

## Freshwater bivalves and their environmental conditions in a Jurassic lacustrine system (Cañadón Asfalto Formation) from Patagonia, Argentina

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**ABSTRACT.** At the moment, two freshwater bivalve species were described for the continental Jurassic of Patagonia: *Diplodon simplex* Morton and *Diplodon matildensis* Morton from La Matilde Formation of the Santa Cruz province. The Cañadón Asfalto Formation located in Chubut province exhibits a high diverse invertebrate fossil fauna preserved mainly in lacustrine facies, which includes clam shrimps, bivalves, gastropods, ostracods and insects. However, few studies have been carried out on freshwater bivalve of this geological unit. In this work, a morphological description of bivalve assemblage and paleoenvironment analysis from the Cañadón Asfalto Formation was performed. Forty samples were collected from three stratigraphic levels at the Cañadón Asfalto locality. These levels are ash fall tuffs rich in glass particles accumulated in a lacustrine system with development of microbial activity. Morphological analyzes of outline and sizes were performed at each level. Our results showing the smallest-sized association of unionids recorded for the Jurassic time with size ranging from 7.6-11.7 mm long and 5.2-7.6 mm high. The environmental influence of pyroclastic falls could have played an important role in the development of the sizes of populations and shells.

*Keywords:* Paleoenvironment, Bivalves, Unionids, Jurassic.

**RESUMEN.** Bivalvos de agua dulce y sus condiciones ambientales en un sistema lacustre del Jurásico (Formación Cañadón Asfalto) de la Patagonia, Argentina. Actualmente se han descrito dos especies de bivalvos de agua dulce para el Jurásico continental de la Patagonia: *Diplodon simplex* Morton y *Diplodon matildensis* Morton de la Formación La Matilde en la provincia de Santa Cruz. La Formación Cañadón Asfalto ubicada en la provincia de Chubut exhibe una fauna fósil de invertebrados muy diversa conservada principalmente en facies lacustres, que incluyen "conchostracos", bivalvos, gasterópodos, ostrácodos e insectos. Sin embargo, se han efectuado pocos estudios sobre los bivalvos representados de esta unidad geológica. En este trabajo se realizó una descripción morfológica de restos de conchillas de bivalvos y el análisis del paleoambiente de la Formación Cañadón Asfalto. Se recolectaron cuarenta muestras de tres niveles estratigráficos en la localidad de Cañadón Asfalto. Estos niveles son tobas de caída de ceniza, ricas en partículas de vidrio acumuladas en un sistema lacustre con desarrollo de actividad microbiana. Se hicieron análisis morfológicos de contorno y tamaños en cada nivel. Nuestros resultados muestran la asociación de unionidos de menor tamaño registrada para el Jurásico, con tamaños que oscilan entre 7,6 y 11,7 mm de largo y entre 5,2 y 7,6 mm de alto. La influencia ambiental de la caída de material piroclástico podría haber jugado un papel importante en el desarrollo de los tamaños de las poblaciones y conchillas.

*Palabras clave:* Paleoambiente, Bivalvos, Uniónidos, Jurásico.

## 1. Introduction

Freshwater mollusks are habitual members of the paleofauna from Triassic-Jurassic continental sequences all over the world; they have been studied in several deposits such as in China (Pan and Sha, 2009), Africa (Van Damme et al., 2015), South America (Frengüelli, 1945; Martínez and Figueiras, 1991; Martínez et al., 1993; Morton and Herbst, 2001), USA (Good, 1993, 2004) and Europe (Hendry et al., 2001; Delvene et al., 2013). However, they are poorly known in South America, and in fact only few species have been described.

In the Jurassic record of Argentina and Uruguay there are few unionid species identified: *Diplodon dasilvai* Martínez and Figueiras, 1991, *Diplodon batoviensis* Martínez and Figueiras, 1991 and *Tacuarembóia caorsii* Martínez, Figueiras and Da Silva, 1993 from the Tacuarembó Formation from Uruguay, *Diplodon simplex* Morton and *Diplodon matildensis* Morton in Morton and Herbst, 2001 from the La Matilde Formation of Argentina, and *Cardinioides lanesae* Damborenea in Damborenea and Lanés, 2007 from Puesto Araya Formation (Neuquén Basin). In addition, *Diplodon esperanzaensis* Camacho, 1957 was described for the Jurassic of Antarctica. Therefore, the Jurassic unionids from South America are characterized by the appearance of *Diplodon*-like species, but the absence of diagnostic characters in most of these species implies that this resemblance can be only superficial (e.g., Martínez et al., 2019 regarding *D. esperanzaensis*).

The Cañadón Asfalto Formation is a sedimentary unit of the homonymous basin; it was defined by Stipanovic et al. (1968), and later reinterpreted by Cabaleri et al. (2010a). It is constituted by two distinct volcano-sedimentary sections (Las Chacritas and Puesto Almada members) (Silva Nieto et al., 2003) corresponding to balance-fill and underfilled lacustrine systems (Cabaleri and Benavente, 2013; Cabaleri et al., 2013). Regarding invertebrate records, the clam shrimps are the most diverse component of aquatic fauna which were described by Tasch and Volkheimer (1970), Vallati (1986), Gallego et al. (2010, 2011) and Monferran et al. (2013, 2016, 2020). Ostracod and insect species were studied mainly by Mussachio (1970, 1995, 2001) and Genise et al. (2002) respectively. Bivalves are also conspicuous components of the paleofauna of the Cañadón Asfalto Formation but were only mentioned by

Martínez et al. (2007), Gallego et al. (2011), and Zacarías et al. (2019). In this sense, the aim of this paper is to describe a new bivalved mollusk assemblage and analyze its paleoenvironmental conditions of the Cañadón Asfalto Formation at the Cañadón Asfalto locality, about 8 km south of the Cerro Cóndor village (middle Chubut River).

## 2. Geological setting

The Jurassic continental sedimentary rocks of Argentina are also present in Patagonia, where the Jurassic basins are associated with intense volcanism and plutonism, which was the result of subduction at the western margin of Gondwana (Spalletti and Franzese, 2007). The Cañadón Asfalto Basin is a rift basin of Middle to Late Jurassic age (Figari and Courtade, 1993; Silva Nieto et al., 2002; Hauser et al., 2017) in the Extra-Andean Patagonia (Chubut province, Fig. 1) and contains the most complete paleontological record of the continental Jurassic of South America. The extensional process that originated this basin was accompanied by the effusion of olivine basalt flows. The Cañadón Asfalto Basin has several isolated sub-basins. The Cerro Cóndor sub-basin is limited by NW oriented faults and occupies the central region of the basin (Fig. 1A) (Cabaleri et al., 2006, 2010a; Silva Nieto et al., 2007). The basement of the sub-basin consists of granitoids of the Mamil Choique Formation, of Carboniferous-Permian age. This unit is unconformably covered by the Lower Jurassic continental fluvio-deltaic deposits sequence of the Las Leoneras Formation (Nakayama, 1973), and underlies Lower-Middle Jurassic volcanites (U-Pb  $172 \pm 2$  Ma, Hauser et al., 2017; K-Ar 173 Ma, Silva Nieto, 2005) of the Lonco Trapial Formation (Lesta and Ferello, 1972), with an unconformity at the basal contact. The Lonco Trapial Formation is then unconformably overlain by the Cañadón Asfalto Formation (Fig. 1B). To the east of the Chubut River, the Cañadón Asfalto Formation occurs in tectonic contact with the Cañadón Calcáreo Formation (Proserpio, 1987) of Berriasian-Hauterivian age (Volkheimer et al., 2009). Continental units of the Chubut Group (Los Adobes and Cerro Barcino formations; Barremian/Cenomanian) cover the Cañadón Asfalto Formation in a low-angle unconformity (Lesta, 1968; Codignotto et al., 1978). In the northern area of the Cerro Cóndor locality (Fig. 1), the Cañadón Asfalto Formation is covered by the Lefipán (Campanian) and Paso del Sapo

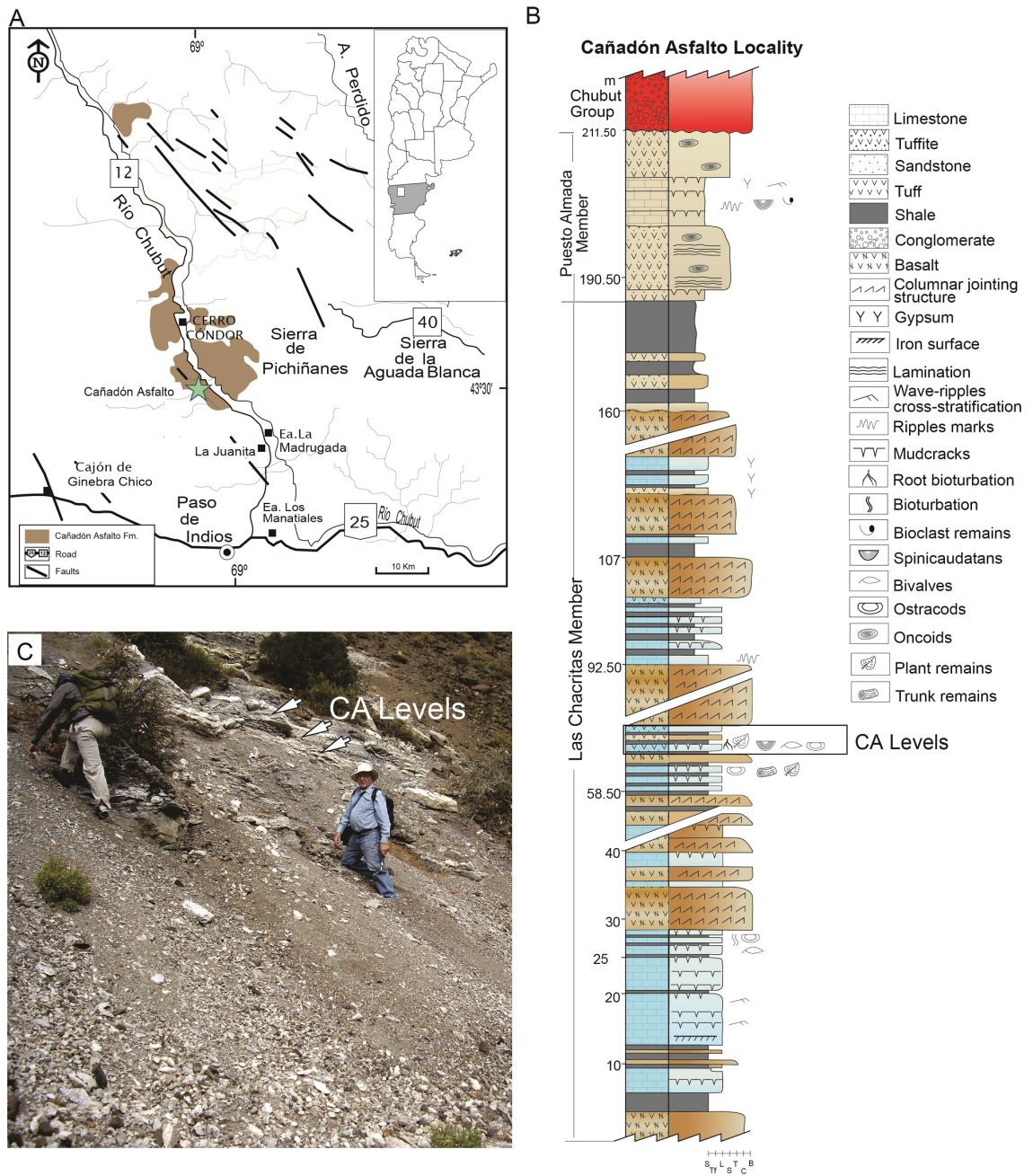


FIG. 1. Cañadón Asfalto locality. **A.** Geological map and location of the Cañadón Asfalto creek in the Cerro Cándor Sub-basin (green star), central Chubut Province. **B.** Stratigraphic section of the Las Chacritas Member (Cañadón Asfalto Formation) in Cañadón Asfalto locality, modified from Cabaleri *et al.* (2010b). CA are the fossiliferous levels. **C.** Field view of the fossiliferous levels at Cañadón Asfalto locality, these are tuffitic layers (*ca.* 5 m thick) interbedded with shale.

formations (Campanian/Maastrichtian) (Lesta and Ferello, 1972).

The Cañadón Asfalto Formation is composed by the Las Chacritas Member (U-Pb age 168±2 Ma, Hauser *et al.*, 2017; K-Ar age 170±4 Ma, Salani, 2007), and the Puesto Almada Member (U-Pb age 160±2 Ma, Hauser *et al.*, 2017; Gallego *et al.*, 2011; K-Ar age 147±3.3 Ma, Cabaleri *et al.*, 2010b).

The type locality of the Las Chacritas Member is the Cerro Cóndor locality (Cerro Cóndor sub-basin). There, the member is composed by sedimentary rocks (limestone and shale) interbedded with pyroclastic deposits and basalt flows (Cabaleri and Armella, 1999). This unit ends with limestones interbedded with shales and tuffaceous levels with clam shrimps, bivalves, ostracods and coal remains. This sedimentary-volcanic sequence is interpreted as a carbonate rich lacustrine system episodically affected by intense volcanic activity developed in the margin of the Cañadón Asfalto rift basin during the synrift stage (Cabaleri *et al.*, 2010a). These authors identified three depositional subenvironments: lacustrine, palustrine, and pedogenic. Freshwater bivalve assemblages hosted

in volcanic and sedimentary rocks of the Cañadón Asfalto locality were found in tuffitic and vitreous tuff levels accumulated in a lacustrine sedimentary system with the development of microbial activity.

The Puesto Almada type section crops out in the Estancia El Torito locality (Cerro Cóndor sub-basin). This member is mainly composed of tuffs and tuffites, interbedded with brown yellowish laminated limestones that contain fish, plant remains, clam shrimps, bivalves, gastropods, ostracods, and caddisfly cases (Cabaleri *et al.*, 2010a). The facies correspond to palustrine-lacustrine and fluvial, alkaline carbonate systems. The main environments are shallow lacustrine (ponds) and palustrine, associated with wetland sub-environments (Table 1).

### 3. Materials and methods

The materials analyzed were collected in the field trip in 2009 and they are housed in the Palaeozoology section of the Palaeontological Collections “Dr. Rafael Herbst” of the Universidad Nacional del Nordeste (Corrientes, Argentina) which are hosted at the CECOAL-CONICET-UNNE, under the collection

**TABLE 1. FACIES AND FACIES ASSOCIATIONS FROM CAÑADÓN ASFALTO FORMATION AT THE CAÑADÓN ASFALTO LOCALITY.**

Locality	Facies/Microfacies	Facies association/ Paleoenvironments	Associated fauna
Cañadón Asfalto	Basalt deposit	Lava flows	-
	Tuffs, tuffites	Shallow water lake	-
	Tuffitic levels and vitreous tuff*	Pyroclastic input.	Mollusk bivalve Spinicaudatans Ostracods
	Black shales	Lacustrine	-
	Sandstones/conglomerates	Fluvial input	-
	Microbialite/Stromatolites	Shallow water lake	-
	Laminated mudstone with subaerial exposure		-
	Peloidal wackestone	Eulittoral with fluvial channel	-
	Siliciclastic wackestone		-
	Intraclastic graisntone	Shallow littoral	-
	Mudstone with mudcracks and rhizobrecciation	Marginal zone, lacustrine/palustrine. Paleosoils	Spinicaudatans
	Nodular mudstone		

Facies and facies associations from Cañadón Asfalto Formation at the Cañadón Asfalto locality, \*Studied level. Modified from Gallego *et al.* (2022).

numbers: CTES-PZ 7374-7378. Additional materials are deposited in the Palaeoinvertebrate Collection of the Museo Paleontológico "Egidio Feruglio", Trelew, Argentina (MPEF-PI1190-1991).

### 3.1. Sedimentological analysis

Field description included the record of thickness, color, and lithology in vertical succession, including lateral variations. The color of the different lithological units was defined according to the Munsell Rock Color Chart from Geological Society of America. Sampling was carried out according to Flügel (2004), with 10 samples collected at a centimeter scale, and five additional samples collected from each of the previously defined microfacies. Samples were sent to the Rock Cutting and Thin Sectioning Laboratory of the Instituto de Geocronología y Geología Isotópica (INGEIS-CONICET-UBA, Buenos Aires) for production of polished slabs and standard thin sections (7.5 cm<sup>2</sup>). The polished slabs were described using a low-magnification stereo microscope (Leica S8 APO). Thin sections were stained with Alizarin Red S to differentiate calcite from dolomite and were observed and photographed using a Zeiss Axioskop 40 petrographic microscope.

### 3.2. Morphological analysis

Bivalves were obtained from forty samples recorded in three fossiliferous levels from the tuffitic facies, labeled as CA1, CA2 and CA3, based upon their stratigraphic position (Fig. 1). Thirty specimens were measurement in CA1 and CA2 levels, and only nine specimens in CA3 because the state of preservation prevented observing outlines. The morphological descriptions of mollusks were carried out according to sizes and outlines. The analysis of the sizes and graphical representations were performed using R software. Specimens were observed and photographed under a Stereoscopic Microscope Olympus SZ51 and a camera CANON EOS 6 at the Centro de Ecología Aplicada del Litoral (CECOAL- CONICET- UNNE) Corrientes, Argentina.

## 4. Results

### 4.1. Analysis of the fossiliferous levels

In the Cañadón Asfalto Creek the Las Chacritas Member is *ca.* 187 m thick and the Puesto Almada

Member is 25 m thick. In this section, the Las Chacritas Member is characterized by thick olivine basalts levels intercalated with volcano-sedimentary sequences. Throughout the sequence, 12 basaltic sections are exposed, with thicknesses ranging from 1 to 15 m (Silva Nieto *et al.*, 2002). The sedimentary sequence is represented by limestones, stromatolitic limestones, tuffites, tuffs, bituminous shale and evaporites, frequently in layers with wave cross-stratification and mudcracks, Chert nodules are common in brown limestone levels (Cabaleri and Armella, 1999; Cabaleri *et al.*, 2005). Tempestite levels with intraclasts and silicified trunks remains are present. In the upper section of the stratigraphic section (Fig. 1B), the limestones are interbedded with conglomerates bearing chert clasts. An evaporite sequence is recorded, where breccias, gypsum, and silica layers were identified, together with algal limestones with gypsum interbeddings. The Las Chacritas Member ends with a bed of 18 m thickness composed of black shales interbedded with tuffs, tuffites, and limestones.

The Puesto Almada Member begins with tuffs and tuffites, with mudcracks and wave-ripple cross-stratification. In these beds clam shrimps carapaces and fragments of reworked bivalves were recognized. The sandstones and conglomerates of the Bardas Coloradas Member of the Los Adobes Formation (Chubut Group, Early Cretaceous) cover in angular unconformity the Jurassic sequence.

### 4.2. Petrographic analysis

The tuffitic levels and vitreous tuff are composed of thin tabular beds of 5 cm thickness, with yellowish brown (10 YR 5/4) and yellowish gray (7 Y 7/2) irregular laminae of 0.5 cm and 1 cm thickness respectively. The stratal surface is wavy, with mudcracks and scattered carbonaceous remains (20%).

The microscopic study reveals that the contacts among laminae are transitional to well defined sharp; the darkest ones, 5,000 to 4,000  $\mu\text{m}$  thick, have vitreous texture with a matrix composed of fine vitreous material, altered to clay minerals, and microcrystalline silica (Fig. 2A-B-D). The vitroclasts correspond to subparallel glass shards (Fig. 2B), colorless (5%), 1,120  $\mu\text{m}$  in length, and dark reddish brown (<1%) of 1,680  $\mu\text{m}$  in length. A lesser amount (1%) of fine sand size (250-125  $\mu\text{m}$ ) crystals of quartz, potassium feldspar, plagioclase crystals replaced by calcite, and biotite replaced by iron oxides was observed.

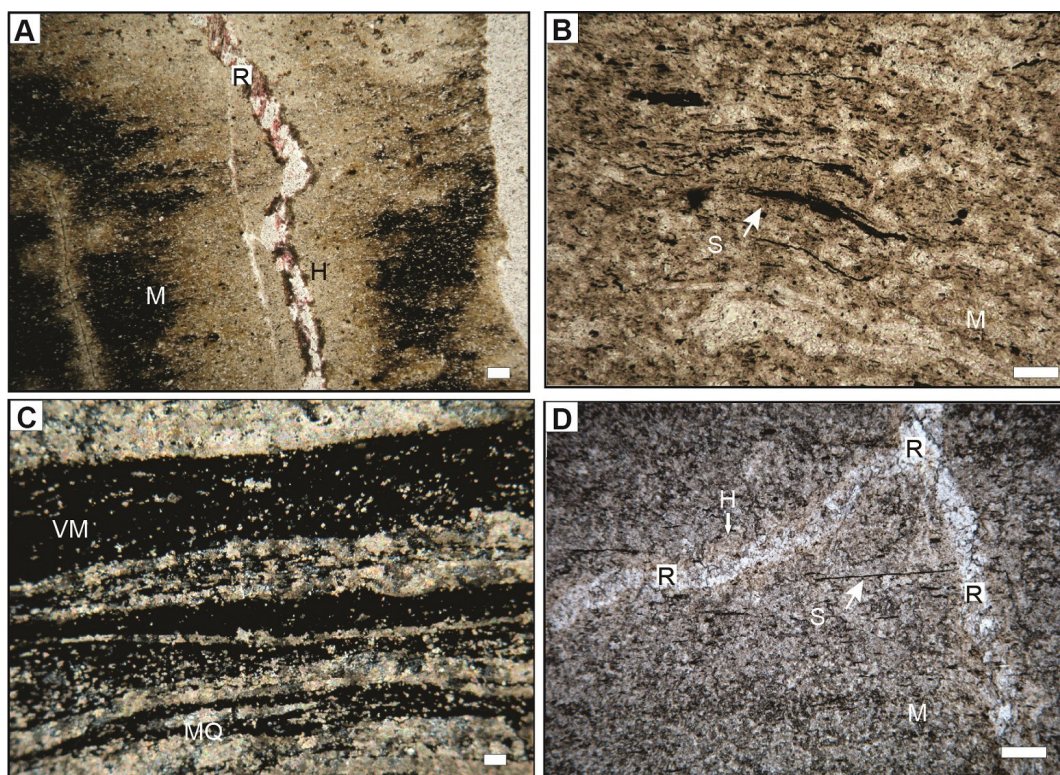


FIG. 2. Tuffitic levels and vitreous tuff microphotographies. Sample CA2: **A**. Vitreous matrix (**M**) altered to clay minerals, root cavity filled with micrite and silica (**R**), bleached halo (**H**) of microcrystalline silica. Sample CA3: **B**. Subparallel glass shard (**S**), some of them are dark reddish brown, vitreous matrix with clay minerals (**M**). **C**. Intercalations of vitreous matrix (**VM**) and sparite with microcrystalline quartz (**MQ**). Sample CA1: **D**. Roots (**R**) filled with microcrystalline silica, with discolored micrite halo (**H**) around them. Microcrystalline silica matrix (**M**) with glass shard (**S**). Bar scale: 2 mm.

Small remains (<1%) of thin unidentified shell were recognized. The thinnest laminae (1,000  $\mu\text{m}$  thick) are of tuffitic or sparitic composition (Fig. 2C). Tuffitic laminae have a matrix with crystalloclasts (<1%) of very fine sand size (125-62  $\mu\text{m}$ ). The vitroclasts are more abundant (15%), composed of glass shards, 1,150  $\mu\text{m}$  long by 225  $\mu\text{m}$  thick (10%) (Fig. 2D), bent and reworked. In addition, there are highly altered pumice fragments (5%), replaced by microsparite and microcrystalline silica. Elongated (1.5 to 2 cm) and circular (0.57 cm in diameter) cavities filled with amorphous silica, microcrystalline quartz and micrite were observed; together with elongated cavities (Fig. 2A, D) (0.5 cm thick and 1.5 cm long) filled with quartz and clay minerals. Associated with these filled cavities, other smaller ones (0.038 cm thick and 0.5 cm long) with undistinguished filling were recorded. These structures are surrounded by a bleached halo in the matrix (Fig. 2A, D).

Fractured bioclasts (2%) of shell remains and scarce (<1%) opaque iron oxide was observed.

**Interpretation:** The well sorted vitroclasts and the dusty vitreous matrix indicates that the region was affected by ash fall. The elongated cavities described correspond to plant root systems (Alonso-Zarza and Wright, 2010; Košir, 2004), and the bleached areas of siliceous and micritic composition surrounding these radicular structures are interpreted as rizohaloes, indicating the zone of activity of the roots (Kraus and Hasiotis, 2006) with impoverishment of some element of the matrix (*e.g.*, iron or manganese) and the disintegration of organic matter by bacterial activity (Bullock *et al.*, 1985). The fragments of shells belong to bivalve and clam shrimp remains. The reworked particles of the tuffitic layer evidence movement of the water film. The mudcracks record desiccation episodes in a shallow subaqueous pond type environment affected by pedogenetic processes.

### 4.3. Bivalve assemblages

The fossil remains recovered from the vitreous tuff and tuffitic levels were mostly bivalves (80%) and clam shrimps (20%). Regarding the mode of preservation, this assemblage is remarkable for its preservation as internal molds by silicification (levels CA1 and CA2) and less commonly imprints and replacement (level CA3) (Fig. 3). The molds

were arranged parallel to the bedding planes in cross section, described as concordant according to Kidwell *et al.* (1986). In two-dimensional view on the bedding-plane, the shell accumulations can be described as a pavement (Kidwell *et al.*, 1986). Some molds show a low degree of superficial fragmentation.

The specimens are small-sized, length is between 7.6 and 11.7 mm and height between 5.2 and 7.6 mm (height/length ratio 0.56-0.88). The anterior margin

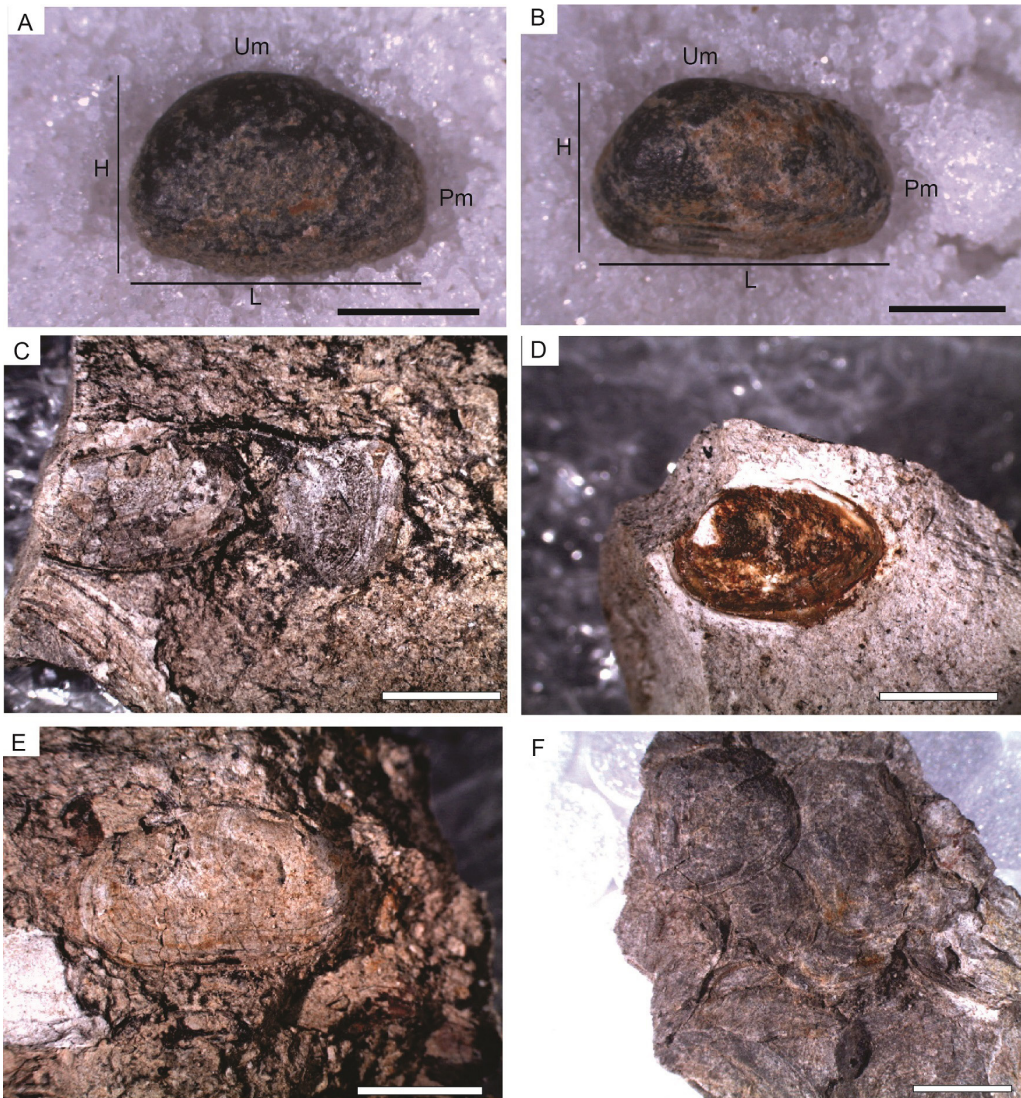


FIG. 3. Fossil bivalves from Cañadón Asfalto locality. **A.** Internal mold from left valve of the Morphotype 1 in lateral view from CA1 level (MPEF-PI1190). **B.** Internal mold from left valve of the Morphotype 2 in lateral view from CA1 level (MPEF-PI1190). **C-E.** Replacement of the shell in CA3 level (MPEF-PI1191). **F.** Molds from CA2 level (MPEF-PI1190). **Um:** umbo; **Pm:** posterior margin; **H:** height; **L:** length. Bar scale=5 mm.

is rounded, the posterior one obtusely pointed; the ventral margin is straight or slightly concave, the dorsal one nearly straight or slightly arched. The umbo cannot be distinguished in most specimens because of the type of preservation; when they are visible, they are situated at about ¼ of the shell length from the anterior end, and do not protrude from the dorsal margin. The shape resembles that of modern unionids; however, the absence of distinctive characters, such as hinges, sculpture, or muscle impressions, prevents a formal determination. At least two morphotypes has been recognized based on shape and height/length (H/L) variation. Morphotype 1 (M1) has suboval or subcircular-subtriangular outline with a convex ventral margin, the anterior margin being rounded and the posterior one with a marked angle (Fig. 3A). Morphotype 2 (M2) is transversely elliptical, with a slightly straight dorsal margin and sharp anterior margin (Fig. 3B).

Thirty specimens were analyzed in CA1 and CA2 levels, and nine specimens in CA3 due to the bad preservation, which prevents recognizing outlines. In table 2 and figure 4 the differences and similarities among the assemblages of the three levels are shown (supplementary data, Appendix 1). The smallest specimen is 6.9 mm long and 5.4 mm high and the larger specimen is 11.7 mm long and 6.5 mm high. We calculated the Shapiro-Wilk normality test for length in each bivalve levels (Table 2), and this analysis evidence that the three levels have a normal distribution ( $p > 0.05$ ). The size-frequency histogram based on length exhibits a mode at 8.5-9 mm in CA1 and 9.5-10 mm in CA2, while the two peaks at CA3 level is unreliable due

to the low number of individuals (Fig. 4A-C). The size-frequency histogram based on height exhibits a mode at 6-6.5 mm in CA1, 6-7 mm in CA2, and 6-6.5 mm in CA3 (Fig. 4D-F).

ANOVA analysis evidence that there are differences between mean length of the three levels (supplementary data, Appendix 2). CA2 and CA3 assemblages are similar in size and different to CA1, suggesting probably different environment conditions (Fig. 5A). Additionally, similar results are obtained for H/L ratio from three levels. CA1 shows a wider range of the H/L ratio than CA2 and CA3 (Fig. 5B). However, comparisons with the last assemblage are not reliable due to the sample size (Appendix 2). Finally, scatterplots show height-length proportion for the three levels (Fig. 5C).

### 5. Discussion

Previous records of bivalves from the Cañadón Asfalto Formation refer mainly to indeterminate taxa related to *Diplodon* (Martínez et al., 2007; Gallego et al., 2011). In fact, unionid characters such as inner nacreous shell layer, characteristic umbonal sculptures and muscular scars are not visible in the fossil bivalves from the Cañadón Asfalto Formation, and as a result, a proper classification is difficult. Based on the fossil records of Jurassic unionids and the external appearance of the bivalves from CA levels, we could be related to Unionida like *Diplodon*, *Unio* or *Cuneopsis* by their shape; particularly it resembles *Diplodon matildensis* from the La Matilde Formation (Morton and Herbst, 2001). The recognition of morphotypes in CA levels

TABLE 2. MEASUREMENTS (IN MM) OF BIVALVE SHELLS FROM THE CAÑADÓN ASFALTO FORMATION.

		Length	Height	Inflation	Convexity	H/L	Shapiro-Wilk (Length)
Level CA1	Min	6.9	5.2	4	2	0.59	p=0.7887
	Max	10.9	7	5.4	2.7	0.88	
	Media	8.7	6.28	4.56	2.25	0.73	
Level CA2	Min	7.6	5.3	3.7	-	0.56	p=0.5369
	Max	11.7	7.6	5.5	-	0.84	
	Media	9.54	6.58	4.81	-	0.69	
Level CA3	Min	8.6	5.6	4.1	-	0.57	p=0.8621
	Max	11.5	7.4	5.3	-	0.72	
	Media	9.88	6.42	4.86	-	0.65	



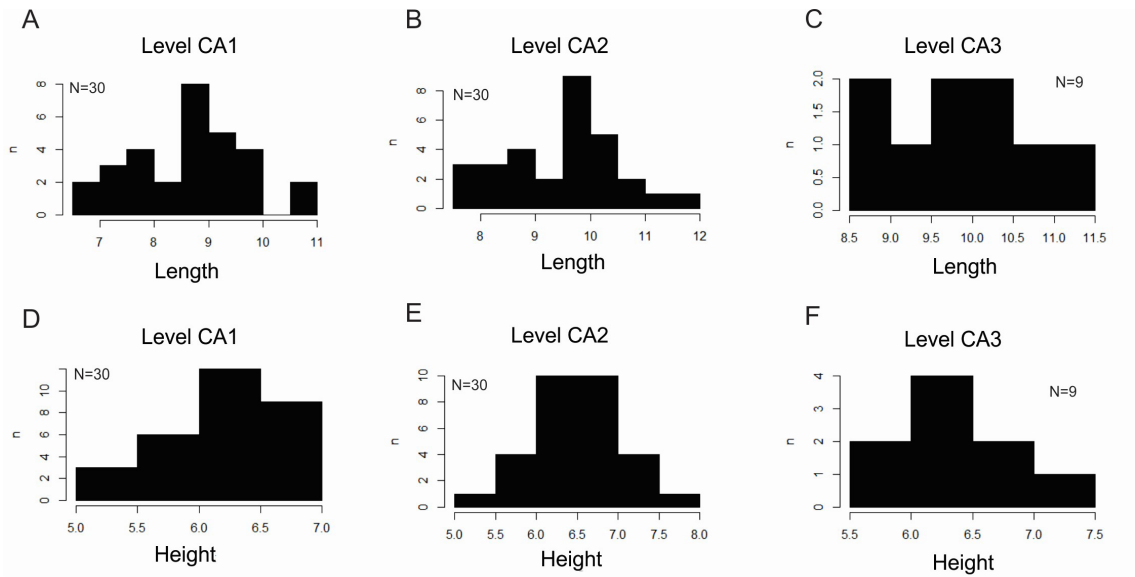


FIG. 4. Size-frequency distribution of length (A-C) and height (D-F) ratios from Cañadón Asfalto locality, using R program.

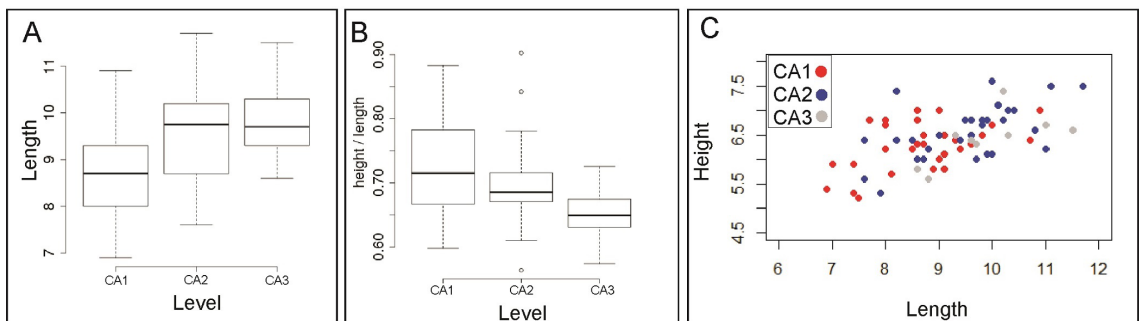


FIG. 5. Box plot illustrating significant difference between length median (A) and Height/length ratio (B), and Scatter diagrams of Height/length ratio (C) from Cañadón Asfalto locality, using R program.

indicate that this species is morphologically variable as it happens in several freshwater bivalve species like *Cuneopsis johannisboehmi* Frech, 1911 (Pan and Sha, 2009). Anyhow, our identification of the specimens are shape and contextual based, and new specimens with better preservation are necessary for a safer procedure.

### 5.1. Palaeoenvironment and palaeoecology

Facies associations at the Cañadón Asfalto locality reflect a sedimentary depositional process in a lacustrine system intermittently affected by volcanic episodes (Cabaleri *et al.*, 2010a) (Table 1).

An autochthonous benthic fauna was settled in the water body where unionids were the main component. The presence of clam shrimps provides additional information on the palaeoenvironment. They have a specialized life cycle that is adapted to life in ephemeral pools and live within a temperature range from 13 to 25 °C with pH conditions from neutral to alkaline (Tasch, 1969; Webb, 1979; Frank, 1988). Unionids are also good environmental indicators, and their size and shape allow reconstructing environmental conditions. In general, the optimal unionid ecological habitat comprises clean and shallow water, pH slightly >7, perennial aquatic habitat, and stable substrate (Good, 2004). The relationship between morphotype

and habitat has been studied in unionids for over 100 years (Zieritz and Aldridge, 2009). They are one of the most significant members of benthic freshwater systems, notable for their ecophenotypic plasticity (Cummins, 1994). Hinch *et al.* (1986) observed shells of the same species to be more elongated in sand than in mud. On the other hand, the shell elongation and shape of the dorso-posterior area were associated with the different hydrological characters of the habitat, where shell thickness generally increases as the water speed increases, and in consequence fluvial unionids have thicker shells than lacustrine ones (Ball, 1922; Eager, 1948; Tevesz and Carter, 1980; Burkey, 1983; Good, 2004; Zieritz and Aldridge, 2009).

In Cañadón Asfalto locality, the abundant record of unionid specimens confirms that the environmental conditions were favorable for the development of their populations and the distinction of morphotypes indicates ecophenotypic plasticity. However, the ranges in the shell size of the assemblages from the three fossiliferous levels suggest that the environment was not always favorable, and some individuals died before reaching the maximum or medium sizes. According to the quantitative analysis, in level CA1 the bivalve assemblage shows more small-sized exemplars, indicating probably unfavorable conditions than CA2 and CA3 assemblages. The sedimentary analysis records periods of stability in the lacustrine system (with the development of microbial activity) and volcanic episodes with ash fall that was unfavorable to the development of the fauna. Ash influence in aquatic environments and its consequences (mainly abundance and size) on benthic organisms, including bivalves, has been proven both experimentally (*e.g.*, Salas-Yanquin *et al.*, 2018) and descriptively (*e.g.*, Brzezinski and Holton, 1983) in recent settings, and hypothesized for the fossil record (*e.g.*, Good, 2004; Maguire *et al.*, 2016). Volcanic ash contributed to the alkalinity of water through hydration and alteration of silicic volcanic glass, which is highly active (Hay, 1966; Jones, 1969; Sheppard and Gude, 1969). In addition, the poor preservation of the shell reflects the general conditions and water chemistry of these environments, which were heavily influenced by volcanic processes. Frequent ash deposition and alteration of volcanic glass particles locally created an acidic environment within the alkaline lake, which led to early diagenetic formation of authigenic alumino-silicate minerals, ferruginous internal moulds, dissolution of the

carbonate shell and silicification of shells (Fürsich and Pan, 2016).

Table 3 shows unionid species recorded from fluvial deposits or sandy substrates in different Jurassic basins, where they are mainly large, more than 30 mm in length. North America, Europe and Africa contain larger forms compared to China, Antarctica, and South America species. *Tacuarembioia caorsii* from Uruguay is the only giant species from South America; the unionids from Argentina are characterized by small forms, less than 15 mm in length (Cañadón Asfalto and La Matilde formations). *Cardinoides lanesae* appears in lagoonal facies with frequent changes in salinity, suggested by a trapezoidal globose shell with posterior umbonal carina and a truncated posterior margin (Damborenea and Lanés, 2007). Species from Jurassic and Lower Cretaceous of northeastern China show frequently small sizes (*ca.* 10 mm) recorded in lacustrine deposits (Fürsich and Pan, 2016). *Cuneopsis johannisboehmi* shows a wide range of sizes (15-68 mm long) where the smallest specimens are 15 mm long and 9.5 mm high. Therefore, the bivalve freshwater fauna from Patagonia described here show the smallest-sized association of unionids recorded for the Jurassic time.

Finally, according to preservation mode remarks, bivalve populations died and accumulated in the same place where they lived in the lake. Transport is not evidenced here; the remains do not have preferential orientation or wear. However, time averaging is considered because these environments possess low sedimentation rates, subsequently generating accumulation of specimens remains (see Kidwell and Bosence, 1991). Thus, the characteristics of the three assemblages suggest an accumulation of mixed populations classified as within-habitat time-averaged assemblage (Kidwell and Bosence, 1991).

## 6. Conclusion

Bivalve specimens are broadly similar to modern unionids; however, the absence of distinctive characters such as hinges, sculpture or muscle impressions, prevents a formal determination. Probably, the bivalves from Cañadón Asfalto Formation could be related to unionids like *Diplodon*, *Unio* or *Cuneopsis*, resembling particularly to *Diplodon matildensis* from the La Matilde Formation of the Santa Cruz province.

A characteristic of these assemblages is the small size of the specimens compared to other

TABLE 3. EXAMPLES OF FRESHWATER BIVALVE RECORDS FROM THE JURASSIC OF NORTH AMERICA, EUROPE, AFRICA, CHINA, SOUTH AMERICA AND ANTARCTICA.

	Length (mm)	Palaeoenvironment	Age/Stratigraphic unit
<b>North America</b>			
<i>Vetulonaia faberi</i> Holt, 1942	55	Fluvial channels and floodplain ponds	Late Jurassic/Morrison Formation
<i>Vetulonaia whitei</i> Branson, 1935	50	Fluvial channels and in floodplain ponds	Late Jurassic/Morrison Formation
<i>Hadrodon lateralis</i> Yen, 1952	67	Fluvial channels and floodplain ponds	Late Jurassic/Morrison Formation
<i>Unio felchii</i> White, 1886	80	Fluvial channels and floodplain ponds	Late Jurassic/Morrison Formation
<i>Unio subspatulatus</i> Meek and Hayden, 1858	70		Jurassic/Judith River Formation
<b>Europe</b>			
<i>Margaritifera cf. valdensis</i> (Mantell, 1844)	81	Brackish	Late Jurassic/Villar del Arzobispo Formation (Spain)
<i>Mujanaia abeuensis</i> Delvene <i>et al.</i> , 2016	69	Wetland	Late Jurassic/Vega Formation (Spain)
' <i>Unio</i> ' <i>asturianus</i> Delvene <i>et al.</i> , 2016	55	Deltaic system	Late Jurassic/Lastres Formation (Spain)
<i>Margaritifera?</i> <i>Lagriega</i> Delvene <i>et al.</i> , 2016	107	Alluvial channel	Late Jurassic/Terenes Formation (Spain)
<i>Mezounio zverkovi</i> Zakharov <i>et al.</i> , 2020	60	Shallow-water	Middle Jurassic/Izhma river basin (Russia)
<i>Unio andersoni</i> Hudson, 1963	¿	Brackish	Middle Jurassic/Lealt Shale Formation (Scotland)
<b>Africa</b>			
<i>Unionelloides bellalensis</i> Van Damme and Bogan (Van Damme <i>et al.</i> , 2015)	76	Fluvial deposits	Middle to Late Jurassic/Irhazer Group
<i>Afrohyrioides jowikolensis</i> (Newton, 1909)	47	Fluvial deposits	Middle to Late Jurassic/Irhazer Group
<i>Saharella tedreftensis</i> (Mongin, 1963)	70	?Fluvial deposit	Middle to Late Jurassic/Irhazer Group
<i>Tuaregunio agadesensis</i> (Mongin, 1963)	68	?Fluvial deposit	Middle to Late Jurassic/Irhazer Group
<i>Tameselloides lithoides</i> Van Damme and Bogan (Van Damme <i>et al.</i> , 2015)	30	?Fluvial deposit	Middle to Late Jurassic/Irhazer Group
<i>Tamesnella amatouensis</i> (Newton, 1909)	32	?Fluvial deposit	Middle to Late Jurassic/Irhazer Group
<i>Tegulaedon humei</i> (Newton, 1909)	75	?Fluvial deposit	Middle to Late Jurassic/Irhazer Group
<i>Paraheudeana soudanensis</i> Van Damme and Bogan (Van Damme <i>et al.</i> , 2015)	121	Lentic environment	Middle to Late Jurassic/Irhazer Group-Nubian 'Sandstone' complex
<i>Margaritifera crosthwaitei</i> (Newton, 1909)	47	?Fluvial deposit	Late Jurassic (Tithonian?)/Nubian 'Sandstone' complex
<i>Coactunio iguallalensis</i> (Mongin, 1963)	110	?Fluvial deposit	Middle to Late Jurassic/Irhazer Group
<b>China</b>			
<i>Cuneopsis johannisboehmi</i> (Frech, 1911)	40	Fluvial deposit	Middle Jurassic/lower member of the Nadang Formation
<i>Potomida</i> sp.	35	Fluvial deposit	Middle Jurassic/lower member of the Nadang Formation
<i>Margaritifera cf. mengyinensis</i> Grabau, 1923	50	Fluvial deposit	Middle Jurassic/lower member of the Nadang Formation
<i>Ferganoconcha sibirica</i> Tschernyshev (Jiang, 2006)	13	Lacustrine	Jurassic Daohugou Fossil Beds
<i>Yananconcha zaoyuanensis</i> Yu and Zhang 1980	20	Lacustrine	Middle Jurassic/Yungang Formation

table 3 continued.

	Length (mm)	Palaeoenvironment	Age/Stratigraphic unit
<b>South America</b>			
<i>Tacuaemboia caorsii</i> Martínez, Figueiras y da Silva, 1993	310	Fluvial deposits	Late Triassic-Late Jurassic/Tacuaembó Formation
<i>Diplodon dasilvai</i> Martínez and Figueiras, 1991	34.5	?Fluvial deposits	Late Triassic-Late Jurassic/Tacuaembó Formation
<i>Diplodon batoviensis</i> Martínez and Figueiras, 1991	32.4	?Fluvial deposits	Late Triassic-Late Jurassic/Tacuaembó Formation
<i>Diplodon simplex</i> Morton (Morton and Herbts 2001)	11.8	Lentic environment	Middle Jurassic/La Matilde Formation
<i>Diplodon matildensis</i> Morton (Morton and Herbts, 2001)	9.27	Lentic environment	Middle Jurassic/La Matilde Formation
? <i>Diplodon</i> sp.	10	Lentic environment	Middle Jurassic/Cañadón Asflato Formation
<b>Antarctica</b>			
<i>Diplodon esperanzaensis</i> Camacho, 1957	38	Lentic environment	Jurassic/Lower Member of the Mount Flora Formation

In most cases the length variable is obtained from the holotypes (extracted from Martínez and Figueiras, 1991; Jingshan *et al.*, 1993; Watters, 2001; Morton and Herbst, 2001; Good, 2004; Pan and Sha, 2009; Van Damme *et al.*, 2015; Delvene *et al.*, 2016).

freshwater bivalve assemblages from Jurassic times, with size ranging from 7.6-11.7 mm long and 5.2-7.6 mm high. In the CA1 fossiliferous level the bivalve assemblage is composed by a higher proportion of small individuals than levels CA2 and CA3, likely indicating probably different environmental conditions. The three assemblages studied represent mixed populations and our results suggest that the environmental influence of pyroclastic falls played an important role in the size of populations and shells.

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## Appendix 1

CA1 LEVEL					
N	Length	Height	Inflation	Convexity	H/L
1	7.4	5.3	4.4	2.2	0.72
2	9.8	6.5	4.9	2.4	0.663
3	8	6.2	4.6	2.3	0.775
4	9	7	4.2	2.1	0.778
5	9	6	4.5	2.2	0.667
6	8.6	7	4.4	2.2	0.814
7	6.9	5.4	4	2	0.783
8	8.7	6.3	4.3	2.2	0.724
9	10	6.7	4.8	2.4	0.67
10	9.6	6.8	4.9	2.4	0.708
11	8.6	6.3	4.3	2.1	0.733
12	9.1	6.1	4.5	2.2	0.670
13	10.9	7	5.4	2.7	0.642
14	10.7	6.4	5	2.5	0.598
15	9.4	6.2	4.6	2.3	0.660
16	8.6	6.8	4.4	2.2	0.791
17	9.1	5.8	4.7	2.3	0.637
18	8.1	5.7	4.5	2.2	0.704
19	9.1	6.5	4.6	2.3	0.714
20	8.7	6.5	4.9	2.4	0.747
21	8	6.8	4.4	2.2	0.85
22	9.6	6.3	4.3	2.1	0.656
23	8.9	5.8	4.9	2.4	0.652
24	8.5	6.2	4.7	2.3	0.729
25	7.5	5.2	4.1	2	0.693
26	9.3	6.4	4.5	2.2	0.688
27	7.7	6.8	4.2	2.1	0.883
28	7	5.9	4.3	2.1	0.843
29	8	6.7	4.8	2.4	0.838
30	7.4	5.9	4.7	2.3	0.797

0.73

**CA2 LEVEL**

N	Length	Height	Inflation	Convexity	H/L	LEVEL 50				
						Length	Height	Inflation	Convexity	
1	10.4	7	5.4	2.7	0.673					
2	11.1	7.5	4.9-4.4	0	0.676	<b>Min</b>	7.6	5.3	3.7	-
3	11.7	7.5	5.5	2.7	0.641	<b>Max</b>	11.7	7.6	5.5	-
4	7.9	5.3	4.6	2.3	0.671	<b>Media</b>	9.54	6.58	4.81	-
5	8.5	6.4	4.8-4.4	2.2	0.753					
6	8.2	6.4	5	0	0.780					
7	10	6.1	4.9	2.4	0.61					
8	10.3	7	5.2-4.2	0	0.680					
9	10	7.6	5.3	0	0.76					
10	8.2	7.4	4	2	0.902					
11	9.6	6.8	5.5	0	0.708					
12	9.4	6.4	5	2.5	0.681					
13	8.8	6.2	4.6	2.3	0.705					
14	9.7	6	4.8	2.4	0.619					
15	9.5	6.8	4.9	2.4	0.716					
16	10.8	6.6	5.2	0	0.611					
17	9.6	6.5	5	0	0.677					
18	7.6	6.4	4.3	0	0.842					
19	10.1	7.1	5.3	0	0.703					
20	9.8	6.8	4.4	0	0.694					
21	9.9	6.8	5.3	0	0.687					
22	10.2	6.8	5	0	0.667					
23	9.9	6.1	4.7	0	0.616					
24	9.8	6.7	5	0	0.684					
25	7.6	5.6	4.5	0	0.737					
26	10.3	7	4.6	0	0.680					
27	9	6.5	4.3	0	0.722					
28	11	6.2	3.7	0	0.564					
29	8.7	6	4.8	0	0.690					
30	8.6	6	4.3	0	0.698					
					0.695					

**CA3 LEVEL**

N	Length	Height	Inflation	H/L	LEVEL 51				
					Length	Height	Inflation	Convexity	
1	11.5	6.6	5.1	0.574					
2	11	6.7	5.3	0.609	<b>Min</b>	8.6	5.6	4.1	-
3	9.6	6.4	5	0.667	<b>Max</b>	11.5	7.4	5.3	-
4	10.3	6.5	5.1	0.631	<b>Media</b>	9.88	6.42	4.86	-
5	8.6	5.8	4.5	0.674					
6	9.3	6.5	5	0.699					
7	10.2	7.4	5	0.725					
8	9.7	6.3	4.1	0.649					
9	8.8	5.6	4.7	0.636					
					0.652				

## Appendix 2

1. Normality tests were applied regarding length and height of the bivalves from each level.

**a) Shapiro-Wilk test:** The null hypothesis for this test is that the data are normally distributed. The Prob <W value listed in the output is the p-value. We chosen 0.05 as alpha level and the p-value is less than 0.05, then the null hypothesis that the data are normally distributed is rejected (Royston, 1992). In this case, these results show for all levels  $p > 0.05$  for the length variable, indicating a normal distribution (Table 1). However, in CA2 level doesn't show H/L normal distribution.

**TABLE 1. SHAPIRO-WILK TESTS IN THE DIFFERENT POPULATIONS OF BIVALVES FROM CAÑADÓN ASFALTO LOCALITY.**

Levels	Length		H/L	
	Shapiro-Wilk	p(normal)	Shapiro-Wilk	p(normal)
CA1	0.9787	0.7887	0.96016	0.3128
CA2	0.9699	0.5369	0.91617	0.02136
CA3	0.9664	0.8621	0.99463	0.9996

**b) Qq-plots (Fig.1):** a Q-Q (quartile-quartile) plot is a probability plot, which is a graphical method for comparing two probability distributions by plotting their quantiles against each other (Wilk and Gnanadesikan, 1968).

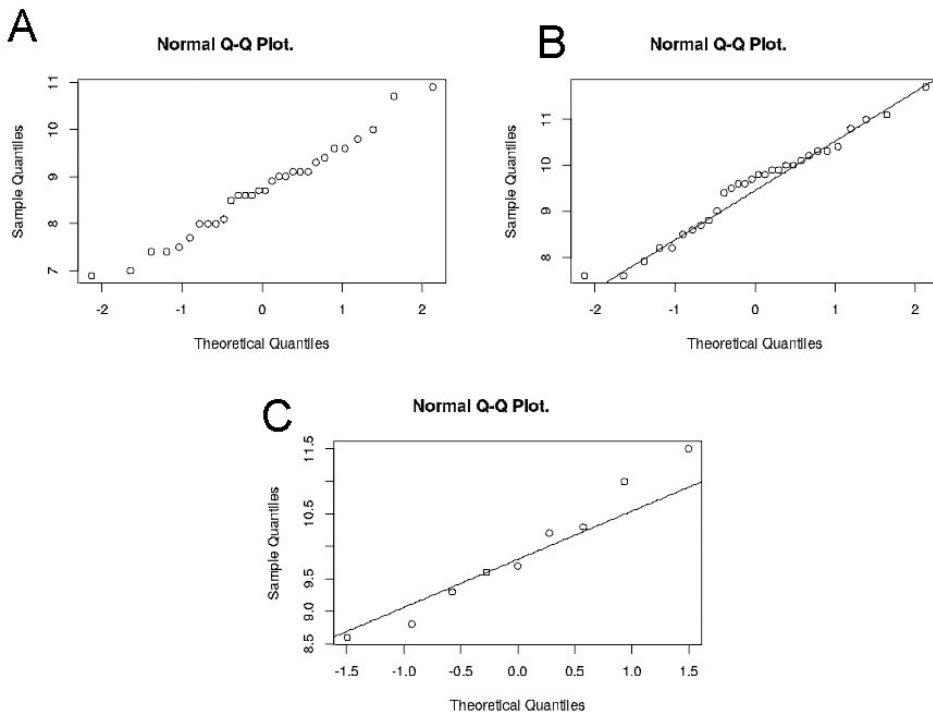


Fig. 1. Qq-plots results. **A.** level CA1. **B.** level CA2. **C.** level CA3.

2. We compared length and height between levels through the Kruskal-Wallis test and ANOVA. Kruskal-Wallis results show that there is a significant difference between sample length medians and H/L relationship ( $p > 0.05$ ). ANOVA results indicate the same results of length medians relationship (Table 2).

**TABLE 2. RESULTS FROM KRUSKAL-WALLIS TEST AND ANOVA ANALYSIS.**

Variables	Kruskal-Wallis		ANOVA
	H (chi <sup>2</sup> )	p-value	p-value
Length	12.45	0.001961	0.001367
H/L	8.4677	0.0145	X

3. Finally, we evaluated if the data size is enough for the comparison of means. We have compared between levels, and our results show that in 95% of cases the size data appropriate have to be  $n=32$ . Therefore, as CA3 level has only 9 specimens we must be careful with comparisons with this level.

**Script applied in R program:**

**Shapiro-Wilk test:**

Length:

```
> shapiro.test(lvlCA1_length)
> shapiro.test(lvlCA2_length)
> shapiro.test(lvlCA3_length)
```

H/L:

```
> shapiro.test(lvlCA1_ratioHL)
> shapiro.test(lvlCA2_ratioHL)
> shapiro.test(lvlCA3_ratioHL)
```

Kruskal-Wallis test:

```
> kruskal.test(length~Level, data=bivalve)
> kruskal.test(ratioHL~Level, data=bivalve)
```

**ANOVA:**

Length:

```
mod2 <- aov(Length~Level, data=bivalve)
anova(mod2)
```

```
>anova(mod2)
```

Analysis of Variance Table

Response: Length

Df Sum Sq Mean Sq F value Pr(>F)

Level2 15.0037.50177.3004 0.001367 \*\*

Residuals 66 67.8201.0276

contrast analysis

```
>TukeyHSD(mod2)
```

Tukey multiple comparisons of means

95% family-wise confidence level

```
Fit: aov(formula=Length ~ Level, data=bivalve)
```

```
$Level
diffwruwr p adj
50-43 0.83333330.2057734 1.460893 0.0061997
51-43 1.18222220.2584790 2.105965 0.0086463
51-50 0.3488889 -0.5748543 1.272632 0.6387172
```

### Comparison between data size:

```
alfa<- 0.05
alfa_2 <- alfa/2
Z <- qnorm(alfa_2, lower.tail = FALSE)
B <- 0.5
```

```
TamMuestrealCA1_CA2 <- (Z^2 * ( sd(lvl43_Length)^2 + sd(lvl50_Length)^2 )) / B^2
> TamMuestrealCA1_CA2
[1] 32.00898
```

```
TamMuestrealCA1_CA3 <- (Z^2 * ( sd(lvl43_Length)^2 + sd(lvl51_Length)^2 )) / B^2
> TamMuestrealCA1_CA3
[1] 29.46843
```

```
TamMuestrealCA2_CA3 <- (Z^2 * ( sd(lvl50_Length)^2 + sd(lvl51_Length)^2 )) / B^2
> TamMuestrealCA2_CA3
[1] 31.00149
```

### References

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