Lancettopsis harringtonii sp. nov, a new acritarch and related morphotypes from the Sauce Grande Formation of Pennsylvanian-Cisuralian age, Claromecó Basin, Argentina

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ABSTRACT

A new acritarch, *Lancettopsis harringtonii* sp. nov, is proposed for the glacio-marine Sauce Grande Formation of Pennsylvanian-Cisuralian age, located in the Claromecó Basin, Argentina. The genus *Lancettopsis* emended in this work was originally defined as part of the life cycle of the genus *Campenia*. However, our records indicate that *Lancettopsis* may represent the final stage of the repeated curling inward of the vesicle wall of originally spheroidal morphotypes. In this regard, *Lancettopsis harringtonii* sp. nov. is interpreted as the repeated curling inward of the vesicle wall of a sphaeromorph palynomorph, gen. et sp. indet. The genus *Lancettopsis*, to date only registered in unequivocal marine successions of Phanerozoic rocks, is here considered to be constituent of the organic-walled marine microplankton, although its biological affinity cannot be confirmed.

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1. Introduction

The genus *Lancettopsis* was erected by Mädler (1963) to include flat lanceolate vesicles recovered from the Lower Toarcian Posidonia Shale, northwestern Germany. Subsequent references to this genus have been made in the Mesozoic (e.g., Lower Jurassic and Aalenian Los Molles and Sierra de Chacaico formations in Volkheimer, 1974; Maastrichtian/Danian Jagüel Formation in Pérez Pincheira and di Pasquo, 2021) and more rarely in the Paleozoic (Permian Copacabana Formation in Doubinger and Marocco, 1981), and Cenozoic (Early-Middle Miocene Nanati Formation in Takahashi and Matsuoka, 1981). The biological affinity of *Lancettopsis* is controversial, as it has been considered an acritarch (Mädler, 1963; Volkheimer, 1974), a prasinophyte (e.g., Prauss, 2015), and even a pollen grain (Doubinger and Marocco, 1981).

Originally, Mädler (1963, 1967) interpreted the genus *Lancettopsis* as part of the life cycle of *Campenia*. This author considered that by

growth and unfolding, *Lancettopsis* would evolve into *Campenia*, a proposition not widely accepted.

Cultivation is an essential methodology to discriminate between the different stages of the life cycle of many unicellular modern algae (Starr, 1955; Lindgren, 1981). However, in fossil associations, it is possible to employ other evidence, with different degrees of certainty, to suggest that two or more morpho-species constitute developmental stages (including vegetative ones) of the life cycle of the same microorganism. Evidence that may offer a guide to relating different morphotypes in a unique life cycle would involve morphological similarity (e.g., in the wall type), the presence of transitional forms especially if they are identified in a single sample, and their recurrent co-occurrence in the fossil record (e.g., *Maranhites* in González, 2009).

The palynological study of core samples obtained from the Pennsylvanian-Cisuralian Sauce Grande Formation in the PANG 0002 drilled in the Sierras Australes area (Claromecó Basin, Argentina, Fig. 1) has revealed an association of abundant lanceolate morphotypes, here assigned to *Lancettopsis harringtonii* sp. nov., together with sphaeromorphs and transitional forms. These findings allow us to suggest a potential relationship among these morphotypes and to discuss the life cycle of *Campenia* and *Lancettopsis* originally suggested by Mädler (1963). The genus

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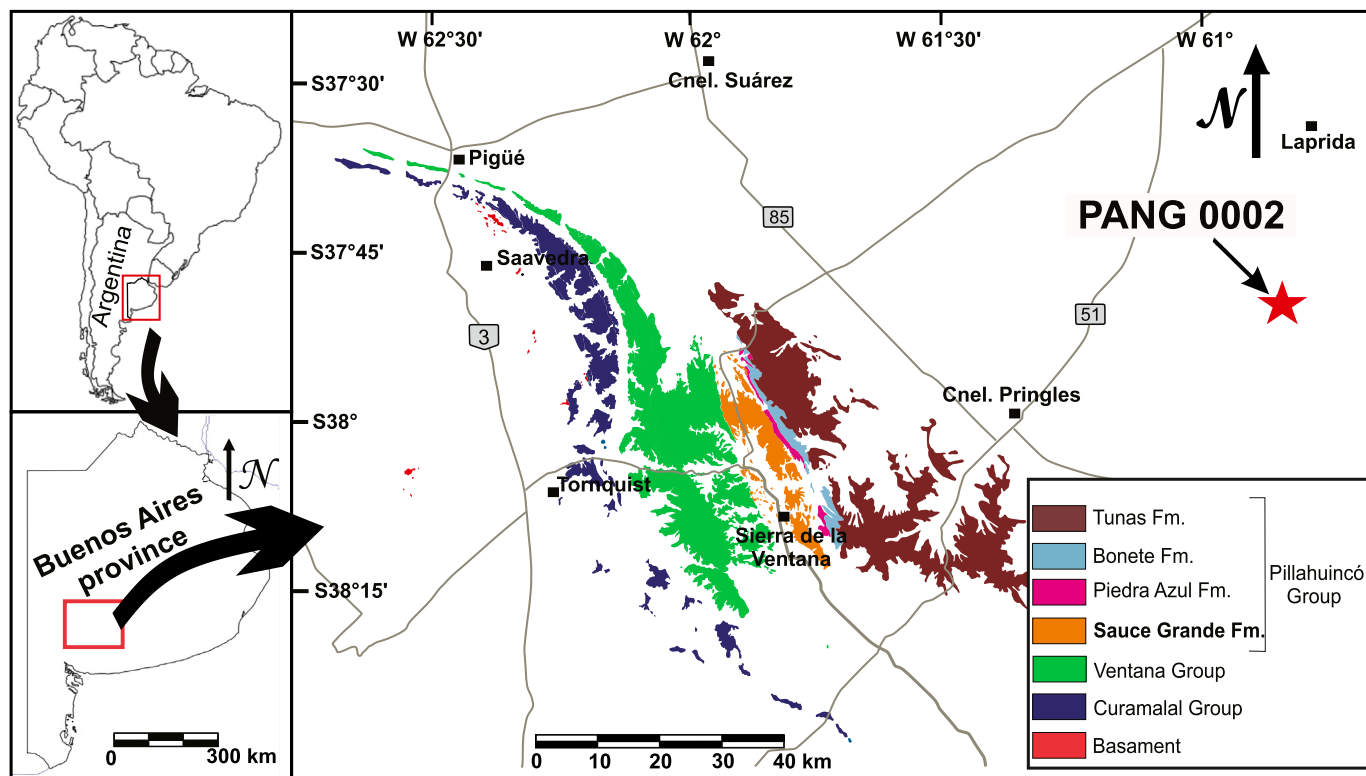
Fig. 1. Location map of PANG 0002 borehole in the Claromecó Basin, Buenos Aires Province, Argentina. Lithoestratigraphic units are also indicated (modified after Harrington, 1947, and Furque, 1973, 1979).

Lancettopsis is emended, and the biological affinities of *Lancettopsis* and *Campenia* are discussed.

2. Geological setting

The Claromecó Basin (Kostadinoff and Font de Affoler, 1982) in central-eastern Argentina covers an area of approximately 50,000 km^2 in Buenos Aires Province, and it underlies the Colorado Basin in an offshore position (Lesta and Sylwan, 2005). The former basin is composed of Paleozoic metamorphic and sedimentary rocks, which crop out mostly along the Sierras Australes (Ventania System) and in small isolated outcrops located near Lumb, Gonzales Chaves, De la Garma, and Mariano Roldán localities (Andreis et al., 1987 and cites therein) (Fig. 1).

The stratigraphy of the Sierras Australes and Claromecó Basin was defined by Harrington (1947, 1970), and it comprises the Curamalal, Ventana (Lower Paleozoic), and Pillahuincó groups. The Pillahuincó Group includes, from base to top, the Upper Paleozoic Sauce Grande, Piedra Azul, Bonete, and Tunas formations. The Sauce Grande Formation overlies the Devonian Lolén Formation (Ventana Group) in an angular unconformable contact (Keidel, 1947; Andreis et al., 1987; Japas, 1989), and grades up into the Piedra Azul Formation (Harrington, 1947, 1970; Andreis et al., 1989). The Sauce Grande Formation is composed of a series of glaciomarine facies (Coates, 1969; Frakes et al., 1969; Harrington, 1970, 1972; Andreis et al., 1989; Andreis and Torres Ribeiro, 2003), in which diamictites predominate, whereas conglomerates, sandstones, and mudstones are subordinated. This unit was deposited in a proximal neritic environment (Harrington, 1947, 1972; Frakes et al., 1969; Andreis, 1984; Andreis et al., 1989). Paleontological data support a late Pennsylvanian- Cisuralian marine influence, due to the presence of acritarchs (di Pasquo et al., 2008; Di Nardo et al., 2021), and a poorly preserved marine invertebrate (without stratigraphic value) defined by Harrington (1955) as *Astartella? pussilla*.

Andreis and Torres Ribeiro (2003) recognized three megacycles in the Sauce Grande Formation. The two lower megacycles were interpreted by López-Gamundí et al. (2021) as a lower deglaciation sequence sensu Visser (1996, 1997). The upper megacycle was related to a transgressive process associated with the Tastubian (= early Sakmarian in Gradstein et al., 2012) transgression that continued in the Piedra Azul Formation (Andreis and Torres Ribeiro, 2003) or as an upper deglaciation sequence together with the lower part of the Piedra Azul Formation (López-Gamundí et al., 2021).

The PANG 0002 borehole (S 37°46′58.50″, W 60°44′34.86″) analyzed herein was drilled 26 km south of Laprida locality at the Claromecó Basin depocenter, northeast of the Sierras Australes (Fig. 1). The continuous core of PANG 0002 registers 219 m of sedimentary rocks with a predominance of matrix-supported diamictites and subordinated, interbedded levels of sandstones, conglomerates, and mudstones (Fig. 2). Sandstones and conglomerates intercalate with diamictites mainly at the basal part of the succession, whereas thin levels of mudstones predominate in the middle-upper section of the well. The sedimentary sequence clearly correlates to the Sauce Grande Formation based on its lithological content (Zavala et al., 2008; Garat et al., 2018). Considering the thickness and lithology, PANG 0002 may represent the uppermost portion of the middle and upper sections of the unit, in agreement with Harrington (1947) and Zavala et al. (2008).

3. Palynological background of Sauce Grande Formation

There are few published accounts of palynomorphs from the Sauce Grande Formation. Archangelsky and Gamerro (1980) and Archangelsky (1996) studied cutting samples from Puelches X-1 offshore drilling, located in the Argentine Continental Shelf. A thick succession of sedimentary rocks was drilled, whose last hundreds of meters at the bottom were attributed to the Sauce Grande Formation. At these depths, Archangelsky and Gamerro (1980) reported from diamictite
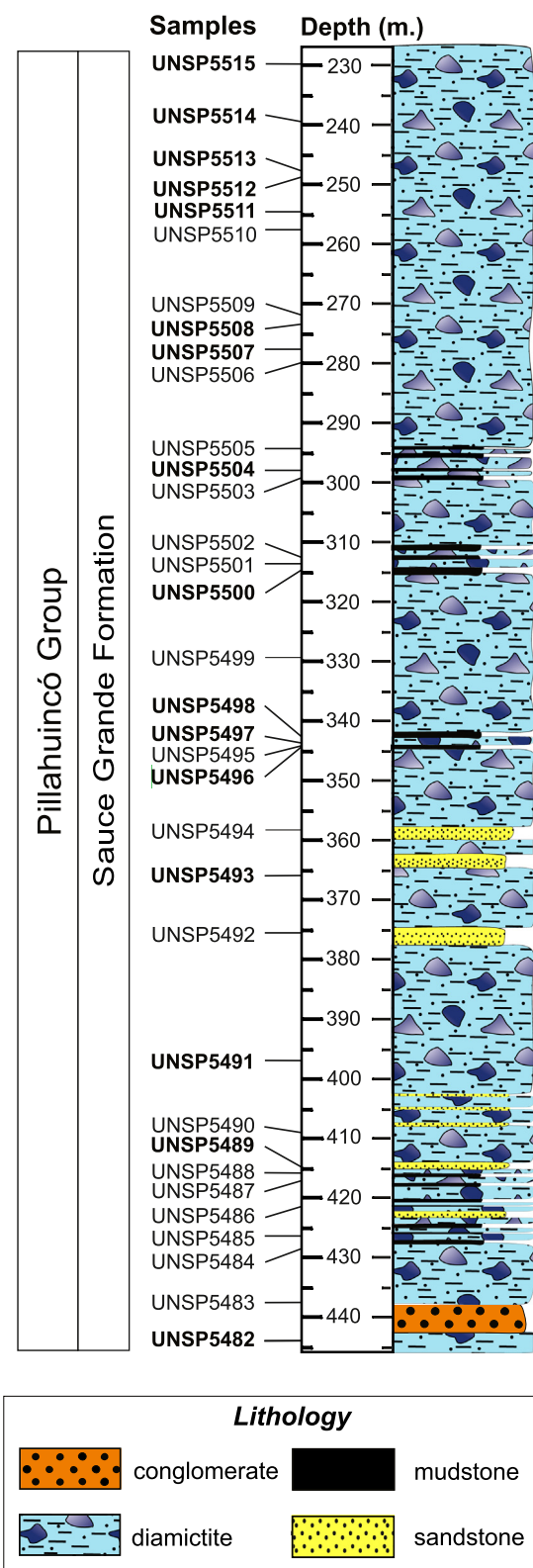
Fig. 2. Generalized stratigraphic column of PANG 0002 borehole. Fertile palynological samples are highlighted in bold letters.

Lesta and Sylwan (2005) mentioned the existence of palynological data of the Sauce Grande Formation from Paragüil drilling, located in the Claromecó Basin. Unfortunately, this information comes from unpublished works (Archangelsky, 1998, in Lesta and Sylwan, 2005), and there are no descriptions or illustrations. The association *Lundbladispora-Granulatisporites-Cristatisporites* was reported for the middle member of the Sauce Grande Formation, and a Pennsylvanian age was suggested.

Di Pasquo et al. (2008) described the first and only palynological association recovered from outcrop samples, also referred to the Middle Member of the Sauce Grande Formation. The palynological association is composed of one pollen grain, one acritarch, and nine species of trilete spore, showing a low degree of preservation. These authors suggested an Upper Pennsylvanian-Cisuralian age based on the stratigraphic range of recognized species.

More recently, Di Nardo et al. (2021) presented an association of acritarchs recovered from core samples of the PANG 0002 borehole, including the Pennsylvanian- Cisuralian *Deusilites tenuistriatus* Gutiérrez, Césari and Archangelsky 1997, giving palynological support to the age of the unit.

4. Materials and methods

The rock samples concerning the present study consist of cores obtained from the PANG 0002 well (Fig. 1) drilled by Río Tinto Mining Exploring Company as part of a drilling project carried out in 2008. Subsequently, the complete PANG 0002 borehole, along with two more wells comprising the Tunas Formation (PANG 0001 and PANG 0003), was ceded to Universidad Nacional del Sur for academic purposes.

Thirty-four samples were taken from the interval between 445,7 and 227,50 m bearing laminate mudstone and massive matrix-supported diamictites, both lithologic types, dark gray in color. Organic matter was extracted by applying conventional techniques with hydrochloric and hydrofluoric acids (Volkheimer and Melendi, 1976). Sixteen productive residues were mounted using UV-curable acrylate (Trabasil ® NR2) media (Noetinger et al., 2017). Slides were studied using a Nikon eclipse50i transmitted white light microscope. The illustration of specimens was performed with an AmScope 14 Mp video camera. The location of specimens is given in England Finder coordinates. Materials (rock samples, residues, and slides) are housed at Instituto Geológico del Sur-Universidad Nacional del Sur, Bahía Blanca, Buenos Aires, Argentina. They are identified by catalog numbers preceded by the acronym UNSP (Universidad Nacional del Sur, Palynology).

5. Results

The sixteen productive samples correspond to levels at depths of 444.2 m (UNSP 5482), 414.75 m (UNSP 5489), 395.94 m (UNSP 5491), 366.05 m (UNSP 5493), 344.98 (UNSP 5496), 343.63 m (UNSP 5497), 342.38 m (UNSP 5498), 314.89 m (UNSP 5500), 298 m (UNSP 5504), 277.58 m (UNSP 5507), 273.28 m (UNSP 5508), 254.8 m (UNSP 5511), 248.71 m (UNSP 5512), 247.74 m (UNSP 5513), 239.37 m (UNSP 5514), and 299.75 m (UNSP 5515) (Fig. 2).

Lanceolate forms and potentially related sphaeromorphs, documented in many samples along the interval, are morphologically and taxonomically described.

5.1. Taxonomic descriptions

Group: ACRITARCHA Evitt 1963
Genus: **Lancettopsis** Mädler, 1963 emend. Di Nardo, Martínez, and di Pasquo
Type species: *Lancettopsis lanceolata* Mädler, 1963
Original diagnosis (in German): Flache, lanzettliche, ± schmale Gebilde, die ursprünglich wohl spindel- förmig waren. Spitzen anfangs

sequences a decrease in striated pollen grains and an increase in spores and monosaccate pollen grains in comparison with the overlying section of the drilling. No microplankton was recovered from the diamictites. This sequence was correlated to the uppermost part of the *Potonieisporites-Lundbladispora* Zone Archangelsky and Gamerro (1979) of the Chacoparaná Basin.

verdichtet, nach weiterer Entwicklung durch feine Linien als zusammengerollt erkennbar. Durch meridionale, bogenläufige Streifen und einen Mittelstreifen von innen nach außen weniger dicht. Manchmal teilweise zurückgerollt, dann allmählich in *Campenia* übergehend, auch mehrere; zusammenhängend oder ineinandegerollt.

Translation from German: Flat, lanceolate, ± narrow structures that were originally probably spindle-shaped. Tips initially compacted, after further development recognizable as a curling inward with fine lines. Meridional arcuate stripes, which become less dense from the inside to the outside. Sometimes partially rolled back, then gradually changing to *Campenia*; also several connected or rolled into one another.

Emended diagnosis: Elongate bodies with a lanceolate or fusiform outline. One-layered, thin, and psilate wall. Narrow longitudinal split bordered with distinctive folds, which result from a repeated curling inward of the originally spheroidal vesicle, after the vesicle is divided into two halves. Commonly, both halves completely separated, and they may exceptionally remain partially attached.

Comparisons: Schizofusa Yan, 1982 is a fusiform to ellipsoidal vesicle with a slit-like opening, which may or may not have bordered folds extending from pole to pole (Yan, 1982, in Miao et al., 2019). This genus has been registered in the Middle and Late Paleoproterozoic of China (see references in Loron and Moczydłowska, 2017, and Miao et al., 2019) and in the Late Proterozoic of Sweden (Loron and Moczydłowska, 2017). *Schizofusa* includes a broader range of morphologies, while *Lancettopsis* is restricted to fusiform or lanceolate forms, not ellipsoidal, with pointed ends, and always with the extremities of walls curled up.

Remarks: Mädler (1963, 1967) considered the genus *Lancettopsis* to be a youth stage of genus *Campenia,* based on the presence of the tips of lanceolate bodies in the split of some specimens of *Campenia gigas*. By growth and unfolding, *Lancettopsis* would transitionally evolve into *Campenia* (see discussion of the relationship between *L. harringtonii* and sphaeromorohs further below). The specimens selected by Mädler to illustrate such a situation (pl. 27, figs. 3, 4) are not clear, weakening support for this interpretation. We agree with Peat et al. (1978) that there would be no ontogenetic relationship between *L. lanceolata* and *C. gigas*.

We emend the genus *Lancettopsis* to allude to the ornamentation of the wall, to include the presence of a longitudinal split in the vesicle, and to exclude the ontogenetic relationship between *Campenia* and *Lancettopsis* as interpreted by Mädler in the original diagnosis.

Lancettopsis lanceolata represents the type species of the genus, and to date, it is the only species formally established. The body dimensions are restricted to 230–330 μm in length and 50–80 μm in width. Nevertheless, some specimens illustrated in Mädler's publication exceed both the length (p.403, fig. 29–2) and the width (p. 403. fig. 29–3).

Lancettopsis harringtoni Di Nardo, Martínez and di Pasquo sp. nov.
Plate I, 1–8; Plate II, 1–4.
1958 *Leiosphaeridia* sp. Eisenack, p. 403, pl. 1 figs. 7–8.
1981 *Lancettopsis lanceolata* Doubinger and Marocco, p. 1097, pl. 2, fig. 37.
2015 *Lancettopsis* sp. Prauss, p. 32, fig. 13k.

Etymology: The new species is dedicated to geologist Dr. Horacio Harrington, whose work contributed to establishing the stratigraphic regional scheme of the Sierras Australes of Buenos Aires.

Locality: PANG 0002 borehole (Sauce Grande Formation), Buenos Aires, Argentina.

Holotype: Plate I, fig. 1 (UNSP 5498 (2) Z39/0).

Additional studied material: 5493J25/0; 5496 P24/2; 5496 X24/0; 5496 Q38/1; 5496 U20/2; 5496–2 D36/2; 5496–3 B32/1; 5497–2 L29/2; 5497 Y32/2; 5498(3) D28/2; 5507 Q25/0;

Stratigraphic horizon: PANG 0002 at 342.38 m.

Diagnosis: Elongate vesicles with lanceolate or fusiform outline and pointed ends. One-layered, laevigate wall ca. 1 μm. Longitudinal split, narrow, parallel to the length of the vesicle, and bordered by distinctive folds which result from the repeated curling inward of the vesicle. Length/width ratio ranges between 2.2 and 5.8.

Dimensions: Length (125 specimens): 104 (137) 210 μm; width (105 specimens): 20 (44) 76 μm; length/width ratio (81 specimens): 2.2 (3.4) 5.8.

Description: Vesicles with lanceolate outline, thin and psilate wall. Conspicuous folds parallel to the major axis of the vesicle producing darker bands in the inner part and lighter in color towards the outer part. The major axis measures between 104 and 210 μm and the minor axis between 20 and 76 μm. The vesicle wall is smooth although it shows a certain degree of deterioration (predominance of degradation, and secondarily, corrosion and mechanical damage sensu Delcourt and Delcourt, 1980).

Comparisons: Lancettopsis harringtonii sp. nov. resembles the type species of the genus, *L. lanceolata*. The size range of longitudinal axes of the former is restricted to 104–210 μm, and *L. lanceolata* is larger, between 230 and 330 μm. No overlapping exists between the dimensions of the species, justifying their separation as independent entities.

Leiosphaeridia sp. Eisenack, 1958 (p. 403, pl. 1, figs. 7–8) from the Lower Ordovician of Estonia, *Lancettopsis lanceolata* illustrated by Doubinger and Marocco (1981) from the Lower Permian Copacabana Group, and *Lancettopsis* sp. Prauss, 2015 from the Upper Turonian to Lower Santonian at Tarfaya (Morocco, NW Africa) agree with the main features (amb, size) of *Lancettopsis harringtonii* sp. nov. Hence, they are included in this new species.

Lancettopsis sp. Takahashi and Matsuoka, 1981 (p. 119, pl. 13, fig. 11) described for the Nantani Formation (Early-Middle Miocene) from Niigata Prefecture, central Japan, is similar in dimensions to *Lancettopsis harringtonii* sp. nov. However, the former has an irregular outline and a wrinkled appearance (Takahashi and Matsuoka, 1981). *Lancettopsis* sp. Volkheimer, 1974 (p. 165, pl. 8, fig. 69), described for the Sierra Chacai Có and Los Molles formations (Liass-Aalenian), Neuquén Basin, is smaller than *Lancettopsis harringtonii* sp. nov.

Acritarcha sp. A Ottone, 1991 (p. 129, pl. 3, fig. 5), found in the Guandacol Fm. (Late Carboniferous) has a thicker wall (1.5–2.3 μm), and its ornamentation varies from psilate to granulate, verrucate, and apiculate.

Acritarca sp. A García, 1996 (p. 21, pl. 5, fig. 11), registered in the Pennsylvanian- Cisuralian Imperial Formation of San Rafael Basin, Argentina, shows similar features to *Lancettopsis harringtonii* sp. nov. However, only two partially preserved specimens were recovered, thus preventing the transference of this morphotype to *Lancettopsis harringtonii* sp. nov.

Brazilea scissa (Balme and Hennelly) Foster, 1975 (see Carboniferous-Permian records in Gutiérrez et al., 2015) = *Ovoidites scissus* (Balme and Hennelly) Zavattieri et al., 2020 resembles to *Lancettopsis harringtonii* sp. nov. (e.g., Plate I, fig. h). However, the former is originally ellipsoidal in shape, considerably smaller (generally not larger than 100 μm), and has an open mechanism that has been described as follows: 1- partial or complete rupture (Foster, 1975, 1979); 2- frequently with both halves partially attached (Archangelsky and Gamerro, 1979); 3- with a dehiscence suture that does not surround the vesicle, so it remains joined when it opens (Zavattieri et al., 2020).

Brazilea sp. A Playford and Dino, 2000, recorded in the Amazon Basin, differs from *Lancettopsis harringtonii* sp. nov. in its elongated-oval or elliptical shape, smaller size, and thicker wall. Besides, the former does not show the repeated curling inward of the vesicle of the latter species. The wall thickness of *Brazilea* sp. A Playford and Dino, 2000 in Gutiérrez et al., 2015 (p. 130, fig. 3N) is similar to that of *Lancettopsis harringtonii* sp. nov., but differs in being smaller.

Calamospora fissurata Gutiérrez and Balarino, 2018, defined in the Ordoñez Formation (Pennsylvanian), Chacoparaná Basin, partially resembles to *Lancettopsis harringtonii* sp. nov. However, the former has a trilete mark and is smaller than *Lancettopsis harringtonii* sp. nov.

Cycadopites cymbatus (Balme and Hennelly) Potonié and Lele 1961, widely documented in Pennsylvanian-Permian palynoassociations of
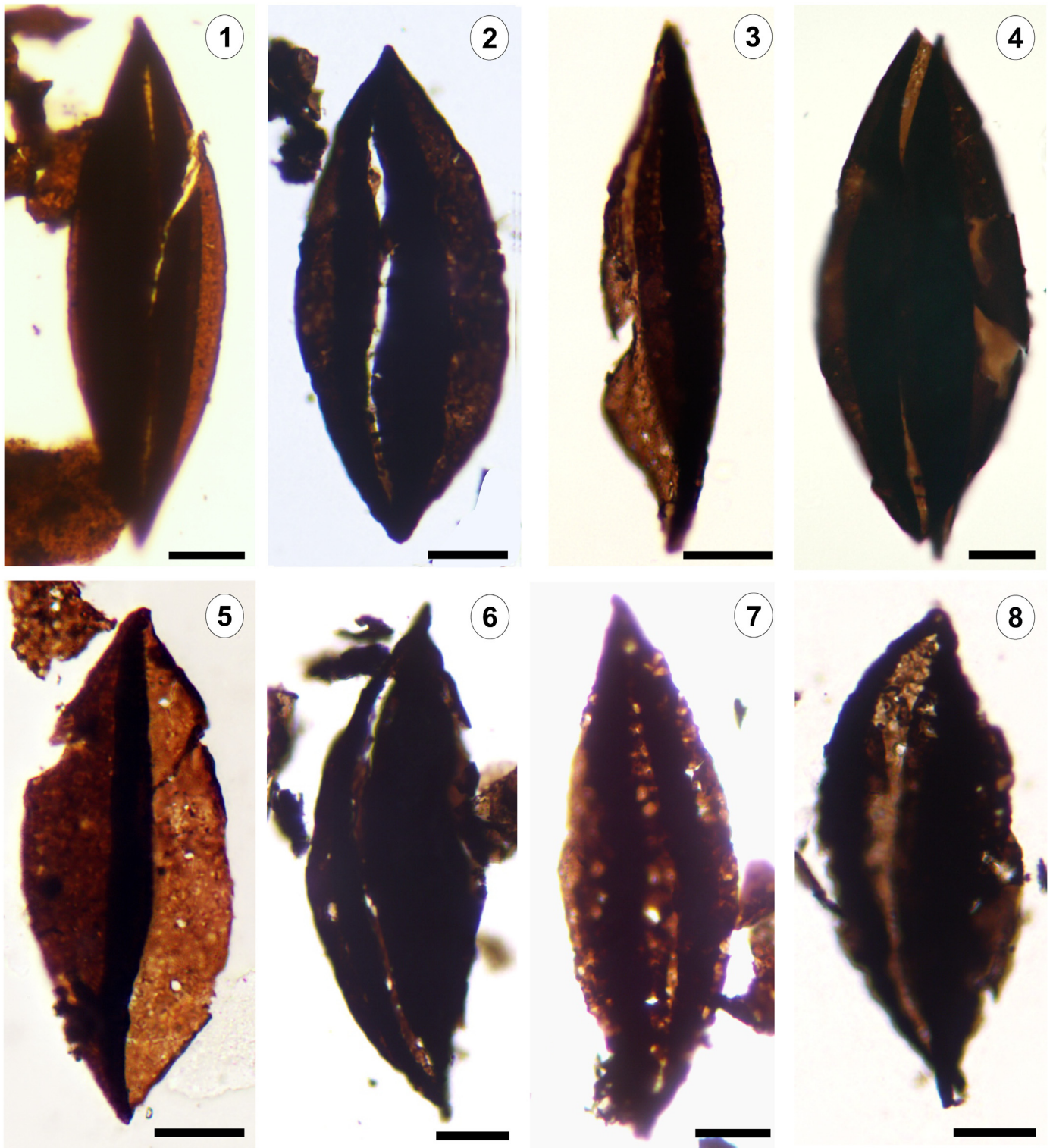
Plate I. Figs. 1–8. *Lancettopsis harringtonii* sp. nov. a. Holotype. 1. 5498(2) Z39/0; 2. 5496 P24/2; 3. 5496–3 B32/1; 4. 5498(3) D28/2; 5. 5496 Q38/1; 6. 5496 U20/2; 7. 5497–2- L29/2. 8. 5496 X24/0. Scale bar = 20 μm.

South America has a similar amb, but it is much smaller than *Lancettopsis harringtonii* sp. nov. Dimensions of *Cycadopites grandus* Bharadwaj et al., 1976, from Cisuralian Rio Bonito and Iratí formations in northern Brazil, are in the range of those of *Lancettopsis harringtonii* sp. nov. However, these pollen grain species with ginkgo/cycadophytic affinities among other species of this genus (Cards 5072–5073 of Jansonius et al., 1998) have a faintly microgranular exine wall and a

sulcus extending the full length of the grain more or less open at its ends, and more or less constricted in the middle, with two longitudinal semilunar folds all along.

Remarks: The fact that only three partially attached specimens were found in all the studied samples (see Plate II, figs. 2–4) indicates that the two halves of the originally spheroidal vesicles would exceptionally remain partially attached.
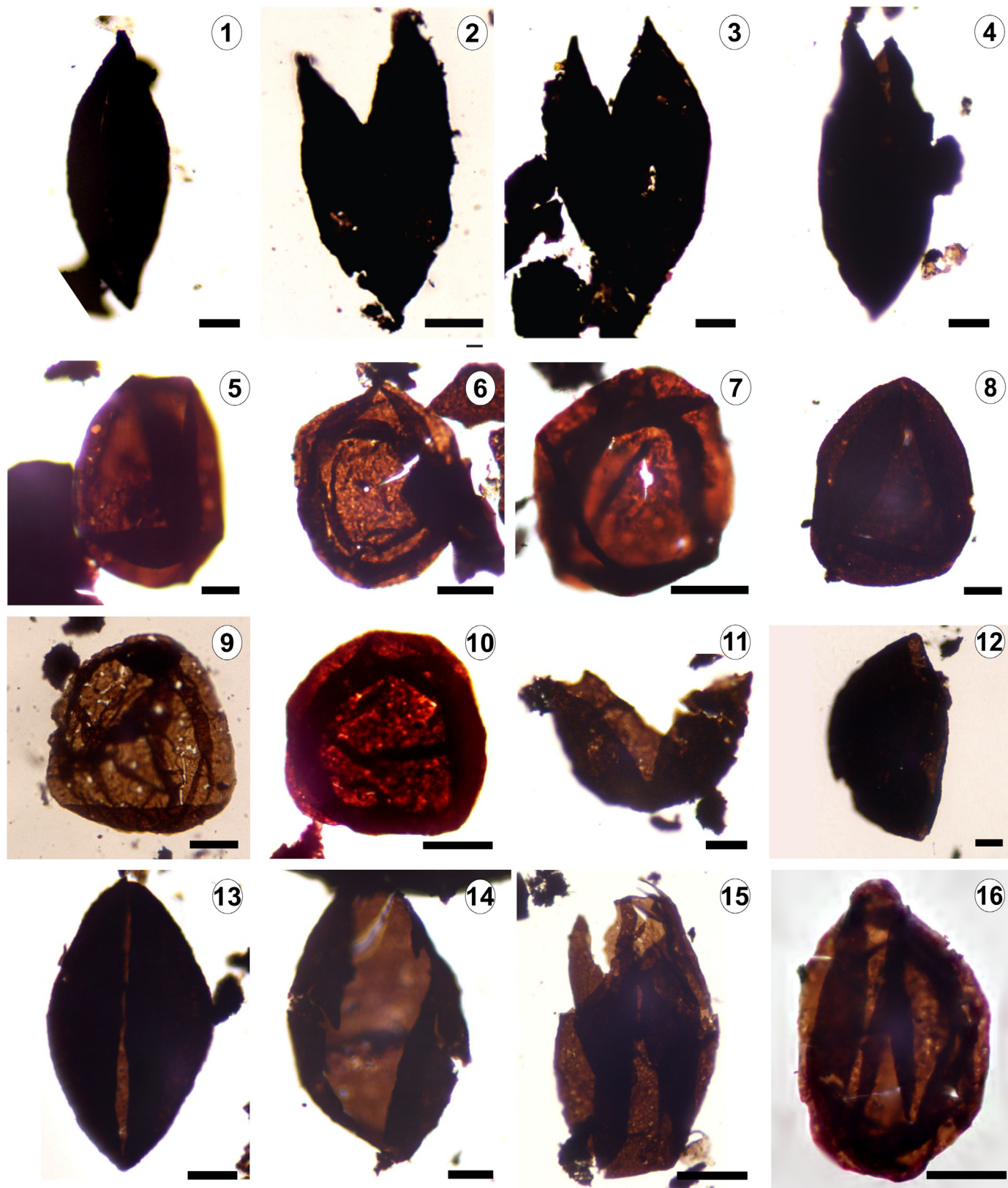
Plate II. Figs. 1–4. *Lancettopsis harringtonii* sp. nov. 1. 5496-2 D36/2.; 2. 5497 Y32/2; 3. 5507 Q25/0; 4. 5493J25/0. 5–12. Sphaeromorph gen. et sp. indet. Morphotype 1. 5. 5498–5, C45/2; 6. 5496 C18/0; 7. 5493 H12/1; 8. 5496 Y41/2; 9. 5512 P37/4; 10. 5498 Y19/0; 11. 5496 V21/0; 12. 5496 Q15/4. 13–16. Sphaeromorph gen. et sp. indet. Morphotype 2. 13. 5496 D36/; 14. 5411 L27/3; 15. 5498 F14/0; 16. 5504 G30/3. Scale bar = 20 µm.

Geographic and stratigraphic distribution: Lancettopsis harringtonii is registered in the Lower Ordovician of Estonia (Eisenack, 1958), in the Permian Copacabana Formation, Peru (Doubinger and Marocco, 1981), in the Upper Turonian to Lower Santonian at Tarfaya, Morocco, NW Africa (Prauss, 2015), and in Pennsslyvanian-Cisuralian Sauce Grande Formation, Argentina (this paper).

Subgroup: SPHAEROMORPHITAE Downie and Sarjeant, 1963

This subgroup includes acritarchs with a circular to ellipsoidal amb, granular, smooth, punctate, or perforate wall, lacking an opening, or bearing a simple circular pylome or a split. The numerous sphaeromorphs with circular to ellipsoidal amb, described below as Morphotypes 1 and 2, respectively, are interpreted as previous developmental stages of *Lancettopsis harringtonii* sp. nov.

Species: Sphaeromorph gen et sp. indet.

Morphotype 1.

Plate II, 5–12.

Description: Vesicle circular to oval in outline. Psilate thin wall. Circumpolar folds (equatorial to subequatorial) developed in variable degrees resulting from the curling inward of the vesicle after it is divided into two hemispheres. Rarely, both halves partially remain attached (Plate II, figs. 2–4).

Dimensions (86 specimens): diameter of vesicles, 58 (99) 175 µm in length, 46 (82) 175 µm in width, length/width ratio: 1 (1.2) 1.6.

Main material studied: 5493 H12/1; 5496 C18/0; 5496 Y41/2; 5496 V21/0; 5496 T26/2; 5496 Q15/4; 5497–2 P12/0; 5498 Y19/0; 5498–5 C45/2; 5498–5 F42/0; 5510 B29/3; 5512 P37/4.

Comparisons: *Leiosphaeridia simplex* Sinha 1969, illustrated by Gutiérrez et al. (2015) (p. 130, fig. 3 o–p) for the Cisuralian of Paraná Basin in Uruguay, is similar to morphotype 1. However, *L. simplex* lacks an equatorial dehiscence.

Brazilea helbyi Foster, 1979 has a thicker wall (2–4 um, rarely 1 um), a maximum dimension smaller than Morphotype 1, and a tendency to remain intact or only partially open or broken. This species can also occur in chains of 2–6 specimens, specimens referred to as *B. helbyi* forma *gregata* Foster (1979).

Ovoidites circumplicatus Zavattieri et al., 2020, defined from samples of a continental Middle Triassic succession of the Puesto Viejo Basin, Argentina, comprises spherical to elongate-subspherical zygospores, splitting into two approximately equal halves that usually remain attached, with fine subequatorial folding developed over the detached parts of the valves. The circumpolar folds in our specimens are thicker, and both halves rarely remain attached. Besides, maximum diameter of Morphotype 1 is considerably larger than that of *O. circumplicatus*. These features and a different paleoecology (see "biological affinities" section) exclude our material from *O. circumplicatus*.

Other similar forms have been assigned to the spore-genus *Calamospora* Schopf, Wilson and Bentall 1944, illustrated from the Carboniferous-Permian of Chacoparaná and Paraná basins, such as *Calamospora hartungiana* Schopf, Wilson and Bentall 1944 in Beri et al. (2011) (p. 461, fig. 11.1) and *Calamospora fissurata* Gutiérrez and Balarino, 2018. However, these spore taxa mostly differ from morphotype 1 in having a trilete mark, simple and short to slightly larger, depending on the species.

Remarks: As pointed out by Peat et al. (1978); Peat (1979) for Proterozoic disphaeromorphs of the Roger Group, in a compressed state, it is difficult to distinguish in some specimens whether the rounded vesicles are folded spheres or hemispheres. The specimens show variable degrees of preservation comparable to that of *Lancettopsis harringtonii* sp. nov.

Morphotype 2.

Plate II, 13–16

Description: Vesicle oval in outline, with rounded to slightly pointed ends. Psilate thin wall. Folds parallel to maximum dimension of the vesicle, which results from the curling inward of the vesicle in variable degrees.

Dimensions (22 specimens): diameter of vesicles, 75 (105) 141 µm in length, 30 (57) 82 µm in width, length/width ratio 1.4 (1.9) 2.6.

Main material studied: 5493 J25/0; 5496–2 D36/0; 5497 Y32/2; 5498 F14/0; 5498–5- D55/0; 5504 G30/3; 5507 Q25/0; 5411- L27/3; 5514 D11/4.

Comparisons: Morphotype 2 slightly differs from morphotype 1 in having a greater length/width ratio, as a result of a more elongate overall shape.

Remarks: The preservation state of specimens assigned to Morphotype 2 is similar to that of *Lancettopsis harringtonii* sp. nov. and Morphotype 1.

6. Relationship between *Lancettopsis harringtonii* sp. nov. and sphaeromorphs

The co-occurrence of lanceolate specimens, sphaeromorphs, and transitional forms led us to interpret that there is a relationship among all these morphotypes. We believe that the life cycle proposed by Mädler, which relates genera *Campenia* and *Lancettopsis,* does not constitute an acceptable explanation for the findings in the samples from Sauce Grande Formation.

Mädler (1963, 1967) considered the genus *Lancettopsis* as a youth stage of the genus *Campenia.* By growth and unfolding, *Lancettopsis* would transitionally evolve into *Campenia* (Fig. 3.1a-d). This idea was also followed by Volkheimer (1974) when describing *Campenia austroamericana* and *Lancettopsis* sp. from the Early-Middle Jurassic of the Neuquén Basin.

Mädler's evolutionary hypothesis of *Lancettopsis* as a young stage of *Campenia* was based on the presence of tips of lanceolate bodies in the slit of some specimens of *Campenia* (Fig. 3.1d). This situation is not clear in the specimens illustrated by Mädler (pl. 27, figs. 3, 4). Even if the ontogenetic relationship between *Campenia* and *Lancettopsis* is accepted as valid, the different juvenile and adult specimens of *Lancettopsis* should be found. Mädler interpreted that the juvenile forms were those that were partially attached, rolled up next to each other (Fig. 3.1a). He made this interpretation based on the small size of many of these forms. However, the specimens illustrated exhibiting such features are large, all being in the range established for the species *L. lanceolata*, except for one of them (pl. 28, fig. 6), whose dimensions even exceed its limits. We agree with Peat et al. (1978) that there would be no ontogenetic relationship between *L. lanceolata* and *C. gigas* sensu Mädler (1963).

Peat (1979) proposed a life cycle of Proterozoic disphaeromorphs (Fig. 3.2) that involved, as a final stage, folded vesicles comparable to those of *Lancettopsis*. He reported specimens with both valves joined (Fig. 3.2b) and other specimens with folded valves (Figs. 3.2c–d). We believe that Peat's proposal, though put forward for Proterozoic material, is more coherent and can be applied to Madler's and our specimens. Eisenack (1958) first suggested that some Ordovician fusiform vesicles (e.g., *Leiosphaeridia* sp. pl. 1 figs. 7–8 in Eisenack, 1958) could represent rolled-up leiospheres, an idea questionned by Mädler (1963). A similar relationship has been suggested between *Leiosphaeria* and *Schizofusa* found in permineralized samples of Proterozoic age in China (Wang et al., 2015). These authors interpreted the genus *Schizofusa* as the curling inward of some species of *Leiosphaeridia* with a median split.

Similarly, we propose that *L. lanceolata* and *L. harringtonii* may constitute the final stage of the curling of hemispheres completely detached (Fig. 3.3 b–d) or, more rarely, partially attached (Fig. 3.3 b'–d'). The median splitting of sphaeromorphs (Fig. 3.3 a) would evolve into morphotype 1 (Fig. 3. 3 b, b'; Plate II, figs. 5–12), then morphotype 2 (Fig. 3. 3 c, c'; Plate II, figs. 13–16), and finally, into *Lancettopsis* as a final result. Exceptionally, the open mechanism of the sphaermorphs is partial rupture (Fig. 3.3. b'– c'; Plate II, fig. 11) resulting in two partially attached specimens of *Lancettopsis* (Fig. 3.1 a, 3. 3 d', Plate II, figs. 2–4).
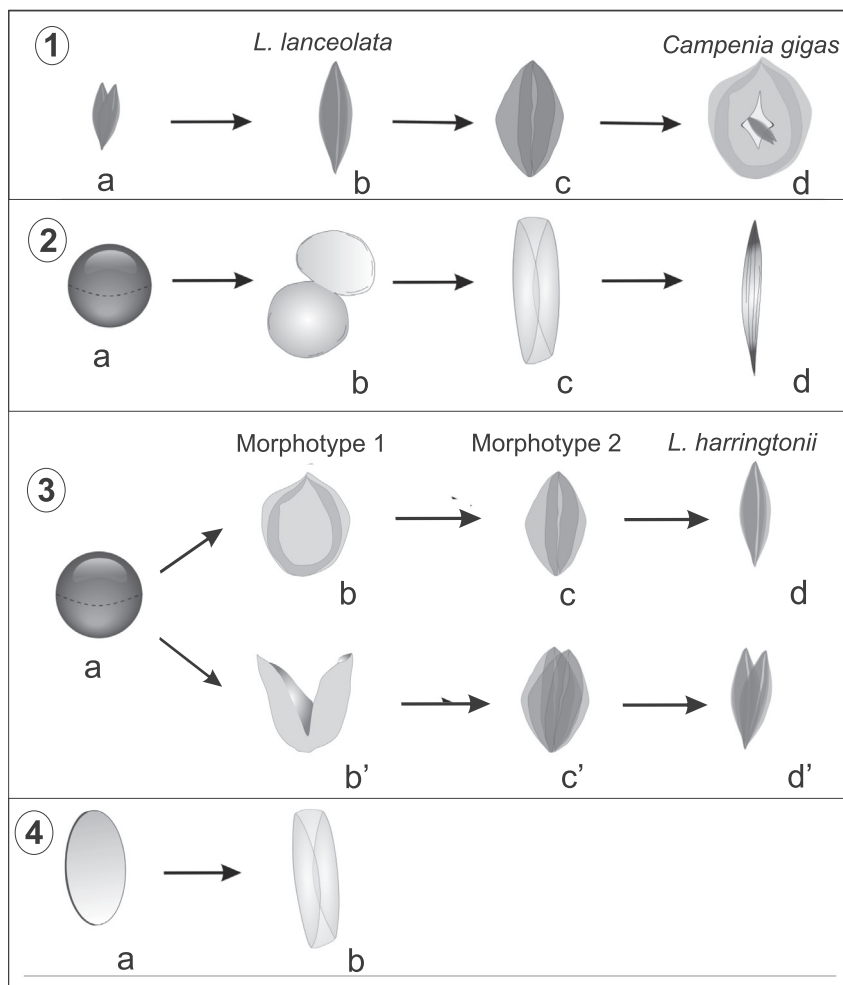
Fig. 3. Hypothetical relationships between spheroidal, transitional, and lanceolate morphotypes proposed by different authors. 1. Mädler' s interpretation of the life cycle of *Lancettopsis lanceolata* and *Campenia gigas*. Mädler (1963, 1967) proposed that lanceolate forms become spheroidal by growth and unfolding. See detailed explanation in the text. 2. Peat's interpretation (1979) of the life cycle of disphaeromorphs of the Proterozoic of Roger Group from Australia, relating morphotypes 3 (Fig. a), 10 (Fig. b), 12 (Fig. c) and 11 (Fig. d). Redrawn from Peat (1979). See detailed explanation in the text. 3. Interpretation proposed in this paper for the origin of *Lancettopsis harringtonii* sp. nov. Two possibilities are shown depending on whether the rupture of the sphaeromorphs is complete (Figs. 3 a, b, c, d) or partial (Figs. 3 a, b', c', d') interpretation is extensible to other species of *Lancettopsis*. 4. a–b. Interpretation proposed for the origin of some specimens belonging to Peat's morphotype 12 (1979). These elongate forms, with nearly straight edges and without acuminate ends (fig. 4.b) would be interpreted as the folding of originally discoidal vesicles (4.a) but not spheroidal.

In broad terms, we agree with the interpretation made by Peat et al. (1978) for Proterozoic disphaeromorphs. However, we consider that some specimens that he included in morphotype 12 (Fig. 3.2 c; see Peat, 1978, fig. 59; pl. 14a), those with more or less parallel edges and without acuminate endings, more probably result from the folding of originally disc-shaped but not spheroidal specimens, as shown in Fig. 3.3 e and f. All of our *Lancettopsis* specimens have acuminate terminations in response to repeated folding of hemispheroidal vesicles.

7. Biological affinities of *Campenia* and *Lancettopsis*

The biological affinities of *Campenia* and *Lancettopsis* have been interpreted in different ways. Initially, Mädler (1963, 1967) included the genera *Campenia* and *Lancettopsis* within the family Leiosphaeridiaceae (Eisenack) Mädler. Tappan (1980), in Guy-Ohlson, 1996) transferred the Leiosphaeridiaceae family, encompassing *Leiosphaeridia* and *Campenia* (and hence, *Lancettopsis*), to the prasinophytes. Several authors have subsequently questioned this idea, mainly regarding the genus *Leiosphaeridia* (see Lindgren, 1981; Colbath and Grenfell, 1995; Ströther, 1996; Martínez et al., 2005; Moczydlowska, 2010; Zavattieri et al., 2017), since evidence indicates that this genus is polyphyletic. However, the discussion did not extend to *Campenia*, and some authors have

maintained this genus within prasinophytes (e.g., Prauss et al., 1991; Prauss, 1996, 2006, 2015). *Campenia gigas* has also been listed as an acritarch, possibly a zygospore of green algae (Feist-Burkhardt et al., 2009). On the other hand, *Campenia* has been considered a terrestrial palynomorph (Schulz, 1967; Guy-Ohlson, 1982; Riding et al., 1991; Seidenkrantz et al., 1993). Schulz (1967) tentatively included *Campenia* within asaccate gymnosperm pollen grains (in Jansonius et al., 1998, card 373). In particular, *C. gigas* is considered a pollen grain marker of the Early Jurassic (Guy-Ohlson, 1982) or specifically of the Toarcian stage (Riding et al., 1991 and cites therein). In summary, there is no consensus about the biological affinity of the genus *Campenia*.

Lancettopsis has been regarded mainly as a constituent of the organic wall microplankton, considered as an acritarch (Mädler, 1963, 1967; Volkheimer, 1974; Takahashi and Matsuoka, 1981; González-Amicón and Volkheimer, 1982; Iosifova, 1996), a prasinophyte (Prauss, 2015) or Chlorophyte (Pérez Pincheira and di Pasquo, 2021) in a broader sense. More rarely, *Lancettopsis* has been listed within terrestrial palynomorphs, such as sporae *incertae sedis* (Doubinger and Marocco, 1967), or a monocolpate pollen grain (Doubinger and Marocco, 1981).

From our point of view, *Lancettopsis* is not a terrestrial palynomorph because it does not show any mark indicating that it is a trilete spore (as occurs in *Calamospora fissuratta*) or a monosulcate pollen grain of

Cycadopites- type. Moreover, no specimen has been found in organic connection with any reproductive structure of terrestrial plants. Conversely, there are reasons to interpret *Lancettopsis* as an organic walled marine microplankton (OWMM) since it has been widely registered in marine successions of Phanerozoic rocks, associated with other constituents of the OWMM, such as acritarchs, dinocysts, and prasinophytes (see Eisenack, 1958; Mädler, 1963, 1967; Volkheimer, 1971, 1974; González-Amicón and Volkheimer, 1982; Volkheimer and Quattrocchio, 1975; Takahashi and Matsuoka, 1981; Leckie et al., 1990; Iosifova, 1996; Prauss, 2015; Pérez Pincheira and di Pasquo, 2021). One exception is *L. lanceolata* (here transferred to *Lancettopsis harringtonii* sp. nov.) registered in black mudstones of the Copacabana Group by Doubinger and Marocco (1981), although other evidence has confirmed a marine environment for the deposition of this unit (Newell et al., 1953; di Pasquo and Grader, 2012).

Although the excystment type of sphaeromorph gen. et sp. indet. here described resembles that of some freshwater species affiliated to the zygnemataceae widely registered in Gondwana (e.g., *Brazilea scissa*), the partial and complete rupture along a median split is not exclusive to this group of algae. *Schizofusa sinica* Yan, 1982, a Proterozoic acritarch comparable to *Lancettopsis*, also interpreted as the curl inward of some leiospheres by Wang et al. (2015), has always been registered in marine sediments (see discussion in Loron and Moczydłowska (2017)), and morphologically compared to the extant marine alga *Nannochloropsis* (Lamb et al., 2009). Some Proterozoic sphaeromorphs assigned to the genus *Leiosphaeridia* also exhibiting median split and partial rupture (e.g., *L. crassa* Naumova emend. Jankauskas 1989 in Knoll, 1996 p. 69; *L.* spp. in Loron and Moczydłowska (2017)) have been referred to marine paleoenvironments as well. Other genera that include sphaeromorphs with a median split that tends to separate the vesicle into halves are *Dichotisphaera* Turner, 1984, an OWMM acritarch of Caradoc Series of England, and *Hemiruptia* Ottone 1996, defined for the Devonian Los Monos Formation (Tarija Basin, Argentina), considered an acritarch (Ottone, 1996) or prasinophyte (Turnau and Racki, 1999; Turnau, 2000; di Pasquo, 2002; Mullins et al., 2007; García Muro et al., 2017; Abreu, 2019; Abreu et al., 2019). These two genera are fully comparable to zygospores of the Zygnemataceae family since they share morphologic features with modern zygospores (Colbath and Grenfell, 1995), although this affiliation has not been suggested, and both have been registered in association with other marine constituents (cf. Turner, 1984; Ottone, 1991).

One hypothesis that cannot be discarded is that Sphaeromorph gen. et sp. indet. and *Lancettopsis harringtonii* could also represent metazoan eggs of planktonic crustaceans affiliated to copepods. From Pleistocene marine sediments of eastern Banda Sea, Indonesia, Van Waveren (1992) described twenty morphotypes of copepod eggs. Most of them were originally spherical, with a size range between 60 and 220 μm, displaying equatorial dehiscence partially to completely developed, with thin to thick, psilate to ornamented walls. Some morphotypes also show a fusiform outline, with vesicle edges folded inward (see also Matsuoka et al., 2017, p.18, Fig. 2j), or occurring as opened hemispheres (see di Pasquo et al., 2019; Pérez Pincheira and di Pasquo, 2021). It is interesting to note that fragments of micro-crustaceans including copepods have been recorded from samples of at least Carboniferous times (Selden et al., 2010). As suggested by Arai (2000), copepod eggs may have been largely ignored in palynological preparations, some of them misinterpreted as leiosphaerids, Schizomorphitae acritarchs, or even as dinocysts (e.g., *Cobricosphaeridium giganteum* McMinn 1991).

We consider that it would not be appropriate to relate all simple forms with circular to oval outline that tend to separate into halves with zygospores of freshwater zygnemataceae without bearing in mind the fossil association and other paleoenvironmental evidence. Assigning our specimens to *Brazilea* (*Ovoidites*), a genus widely accepted as of freshwater origin and registered in the Pennsylvanian-Permian of Gondwana, would not enable discussion of its biological affinity and paleoecological requirements.

In the current state of knowledge, the genus *Lancettopsis* cannot be assigned to a particular natural group, and more than one affiliation is possible (polyphyletic origin). For this reason, it is preferable to retain it within the Group Acritarcha. Based on the great number of specimens in different developmental stages and the accompanying marine microflora (Di Nardo et al., 2021), a general affinity with the OWMM is proposed for *Lancettopsis harringtonii* and sphaeromorph gen. et sp. indet., although a particular natural group cannot be defined. This interpretation agrees with the glaciomarine origin proposed for the Sauce Grande Formation (Coates, 1969; Frakes et al., 1969; Harrington, 1970, 1972; Andreis and Torres Ribeiro, 2003) and with the records of the genus *Lancettopsis* in association with other OWMM.

8. Stratigraphic significance of *Lancettopsis harringtonii*

Lancettopsis harringtonii sp. nov. has been registered worldwide in units from different ages in the Paleozoic and Mesozoic periods (Ordovician, Late Pennsylvanian- earliest Cisuralian and Cretaceous). Another explanation lies in the reworking process of older (at least Ordovician) into younger deposits (Permo-Carboniferous and Cretaceous).

According to Batten (1991), the recognition of reworked palynomorphs mainly depends on taxonomic identification (with reference to the known age of the taxon), and differences in their color, state of preservation, and fluorescence in comparison with autochthonous palynomorphs can be useful as well.

We evaluated whether the specimens found in the Sauce Grande Formation may be interpreted as indigenous or reworked from older units. On the one hand, current studies indicate that there are no other species older than Late Pennsylvannian- early Cisuralian in the analyzed samples. Therefore, the process of reworking of pre-Pennsylvanian deposits cannot be confirmed in the recovered palynological association. In addition, the similar degree and type of preservation (including corrosion, degradation, and mechanical damage sensu Delcourt and Delcourt, 1980), the color variation (TAI 3 to −4 after Utting and Wielens, 1992), and the absence of fluorescence in all identified palynomorphs characterize the complete palynological association. In conclusion, no evidence indicates that *Lancettopsis harringtonii* sp. nov. represents a reworked palynomorph.

On the other hand, the proposition that *Lanceottopsis harringtonii* sp. nov. has a wide spatial and temporal distribution is feasible since it represents a simple morphology of polyphyletic origin, and hence it may be recurrent in the fossil record. The broad distribution of *Lancettopsis harringtonii* sp. nov. could be explained by its ability to survive and adapt to different contexts along a wide stratigraphic interval. A similar situation occurs with the morphologically simple and very frequent leiospheres recovered in palynologic associations worldwide from the Proterozoic to Recent. In general, these simple morphotypes are interpreted as autochthonous, and they are referred to different species of *Leiosphaeridia* depending on the age of each association, even when they may be assigned to species first defined from older or younger units.

In conclusion, we suggest that *Lancettopsis harringtonii* sp. nov. can be effectively interpreted as an autochthonous palynomorph in the Sauce Grande Formation. This species lacks stratigraphic value due to its wide temporal distribution.

9. Conclusions

The palynological study of core samples from PANG 0002 (Sauce Grande Formation, Pennsylvanian- Cisuralian), located in the Claromecó Basin, Argentina, revealed a new association of organic-walled marine microplankton. The new species *Lancettopsis harringtonii* is proposed and interpreted as the repeated curling inward of vesicle walls of Sphaeromorph gen. et sp. indet.

Lanceolate morphotypes were assigned to *Lancettopsis*, a genus here emended and interpreted as the final stage of the repeated curling

inward of spheromorphs with median split or, more rarely, partial rupture. This genus would not have an ontogenic relationship with the misunderstood acritarch, prasinophyte, or pollen grain *Campenia*, as originally interpreted by Mädler (1963).

The genus *Lancettopsis* is widely registered in marine successions of Phanerozoic rocks, associated with other constituents of the organic wall marine microplankton. This recurrent association and the fact that no specimen has been registered in confirmed continental environments yet allow us to consider the genus *Lancettopsis*, and in particular, the species *Lancettopsis harringtonii* sp. nov., as a representative of the organic-walled marine microplankton. This interpretation is in line with the glacimarine origin of the Sauce Grande Formation, as previously interpreted based on sedimentological, stratigraphical, and paleontological data.

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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.

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