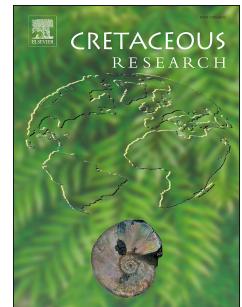


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Author Statement.

Andrea De Sosa Tomas has carried out the field trips, has sampled and processed all the samples mentioned in the manuscript. Besides, she studied and dealt with the description and interpretation of the stratigraphic section where the samples come from. Carles Martín-Closas has contributed to the analysis of the results and to the writing of the manuscript.

Patricia Vallati has contributed with the analysis and description of the palynomorphs and to the writing of the manuscript..

Marcelo Krause has contributed to the geology of the study area, the description and interpretation of the stratigraphic section.

All authors have approved the final version of the manuscript.

Early Cretaceous *Mesochara*-rich assemblages from central Patagonia, Argentina, predate the origin of homogenous Charoidean floras by about 30 million years

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ABSTRACT

During the Early Cretaceous charophyte assemblages were dominated by the family Clavatoraceae, especially in low latitudinal lakes from the Peri-Tethyan basins. In higher latitudes, however, charophyte assemblages were mainly formed by early characeans associated to a reduced diversity of clavatoraceans. The charophyte studied assemblages from the Los Adobes Formation in the Cañadón Asfalto Basin (central Patagonia) are unique as they are exclusively composed of several species belonging to

the early characean genus *Mesochara*, which is considered the ancestor of modern species of the subfamily Charoideae. These assemblages show well-preserved gyrogonites and unusual species richness for this genus, including *Mesochara maruchoensis*, aff. *Mesochara harrisii*, *Mesochara stipitata* and *Mesochara adobensis* sp. nov. Two of these species display a worldwide distribution (*M. harrisii* and *M. stipitata*), while two (*M. maruchoensis* and *M. adobensis* sp. nov.) were only recorded in Patagonia, Argentina, being considered endemic to this region. The charophyte assemblages of the Los Adobes Formation represent autochthonous floras of alkaline ponds or small lakes in distal fluvial floodplains, developed under dry climatic conditions, as indicated by sedimentary facies analysis of the studied beds, and taphonomic and palaeoecological analyses of charophytes and associated fossil groups, such as palynomorphs and ostracods.

This type of charophyte assemblage predates by about 30 million years the first floras composed exclusively of members of the subfamily Charoideae, which radiated worldwide in the Late Cretaceous and continued to dominate the charophyte floras during the Cenozoic until the present.

Keywords

Palaeobotany, Palaeoenvironment, Palaeogeography, Gondwana, Lower Cretaceous, Los Adobes Formation.

1. Introduction

Charophytes are non-marine aquatic plants that include the living and fossil representatives of the Charales and the extinct orders of the Sycidiales and Moellerinales (Feist et al., 2005). They appeared in the late Silurian, ~425 Ma (Conkin

and Conkin, 1992; Mamet et al., 1992; Feist et al., 2005), and diversified at several stages, i.e., the expansion of Sycidiales and Moellerinales in the Devonian–early Carboniferous, the diversification of the first modern Charales (family ‘Porocharaceae’) in the Triassic and Jurassic, the origin and diversification of Clavatoraceae in the Late Jurassic and Early Cretaceous and the radiation of the Characeae from the Late Cretaceous to Paleogene (Grambast, 1974). From the Neogene to the present, charophytes just include a relictual portion of its total diversity in the geological past, with a single family, the Characeae, and seven extant genera, *Chara*, *Nitellopsis*, *Lamprothamnium*, *Lychnothamnus*, *Nitella*, *Sphaerochara*, and *Tolypella* (Soulié-Märsche, 1989).

According to Feist et al. (1991), the Characeae first appeared in the fossil record in the Early Jurassic (Lias), represented by the genus *Aclistochara* Peck. During the Jurassic and Early Cretaceous this family usually played a minor role in charophyte assemblages (e.g., Vicente and Martín-Closas, 2013; Tiss et al., 2019), and was mainly represented by the genera *Aclistochara* Peck, *Sphaerochara* Mädlar, *Tolypella* Braun and *Mesochara* Grambast (Grambast, 1974; Martín-Closas et al., 2018). Regarding the last-mentioned taxon, Soulié-Märsche (1989) synonymized it with the living genus *Chara*, taking into account morphological similarities. However, *Mesochara* differs from *Chara* by the absence of any apical modification, and especially by the lack of apical enlargement of the spiral cells, which is characteristic of genus *Chara*. This difference is considered a valid generic criterion to differentiate both taxa within the family (Feist et al., 2005).

The fossil genus *Mesochara* (meaning “Mesozoic *Chara*”) is considered the earliest and most plesiomorphic taxon belonging to the subfamily Charoideae (Martín-Closas et al., 2018). This genus appeared in the Middle Jurassic (Tiss et al., 2019) and developed

mainly during the Late Jurassic and Early Cretaceous, becoming later a minor component of charophyte assemblages until its extinction during the latest Cretaceous (Feist et al., 2005). The genus *Mesochara*, although generally not abundant, is very significant from an evolutionary point of view. It is considered to contain the ancestors of the subfamily Charoideae, which expanded mainly during the Late Cretaceous and Cenozoic and contains most of the living charophytes.

Mesochara is exceptionally species-rich in the Early Cretaceous charophyte assemblages from the Los Adobes Formation at Sierra de La Manea, Argentina. These floras differ from those previously studied in Lower Cretaceous deposits of Argentina (Musacchio and Chebli, 1975; Musacchio, 1978, 1979, 1981; Musacchio et al., 1986) and elsewhere, which include several genera of early characeans (represented both by the Charoideae and the Nitelloideae) and clavatoraceans. Although Musacchio (1995) mentioned three species of the genus *Mesochara* from the Los Adobes Formation in the Cañadón Asfalto Basin, the assemblages lacked a complete biometric and taxonomic treatment and a thoughtful palaeoecological and palaeobiogeographic analysis. The unique charophyte floras studied herein are of interest to understand the diversification of the subfamily Charoideae during the Late Cretaceous. The present study aims to provide a detailed description of these assemblages and discuss some hypotheses regarding the reasons for its particular taxonomic composition.

2. Materials and methods

The charophytes described in this study were obtained by the prospection and sampling of mudstones and claystones from the Los Adobes Formation at Sierra de La Manea (Fig. 1). Up to eight sites were sampled for charophytes, ostracods and pollen by one of the authors (ADST), between years 2018 and 2020. Seven of these sites are isolated

outcrops (labelled S1 to S7) and one is a complete stratigraphic succession labelled P1. The charophytes studied herein were recovered only in four of the isolated outcrops (S1, S2, S4, S6), sometimes associated to ostracods or palynomorphs. Site S7 and especially the stratigraphic section P1 did not provide charophytes, but only ostracods or palynomorphs, while sites S3 and S5 were devoid of microfossil-bearing rocks. The geographic location of the sites with microfossils and the distribution of samples (labelled M) are shown in Fig. 1 and Table 1.

-----Insert Table 1 here-----

The charophyte fossil remains were released from the matrix using the gasoline method. This method consists in completely submerging perfectly dried rock (broken into pieces about 3 cm in diameter) in gasoline for a few hours, then removing the gasoline excess and adding boiling water in order to disaggregate the rock. This sediment was finally wet-sieved. The mesh sizes used during the process were 1 mm and 70 μm . Microfossils were later picked out under a binocular microscope. Occasionally, it was necessary to use ultrasound cleaning to remove material adhering to the surface of the fructifications. Gyrogonites were measured using the Motic Images Plus 3.0 software in a Motic SMZ-168 stereomicroscope at the Biostratigraphic Laboratory of the Universidad Nacional de la Patagonia San Juan Bosco (UNPSJB, Comodoro Rivadavia). Thin sections from the gyrogonites about 30 μm thick were prepared to observe internal features, such as the basal plate. They were studied by using an Optika B-383POL petrographic microscope. Selected charophytes were photographed using the Scanning Electron Microscope at Aluar Aluminio Argentino (Puerto Madryn), a JEOL JSM-6510LV Scanning Electron

Microscope at the UNPSJB, and a Quanta 200 Scanning Electron Microscope (SEM) the Serveis Científics i Tecnològics of the Universitat de Barcelona.

The specimens and the thin sections are housed in the microfossil collection of the “Dr. Eduardo A. Musacchio Scientific and Educational Repository” of the UNPSJB, in Comodoro Rivadavia with catalog numbers: UNPSJB-MFC 225 to UNPSJB-MFC 242, and UNPSJB-MFC 252 to UNPSJB-MFC 254.

Grey laminated and light brown mudstones were recently sampled for palynological studies during the prospection for calcareous microfossils with the objective of providing additional palaeoenvironmental information. Four fertile samples were obtained in three different sites at Sierra de La Manea (S4, S7 and P1, Fig. 1, Table 1).

Standard palynological methods, including hydrochloric and hydrofluoric attack, allowed the removal of carbonates and silicates from the sedimentary rocks. Occasionally, the residue was oxidized with nitric acid to remove unwanted amorphous organic material. The organic residue was mounted on microscope slides using glycerine jelly and the samples were studied with a Carl Zeiss KF2 microscope. Micrographs were obtained with a digital Nikon Coolpix P2 camera at the Biostratigraphic Laboratory of the UNPSJB. The slides are stored in the palynological collection of the “Dr. Eduardo A. Musacchio Scientific and Educational Repository” of the UNPSJB, in Comodoro Rivadavia (catalog numbers: UNPSJB-MFP 243 to UNPSJB-MFP 251).

3. Geological setting

The fossils studied herein were found in the southern flank of the Sierra de La Manea, northern Chubut province, Argentina (Fig. 1A–B). In this area, the Mesozoic sequences

are folded and affected by reverse and strike-slip faults (Fig. 1C–D) and unconformably covered by Quaternary deposits (Figari, 2005; Figari et al., 2015). The Mesozoic rocks cropping out at the Sierra de La Manea and surrounding areas include the Jurassic Lonco Trapial, Cañadón Asfalto and Cañadón Calcáreo formations, the Lower Cretaceous Los Adobes Formation and the Aptian–Albian Puesto La Paloma and Cerro Castaño members, belonging to the lower part of the Cerro Barcino Formation (Tasch and Volkheimer, 1970; Codignotto et al., 1978; Proserpio, 1987; Anselmi et al., 2004; Figari, 2005).

Volcaniclastic, alluvial, and lacustrine deposits constitute the infilling of the Cañadón Asfalto Basin (Figari and Courtade, 1993; Figari, 2011). The Lonco Trapial, Cañadón Asfalto and Cañadón Calcáreo formations were deposited during the syn-rift stage of the basin evolution, while Los Adobes and Cerro Barcino formations correspond to the post-rift stage (Figari and Courtade, 1993; Figari, 2005; Figari et al., 2015). Syn-rift depositional systems, are up to 2600 m thick (Figari, 2005), Pliensbachian to Kimmeridgian in age (Cúneo et al., 2013; Hauser et al., 2017), while post-rift depositional systems are only up to 420 m thick (Anselmi et al., 2004), and were assigned to the Barremian–Cenomanian (Umazano et al., 2017; Krause et al., 2020).

The Los Adobes Formation (Tasch and Volkheimer, 1970), which is the lowermost unit of the Chubut Group (Lesta and Ferello, 1972), includes the Arroyo del Pajarito and the Bardas Coloradas members. The upper part of the Bardas Coloradas Member, mainly formed by sandstones and mudstones, is the object of this study. These beds were interpreted as deposited in fluvial-channel belts (e.g., Chebli et al., 1976; Codignotto et al., 1978; Allard et al., 2009; Villegas et al., 2015). Regional palaeocurrent patterns from the Los Adobes Formation suggest that rivers from the Bardas Coloradas Member

succession drained southward towards the Golfo San Jorge Basin (Figari and García, 1992; Allard et al., 2015; Figari et al., 2015).

-----Insert figure 1 here-----

Previous regional geological studies suggested that the deposition of the Los Adobes Formation took place during the Early Cretaceous, precisely in the Hauterivian–Aptian time interval (Tasch and Volkheimer, 1970; Turner, 1983). Later, biostratigraphic studies based on calcareous microfossils (ostracods and charophytes) and palynomorphs calibrated its age to the “pre-upper Barremian” (Musacchio, 2000) and finally to the Hauterivian–Barremian (Vallati, 2002). In contrast with these results, Marveggio and Llorens (2013) proposed an Albian age for the lowermost beds of the Los Adobes Formation based on the record of tricolpate pollen grains from subsoil samples at Cerro Solo. An ostracod fauna from the same beds of the Bardas Coloradas Member (Table 1, Fig. 2) is now being studied, and preliminary results suggest a pre-Aptian age (Carignano, pers. comm.). Recently, a U-Pb age of $118.497 \pm 0.063/0.095/0.16$ Ma was obtained by Krause et al. (2020) from a tuffaceous bed near the base of the Puesto La Paloma Member (lowermost Cerro Barcino Formation) at Puesto Limonao (Fig. 1C). This layer is stratigraphically equivalent to the Bardas Coloradas Member, resulting in an early Aptian minimum age for the unit. In sum, a Barremian age seems to be most probable for the studied deposits.

The rocks bearing the charophytes here studied consist of massive, greyish green and pinkish white to very pale brown mudstones of the Bardas Coloradas Member, discontinuously cropping out on top of badlands. A stratigraphic section (P1 in Fig. 1D;

Fig. 2) was studied in a better-exposed badland located around 2 km southeast of the sampling sites (S1, S2, S4, S6 and S7 in Fig. 1D). Charophyte-rich levels were not identified in this section, but, based on lithostratigraphic and cartographic correlation, we consider that the fossiliferous beds bearing charophytes (Table 1) are lateral equivalents of the basal part of the section represented in Fig. 2).

-----Insert figure 2 here-----

Regional tectonostratigraphic reconstructions in the study area suggest that the deposits bearing the charophytes studied herein occurred in upland settings (see Figari et al., 2015), where the deposits of the Bardas Coloradas Member were relatively thin. Similarly, reduced thicknesses of about 20 m were recorded in Cerro Los Chivos section (Rauhut et al., 2003) and in Estancia Aguada La Piedra locality (Brea et al., 2016), while a slightly thicker succession (40 m according to Villegas, 2015) was recorded in Puesto Mesa (Fig. 1C–D). Finally, a significantly thicker succession (90 m) crops out at Puesto Limonao, suggesting deposition in lowlands for this area, located 60 km south of the Sierra de La Manea.

4. Systematic palaeobotany (Charophytes)

We have followed the classification system of Martín-Closas (2000), particularly for the grouping of *Mesochara* species in morphological groups.

Division: Charophyta Migula, 1897

Class: Charophyceae Smith, 1938 emend. Schudack, 1993

- 218 Order: Charales Lindley, 1836
- 219 Family: Characeae Richard ex Agardh, 1824 emend. Martín-Closas and Schudack, 1991
- 220 Subfamily Charoideae Braun in Migula, 1897
- 221 Genus *Mesochara* Grambast, 1962
- 222 *Mesochara* gr. *voluta* subgr. *voluta* sensu Martín-Closas (2000)
- 223
- 224 **aff. *Mesochara harrisii*** (Mädler, 1952) Shaikin, 1967
- 225 Fig. 3A–F
- 226 1952 *Tolypella harrisii* Mädler, pp. 31, 32, pl. B, figs. 31–35.
- 227 1967 *Mesochara harrisii* (Mädler) nov. comb.; Shaikin, p. 47.
- 228
- 229 Material. Over 50 gyrogonites from the Bardas Coloradas Member, Los Adobes
- 230 Formation, most of them (33 specimens) in sample S1M3. Less than 10 gyrogonites
- 231 occurred in other samples (Tables 1, 2).
- 232 Description. Gyrogonites are generally very small in size, 204–351 μm high (mean 282
- 233 μm) and 174–286 μm wide (mean 232 μm), with a subprolate spheroidal to prolate
- 234 shape (usually subprolate) and an isopolarity index of 101–147 (mean 121) (Fig. 3A–F,
- 235 Fig. 4). Apex rounded to slightly pointed, showing the junction of apical cells without
- 236 any periapical modification (Fig. 3B). The spiral cells are unornamented, with a variable
- 237 degree of calcification, concave (30–52 μm wide) to almost flat, with 6–8 spiral turns
- 238 visible in lateral view (mean 7). The basal plate could not be observed in the present
- 239 material. The basal pore is pentagonal in shape (Fig. 3C), 15–30 μm in wide.

Remarks. The biometric characterization of a representative population of this species reflects a moderate intraspecific polymorphism (Fig. 3A, D–F). Variation in size of the fructifications is evidenced in the dispersion graph (Fig. 4E).

Mesochara harrisii and *Tolypella grambastii* subsp. *arctica* Feist et Brouwers 1990 display similar external features in their gyrogonites, both species differing especially in their basal plate, as stated by Martín-Closas et al. (2018). While genus *Mesochara* bears a unicellular basal plate, this plate is multipartite in genus *Tolypella*. This led us to consider the studied material as only having affinity to *M. harrisii*, since the basal plate was not observed.

Distinction from *M. voluta* (Peck, 1937) Grambast, 1965 is based on its characteristic subovoidal shape and a lower ISI in comparison to *M. harrisii*.

Distribution. *M. harrisii* has a wide biogeographic distribution in the Northern Hemisphere, but until now it had not been recorded in South America. (1) In Europe this species has been recorded in the Kimmeridgian to Berriasian of Germany (Schudack, 1993; 1996), in the Kimmeridgian to Barremian of Spain (Brenner, 1976; Martín-Closas and Grambast-Fessard, 1986; Schudack, 1987, 1989, 1993; Martín-Closas, 2000; Vicente and Martín-Closas, 2013), upper Tithonian to lower Berriasian (?) of Portugal (Pereira et al., 2010); Berriasian of the Aquitaine Basin, France (Colin et al., 2004; El Albani et al., 2004; Benoit et al., 2017), the Barremian–lower Aptian of the Northern Subalpine Chains, France (Martín-Closas et al., 2009); the Berriasian and Barremian of the South Dobrogea, Romania (Sanjuan et al., 2021a), and in the Kimmeridgian–Tithonian of Russia and Ukraine (Shaikin, 1967, 1976). (2) In Africa and the Middle East the species has been documented in the in the Upper Jurassic of Tanzania (Schudack, 1999) and in the upper Barremian deposits of Lebanon (Middle East) by Sanjuan et al. (2021b). (3) In Asia *M. harrisii* was found in the Lower and

Upper Cretaceous of China (Wang, 1965; Hao et al., 1983; Liu and Wu, 1985) and in the Barremian of Japan (Kubota, 2005). (4) In America gyrogonites of aff. *M. harrisii* were found in the Berriasian of the United States (Martín-Closas et al., 2013).

-----Insert Table 2 here-----

-----Insert figure 3 here-----

-----Insert figure 4 here-----

Mesochara gr. *voluta* subgr. *stipitata* sensu Martín-Closas (2000)

Mesochara maruchoensis Simeoni and Musacchio, 1986

Fig. 5A–C

1986 *Mesochara* cf. *maruchoensis*, Musacchio et al. (Lám. 6, Fig. 4–6, 8–10)

Material. Over 60 gyrogonites from the Bardas Coloradas Member, Los Adobes Formation, with 19 specimens in sample S4M2, 12 in S1M3, 3 in S2M2, 15 in S4M3, and 14 in S6M1 (Tables 1, 2).

Description. Gyrogonites are generally small in size, 214–343 μm high (mean 268 μm) and 190–317 μm wide (mean 250 μm), inversely pear-shaped, oblate to prolate-spheroidal (usually prolate-spheroidal) with an isopolarity index of 96–114 (mean 109) (Fig. 5A–C, Fig. 6). Apex broadly rounded to slightly truncated, without periapical modifications (Fig. 5B). Base tapering into a prominent and wide basal prolongation. The basal plate was not observed. Basal pore is subpentagonal (Fig. 5C), 20–30 μm

across in external view. Spiral cells, with a variable degree of calcification, are unornamented and mainly concave (40–60 μm wide), with 5–7 spiral turns visible in lateral view (mean 6).

Remarks. Musacchio et al. (1986) included the species *Mesochara* cf. *maruchoensis* within the ostracod assemblage of *Looneyellopsis* cf. *barrancalensis*, from the Berriasian–Hauterivian interval. This species was considered a secondary marker of the ostracod *Gomphocythere dorsoacuminata* Biozone of the early Hauterivian in the Neuquén Basin (Musacchio, 1989).

Distribution. The biogeographic distribution of *M. maruchoensis* during the Early Cretaceous is limited to Argentina. It was first defined by Simeoni and Musacchio (1986) in the Hauterivian of the Agrio Formation at the El Marucho locality, Neuquén Basin. Besides, Musacchio et al. (1986) found *Mesochara* cf. *maruchoensis* at Cerro Ferrarotti in the domain of the Golfo San Jorge Basin. Later, Musacchio (1995) reported, but did not illustrate, *Mesochara maruchoensis* in Lower Cretaceous deposits of the lower part of the Los Adobes Formation at Sierra de La Manea.

-----Insert figure 5 here-----

-----Insert figure 6 here-----

Mesochara stipitata (Wang, 1965) Wang, 1981

Fig. 5D–F

1965 *Tolypella stipitata* Wang: p. 482, pl. I, figs. 19–42.

1981 *Mesochara stipitata* Wang: p. 320, pl. I, figs. 8–13.

311

312 Material. Over 680 gyrogonites from the Bardas Coloradas Member, Los Adobes
313 Formation, most of them (263 specimens) in sample S4M2, 44 in S1M3, 148 in S4M3,
314 1 in S4M4 and 226 in S6M1 (Tables 1, 2).

315 Description. Gyrogonites are small, 202–481 μm high (mean 294 μm) and 136–385 μm
316 wide (mean 207 μm). Subprolate to perprolate (usually prolate) in shape. Isopolarity
317 index ranges from 113 to 205 (mean 134) (Fig. 5D–F, Fig.7). Six to eight (mean 7)
318 spiral turns are visible in lateral view (Fig. 5D). Spiral cells are concave, 40–64 μm
319 high, usually devoid of ornamentation, but occasionally showing a continuous sutural
320 crest (Fig. 5D, F). Apex rounded to pointed, without periapical modifications (Fig. 5E).
321 Tapered base, usually forming a stout basal column, which displays a pentagonal basal
322 pore (Fig. 5F), 20–30 μm wide.

323 Remarks. A biometric characterization of a representative population of *M. stipitata* and
324 its intraspecific polymorphism was provided by Li et al. (2018) and Li et al. (2020) in
325 gyrogonites from the Jiuquan Basin, Northwest China. The specimens from Sierra de La
326 Manca compare best with those studied by Li et al. (2020) in the Xiagou Formation.

327 Distribution. This species was originally reported in the Lower Cretaceous of China
328 (Wang, 1965; Wang, 1981; Li, 1988; Fu and Lu, 1997; Lu and Wang, 1999; Wang et
329 al., 2000; Wang, et al., 2003; Li et al., 2018; Li et al., 2020), including Inner Mongolia
330 (Peng et al., 2003; Yang et al, 2003). Later, it was also found in Europe, i.e., in the
331 Berriasian of Northwest Germany, Serpulit and Purbeck units (Feist and Schudack,
332 1991), in the Barremian of Japan (Kubota, 2005) and in the Hauterivian–Barremian of
333 Argentina (Simeoni and Musacchio, 1986; Musacchio, 1990).

334

-----Insert figure 7 here-----

Mesochara gr. *voluta* sensu Martín-Closas (2000)

subgr. Indet.

Mesochara adobensis De Sosa Tomas and Martín-Closas sp. nov.

Fig. 8A–L

Holotype. Fig. 8A; sample S4M3; UNPSJB-MFC 231.

Paratypes. Fig. 8B–G; samples S4M2, S4M3; UNPSJB-MFC 232–237.

Repository. “Dr. Eduardo A. Musacchio” of the UNPSJB at Comodoro Rivadavia.

Type locality. Sierra de La Manea, Paso de Indios Department, Chubut Province,

Argentina (43° 9'21.70"S; 68°48'11.78"W).

Stratigraphic horizon. Bardas Coloradas Member, Los Adobes Formation at Sierra de

La Manea.

Derivation of name. From the name of the stratigraphic unit Los Adobes Formation

yielding the gyrogonites of the type population.

Diagnosis. Gyrogonites small, tronco-conical to cylindrical in shape, with truncated to

slightly rounded summit and truncated broad base. Spiral cells concave to flat with 6–8

spiral turns visible in lateral view.

Material. Over 190 specimens from the Bardas Coloradas Member, Los Adobes Formation, most of them (123 specimens) in sample S4M3 66 in sample S4M2, 4 in S4M4 and 4 in S6M1 (Tables 1, 2).

Description. Small gyrogonites, 242–496 μm in height (mean 352 μm) and 158–346 μm in width (mean 230 μm). General shape tronco-conical to cylindrical, usually with the upper part enlarged towards the apex. Few specimens show almost a rectangular shape in lateral view (Fig. 8F–G). Isopolarity index ranges from 111 to 213 (mean 154) (Fig. 9). Spiral cells are concave to flat, 40–60 μm high, usually devoid of ornamentation, but with continuous, narrow intercellular ridges, occasionally bicarinate (Fig. 8K). Six to eight spiral turns are visible in lateral view (mean value 7). Intercellular ridges usually decrease in height at the apical area (Fig. 8A–G) and become very prominent to the base. Apex rounded to truncated, without any peri-apical modification. Truncated broad base, with very wide spiral cells that become narrower upwards. Basal pore pentagonal in shape (Fig. 8K–L), 30–40 μm across. The basal plate could not be observed in thin sections of selected gyrogonites but these sections revealed a narrow basal canal, only visible from the inside of the gyrogonite (Fig. 8H).

Remarks. The occurrence of both tronco-conical and cylindrical gyrogonites, with all intermediates between both shapes, in *Mesochara adobensis* sp. nov. results in a moderate intraspecific polymorphism. Precisely, the unique morphology of these gyrogonites which has never been observed before in the genus, allows differentiating the new taxon from previously known species of *Mesochara*.

The monotypic genus *Stylochara* Jiang, Zhang et Meng, 1985, with the species *S. xitanlouensis* Jiang et Zhang in Jiang et al. (1985) includes also small cylindrical gyrogonites with truncated apex and base. The main difference with *M. adobensis* is the

apical zone that is rounded to truncated and without periapical modifications in the new species, while it is sunken and with periapical thinning in the genus *Stylochara*.

Taking into account the size of the gyrogonites, *M. adobensis* can be included in *Mesochara* gr. *voluta* sensu Martín-Closas (2000). However, the particular morphology of the gyrogonites studied, which exhibit a truncated broad base, do not fit well in any of the currently known subgroups.

-----Insert figure 8 here-----

-----Insert figure 9 here-----

Charophyte thalli

Over 200 calcified portions of cylindrical tubes (300 µm mean wide) were recovered from samples S4M2, S4M3 and S6M1 (Fig. 5G–I). They are attributed here to internodes of charophyte ecorticate thalli. So far, fructifications have not been found attached to these vegetative remains but, considering that the gyrogonite assemblage associated with the thalli is solely composed of species belonging to genus *Mesochara*, it is probable that both kinds of remains were related to each other. This hypothesis should be confirmed by further search of anatomically connected thalli and fructifications in this early characean genus. Other macroalgae recorded in the palynological analysis in the same formation, especially the representatives of Zygnematales, are excluded as possible producers of these thalli, since they do not calcify.

5. Palynomorphs from the Bardas Coloradas Member of the Los Adobes

Formation

The fairly well preserved palynoflora of the Bardas Coloradas Member at Sierra de La Manea (Fig. 10) is dominated by gymnosperm pollen grains, mainly belonging to the conifers, such as cheirolepidiaceans, araucariaceans and podocarpaceans. Rimulate pollen grains of the genus *Classopollis* (Fig. 10D), which belong to the extinct conifer family Cheirolepidiaceae, account for more than 60% of the palynological assemblage of the Los Adobes Formation, as documented in a nearby section at Sierra de La Manea (Vallati, 2002). Araucariaceans are represented by *Cyclusphaera* (*C. psilata* Volkheimer and Sepúlveda, 1976; *C. cf. patagonica* Archangelsky, 1983 in: Archangelsky et al., 1983 and *Cyclusphaera* sp.; Fig. 10H–I), *Araucariacites australis* Cookson, 1947 and *Balmeiopsis limbatus* (Balme) Archangelsky, 1977 (Fig. 10G), which are all common pollen types in Early Cretaceous Gondwanan forests (Archangelsky and Del Fueyo, 2010). The saccate pollen grains *Callialasporites* spp. (Fig. 10F), *Microcachrydites antarcticus* Cookson, 1947, *Trisaccites* sp., and *Podocarpidites* spp. (Fig. 10E) would represent the Podocarpaceae, while *Alisporites similis* (Balme) Dettmann, 1963 has affinity with the pteridosperms. Up to now, no angiosperm pollen grains were recognized in this palynoflora.

The assemblage includes also spores of Bryophyta and Monilophyta, which are represented by *Interulobites triangularis* Phillips and Felix, 1971; *Taurocusporites segmentatus* Stover, 1962 (Fig. 10C); *Leptolepidites* sp.; *Klukisporites* sp. (Fig. 10B) and *Cyathidites* sp.

The aquatic palynological record includes *Botryococcus*, a genus of colonial (syncytial) green algae (Botryococcaceae/ Dictyosphaeriaceae) (Fig. 10A) and scarce zygospores of *Ovoidites elongatus* (Hunger) Krutzsch, 1959 (Zygnemataceae). Besides, the dominance

of subspherical cysts of *Leiosphaeridia* (a probably polyphyletic taxon, see Mays et al., 2021) was reported in previously studied samples of this unit (Vallati, 2002).

-----Insert figure 10 here-----

6. Sedimentology, taphonomy and palaeoecology

The section studied is ~14 m thick with-unexposed base, and consists of a monotonous succession of mudstones, only interrupted by two gravelly to sandy beds that occur in the upper part, at nearly 9 meters and 13 meters from the base respectively (Fig. 2).

They display an erosive base and a fining-upward arrangement. The mudstones form tabular and generally massive beds, holding occasionally, poorly preserved parallel lamination. They change in colour from greenish to reddish, both coexisting often within a same bed in an irregular mottling pattern. Alternatively, they contain iron (III) glaeboles, as well as calcium carbonate and gypsum concentrations.

These deposits are interpreted as representing shallow temporary ponds or small lakes from distal river floodplain areas. The changes in colour of the mudstones are interpreted as produced by gleying, probably due to seasonal alternation of a high-water table and subaerial exposition. Mottling suggests alteration of mudstones by re-dox processes in hydromorphic paleosols. The same conditions were previously recognized in paleosols from the overlying lower Cerro Barcino Formation (Krause et al., 2014).

The small gyrogonites and thalli studied herein show a low degree of abrasion, indicating limited transport in the floodplain. This, along with the joint occurrence of vegetative and reproductive charophyte remains suggests a parautochthonous assemblage.

Likewise, the aquatic palynomorphs present in the studied samples reflect a freshwater ecosystem. *Botryococcus* is the best represented planktonic alga in the studied palynoflora and is particularly abundant in the sample S4M1 of the studied section (Fig. 1, Table 1), with middle sized and relatively well-preserved colonies probably reflecting an occasional phytoplanktonic bloom. This genus is distributed mainly in temperate and tropical regions and its predominance could indicate shallow water and calm, mesotrophic conditions (Worobiec, 2014 and references therein). The occurrence of such algal blooms would indicate that episodes of high nutrients would alternate in the lakes with episodes of low nutrients, which are preferred by charophytes (Blindow, 1992).

7. Palaeoclimatic control

The palaeoclimatic estimates presented herein take into consideration both the sedimentological characteristics of the rocks studied and the palynological record in the Bardas Coloradas Member at Sierra de La Manea. The presence of calcium carbonate nodules in palaeosols is suggestive of semi-arid climate, with an annual precipitation below 500–600 mm (Jenny, 1941; Sheldon, 2003). Moreover, the presence of gypsum, here tentatively considered as primary in origin, would suggest similar or even drier climatic conditions (e.g., Retallack and Huang, 2010). On the other hand, the repeated upward trend from greenish to reddish colours in the section studied herein, suggests a cyclic increase in soil oxidation conditions with time, probably controlled also by the climate.

The palynoflora is dominated by the pollen of the extinct family Cheirolepidiaceae (Coniferales). These thermophilic and drought-resistant plants probably thrived under hot and semi-arid to arid conditions (Cors et al., 2015). Similarly, warm and dry

climatic conditions were interpreted for different Lower Cretaceous deposits studied southward of the present study area, in the Cañadón Asfalto Basin (Krause et al., 2014) and in the Golfo San Jorge Basin (Vallati, 2002, 2013; Greppi et al., 2020).

8. Palaeobiogeography

The charophyte assemblages from the Bardas Coloradas Member studied here include four species of the genus *Mesochara*. Among them, *Mesochara adobensis* sp. nov. and *Mesochara maruchoensis*, are endemic in Patagonia, the latter taxon being found in the Cañadón Asfalto and Neuquén basins (Simeoni and Musacchio, 1986; Musacchio, 1995). The other species of *Mesochara* recognized in the studied assemblage, i.e., aff. *Mesochara harrisii* and *Mesochara stipitata* have a cosmopolitan or subcosmopolitan distribution with several reports from the Tethyan Region, Asia and possibly North America. This would be the first record of the species *M. harrisii* in Patagonia, extending its geographic distribution to West Gondwana (Fig. 11).

To date, the dispersal mechanisms of these cosmopolitan charophytes is poorly known. The possible dispersion of non-marine ostracods, passively transported by larger animals, particularly birds or pterosaurs, was discussed by Trabelsi et al. (2015). Besides, several authors, such as Martín-Closas and Wang (2008) and De Sosa Tomas et al. (2017), suggested that migratory herbivorous dinosaurs, especially those living in wetlands where charophytes thrived, might have been the vectors of dispersal, in a similar way as ducks and other migratory birds disperse the gyrogonites of living charophytes (Proctor, 1980).

-----Insert figure 11 here-----

8. Discussion

Charophyte floras show different compositions in successive time intervals (Grambast, 1974; Martín-Closas, 2003; Martín-Closas and Soulié-Märsche, 2016). In the Palaeozoic (Silurian–middle Permian), charophyte assemblages were dominated by different species of the orders Sycidiales and Moellerinales, with a minor representation of the Charales (e.g. Lu et al., 1996). Late Permian–Middle Jurassic charophyte assemblages were dominated by the early Charales, mainly by representatives of the paraphyletic family Porocharaceae. After the Middle Jurassic, these floras formed mixed assemblages with the early Characeae (e.g. Tiss et al., 2019). The Late Jurassic and Early Cretaceous were characterized by the abundance of charophyte species belonging to the family Clavatoraceae, especially in the tropical and subtropical Tethyan region (e.g., Pérez-Cano et al., 2020). Elsewhere, few species of this family coexisted with early Characeae. Alternatively, mixed Charoideae and Nitelloideae assemblages occurred without clavatoraceans (e.g., Wang and Lu, 1982; Schudack, 1993). It was not until the Late Cretaceous that modern floras dominated by the subfamily Charoideae (family Characeae) appeared in the fossil record (Grambast, 1974).

The Early Cretaceous assemblages from the Bardas Coloradas Member at Sierra de la Manera, Patagonia Argentina, should be included in the period of dominance of Clavatoraceae associated with early Characeae. However, in contrast to other floras at a worldwide scale, these assemblages lack clavatoraceans and are uniquely composed of species belonging to early representatives of the subfamily Charoideae, i.e., genus *Mesochara*. Considering the charophyte evolutionary history, Charoideae-dominated assemblages did not develop until the Late Cretaceous (e.g., Li et al., 2019), meaning

that the floras studied herein predate such assemblages worldwide by about 30 million years.

This unusual composition has been analysed here under the scope of palaeoecology and palaeobiogeography. From the palaeoecological viewpoint, the *Mesochara*-rich assemblages of Sierra de la Manea were growing in alkaline temporary lakes within distal floodplains. Such environments were already known to exhibit low diversified charophyte assemblages, formed by charophytes with small fructification sizes when compared to those of permanent lake deposits (Vicente and Martín-Closas, 2013; Vicente et al., 2015; Sanjuan et al., 2017). Both characteristics (low diversity and selection of small sized gyrogonites) are present in the assemblages studied here. Based on experiments with extant *Chara*, these features have been interpreted as an opportunistic strategy developed by charophytes to thrive in shallow short-lived ponds, subjected to extremely high temperatures and light intensities before desiccation (Sanjuan et al., 2017).

Besides, the absence of clavatoraceans in the assemblages from the Bardas Coloradas Member could also be produced by palaeobiogeographic constraints. In fact, Clavatoraceae were not recorded in Argentina until the Barremian–Aptian interval. Three subcosmopolitan species of this family colonized South America from the Tethyan area, where their ancestors were recorded (Musacchio, 2000; Martín-Closas and Wang, 2008; Martín-Closas, 2015). These species are *Atopochara trivolis triquetra* Grambast, 1968; *Clavator harrisii* Peck, 1941 and *Clavator calcitrapus jiangluoensis* nov. comb. Pérez-Cano, Bover-Arnal and Martín-Closas, 2020 (= *Triclypella patagonica* Musacchio, 1989). Recently, Pérez-Cano et al. (2020) noticed that a fourth South American clavatoracean, *Diectochara andica* Musacchio-1971, could also be conspecific with the Tethyan *Echinochara lazarii* (Pérez-Cano et al. 2020

ex Mojon)-*Charaxis spicatus* Martín-Closas et Diéguez 1998 plant (both parataxa corresponding respectively to fructifications and thalli of the same charophyte species). The Argentinian taxon would eventually have nomenclatural priority over it. Particularly, Musacchio (1971) reported abundant specimens of *A. trivolis triquetra* in the flora of the Barremian La Amarga Formation in the Neuquén Basin. Besides, several morphotypes of the species *Clavator harrisii* were reported in different Barremian–early Albian assemblages of the Cañadón Asfalto and Golfo San Jorge basins (Musacchio and Chebli, 1975; Musacchio in Hechem et al., 1987; Carignano, et al., 2017; De Sosa Tomas et al., 2017). Finally, *Clavator calcitrapus jiangluoensis* (= *Triclypella patagonica*) was documented in the La Amarga Formation (Musacchio, 1989). The arrival of Tethyan clavatoraceans to the Patagonian domain did not occur before the Barremian, while they were thriving in the Northern Hemisphere since the Late Jurassic. The absence of this charophyte family in Valanginian–Hauterivian non-marine deposits of Patagonia, led Musacchio (2000) to hypothesize that a geographic barrier hindered the floral exchange between South America and the tropical latitudes, particularly the Tethyan domain, before the Barremian. However, taking into account the probable Barremian age of the Patagonian assemblages presented herein, devoid of clavatoraceans but with subcosmopolitan characeans, other reasons than those strictly related to palaeogeography should be considered to explain their unusual composition.

9. Conclusions

The Early Cretaceous charophyte floras from the Bardas Coloradas Member of the Los Adobes Formation are unique in being formed exclusively by well-preserved gyrogonites of the ancient genus *Mesochara*, which is considered the ancestor of

modern Charoideae. These Patagonian floras predate the worldwide assemblages dominated by this subfamily by approximately 30 million years. The floras present probable endemic species such as *M. maruchoensis* and *Mesochara adobensis* sp. nov. associated to species that display intercontinental geographic distribution, such as *M. stipitata* and *M. harrisii*. The new species *M. adobensis* is easily recognizable by the unique elongate tronco-conical shape of the gyrogonite, which has never been reported before in the genus *Mesochara*. Sedimentological, taphonomic, and palynological data suggest that the habitat of the studied charophytes in temporary ponds of distal river floodplains, developed under warm and seasonally dry palaeoclimatic conditions. Such palaeoenvironmental factors are known to enhance the development of small sized gyrogonites from a reduced number of taxa, both features being recognized in the studied charophyte assemblages. The occurrence of both endemic and subcosmopolitan species of *Mesochara*, in the Bardas Coloradas Member of the Los Adobes Formation suggests that the unique composition of these Early Cretaceous Charoideae-dominated assemblages cannot be explained solely on the basis of palaeogeographic isolation.

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Figure captions

Table 1. Geographic coordinates of the sampling sites and indication of the fertile samples bearing microfossils.

Table 2. Relative abundance of charophyte species in the studied sites at Sierra de La Manea.

Figure 1. Geographic and geological setting of the study area with indication of key localities referenced in the text. **A.** Regional setting in Argentina. The black area encompasses the Chubut province. **B.** Regional setting in the Chubut province. The black box encompasses the map in C. **C.** Geological map with location of the main localities referenced in the text. The black box encompasses the map in D. **D.** Detail of the Sierra de La Manea range area with location of the sites sampled (S) or studied in stratigraphic sections (P). The geology is based on Proserpio (1987), Anselmi et al. (2004), and Figari (2005). The position of tectonic features is approximate, for more precise structural maps please refer to Figari (2005).

Figure 2. A. Schematic stratigraphic section of the Bardas Coloradas Member in the southern flank of the Sierra de la Manea (P1). The position of samples with palynomorphs and ostracods is indicated. No charophytes were found in this section. The asterisk indicates the estimated stratigraphic position of the charophyte-bearing beds according to cartographic correlation. **B.** Aerial photograph of the studied sites S1 and S4. Scale bar: 100 m. **C.** Aerial photograph of the section P1 represented in A. Scale bar: 5 m.

989

990 **Figure 3.** Charophytes from the Bardas Coloradas Member, Los Adobes Formation at
 991 Sierra de la Manea. **A–F.** aff. *Mesochara harrisii*. **A–C.** UNPSJB-MFC 225, sample
 992 S4M2. **D–E.** UNPSJB-MFC 252–253, sample S1M3. **F.** UNPSJB-MFC 254, sample
 993 S4M2. **A, D–F.** Lateral views; **B.** Apical view; **C.** Basal view. Scale bar: 100 μm .

994

995 **Figure 4.** Biometric values of aff. *Mesochara harrisii* from the Bardas Coloradas
 996 Member, Los Adobes Formation at Sierra de la Manea. **A.** Gyrogonite height (μm); **B.**
 997 Gyrogonite width (μm); **C.** Number of spiral turns; **D.** Isopolarity index; **E.**
 998 Height/width dispersion graph.

999

1000 **Figure 5.** Charophytes from the Bardas Coloradas Member, Los Adobes Formation at
 1001 Sierra de la Manea. **A–C.** *Mesochara maruchoensis*, UNPSJB-MFC 226, sample S2M2.
 1002 **D–F.** *Mesochara stipitata*, UNPSJB-MFC 227, sample S6M1; **G–I.** Calcified portions
 1003 of thalli; **G–H.** UNPSJB-MFC 228–229, sample S4M3, **I.** UNPSJB-MFC 230, sample
 1004 S4M2. **A, D.** Lateral views; **B, E.** Apical views; **C, F.** Basal views; **G, H.** longitudinal
 1005 views of internode; **I.** transversal section of internode. Scale bar: 100 μm .

1006

1007 **Figure 6.** Biometric values of *Mesochara maruchoensis* from the Bardas Coloradas
 1008 Member, Los Adobes Formation at Sierra de la Manea. **A.** Gyrogonite height (μm); **B.**
 1009 Gyrogonite width (μm); **C.** Spiral turns; **D.** Isopolarity index; **E.** Height/width
 1010 dispersion graph.

1011

Figure 7. Biometric values of *Mesochara stipitata* from the Bardas Coloradas Member, Los Adobes Formation at Sierra de la Manea. **A.** Gyrogonite height (μm); **B.** Gyrogonite width (μm); **C.** Spiral turns; **D.** Isopolarity index; **E.** Height/width dispersion graph.

Figure 8. Charophytes from the Bardas Coloradas Member, Los Adobes Formation at Sierra de la Manea. **A–L.** *Mesochara adobensis* sp. nov. **A–G.** Lateral views, UNPSJB-MFC 231–237, samples S4M3 and S4M2; **H.** Thin section of a gyrogonite, UNPSJB-MFC 238, sample S4M2; **I–J.** Apical views, UNPSJB-MFC 239–240, sample S4M2; **K–L.** Basal views, UNPSJB-MFC 241–242, sample S4M3. Scale bar: 100 μm .

Figure 9. Biometric values of *Mesochara adobensis* sp. nov. from the Bardas Coloradas Member, Los Adobes Formation at Sierra de la Manea. **A.** Gyrogonite height (μm); **B.** Gyrogonite width (μm); **C.** Spiral turns; **D.** Isopolarity index; **E.** Height/width dispersion graph.

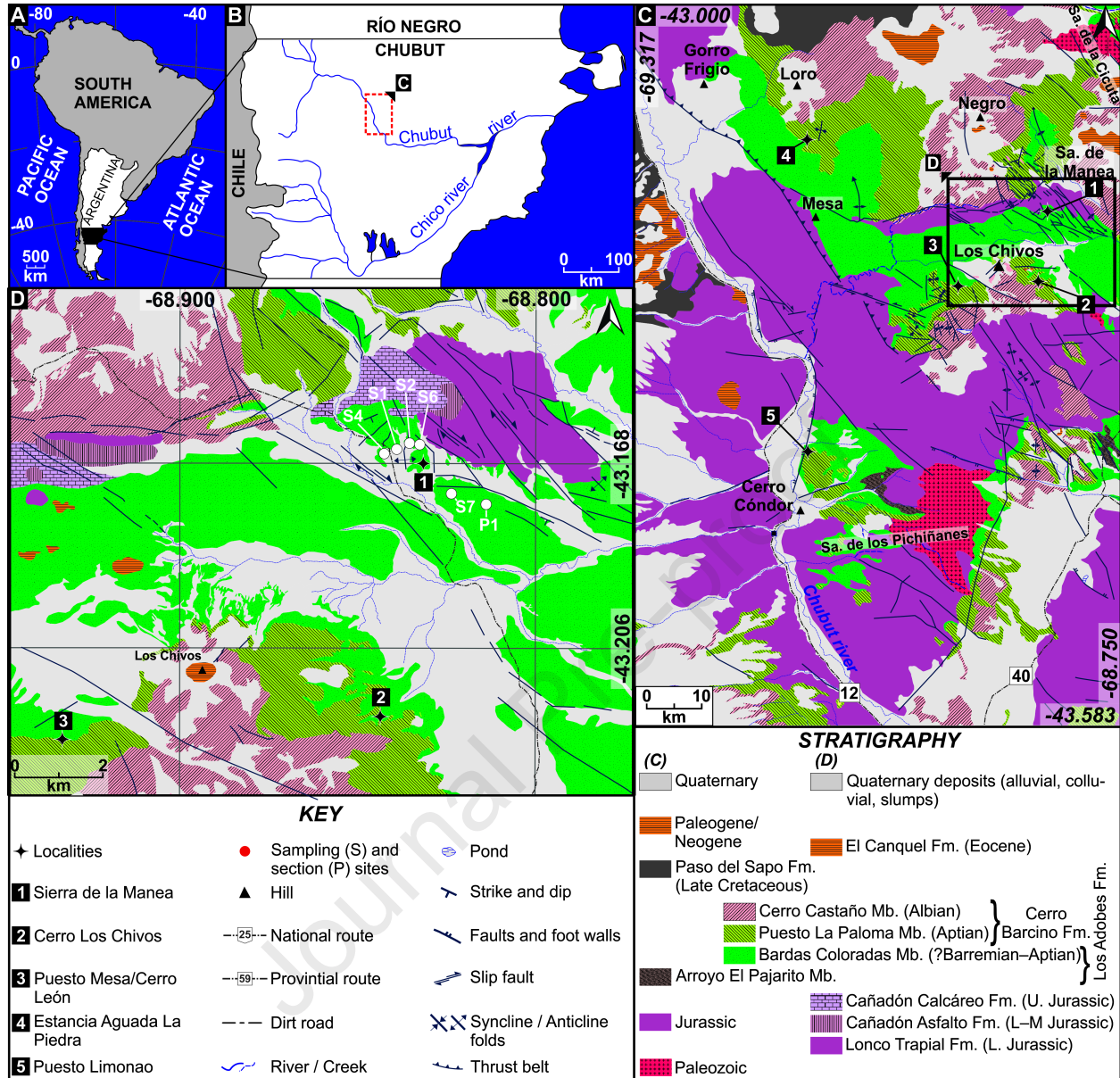
Figure 10. Selected palynomorphs from the Bardas Coloradas Member, Los Adobes Formation at Sierra de la Manea. **A.** *Botryococcus* sp., sample P1M3; **B.** *Klukisporites pseudoreticulatus*, sample P1 M3; **C.** *Taurocusporites segmentatus*, sample P1M3; **D.** *Classopollis classoides*, sample P7M1; **E.** *Podocarpidites* sp., sample P1M3; **F.** *Callialasporites* sp., sample P1M3; **G.** *Balmeiopsis limbatus*, sample P1M4; **H.** *Cyclusphaera psilata*, sample P1M4; **I.** *Cyclusphaera* cf. *patagonica*, sample P1M3. Scale bar: 10 μm .

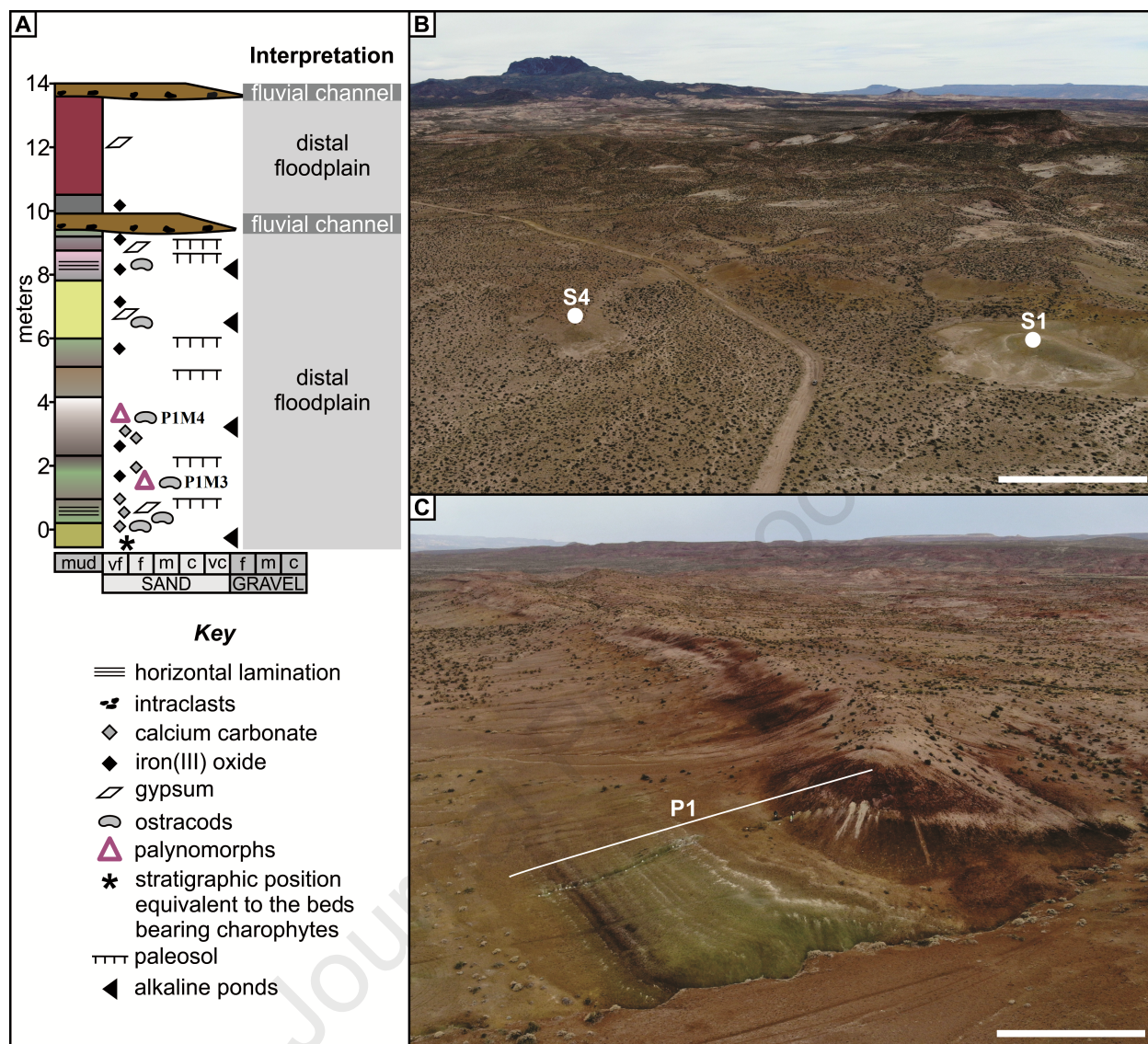
Figure 11. Palaeogeographic map showing the distribution of *M. harrisii*, *M. stipitata*,
M. maruchoensis, and *M. adobensis* sp. nov. in the Early Cretaceous, modified from
Blakey (2020).

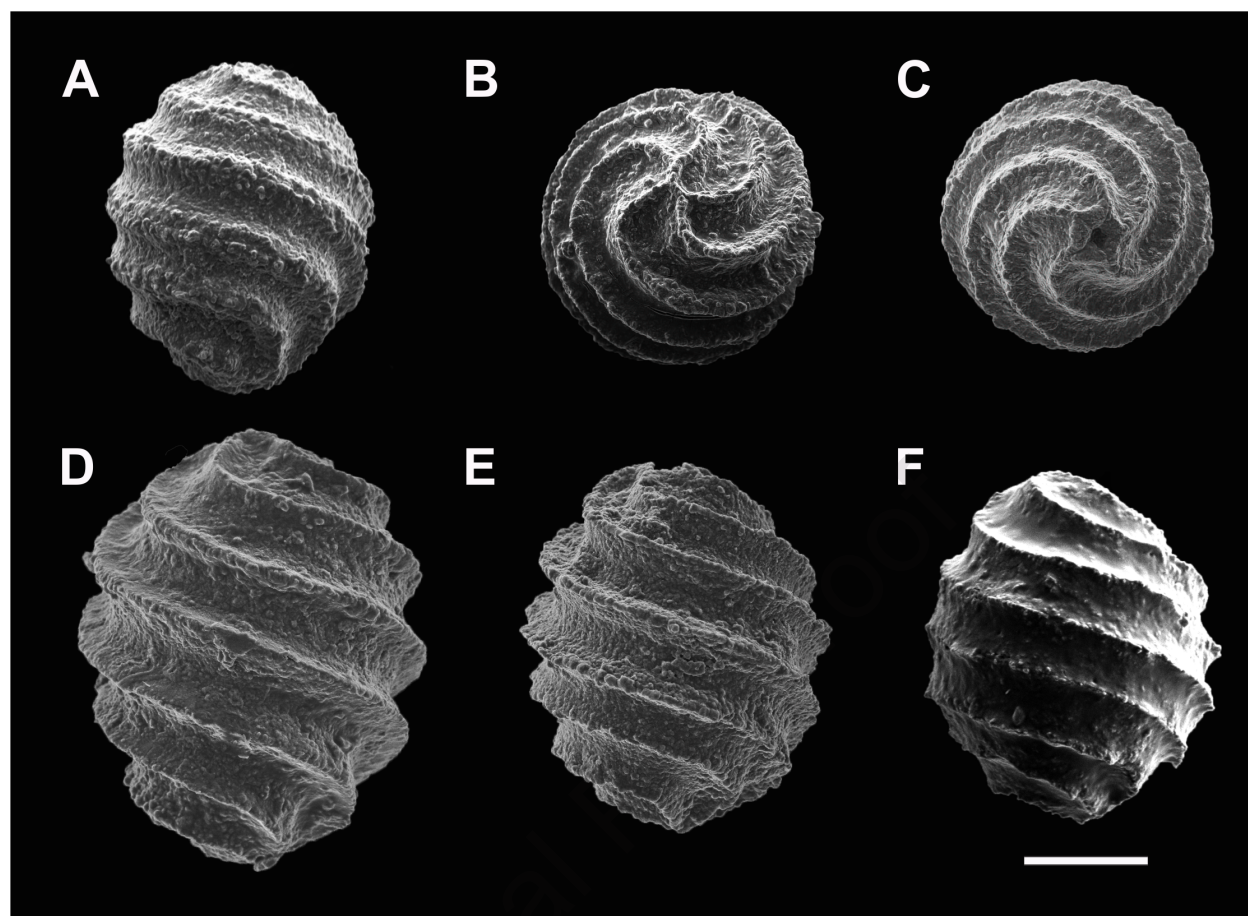
SAMPLING SITES	S1	S2	S4	S6	S7	P1
COORD.	43° 9'54.32"S 68°50'20.60"W	43° 9'49.82"S 68°50'7.63"W	43° 9'57.60"S 68°50'33.26"W	43° 9'50.86"S 68°49'57.33"W	43°10'16.00"S 68°49'37.00"W	43°10'35.00"S 68°48'50.00"W
FERTILE SAMPLES	M3  	M2 	M1  M2   M3   M4  	M1  	M1  	M1  M2  M3   M4   M18  M20 
Key	 Charophytes  Palynomorphs  Ostracods					

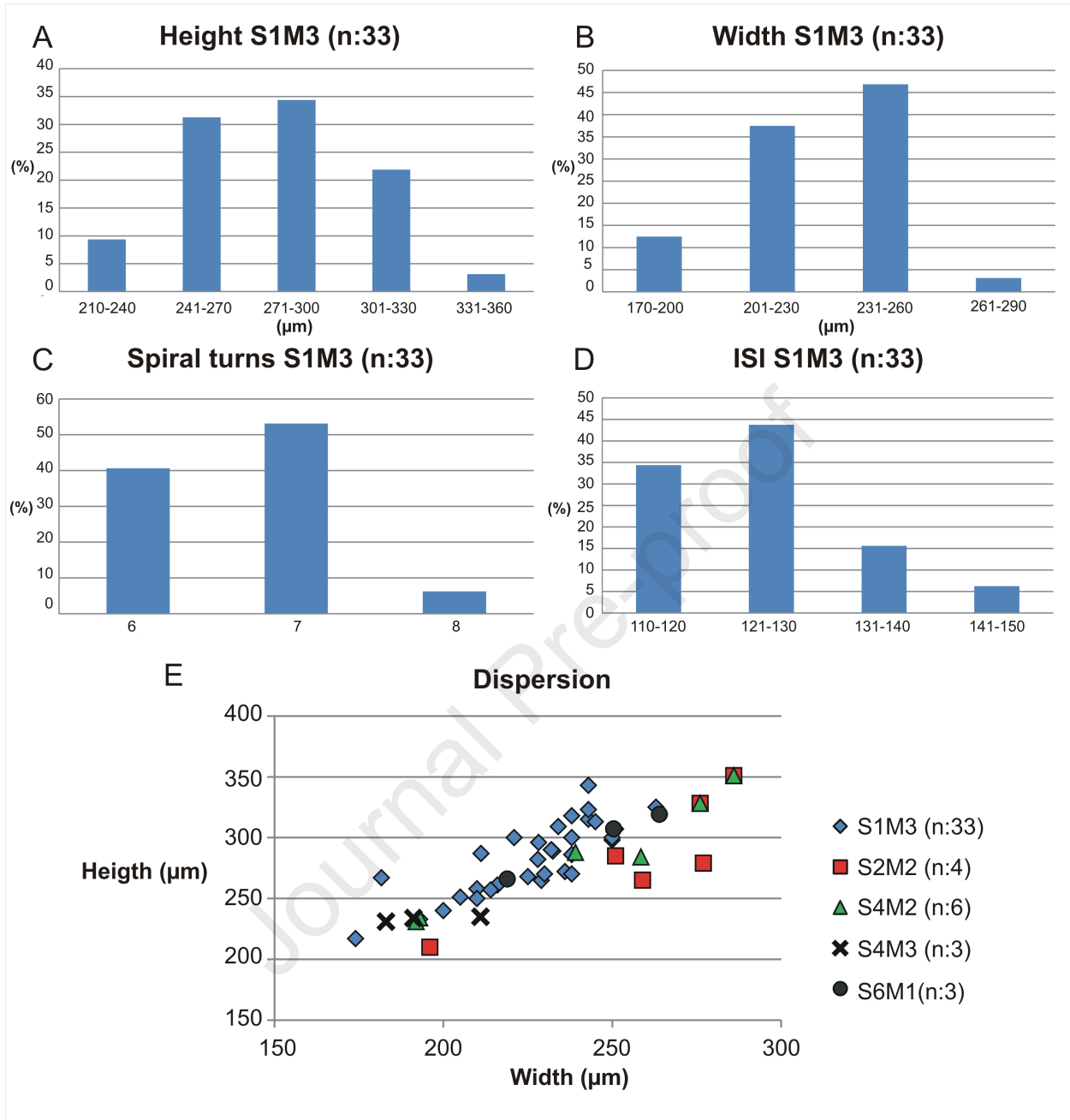
Localities	S1	S2	S4			S6
Species \ Samples	M3	M2	M2	M3	M4	M1
<i>aff. Mesochara harrisii</i>	●	●	●	●	●	●
<i>Mesochara maruchoensis</i>	●	●	●	●		●
<i>Mesochara stipitata</i>	●		●	●	●	●
<i>Mesochara adobensis</i> sp nov.			●	●	●	●

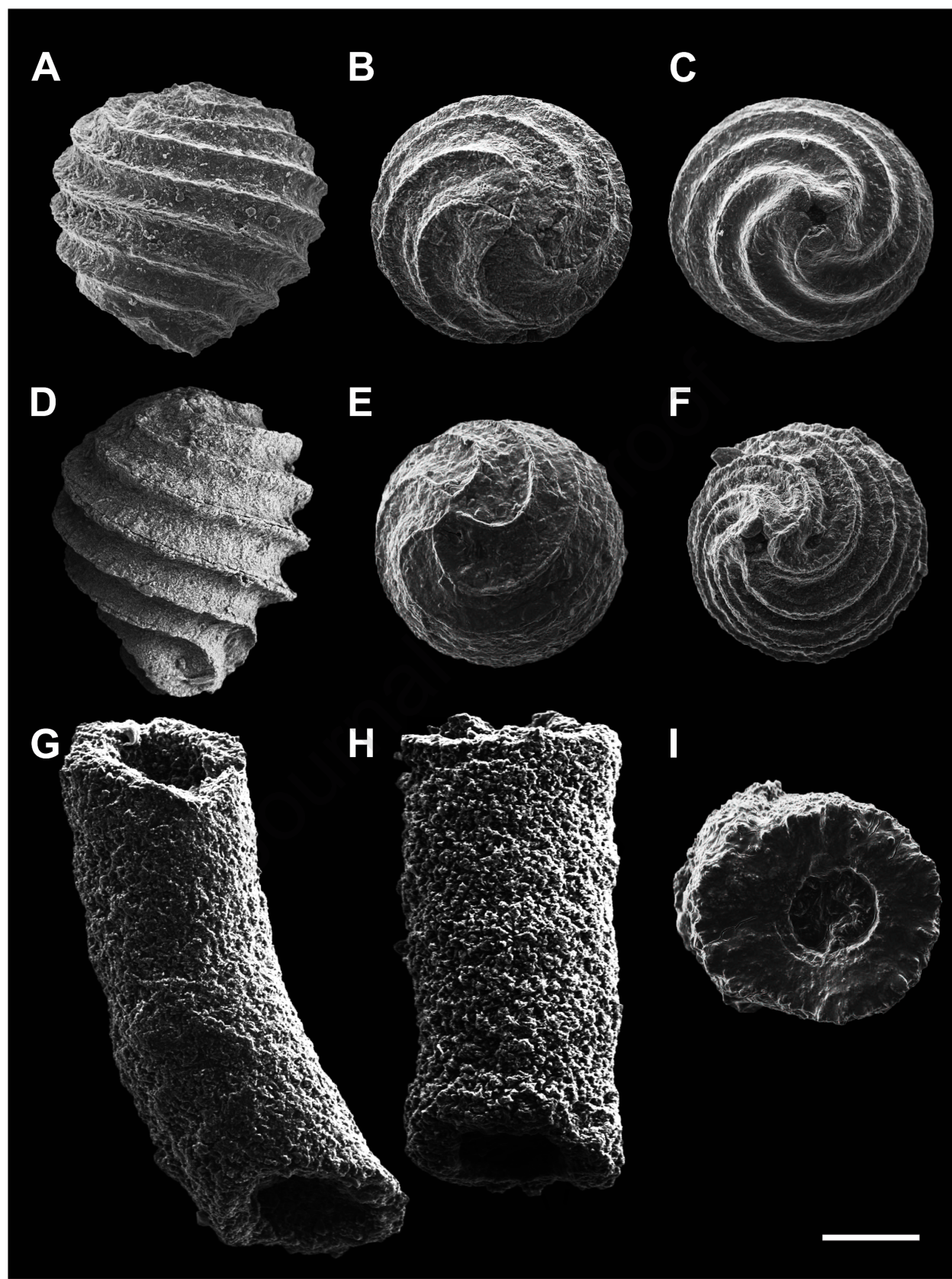
Number of gyrogonites per sample ● 0-10 ● 11-50 ● 51-100 ● >100

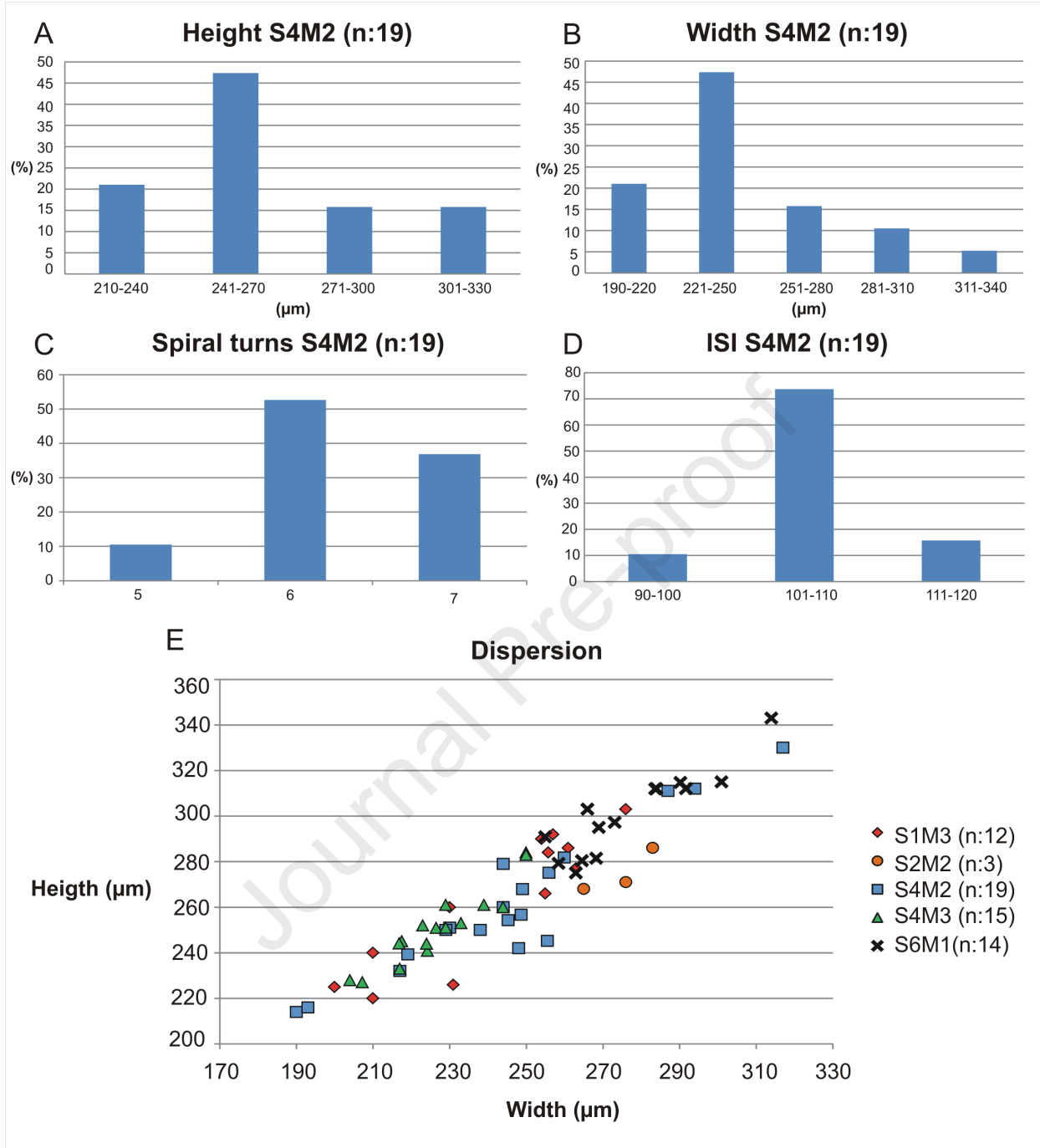


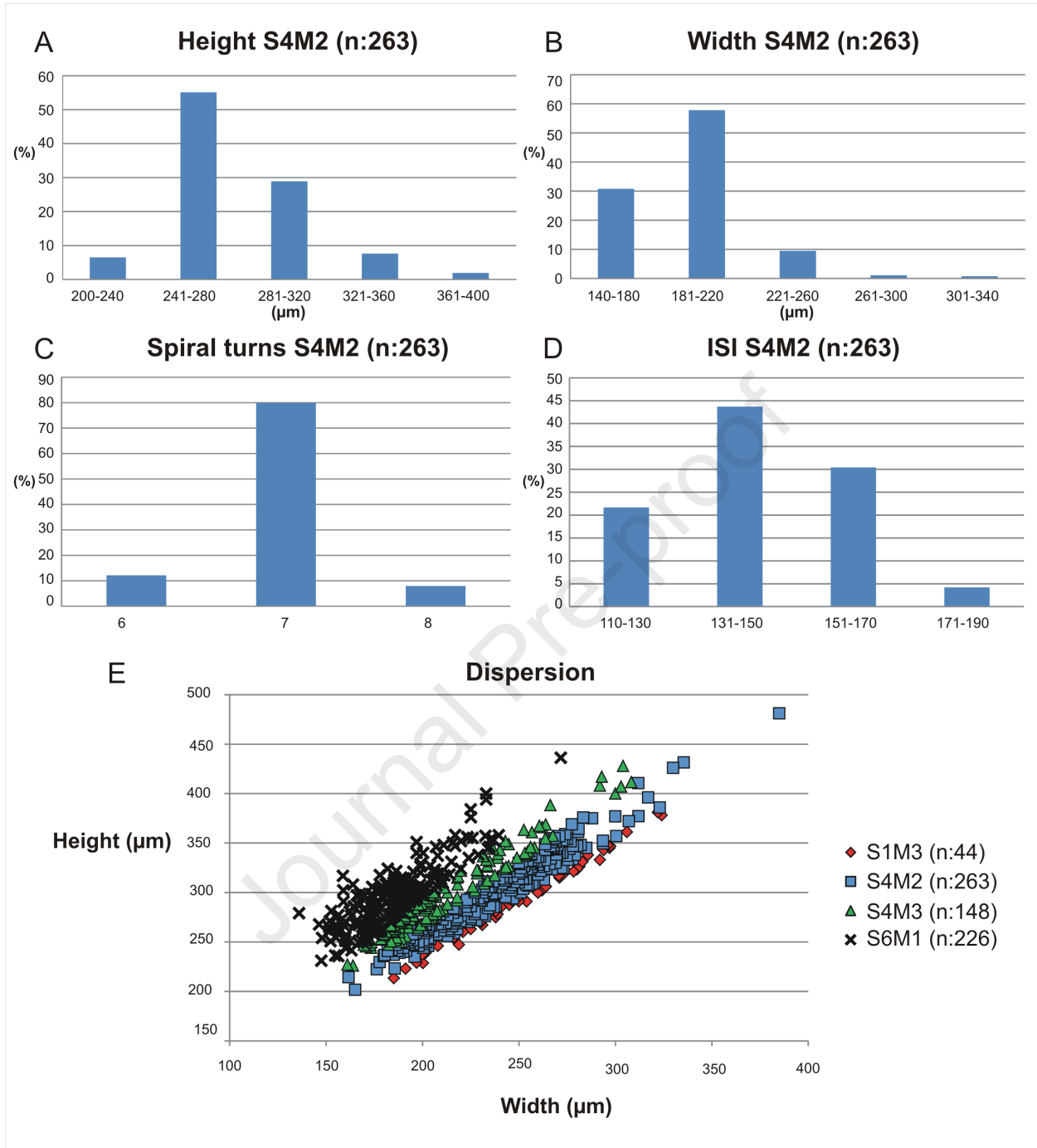


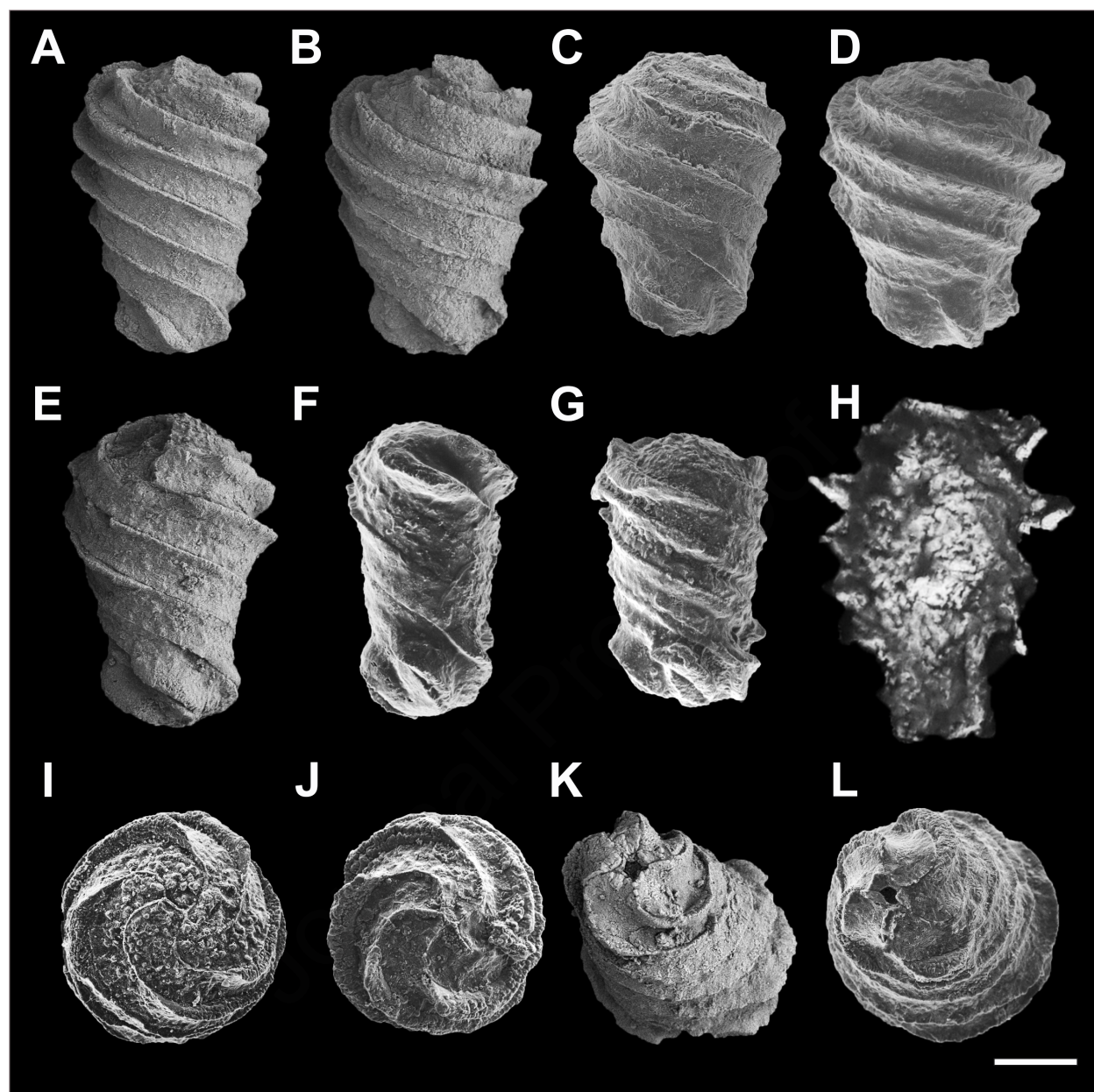


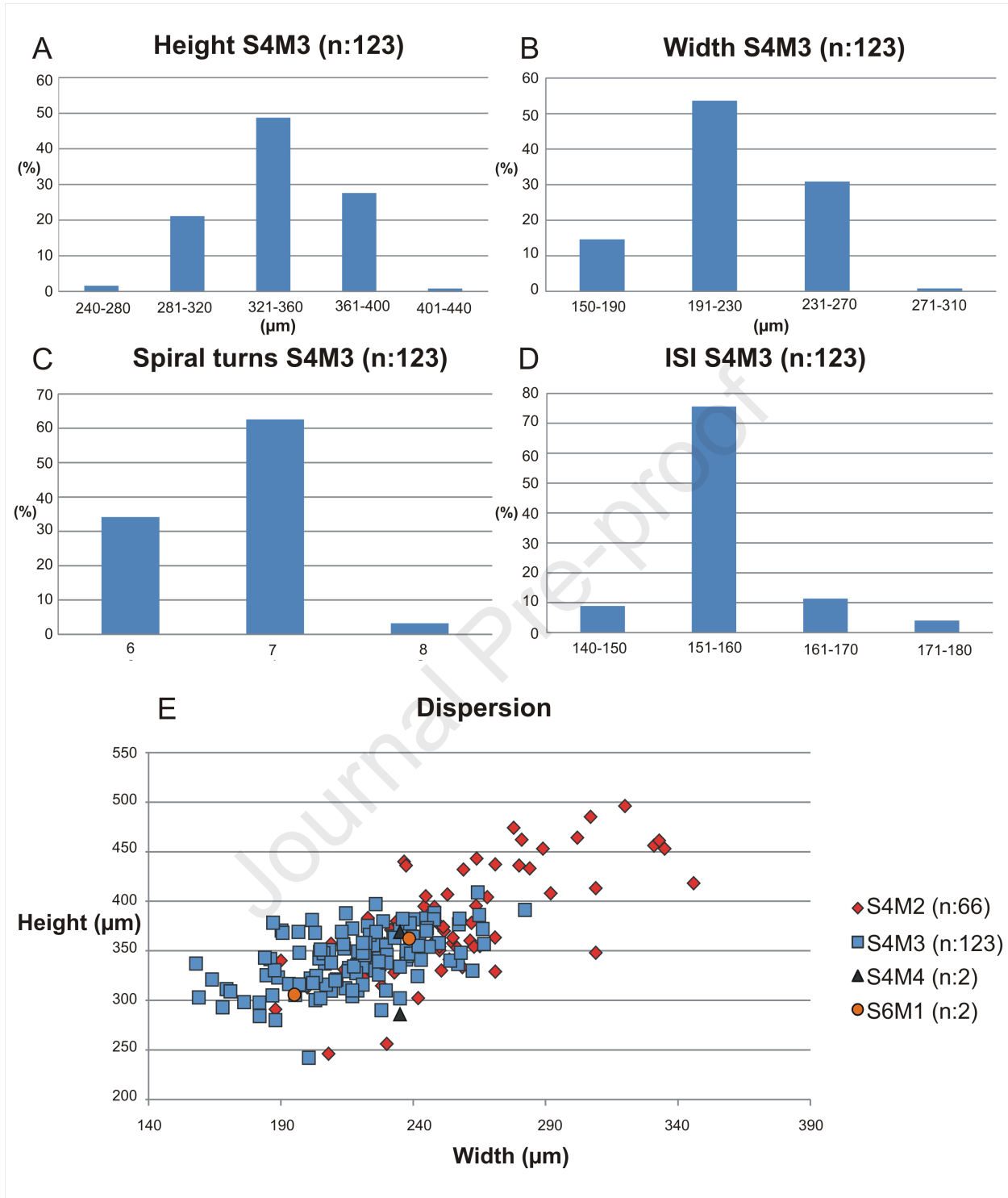


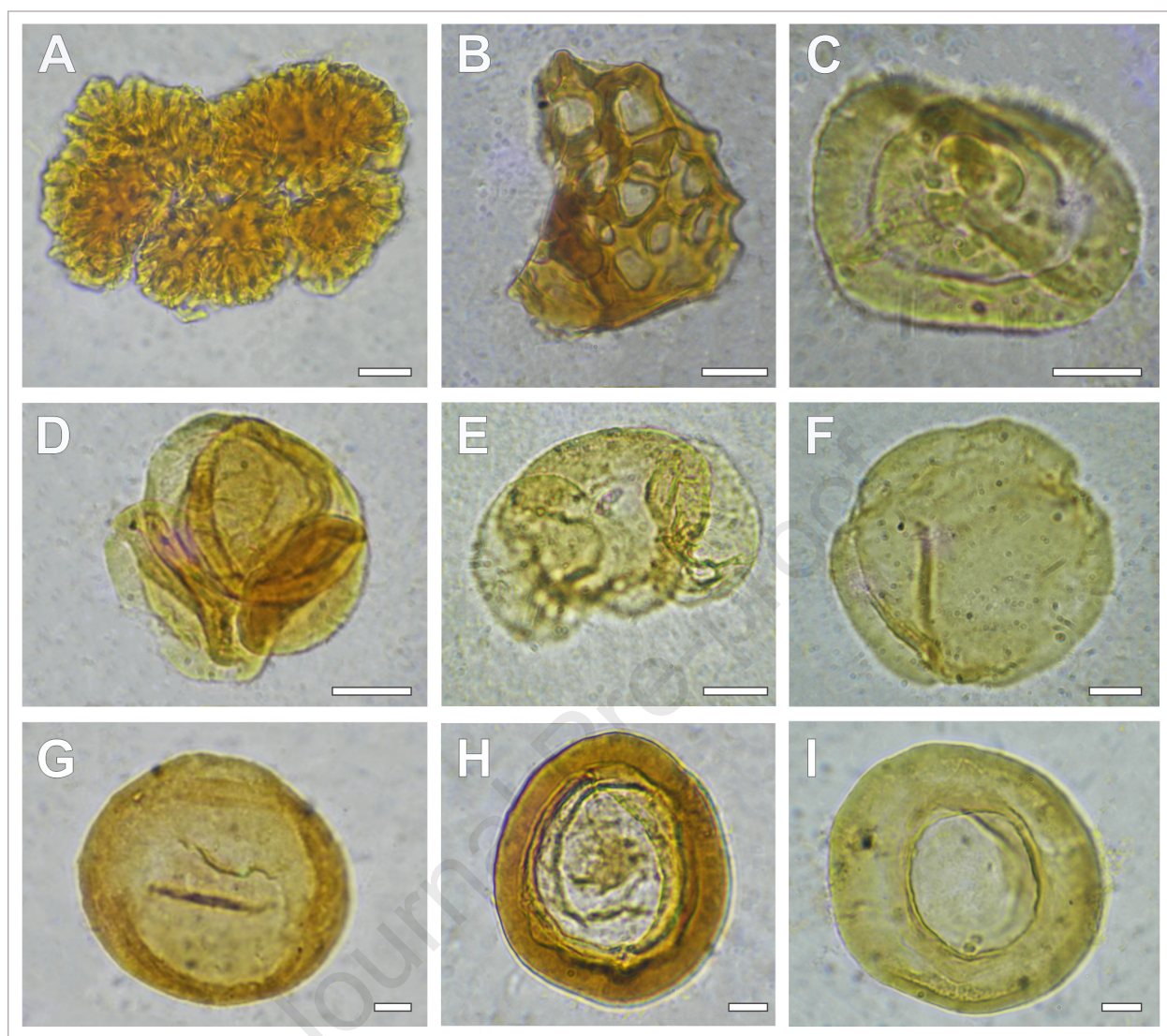


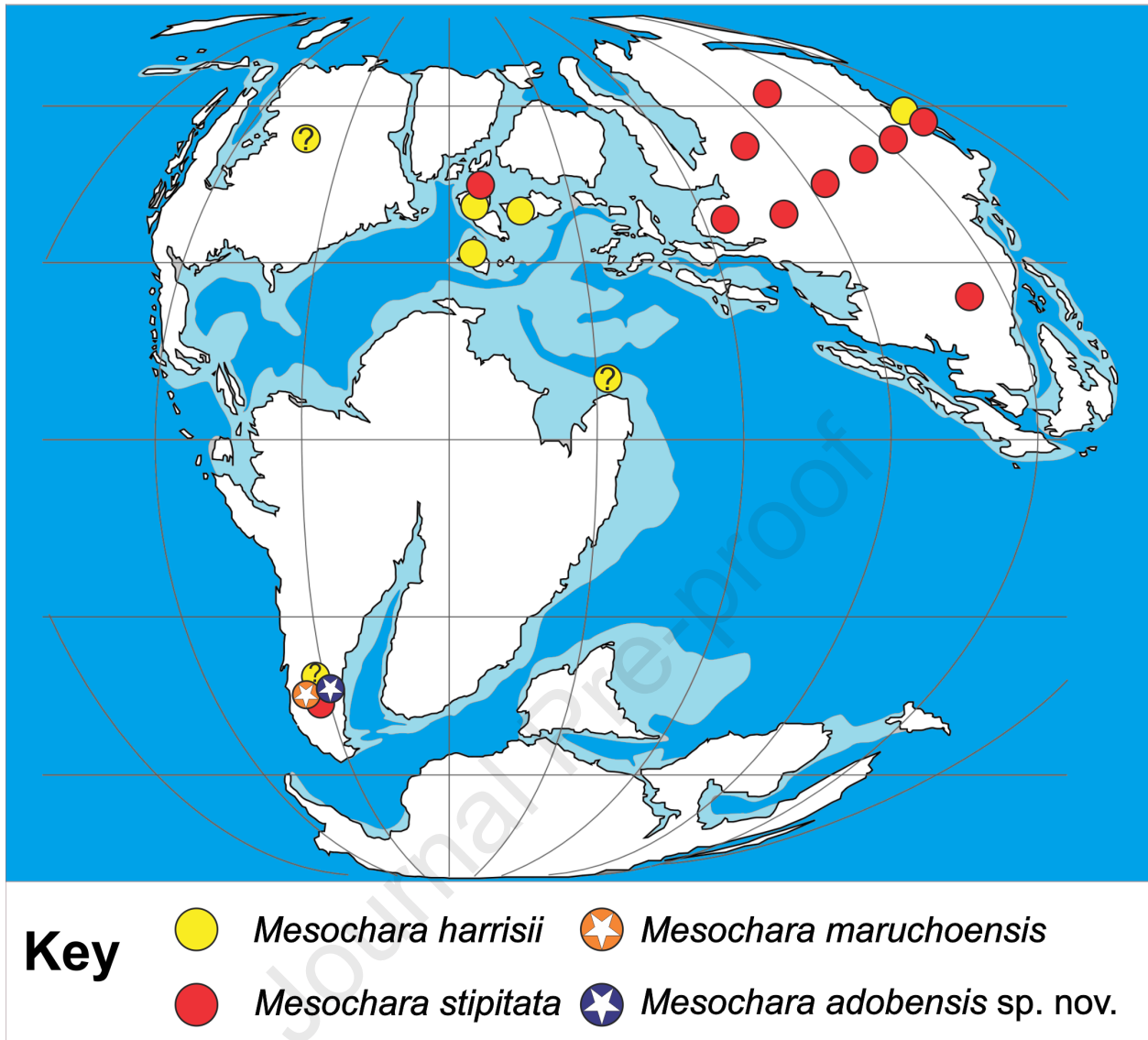












Highlights

- A unique *Mesochara*-rich flora is reported from the Lower Cretaceous of Patagonia.
- The assemblage includes two endemic and two cosmopolitan species of *Mesochara*.
- *Mesochara adobensis* sp. nov. shows a unique tronco-conical gyrogonite shape.
- The assemblage grew in floodplain ponds under warm and dry climatic conditions.
- Such homogeneous Charoidean assemblages were unknown before the Late Cretaceous.

SAMPLING SITES	S1	S2	S4	S6	S7	P1
COORD.	43° 9'54.32"S 68°50'20.60"W	43° 9'49.82"S 68°50'7.63"W	43° 9'57.60"S 68°50'33.26"W	43° 9'50.86"S 68°49'57.33"W	43°10'16.00"S 68°49'37.00"W	43°10'35.00"S 68°48'50.00"W
FERTILE SAMPLES	M3  	M2 	M1  M2   M3   M4  	M1  	M1  	M1  M2  M3   M4   M18  M20 
Key	 Charophytes		 Palynomorphs		 Ostracods	

Localities	S1	S2	S4			S6
Samples Species	M3	M2	M2	M3	M4	M1
<i>aff. Mesochara harrisii</i>	●	●	●	●	●	●
<i>Mesochara maruchoensis</i>	●	●	●	●		●
<i>Mesochara stipitata</i>	●		●	●	●	●
<i>Mesochara adobensis</i> sp nov.			●	●	●	●

Number of gyrogonites per sample	0-10 ●	11-50 ●	51-100 ●	>100 ●
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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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