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Ontogeny of the Early Ordovician olenid trilobite *Jujuyaspis keideli* Kobayashi from northwestern Argentina

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Abstract. The Early Ordovician olenid trilobite *Jujuyaspis keideli* Kobayashi is well-preserved in black shale facies of the Santa Rosita Fomation at Purmamarca, northwestern Argentina. Although protaspides are not represented in the collections, isolated tagmata and articulated specimens from the early meraspid stages onwards are available for ontogenetic study. Meraspid Group 1 is characterized by having an hexagonal cephalic outline, three distinct glabellar furrows, and seven marginal spines. In meraspid Group 2 the cephalon has become reniform in outline, the glabellar furrows are less developed, and the fixigenae exhibit a pair of ocular ridges. Meraspid Group 3 is characterized by an adult-like cephalon lacking both ocular ridges and paired marginal spines. At this stage the thorax has very long pleural spines which, contrasting greatly with those of the adult, are laterally splayed out. In meraspid Group 4 the cephalon bears a well-developed occipital spine or a conspicuous occipital node, the glabella possesses two pairs of lateral furrows, and the thorax exhibits axial nodes on the anterior segments and shorter, more posteriorly directed lateral spines. Early holaspides retain some of the later meraspid morphological features. The hypostome of the species is documented for the first time. Information on the intraspecific variability of *J. keideli* enables us to discuss its systematic affinities in a new context. A monospecific, age-sorted clustered assemblage assignable to holaspid Group 1 could represent specimens that aggregated together for synchronized exuviation. Early meraspides of *Jujuyaspis* are assumed to be pelagic, a fact that must have facilitated the worldwide distribution of the genus, whereas holaspides may have had a nekto-benthic mode of life.

Resumen. ONTOGENIA DEL TRILOBITE OLÉNIDO *JUJUYASPIS KEIDELI* KOBAYASHI (ORDOVÍCICO TEMPRANO) DEL NOROESTE ARGENTINO. El trilobite olénido *Jujuyaspis keideli* Kobayashi se encuentra bien preservado en la facies de lutitas negras de la Formación Santa Rosita (Ordovícico Temprano) en Purmamarca, noroeste de Argentina. Aunque la fase protaspis no está representada en las colecciones, éstas contienen tagma aislados y ejemplares completos asignables a estadios meráspidos tempranos y siguientes. El grupo meráspido 1 está caracterizado por su contorno cefálico hexagonal, tres pares de surcos glabelares conspicuos y siete espinas marginales. En el grupo meráspido 2 el céfalo adquiere un contorno reniforme, los surcos glabelares están menos desarrollados, y las mejillas fijas exhiben un par de aristas oculares. El grupo meráspido 3 está caracterizado por un céfalo de aspecto similar al del adulto, desprovisto de aristas oculares y espinas marginales pares. En este estadio el tórax presenta espinas pleurales muy largas que, contrastando en gran medida con las del adulto, están expandidas lateralmente. En el grupo meráspido 4 el céfalo posee una espina occipital bien desarrollada o un nodo occipital conspicuo, la glabela presenta dos pares de surcos glabelares someros, y el tórax exhibe nodos axiales sobre los primeros segmentos y espinas laterales más cortas que las de estadios anteriores, dirigidas más posteriormente. Los ejemplares holáspidos tempranos retienen estos últimos caracteres. Se documenta por primera vez el hipostoma de la especie. Información sobre la variabilidad intraespecífica de *J. keideli* permite discutir sus afinidades sistemáticas en un nuevo contexto. Una asociación mono-específica compuesta por numerosos ejemplares asignables al grupo holáspido 1 podría representar individuos reunidos para mudar en forma sincronizada. Los meráspidos tempranos de *Jujuyaspis* son considerados formas pelágicas, hábito que debe haber facilitado la amplia distribución del género, mientras que los holáspidos podrían haber tenido un modo de vida necto-bentónico.

Key words. *Jujuyaspis*. Trilobita. Olenidae. Early Ordovician. Argentina. Ontogeny. Ecdysis. Paleoecology.

Palabras clave. *Jujuyaspis*. Trilobita. Olenidae. Ordovícico Temprano. Argentina. Ontogenia. Ecdisis. Paleoecología.

Introduction

The Santa Rosita Formation (lower part), Iscayachi Formation and equivalents of latest Cambrian and earliest Ordovician age are widely distributed in the Eastern Cordillera of Argentina and southern Bolivia (e.g. Harrington *in* Harrington and Leanza, 1957; Turner, 1960; Branisa, 1965; Aceñolaza, 1968; Suárez Soruco, 1976). Lithologically, they are characterized by greenish and black shales and sandstones, with rare interspersed marl and limestone layers, representing both shallow marine settings affected by storms and waves and outer shelf

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environments below storm-wave base. These units lie on Cambrian quartzites of the Meson and Tucumilla groups in Argentina and Bolivia respectively (Turner, 1960; Schlatter and Nederloff, 1966). In addition, the Upper Cambrian-lowest Ordovician is locally represented in the Famatina Range (La Rioja Province, Argentina), where the lower member of the Volcancito Formation is mainly composed of outer shelf marls and shales and inner shelf sandstones and mudstones, resting unconformably upon the metamorphosed Cambrian rocks of the Negro Peinado Formation (Harrington *in* Harrington and Leanza, 1957; Esteban, 1999).

Fossils are abundant in these formations. Trilobites and brachiopods are especially rich, as well as graptolites, conodonts, gastropods and echinoderms. As is usual in other parts of the world, olenid and agnostoid trilobites are better represented in dark and black shale facies, often occurring in a good state of preservation. After early studies by Kayser (1876, 1897), Kobayashi (1936, 1937) and Harrington (1938), Harrington and Leanza (1957) described in great detail numerous species of trilobites and provided a biostratigraphic scheme which, with slight modification, is still standing. The *Parabolina* (*Neoparabolina*) *frequens argentina* Zone, originally wholly assigned to the lower Tremadoc, provides a unique opportunity to evaluate the Cambrian-Ordovician transition in South America. A varied agnostoid fauna, which occurs along with some olenid species, characterizes the lower part of this biozone, indicating a latest Cambrian age (Tortello and Esteban, 1999, 2003; Tortello, 2003). On the other hand, the upper part of the unit is dominated by the lower Tremadoc olenid *Jujuyaspis keideli* Kobayashi.

Jujuyaspis keideli is one of the most abundant taxa in northwestern Argentina (Harrington and Leanza, 1957). It has been described from both thick stratigraphic sections, in which the sequences are well represented (Tortello and Esteban, 1999; Tortello *et al.*, 1999), and smaller, isolated exposures. The type area of *Jujuyaspis keideli* belongs to the later category. It is at Purmamarca, in the Quebrada de Humahuaca (Jujuy Province) (Kobayashi, 1936), where a series of west and east verging thrusts bounds thin tectonic slides comprising the Upper Precambrian-Lower Cambrian Puncoviscana Fm., the Upper Cambrian Meson Group, and the lowest Ordovician Purmamarca Shales (=upper part of the Casa Colorada Formation) (Harrington *in* Harrington and Leanza, 1957).

The Purmamarca Shales are 85-100 m thick and composed of pyritiferous black shales with scarce interbedded sandstone layers. *Jujuyaspis keideli* is the most common species in the formation, representing more than 90 per cent of the assemblages. It occurs together with the olenids *Parabolinella argentinensis* Kobayashi, *Angelina hyeronimi* (Kayser), *Bienvillia* sp. and *Plicatolina* sp., and the agnostoids *Micragnostus* sp., *Anglagnostus* sp. and *Gymnagnostus* sp. (Kobayashi, 1936; Harrington, 1938; Harrington and Leanza, 1943, 1952, 1957; Aceñolaza and Aceñolaza, 1992; Aceñolaza, 1996; Mángano *et al.*, 1996; Tortello and Aceñolaza, 1999; Aceñolaza *et al.*, 2001). The depositional environment of the Purmamarca Shales, dominated by quiet, low-oxygen-water bottom conditions, resulted in the accumulation of many articulated specimens with a good state of preservation.

Although the genus *Jujuyaspis* has been described from different lithology in numerous localities in the world, references to material assignable to early ontogenetic stages are scarce. Dense clusters of well-preserved individuals of *J. keideli*, and numerous specimens assignable to early meraspid stages onwards have been recently found in the Alta Creek (Purmamarca area) (figure 1). In order to emend the original description of *J. keideli* and to discuss its affinities and possible mode of life, the ontogeny, intraspecific variability, and moulting of the species are herein described. New morphological and biostratigraphic data enable us to debate the ecological role of this taxon in the olenid communities of the lowest Ordovician of Argentina.

The genus *Jujuyaspis*: occurrence and importance

Jujuyaspis Kobayashi, 1936, is a cosmopolitan olenid that has been recorded in both shales and limestones close to the Cambro-Ordovician boundary. In the absence of graptolites and conodonts, the genus has proved to have great biostratigraphic value as an international guide for the lowermost Tremadoc (see Aceñolaza and Aceñolaza, 1992; Cooper *et al.*, 2001).

In North China and Korea, the species *Jujuyaspis sinensis* Zhou was documented from the *Yosimuraspis* Zone (Early Ordovician) (e.g. Chen *et al.*, 1980; Zhou and Zhang, 1985; Kim and Choi, 2000), and *J. kelleri* (Balashova) was described from similar stratigraphic levels in Kazakhstan (Balashova, 1961; see Nikolaisen and Henningsmoen, 1985).

Likewise, the occurrences of *Jujuyaspis* in North America characterize the *Symphysurina bulbosa* Subzone of the *Symphysurina* Zone in several sections of the Cambrian-Ordovician transition. In southwestern USA (New Mexico), the species *Jujuyaspis borealis* Kobayashi occurs in association with conodonts that indicate a lowest Ordovician age (e.g. *Iapetognathus* sp., *Cordylodus angulatus* Pander), close to the occurrence of *Rhabdinopora flabelliformis* (Eichwald) (Taylor and Repetski, 1995). In British Columbia (e.g.

Figure 1. Location map (modified from Aceñolaza *et al.*, 2001). The asterisk (*) shows the position of the Alta Creek, where the trilobites were collected / *Mapa de ubicación (modificado de Aceñolaza* et al.*, 2001). El asterisco (*) muestra la posición de la quebrada Alta, donde fueron coleccionados los trilobites estudiados.*

Kobayashi, 1955; Norford, 1969), Alberta (Westrop, 1986; Dean, 1989), Utah (Stitt and Miller, 1987; Miller and Taylor, 1995; Loch *et al.*, 1999) and Texas (Winston and Nicholls, 1967; Stitt and Miller, 1987; Miller and Stitt, 1995) *Jujuyaspis borealis* have been recovered together with *Iapetognathus*. Miller and Stitt (1995) correlated the bases of the *Symphysurina bulbosa* Subzone and the *Iapetognathus* Zone with the base of the Tremadoc, pointing out the biostratigraphic value of *Jujuyaspis* in these units (see also Stitt and Miller, 1987).

Jujuyaspis was also adapted to paleoenvironmental conditions that prevailed at the edges of the paleocontinents of Gondwana and Baltica, providing a firm basis for intercontinental correlation among these regions (McCormick and Fortey, 1999). In southern Norway, *Jujuyaspis keideli norvegica* Henningsmoen occurs associated with *Cordylodus lindstromi* Druce and Jones and *Iapetognathus* (Henningsmoen, 1957; Bruton *et al.*, 1982, 1988), whereas *Jujuyaspis angusta* Henningsmoen occurs within the range of *Rhabdinopora flabelliformis socialis* (Salter) (Henningsmoen, 1957). "*Jujuyaspis colombiana*" was documented in the lower Tremadoc of Colombia (Baldis *et al.*, 1984). On the other hand, J*ujuyaspis keideli keideli* Kobayashi has a wide geographic distribution that includes northern Norway (Nikolaisen and Henningsmoen, 1985), Colombia (Baldis *et al.*, 1984; see Aceñolaza and Aceñolaza, 1992), Bolivia (Přibyl and Vaněk, 1980) and Argentina (e.g. Kobayashi, 1936; Harrington, 1938; Harrington and Leanza, 1957). *Jujuyaspis* is also represented in the onshore Bonaparte Basin of Western Australia, within the *Cordylodus lindstromi* Zone (Shergold, 2000). In addition, fragments from Celtiberia (Spain), described by Shergold and Sdzuy (1991) as an undetermined olenid, are possibly assignable to this genus (Shergold, 2000: 129).

Occurrences of *Jujuyaspis keideli keideli* in Argentina are well constrained biostratigraphically in Santa Victoria, Cajas, Purmamarca and río Volcancito (Kobayashi, 1936; Harrington and Leanza, 1957; Ortega and Rao, 1995; Tortello and Esteban, 1999; Tortello *et al.*, 1999). Since this taxon occurs with or close to *Rhabdinopora flabelliformis* s.l. in the upper part of the *Parabolina* (*Neoparabolina*) *frequens argentina* Biozone (lowest Tremadoc), it is a valuable key for defining the Cambrian-Ordovician boundary in South America (Aceñolaza, 1983).

Previous studies on the ontogeny of the Pelturinae

Studies on comparative ontogeny provide morphological information vital for determining phylogenetic relationships between established taxa, and heterochronic patterns of evolution. In many cases, ontogenetic studies also provide clues to the biology, evolutionary ecology and biogeographic distribution of trilobite taxa (Chatterton and Speyer, 1990).

First investigations on olenid ontogeny demonstrated that the morphological development mainly occurs in the meraspid period (Raw, 1925). Clarkson and Taylor (1995), Clarkson *et al.* (1997), and Chatterton and Speyer (1997) compiled a series of studies on olenid ontogeny, which include description of juvenile stages of *Triarthrus*, *Bienvillia*, *Olenus*, *Leptoplastides*, *Leptoplastus*, *Parabolinella*, *Ctenopyge*, *Hedinaspis* and *Highgatella*, among others. As is usual in this kind of research, most of the studies were based on specimens preserved in limestones.

Studies on the ontogeny of pelturines are relatively few. Holtedahl (1910) illustrated incomplete juvenile cephala of *Protopeltura holtedahli* Henningsmoen from the Upper Cambrian of Norway (Holtedahl, 1910: pl. 2, figs. 9-10 -figured as *Peltura praecursor*, see Henningsmoen, 1957: 227-). Subsequently Poulsen (1923), Whittington (1958) and Hu (1964) described in detail several larval stages of *Peltura scarabaeoides* (Wahlenberg, 1821) from the Upper Cambrian of Denmark and Norway, showing the presence of lateral glabellar furrows, genal pits, and fixigenal and occipital spines in early meraspides, as well as changes in the outline of free cheeks, glabella and anterior cephalic margin during ontogeny. In addition, Hu (1971) described the ontogeny of *Acerocare ecorne* Angelin from the Uppermost Cambrian of Sweden, also indicating changes in the outline of the glabella and the development of frontal area and glabellar furrows, and the presence of occipital and fixigenal spines in the early stages [see also Moberg and Möller (1898) and Henningsmoen (1957: pl. 30, fig. 1)]. A study on the ontogeny of *Peltura scarabaeoides westergaardi* Henningsmoen, based upon largely complete and intact larval stages, is currently in review (Bird and Clarkson, in press).

Although the complete ontogeny of *Jujuyaspis* has not been previously described, some references to juvenile stages have been provided by several authors. Winston and Nichols (1967: pl. 12, fig. 23) illustrated an “immature” cranidium of *Jujuyaspis borealis* Kobayashi from the Wilberns Formation in Central Texas, characterized by having a pair of metafixigenal spines. Similarly, Westrop (1986: pl. 20, figs. 8-9) figured a small cranidium with fixigenal spines from the Survey Peak Formation in Alberta. Dean (1989: pl. 8, fig. 3) also illustrated a poorly preserved cranidium from the same region, that was tentatively assigned to a meraspid stage. All these specimens show indications of a small occipital node, which is absent in the holaspides. Similarly, Kim and Choi (2000: fig. 5.32) figured a juvenile cranidium of *Jujuyaspis sinensis* Zhou *in* Chen *et al.*, from the Mungok Formation in Korea, indicating the presence of a minute occipital node.

Aceñolaza *et al.* (2001: fig. 3.4 and 3.7) illustrated a juvenile eye of *Jujuyaspis keideli* from the Purmamarca Shales that shows a small number of lenses as compared with that of the adult. In addition, S. B. Esteban (Univ. of Tucumán) and one of the authors (MFT) have collected six small, poorly preserved cranidia of *J. keideli* from the Volcancito Formation (Famatina Range) bearing an occipital spine, a deep occipital furrow, and faint indications of a pair of glabellar furrows (La Plata Museum, MLP 28289, 28293, 28294, 28296). These meraspid specimens have been included in the present study for comparison.

Material and methods

The material comes from the upper part of the Purmamarca Shales (= Casa Colorada Formation) (lower Tremadoc) in the Alta Creek (Purmamarca area, Tumbaya Department, Jujuy Province, Argentina). *Jujuyaspis keideli* occurs in association with *Parabolinella argentinensis* Kobayashi, *Angelina hyeronimi* (Kayser), *Gymnagnostus* sp., *Micragnostus* sp. and “inarticulate” brachiopods. *Jujuyaspis keideli* dominates the assemblages, representing 94 per cent of the total fauna. The material is housed in the paleontological collections of La Plata Museum (La Plata, Argentina), with specimen numbers prefixed by MLP.

Specimens preserved in shales are not usually ideal for ontogenetic studies. The methods used in this work are similar to those applied by Berard *et al.* (2000) who described the larvae of *Taihungshania miqueli* (Bergeron) from the siliciclastic Arenig of France. A selected four kg of grey and black shale was used in this study. A total of 233 rock pieces were searched for adult and juvenile specimens. As a result, about 500 specimens of *J. keideli* were identified in the samples, comprising both articulated and disarticulated shields. Forty-three per cent of these specimens are meraspides and early holaspides (less than 7.5 mm total exoskeleton sagittal length), whereas no protaspides were recovered for study.

The material was cleaned by using conventional paleontological techniques. Many latex replicas of external and internal moulds were prepared. All well preserved specimens were drawn to scale by using a camera lucida microscope. For light macrophotography, the late meraspid and holaspid specimens were coated with magnesium oxide. On the other hand, latex replicas of the early meraspides with gold-palladium coating were examined under SEM. Based on techniques by Clarkson and Taylor (1995), Berard *et al.* (2000) and Clarkson and Ahlberg (2002), the reconstructions of larger specimens were made from scaled camera lucida drawings, whereas the reconstructions of the smaller stages were made from the SEM photographs by drawing a squared grid on each illustration (the dimensions given by the scale bar) and transposing this on to millimetre-squared graph paper to give a constant scale. Similarly, measurements of the larger and smaller individuals were taken from camera lucida drawings and SEM photographs, respectively.

Description of meraspid-holaspid ontogeny of *Jujuyaspis keideli*

Family OLENIDAE Burmeister, 1843
Subfamily PELTURINAE Hawle
and Corda, 1847

Genus ***Jujuyaspis*** Kobayashi, 1936

Type species. *Jujuyaspis keideli* Kobayashi, by original designation.

Jujuyaspis keideli keideli Kobayashi, 1936
Figures 2-11

1936. *Jujuyaspis keideli* n. sp. Kobayashi, p. 90, pl. 16, figs. 5-9.
1938. *Jujuyaspis keideli* Kobayashi. Harrington, p. 206, pl. 9, figs. 2-4, 10.
1943. *Jujuyaspis keideli* Kobayashi. Harrington and Leanza, p. 352, pl. 2, figs. 2, 7.
1952. *Jujuyaspis keideli* Kobayashi. Harrington and Leanza, p. 201, pl. 1, fig. 8.
1955. *Jujuyaspis harringtoni* n. sp. Kobayashi, p. 467.
1957. *Jujuyaspis keideli* Kobayashi. Harrington and Leanza, p. 99, figs. 33, 34.1-34.7.
1957. *Jujuyaspis keideli keideli* Kobayashi. Henningsmoen, p. 262, pl. 2, fig. 7.
1965. *Jujuyaspis keideli* Kobayashi. Branisa, pl. 1, figs. 3-4.
1980. *Jujuyaspis keideli keideli* Kobayashi. Přibyl and Vaněk, p. 15, pl. 11, figs. 2-3.
1984. *Jujuyaspis truncaticonis* n. sp. Baldis and González *in* Baldis *et al.*, p. 29, pl. 2, figs. 1-4.
?1984. *Jujuyaspis colombiana* n. sp. Baldis and González *in* Baldis *et al.*, p. 31, pl. 3, figs. 1-4.
1985. *Jujuyaspis keideli keideli* Kobayashi. Nikolaisen and Henningsmoen, p. 26, fig. 18A-L.
1992. *Jujuyaspis keideli* Kobayashi. Aceñolaza and Aceñolaza, fig. 2A-C, G-H.
1999. *Jujuyaspis keideli* Kobayashi. Tortello and Esteban, fig. 4.
1999. *Jujuyaspis keideli keideli* Kobayashi. Tortello, Rábano, Rao and Aceñolaza, p. 565, fig. 4.G-M.
2001. *Jujuyaspis keideli keideli* Kobayashi. Aceñolaza, Tortello and Rábano, p. 348, figs. 2.1-2.3 and 3.1-3.7.

Remarks. The late holaspid morphology was fully described by Kobayashi (1936) and Harrington and Leanza (1957). In addition, the eye morphology were provided by Aceñolaza *et al.* (2001). Since the material from Colombia described by Baldis and González *in* Baldis *et al.* (1984) is very similar to that of *Jujuyaspis keideli* described here, it is regarded as conspecific (see below).

Meraspid morphology

The traditional descriptive methodology by Raw (1925), consisting of the division of the meraspid period into degrees (1, 2, 3, etc.), marked by the addition of succesive segments to the thorax, can be confidently applied here only in late meraspid stages, whereas there remains some uncertainty in the ascription of early meraspid individuals to their appropriate degrees. Therefore, the simple terminology of Whitworth (1970), who designated groups 1, 2, 3 to define specific ontogenetic morphology, is used here (see also Clarkson and Taylor, 1995; Clarkson *et al.*, 1997; Berard *et al.*, 2000; Clarkson and Ahlberg, 2002).

Group 1. This developmental stage is represented by three minute cranidia. The specimen figured here (figures 2.A, 3.A) is 523 µm in sagittal length and 571 µm in maximum width (excluding spines), lacking a transitory pygidium. It is hexagonal in form, 0.82 as long as wide, with an anterior margin strongly concave forwards. The protoglabella (as defined by Whittington, 1997, excluding L0) is very long and narrow, remarkably convex, with the anterior half slightly tapered forwards and the posterior part subparallel sided, rounded anteriorly and reaching the anterior border, occupying 75 per cent of the cephalic length and about one-third of the cephalic width (at midlength); it is well defined by a pair of deep, narrow axial furrows. In addition, the protoglabella

Figure 2. ***Jujuyaspis keideli*** Kobayashi; scale reconstructions of Groups 1 (A) and 2 (B) meraspid / *reconstrucciones a escala de los grupos meráspidos 1 (A) y 2 (B)*, X40.

has three transverse furrows, approximately of equal spacing, curving slightly posteriorly; S1 and S2 are distinct, transglabellar, defining two well-differentiated protoglabellar lobes (L1, L2), whereas S3 are represented by a pair of faint lateral furrows, not connected in the middle, separating L3 from the frontal lobe. The occipital furrow is well defined, transverse, with its median part straight and the lateral tips slightly curved forwards. The occipital ring is prominent, triangular in form, showing a median indentation which can be interpreted as a spine base. Preglabellar field absent.

The narrow anterior border, occupying about 4 per cent of the total cephalic length (sag.), is of nearly constant width, and defined by a weak border furrow; it bears a pair of long, sharp antero-lateral spines, anteriorly projecting at about 45 degrees to the sagittal plane. The lateral parts of the specimen are somewhat inflated; they are slightly damaged, but it is possible to recognize the indications of an additional pair of spines, located on the lateral border, slightly in front of S3. Posteriorly, there is a poorly defined border that shows the bases of a pair of strong intergenal spines.

The specimen described above is the smallest element suitable for description in the collections. It may correspond to the degrees 0-1. Some comments on the significance of bearing seven marginal spines are made below.

Group 2. This stage of development is represented by three specimens about 0.53 mm in length and 0.68 mm in width (excluding spines). A well preserved cephalon (figures 2.B, 3.B) is the most suitable for description. At this stage, the cephalon is reniform in outline and is 0.66 (restored) as long as wide; although it is proportionally wider than that of Group 1, it is still narrower (tr.) than that of holaspides. The glabella has undergone a significant change in shape when compared to that of Group 1: its anterior part is wider (tr.), the lateral margins uniformly converge forwards, and its convexity is not very high. In addition, the glabellar lateral furrows are less developed, with only faint indications of S1. The occipital ring seems to be less distinct, slightly convex, occupying only 12.5 per cent of the total cephalic length (sag.) (excluding spines), prolonged posteriorly to form a pronounced median spine which is at least as long as 25 per cent the sagittal cephalic length. The occipital segment is well defined by a narrow, faint, rearwardly curving occipital furrow. The frontal area is slightly wider (sag.) than that of Group 1.

The fixigenae are somewhat inflated and a pair of curved ocular ridges are present, connecting the anterolateral corners of the glabella with a pair of faint palpebral lobes. The facial suture is very adult-like: anterior branches are slightly convergent forwards whereas posterior branches are directed outwards and rearwards, and curve rearwards in a semicircle close to the marginal border. The posterior border has become more distinct. A pair of narrow librigenae are present, each with a poorly preserved border. Since we discovered no detached librigenae at this stage, the facial suture could have not become functional until a later stage in development. The eye lobes are prominent, subparallel to the exsagittal plane, located far from the glabella and closer to anterior than posterior margin of the cephalon. Seven marginal cephalic spines are still present at this stage of development. The specimen figured shows the base of an antero-lateral spine on its right hand side. Similarly, a lateral spine on the left hand side of the cephalon appears to be broken off and lies to the side. The intergenal spines are long and sharp, posterolaterally projecting at about 45 degrees to the sagittal plane.

Group 3. Twenty-eight specimens with a rather wide size range (0.83 to 1.28 mm cranidium length -sag.-) are assigned to this group. Although the cephalon and the central part of the body of many of these individuals are absent or indistinct, the post-cephalic pleural spines are well preserved, showing a unique arrangement (see below). The best preserved specimen is illustrated in figure 3.C, and additional individuals are shown in figures 3.D, 3.F-H, 4.A-B (in part) (see also figure 5.A).

The cephalon is very adult-like, subsemicircular to reniform in outline, proportionately wider (tr.) than that of Group 2, 0.45-0.60 as long as wide. The anterior cephalic margin is slightly curved backwards, straight, or slightly curved forwards. The glabella is large, slightly raised above the level of the fixigenae, subparallel sided to slightly tapering forwards, rounded anteriorly, 1.15-1.50 as long as wide, smooth or with faint indications of S1 and S2. The preglabellar field is contracted. The occipital ring is defined by a shallow, straight to slightly backwardly curving occipital furrow; its width (sag.) is more uniform than that of earlier stages of ontogeny, and it retains a well developed median spine or a conspicuous median node. The eyes have shifted inwards, located close to the glabella. The ocular ridges are absent. Furthermore, the librigenae are wider (tr.) than those of Group 2, occupying 51-52 per cent (small specimens) and 54-58.3 per cent (large specimens) of the total cephalic width (measured at the posterior margins of the eyes). There are some axial shields and displaced librigenae of this group in the collections, indicating that the facial suture has become functional at this stage of development. The cephalic border is well defined; its posterior portion is a little wider (exsag.) than the anterior portion. The antero-lateral, lateral and fixigenal spines have disappeared.

Figure 3. ***Jujuyaspis keideli*** Kobayashi; **A,** Group 1 meraspid, cephalon / *Grupo meráspido 1, céfalo*, MLP 30304, X48. **B,** Group 2 meraspid, cephalon / *Grupo meráspido 2, céfalo*, MLP 30367, X47. **C-D,** Group 3 meraspid / *Grupo meráspido* 3; **C,** axial shield / *escudo axial*, MLP 30359a, X20,1; **D,** complete specimen / *ejemplar completo*, MLP 30359b, X20,4. **E,** Group 4 meraspid, thorax / *Grupo meráspido 4, tórax*, MLP 30344, X20,2. **F-H,** Group 3 meraspid / *Grupo meráspido 3*; F, thoracopygon / *toracopigidio*, MLP 30340, X10; **G,** thoracopygon / *toracopigidio*, MLP 30359c, X20; **H,** thoracopygon / *toracopigidio*, MLP 30359d, X19. **I-K,** Group 4 meraspid / *Grupo meráspido 4*; **I,** cephalon / *céfalo*, MLP 30268, X19,4; **J,** cranidium / *cranidio*, MLP 30358, X15; **K,** cephalon-thorax / *céfalo-tórax*, MLP 30344, X11,5.

Many specimens have 5 to 8 pairs of long, stout, parallel thoracic spines, rounded in cross-section, which, contrasting greatly with those of the adult, occupy more than 50 per cent the pleural length (tr.) and are laterally splayed out. Even in specimens where the axis and adjacent areas are poorly preserved, the spines are retained. Some individuals retain at least part of the central part of the thorax, and show a strap-like, transverse, upraised axis, ornamented with small tubercles. Because of incomplete preservation, the junction between the thorax and the transitory pygidium is not clearly seen, which makes it difficult to establish the exact degrees of these specimens. Based on the size and general post-cephalic morphology, this group may comprise meraspid degrees 4-8.

Group 4. This includes specimens of 3.75-5.9 mm exoskeleton length (sag.) (1.4-2.1 mm cephalon length) (figures 3.E, 3.I-K, 4.C-K, 5.B). Since several individuals are complete, with exoskeletons bearing 9 to 11 thoracic segments, Group 4 represents the late meraspid stages of development. The cephalon is very adult-like, though it retains some juvenile characters. There is a well-developed occipital spine (figures 3.J-K, 4.D, 4.I) or, in some specimens, a conspicuous occipital node (figures 4.E-F). Although some have a smooth glabella, others show faint indications of two pairs of lateral furrows (S1 and S2); both furrows are slightly curved, disconnected at the middle, and set obliquely backwards (figure 4.C).

In most specimens, the anterior thoracic pleural spines have become shorter and flatter, and the rear spines are losing the lateral splay and are becoming directed more posteriorly (figures 3.E, 3.K, 4.C, 4.F, 4.I, 5.B). Nevertheless, some individuals bear exceptionally developed, straight, laterally splayed out pleural spines (figures 4.D, H, J, K). These individuals, bearing 10 and 11 thoracic segments, are rather larger than the rest of the material of this group, illustrating a singular case of intra-specific variability. The expression of the axial nodes on the thorax is also variable in Group 4. Some specimens bear distinct nodes on the first seven segments; in other cases the nodes are expressed only on the first three segments, or are absent.

The pygidium is not very well preserved. It approaches the adult form, but lacks the terrace lines.

Holaspid morphology

Group 1. This group is represented by numerous specimens (complete exoskeletons, axial shields, cephala, cranidia, librigenae, thoracopygon and pygidia) of exoskeleton length 6.1-9 mm (figures 4.A-B -in part-, 6.A-N, 7). Many of them occur in a clustered assemblage (see below). Since 12 thoracic segments are already present, this group represents the smallest holaspid stage. As in the meraspides, these small adults have either a well-developed occipital spine or an occipital node and some individuals show indications of a pair of glabellar furrows and thoracic median nodes. On the other hand, the librigenae become wider, representing 55-65 per cent of the maximum cephalic width (tr.).

Although *J. keideli* is well represented in northwestern Argentina, the hypostome of this species has not been previously reported, suggesting that it was not attached to the cephalic doublure (natant condition). The material from Purmamarca contains only one adequately preserved hypostome, which is assignable to the holaspid Group 1 (figure 6.A), and three imperfect early and late holaspid specimens (figures 6.I, 6.K, 8.K). The former is about 1.17 mm in length and 0.95 mm in maximal width; the anterior margin is slightly bowed forwards; the anterior wings are well defined, narrow (tr.), and sharply pointed. Behind these the lateral hypostomal margins diverge backwards, defining a wider hypostomal rear part. The posterior margin is semicircular. The middle body is long, wide, and highly convex; it merges forwardly with the anterior part of the hypostome, and is posteriorly well defined by a deep, uniformly impressed furrow. There is a distinct brim, crescentic in form, occupying more than half the length (sag.) of the hypostome, with a narrow posterior border.

The thoracic pleural spines have completely lost the lateral splay shown in the preceding stages; they are directed posteriorly, in an adult-like general arrangement (figures 6.D-F, I, N). At this stage, the pygidium shows indications of terrace lines.

Group 2. Specimens of this group (figures 8.A-K, 9.A-K) have been described from other localities of Argentina. The glabellar furrows are not visible at this stage. On the other hand, the occipital segment and the

Figure 4. ***Jujuyaspis keideli*** Kobayashi; **A,** Groups 3 meraspid (cephalon-thorax, left) and 1 holaspid (thoracopygon, center) / *Grupos meráspido 3 (céfalo-tórax, izquierda) y holáspido 1 (toracopigidio, centro)*, MLP 30340, X8,6. **B,** Groups 3 meraspid (cephalon-thorax, up) and 1 holaspid (cephalon-thorax, center) / *Grupos meráspido 3 (céfalo-tórax, arriba) y holáspido 1 (céfalo-tórax, centro)*, MLP 30359, X 8; **C,** Group 4 meraspid, axial shield and free cheeks / *Grupo meráspido 4, escudo axial y mejillas libres*, MLP 30277, X7,4. **D,** Group 4 meraspid, axial shield / *Grupo meráspido 4, escudo axial*, MLP 30361, X6,9. **E,** Groups 1 holaspid (cephalon, left) and 4 meraspid (cranidium-thorax, right) / *Grupos holáspido 1 (céfalo, izquierda) y meráspido 4 (cranidio-tórax, derecha)*, MLP 30330, X9. **F-K,** Group 4 meraspid / *Grupo meráspido 4*; **F,** complete specimen (left) and axial shield (right) / *ejemplar completo (izquierda) y escudo axial (derecha)*, MLP 30305, X6,6; **G,** cephalon / *céfalo*, MLP 30268, X10,2; **H,** thoracopygon / *toracopigidio*, MLP 30365, X13,6; **I,** cephalon-thorax / *céfalo-tórax*, MLP 30344, X9,7; **J,** thoracopygon / *toracopigidio*, MLP 30335, X9,2; **K,** thoracopygon / *toracopigidio*, MLP 30362, X8,1.

Figure 5. ***Jujuyaspis keideli*** Kobayashi; scale reconstructions of Groups 3 (A) and 4 (B) meraspid / *reconstrucciones a escala de los grupos meráspidos 3 (A) y 4 (B),* X16,8.

thoracic axial rings of most specimens of this group are smooth, whereas some individuals from Purmamarca retain an occipital spine (or a node) and well-developed thoracic axial nodes (figures 8.K, 9.B, 9.I). As noted by Harrington and Leanza (1957), the degree of expression of the preglabellar field, as well as the outline of the glabella, which is parallel sided or slight tapered forwards, are highly variable features. Similarly, the pleural spines of the 9th thoracic segment show a very variable length. In some specimens, these spines reach three times the total length (sag.) of the pygidium.

Group 3. Here are grouped a few specimens characterized by having a very large exoskeleton, which is in the range of 32-40 mm in sagittal length. The morphology remains similar to that of Group 2, but the convexity is extremely low and the axial and occipital furrows are shallower (figures 8.L-M). This group represents the latest holaspid stage of the species.

Growth and moulting

Growth

In order to show how *Jujuyaspis keideli* increases in size during ontogeny, the sagittal length of the glabella and maximum width have been plotted graphically for meraspid and early holaspid stages (figure 10). The result shows no well-defined instar groupings. The length / width of the glabella is higher during the first meraspid stages (1.75 in Group 1) and later it stabilizes in the range of 1.1-1.3, showing an increasing variability in holaspid degrees. Individual variability in growth rates usually causes instars to overlap in size. An evident overlap in size between meraspid and holaspid stages was identified, since a small holaspid with 12 thoracic segments (specimen MLP 30347, marked with an “x” in figure 10) lies within the size range of the largest meraspides. Another singular case of intraspecific variability is cited above (see Group 4 M).

Moulting clusters

Clusters of well-preserved trilobites have been previously described from many stratigraphic levels throughout the lower and middle Paleozoic (see Speyer and Brett, 1985). According to Speyer and Brett (1982, 1985), some clustered trilobite assemblages reflect gregarious trilobite behavior and,

Figure 6. ***Jujuyaspis keideli*** Kobayashi; **A-N,** Group 1 holaspid / *Grupo holáspido* 1; **A,** cephalon and hypostome / *céfalo e hipostoma,* MLP 30348, X7,6; **B,** free cheek / *mejilla libre,* MLP 30326, X7; **C,** cephalon and fragmentary thorax / *céfalo y tórax fragmentario,* MLP 30285, X9,5; **D,** complete specimens / *ejemplares completos,* MLP 30323, X5; **E,** complete specimen / *ejemplar completo,* MLP 30310, X7; **F,** incomplete carapace / *exoesqueleto incompleto,* MLP 30323, X7,7; **G,** cranidium / *cranidio,* MLP 30358b, X7,2; **H,** cranidium / *cranidio,* MLP 30358a, X10,7; **I,** free cheeks, hypostome and thoracopygon / *mejillas libres, hipostoma y toracopigidio,* MLP 30280, X5,5; **J,** cranidium / *cranidio,* MLP 30306, X7,9; **K,** cephalon and hypostome / *céfalo e hipostoma,* MLP 30352, X6; **L,** cranidium / *cranidio,* MLP 30369, X8,1; **M,** cephalon / *céfalo,* MLP 30307, X7,7; **N,** axial shield / *escudo axial,* MLP 30297, X8,3.

Figure 7. *Jujuyaspis keideli* Kobayashi; reconstruction of Group 1 holaspid / *reconstrucción del Grupo holáspido 1*, X11.

therefore, provide excellent opportunities to evaluate paleoecological and ethological aspects of the species involved.

A trilobite cluster was found in a narrow interval of the upper part of the Purmamarca Shales. This part of the section is characterized by fine grained, pyritiferous, dark sediments, lacking visible sedimentary structures or bioturbation. This sedimentary feature indicates deposition in a low energy, muddy environment below normal wave base. The specimens display a good preservation and no preferred orientation, indicating that current action did not play an important role in their aggregation. Besides, the cluster shows other distinctive features: 1) in contrast to other parts of the section, in which *J. keideli* occurs in association with other olenids and agnostoids, the assemblage is composed exclusively of *J. keideli*; 2) the size range documented from this bed is 7 to 8.5 mm in exoskeleton length (sag.), whereas the ranges noted within other beds of the section are considerably larger; according to the pattern of growth of *Jujuyaspis keideli* described above, the specimens of the cluster fall within the late Group 1 (H); 3) the cluster is composed of densely packed, often overlapping exoskeletal parts which are arranged in different configurations: a) complete specimens with the librigenae slightly displaced backwards, b) axial shields (cranidium + thorax + pygidium) either entire or broken along one or more joints, the latter showing their different parts only slightly displaced, c) isolated pairs of librigenae with, in one case, the corresponding hypostome, and d) thoracopygon; 4) as documented in similar assemblages, some specimens are orientated dorsal shield upwards, whereas others are typically inverted (figure 11).

This assemblage is rather similar to that found on a bedding surface in a limestone concretion in the Alum Shales (Upper Cambrian) at Naersnes, Norway (Henningsmoen, 1957: pl. 31). The latter represents a cluster composed of about 250 tightly arranged early holaspides (4 to 8 mm long) of *Acerocare ecorne* Angelin, partially overlapping each other, with the dorsal shields both upwards and inverted in similar proportions, lacking a preferred orientation in the plane of bedding surface. Characteristically, the specimens are represented by different tagmata in diverse arrangements. Henningsmoen (1957) interpreted them as exuviae shed where they were embedded.

Speyer and Brett (1985) postulated that clustering represents an aspect of trilobite growth and reproductive behavior. In addition, Henningsmoen (1975: 198, fig. 14) proposed some configurations of exoskeleton units as indicative of exuviae (e.g. axial shield; yoked librigenae + rostral plate + hypostome; exoskeleton showing the free cheeks displaced backwards below the axial shield). Taking into account such criteria, we consider that the monospecific, age-sorted clustered assemblage described here may well represent specimens that aggregated together for synchronized exuviation. Since ecdysis of modern marine arthropods is currently related to the organism's reproductive cycle, mass copulation could have followed such metabolic process. As in previously described moult trilobite clusters, no evidence of morphological sexual dimorphism has been identified in the sample.

It is interesting to note the contrast between the assemblages described for *Jujuyaspis keideli* and *Acerocare ecorne*, and the occurrence of clustered specimens of *Parabolina spinulosa* (Wahlenberg) from southern Sweden described by Clarkson *et al.* (1997). In the latter case, individuals are represented by a wide range of sizes and all stages of development, rather than falling within a narrow size range, and

Figure 8. *Jujuyaspis keideli* Kobayashi; **A-K,** Group 2 holaspid / *Grupo holáspido 2*; **A,** cephalon, fragmentary thorax, and pygidium / *céfalo, tórax fragmentario y pigidio*, MLP 30296, X4,6; **B,** cephalon / *céfalo*, MLP 30283, X6,3; **C,** free cheek / *mejilla libre*, MLP 30298, X5,8; **D,** cranidium / *cranidio*, MLP 30337, X7,1; **E,** cranidium / *cranidio*, MLP 30342, X6,7; **F,** free cheek / *mejilla libre*, MLP 30357, X5,4; **G,** cephalon / *céfalo*, MLP 30343, X8,2; **H,** cranidium and fragmentary thorax / *cranidio y tórax fragmentario*, MLP 30316, X4,4; **I,** free cheeks / *mejillas libres*, MLP 30287, X4; **J,** cephalon / *céfalo*, MLP 30308, X5; **K,** cephalon and hypostome / *céfalo e hipostoma*, MLP 30372, X3,9. **L-M,** Group 3 holaspid / *Grupo holáspido 3*; **L,** cephalon / *céfalo*, MLP 30351, X2,9; **M,** cephalon / *céfalo*, MLP 30289, X2,2.

this *Parabolina* assemblage was interpreted as a result of mass mortality due to an influx of toxic or stagnant water.

Probable moulting clusters have been described for the leptoplastine olenid *Ctenopyge* (*Eoctenopyge*) *angusta* Westergård in material from Västergötland, central Sweden (Clarkson *et al.*, 2003). These, however, consist of many instars with few individuals, and do not overlap. We might tentatively suggest some difference between leptoplastine and pelturine moulting behaviour, which needs to be tested by further evidence.

Relationships

Possible suprageneric affinities based on earliest stages of development

Fortey (1974) discussed the phylogenetic implications of early meraspid cranidia within the Olenidae. The meraspid Group 1 of *J. keideli* is similar to the earliest stages of *Leptoplastides salteri* (Callaway) from the Tremadoc of Shropshire (Raw, 1925; Fortey and Owens, 1991), in having seven marginal spines ("Heptacicephalic stage" *sensu* Raw, 1925), a cephalon narrower for its length than in succeeding stages, a glabella narrower than the cheeks, and in lacking evidence of a preglabellar field. Based on these observations, a possible relationship of *Leptoplastides* with the Subfamily Pelturinae is suggested. Early stages of Upper Cambrian pelturines, like *Peltura scarabaeoides* (Wahlenberg, 1821) (Poulsen, 1923; Whittington, 1958; Hu, 1964) and *Acerocare ecorne* Angelin (Hu, 1971), do not seem to have seven marginal spines, so the peculiar arrangement observed in *Jujuyaspis* and *Leptoplastides* may have arisen later in the early Tremadoc.

The adult morphology of the earliest Ordovician *Jujuyaspis* and the Upper Cambrian *Acerocare* (see Henningsmoen, 1957; Hu, 1971) is very similar, suggesting a close affinity between these taxa. Nevertheless, the earliest meraspides of *Jujuyaspis* strongly differ from those of *Acerocare* mainly in having a tapered anterior part of the glabella and smooth cheeks.

Jujuyaspis keideli: *comparison with other species of the genus*

Jujuyaspis keideli clearly differs from *Jujuyaspis angusta* Henningsmoen from the Lower Tremadoc of Norway (Henningsmoen, 1957), because the latter has palpebral lobes relatively far back, opposite S1, and an extremely narrow (tr.) pygidium. It is interesting to note that *J. angusta* possesses some characters that have been identified in early stages of *J. keideli*. According to Henningsmoen (1957), the Norwegian species has a well developed occipital spine, clear indications of a pair of glabellar furrows, and some thorax segments bearing both axial spines and well developed pleural spines. As discussed above, these features are well represented in the late meraspides and early holaspides of *J. keideli*. Since *J. angusta* was described on the basis of a few cranidia about 3 mm in length (Henningsmoen, 1957), these may correspond to similar ontogenetic stages.

Figure 10. Plot of glabellar length versus maximum width of meraspid and early holaspid stages of *Jujuyaspis keideli* / *Representación gráfica de la longitud versus la máxima anchura de la glabela en estadios meráspidos y holáspidos tempranos de* Jujuyaspis keideli.

Jujuyaspis keideli keideli hardly differs from *J. keideli norvegica*, from the Lower Tremadoc of Norway (Henningsmoen, 1957) only in having the palpebral lobes set slightly forwards (Henningsmoen, 1957). As in many specimens of *keideli* described in this paper, the holotype of *norvegica* bears a delicate occipital node (Henningsmoen, 1957: pl. 28, fig. 21; see also Bruton *et al.*, 1982: pl. 1, fig. 16). Occipital nodes have been also described in *Jujuyaspis truncaticonis* Baldis and González and *Jujuyaspis colombiana* Baldis and

Figure 9. ***Jujuyaspis keideli*** Kobayashi; **A-K,** Group 2 holaspid / *Grupo holáspido 2*; **A,** incomplete carapace / *exoesqueleto incompleto*, MLP 30269, X1,9; **B,** axial shield and free cheek / *escudo axial y mejilla libre*, MLP 30303, X4,8; **C,** thoracopygon / *toracopigidio*, MLP 30336, X2,5; **D,** thoracopygon / *toracopigidio*, MLP 30292, X2,5; **E,** axial shield / *escudo axial*, MLP 30272, X5; **F,** thoracopygon / *toracopigidio*, MLP 30328, X3,3; **G,** thoracopygon / *toracopigidio*, MLP 30367, X3,3; **H,** pygidium / *pigidio*, MLP 30291, X5; **I,** cranidium-thorax / *cranidio-tórax*, MLP 30353, X3,6; **J,** fragmentary thorax and pygidium / *tórax fragmentario y pigidio*, MLP 30281, X6,7; **K,** fragmentary thorax and pygidium / *tórax fragmentario y pigidio*, MLP 30331, X3,9.

González, from the Lower Tremadoc of Colombia (*in* Baldis *et al*., 1984). Aceñolaza and Aceñolaza (1992) suggested that *J. truncaticonis* may be a junior synonym of *J. keideli*. Baldis *et al.* (1984) postulated that *J. truncaticonis* is distinguished from *J. keideli* in having a narrower anterior cephalic border, a subtrapezoidal to subconical glabella, a deep occipital furrow, a convex occipital ring bearing a mesial node, axial nodes in the first six thoracic segments, and straighter pleural spines. However as noted above, some of these characters are well represented in meraspid and early holaspid stages of *J. keideli*. In addition, the outlines of the anterior border and the glabella have proved variable, even within a species in other pelturines (Poulsen, 1923; Whittington, 1958; Harrington and Leanza, 1957). Concurring with Aceñolaza and Aceñolaza´s suggestion, *J. truncaticonis* is considered as a junior synonym of *J. keideli*.

Similarly, *Jujuyaspis colombiana* Baldis and González was originally defined on the basis of some characters that are well developed in late meraspides and early holaspides of *J. keideli* (e.g. indications of glabellar furrows; axial nodes on the occipital and thoracic segments) (Baldis *et al*., 1984). According to Baldis *et al.* (1984), *J. colombiana* differs from *J. keideli* by its divergent convex posterior branch of facial suture. Unfortunately, the state of preservation of the type material of *J. colombiana* precludes the adequate evaluation of such a character.

Jujuyaspis keideli closely resembles *Jujuyaspis borealis* Kobayashi, from the lowest Ordovician of North America (Kobayashi, 1955; Winston and Nicholls, 1967; Norford, 1969; Westrop, 1986; Stitt and Miller, 1987; Dean, 1989). The features commonly used to distinguish these species (e.g. dimensions of frontal area, width of fixigenae, outline of pygidium; see Norford, 1969; Westrop, 1986; Stitt and Miller, 1987) are rather variable in *Jujuyaspis keideli*. However, the librigenal border of all holaspid stages of the latter is narrower than that of *J. borealis* (cf. Stitt and Miller, 1987), genae are smooth, and the postaxial part of the pygidium is slightly longer (sag.).

Adults of *Jujuyaspis keideli* also differ from *Jujuyaspis sinensis* Zhou *in* Chen *et al.*, from the lowest Ordovician of China and Korea (Chen *et al.*, 1980; Zhou and Zhang, 1985; Kim and Choi, 2000), in having a contracted cephalic border and a slightly longer (sag.) postaxial part of the pygidium. In addition, cranidia of holaspid stages of *J. keideli* show a straight or rearward arcuate anterior margin.

Figure 11. ***Jujuyaspis keideli*** Kobayashi, partial view of a clustered assemblage of Group 1 holaspides from the Santa Rosita Formation at Purmamarca, northwestern Argentina/ Jujuyaspis keideli *Kobayashi, vista parcial de una asociación compuesta por numerosos ejemplares del Grupo holáspido 1 (Santa Rosita Formation, Purmamarca, noroeste de Argentina).*

Paleoecology

Functional morphology / mode of life

The mode of life of the holaspid stages of *Jujuyaspis* was first referred by Henningsmoen (1957) and Bergström (1973), who considered that the Family Olenidae include predominantly pelagic species. In the context of the morphological types defined by Henningsmoen (1957), Bergström (1973) interpreted *Jujuyaspis* as a vigorous, active swimmer assignable to the "*Peltura* type". On the other hand, Fortey (1974, 1985) demonstrated that most olenids were benthic forms inhabiting a low-oxygen environment, though some species could have been pelagic. Fortey (1985) suggested that *Jujuyaspis* is a possible example of the "*Irvingella* type morphology", typified by the Upper Cambrian genus *Irvingella* Ulrich and Resser in Walcott, 1924. This morphology, with an elongate exoskeleton, wide rachis, large eyes, and posterior thoracic pleurae extended as parallel spines which reach beyond the posterior pygidial margin, is considered as a candidate for pelagic habits (Fortey, 1985). Aceñolaza *et al.* (2001) provided a new evidence in favour of such a habit, showing that *J. keideli* had a visual field wider than that of most benthic olenids. The wide geographic distribution of the genus and its occurrence in different lithologies are also compatible with a non-benthic mode of life (Fortey, 1985).

Since the present study provides information on the morphology of the early ontogenetic stages of *Jujuyaspis keideli*, it is appropriate to discuss the possible adaptive morphology of some of the features described. As noted above, the presence of seven cephalic marginal spines characterizes the smallest meraspid stages (Groups 1 and 2). These long, stout spines pointing in different directions could have favoured the permanence of the animal in the water column, preventing a rapid sinking. Since similar marginal spines have been also described from many planktonic larvae of recent Crustacea, a comparable mode of life can be suggested for these minute meraspides.

Likewise, the degree of development and disposition of the thoracic pleural spines of Group 3 (M) are rather interesting. These meraspides greatly differ from the adults in having long, parallel, laterally splayed out thoracic spines. In small organisms, such structures can represent an adaptation to a floating or swimming mode of life by frictional retardation of sinking in the water column. A comparable arrangement was reported in the miniaturised olenid *Ctenopyge ceciliae* (Clarkson and Ahlberg, 2002). Besides, a very similar pattern was described in meraspid stages of the genus *Selenopeltis* Hawle and Corda, 1847 (Snajdr, 1984). According to Hammann *et al.* (1986), the general aspect of the juveniles of *Selenopeltis* is closely similar to that of planktonic larvae of extant arthropods. We postulate a pelagic mode of life for the meraspid stages of *J. keideli*, a fact that must have facilitated the worldwide distribution of the taxon.

As in adults of *Jujuyaspis*, the holaspid specimens of *Selenopeltis* have posterior thoracic pleurae extended strongly backwards as parallel spines. This hydrodynamic configuration is compatible with active swimming (Hammann *et al.*, 1986). On the other hand, the presence of a hypostome detached from the cephalic doublure (natant condition; Fortey and Owens, 1999) suggests that holaspides of *Jujuyaspis keideli* lived by particle feeding. The adult *Jujuyaspis* could have been a rather versatile nektobenthic animal, capable of both swimming and spending shorter or longer periods of time on the sea floor, feeding as an organic particle processor.

Final remarks

Uppermost Cambrian grey and black shales of Eastern Cordillera are characterized by a varied fauna of agnostoids [e.g. *Lotagnostus* (*Lotagnostus*), *Lotagnostus* (*Semagnostus*), *Lotagnostus* (*Distagnostus*), *Pseudorhaptagnostus* (*Machairagnostus*), *Gymnagnostus*, *Micragnostus*] and olenids (*Parabolina*, *Parabolinella*, *Angelina*, *Plicatolina*, *Beltella*), which represents the lower part of the *Parabolina frequens argentina* Biozone (Tortello, 2003; Tortello and Esteban, 2003). The benthic genera *Parabolinella* and *Plicatolina* were especially adapted to live in deep, oxygen-depleted environments (Fortey, 1985). On the other hand, *Beltella* could have had a nekto-benthic mode of life. The morphology of the latter is characterized by a convex exoskeleton, wide cephalon and rather small pleural areas, suggesting that it could have been able to respond to a further lowering of oxygen in the environment by rapid escape and active swimming (Fortey and Owens, 1989).

The upper part of the *P. frequens argentina* Biozone (Lower Tremadoc) is characterized by the disappearance of some Upper Cambrian taxa [e.g. *L.* (*Lotagnostus*), *L.* (*Semagnostus*), *L.* (*Distagnostus*), *Pseudorhaptagnostus*, *Beltella ulrichi*] and the occurrence of *Jujuyaspis keideli*. As noted above, in Purmamarca *J. keideli* is recorded together with the olenid *Parabolinella argentinensis* Kobayashi, *Angelina hyeronimi* (Kayser), *Bienvillia* sp. and *Plicatolina* sp., and the agnostoid *Micragnostus* sp., *Anglagnostus* sp. and *Gymnagnostus* sp. It is likely that holaspides of *J. keideli* in the communities of the earliest Ordovician of Argentina occupy the same ecological niche as that of *Beltella* in the latest Cambrian.

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The Ordovician system is well represented in northwestern Argentina, and the body and trace fossils are frequently very well-preserved. Many classic studies have been undertaken on this material, such as Harrington and Leanza´s renowned monograph (1957) *Ordovician Trilobites of Argentina.* Yet much of the voluminous literature which was accumulated in recent years remains scattered, and sometimes difficult of access. Accordingly, and just after the 8th International Symposium on the Ordovician (ISOS) in Prague in 1999, Luis Benedetto and his colleagues concieved this new and major work, intended to be a comprehensive synthesis of all available information on the Ordovician palaeontology of Argentina. A formidably strong team was assembled, centred on Córdoba but with experts from other Argentine universities and institutes, and as a result of their hard work and dedication this magnificent publication was ready for the 9th ISOS in San Juan in August 2003. It is a tribute to all the contributors and the editor that all this information could be put together in less than four years, and assembled in so attractive a form.

Ordovician Fossils of Argentina has an appealing green cover, illustrating a ring of different invertebrate fossils set against a south polar projection of Gondwanaland, and so enticing the prospective reader to enquire within. And the contents do not disappoint. Within this book one finds twelve chapters, of which the first five provide the sedimentary, tectonic, palaeogeographical and ecological setting for our understanding of the faunas, and the remaining are essentially systematic treatments of particular fossil groups. There is such a wealth of information here that it would be hard to single out specific points. Ch. 1, by R. Astini, *The Ordovician Proto-Andean Basins* (74 pp., 40 figures) details the history of the various Ordovician depocentres and integrates them into the larger picture of the evolution of western Gondwanaland. Ch. 2, by E.D. Brussa *et al.*, *Biostratigraphy* (16 pp., 4 figures) provides an essential chrono- and biostratigraphical framework for the Argentine Ordovician. Ch. 3, by J.L. Benedetto, *Palaeobiogeography* (38 pp., 7 figures) gives an overall framework and sets out the case for a Laurentian origin for the Precordilleran terrane. In Ch. 4 by T.M. Sánchez *et al.*, *Palaeoecology and global events* (18 pp., 8 figures) there are presented attractive palaeocommunity reconstructions. Some of these are in colour. Ch. 5 by F.L. Cañas and M.G. Carrera (12 pp., 5 plates) describes *Precordilleran reefs*, with particular reference to sponge-microbial associations. There follows the systematic section. Ch. 6 by M.G. Carrera: *Sponges and bryozoans* (30 pp. incl. 9 plates); Ch. 7 by J.L. Benedetto: *Brachiopods* (102 pp. incl. 24 plates); Ch. 8 by T.M. Sánchez: *Bivalves and Rostroconchs* (20 pp. incl. 3 figures and 4 plates); Ch. 9 by B.G. Waisfeld and N.E. Vaccari: *Trilobites* (144 pp. incl. 34 plates); Ch. 10 M.J. Salas: *Ostracods* (28 pp. incl. 8 plates); Ch. 11 by B.A. Toro and E.D. Brussa: *Graptolites* (64 pp. incl. 16 plates, both photographs and drawings) and Ch. 12 by M.G. Mángano and L.A. Buatois: *Trace fossils* (49 pp. incl. 9 plates). The length of the chapter on brachiopods and trilobites reflects the diversity and abundance of these groups, but also the fact that they have already been extensively treated systematically. A brief appendix includes references to other groups such as cephalopods, which are otherwise not covered here, and which points the way for future research. There is also a useful systematic index.

The standards of production are exceptionally high. All the papers without exception are easy to read, and well written in good English, the text figures are clear and explicative. Each chapter has an extensive and comprehensive bibliography. But perhaps the most excellent thing about this book is the exceptionally high quality of the 109 plates. Each photograph has been carefully scanned in to an appropriate size, and the tones match perfectly. The result is that each plate is a pleasure to look at and a work of art in itself, quite apart from its scientific value. This must have been a major undertaking, considering that there are 1885 separate photographs, if I have counted correctly.

In all respects this book is quite outstanding, and will surely become an essential reference for all Ordovician workers, and not just those who specialise on Gondwanan faunas. The editor and his team have given us a work of great appeal and enduring usefulness, and one which no-one interested in the Ordovician should be without. Let us hope that it receives the global attention which it so clearly deserves.

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