimens. – **A:** CORD PZ 12846, complete carapace (valves dorsally disjoined) showing traces of longitudinal coiling; **B:** CORD PZ 12860, carapace with both sides in dorsal connection with partly coiled right (anterior) and left valve (anteroventral); **C:** CORD PZ 14150, poorly preserved carapace with both sides in connection and showing coiling features (the thin longitudinal, almost undiscernible lines may represent external ornament); **D:** CORD PZ 11576, carapace with both valves slightly displaced, folded up transversally at about midlength.

graphic illustration of the holotype of *C. acuta* BULMAN 1931 (a right valve with the anterior and posterior tips obviously broken) nor the sketches of two additional valves made by BULMAN (1931) are sufficient to allow detailed comparisons with *C. delicatus* n. sp. Besides, BULMAN's (1931) description refers to a very limited number of diagnostic features, mainly the carapace outline. *C. acuta* superficially resembles *C. delicatus* in having a long ventral rim and hypothetical slight indentations along the posterior margin of the carapace (BULMAN 1931: pl. 11, fig. 7). Two other forms occur in Argentina, one from the lower Ordovician of the Catamarca Province (*Caryocaris* sp.; ACEÑOLAZA et al. 1976: pl. 2, figs. 2, 6, 7), the other one from the Arenig of the Salta Province (*Caryocaris* sp. RAMOS 1984: pl. 1, figs. a-f). Both seem to be smaller than *C. delicatus* (the carapace of *Caryocaris* sp. from Catamarca is about 12 mm long and 4-5 mm high). The tail-piece of *Caryocaris* sp. from Salta has a very stout telson almost as long as the rami which differs from that of *C. delicatus*. The general poor state of preservation of the material does not allow further comparisons.

C. bodenbenderi ACEÑOLAZA & ESTEBAN 1996 is more accurately documented. However, the type specimens were mistakenly identified by the authors as carapaces whereas they are furcal rami. The holotype is not a left valve with a very prominent rostrum as claimed by ACEÑOLAZA & ESTEBAN (1996) but is actually a left isolated leaf-like furcal ramus with coarse indentations along its outer margin. It is the relatively large size (8.5 mm long) of the ramus which probably misled the authors in their morphological interpretations. *C. delicatus* n. sp. differs from *C. bodenbenderi* in having small articulated spinules instead of coarse indentations (compare ACEÑOLAZA & ESTEBAN 1996: fig. 2 and Fig. 8B, present paper).

C. delicatus can be easily distinguished from *Caryocaris wrightii* SALTER 1863 (type species) from the Arenig of the British Isles and Ireland (see RUSHTON & WILLIAMS 1996) and the Arenig/Llanvirn deposits of numerous other localities throughout Europe (Bohemia, Germany and Norway; see CHLUPAC 1970, KOCH & BRAUCKMANN 1998, STÖRMER 1937, respectively) by its oblique posterior margin lacking any posteroventral indentations and by a prominent rostrum. The tail-pieces of the two species also differ in many important aspects (furcal rami are v-shaped in *C. wrightii* and leaf-shaped in *C. delicatus*; *C. delicatus* has a median ridge on its

telson which *C. wrightii* does not possess; Fig. 13A-C). However, it is worth noting here that the marginal pits of *C. wrightii* mentioned by CHLUPAC (1970: 48) in several specimens from the Sárka and Dobrotivá Formations (Llanvirn) of Bohemia most probably represent the actual insertion spots of setae (see analogous features in the Recent phyllocarid *Nebalia*, Fig. 6). If this interprepation is correct, then *C. delicatus* and *C. wrightii* may have born a similar type of articulated setae along their furca.

Contrasting with *C. delicatus* (Fig. 13 C), most species assigned to *Caryocaris* typically exhibit a vertical posterior margin, for example *C. stewarti* JELL 1980 from the middle Tremadoc of Australia (Fig. 13D), *C. zhejiangensis* SHEN 1986 from the Arenig of SE China (Fig. 13E), *C.* cf. *monodon* (GURLEY 1896) from the Arenig of Norway (Fig. 13F; see also STÖRMER 1937) and *C. curvilata* GURLEY 1896 from the Arenig/Llanvirn of Alaska and Nevada (Fig. 13G; see also CHURKIN 1966).

C. delicatus n. sp. closely resembles *Caryocaris subula* CHLUPAC 1970. Both species have in common a slender streamlined carapace with an oblique posterior margin fringed with spinules (Fig. 13B, C). However, no strong posteroventral spine is present in *C. delicatus*. Besides, the outer margin of the furcal rami is fringed with 7-8 spine-like posteriorly directed outgrowths in *C. subula* whereas it bears distinctive 6-7 articulated spinules in *C. delicatus*. Although the scarcity of the South American material does not allow accurate biometrical comparison with other species, the size range of *C. delicatus* n. sp. seems to be smaller than that of *C. subula* (see CHLUPAC 1970: 57, fig. 9). The morphology of the carapace and tail piece of *Caryocaris stewarti* JELL 1980 is unique (Fig. 13D) and shows no close resemblances with that of *C. delicatus* n. sp.

Preservation of specimens and interpretation: Most of our specimens were found in grey, laminated, fine-grained siltstones in association with graptolites, the tail-pieces being mostly disarticulated and always dissociated from the animal's exoskeleton. Carapaces are usually flattened with the two sides ('valves') pressed on top of each other. Careful examination of these specimens revealed that the valve margins were often folded (see Fig. 26A-C), suggesting that a spiral coiling of the carapace occurred before compaction in sediment and probably in a very early post-mortem or post-exuvial stage before any mineralization process began. Coiling may have been greatly facilitated by the mechanical properties and architecture of the exokeleton itself, i.e. a very thin and flimsy carapace with a very high L:H ratio. This peculiar taphonomic trait is very common among *Caryocaris* [material from Bohemia (CHLUPAC 1970), Sweden (ECKSTRÖM 1937) and North America (CHURKIN 1966)], some carapaces showing remarkable uncompressed involute features (CHURKIN 1966: pl. 65, fig. 9). To us, such spiral coiling may have preferentially affected exuviae or free carapaces than dead animals in which the soft parts still attached to the exoskeleton, would have hindered part of the mechanical process of coiling. *Caryocaris* has been classically referred (e.g. RUEDEMANN 1934; CHLUPAC 1970) to as a pelagic animal and a possible active swimmer (VANNIER et al. in prep.) mainly because of its streamlined carapace and its frequent occurrence with graptolites. Its inferred midwater habitat added to the fact that its carapace was probably uncalcified, thin and therefore very light, imply that the exuviae of *Caryocaris* would have sunk relatively slowly in the water column. Passive sinking rates of small pelagic Recent crustaceans such as halocyprid ostracodes range between 0.6 and 2.5 cm x sec-1 (ANGEL 1993) which means that a vertical descent over 200 m takes about 6 hours. The sinking of exuviae is obviously much slower. As for *Caryocaris*, it seems reasonable to think that the coiling process took place during the vertical drifting of exuviae before they reached the bottom, as the possible result of changes in the mechanical properties of the organic compounds of the carapace (chitin + proteins) due to decay. Dead specimens of *Caryocaris* are likely to have been disarticulated within the water column, thus producing drifting carapaces similar to exuviae and separate body parts. Further fragmentation (e.g. abdominal segments/furcal rami; telson/rami) aided by microbial activity probably took place on the bottom. This would explain the absence of complete specimens in our material. No experimental studies on the decay and early mineralization of 'soft' crustacean exoskeletons (e.g. phyllocarids, pelagic ostracodes, etc.) have been made yet (for calcified shrimps see BRIGGS & KEAR 1994).

Caryocaris sp. 1
Fig. 8A

Horizon and age: Parcha Formation, in beds belonging to the *Tetragraptus phyllograptoides* and *Tetragraptus akzharensis* Zones of early Arenig age.

Material: Internal and external moulds of two complete tail-pieces (CORD PZ 19072A, B) from between Parcha and Abra de Sococha (Fig. 1, loc. 8) and 2 tail-pieces (CORD PZ 19151-19152) from La Perdrera Creek (Fig. 1, loc. 9), both localities of the Salta Province, Eastern Cordillera.

Description

Carapace: Unknown.

Abdominal somites: Although slightly disarticulated, the last abdominal somites of two specimens (CORD PZ 19151, 19072) are still connected (although slightly disarticulated) to the telson. In specimen CORD PZ 19151, these somites are very short (length less than 1 mm; width between 2.25 mm to 2.3 mm), each bearing a pair of convex dorsolateral tubercles.

Tail-piece: The telson is triangular in outline, dorsoventrally flattened with a pointed extremity. Maximum length L = 3.8 mm; width of proximal part W = 1.7 mm. L:W = 2.23 and 2.30 for specimens CORD PZ 19072 and 19151, respectively. The dorsal side of the telson is moderately convex, evenly arched transversally without ridge or longitudinal carina. Telson margins with no spinosity.

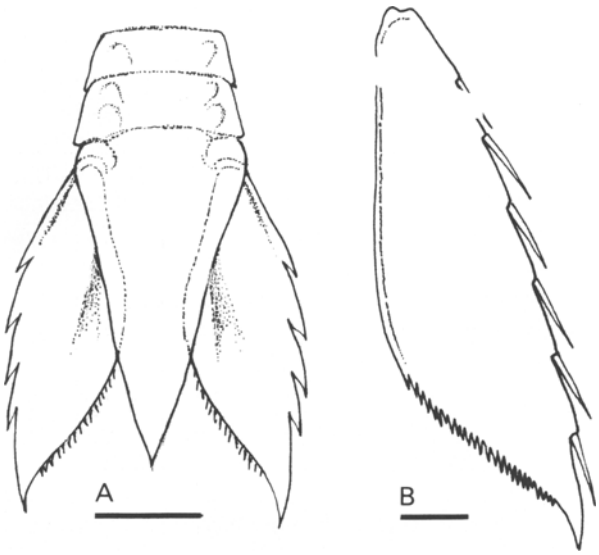

Fig. 8. A: *Caryocaris* sp. 1 – Early Arenig, Parcha Formation, Eastern Cordillera, Argentina. CORD PZ 19072, complete tail-piece showing two abdominal somites in connection with the telson. **B:** *Caryocaris delicatus* n. sp. – Early to late Llanvirn, Los Azules Formation, Precordillera, Argentina. CORD PZ 13256, right furcal ramus showing articulated spinules and setae along its outer and inner margin, respectively. – Camera lucida drawings. Scale bar = 1 mm.

The furcal rami are leaf-shaped, pointed and longer than the telson. Their length reaches 4.4 mm in specimen CORD PZ19151 (telson 3.8 mm long). They are elongated and relatively narrow; (L:W = 3.18 and 3.38 in CORD PZ 19072 and 19151, respectively). Their outer margins bear 3 relatively large, triangular, flattened, and posteriorly directed spine-like outgrowths. The distal inner margin of the ramus has very small spinules (about 0.1 mm long; more than 10 per mm). Each furcal ramus has a shallow concave ridge originating from the condyle and is well-developed in the proximal half of the ramus only.

Comparison: This form (tail-piece) possesses the major diagnostic features of *Caryocaris*. It can easily be distinguished from *Caryocaris delicatus* n. sp. by its wide, flattened, and weakly convex telson without ridge or carina and its relatively short furcal rami bearing only 3 to 4 spine-like outgrowths and not 6 to 7 elongated and articulated spines as in *C. delicatus* (compare Figs. 4E and 7A).

Caryocaris sp. 1 may be tentatively compared with the holotype of *C. bodenbenderi* ACEÑOLAZA & ESTEBAN 1996 (a furcal ramus and not a carapace). Both have furcal rami with large spine-like outgrowths (3 in *C. bodenbenderi*). However, *C. bodenbenderi* has no spinules along the outer furcal margins and bears a conspicious reticulated ornament unknown in other congeneric forms including *C. delicatus* and *C.* sp.1. These unconclusive comparisons added to the absence of carapace led us to maintain *C.* sp.1 in open nomenclature.

?*Caryocaris* sp. 2

Horizon and age: Las Plantas Formation, *Climacograptus bicornis* Zone, early Caradoc. The specimens have been collected a few meters below the layers which yielded *Pumilocaris granulosus* n. gen., n. sp.

Material: Four very poorly preserved carapaces (CORD PZ 19313-19316) from the Western side section of the Cerro Potrerillo (Fig. 1, loc. 3), San Juan Province, Precordillera.

Description: Carapaces are about 20 mm long and seem to have been flattened after spiral coiling (see remarks on preservation and taphonomy). The exact outline of the anterior and posterior ends is uncertain. However, no trace of prominent features such as a rostrum or a posterior spiny termination is discernible. This form is questionably assigned to the genus *Caryocaris*.

Family Ceratiocarididae SALTER 1860

Genus *Pumilocaris* n. gen.

Type species: *Pumilocaris granulosus* n. gen., n. sp.
Derivatio nominis: from pumilus (lat.), dwarf, alluding to the small size of this species, and the suffixe -caris, referring to its phyllocarid affinities.

Diagnosis: Carapace subovate in outline, about 2.5 times longer than high; posteroventral margin markedly rounded; posterior margin oblique, weakly concave; anterior and ventral margins of the carapace with a very narrow border; anterior of right valve with a small node near the dorsal line; anterodorsal section of the free margin straight or weakly concave suggestive of a frontal incisure. Microornamented carapace (e.g. small granulation). No marginal spinosity.

Comparison: *Pumilocaris* n. gen. differs from *Caryocaris* in important aspects of the carapace morphology, chiefly (1) the rounded aspect of its posterior margin lacking any spinosity, (2) the presence of a conspicious anterodorsal indentation of the free margin and (3) the presence of an anterodorsal node. These features typically occur in the representatives of Ceratiocarididae (ROLFE 1962) although the size of all ceratiocariids far exceeds that of *Pumilocaris* n. gen. We may speculate that the frontal gap created by the frontal indentation of each valve accomodated a rostral plate as it is the case in numerous ceratiocarids (ROLFE 1962, 1969). However, no such exoskeletal piece was found in our material. No anastomising longitudinal striae also typical of ceratiocaridids exist in *Pumilocaris* n. gen. which, instead, has a granulose ornament. Since the tail-piece of *Pumilocaris* n. gen. is still unknown, no conclusive familial assignment of this new genus will be given here.

Pumilocaris granulosus n. sp.
Figs. 9, 10; Tab. 2

Derivatio nominis: Alluding to the peculiar granulose ornament of this phyllocarid.

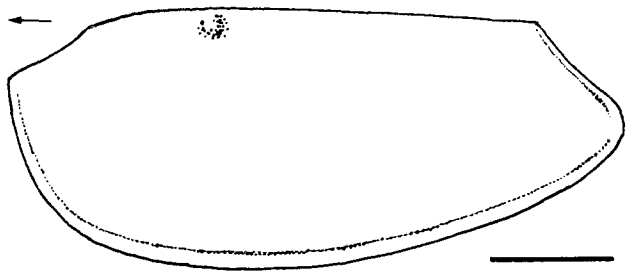

Fig. 9. *Pumilocaris granulosus* n. gen., n. sp. – Early Caradoc, Las Plantas Formation, Precordillera, Argentina. Reconstruction of the holotype CORD PZ 19371, lateral view of left side of the carapace (see Fig. 10A). – Scale bar = 1 mm.

Tab. 2. – *Pumilocaris granulosus* n. gen., n. sp. – Early Caradoc, Las Plantas Formation, Precordillera, Argentina. Measurements (in mm); L = carapace length, H = carapace height; DML = length of the dorsal margin; DIL = length of the anterodorsal indentation.

Specimen n°	L	H	L/H	DML	DIL
19368	8.7	3.6	2.41	6.2	1.6
19369	9.9	3.8	2.63	7.7	1.7
19370	9.7	4.0	2.42	7.1	1.4
19371 (hol.)	9.1	3.7	2.46	6.3	1.3
19373	9.1	3.1	2.93	6.2	1.6
19375	?	3.7	–	7.3	?
19377	9.3	3.4	2.73	7.0	1.3

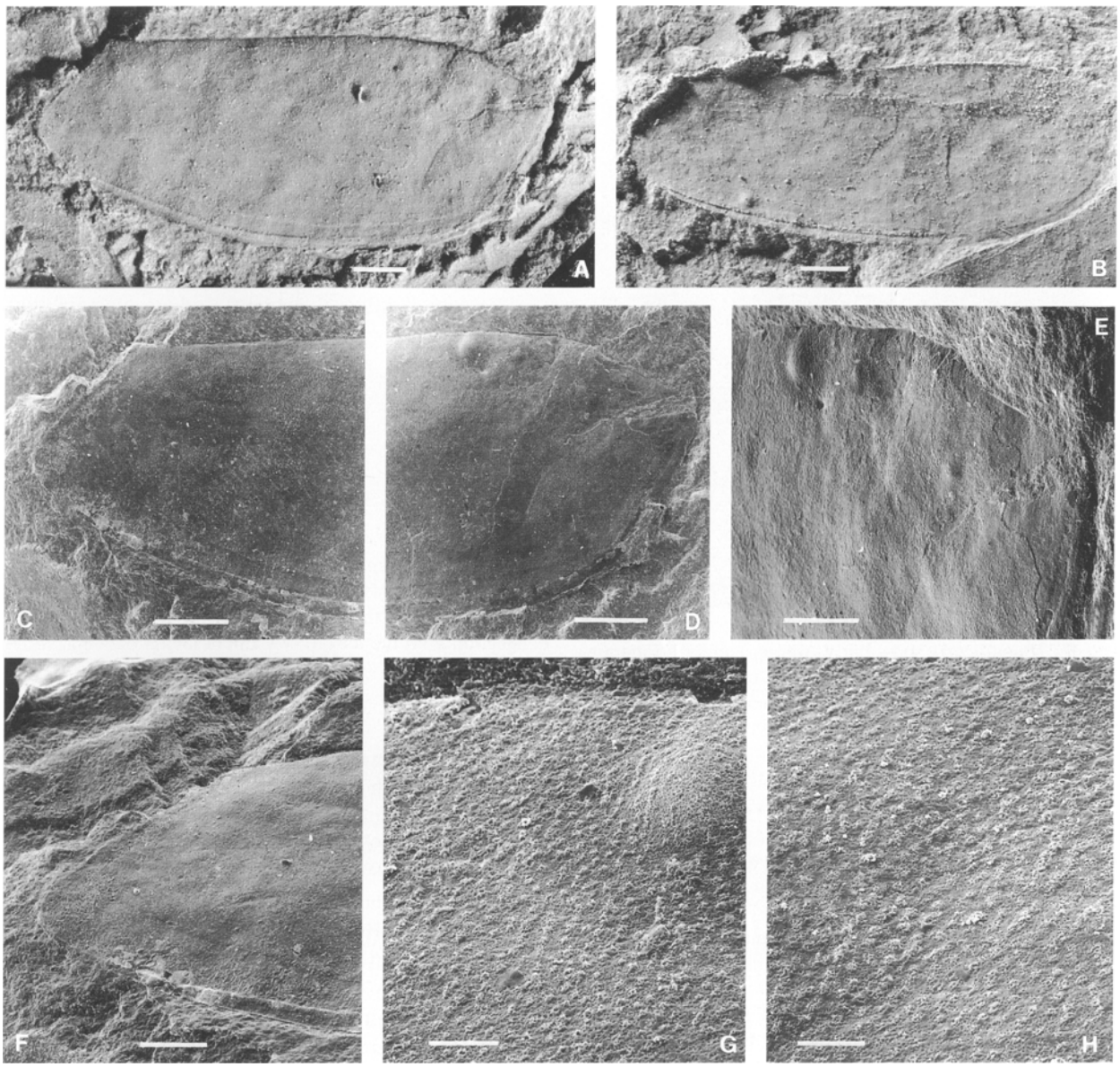

Fig. 10. *Pumilocaris granulosus* n. gen., n. sp. – Early Caradoc, Las Plantas Formation, Precordillera, Argentina. All latex casts of external moulds. All SEM micrographs except A, B. Scale bar = 1 mm in A-D, 500 µm in E, F and 100 µm in G, H. – **A, C-H:** holotype CORD PZ 19371; **A:** lateral view of right valve; **C, D:** posterior and anterior end, respectively; **E:** intermediate anterior view; **F:** intermediate ventral view; **G, H:** microornament on the posterior and anterior (including node) part of the valve, respectively. **B:** CORD PZ 19377a , right valve, lateral view.

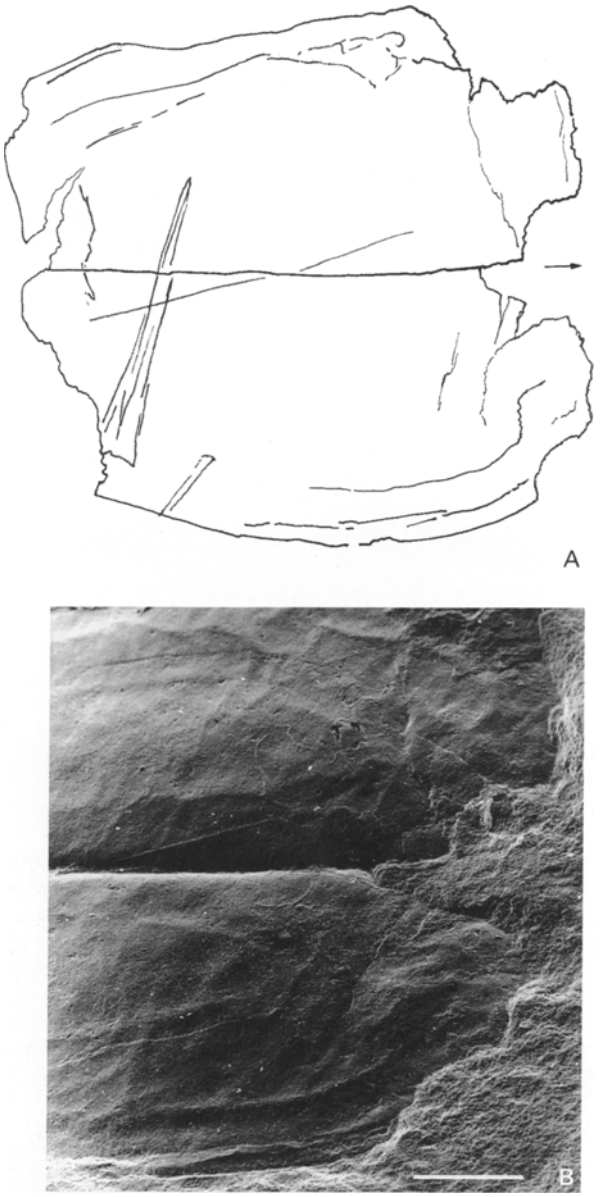

Fig. 11. ?*Pumilocaris* sp. – Early Arenig, Parcha Formation, Eastern Cordillera, Argentina. CORD PZ 18924, latex casts of external mould. Scale bar = 1 mm. – **A:** Camera lucida drawing; **B:** SEM micrograph.

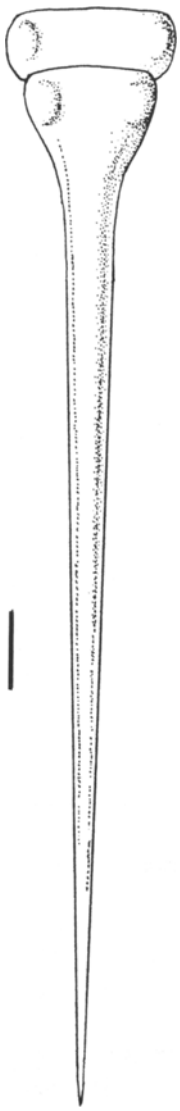

Fig. 12. Undeterminated phyllocarid. – Early Arenig, Parcha Formation, Eastern Cordillera, Argentina. CORD PZ 19075, reconstruction of the tail-piece (last abdominal somite in connection with the telson). – Camera lucida drawing. Scale bar = 1 mm.

Holotype: External mould of the right valve of the carapace CORD PZ 19371.

Type locality: Western side section of the Cerro Potrerillo, NE of Jachal (Fig. 1, loc. 3), San Juan, Precordillera, Argentina.

Horizon and age: Las Plantas Formation, in beds with *Climacograptus bicornis*, *Nemagraptus gracilis* and *Orthograptus* spp., assigned to the *C. bicornis* Zone of early Caradoc age (ORTEGA & ALBANESI 1998).

Material: 7 external and 1 internal moulds of isolated valves: CORD PZ 19368, 19369, 19370, 19371 (holotype), 19373, 19375 and 19377A-B.

Diagnosis: As for the genus.

Description

Carapace: Carapace subovate in outline. Maximum length 10 mm. Maximum height (H) located at one-third of the valve length (L) from anterior margin. 2.41 <L:H< 2.93 (6 specimen measured). Anterodorsal part of the free margin as a well-defined straight or very weakly concave section possibly representing the margin of a frontal incisure between the two valves. Dorsal margin weakly arched in the anterior half of the valve, becoming straight posteriorly. Carapace convex (radial breaks due to compaction in several specimens). Anterodorsal node, located at one-third of the valve length from anterior margin. Ventral margin weakly arched. Posteroventral margin strongly convex, becoming concave posterodorsally before the junction between the two valves. Angle between the posterodorsal margin and dorsal line = 45°.

Tail-piece: Unknown.

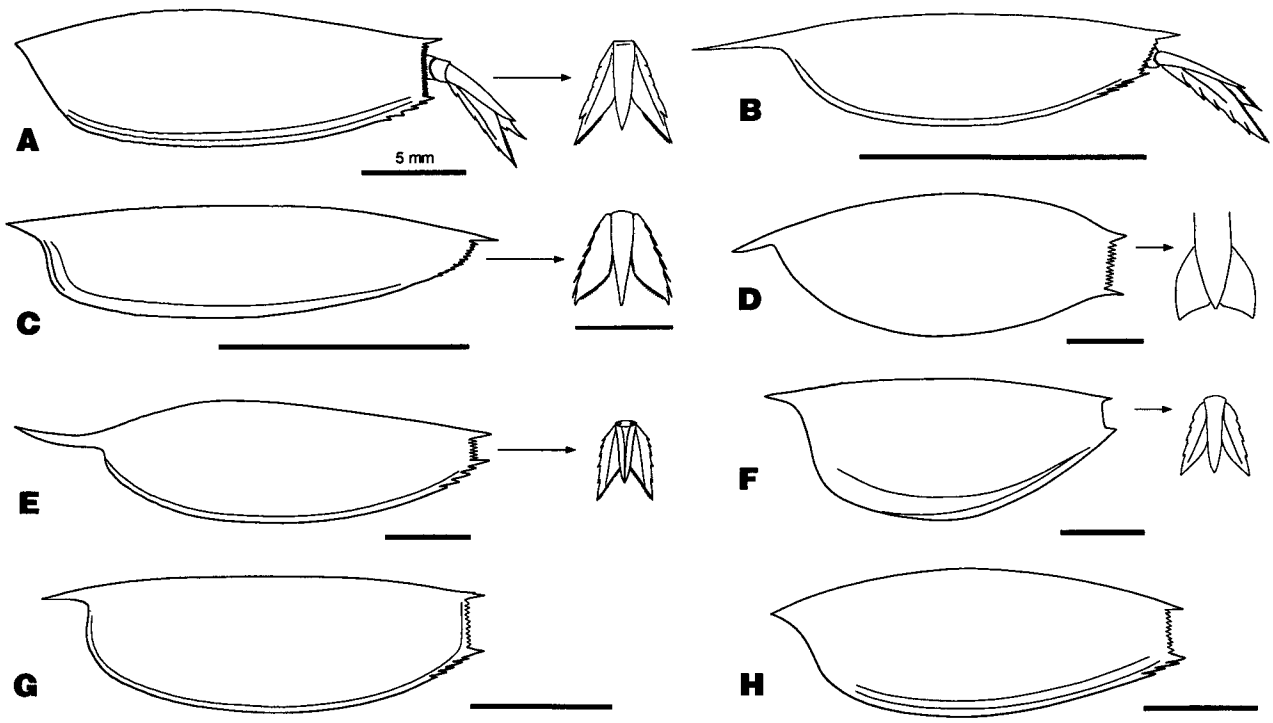

Fig. 13. Morphological comparisons of the main Ordovician representatives of *Caryocaris*. – **A, B:** *Caryocaris wrightii* SALTER 1863 and *C. subula* CHLUPAC 1970 from the Llanvirn of Bohemia (after CHLUPAC 1970), respectively; **C:** *C. delicatus* n. sp. from the Llanvirn of Argentina (this paper); **D:** *C. stewarti* JELL 1980 from the middle Tremadoc of Australia (after JELL 1980); **E:** *C. zhejiangensis* SHEN 1986 from the lower Ordovician of SE China (from SHEN 1986); **F:** *C.* cf. *monodon* (GURLEY 1896) from the Arenig of Norway (from STÖRMER 1937); **G:** *C. curvilata* GURLEY 1896 from the Arenig/Llanvirn of Alaska (from CHURKIN 1966); **H:** *Caryocaris* sp. from the Caradoc of Southern Peru (from HANNIBAL & FELDMANN 1996). Carapace and tail-pieces of each taxa represented in lateral and dorsal view, respectively and at the same scale except C. (*C. delicatus*). Inferred life attitude reconstructed for *C. wrightii* and *C. subula*. – Scale bar = 5 mm.

Remarks: The carapaces of *Pumilocaris granulosus* n. sp. show no trace of coiling whereas *Caryocaris* found in the same beds do exhibit such taphonomic features. We conclude that the carapace of *Pumilocaris* was possibly thicker and/or more mineralized (?) than that of *Caryocaris*.

?*Pumilocaris* sp.
Fig. 11

Material: One poorly preserved carapace with both valves in connection (CORD PZ 18924) from the Incamayo Creek, 3 km S. of Incahuasi (Fig. 1, loc. 11), Salta Province, Eastern Cordillera.

Horizon and age: Parcha Formation, in beds belonging to the *Tetragraptus phyllograptoides* and *Tetragraptus akzharensis* Zones of early Arenig age.

Discussion: Valves of about 9 mm long and 3.8 mm high. Outline and morphology closely similar to those of *Pumilocaris granulosus* n. gen., n. sp. from the Las Plantas Formation (Caradoc) except that their postero-ventral margin is more rounded and that the dorsal line is almost perpendicular to the posterodorsal margin (not 45° as in *P. granulosus*). CORD PZ 18924 exhibits the superimposed imprint of an elongated structure which is interpreted as a telson (Fig. 11A) comparable to that of the undetermined phyllocarid from the Parcha Formation (see text and Fig. 12). Both forms have a similar age (early Arenig) but more material is needed before we could state about their conspecificity.

Undetermined phyllocarid
Fig. 12

Material: Two tail pieces with the last abdominal somite in connection with the telson (CORD PZ 18962 and 19075).

Horizon and age: Parcha Formation, in beds belonging to the *Tetragraptus phyllograptoides* and *Didymograptus balticus* Zones of early Arenig age.

Description

Abdominal somites: Two abdominal somites connected to the telson are present in CORD PZ 18962 and only one in CORD PZ 19075. They are short (L = 0.35 mm and 0.5 mm in CORD PZ 18962 and 19075, respectively) and about three times wider than long. Each somite bears two oblique, elongated, and weakly differentiated lateral tubercles.

Tail-piece: The telson of the largest specimen (CORD PZ 19075) is style-shaped (length = ca. 10 mm, head width = 1.5 mm). None of the three available tail-pieces exhibit furcal rami. The telson head is subtriangular, dorsally rounded and evenly arched, with two lateral, weakly developed tubercles. The rest of the telson is convexo-con-

cave in cross section; its dorsal side has a long median ridge (convex in section) flanked with shallow furrows. The telson is outlined by very narrow rounded ridges. No traces of insertion of spinules.

Discussion: In most Recent and fossil phyllocarids, the furcal rami are tightly articulated with the telson. This form shows no visible trace of such articulation along its telson. We conclude that the lack of furcal rami was an original characteristic of the abdominal termination.

Styliform telsons with no furcal rami are known to occur in a few phyllocarid genera such as *Heroldina* (?Ceratiocarididae) and representatives of the family Aristozoidae. However, no taxonomic conclusion can be drawn from this feature only.

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References

ACEÑOLAZA, F.G. 1966. Geología estratigráfica de la región de la Sierra de Cajas, Dpto. Humahuaca, Prov. de Jujuy. – Revista de la Asociación Geológica de Argentina **23**: 207-222, Buenos Aires.

ACEÑOLAZA, F.G. & ESTEBAN, S. 1996. Filocáridos (Crustacea) en el Tremadociano del Sistema de Famatina, Provincia de La Rioja, Argentina. – Actas del XII Congreso Geológico de Bolivia: 281-288, Tarija.

ACEÑOLAZA, F.G.; GORUSTOVITCH, S. & SOLIS, J. 1976. El Ordovícico del Rio La Alumbrera, Departamento Tinogasta, Provincia de Catamarca. – Ameghiniana **13**: 269-288, Buenos Aires.

AHLFELD, F. & BRANISA, L. 1960. Geología de Bolivia. – Instituto Boliviano del Petroleo: 245 pp., La Paz (d. Bosco edit.).

ALBANESI, G.L. & ORTEGA, G. 1997. La fauna de conodontes caradociana de la Formación Los Azules, Precordillera de San Juan, Argentina. – Ameghiniana **34**: 113, Buenos Aires.

ALBANESI, G.L.; ORTEGA, G.; BARNES, C.R. & HÜNICKEN M.A. 1999. Conodont-graptolite biostratigraphy of the Gualcamayo Formation (Middle Ordovician) in the Gualcamayo-Guandacol rivers area, Argentine Precordillera. – [In:] KRAFT, P. & FATKA, O. [eds.] Quo vadis Ordovician? Short Papers of the 8th International Symposium on the Ordovician System. – Acta Universitatis Carolinae, Geologica: 45-48, Praha.

ALBANESI, G.L.; ORTEGA, G. & HÜNICKEN, M.A. 1998. High resolution conodont-graptolite biostratigraphy controlling the diachronous boundary between the San Juan and Gualcamayo formations (Arenig-Llanvirn) in the Argentine Precordillera. – ECOS VII, 7th International Conodont Symposium held in Europe, Abstracts: 2-4, Bologna, Modena.

ALBANESI, G.L.; ORTEGA, G.; TORTELLO, M.F. & ACEÑOLAZA, F.G. 1997. Conodontes, graptolitos y trilobites de la Formación Parcha en la Cordillera Oriental de Salta, Argentina. – Ameghiniana **34**: 114, Buenos Aires.

ANGEL, M.V. 1993. Marine planktonic ostracods. – Synopses of the British Fauna (New Series) **48**: 1-240, London (Linnean Society of London and the Estuarine and Coastal Sciences Association).

BENEDETTO, J.L.; HERRERA, Z.A. & ORTEGA, G. 1991. Bioestratigrafia del Ordovícico en el flanco occidental del Cerro Potrerillo, provincia de San Juan. – Revista de la Asociación Geológica de Argentina **46**: 60-68, Buenos Aires.

BORDONARO, O.L. & PERALTA, S.H. 1987. El Arenigiano Inferior de la Formación Empozada en la localidad de San Isidro, Mendoza, Argentina. – Actas del X Congreso Geológico Argentino **3**: 81-84, Tucumán.

BRIGGS, D.E.G. & KEAR, A. J. 1994. Decay and mineralization of shrimps. – Palaios **9**: 431-456, Tulsa/Okl.

BULMAN, O.M.B. 1931. South American Graptolites with special references to the Nordenskiöld collection. – Arkiv för Zoologi **22A**: 1-111, Stockholm.

CHAPMAN, F. 1903. New or little known Victorian fossils in the National Museum, I. Some Palaeozoic species. – Proceedings of the Royal Society of Victoria **15**: 104-122, Melbourne.

CHLUPAC, I. 1970. Phyllocarid crustaceans of the Bohemian Ordovician. – Sborník Geologickych Ved **12**: 41-75, Praha.

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

ECKSTRÖM, G. 1937. Upper *Didymograptus* Shale of Scania. – Sveriges Geologiska Undersökning, (C) **403**: 1-51, Stockholm.

FORTEY, R. 1995. A revision of Ordovician series and stages from the historical type area. – Geological Magazine **132**: 15-30, London.

GURLEY, R.R. 1896. North American graptolites; new species and vertical range. – Journal of Geology **4**: 291-311, Chicago.

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

HARRINGTON, H.L. & LEANZA, A.F. 1957. Ordovician trilobites of Argentina. – University of Kansas, Special Publication **1**: 1-276, Lawrence/Ks.

HUFF, W.D.; BERGSTRÖM, S.M.; KOLATA, D.R.; CINGOLANI, C. & DAVIS, D.W. 1995. Middle Ordovician k-bentonites discovered in the Precordillera of Argentina: Geochemical and paleogeographical implications. – [In:] COOPER, I.D.; DROSER, M.L. & FINNEY, S.C. [eds.] Ordovician Odyssey. – Short Papers of the Seventh International Symposium on the Ordovician System: 343-349, Las Vegas.

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

JELL, P.A. 1980. Two arthropods from the Lancefieldian (La 1) of central Victoria. – Alcheringa **4**: 37-46, Sydney.

KEIDEL, J. 1937. La Prepuna de Salta y Jujuy. – Holmbergia **1**: 163-180, Buenos Aires.

KOCH, L. & BRAUCKMANN, C. 1998. Phyllocariden (Crustacea) aus dem Unteren Llanvirn (Ordovizium) des Ebbe-Sattels (Rheinisches Schiefergebirge). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte **1998** (1): 55-64, Stuttgart.

LEVY, R. 1971. Noticia sobre el hallazgo de apéndices ventrales de trilobites en la Formación Parcha (Salta). – Ameghiniana **8**: 73-76, Buenos Aires.

MANCA, N. 1991. Organismos planctónicos en el Tremadociano Inferior de los alrededores de la quebrada de Humahuaca, Provincia de Jujuy, Argentina. – Revista del Instituto Geológico y Minero **8**: 141-150, Madrid.

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, Buenos Aires.

ORTEGA, G. 1987. Las graptofaunas y los conodontes de la Formación Los Azules, cerro Viejo, zona de Huaco, departamento Jáchal, San Juan. – Tesis doctoral, Universidad Nacional de Córdoba: 210 pp., Córdoba. [unpublished]

— 1995. Graptolite zones of the Los Azules Formation (Middle Ordovician) from Precordillera, western Argentina. – Graptolite News **8**: 57-59.

ORTEGA, G. & ALBANESI, G.L. 1998. The record of the *Nemagraptus gracilis* Zone in the Argentine Precordillera. – VI Graptolite Conference and 1998 Field Meeting of the IUGS Subcommission on Silurian Stratigraphy: 231-235, Madrid.

ORTEGA, G.; ALBANESI, G.L.; OTTONE, E.G. & HOLFELTZ, G.D. 1996. Conodonts, palynomorphs and graptolites from Los Azules Formation, Argentine Precordillera. – ECOS VI, 6th European Conodont Symposium, Abstracts: 44, Warszawa.

ORTEGA, G.; ALBANESI, G.L. & RAO, R.I. 1998. Lower Ordovician graptolites and conodonts from Cajas range and Parcha area, Eastern Cordillera, Northern Argentina. – VI Graptolite Conference and 1998 Field Meeting of the IUGS Subcommission on Silurian Stratigraphy: 236-240, Madrid.

ORTEGA, G.; TORO, B. & BRUSSA, E. 1993. Las zonas de graptolitos de la Formación Gualcamayo (Arenigiano tardio-Llanvirniano temprano) en el norte de la Precordillera (Provincias de La Rioja y San Juan), Argentina. – Revista Española de Paleontología **8**: 207-219, Madrid.

OTTONE, E.G.; ALBANESI, G.L.; ORTEGA, G. & HOLFELTZ, G.D. (in press). Plant microfossils, conodonts and associated graptolites from the Ordovician Los Azules Formation, Central Precordillera, Argentina. – Micropaleontology **45**: 225-250, New York.

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. – Tesis doctoral, Universidad de Buenos Aires: 86 pp., Buenos Aires. [unpublished].

— 1984. Filocaridos (Crustacea) del Ordovícico Argentino. – Actas del III° Congreso Argentino de Paleontología y Bioestratigrafía: 29-38, Buenos Aires.

ROLFE, W.D.I. 1962. Grosser morphology of the Scottish Silurian phyllocarid crustacean, *Ceratiocaris papilio* SALTER in MURCHISON. – Journal of Paleontology **36**: 912-932, Lawrence/Ks.

— 1969. Phyllocarida. – [In:] MOORE, R.C. [ed.] Treatise on Invertebrate Paleontology, Part **R**, Arthropoda 4. – **1**: R296-R331, Boulder/Col. (Geological Society of America), Lawrence/Ks. (University of Kansas Press).

RUEDEMANN, R. 1934. Paleozoic plankton of North America. – Memoirs of the Geological Society of America **2**: 1-133, Washington/D.C.

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, Dublin.

SALTER, J.W. 1863. Note on Skiddaw Slate Fossils. – Quarterly Journal of the Geological Society of London **19**: 79-84, London.

SARS, G.O. 1887. Report on the Phyllocarida collected by H. M. S. Challenger during the year 1873-76. – Reports on the scientific results of the voyage of the H. M. S. Challenger during the year 1873-76. Zoology, XIX, part LVI. – 38 pp., London.

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

STÖRMER, L. 1937. Planktonic crustaceans from the Lower *Didymograptus* Shale (3b) of Oslo. – Norsk Geologisk Tidsskrift **16**: 267-278, Oslo.

SUAREZ SORUCO, R. 1976. El Sistema Ordovícico en Bolivia. – Revista Técnica de Yacimientos Petroliferos Fiscales Bolivianos **5**: 111-223, Santa Cruz.

TORO, B.A. 1998. New data about the age of the graptolite fauna from the Santa Victoria area, Salta province, Argentina. – VI Graptolite Conference and 1998 Field Meeting of the IUGS Subcommission on Silurian Stratigraphy: 266-267, Madrid.

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

VANNIER, J.; WILLIAMS, M.; RACHEBOEUF, P.R.; RUSHTON, A.; SERVAIS, TH. & SIVETER, D.J. 1998. The early colonization of pelagic niches by crustaceans and other bivalved arthropods. – Proceedings and Abstracts of the 4th International Crustacean Congress, 20-24 July 1998: 202, Amsterdam.

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