Review of Palaeobotany and Palynology 318 (2023) 104971

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Taxonomy of Early Mississippian gulate megaspore assemblage from northern Bolivia

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ARTICLE INFO

Keywords:
Bolivia
Carboniferous
Lycopsids
Megaspores
Tournaisian

ABSTRACT

A taxonomic study of gulate megaspores, characterised by having an apical prominence associated with the trilete mark, from the Toregua Formation, Retama Group, Early Carboniferous (mid-upper Tournaisian) of northern Bolivia was performed. To achieve this, the general morphology and wall structure of around a hundred of specimens of megaspores isolated from palynologic residues of the Pando X-1 and Manuripi X-1 boreholes were studied in detail and thoroughly described and illustrated using light, fluorescence and scanning electron microscopy. From this analysis, nine morphospecies of the genus *Lagenicula* were identified, including a new species (*L. morbelliae* sp. nov.), of which some were considered Mississippian in age (*L. brasiliensis*, *L. microechinata*, cf. *L. crassiaculeata*, cf. *L. hirsutoida*) and others (*L. devonica, L. illizii, L.magna, L. media*) were interpreted as likely reworked forms from Devonian deposits. The sporoderm morphological features of the studied megaspores confirm the botanical affinity assigned to heterosporous arborescent lycopsids (Lepidocarpaceae/Lepidodendraceae), which would have formed dense forests, not only of great dimensions and variability but also with ecological complexity, during the Early Carboniferous in Bolivia.

1. Introduction

Megaspores are found in the fossil record from sediments as old as Early Devonian (early Emsian; Bonacorsi et al., 2020). From that period, the size differentiation between microspores and megaspores became more pronounced (Chaloner, 1967; Richardson, 1967) and the diversity of megaspores increased (Scott and Hemsley, 1996), reaching its maximum importance during the Carboniferous, in which heterosporous lycopsids had a rapid diversification (Bateman et al., 1992) and dominated major portions of the landscape (Phillips, 1978).

Currently, there are heterosporous plants that produce megaspores (e.g. *Selaginella*, *Isoetes*, *Marsilea* and *Azolla*) however, the study of ancient megaspores such as those from the Devonian and Carboniferous is especially relevant to ascertain the origin and evolution of heterospory and the groups of plants involved in this event (Traverse, 2007). Comparing with the Pennsylvanian epoch, the knowledge on Mississippian dispersed megaspores is still limited due to the scarcity of described assemblages (Arioli et al., 2007; Wellman et al., 2009), and especially from the Tournaisian, where megaspores assemblages revealed a low diversity of morphospecies in relation to those from Late Devonian and Visean age (Scott and Hemsley, 1996).

Within Early Carboniferous assemblages, specifically of Tournaisian age, there are megaspores characterised by having a gula, i.e., a particular form of development of the trilete mark, which is more or less raised, apparently formed also by the contact areas in laterally compressed specimens (Dybová-Jachowicz et al., 1979). These gulate megaspores are assigned to heterosporous arborescent lycopsids of the Lepidocarpaceae or Lepidodendraceae family (Balme, 1995). Previous studies on megaspores with gula suggest they could derive almost exclusively from that family (Arioli et al., 2007), which is generally considered to form dense and diverse forests (Wellman et al., 2009). This is primarily evidenced not only by the preservation of deposits bearing abundant plant material of different parts of lycopsids documented in the Pennsylvanian (DiMichele et al., 2007) and Mississippian (Bell, 1960) but also by the morphological diversity found in gulate megaspore assemblages (Glasspool and Scott, 2005; Arioli et al., 2007; Wellman et al., 2009).

Gulate megaspores have been described within assemblages found in North America (e.g., Chaloner, 1954; Winslow, 1962; Glasspool et al., 2000) and Europe (Mortimer et al., 1970; Hemsley et al., 1994), while in

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https://doi.org/10.1016/j.revpalbo.2023.104971
Received 23 January 2023; Received in revised form 3 August 2023; Accepted 11 August 2023
Available online 17 August 2023
0034-6667/© 2023 Published by Elsevier B.V.

South America they were described mainly from Pennsylvanian and Permian deposits (e.g., Arai and Rösler, 1984; Archangelsky et al., 1989; Cúneo et al., 1991; Ricardi-Branco et al., 2002; Amaral and Ricardi-Branco, 2004; Mune et al., 2011). Regarding Mississippian deposits, and particularly from Bolivia, our study area, only one papers have been published (Quetglas et al., 2019).

The present research concerns northern Bolivia mid-upper Tournaisian gulate megaspore taxonomy, morphology and wall structure; and to achieve this, optical, fluorescence, and scanning electron microscopy were used. This study will broaden the knowledge about Mississippian megaspore diversity, since few researches on megaspores for this region and time period have been made.

2. Material and methods

2.1. Locality and geology

During late Palaeozoic, most of the continents were part of either Euramerica or Gondwana. The latter located in the southern palaeolatitudes, and comprised South America, Africa, the Arabian Plate, India, Australia and Antarctica (Lakin et al., 2016). Through the Devonian–Mississippian time period, the Late Palaeozoic Ice Age was onset, marked by three short glaciations in the latest Famennian, mid-Tournaisian and Visean, respectively (Caputo et al., 2008; Montañez and Poulsen, 2013). In Gondwana, the evidence of these glaciations is based on diamictite deposits and striated pavements in both South America and Africa (Caputo et al., 2008; Isaacson et al., 2008). The Toregua Formation (Retama Group) in northern Bolivia, is an example of these glacial deposits which comprises a continuous succession of sedimentary rocks containing two glacial intervals (Koltonik et al., 2019). The Toregua Formation was deposited in a pro-delta to delta plain subenvironment (Isaacson et al., 1995; Giusiano et al., 1998) and based on palynological data, it corresponds to a mid-upper Tournaisian age due to the presence of miospores such as *Vallatisporites ciliaris*, *Granulatisporites granulatus*, *Reticulatisporites waloweekii*, *Dibolisporites setigerus*, *Crassispora scrupulosa* and *Cristatisporites echinatus* (Di Pasquo, 2015; Di Pasquo et al., 2015, 2019a).

Megaspores were isolated from palynological samples of the Toregua Formation from Pando X-1 (11° 36′ 07″ S, 67° 56′ 45″ W) and Manuripi X-1 boreholes (11° 36′ 01″ S, 68° 08′ 55″ W), northern Bolivia (Fig. 1). Geological information, descriptions of both boreholes and palynological results have been previously published (Isaacson and Díaz Martínez, 1995; Isaacson et al., 1995; Vavrdová et al., 1996; Vavrdová and Isaacson, 1996; di Pasquo, 2008, 2009a, 2015; di Pasquo et al., 2015, 2016). A total of 23 samples, obtained between 1360 and 1240 m depth from the Pando X-1 borehole (CICYTTP 729, 731, 733, 734, 2609, 2610, 2611, 2612, 2613, 2614, 2615) and between 1535 and 1432 m depth from the Manuripi X-1 borehole (CICYTTP 564, 565, 566, 572, 573, 574, 575, 576, 577, 578, 579, 580) were studied (Fig. 2).

Fig. 1. Map of the study area: (1) Pando X-1 and (2) Manuripi X-1 boreholes, Madre de Dios Basin, Bolivia.

2.2. Preparation and techniques

Pieces of rocks greater than 5 mm were selected and not crushed to avoid possible mechanical fragmentation of megaspores and they were processed following standard paleopalynologic techniques using HCl (25%) for 8 h followed by HF (45%) for 48 h (see Steemans et al., 2009). Samples were washed with distilled water to neutralise the acid. Then, residues were sieved using a mesh of 25 μm. Megaspores were hand-picked from residues in a Petry dish under a stereoscopic microscope and temporarily mounted on glass slides using water for a microscopic analysis (LM). This analysis was performed with white and fluorescence lights under a light microscope Leica DM500 bearing a fluorescence device (LED lamp, filter block for fluorescein ca. 450 nm). A video camera Amuscope 14 Mp was used to take pictures of palynomorphs. Different morphologic features of each megaspore were measured using the scale into the LM and through the program ImageJ version IJ 1.46r (Ferreira and Rasband, 2012). Maximum and minimum values were expressed in micrometres (μm).

A detail study under scanning electron microscopy (SEM) of selected megaspores bearing different patterns of ornamentation and fractures in their walls was performed. For this, some of the same megaspores that were previously documented by LM were re-mounted with glue in stubs for SEM observation. Two types of microscopes were used, a JEOL JSM 6360 LV at the *Facultad de Ciencias Naturales y Museo* (UNLP), for which samples were coated with gold, and a JENCK PHENOM PRO at the *Centro de Investigaciones Científicas y Transferencia de Tecnología* (CONICET-Entre Ríos-UADER), for which samples did not require to be coated (di Pasquo and Vilá, 2019).

All the materials analysed (palynologic slides, residues, rock samples, specimens of megaspores) are deposited in the *Laboratorio de Palinoestratigrafía y Paleobotánica* (CICYTTP-CONICET-Entre Ríos-UADER, di Pasquo and Silvestri, 2014) under the acronyms CICYTTP-M for the collection of megaspores and CICYTTP-Pl for the palynologic samples.

3. Systematic palaeontology

In this contribution, we followed Potonié (1893) and Spinner (1969, 1983) for morphotaxonomic classification of megaspores, and Punt et al. (2007) for morphologic terminology. The Chart 1 (suppl. online material) contains the stratigraphic information of the specimens of megaspores (material) analysed in this study.

Anteturma: SPORITES Potonié, 1893

Turma: TRILETES (Reinsch, 1881) Potonié and Kremp, 1954

Subturma: LAGENOTRILETES Potonié and Kremp, 1954 emend. Bhardwaj, 1957

Infraturma: GULATI Bhardwaj, 1957

Genus: **Lagenicula** (Bennie and Kidston) Potonié and Kremp, 1954

Type species: *Lagenicula horrida* Zerndt, 1934.

Generic remarks: this genus established by Bennie and Kidston (1886). Some authors (e.g. Winslow, 1962) considered it as a subdivision of the genus *Triletes* until Zerndt (1934) used it as a genus but without a type species. Potonié and Kremp (1954) validated the genus *Lagenicula* by selecting *Lagenicula horrida* Zerndt, 1934 as the type species. For that time, many new genera for gulate megaspores were erected and their differentiation only based on the ornamentation type (e.g. *Lagenoisporites* Potonié and Kremp, 1954, a laevigate form). Spinner (1969) argued the value of using these differences in ornament to distinguish genera and proposed retaining *Lagenicula*. Afterwards, Piérart (1978) and Dybová-Jachowicz et al. (1979) characterised four

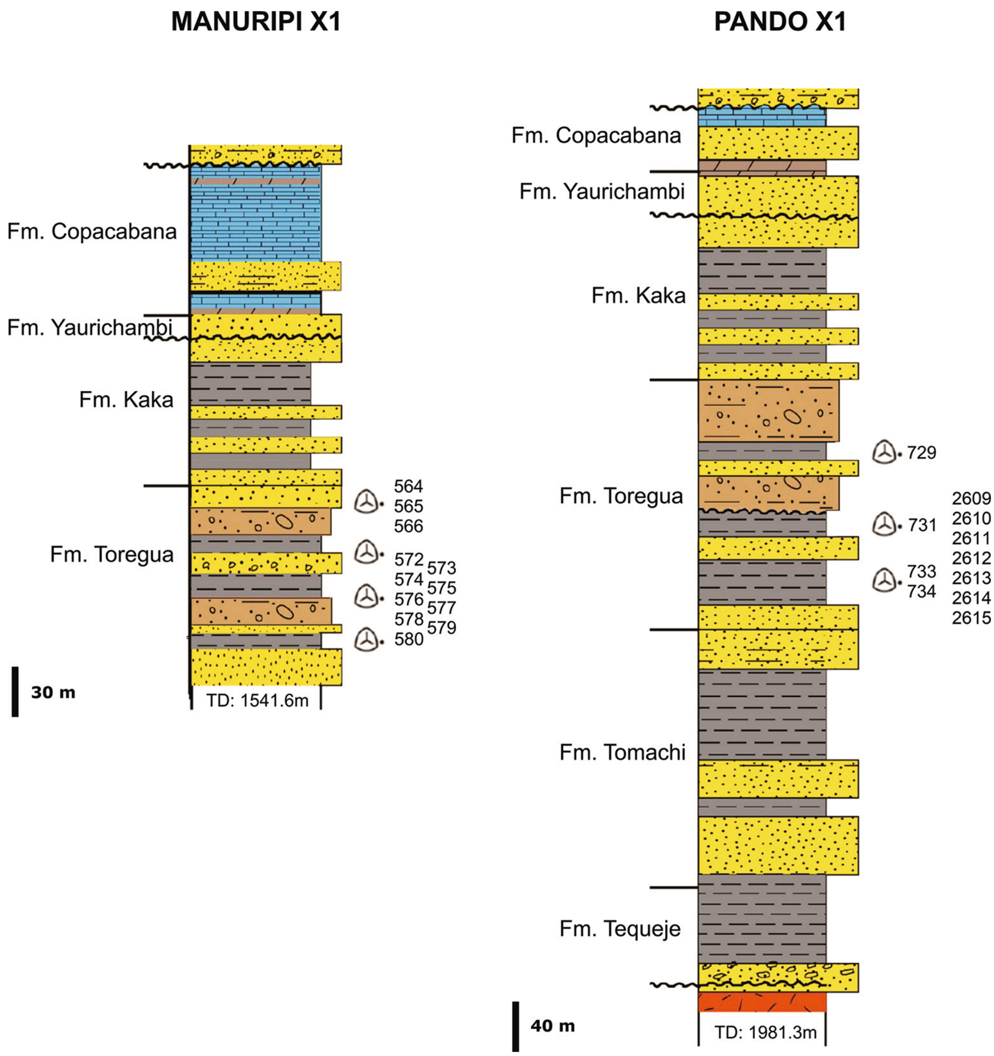

Fig. 2. Stratigraphic columns of Pando X-1 and Manuripi X-1 boreholes (modified from Koltonik et al., 2019) with the location of the studied levels.

different types of gula (hologula, subgula, crassigula, anguligula) and based on them, they proposed four new genera: *Sublagenicula*, *Auritolagenicula*, *Crassilagenicula* and *Zonolagenicula*. Because the diagnoses of the new genera did not adequately differentiate between them, Spinner (1983) completely disagreed with this proposal. Many authors (e.g. Arioli et al., 2007; Wellman et al., 2009) consider that gulate megaspore taxonomy requires clarification. In this research, we prefer to retain the genus *Lagenicula*, rather than those proposed by Piérart (1978) and Dybová-Jachowicz et al. (1979), for the reasons given by Spinner (1969, 1983).

Lagenicula brasiliensis (Dijkstra, 1955a) comb. nov. (Plate I).

Basionym: *Triletes brasiliensis* Dijkstra, 1955a, p. 337, pl. 41, fig. 39; pl. 42, figs. 36–37; pl. 43, figs. 38, 40–41.

For a complete synonymy list see Glasspool (2003, p. 274–275).

Material: Specimens CICYTTP-M2, 15, 17, 28 (see Chart 1, suppl. online material).

Description: Trilete megaspores, laterally compressed, with spheroidal body and gula. The overall length (including the gula) is 550–990 µm and the width of the body is 235–639 µm. The gula measures 151–332 µm high and 154–436 µm wide, bearing a few verrucae of 3–8 µm high. Laterally, the gula presents an auriculae projection. Both gula and megaspore body have a superficial microgranulate ornamentation. These microgranules are either separated from each other or laterally fused, and do not exceed 1.5 µm high. Through the observation of a fracture, the outermost layer of the exospore reveals a spongy structure constituted by a three-dimensional network of fused rodlets, circular in section.

Remarks and comparison: The size, shape and ornamentation of this megaspore are very similar to those specimens described by Dijkstra (1955a, 1955b) as *Triletes brasiliensis*. In addition, the specimens illustrated by this author show little marked auriculae projection as in our case. This taxon shares some similarities with *Sublagenicula nuda* (Nowak and Zerndt, 1936) Dybová-Jachowicz et al., 1979. Both have auriculae projections, however, the studied specimens have a microgranular ornamentation whereas *S. nuda* is completely smooth.

Chronostratigraphic distribution of the studied material: Mid-late Tournaisian of Manuripi X1 borehole (see Chart 1, suppl. online material).

Stratigraphic and geographic range: Mississippian from Egypt and Nigeria. Pennsylvanian from Algeria, Sahara, Libya, Brazil and Argentina. Early Permian of South Africa, Argentina and Brazil (see Glasspool, 2003, pp. 274–275).

cf. *Lagenicula crassiaculeata* Zerndt, 1937 (Plate II)

Material: Specimen CICYTTP-M183 (see Chart 1, suppl. online material).

Description: Trilete megaspores, laterally compressed. The overall length is 370 µm and the width of the body is 281 µm. The surface of the gula is echinate and the remaining surface of the megaspore has an ornamentation composed of broad-based processes, several times

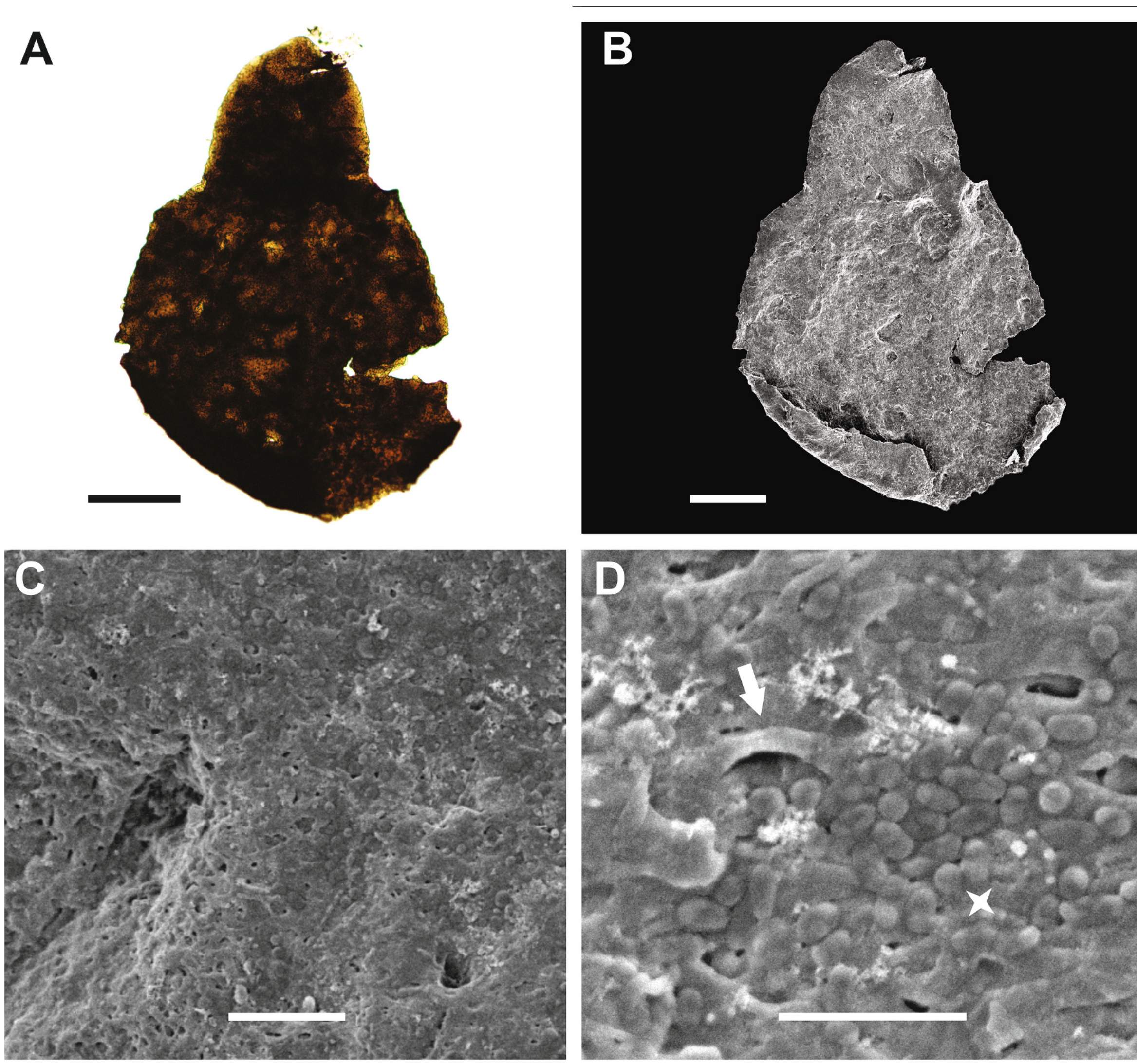

Plate I. *Lagenicula brasiliensis* (Dijkstra 1955) comb. nov. Specimen CICYTTP-M2.
1. Specimen observed with LM. Megaspore laterally compressed with spheroidal body and proximal gula. Scale bar 100 μm.
2–4. Specimen observed with SEM.
2. Megaspore laterally compressed whose gula has an auricular projection (arrow). Scale bar 100 μm.
3. Megaspore surface with microgranulate background ornamentation. Scale bar 10 μm.
4. Detail of the surface where microgranules are either, separated one from the other or laterally fused (star). The outermost layer of the exospore is composed of rodlets (arrow), which merge to form a three-dimensional network. Scale bar 5 μm.

branched, and a thinned apical tip ending in funnel form and by other processes without an apical funnel. Processes are 30–55 μm high and 9–15 μm wide in its base and 2–4 μm in diameter in its apical funnel. These processes are hollow with a wall of 0.6–1.7 μm thick and have transverse partitions located at different heights. The basal part of the processes is thinner, branched and anastomosed forming a reticulum that determined heterogeneous lumens, which constitutes the megaspore background.

Remarks and comparison: The studied megaspore is tentatively assigned to *L. crassiaculeata* due to the body ornamentation composed of processes with or without an apical funnel, which is a characteristic of this morphospecies. However, processes usually measure 200 μm long (Chaloner, 1953), whereas in the studied specimen they never exceed 55 μm high. In addition, the studied megaspore also differed from those described by Zerndt (1937) due to its smaller size. According to some authors, contact areas of the gula of this species are smooth (Zerndt, 1937; Karczewska, 1967), while for others minute spines are documented (Chaloner, 1953; Scott and Meyer-Berthaud, 1985) like in our specimen.

Chronostratigraphic distribution of the studied material: Mid-late Tournaisian of Manuripi X1 borehole.

Stratigraphic and geographic range: Lower Carboniferous of Scotland (Scott and Meyer-Berthaud, 1985; Bateman and Rothwell, 1990; Scott and Hemsley, 1991; Hemsley et al., 1996).

Lagenicula devonica Chaloner, 1959 (Plate III)
1959 *Lagenicula devonica* Chaloner, p. 325, pl. 55: 3.
1971 *Lagenicula devonica* Chaloner; Hills et al., p. 806, pl. 2: 3.
1973 *Lagenicula devonica* Chaloner; Chi and Hills, p. 245, pl. 1: 4.
1976 *Lagenicula devonica* Chaloner; Chi and Hills, p. 730, pl. 8: 1–8.

Material: Specimens CICYTTP-M160, 175 (see Chart 1, suppl. online material).

Description: Trilete megaspores, laterally compressed, with spheroidal body and a proximal gula. Contact areas are limited proximally by laesurae and distally by a well-defined curvaturae perfectae, a curved line joining the laesurae ends. The overall length (including the gula)

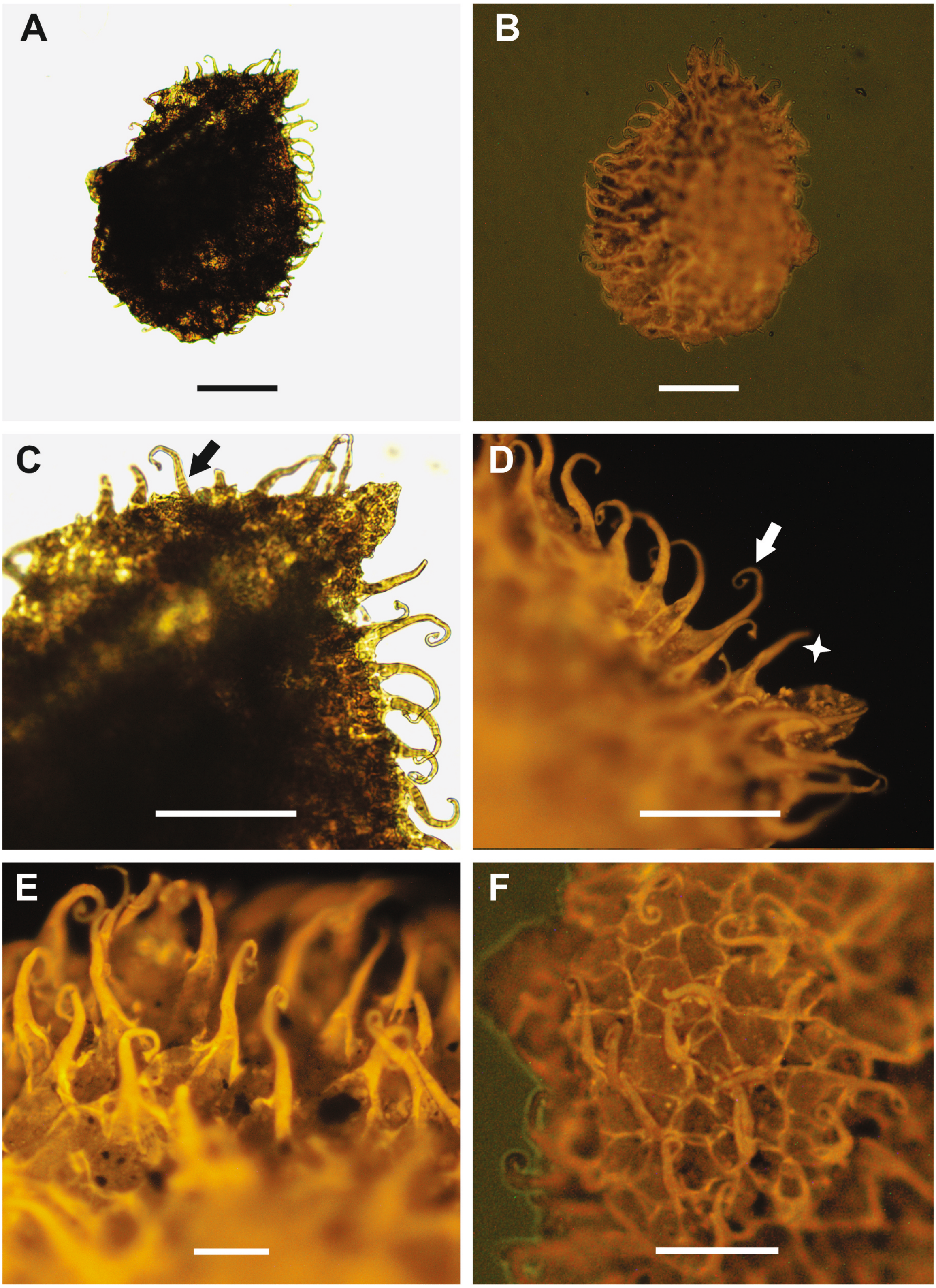

Plate II. cf. *Lagenicula crassiaculeata* Zerndt, 1937. Specimen CICYTTP-M183.
1. Megaspore laterally compressed observed with LM. Scale bar 100 μm.
2. Megaspore laterally compressed observed with fluorescence microscopy. Scale bar 100 μm.
3. Detail of processes that are hollow under LM and have transverse partitions located at different heights (arrow). Scale bar 50 μm.
4. Detail of processes, some with a thinned apical end ending in funnel form (arrow) and other without apical funnel (star). Scale bar 50 μm.
5. Detail of the processes that are observed thinned and branched at its base. Scale bar 20 μm.
6. Processes basis anastomosed forming a reticulum that determined heterogeneous lumens, which constituted the megaspore background. Scale bar 50 μm.

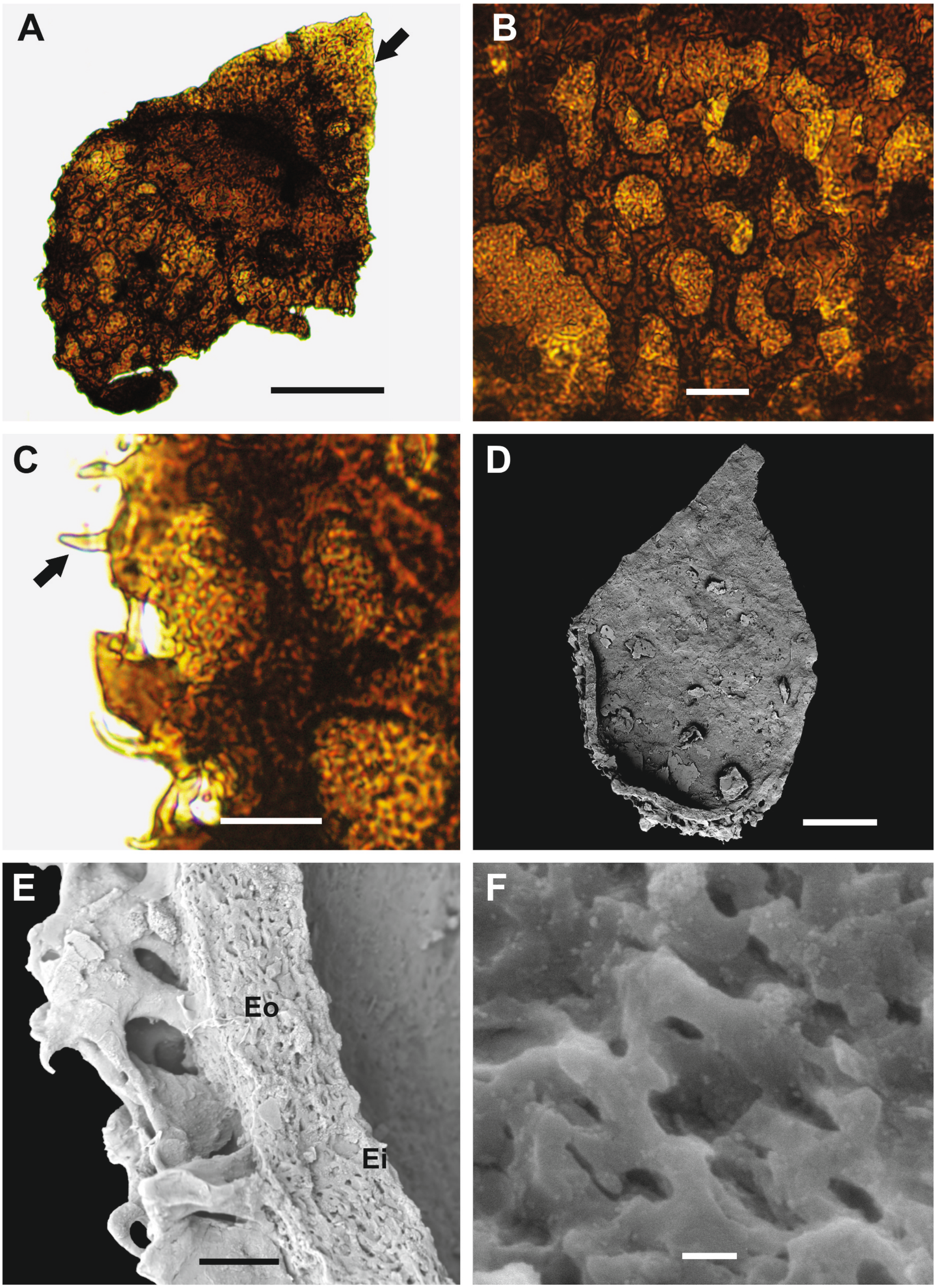

Plate III. *Lagenicula devonica* Chaloner, 1959.
1. Specimen CICYTTP-M160. Megaspore laterally compressed with well-developed gula, with verrucae on its surface (arrow) and well-defined curvaturae perfectae observed with LM. Scale bar 100 μm.
2–6. Specimen CICYTTP-M175 observed with LM (2–3) and SEM (4–6).
2. Megaspore body with muri consisting a well-defined reticulum with heterogeneous lumina. Scale bar 20 μm.
3. Detail of muri where spines with a curved apical end were observed (arrow). Scale bar 10 μm.
4. Megaspore laterally compressed with a fracture. Scale bar 100 μm.
5. Megaspore wall, in section, constituted by the ornamentation (reticulum), an external exospore (Eo) and an innermost exospore (Ei). Scale bar 10 μm.
6. Detail of the external exospore where rodlets located in different directions merged to form a three-dimensional network. Scale bar 1 μm.

ranges from 420 to 550 μm and the width of the body, from 280 to 312 μm, according to the equatorial axis. The gula is 233–320 μm in height and 247–278 μm in width, and in surface presents verrucae of 2–4 μm high. The megaspore body has muri, of 5–12 μm width, consisting in a well-defined reticulum with heterogeneous lumina of 7–30 μm in diameter. Muri are formed by rodlets that are arranged in different directions, some are perpendicular and others are tangentially to the surface. On the muri, spines with a curved apical end are observed. These spines measure 5–10 μm in height.

In section, the megaspore wall is 10–23 μm thick mostly due to the ornamentation (reticulum). The exospore also identified, of 11–16 μm thick, is differentiated into an external exospore (9–11 μm thick), which consisted of rodlets that are arranged in different directions forming a three-dimensional network and, into a compact and thinner innermost exospore (1.5–2.5 μm thick).

Remarks and comparison: The studied specimens are similar to those originally described by Chaloner (1959). In addition, the megaspores present spines on the reticulum as described by Chi and Hills (1976). According to the latter, this pattern of reticulation is due to the fusion of the bases of spines. However, in the studied specimens it is mainly form by rodlets that are arranged in different directions.

Chronostratigraphic distribution of the studied material: It is likely part of the Devonian reworked assemblage of micro-megaspores and other palynomorphs in the Lower Carboniferous of the Pando X1 and Manuripi X1 boreholes (di Pasquo et al., 2019a).

Stratigraphic and geographic range: Upper Devonian of Canada (Chaloner, 1959; Hills et al., 1971, 1984; Chi and Hills, 1973, 1976; Whiteley, 1980), and Greenland (Allen, 1972). Strunian of United States (di Pasquo et al., 2019b).

cf. *Lagenicula hirsutoida* Dijkstra and Piérart, 1957 (Plate IV)

Material: Specimen CICYTTP-M58 (see Chart 1, suppl. online material).

Description: Trilete megaspore, laterally compressed, with spheroidal body and proximal gula. Contact areas limited proximally by the laesura and distally by a well-defined curvaturae perfectae. The total length (including the gula) is 185 μm and the width of the body is 155 μm. The gula, 78 μm high and 136 μm wide, lacks ornamentation. The body of

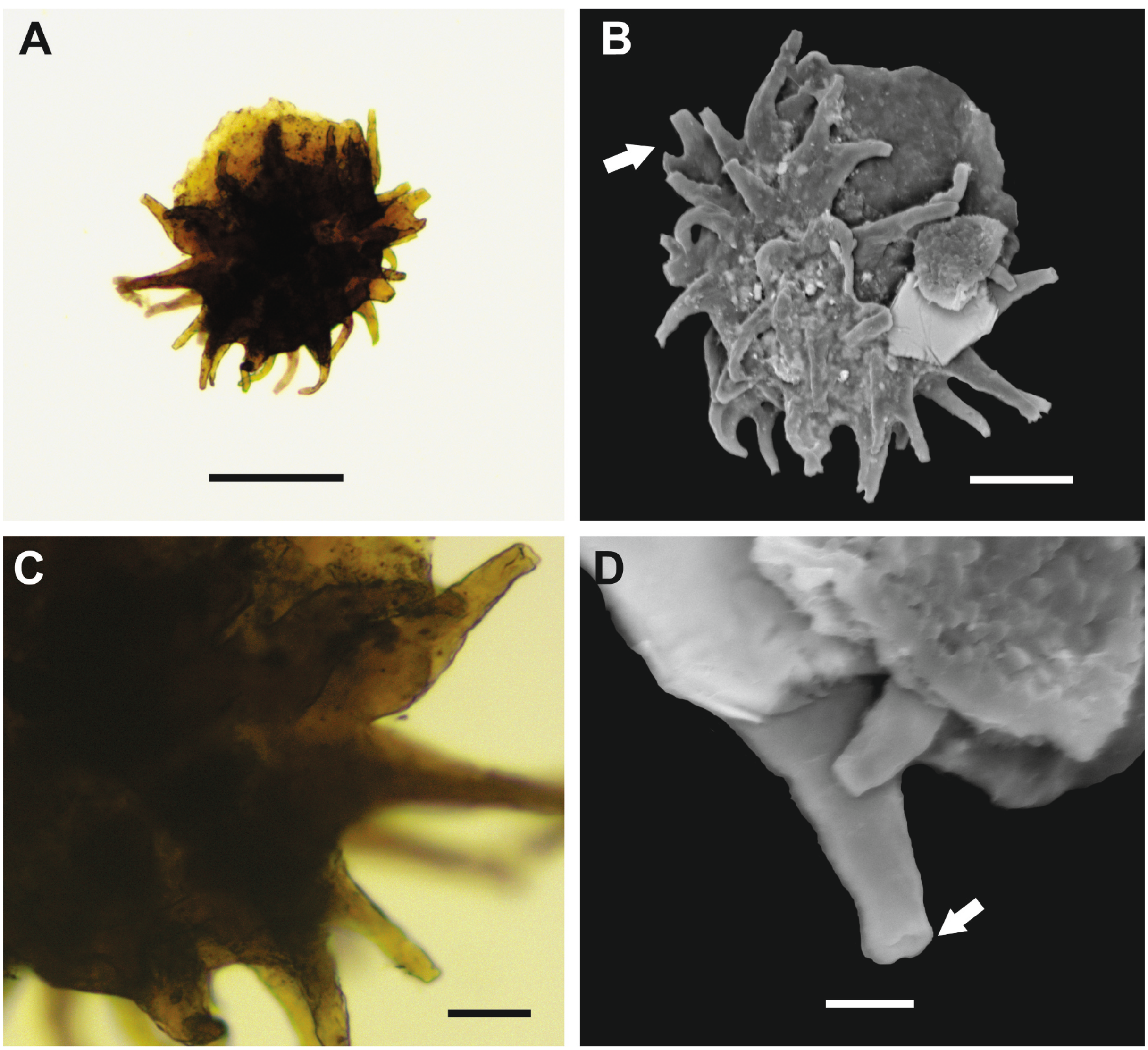

Plate IV. cf. *Lagenicula hirsutoida* Dijkstra and Piérart, 1957. Specimen CICYTTP-M58.
1. Megaspore laterally compressed with spheroidal body, proximal gula and a well-defined curvaturae perfectae. Scale bar 100 μm.
2. Megaspore in general view with a smooth gula and an ornamented body with densely distributed processes that may be laterally fused (arrow). Scale bar 50 μm.
3. Detail of the ornamentation showing elements with a wide base, hollow and blunt apex. Scale bar 20 μm.
4. Detail of processes showing clearly they are hollow (arrow). Scale bar 10 μm.

this megaspore is densely, covered by processes with a broad base and a blunt, hollow apex. The bases may be laterally fused. They are 32–65 μm long, 10–20 μm wide at the base, and 5–8 μm at the apex.

Remarks and comparison: The studied megaspore is tentatively assigned to *L. hirsutoida* due to the similarity in their sculptural elements, both presenting a blunt and hollow apex. Although the processes sizes of the base and apex are similar, the length in the studied specimen is much smaller than in *L. hirsutoida*, in which processes can reach 100 μm in length.

Chronostratigraphic distribution of the studied material: Mid-late Tournaisian of Manuripi X1 borehole.

Stratigraphic and geographic range: Lower Carboniferous of Russia (Dijkstra and Piérart, 1957; Glasspool et al., 2000) and Canada (Glasspool and Scott, 2005).

Lagenicula illizii (Candilier et al., 1982) comb. nov. (Plate V)
Basionym: *Lagenoisporites illizii* Candilier et al., 1982, p. 183, p. 92, pl. 3: 1–8.

Material: Specimens CICYTTP-M90, 199, 218 (see Chart 1, suppl. online material).

Description: Trilete megaspores, laterally compressed, with spheroidal body and gula. The overall length (including the gula) is 168–260 μm and the width of the body is 180–236 μm. The gula is 66–147 μm height, 109–193 μm width and is ornamented by low and broad-based spines. The megaspore body is composed of stout sculptural elements with a wide base that narrows towards the apex, this being blunt, sharp or rounded. These sculptural elements range from 9 to 15 μm high, and 7–13 μm wide in their base and 5–9 μm in their middle portion. Some of these elements are laterally fused forming ridges. Perforations are observed, as background ornamentation, between sculptural elements and in their basal portion.

Remarks and comparison: Candilier et al. (1982) described megaspore specimens bearing a more developed gula and thinner sculptural elements in comparison with the megaspores of this research. Although, we

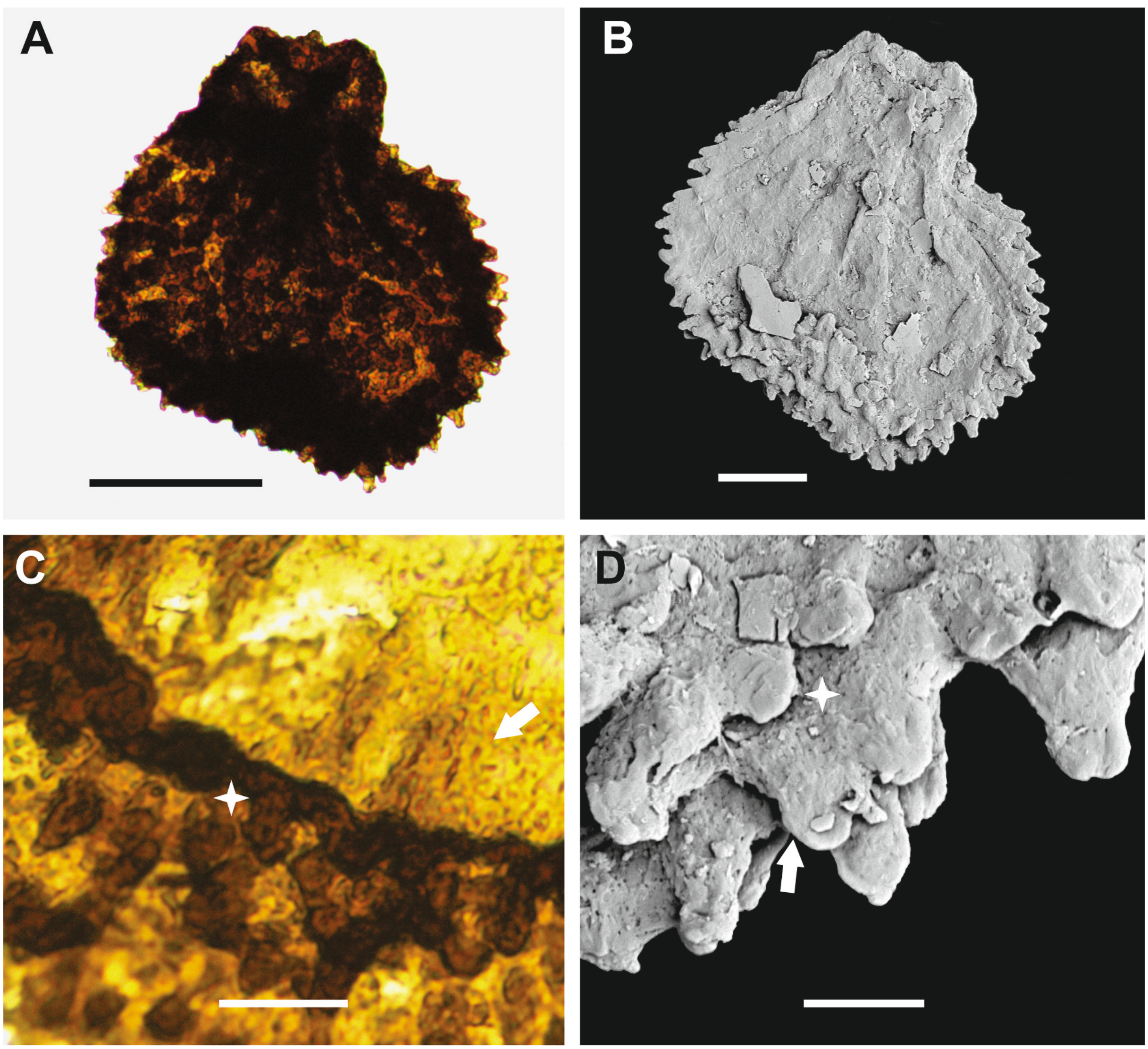

Plate V. *Lagenicula illizii* (Candilier et al., 1982) comb. nov.
1. Specimen CICYTTP-M90. Megaspore laterally compressed with spheroidal body and proximal gula observed with LM. Scale bar 100 μm.
2. Specimen CICYTTP-M90 observed with SEM. Scale bar 50 μm.
3. Specimen CICYTTP-M199. Gula ornamentation represented by spines (arrow) while that of the body is composed of robust sculptural elements laterally fused at the level of the megaspore curvaturae (star). Scale bar 20 μm.
4. Specimen CICYTTP-M90. Detail of the body processes, with elements with a broad base narrowing towards the apex, which can be seen as blunt, pointed or rounded. Some of these sculptural elements are laterally fused forming ridges (arrow). Between these sculptural elements and in their basal portion, perforations can be seen as background (star). Scale bar 10 μm.

consider they are subtle differences to separate them from the *L. illizii*. A similar megaspore is *Lagenicula acuminata* Dijkstra and Piérart, 1957 that shares with this latter stout ornamentation in their main body, however, in *L. acuminata* spines are higher (75 μm high) than the elements presented in *L. illizii*, which do not exceed 15 μm in height.

Chronostratigraphic distribution of the studied material: It is likely part of the Devonian reworked assemblage of micro-megaspores and other palynomorphs in the Lower Carboniferous of the Pando X1 and Manuripi X1 boreholes (di Pasquo et al., 2019a).

Stratigraphic and geographic range: Late Famennian-Strunian of Algerian Sahara and western Libya (Candilier et al., 1982).

Lagenicula magna (Chi and Hills, 1976) comb. nov. (Plate VI)

Basionym: *Verrucisporites medius* var. *magnus* Chi and Hills, 1976, p. 700, pl. 2: 5–8.

1982 *Lagenoisporites magnus* (Chi and Hills, 1976); Candilier et al., 1982: 91, pl. 3: 1–8.

2019 *Lagenoisporites magnus* (Chi and Hills, 1976); Quetglas et al., 2019: 5, fig. 2–4.

Material: Specimens CICYTTP-M55, 112, 119, 122, 124, 129, 130, 131, 135, 136, 139, 140, 141, 144, 151, 152, 162, 163, 380, 406, 411, 428 (see Chart 1, suppl. online material).

Description: Trilete megaspores, laterally compressed, with spheroidal body, gula and a well-defined curvaturae perfectae. Gula has verrucae and the rest of the body, complex processes constituted by a bulbous base and a projection with an acute apex. The gula and the body surface of the megaspores show perforations as a background ornamentation (see Quetglas et al., 2019). Through the observation of a fracture, it is possible to identify the exospore outermost layer, which has a spongy structure formed by a three-dimensional network of fused rodlets delimiting heterogeneous spaces (see Quetglas et al., 2019).

Remarks and comparison: Morpho-structural details, figures and discussion about this species in Quetglas et al. (2019).

Chronostratigraphic distribution of the studied material: Probably as part of the Devonian reworked assemblage of micro-megaspores and other palynomorphs in the Lower Carboniferous of the Pando X1 and Manuripi X1 boreholes (di Pasquo et al., 2019a).

Stratigraphic and geographic range: Givetian-Famennian of Canada (Chi and Hills, 1976), late Famennian-Strunian of Algerian Sahara and western Libya (Candilier et al., 1982).

Lagenicula media (Chi and Hills, 1976) comb. nov. (Plate VII).

Basionym: *Verrucisporites medius* var. *medius* Chi y Hills, 1976, p. 699, pl. 2: 1–4.

1976 *Verrucisporites medius* var. *medius* sp. nov.; Chi and Hills, 1976: 699, pl. 2: 1–4.

1982 *Lagenoisporites medius* (Chi and Hills, 1976); Candilier et al., 1982: 91, pl. 2: 1–4.

Material: Specimens CICYTTP-M92, 123, 147, 165 (see Chart 1, suppl. online material).

Description: Trilete megaspores, laterally compressed, with spheroidal body, well-developed hologula and well-defined curvaturae perfectae. The overall length (including the gula) ranges from 300 to 560 μm and the width of the body, from 245 to 361 μm. The gula is 205–345 μm high and 178–328 μm wide. Gula has dispersed verrucae that do not exceed 1–5 μm high. From the middle portion towards the base of the gula, radially arranged folds are observed. The megaspore body has 3–8 μm high and 4–7 μm wide verrucae, laterally joined forming ridges with a marked radial distribution. As background, the surface of all the specimens of this megaspore is perforated.

Remarks and comparison: The studied specimens differed from other megaspores with verrucae, such as *Lagenicula verrucosa* Spinner, 1965 and *L. irregularis* Spinner, 1965, in which the width of verrucae, especially those of the body, range from 10 to 32 and 15–84 μm respectively. Instead, the verrucae in our specimens do not exceed 7 μm wide that is in agreement with *L. medius*.

Chronostratigraphic distribution of the studied material: It is probably part of the Devonian reworked assemblage of micro-megaspores and other palynomorphs in the Lower Carboniferous of the Pando X1 and Manuripi X1 boreholes (di Pasquo et al., 2019a).

Stratigraphic and geographic range: Givetian-Famennian of Canada (Chi and Hills, 1976), late Famennian-Strunian of Algerian Sahara and western Libya (Candilier et al., 1982).

Lagenicula microechinata Hills et al., 1984 (Plate VIII).

1984 *Lagenicula microechinata* sp. nov.; Hills et al., 1984: 218, pl. 4: 1–9.

Material: Specimens CICYTTP-M134, 170, 423 (see Chart 1, suppl. online material).

Description: Trilete megaspores, laterally compressed, with spheroidal body, proximal gula and a well-defined curvaturae perfectae. The overall length (including the gula) is 360–410 μm and the width of the body is 213–255 μm. The gula ranges from 173 to 212 μm in height and 188–196 μm in width, and has verrucae of 1–3 μm high. The ornamentation of the main body is composed of spines, which are 6–11 μm high and 2–3 μm width in its base. The gula and the body surface show perforations. Through the observation of a fracture of the gula, the outermost layer of the exospore is constituted of fused rodlets that form a reticulated and spongy type structure.

Remarks and comparison: The studied megaspores have a similar ornamentation to those originally described by Hills et al. (1984), except for the basal diameter of the spines, which is smaller in this study. The studied megaspores also show similarity with *Lagenicula constrictus* Chi and Hills, 1976, except for the lack of the typical constriction in spines of the latter.

Chronostratigraphic distribution of the studied material: Mid-late Tournaisian of Pando X1 and Manuripi X1 borehole.

Stratigraphic and geographic range: Tournaisian of Canada (Hills et al., 1984) reconsidered as latest Devonian (Strunian) by Harland et al. (1990).

Lagenicula morbelliae sp. nov. (Plate IX)

Etymology: Dedicated to Dr. Marta Morbelli, professor of Universidad Nacional de La Plata, Argentine, for her valuable contribution in Palynology.

Type material: CICYTTP-M404 (holotype), CICYTTP-M 148 (paratype).

Type locality: Pando X1 borehole.

Type horizon: CICYTTP 2611 (Fig. 2).

Material: Specimens CICYTTP-M142, 148, 384, 404 (see Chart 1, suppl. online material).

Diagnosis: Trilete megaspore with spheroidal body, proximal gula and well-defined curvaturae perfectae. The ornamentation of the gula is characterised by coni, and that of the body, by clavae bearing an apical thin spine. A reticulum with heterogeneous spaces is developed on the surface of the megaspores.

Description: Trilete megaspore with spheroidal body, well-developed gula and well-defined curvaturae perfectae. The overall length (including the gula) ranges from 270 to 560 μm and the width of the body ranges from 165 to 314 μm. The gula ranges from 102 to 286 μm high and 124–301 μm wide. The surface of the gula has coni with an acute apex and a basal spheroidal outline. Coni are 4–7 μm high, 2–4 μm wide in the base and 0,5–1 μm in the apex. These elements are densely distributed in the area near the curvaturae. The body has clavae with an apical projection like a thin spine with a height of 5–8 μm, and 1–2 μm wide at the base and the apical portion 2–3 μm. In some cases, the clavae are laterally fused. In addition, a reticulate type background with heterogeneous spaces giving rise to a close and dense structure is observed.

Remarks and comparison: The studied megaspores are similar to *Lagenoisporites clavatus* (Karczewska, 1967) Dybová-Jachowicz et al., 1979, sharing a clavate ornamentation, although the elements are longer (16–40 μm), and wider in their base (6–9 μm wide) and apex

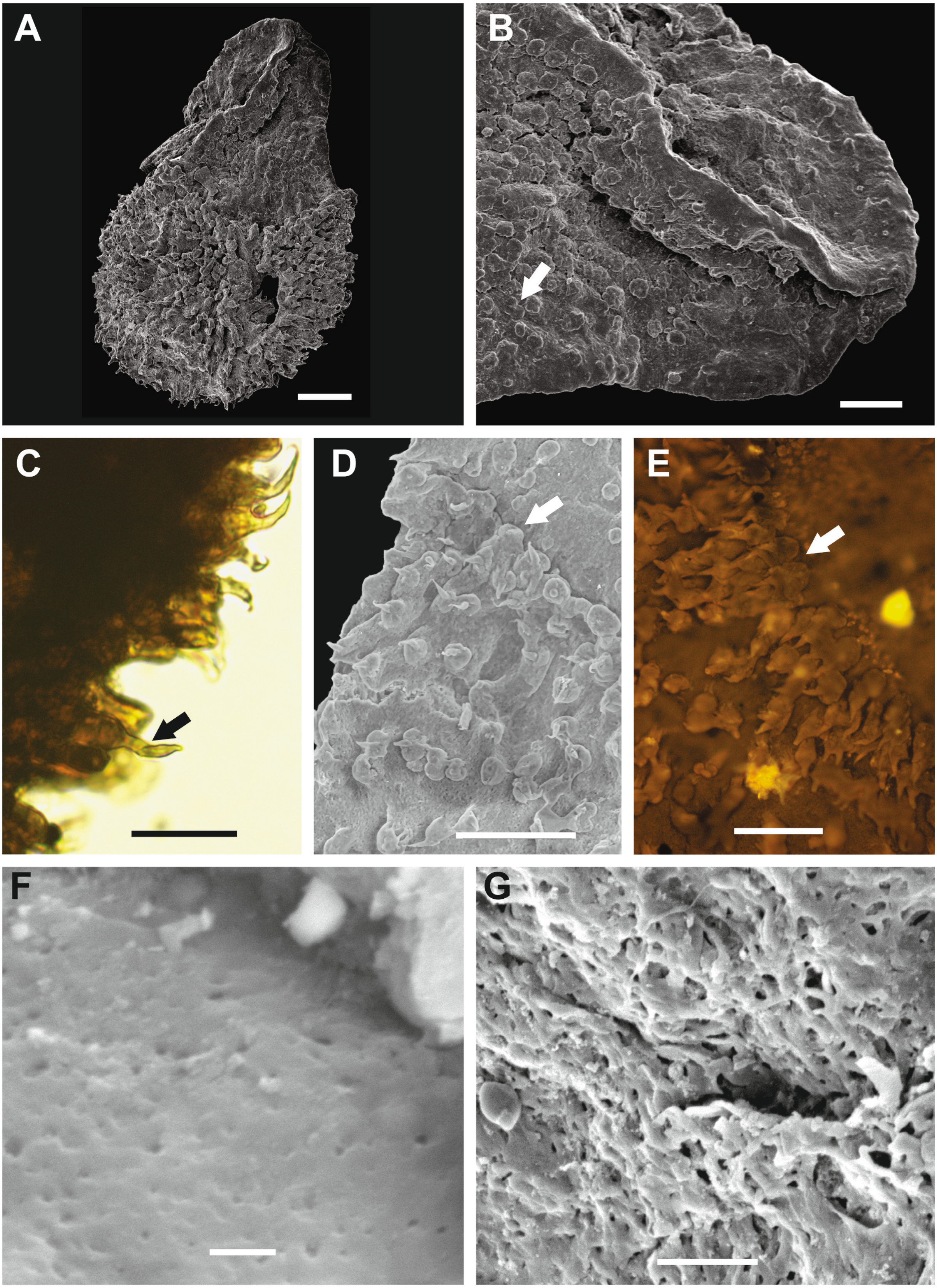

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Plate VI. *Lagenicula magna* (Chi and Hills, 1976) comb. nov.
1. Specimen CICYTTP-M162 observed with SEM. Megaspore laterally compressed where the body, the gula and the curvaturae perfectae are distinguished. Scale bar 50 μm.
2. Specimen CICYTTP-M162 observed with SEM. Gula with verrucae ornamentation, some of them con be fused (arrow). Scale bar 20 μm.
3. Specimen CICYTTP-M162 observed with LM. Detail of the complex processes on the spore body, constituted by a bulbous base and a projection, internally septate (arrow), with an acute apex. Scale bar 20 μm.
4. Specimen CICYTTP-M428 observed with SEM. Detail of the curvaturae perfectae surface (arrow). Scale bar 30 μm.
5. Specimen CICYTTP-M144 observed with fluorescence microscopy. Complex processes, in the curvaturae perfectae, with their bases laterally fused (arrow). Scale bar 20 μm.
6. Specimen CICYTTP-M162 observed with SEM. Detail of the body megaspore surface showing perforations. Scale bar 2 μm.
7. Specimen CICYTTP-M136 observed with SEM. Detail of a fractured megaspore where the exospore outermost layer can be seen, bearing a spongy structure formed by a three-dimensional network of fused rodlets delimiting heterogeneous spaces. Scale bar 2 μm.

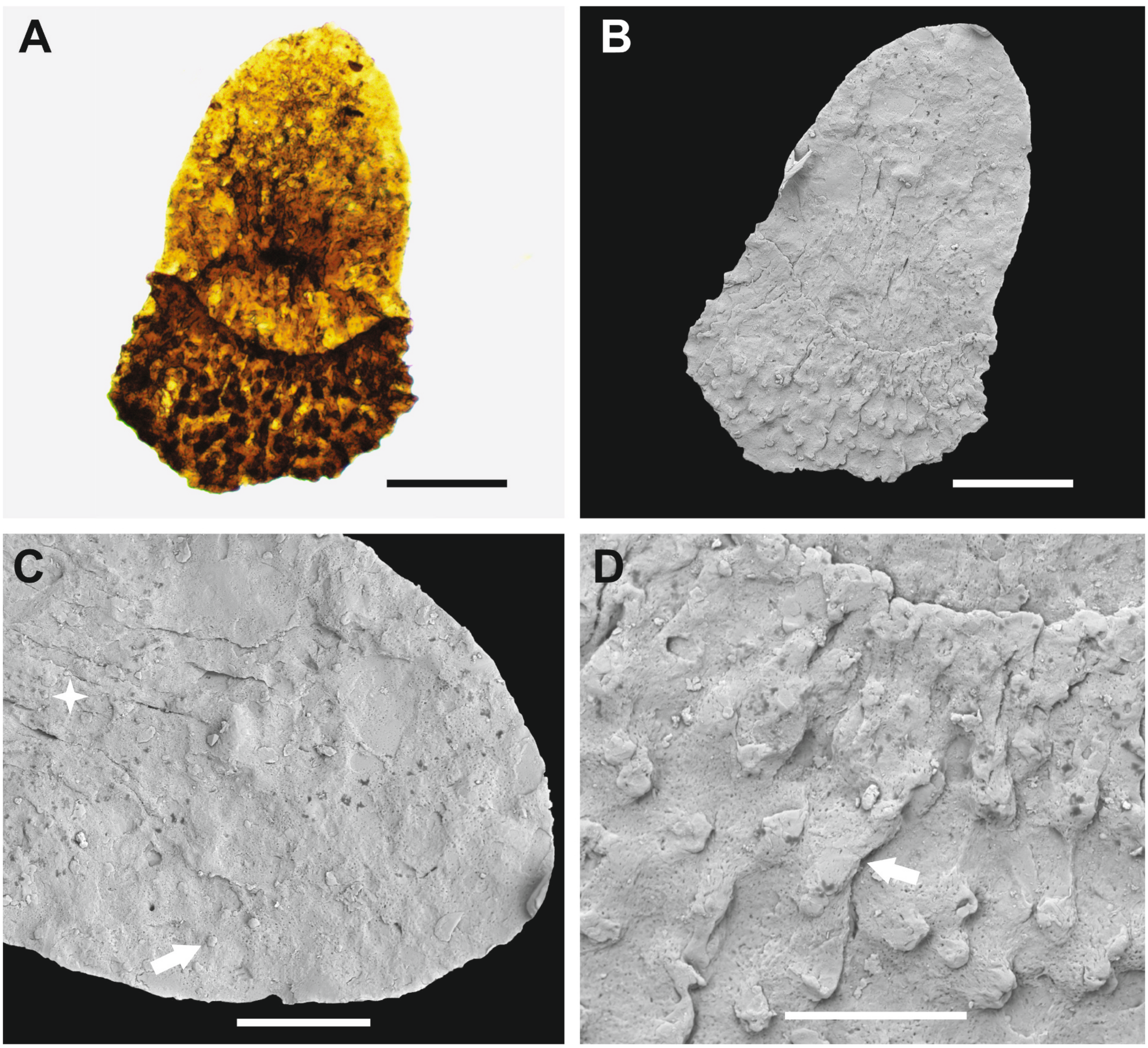

Plate VII. *Lagenicula media* (Chi and Hills, 1976) comb. nov. Specimen CICYTTP-M123.
1. Megaspore, observed with LM, laterally compressed with spheroidal body, a highly developed proximal gula and a well-defined curvaturae perfectae. Scale bar 100 μm.
2. Megaspore laterally compressed, observed with SEM. Scale bar 100 μm.
3. Gula with dispersed verrucae (arrow) and folds (star) radially arranged from the middle portion towards their base. Scale bar 50 μm.
4. Megaspore body with verrucae that are laterally joined forming ridges with a marked radial distribution (arrow) and perforations in the surface. Scale bar 20 μm.

(9–16 μm high), and lack an apical spine. The gula supports its assignment to the genus *Lagenicula* and the presence of a spine in the clavae considered a diagnostic character to support the definition of a new species.

Chronostratigraphic distribution of the studied material: Mid-late Tournaisian of Pando X1 and Manuripi X1 boreholes.

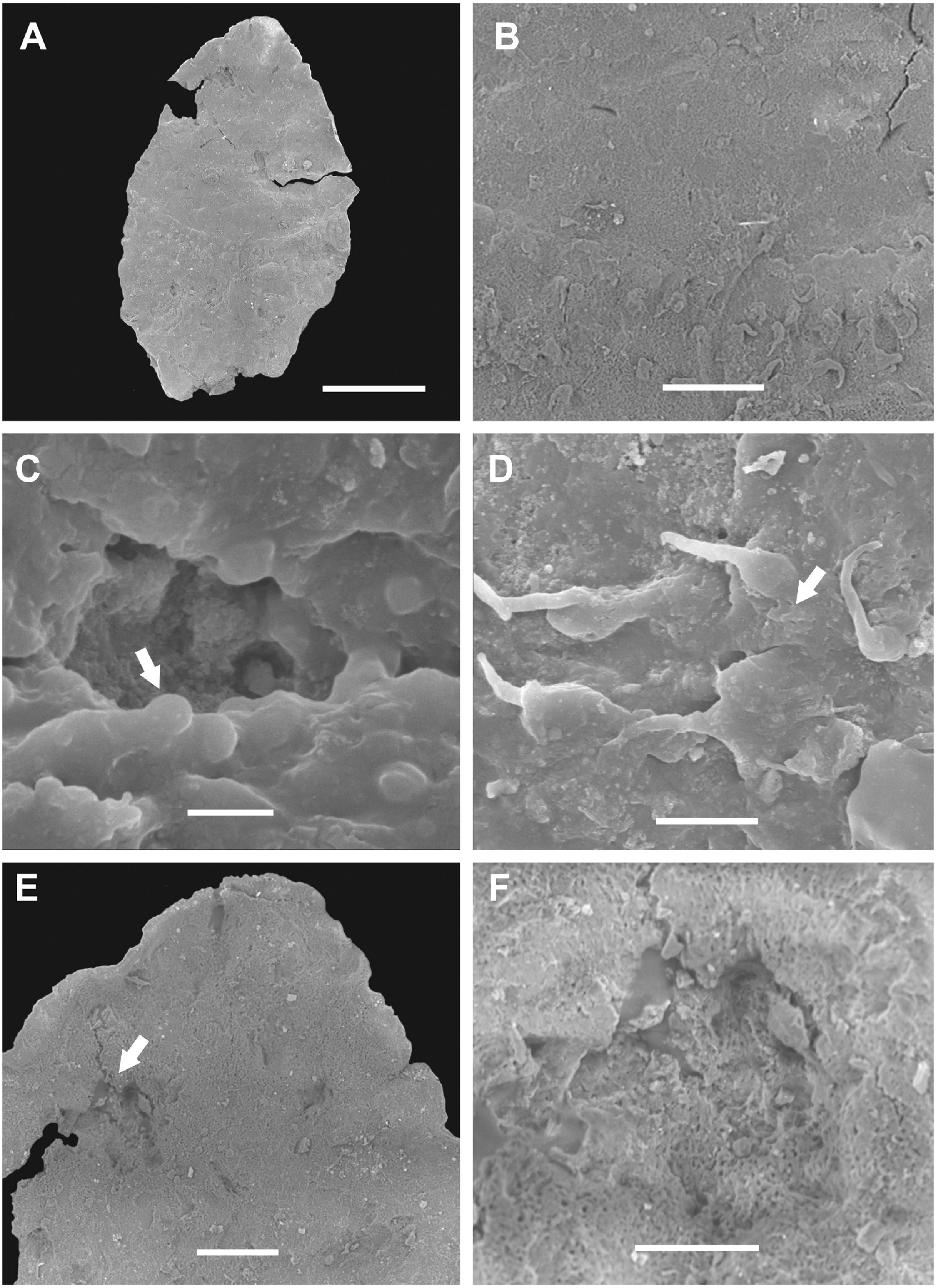

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Plate VIII. *Lagenicula microechinata* Hills et al., 1984.
1. Specimen CICYTTP-M423 observed with SEM. Megaspore laterally compressed with spheroidal body, proximal gula and a well-defined curvaturae perfectae. Scale bar 100 μm.
2. Specimen CICYTTP-M423. Detail of the curvaturae perfectae where the differentiation of ornamentation between the gula and the rest of the body can be observed. Scale bar 20 μm.
3. Specimen CICYTTP-M134 observed with SEM. Detail of the gula with dispersed verrucae (arrow) of reduced size and circular amb. Scale bar 5 μm.
4. Specimen CICYTTP-M134. Detail of the megaspores body with spines and perforations (arrow) in the surface. Scale bar 5 μm.
5. Specimen CICYTTP-M423. Megaspore fractured at the level of the gula where the outermost layer of the exospore can be seen (arrow). Scale bar 20 μm.
6. Specimen CICYTTP-M423. Detail of photo 5, where the exospore constitutes of fused rodlets forming a reticulated and spongy type structure is observed. Scale bar 10 μm.

4. Discussion

4.1. Taxonomy

The mid-late Tournaisian megaspore assemblage of Toregua Formation, Bolivia, was diverse. It was composed of nine morphospecies of the genus *Lagenicula*, including a new one. The taxonomic history of the genus *Lagenicula* is highly complex (Wellman et al., 2009). Some authors (e.g. Archangelsky et al., 1989; Glasspool et al., 2000) follow Piérart (1978) and Dybová-Jachowicz et al. (1979) and agree to differentiate gulate megaspores genera by using ornamentation and type of gula as diagnostic characters. Others (e.g. Arioli et al., 2004, 2007; Wellman et al., 2009) prefer to follow Spinner (1969, 1983), who proposed to avoid the use of different types of gula to support different genus, because of the difficulties to distinguish subtle features of the gula in specimens preserved in polar and oblique compressions or even worse, when the gula is broken. We also agree with Spinner (1969, 1983) that there is no need to maintain the genus *Lagenoisporites* Potonié and Kremp, 1954 only for smooth/laevigate forms. Therefore, we prefer to retain *Lagenicula* as the senior synonym of the genera *Lagenoisporites, Sublagenicula*, *Auritolagenicula*, *Crassilagenicula* and *Zonolagenicula* in accordance with Spinner and other authors (e.g. Arioli et al., 2007; Wellman et al., 2009), until gulate megaspore taxonomy can be clarified.

4.2. Botanical affinity

The incipient megaspore *Acinosporites macrospinosus* Richardson 1965, produced by one of the first groups of heterosporous lycopsids, is considered the earliest report of an apical prominence or gula, an attribute that went on to characterise many megaspores of later lycopsids (Wellman, 2022) as in *Lagenicula* which could derivate, almost exclusively, from the Lepidocarpaceae/Lepidodendraceae family (Arioli et al., 2007).

This family of heterosporous arborescent lycopsids are considered to have formed dense forest, not only of great dimensions and variability but also with ecological complexity, especially, in the Mississippian and Pennsylvanian of northern Hemisphere (Bell, 1960; Glasspool and Scott, 2005; DiMichele et al., 2007; Arioli et al., 2007; Wellman et al., 2009). Their record is here geographically extended up to the Early Carboniferous in northern Bolivia.

According to Glasspool et al. (2000), the exospore ultrastructure of gulate megaspores is divided into an external, intermediate, internal layer and a basal lamina, while for Arioli et al. (2007) and Wellman et al. (2009), the exospore presents two layers (external and internal). The megaspores studied in this research revealed having the latter two layers of exospore, and the external composed of a three-dimensional network of fused rodlets giving the appearance of a spongy structure. This wall structure demonstrates the close phylogenetic relationship with heterosporous arborescent lycophytes of the Lepidocarpaceae family.

Within the Lycophyte lineage, it is proposed that heterospory would have evolved once (Bateman and DiMichele, 1994), that is, a monophyletic group of heterosporous lycophytes could have inherited the mode of the megaspore wall formation, which evolved from a simple modification of the basic developmental process of homosporous spores (Arioli et al., 2007). This mode of megaspores wall formation, and thus their ultrastructure, persisted relatively unchanged (stasis) from those with gula (Wellman et al., 2009) to present-day heterosporous lycophytes (Tryon, 1986; Arioli et al., 2007). According to Arioli et al. (2007), this stasis would only be present in the Selaginellaceae Willk. However, stasis has also been observed in the wall structure of Isoetaceae Reichenb (Wellman, 2002), in which its outermost portion would present a variable structure with the ability to differentiate in response to external factors, allowing adaptations to special environmental conditions (Tryon, 1986).

Therefore, like numerous fossil megaspores assigned to lycophytes that show similarities in their ultrastructure with Isoetales (Macluf et al., 2003), our species of megaspores present an exospore with a spongy structure referred to a three-dimensional network of fused rodlets forming heterogeneous spaces. This pattern agrees with the general scheme described by Lugardon et al. (2000) for current lycophytes and supports Tryon's (1986) proposal of the stasis of the wall structure of megaspores like in current Isoetales. The stability in the mode of the wall formation of Lycophytes turns out to be the most interesting phenomenon in their evolution since it could allow us to understand even more the morphological progression from homospory to heterospory.

4.3. Biostratigraphy

Records of Tournaisian megaspores are still scarce worldwide (e.g. Chaloner, 1954; Winslow, 1962; Mortimer et al., 1970; Hills et al., 1984; Scott and Meyer-Berthaud, 1985; Hemsley et al., 1994; Glasspool et al., 2000; Glasspool and Scott, 2005) and Bolivia is no exception, since there are no previous researches on this type of megaspores for this period of time. In turn, Mississippian records of *Lagenicula* species have not been documented from other South American countries, but they are known from Pennsylvanian and Permian deposits mainly from Argentina and Brazil (e.g. Arai and Rösler, 1984; Archangelsky et al., 1989; Cúneo et al., 1991; Ricardi-Branco et al., 2002; Amaral and Ricardi-Branco, 2004; Mune et al., 2011). Gulate megaspores appear in the Devonian, specifically in the Frasnian (Chaloner, 1967). However, the genera *Lagenicula* begun to become more abundant during the Mississippian to become dominant during the Pennsylvanian (Scott and Hemsley, 1996). Despite the fact that the gulate megaspores of this study were identified in Mississippian deposits (see di Pasquo et al., 2015, 2019a), some of the morphospecies are considered Mississippian in age (*Lagenicula brasiliensis*, *Lagenicula microechinata*, cf. *Lagenicula crassiaculeata*, cf. *Lagenicula hirsutoida*). Others (*Lagenicula devonica, Lagenicula illizii, Lagenicula magna, Lagenicula media*) are interpreted as likely reworked forms from Devonian deposits, following their previous records (Fig. 3). The frequent record of Devonian spores and marine taxa (acritarchs, prasinophytes, chitinozoans, others) in Mississippian and Pennsylvanian deposits of the Pando X1 and Manuripi X1 boreholes is due to the erosion of underlying Devonian rocks (see di Pasquo et al., 2015, 2019a, 2022). The same evidence documented in previous works carried on in Bolivia and northern Argentina (e.g. di Pasquo, 2003, 2007a, 2007b, 2009a, 2009b, 2022; di Pasquo and Streel, 2022; di Pasquo et al., 2017, 2022) allows us to support this interpretation.

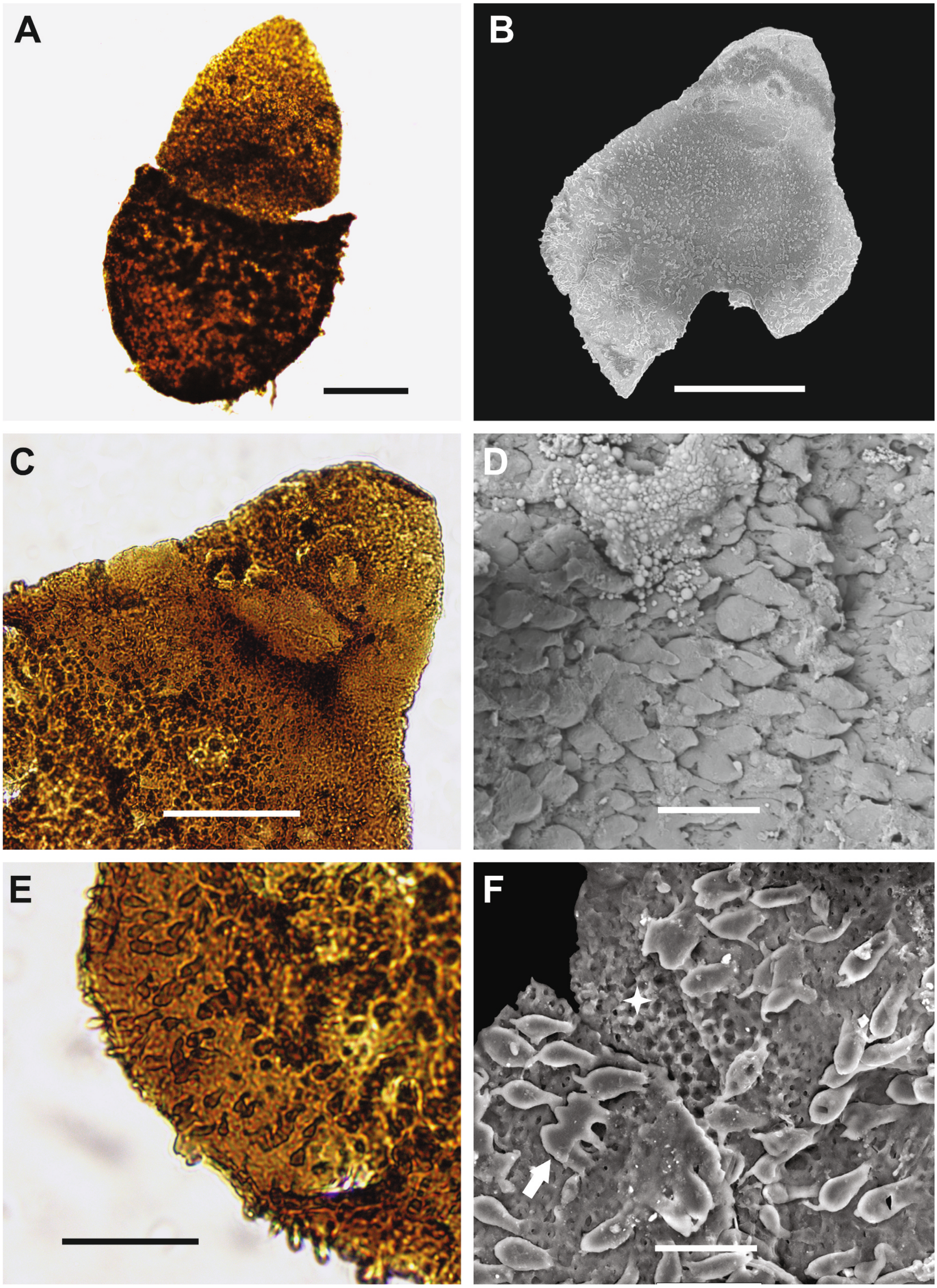

Plate IX. *Lagenicula morbelliae* sp. nov.

1. Specimen CICYTTP-M148 observed with LM. Megaspore laterally compressed with proximal gula and a well-defined curvaturae perfectae. Scale bar 100 μm.
2. Specimen CICYTTP-M404 observed with SEM, laterally compressed. Scale bar 100 μm.
3. Specimen CICYTTP-M404 observed with LM. Detail of the gula surface with coni densely distributed in the area near the curvaturae. Scale bar 20 μm.
4. Specimen CICYTTP-M148 observed with SEM. Detail of coni with the acute apex and spheroid amb. Scale bar 10 μm.
5. Specimen CICYTTP-M404 observed with LM. Megaspore body ornamentation represented by clavate elements bearing apical thin spine. Scale bar 20 μm.
6. Specimen CICYTTP-M404 observed with SEM. Detail of clavae where in some cases, the clavae enlarged portion are laterally fused (arrow). A reticulate dense pattern with heterogeneous spaces is observed (star). Scale bar 10 μm.

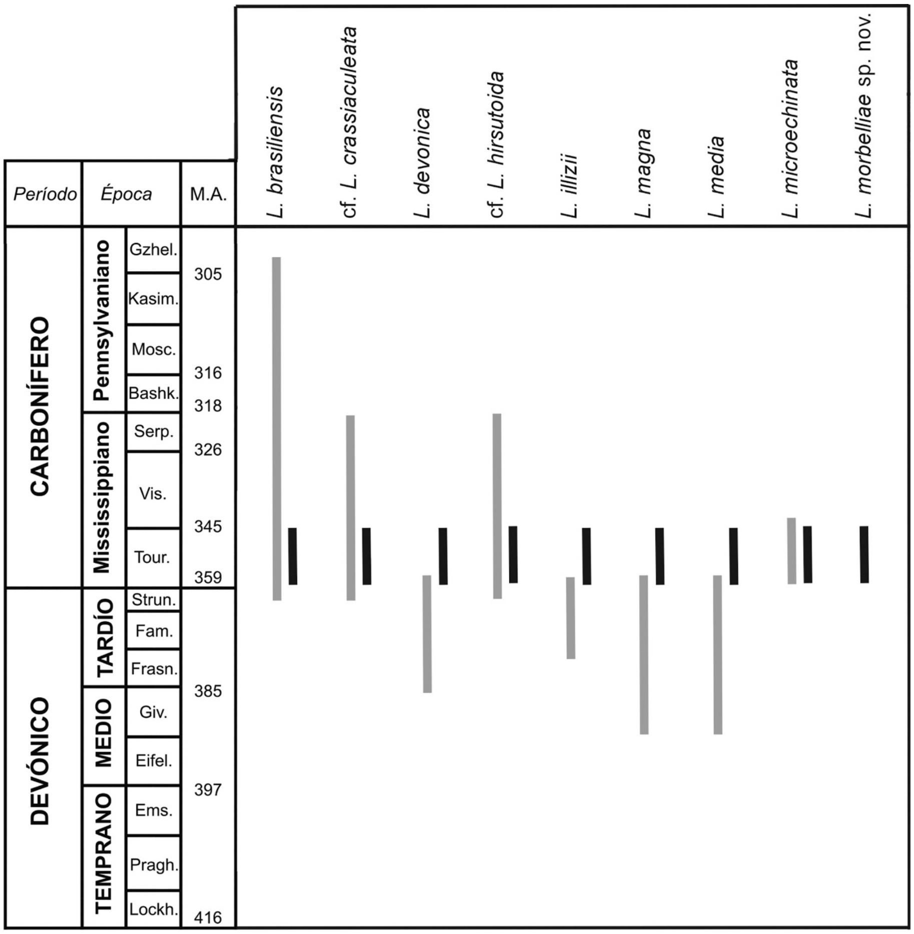

Fig. 3. Range chart of the megaspores analysed in this study. Grey bars indicate the stratigraphic range of the morphospecies and black bars, the stratigraphic range of the studied material.

5. Conclusion

This research contributes with information about gulate megaspores from Early Carboniferous (lower Mississippian, Tournaisian) of Bolivia providing the first evidence for these megaspores from this region. The excellent preservation of specimens recovered, plus the combination of optical, fluorescence and scanning electron microscopy, allowed us a thorough and detailed study not only of the ornamentation, but also, in some cases, of the sporoderm structure, more specifically of the exospore.

The taxonomic study of gulate megaspore performed allowed us to described nine morphospecies of the genus *Lagenicula*, including the combination of *Lagenicula brasiliensis*, *Lagenicula illizii, Lagenicula magna, Lagenicula media*, and a new one, *Lagenicula morbelliae nov.* sp., which is distinguished from other species due to the presence of a spine surmounted on the clavae conforming the ornamentation. A work ongoing will analyse the megaspores found with transmission electron microscopy (TEM) in order to be able to describe in detail the ultrastructure of the wall and therefore, provide new evidence on their botanical affinity to heterosporous arborescent lycopsids (Lepidocarpaceae/Lepidodendraceae), and their evolution.

Declaration of Competing Interest

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.

Data availability

No data was used for the research described in the article.

Acknowledgements

This study was part of a Ph.D. thesis (Quetglas, 2021). The authors deeply thank Diego Di Pietro for reading a preliminary version and Dr. Marta Morbelli for her valuable contributions and unconditional support. The authors also thank Leonardo Silvestri for his assistance in the laboratory processing, and the assistance of Patricia Sarmiento for taking pictures in SEM at the *Museo de Ciencias Naturales de La Plata* (Buenos Aires province), and MSc. Ing. José Félix Vilá in SEM at CICYTTP-CONICET-ER-UADER (Entre Ríos province). This research was supported by grants given by the Consejo de Investigaciones Científicas y Técnicas to M. di Pasquo (CONICET-PIP 0812) and the Universidad Nacional de La Plata to C. Macluf (UNLP-PPID N028).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2023.104971.

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