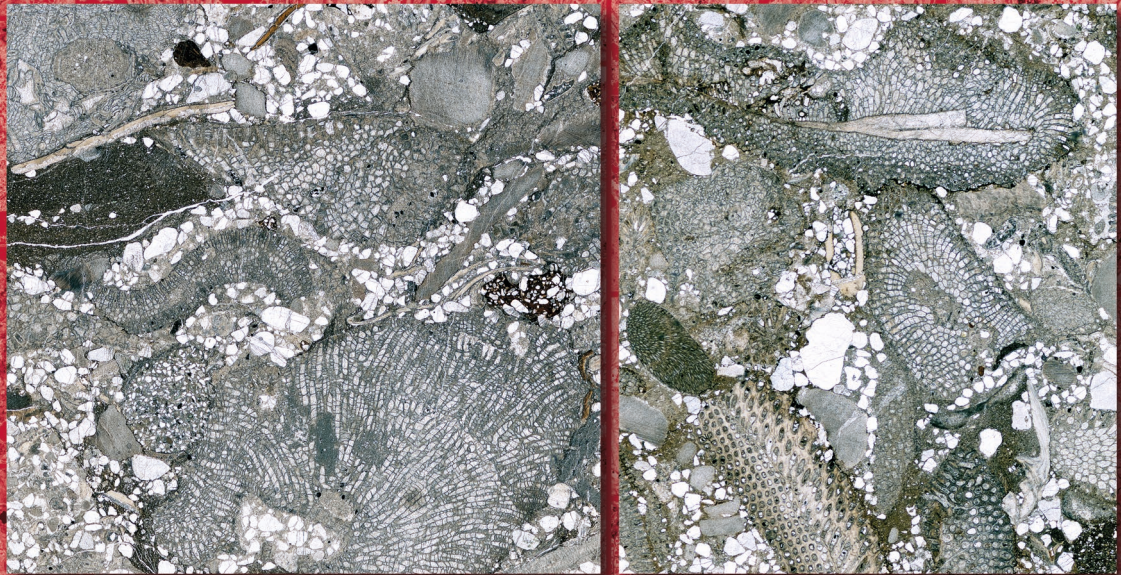


## A cool-water bryozoan association from the La Pola Formation (Sandbian, Ordovician) of Argentine Precordillera

Andrej ERNST & Marcelo CARRERA



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# A cool-water bryozoan association from the La Pola Formation (Sandbian, Ordovician) of Argentine Precordillera

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## ABSTRACT

Nineteen bryozoan species belonging to 18 genera are described from the La Pola Formation (Sandbian, Upper Ordovician) of Argentine Precordillera. Two trepostome genera each with one new species, respectively, are new: *Albardonia bifoliata* n. gen., n. sp. and *Argentinopora robusta* n. gen., n. sp. Five more species are new: a cystoporate *Xenotrypa argentinensis* n. sp., two trepostomes *Heterotrypa enodis* n. sp. and *Nicholsonella spinigera* n. sp., as well as two ptilodictyines *Pseudostictoporella simplex* n. sp. and *Chazydictya ornata* n. sp. The studied fauna shows some connection with Laurentia and Baltica on the species level and is similar to Siberia on the generic level. Furthermore, the generic composition of the La Pola fauna is similar to contemporary faunas of Las Aguaditas and Las Plantas formations of the Argentine Precordillera. The described fauna comes from mixed carbonate-siliciclastic deposits and represents a largely para-autochthonous association, with few autochthonous elements. The bryozoan growth forms indicate shallow shelf conditions. Bryozoans are associated with brachiopods, red algae, and echinoderms indicating heterozoan community typical for temperate to cool water environments with high primary production.

## KEY WORDS

Ordovician,  
Sandbian,  
cool-water environment,  
Bryozoa,  
palaeogeography,  
palaeoecology,  
new genera,  
new species.

## RÉSUMÉ

*Une association de bryozoaires d'eau froide de la Formation de La Pola (Sandbien, Ordovicien) de la Précordillère argentine.*

Dix-neuf espèces de bryozoaires appartenant à dix-huit genres sont décrites au sein de la Formation de La Pola (Sandbien, Ordovicien supérieur) de la Précordillère argentine. Deux genres de trépostomes, incluant chacun une nouvelle espèce, sont nouveaux : *Albardonia bifoliata* n. gen., n. sp. et *Argentinopora robusta* n. gen., n. sp. Cinq autres espèces sont nouvelles : le cystoporate *Xenotrypa argentinensis* n. sp., les trépostomes *Heterotrypa enodis* n. sp. et *Nicholsonella spinigera* n. sp., ainsi que les ptilodictyines *Pseudostictoporella simplex* n. sp. et *Chazydictya ornata* n. sp. La faune étudiée présente un lien évident avec Laurentia et Baltica au niveau des espèces et est proche de Siberia au niveau générique. En outre, la composition générique de la faune de La Pola est proche des faunes contemporaines des formations de Las Aguaditas et de Las Plantas de la Précordillère argentine. La faune décrite provient de dépôts mixtes carbonatés-silicoclastiques et représente une association largement parautochtone, avec peu d'éléments autochtones. Les formes de croissance rencontrées chez les bryozoaires indiquent des conditions de plateforme peu profonde. Ces organismes sont associés à des brachiopodes, des algues rouges et des échinodermes, ce qui indique une communauté hétérozoïque typique des environnements d'eau tempérée à froide avec une production primaire élevée.

## MOTS CLÉS

Ordovicien,  
Sandbien,  
environnement d'eau  
froide,  
Bryozoa,  
paléogéographie,  
paléocologie,  
genres nouveaux,  
espèces nouvelles.

## INTRODUCTION

The present contribution represents the latest taxonomic work on bryozoans from the Argentine Precordillera. After field work and collection of Ordovician bryozoans from Argentina (MC) during the last 30 yr and a decade from the beginning of the study of this important collection, the results have been 29 species. All these studies intend to fill a gap in the bryozoan record from the Southern Hemisphere. In the present contribution we have added 19 more bryozoan species to this record.

The previous studies on bryozoans from the Ordovician of Argentine Precordillera reported material from Lower and Middle Ordovician (Tremadocian to Darriwilian) limestones (Carrera & Ernst 2010). This poorly diversified bryozoan fauna (only four species) is outnumbered in comparison with other sessile organisms, such as demosponges and echinoderms that fully developed in these typical warm water carbonate environments. On the other hand, bryozoans are particularly diverse and abundant in the Sandbian units, of which the Las Plantas and Las Aguaditas formations are the most characteristic (Carrera 2003; Ernst & Carrera 2012). There are also records from the Katian Sassito Formation (Ernst & Carrera 2008) and from the Hirnantian postglacial deposits (Halpern & Carrera 2014) with lower diversity. So, the records in the Argentine Precordillera and their particular paleogeographic history (see Astini *et al.* 1995; Benedetto *et al.* 1999; Benedetto 2003a, Benedetto *et al.* 2009) provide the opportunity to outline the whole Ordovician bryozoan diversification patterns from warmer to colder climates.

The aim of the present paper is the taxonomic study of 19 bryozoan species from the La Pola Formation (Sandbian) in San Juan Province, Precordillera of western Argentina (Fig. 1). This fauna includes genera of the orders Cystoporida, Trepostomata, Cryptostomata, and Fenestrata.

Material for the present study was collected from the La Pola creek section (30°13'19.7"S, 68°29'25"W) near Albardon village in Argentine Precordillera (Fig. 1).

## STRATIGRAPHY AND ENVIRONMENTAL SETTING

The Ordovician stratigraphy of the Argentine Precordillera (Fig. 2) includes several depositional sequences (Astini 1998a; Keller *et al.* 1998; Cañas 1999) that mainly comprise the Tremadocian to Darriwilian carbonate sequence, the Sandbian to Katian mixed calcareous-siliciclastic sequence (Las Plantas, Las Aguaditas, La Cantera and Trapiche formations) and the Hirnantian (Don Braulio sequence). The bryozoan fauna studied in this contribution comes from La Pola Formation (included in Las Plantas sequence by Astini 1998b) developed on the top of the La Cantera Formation. The La Pola Formation is slightly younger than Las Aguaditas formations and partially equivalent to the Las Plantas Formation (Fig. 2).

Sedimentation of the Las Plantas sequence started with the drowning of the underlying carbonate platform (San Juan Formation limestones). In the Darriwilian, a rapid eustatic sea-level rise led to the deposition of graptolitic black shales and mudstones. After a hiatus in sedimentation, the Sandbian deposits were associated with a different tectono-stratigraphic regime. Mixed calcareous-siliciclastic sedimentation dominated during the Sandbian (Las Aguaditas and Las Plantas formations). These deposits also include thick intrabasinal limestone olistoliths mixed with extrabasinal resedimented conglomerates (La Cantera and Las Vacas formations; Keller *et al.* 1993; Astini 1998b).

Las Aguaditas Formation includes the *Nemagraptus gracilis* Biozone (Brussa 1996). The Las Plantas Formation is Sandbian in age, but it records the *Climacograptus bicornis* Biozone, located immediately above the *Nemagraptus gracilis* Biozone (Ortega & Brussa 1990; Astini & Brussa 1997).

The overall setting for most of the Middle and Upper Ordovician (Late Darriwilian-Katian) can be visualized as partitioned, block-faulted platform with topography of horsts and grabens (Astini 1998a; Keller *et al.* 1998). Extensional tectonism generated a horst and graben topography that

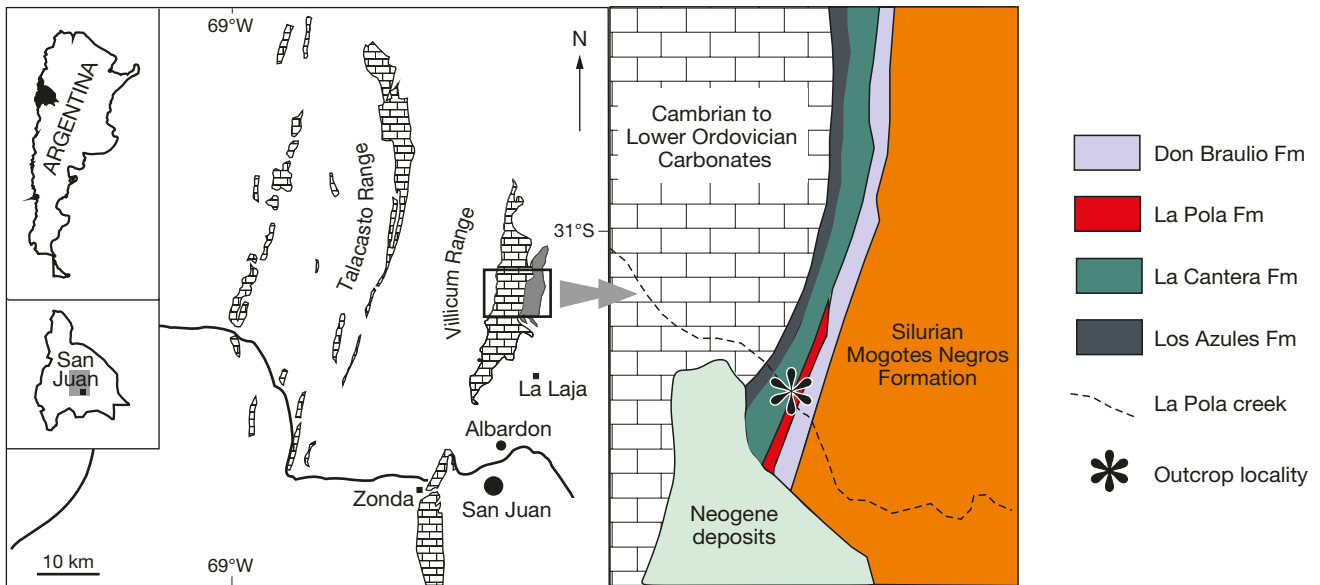


FIG. 1. — Geologic map of the study area showing the location of the La Pola creek and the fossiliferous locality in the Villicum range, San Juan Province, Argentina.

produced shallow calcareous or siliciclastic platforms, and local slopes and basin deposits. Predominantly siliciclastic sedimentation continued during the Late Ordovician, mainly in the northern part of the basin (Trapiche Formation, Trapiche Sequence of Astini [1998b]).

In the Villicum range, easternmost Precordillera basin (Fig. 1), the La Cantera Formation served as the base of the Sandbian units. This unit is partially a lateral equivalent to the mixed siliciclastic carbonate Las Aguaditas Formation with its diverse bryozoan fauna studied by Ernst & Carrera (2012).

The La Cantera Formation is a sand-dominated unit that yields massive polymictic conglomerates at its base and fines upwards. Age constraints at its top suggests a Sandbian age based on the presence of *Nemagraptus gracilis* (Hall, 1847) by Peralta (1986) within the silty shales near its top.

The Hirnantian Don Braulio Formation rests unconformably on the La Cantera Formation (Baldis *et al.* 1982). However, locally in the La Pola creek exposure (Fig. 1), a separate mainly conglomeratic interval develops in between. This unit designated as La Pola Formation by Astini (2001) shows sharp erosive contacts at its bottom and top and constitutes a local relict that survived the strong erosion that occurred during the Late Ordovician glaciation. Both the La Cantera and the La Pola Formations are sharply overlain by glacial diamictites of the Don Braulio Formation. This unit assigned to the Hirnantian stage on the base of its abundant shelly fauna (Benedetto 1986) represents the Late Ordovician glacial record of the Argentine Precordillera (Peralta & Carter 1990; Buggisch & Astini 1993).

La Pola Formation has a maximum thickness of 47 m and a proposed Sandbian age (Brussa 2000). This age is confirmed by its rich shelly fauna. The La Pola Formation represents a succession of thick-bedded coarse-grained debris flows (ranging from mud to clast supported) with interbedded pebbly mudstones, amalgamated lenticular quartz-bioclastic-rich

sandstones, as well as a few turbidites and silty shales. Both graptolites and conodonts with older ages have been recovered from various clasts, with the youngest assigned to *Nemagraptus gracilis*/*Dicranograptus clingani* Biozones. Brussa (2000) identified the graptolites *Dicranograptus ramosus ramosus* (Hall, 1847), *Dicranograptus nicholsoni* Hopkinson, 1870, and other taxa which indicate a Sandbian age (Gisbornian 1-2). More recently, a conodont association from the La Pola Formation allowed definition of the *Amorphognathus tvaerensis* Biozone (upper Sandbian-lower Katian), and within this zone the association can be assigned to the *Baltoniodus variabilis* Subzone (Heredia & Milana 2010).

The La Pola Formation consists of debris flow deposits, slumping and slope facies associations suggest a depositional environment related to a proximal deep-marine trough (Astini 2001). Sedimentary provenance points to a high-energy shelfal quartz-rich source and a coeval or intermixed carbonate interval. Abundant resedimented thalli of *Solenopora* and *Girvanella* remains (Astini 2001), as well as bryozoans (this contribution) associated with a rich brachiopod fauna (Benedetto 2003b) constitute a particular association different to those found in the Lower Ordovician calcareous units of the Argentine Precordillera (Fig. 2).

The para-autochthonous nature of the main fossil collection is suggested by their occurrence in the coarse grained debris flow deposits (Fig. 2[LP2 levels]). However, we noted the autochthonous nature of some bryozoans and also brachiopods recovered from the pebbly mudstones and silty green shales and fine sandstones (Figs 2, 3[LP1, LP 3 and LP4 levels], see also Benedetto 2003b). Some bryozoan colonies were found growing around pebbles, and non-abraded articulated brachiopods occur within the mudstones.

The La Pola Formation and coeval or partially coeval units (Las Plantas, Las Aguaditas and Sassito formations) are similar in that their faunas are all dominated by bryozoans (Car-



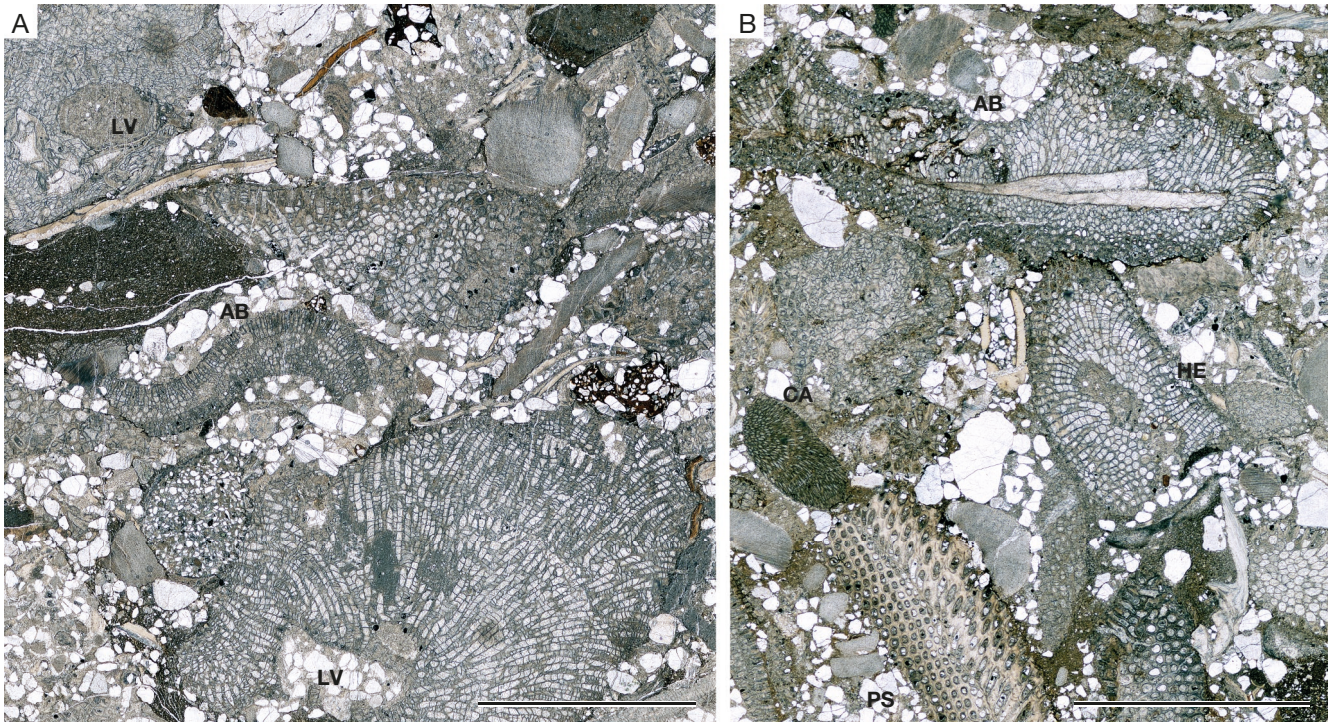


FIG. 3. — Microfacies of the main bryozoan-bearing rocks (lenticular quartz-bioclasic-rich sandstones) containing fragmented bryozoans (PS, *Pseudostictoporella simplex* n. sp.; AB, *Albardonia bifoliata* n. gen., n. sp.; LV, *Lunaferamita virginiensis* Utgaard, 1981; HE, *Heterotrypa enodis* n. sp.), brachiopod shells, crinoids, calcareous algae (CA), as well as lithoclasts in the siliciclastic matrix; A, CEGH-UNC 27520 b; B, CEGH-UNC 27530 e. Scale bars: 5 mm.

ra 2003; Ernst & Carrera 2008, 2012) accompanied by abundant brachiopods. Faunal associations of Las Plantas and Las Aguaditas formations (Fig. 2) also contain tabulate corals (Fernandez-Martinez *et al.* 2004). The Katian Sassito Formation and the Hirnantian Don Braulio Formation are slightly younger than the La Pola Formation and have less bryozoan diversity (Ernst & Carrera 2008; Halpern & Carrera 2014, respectively).

## MATERIAL AND METHODS

The bryozoan fauna was studied in thin sections made from collected rock material. Studied thin sections are housed at the Córdoba University CIPAL-CICTERRA under the prefix CEGH-UNC, numbers 27503-27545.

Bryozoans were investigated in thin sections using binocular transmitted light microscopy. Morphologic character terminology is partly adopted from Anstey & Perry (1970) for trepostomes and Hageman (1993) for cryptostomes. The following morphologic characters were measured and used for statistics in the studied material: Branch diameter, exo- (and endo-) zone width, autozoocial aperture width, autozoocial aperture spacing (along branch and diagonally), acanthostyle diameter, meso- (and meta-) zoecia diameter, autozoocial (mesozoocial) diaphragm spacing, cystiphragm spacing, number of mesozoocia, vesicles, and acanthostyles surrounding each autozoocial aperture, wall thickness in exozone, diameter and spacing of vesicles, lunarium width, length and thickness, and node width (spacing).

The spacing of structures is measured as the distance between their centres. Statistics were summarized using arithmetic mean, sample standard deviation, coefficient of variation, and minimum and maximum values.

## SYSTEMATIC PALAEOLOGY

Phylum BRYOZOA Ehrenberg, 1831  
 Class STENOLAEMATA Borg, 1926  
 Superorder PALAEOSTOMATA  
 Ma, Buttler & Taylor, 2014  
 Order CYSTOPORATA Astrova, 1964  
 Suborder FISTULIPORINA Astrova, 1964  
 Family CONSTELLARIIDAE Ulrich, 1896

Genus *Lunaferamita* Utgaard, 1981

TYPE SPECIES. — *Fistulipora? bassleri* Loeblich, 1942 by subsequent designation (Utgaard 1981), Bromide Formation, lower Sandbian, Upper Ordovician, Oklahoma, United States.

DIAGNOSIS. — Colonies encrusting or ramose. Indistinctly stellate monticules with large, irregular vesicles forming subcircular to elongate centre and radiating inter-rays of vesicles separating rows of loosely aggregated autozoocia. Lunaria on proximal sides of autozoocia nearest the centres of monticules. Autozoocia with thin, transversely laminated walls and many, closely spaced to few, remote diaphragms; isolated by box-like to blister-like vesicles. Acanthostyles few to abundant within laminated vesicle walls or roofs. Lunaria laminated, commonly with hyaline core.

OCCURRENCE. — *Lunaferamita bassleri* (Loeblich, 1942), *L. nevadensis* Utgaard, 1981, and *L. virginiensis* Utgaard, 1981 were reported from the Sandbian of United States. *Lunaferamita nevadensis* Utgaard, 1981 and *L. vesicularis* Chang, Yang & Xigiang, 2011 were reported from the Lianglitag Formation (Upper Ordovician, Katian) of China (Tarym).

#### COMPARISON

*Lunaferamita* differs from *Constellaria* Dana, 1846 by having lunaria and monticules of indistinct stellate shape. Furthermore, *Lunaferamita* possesses vesicles in endozones.

### *Lunaferamita virginiensis* Utgaard, 1981 (Fig. 4A-E; Appendix 1)

*Lunaferamita virginiensis* Utgaard, 1981: 1068-1070, pl. 3, figs 1-9.

MATERIAL EXAMINED. — CEGH-UNC 27506 a, b, CEGH-UNC 27507 c, CEGH-UNC 27513 a-d, CEGH-UNC 27516 c, CEGH-UNC 27520 a, b, CEGH-UNC 27524 a, b, CEGH-UNC 27533 b, CEGH-UNC 27538 b.

OCCURRENCE. — La Pola Formation, Upper Ordovician, Sandbian; La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

#### DESCRIPTION

Massive, encrusting, partly multilayered, or subramose colonies. Massive colony up to 20 mm in height, subramose extensions 3.8-5.0 mm in diameter. Autozoecia growing from thin epitheca, bending in the early exozone to the colony surface. Epitheca 0.003-0.005 mm thick. Basal diaphragms abundant, straight or inclined, thin. Macrozoecia surrounding maculae, 0.14-0.22 mm wide. Autozoecial apertures circular to oval. Lunaria well-developed, rounded to slightly triangular, consisting of granular material; ends of lunaria not indenting autozoecia. Vesicles small to large, not completely separating autozoecia, arranged in 1-2 rows between apertures, 4-8 surrounding each autozoecial aperture, with rounded to flat roofs, polygonal in tangential section. Autozoecial walls granular prismatic, 0.005-0.020 mm thick. Colony surface covered by laminated stereom. Acanthostyles in stereom present, 0.015-0.030 mm in diameter, more abundant in maculae. Maculae consisting of vesicular skeleton with larger vesicles, surrounded by macrozoecia, 0.67-1.25 mm in diameter, spaced 1.13-1.75 mm from centre to centre.

#### COMPARISON

*Lunaferamita virginiensis* Utgaard, 1981 differs from *L. bassleri* (Loeblich, 1942) by having smaller autozoecia, less abundant acanthostyles and more abundant diaphragms. *Lunaferamita virginiensis* differs from *L. vesicularis* Chang, Yang & Xigiang, 2011 by having encrusting and massive colonies instead of ramose ones in the latter species.

### Family XENOTRYPIDAE Utgaard, 1983

#### Genus *Xenotrypa* Bassler, 1952

TYPE SPECIES. — *Fistulipora primaeva* Bassler, 1911 by subsequent designation (Bassler 1952). Lower Ordovician (?Arenig); Russia.

DIAGNOSIS. — Massive or encrusting colonies. Autozoecia slightly indented by acanthostyles. Diaphragms in autozoecia few to absent. Vesicles irregular, isolating autozoecia. Acanthostyles large, generally in autozoecial walls, some in vesicle walls; centres light to dark in colour. Autozoecial walls indistinctly laminated.

OCCURRENCE. — Lower to Middle Ordovician of Russia and Argentina.

#### COMPARISON

*Xenotrypa* Bassler, 1952 differs from *Hennigopora* Bassler, 1952 in acanthostyles which do not significantly indent into the autozoecia, whereas acanthostyles in *Hennigopora* strongly indent autozoecia. Furthermore, vesicles usually completely isolate autozoecia in *Xenotrypa*, whereas the autozoecia in *Hennigopora* often share a common wall.

### *Xenotrypa argentinensis* n. sp. (Figs 4F-G; 5A-E; Appendix 1)

[urn:lsid:zoobank.org:act:67915CAA-948A-462B-A581-8549E84C7F8A](https://doi.org/10.1111/zoo.12584)

HOLOTYPE. — CEGH-UNC 27523 a, b (three thin sections of one colony).

PARATYPE. — CEGH-UNC 27521 a (thin section of one colony).

TYPE LOCALITY. — La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

TYPE HORIZON. — La Pola Formation, Upper Ordovician, Sandbian.

DIAGNOSIS. — Massive multilayered colonies. Autozoecial apertures rounded-polygonal. Autozoecial diaphragms rare to absent in endozone, common in exozone, straight, thin. Vesicles abundant, 4-7 surrounding each aperture, completely isolating autozoecia. Acanthostyles relatively large, 3-6 surrounding each autozoecial aperture. Maculae not observed.

ETYMOLOGY. — The species is named after finding it in Argentina.

#### DESCRIPTION

Massive multilayered colonies. Autozoecia long, having polygonal transverse section in endozone. Autozoecial apertures rounded-polygonal. Autozoecial diaphragms rare to absent in endozone, common in exozone, straight, thin. Vesicles abundant, 4-7 surrounding each aperture, completely isolating autozoecia, angular in cross section, having straight or curved roofs, sealed by calcitic skeleton near colony surface. Acanthostyles relatively large, 3-6 surrounding each autozoecial aperture, originating in endozone, with distinct wide hyaline cores, rarely indenting autozoecia. Autozoecial walls indistinctly laminated, 0.008-0.015 mm thick. Maculae not observed.

#### COMPARISON

The investigated material is similar to representatives of the Family Xenotrypidae which consists of two genera: *Xenotrypa* Bassler, 1952 and *Hennigopora* Bassler, 1952. However, its assignment to a genus is difficult. The genus *Xenotrypa* Bassler,



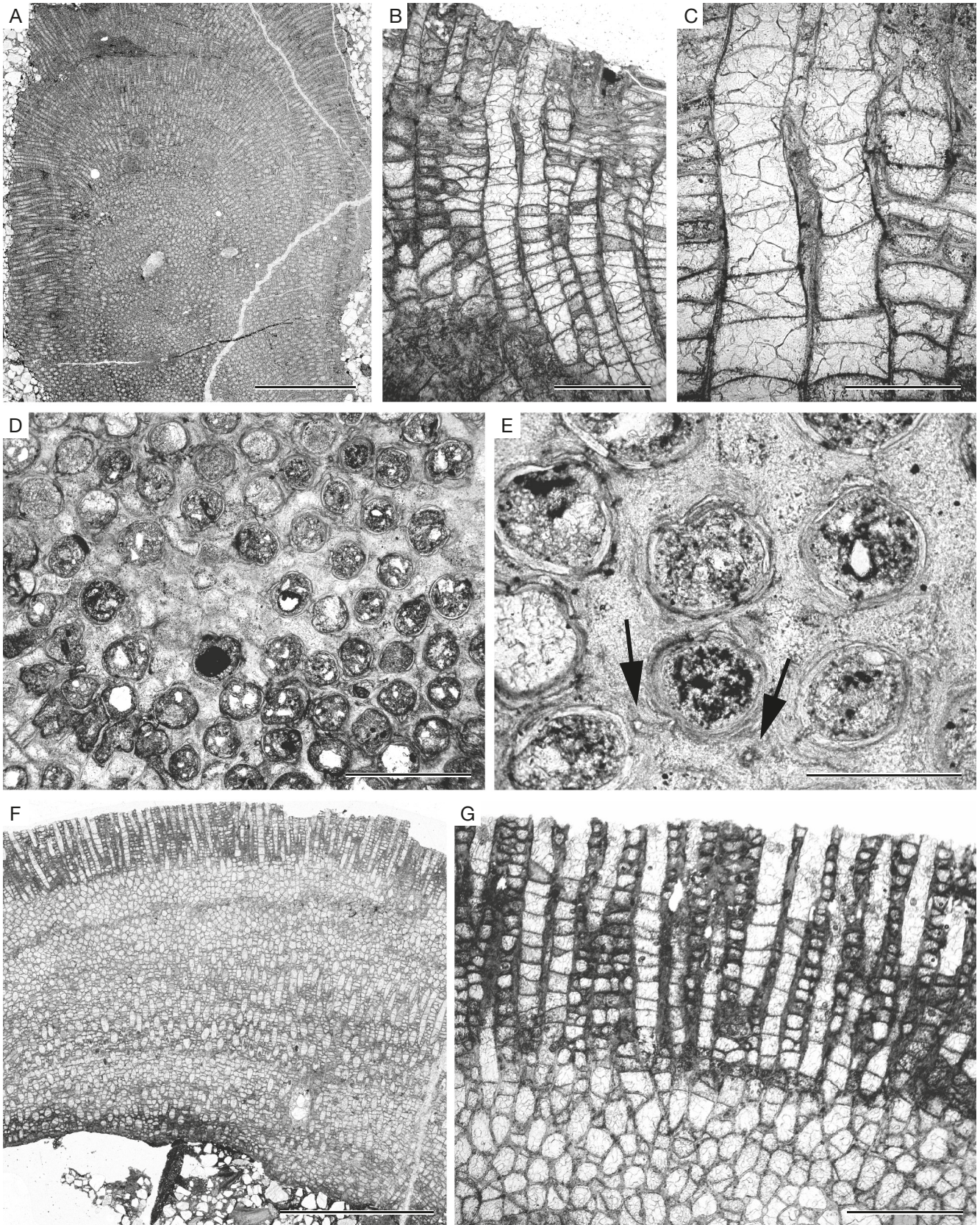


FIG. 4. — **A-E**, *Lunaferamita virginiensis* Utgaard, 1981: **A**, longitudinal thin section of a colony, CEGH-UNC 27524 a; **B, C**, longitudinal section of exozone showing autozoecia with diaphragms and vesicles, CEGH-UNC 27513 c; **D**, tangential thin section showing macula, autozoecial apertures and acanthostyles (arrows), CEGH-UNC 27513 b; **F, G**, *Xenotrypa argentinensis* n. sp., longitudinal thin section, holotype CEGH-UNC 27523 b. Scale bars: A, F, 5 mm; B, D, 0.5 mm; C, E, 0.2 mm; G, 1 mm.

1952 is known with few specimens restricted mainly to the type material of two species of the genus, *Xenotrypa primaeva* (Bassler, 1911) from the Lower Ordovician of Russia, and *X. bassleri* Astrova, 1965 from the Middle Ordovician of Russia. The type species *X. primaeva* reveals large acanthostyles with centres of dark colour (Utgaard 1983: 377, fig. 169). In contrast, acanthostyles in *Hennigopora* have distinct hyaline cores, like in present material. *Xenotrypa argentinensis* n. sp. differs from *X. primaeva* and *X. bassleri* in its smaller autozooeical apertures (aperture width at average 0.16 mm vs 0.36 mm in *X. primaeva*; 0.13–0.21 mm vs 0.22–0.34 mm in *X. bassleri*) as well as in more abundant acanthostyles and abundant diaphragms in autozooeica.

Order ESTHONIOPORATA Astrova, 1978  
Family DIANULITIDAE Vinassa de Regny, 1921

Genus *Dianulites* Eichwald, 1829

TYPE SPECIES. — *Dianulites detritus* Eichwald, 1829 [syn. of *D. fastigiatus*] by subsequent designation (Eichwald 1860). Lower to Middle Ordovician; Russia, Estonia.

DIAGNOSIS. — Colony turbinate, cone or horn-shaped, sometimes compound, occasionally with a conical central cavity, in some species massive hemispherical; zooecia opening on upper, distal surface of colony; colony sides comprising exterior wall; not differentiated into endozone and exozone; maculae variably developed, some monticulate. Zooecia long polygonal tubes, monomorphic or obscurely polymorphic; walls thin, indistinct, granular, inclusion-rich; styles lacking; diaphragms moderately abundant, microstructural fabric strongly radial (modified after Taylor & Wilson 1999).

OCCURRENCE. — Lower to Upper Ordovician; Europe, North and South America, Asia.

#### COMPARISON

*Dianulites* Eichwald, 1829 belongs to its own family (Vinassa de Regny 1921). It shows similarities to the unplaced genus *Nicholsonella* Ulrich, 1890. These genera possess re-crystallized walls which suggest a diagenetically unstable aragonitic (McKinney 1971) or high Mg calcite composition (Taylor & Wilson 1999; Smith *et al.* 2006). *Nicholsonella* differs from *Dianulites* by having abundant mesozooecia and acanthostyles.

*Dianulites rocklandensis* Wilson, 1921  
(Figs 5F–G; 6A; Appendix 1)

*Dianulites rocklandensis* Wilson, 1921: 47, pl. 2, figs 1–2.

MATERIAL EXAMINED. — Single colony (three thin sections) CEGH-UNC 27503 a–c.

OCCURRENCE. — La Pola Formation, Upper Ordovician, Sandbian; La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina. Leray and Rockland formations, Upper Ordovician (Sandbian); Canada.

#### DESCRIPTION

Massive hemispherical colony, 8.5 mm thick in its central part and 20 mm wide at its base. Secondary overgrowth not

observed. Exozone indistinct. Autozooeica long, prismatic, growing from epitheca. Autozooeical apertures polygonal. Diaphragms straight, rare to common in endozone, common in exozone. Autozooeical walls indistinctly granular, irregularly thickened, 0.015–0.040 mm thick. Maculae not observed.

#### COMPARISON

The present material is similar to *Dianulites rocklandensis* Wilson, 1921 from the Ordovician (upper Sandbian) of Canada. This species, as described by Wilson (1921), developed branched ramose colonies. However, Kang (2017) mentioned also hemispheric colonies of this species found at the type locality. *Dianulites rocklandensis* differs from *D. microcellatus* Astrova, 1945 from the Upper Ordovician of Urals in larger autozooeical apertures (0.24–0.36 mm vs 0.19–0.28 mm in *D. microcellatus*).

Order TREPOSTOMATA Ulrich, 1882  
Family MONTICULIPORIDAE Nicholson, 1881

Genus *Monticulipora* d'Orbigny, 1850

TYPE SPECIES. — *Monticulipora mammulata* d'Orbigny, 1850 by original designation. Upper Ordovician (Cincinnatian); North America.

DIAGNOSIS. — Colonies encrusting, hemispherical, massive, frondose or ramose. Autozooeical apertures polygonal. Cystiphagms and planar diaphragms generally occur throughout the zooecia. Acanthostyles are commonly short, generally limited to thick-walled zones and are the best developed in monticules or can be rare or absent. Intermonticular mesozooecia are common to lacking, polygonal in cross section and contain planar, closely spaced diaphragms. Autozooeical walls laminated throughout the colonies. Monticules are marked by thickened zooecial and mesozooecia walls and increased concentrations of enlarged acanthostyles, often with a central cluster of mesozooecia surrounded by enlarged zooecia.

OCCURRENCE. — Middle Ordovician to Lower Silurian, worldwide.

#### COMPARISON

*Monticulipora* d'Orbigny, 1850 differs from *Prasopora* Nicholson & Etheridge, 1877 by having less abundant mesozooecia, polygonal autozooeical apertures, serrated instead of amalgamated wall structure, and usually less abundant cystiphagms.

*Monticulipora* aff. *mammulata* d'Orbigny, 1850  
(Fig. 6B–D; Appendix 1)

For full synonymy of the species *Monticulipora mammulata* d'Orbigny, 1850, see in Brown & Daly (1985: 68).

MATERIAL EXAMINED. — Single colony (three thin sections) CEGH-UNC 27516 a, b, d.

OCCURRENCE. — La Pola Formation, Upper Ordovician, Sandbian; La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

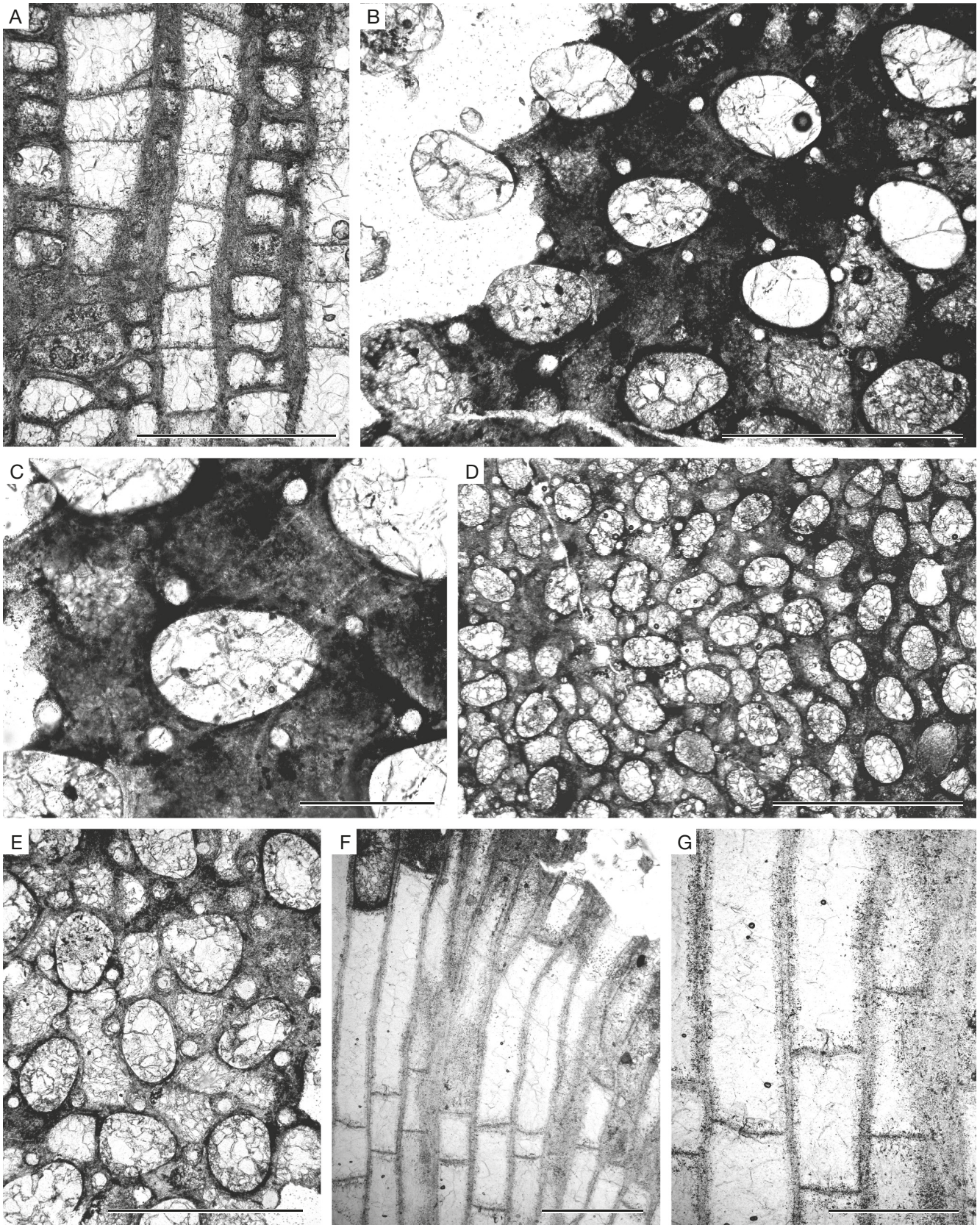


FIG. 5. — **A-E**, *Xenotrypa argentinensis* n. sp.: **A**, longitudinal thin section, showing autozooezia with diaphragms and vesicles, holotype CEGH-UNC 27523 b; **B**, **C**, tangential thin section showing autozooezial apertures, acanthostyles, and vesicles, holotype CEGH-UNC 27523 a; **D**, **E**, tangential thin section showing autozooezial apertures, acanthostyles, and vesicles, paratype CEGH-UNC 27521 a; **F**, **G**, *Dianulites rocklandensis* Wilson, 1921, longitudinal thin section, CEGH-UNC 27503 c. Scale bars: A, B, E, G, 0.5 mm; C, 0.2 mm; D, F, 1 mm.

#### DESCRIPTION

Submassive colony, multilayered, weakly differentiated into exo- and endozone. Autozooezia prismatic, bearing abundant cystiphragms. Autozooezial diaphragms common to abundant, mainly inclined or cystoid. Autozooezial apertures polygonal. Mesozooezia common, polygonal in tangential section, bearing closely spaced diaphragms, locally beaded. Zooeial walls laminated, serrated, 0.01–0.02 mm thick. Acanthostyles rare, 0.030–0.035 mm in diameter. Maculae not observed.

#### COMPARISON

The present material is similar to *Monticulipora mammulata* d'Orbigny, 1850 from the Upper Ordovician of North America. However, the typical monticules consisting of abundant mesozooezia, were not found in the present material. *Monticulipora parallela* McKinney, 1971 from the Middle Ordovician of United States (Alabama) differs from the present material in encrusting colony and larger autozooezial apertures (average aperture width 0.20 mm vs 0.18 mm in the present material).

#### Genus *Orbignyella* Ulrich & Bassler, 1904

TYPE SPECIES. — *Orbignyella sublamellosa* Ulrich & Bassler, 1904 by original designation. Middle Ordovician; United States.

DIAGNOSIS. — Colonies encrusting, massive or globular. Prismatic autozooezia with polygonal apertures. Autozooezial diaphragms abundant, straight or inclined, often cystoid. Exilazooezia rare, short, with or without diaphragms. Acanthostyles small or large, varying in number. Autozooezial walls thin or weakly irregularly thickened, with indistinct laminated microstructure, often serrated.

OCCURRENCE. — Ordovician – Silurian; worldwide.

#### COMPARISON

*Orbignyella* Ulrich & Bassler, 1904 differs from *Cyphotrypa* Ulrich & Bassler, 1904 in having of abundant and inclined diaphragms.

#### *Orbignyella multitabulata* Coryell, 1921 (Fig. 6E–G; Appendix 1)

*Orbignyella multitabulata* Coryell, 1921: 284, pl. 5, figs 3–4.

MATERIAL EXAMINED. — CEGH-UNC 27505 a–c, CEGH-UNC 27518 a–c.

OCCURRENCE. — La Pola Formation, Upper Ordovician, Sandbian; La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina. Pierce Limestone, Upper Ordovician (Sandbian); Tennessee, United States.

#### DESCRIPTION

Massive, subramose multilayered colonies. Secondary overgrowths common, 1–2 mm thick. Autozooezia bending gently from endozone, intersecting colony surface at right angles. Autozooezial apertures rounded to polygonal. Diaphragms in autozooezia common to abundant, straight to curved. Exilazooezia rare, polygonal in cross section, restricted to

exozone. Acanthostyles common, moderately large, situated at junctions of autozooezial apertures. Autozooezial walls granular-prismatic, 0.005–0.010 mm thick in endozone; irregularly thickened, finely laminated, displaying reverse V-structure in longitudinal section, 0.020–0.033 mm thick in exozone. Maculae of macrozooezia 0.70–1.25 mm in diameter, spaced 1.9–2.0 mm from centre to centre.

#### COMPARISON

The present material is morphologically similar to *Orbignyella multitabulata* Coryell, 1921 from the Sandbian of United States. The only metric characteristic for *O. multitabulata* is the number of apertures per 2 mm given as 8–8.5 (Coryell 1921: 284). Interpolated, it gives apertural spacing of *c.* 0.23–0.25 mm what overlaps the range in the present species (0.13–0.22 mm). The present material differs from *Orbignyella wetherbyi* (Ulrich, 1890) from the Upper Ordovician of United States in smaller autozooezia (aperture width 0.11–0.19 mm vs 0.25–0.28 mm in *O. wetherbyi*).

#### Genus *Homotrypa* Ulrich, 1882

TYPE SPECIES. — *Homotrypa curvata* Ulrich, 1882 by original designation. Cincinnati, Upper Ordovician; North America.

DIAGNOSIS. — Ramose and frondose colonies, often flattened, sometimes encrusting and irregularly massive in initial stages. Autozooezia with polygonal, rounded or oval apertures. Walls slightly thickened in exozone, integrate, diagonally and longitudinally laminated. Cystiphragms only in exozone, diaphragms commonly in exozone. Mesozooezia from rare to abundant, sometimes clustering in maculae. Acanthostyles abundant, commonly small.

OCCURRENCE. — Middle Ordovician to Lower Silurian; North America, Europe, Australia, Siberia.

#### COMPARISON

The genus *Homotrypa* Ulrich, 1882 differs from the genus *Monticulipora* d'Orbigny, 1850 by its branched erect colony instead of the encrusting or massive one in *Monticulipora*. Furthermore, cystiphragms in *Homotrypa* are usually concentrated in the inner exozone, whereas cystiphragms in *Monticulipora* occur throughout autozooezial chambers.

#### *Homotrypa subramosa* Ulrich, 1886 (Fig. 7A–C; Appendix 1)

*Homotrypa subramosa* Ulrich, 1886: 81; 1893: 239–340, pl. 19, figs 21–28. — Bassler 1911: 187–189, text-figs 99–100. — Bork & Perry 1968: 1053–1055, pl. 136, figs 1–3. — McKinney 1971: 234–237, pl. 49, fig. 4–8, pl. 50, fig. 1. — Marintsch 1998: 53–55, pl. 9, figs 1–5.

*Homotrypa insignis* Ulrich, 1886: 82.

MATERIAL EXAMINED. — CEGH-UNC 27516 a, d, CEGH-UNC 27519 a, b, CEGH-UNC 27530 a–g, CEGH-UNC 27531 b, CEGH-UNC 27536 a, CEGH-UNC 27537 a, b, CEGH-UNC 27542 a, c, d, e, CEGH-UNC 27545b.

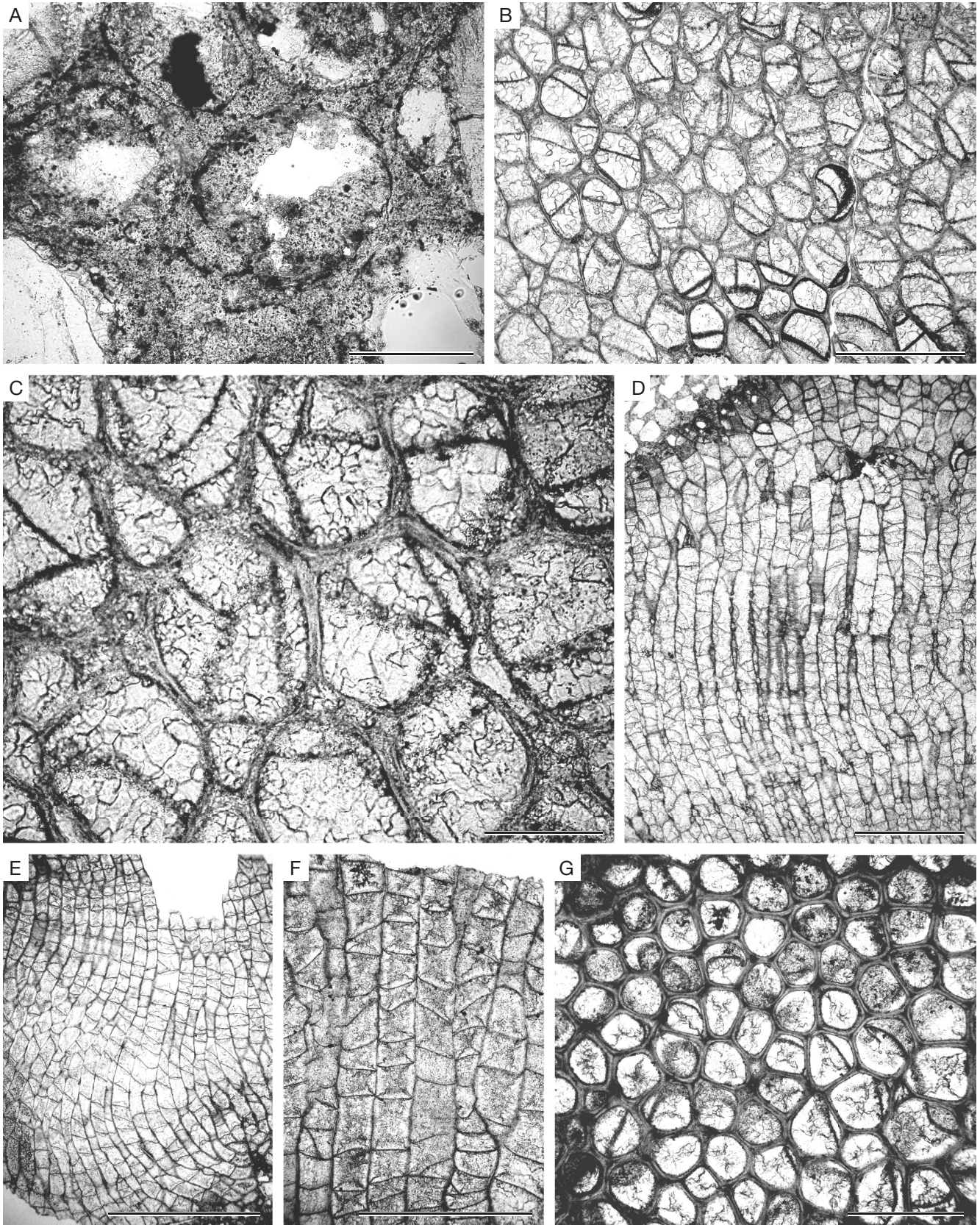


FIG. 6. — **A**, *Dianulites rocklandensis* Wilson, 1921, tangential section showing autozoecial apertures, CEGH-UNC 27503 a; **B-D**, *Monticulipora* aff. *mammulata* d'Orbigny, 1850, CEGH-UNC 27516 d; **B, C**, tangential thin section showing autozoecial apertures; **D**, longitudinal thin section showing autozoecial chambers with cystiphragms; **E-G**, *Orbignyella multitalabulata* Coryell, 1921; **E, F**, longitudinal thin section showing autozoecia with diaphragms, CEGH-UNC 27505 a; **G**, tangential thin section showing autozoecial apertures, CEGH-UNC 27505 b. Scale bars : A, C, 0.2 mm; B, G, 0.5 mm; D, F, 1 mm; E, 2 mm.

#### DESCRIPTION

Irregularly branched, submassive or encrusting colony. Branches and fronds 5.6-9.4 mm thick, encrusting sheets 0.7-1.6 mm thick. Exozones indistinct. Autozooezia prismatic, growing for long distance along branch axis and bending gently to the colony surface. Autozooezial diaphragms common, thin, planar. Autozooezial apertures polygonal in tangential section. Cystiphragms abundant, densely spaced, constricting middle part of zooecia, about a half of their diameter. Mesozooecia few, polygonal. Autozooezial walls granular, 0.003-0.005 mm thick in endozone; amalgamated, 0.02-0.03 mm thick in exozone. Acanthostyles few, small to moderate in size. Maculae consisting of macrozooezia, 0.80-0.95 mm in diameter.

#### COMPARISON

*Homotrypa subramosa* Ulrich, 1886 differs from *H. callosa* Ulrich, 1893 in larger autozooezial apertures (average aperture width 0.16 mm vs 0.14 mm in *H. callosa*; measurements for *H. callosa* from Marintsch, 1998). *Homotrypa subramosa* Ulrich, 1886 differs from *H. tuberculata* Ulrich, 1893 in less abundant and smaller acanthostyles and in smaller autozooezial apertures (average aperture width 0.16 mm vs 0.20 mm in *H. tuberculata*; measurements for *H. tuberculata* from Marintsch 1998).

#### *Homotrypa vacua* McKinney, 1971 (Fig. 7D-I; Appendix 1)

*Homotrypa vacua* McKinney, 1971: 238-241, pl. 50, figs 2-7. — Pushkin 1987: 186.

MATERIAL EXAMINED. — CEGH-UNC 27507 c, CEGH-UNC 27525 a, CEGH-UNC 27529 a, CEGH-UNC 27530 a, b, d-g, CEGH-UNC 27533 d, CEGH-UNC 27541 a, CEGH-UNC 27545 a.

OCCURRENCE. — Lower Chickamauga Group, Upper Ordovician, Sandbian; Alabama, United States. La Pola Formation, Upper Ordovician, Sandbian; La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

#### DESCRIPTION

Ramose colonies, branch diameter 1.45-2.38 mm. Endozone 0.60-1.45 mm wide, exozone 0.25-0.75 mm wide, distinct. Secondary overgrowths not observed. Autozooezia long in the endozone, having larger diameters than in exozone, bending gently and intersecting branch surface at low angles. Autozooezial apertures rounded-polygonal. Autozooezial diaphragms rare to absent in the endozone, concentrated mostly in transitional region between endo- and exozone, common to abundant in outer exozone. Cystiphragms occurring throughout the exozone, occupying about the half of autozooezial diameter. Mesozooecia locally 3-5 surrounding each autozooezial aperture, otherwise rare; small, short, restricted to the outermost part of exozone, containing densely spaced diaphragms. Acanthostyles common, 2-5 surrounding each autozooezial aperture, moderately large, restricted to exozone. Autozooezial walls straight, displaying granular

microstructure, 0.003-0.005 mm thick in endozone; finely laminated with indistinct medial line, 0.023-0.055 mm thick in exozone. Indistinct maculae consisting of macrozooezia.

#### COMPARISON

*Homotrypa vacua* McKinney, 1971 differs from *H. mundula* (Ulrich, 1893) in having smaller colonies (branch diameter 1.45-2.38 mm vs 3.6-4.0 in *H. mundula*, measurements from Karklins [1984: 134]). *Homotrypa vacua* differs from *H. subramosa* Ulrich, 1886 in having thin branched colonies instead subramose and encrusting ones as well as in smaller autozooezial apertures (average aperture width 0.11 mm vs 0.16 mm in *H. subramosa*).

#### Family HETEROTRYPIDAE Ulrich, 1890

#### Genus *Heterotrypa* Nicholson, 1879

TYPE SPECIES. — *Monticulipora frondosa* d'Orbigny, 1850 by subsequent designation (Utgaard & Boardman 1965). Cincinnati, Upper Ordovician; North America.

DIAGNOSIS. — Colonies frondose, ramose or less commonly encrusting. Autozooezial walls can be extremely variable in thickness. Zooecial boundary is a conspicuous dark line in inner exozones and in a broad zone of abutting laminae or completely obscured in outer exozones. Walls generally are amalgamated in appearance. Diaphragms are generally few in endozones, but are moderately abundant in some species. In exozones, diaphragms are closely and regularly spaced, thin, planar and perpendicular to the zooecial walls. Intermonticular mesozooecia range from abundant and regularly arranged to scattered or absent. Mesozooecia develop commonly moniliform chambers at proximal ends and tend to become smaller or are terminated distally within exozones. Diaphragms in mesozooecia noticeably thicker and more closely spaced than zooecial diaphragms. Acanthostyles are at least two kinds within the genus, regular acanthostyles limited to exozone, and the endacanthostyles originating in both endozone and exozone. Endacanthostyles occur in all species. Monticules generally have a central cluster of a few mesozooecia than those in the intermonticular area.

OCCURRENCE. — Middle Ordovician-?Devonian; worldwide.

#### COMPARISON

The genus *Heterotrypa* Nicholson, 1879 differs from the genus *Leioclema* Ulrich, 1882 by abundant diaphragms in autozooezia, more angular apertural shape and two kinds of acanthostyles.

#### *Heterotrypa enodis* n. sp. (Fig. 8A-F; Appendix 1)

[urn:lsid:zoobank.org:act:C5482952-9218-4600-BDBE-C77CE258D9DD](https://doi.org/10.21203/rs.3.rs-1111111/v1)

HOLOTYPE. — CEGH-UNC 27504 a-c (one colony, three thin sections).

PARATYPES. — CEGH-UNC 27519 a, b (two thin sections of one colony), 27542 a, c-e (four thin sections of one colony).

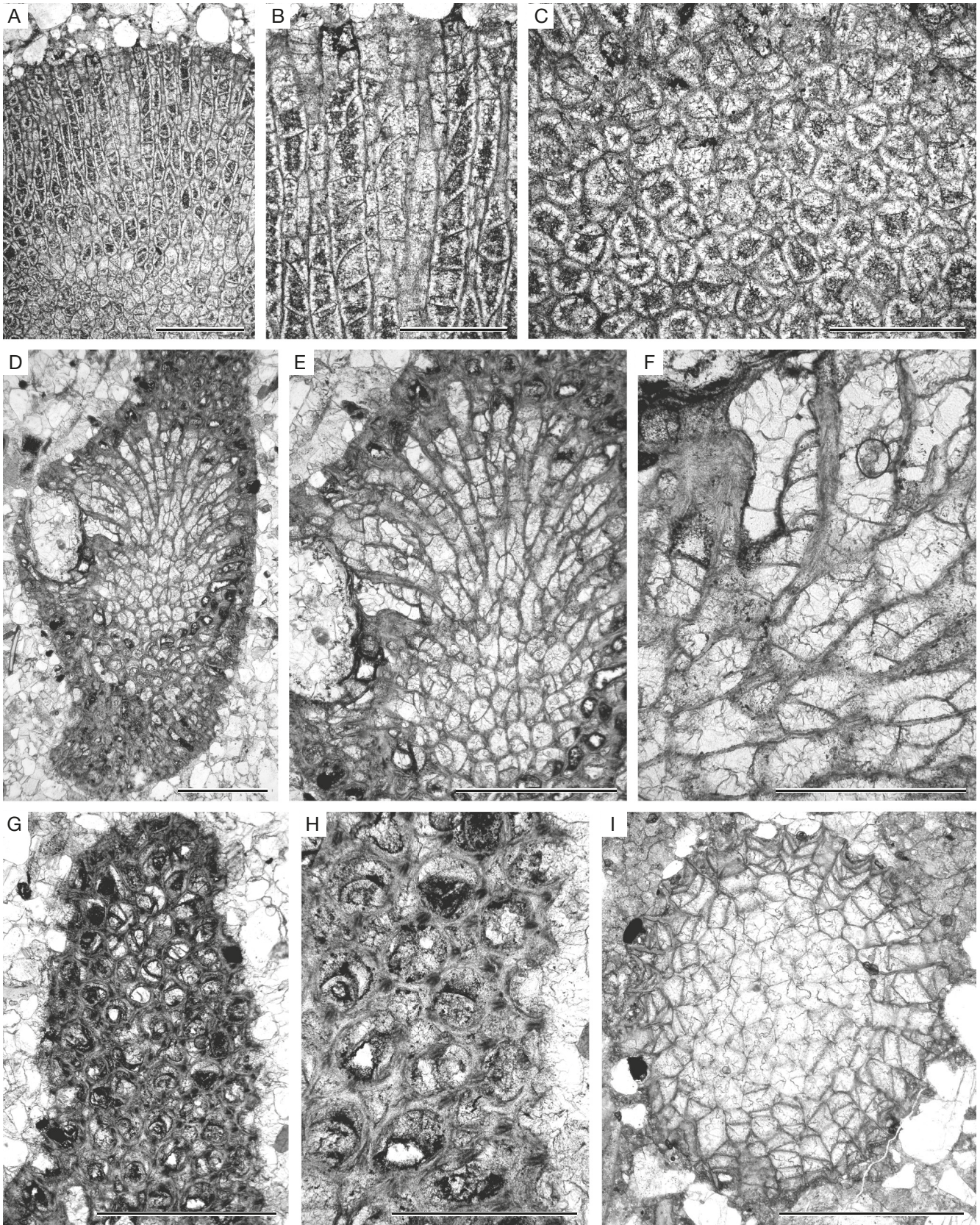


FIG. 7. — **A-C**, *Homotrypa subramosa* Ulrich, 1886, CEGH-UNC 27537 b: **A, B**, longitudinal thin section showing autozooeical chambers with cystiphragms; **C**, tangential thin section showing autozooeical apertures, mesozooeia, and acanthostyles; **D-I**, *Homotrypa vacua* McKinney, 1971: **D, E**, branch longitudinal thin section showing autozooeical chambers with cystiphragms, CEGH-UNC 27545 a; **G, H**, tangential thin section showing autozooeical apertures, mesozooeia, and acanthostyles, CEGH-UNC 27545 a; **I**, branch transverse section, CEGH-UNC 27507 b. Scale bars: A, D, E, G, I, 1 mm; B, C, F, H, 0.5 mm.

TYPE LOCALITY. — La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

TYPE HORIZON. — La Pola Formation, Upper Ordovician, Sandbian.

ETYMOLOGY. — The species name refers to small acanthostyles of the new species (from Latin “*enodis*” – smooth).

DIAGNOSIS. — Ramose colonies with distinct exozones; autozoecia with rounded-polygonal apertures; autozoecial diaphragms rare in endozone, common to abundant in exozone, developed as extension of wall cortex; mesozoecia moderately large, 1-4 surrounding each autozoecial aperture; acanthostyles small, 1-3 surrounding each autozoecial aperture; endozonal styles absent; autozoecial walls with distinct reverse V-shaped lamination with dark autozoecial border and weakly developed wall cortex continued in diaphragms; maculae consisting of macrozoecia.

#### DESCRIPTION

Ramose colonies, branch diameter 3.6 to 3.9 mm. Exozone distinct, 0.68 to 0.78 mm wide, endozone 2.24 to 2.34 mm wide. Autozoecia long, growing parallel to branch axis for a long distance in endozone, in exozone bending sharply and intersecting branch surface at angles of 66 to 74°, having rounded-polygonal shape in transverse section in endozone. Autozoecial apertures oval to polygonal. Autozoecial diaphragms thin, planar, widely spaced in endozone; common to abundant in exozone, planar, rarely inclined, developed as extension of wall cortex. Mesozoecia arising in endozone, polygonal in transverse section, few to common, 1-4 surrounding each autozoecial aperture. Mesozoecial diaphragms planar, densely spaced. Acanthostyles small, having laminated sheaths and indistinct hyaline cores, relatively abundant, 1-3 surrounding each autozoecial aperture. Endozonal styles absent. Autozoecial walls indistinctly laminated, 0.005 to 0.010 mm thick in endozone; displaying distinct reverse V-shaped structure with dark autozoecial border, with weakly developed wall cortex continued in diaphragms, 0.033 to 0.075 mm thick in exozone. Maculae consisting of macrozoecia, 1.25-1.35 mm in diameter.

#### COMPARISON

The present species shows similarities to the genus *Heterotrypa* Nicholson, 1879 in the wall microstructure, abundant diaphragms arising from the wall cortex, presence of mesozoecia and acanthostyles. *Heterotrypa enodis* n. sp. differs from *H. trentonensis* (Ulrich, 1883) from the Upper Ordovician of North America in absence of endozonal styles, smaller exozonal acanthostyles (average acanthostyle diameter 0.03 mm vs 0.05 mm in *H. trentonensis*; measurements from Karklins 1984), and more abundant mesozoecia. *Heterotrypa enodis* differs from *H. subtrentonensis* Marintsch, 1998 from the Upper Ordovician of North America in absence of endozonal styles, less abundant exozonal acanthostyles (1-3 per aperture vs 3-5 in *H. subtrentonensis*), and more abundant mesozoecia.

### Genus *Albardonia* n. gen.

[urn:lsid:zoobank.org:act:CF51A226-FD7D-4583-B045-A26177B30FC0](https://doi.org/10.12110/zoobank.org/act:CF51A226-FD7D-4583-B045-A26177B30FC0)

TYPE SPECIES. — *Albardonia bifoliata* n. sp., by present designation.

ETYMOLOGY. — The new genus is named after Albardon village near which this genus was found.

DIAGNOSIS. — Ramose colony consisting of bifoliate fronds; encrusting sheets and secondary overgrowth common; autozoecia budding from mesotheca or epitheca, having angular shape of transverse section in endozone; autozoecial apertures angular with rounded corners; basal diaphragms common both in endozone and exozone, straight, or inclined; mesozoecia abundant, containing densely spaced diaphragms; aktinostyles moderately large, abundant, originating in exozone, autozoecial walls laminated, integrated with dark median lining, showing reversal V-shaped lamination, without cingulum; maculae lacking.

OCCURRENCE. — La Pola Formation, Upper Ordovician, Sandbian; Argentine Precordillera, western Argentina.

#### COMPARISON

The new genus is characterized by abundant mesozoecia and aktinostyles. It is similar to the genus *Leioclema* Ulrich, 1882 in having abundant and large mesozoecia, but differs in the presence of aktinostyles instead of acanthostyles in the latter genus.

*Albardonia bifoliata* n. gen., n. sp.  
(Figs 8G, H; 9A-F; Appendix 1)

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HOLOTYPE. — CEGH-UNC 27538 c.

PARATYPES. — CEGH-UNC 27507 a, b, CEGH-UNC 27520 a, b, d, CEGH-UNC 27528 a, CEGH-UNC 27529 a, CEGH-UNC 27530 a, b, e, f, g, CEGH-UNC 27532 a, CEGH-UNC 27533 a, b, CEGH-UNC 27537 b, CEGH-UNC 27538 a, b, CEGH-UNC 27539 b, CEGH-UNC 27541 a (in total, 19 thin sections of 10 colonies).

TYPE LOCALITY. — La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

TYPE HORIZON. — La Pola Formation, Upper Ordovician, Sandbian.

DIAGNOSIS. — As for genus.

ETYMOLOGY. — The species name refers to the bifoliate colony shape of the new species.

#### DESCRIPTION

Bifoliate (frondose) colony starting from encrusting sheets. Fronds 0.70-1.30 mm in thickness. Encrusting sheets 0.66-1.31 mm thick. Secondary overgrowths occurring. Autozoecia budding from mesotheca, having angular shape of transverse section in endozone. Autozoecial apertures angular with rounded corners. Mesotheca 0.01-0.02 mm in thickness. Basal diaphragms common both in endozone



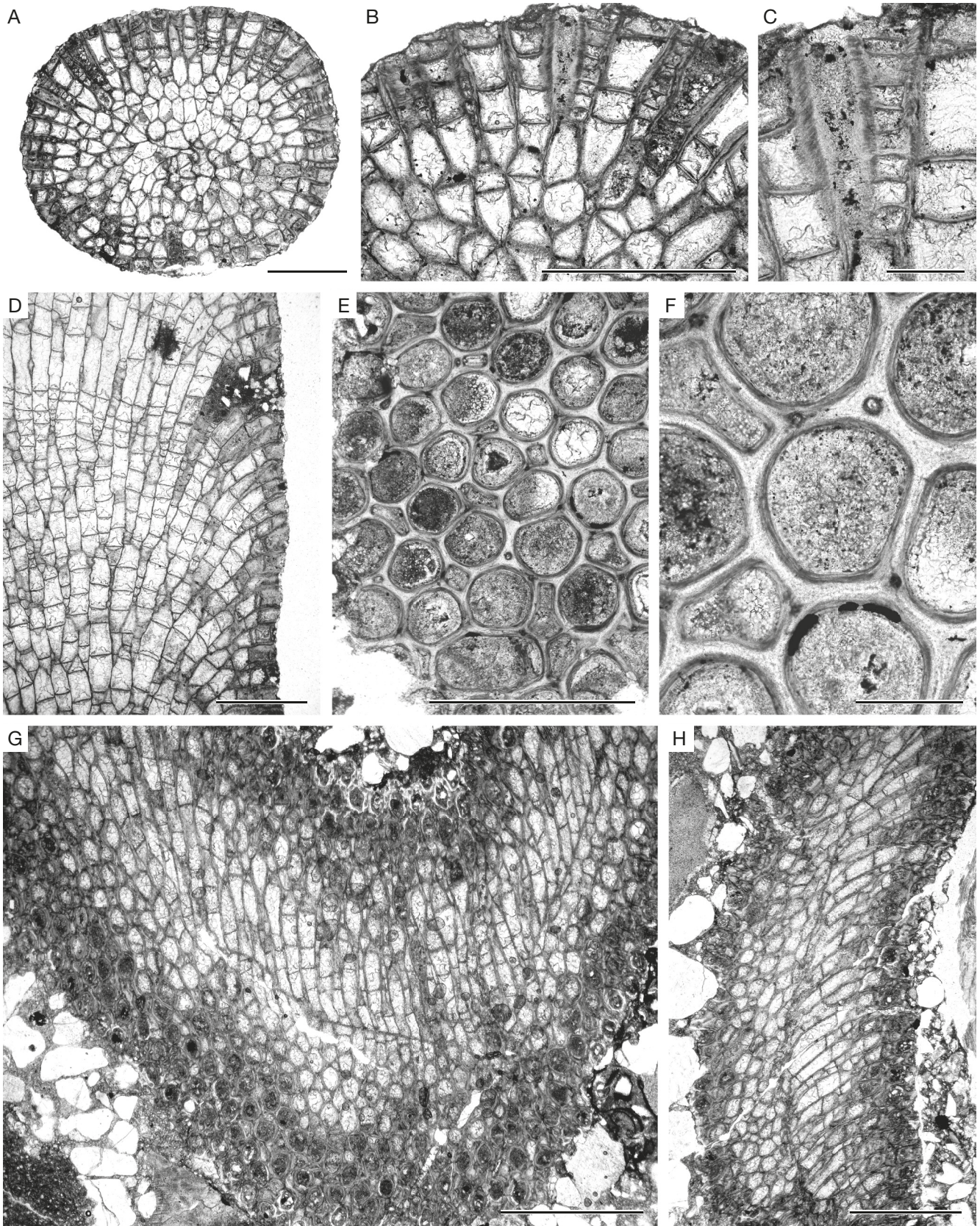


FIG. 8. — **A-F**, *Heterotrypa enodis* n. sp.: **A-C**, branch transverse section showing autozooeical chambers and mesozooeia, holotype CEGH-UNC 27504 b; **D**, branch longitudinal section showing autozooeical chambers with diaphragms and mesozooeia, CEGH-UNC 27504 a; **E, F**, tangential thin section showing autozooeical apertures, mesozooeia, and acanthostyles, CEGH-UNC 27504 c; **G, H**, *Albardonia bifoliata* n. gen., n. sp., oblique thin section through the bifoliate colony, holotype CEGH-UNC 27538 c. Scale bars: A, B, D, E, G, H, 1 mm; C, F, 0.2 mm.

and exozone, straight, or inclined. Mesozooecia abundant, 3-8 surrounding each autozooeal aperture, containing densely spaced diaphragms. Aktinostyles moderately large, abundant, 5-7 surrounding each autozooeal aperture, originating in the outer exozone. Autozooeal walls granular, 0.010-0.015 mm thick, irregularly undulating in endozones; laminated, integrated with dark median lining, showing reversal V-shaped lamination, without cingulum, 0.02-0.05 mm thick in exozones. Maculae not observed.

COMPARISON  
As for genus.

Family HALLOPORIDAE Bassler, 1911

Genus *Diplotrypa* Nicholson, 1879

TYPE SPECIES. — *Monticulipora (Diplotrypa) petropolitana* Nicholson, 1879 by original designation (*non Favosites petropolitaneus* Pander, 1830). Sweden; Middle Ordovician.

DIAGNOSIS. — Massive, variably shaped colonies, exozone poorly developed. Budding pattern interzooeal. Zooeal arrangement disordered; zooecia gradually expand distally through early ontogeny and curve outward toward colony surface; zooecia characterised by ontogenetic progression of mesozooecia expanding into autozooea. Mesozooeal stage of early zooeal ontogeny extended; after mesozooeal stage, diaphragms widely spaced in proximal ends and closely spaced in distal ends of mesozooecia; mesozooecia occasionally fuse to form autozooea; mesozooecia commonly isolate autozooea. Autozooeal apertures polygonal to rounded. Autozooeal walls commonly thin throughout colony and composed of finely crystalline microlaminae. Diaphragms thin, planar, concave, convex or cystoidal, variably spaced. Acanthostyles rare. Maculae usually consisting of macrozoecia.

OCCURRENCE. — Lower Ordovician to Upper Silurian; North America, Asia, and Europe.

COMPARISON

*Diplotrypa* Nicholson, 1879 differs from other genera of the Family Halloporidae by its massive colony form and thin zooeal walls.

*Diplotrypa* sp. A  
(Fig. 9G; 10A-D; Appendix 1)

MATERIAL EXAMINED. — Single colony (two thin sections) CEGH-UNC 27543a, b.

OCCURRENCE. — La Pola Formation, Upper Ordovician, Sandbian; La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

DESCRIPTION

Massive colony, 6.2-6.4 mm in thickness, with indistinct endozone. Autozooea growing from epitheca at high angles. Autozooea in outer exozone often developing from mesozooecia. Autozooeal diaphragms common to rare, planar, curved proximally, irregularly spaced in

autozooea. Mesozooecia common, up to 3 surrounding each autozooeal aperture, bearing abundant straight diaphragms. Autozooeal walls fine fibrous microstructure, 0.005-0.010 mm thick in endozone and 0.02-0.03 mm thick in exozone.

COMPARISON

*Diplotrypa* sp. A is similar to *Diplotrypa catenulata* Coryell, 1921 from the Sandbian of United States. Coryell [1921: 296] gave only the spacing of 4-4.5 apertures per 2 mm (distance from centre to centre 0.44-0.50 mm), which is more than double as large as the aperture spacing of the present material (average distance from centre to centre 0.22 mm). Size of apertures for *Diplotrypa catenulata* recorded by Astrova (1965: 185-186) from the Middle Ordovician of Arctic, was given as 0.42-0.75 mm (with macrozoecia of 0.9-1.0 mm width). *Diplotrypa* sp. A is similar to *D. pusilla* Astrova, 1965 from the Lower Ordovician of the Russian Arctic, but differs from it by less abundant diaphragms in autozooea.

Genus *Tarphophragma* Karklins, 1984

TYPE SPECIES. — *Monotrypella multitabulata* Ulrich, 1886 by subsequent designation (Karklins 1984). Decorah Shale and Prosser Limestone, Mohawkian, Upper Ordovician; Minnesota, United States.

DIAGNOSIS. — Ramose colonies with a few generations of encrusting autozooea at the colony bases; branch cross section shape circular. Irregularly shaped, elevated maculae present and composed of cluster of macrozoecia and mesozooecia. Budding pattern interzooidal. Autozooeal arrangement disordered. Autozooea characterized by ontogenetic progression mesozooecia expanding into autozooea, bending gradually from the endozone through the exozone, having polygonal to subpolygonal to sub-circular shape in the endozone. Autozooeal diaphragms closely spaced in early ontogeny and in late ontogeny in all species and occasionally throughout ontogeny in some species, intersecting walls at different angles, shaped usually planar, convex, concave or cystoidal, spaced variably. Autozooeal wall structure integrate in deep exozone, occasionally less integrate in shallow exozones of some species, having straight to irregular boundary in the exozone; wall laminae sharply convex distally, thickened greatly in exozone. Reduction in abundance of mesozooecia and change in autozooeal living chamber cross section shape in exozone from circular to subpolygonal; deeper sections show autozooea with more circular living chamber cross sections, thinner walls, and almost completely isolated by mesozooecia; shallower sections show autozooea with more subpolygonal living chambers cross sections, thicker walls, and mesozooecia less abundant. Mesozooecia common, but not isolating autozooea; occasionally fusing to form autozooea, having thinner walls than those in autozooea. Acanthostyles, cystiphagms, mural spines or cup-like aparati (*sensu* Conti & Serpagli 1987) absent.

OCCURRENCE. — Middle – Upper Ordovician; worldwide.

COMPARISON

The genus *Tarphophragma* Karklins, 1984 differs from other halloporid genera by the integrate wall structure and the budding pattern of autozooea which derive from mesozooecia in endozone.

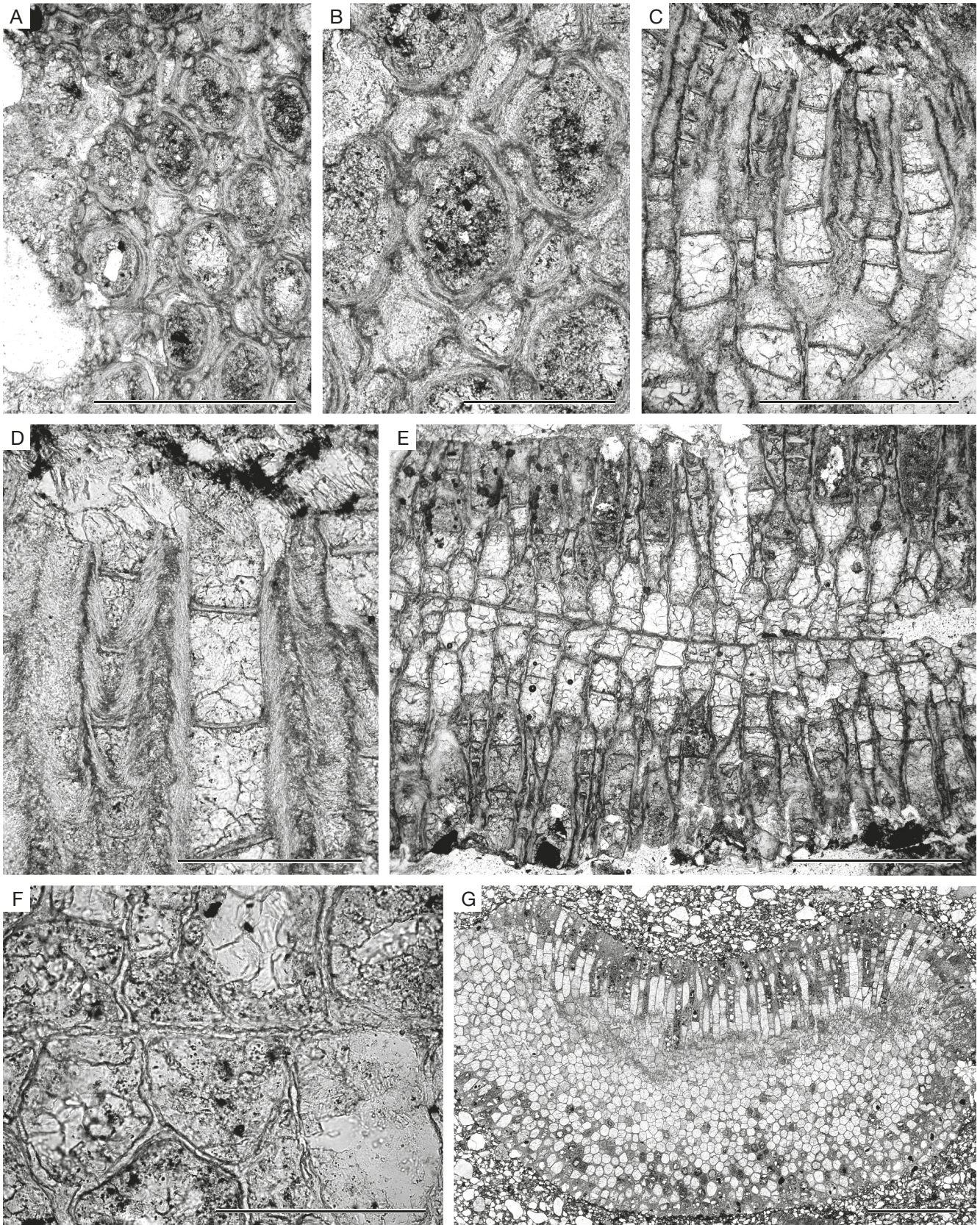


FIG. 9. — **A-F**, *Albardonia bifoliata* n. gen., n. sp.: **A, B**, tangential thin section showing autozooeal apertures, mesozooeia, and aktinostyles, holotype CEGH-UNC 27538 c; **C, D**, longitudinal section showing autozooeal chambers with diaphragms and mesozooeia, paratype CEGH-UNC 27530 a; **E, F**, branch transverse thin section showing autozooeal chambers with diaphragms, mesozooeia, and mesotheca, paratype CEGH-UNC 27541 a; **G**, *Diplotypa* sp. A, CEGH-UNC 27543 a, oblique thin section through the colony. Scale bars: A, C, E, 0.5 mm; B, D, 0.2 mm; F, 0.1 mm; G, 2 mm.

*Tarphophragma macrostoma* (Loeblich, 1942)  
(Figs 10E-G; 11A; Appendix 1)

*Hallopora macrostoma* Loeblich, 1942: 430, pl. 62, figs 12-14.

*Tarphophragma macrostoma* – Key 1991: 207-209, figs 6.1-6.6.

MATERIAL EXAMINED. — CEGH-UNC 27520 c, d, CEGH-UNC 27539 c, d, g, CEGH-UNC 27537 d, CEGH-UNC 27538 d.

OCCURRENCE. — Bromide Formation, Upper Ordovician, lower Sandbian; Oklahoma, United States. La Pola Formation, Upper Ordovician, Sandbian; La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

DESCRIPTION

Ramose colonies, branch diameter 3.0-3.6 mm. Exozone distinct, 0.5-0.6 mm wide, endozone 2.0-2.4 mm wide. Autozoecia long, growing parallel to branch axis for a long distance in endozone and bending sharply in exozone, having rounded-polygonal shape in transverse section in endozone. Autozoecial apertures oval to polygonal. Autozoecial diaphragms thin, planar, widely spaced in endozone; common to abundant in exozone, planar, rarely inclined, developed as extension of wall cortex. Mesozoecia arising in endozone, polygonal in transverse section, 2-6 surrounding each autozoecial aperture. Mesozoecial diaphragms planar, densely spaced. Acanthostyles absent. Autozoecial walls indistinctly laminated, 0.005-0.008 mm thick in endozone; displaying distinct reverse V-shaped structure with dark autozoecial boundary, with weakly developed wall cortex continued in diaphragms, 0.04-0.12 mm thick in exozone. Maculae indistinct, consisting of macrozoecia.

COMPARISON

*Tarphophragma macrostoma* (Loeblich, 1942) differs from *T. ovata* (McKinney, 1971) from the Middle Ordovician of United States in larger autozoecial apertures (average aperture width 0.21 mm vs 0.17 mm in *T. ovata*; measurements for *T. ovata* from McKinney 1971), as well as in less abundant and smaller mesozoecia. *Tarphophragma macrostoma* differs from *T. multitalbulata* (Ulrich, 1886) from the Middle Ordovician of United States in larger autozoecial apertures (average aperture width 0.21 mm vs 0.19 mm in *T. multitalbulata*; measurements for *T. multitalbulata* from Karklins 1984).

Family TREMATOPORIDAE Miller, 1889

Genus *Jordanopora* Ross, 1963

TYPE SPECIES. — *Jordanopora heroensis* Ross, 1963 by original designation. Ordovician, Llanvirn-Llandeilo; United States.

DIAGNOSIS. — Colonies ramose or encrusting, with distinct exozones. Autozoecia prismatic, autozoecial apertures rounded-polygonal. Diaphragms generally lacking in endozones; thin, planar, closely to widely spaced or lacking in exozones. Autozoecial walls thin, laminated, irregularly undulating in endozones; thickly laminated, without cingulum, broadly and irregularly serrated in exozones. Tubules in exozonal walls abundant, thick, hyaline, generally oriented parallel

to autozoecial growth. Mesozoecia rare to common, originating in endozone, containing thick diaphragms. Styles absent. Maculae low to flush, consisting of macrozoecia surround cluster of mesozoecia and massive extrazoooidal skeleton near centres.

OCCURRENCE. — Chazy Series (Darriwilian-Sandbian) of New York, United States, and Sandbian of Argentina.

COMPARISON

*Jordanopora* Ross, 1963 differs from other genera of the Family Trematoporidae in absence of acanthostyles and presence of tubules in zooecial walls.

*Jordanopora heroensis* Ross, 1963  
(Fig. 11B-E; Appendix 1)

*Jordanopora heroensis* Ross, 1963a: 732, pl. 105, figs 1-8, pl. 106, figs 1-4, 6, 7.

MATERIAL EXAMINED. — Single colony (three thin sections) CEGH-UNC 27530 e, f, g.

OCCURRENCE. — Chazy Series (Darriwilian-Sandbian) of New York, United States. La Pola Formation, Upper Ordovician, Sandbian; La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

DESCRIPTION

Colony form uncertain in the present material, possibly branched (bifoliate?) with secondary overgrowth. Exozone distinct, 0.45 mm wide. Autozoecia prismatic, autozoecial apertures rounded-polygonal. Diaphragms thin, planar, widely spaced in exozones. Autozoecial walls 0.010-0.015 mm thick, laminated, irregularly undulating in endozones; thickly laminated, without cingulum, broadly and irregularly serrated, 0.045-0.110 mm thick in exozones. Tubules in exozonal walls abundant, surrounding apertures in one row, hyaline, oriented parallel to autozoecial growth, 0.02-0.05 mm in diameter. Mesozoecia rare to common, occasionally 1-3 surrounding autozoecial apertures, originating in endozone, containing thick diaphragms. Styles absent. Maculae not observed in the present material.

COMPARISON

The present material fits to the species *Jordanopora heroensis* Ross, 1963 in its morphology and dimensions.

Family uncertain

Genus *Argentinopora* n. gen.

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TYPE SPECIES. — *Argentinopora robusta* n. sp., by present designation.

DIAGNOSIS. — Ramose colonies with multiple secondary overgrowths; autozoecia tubular, shape of transverse section angular in endozone and rounded-angular in exozone; basal diaphragms common both in endozone and exozone; cystiphagms common in exozone; autozoecial apertures rounded-polygonal, often petaloid; mesozoecia abundant,

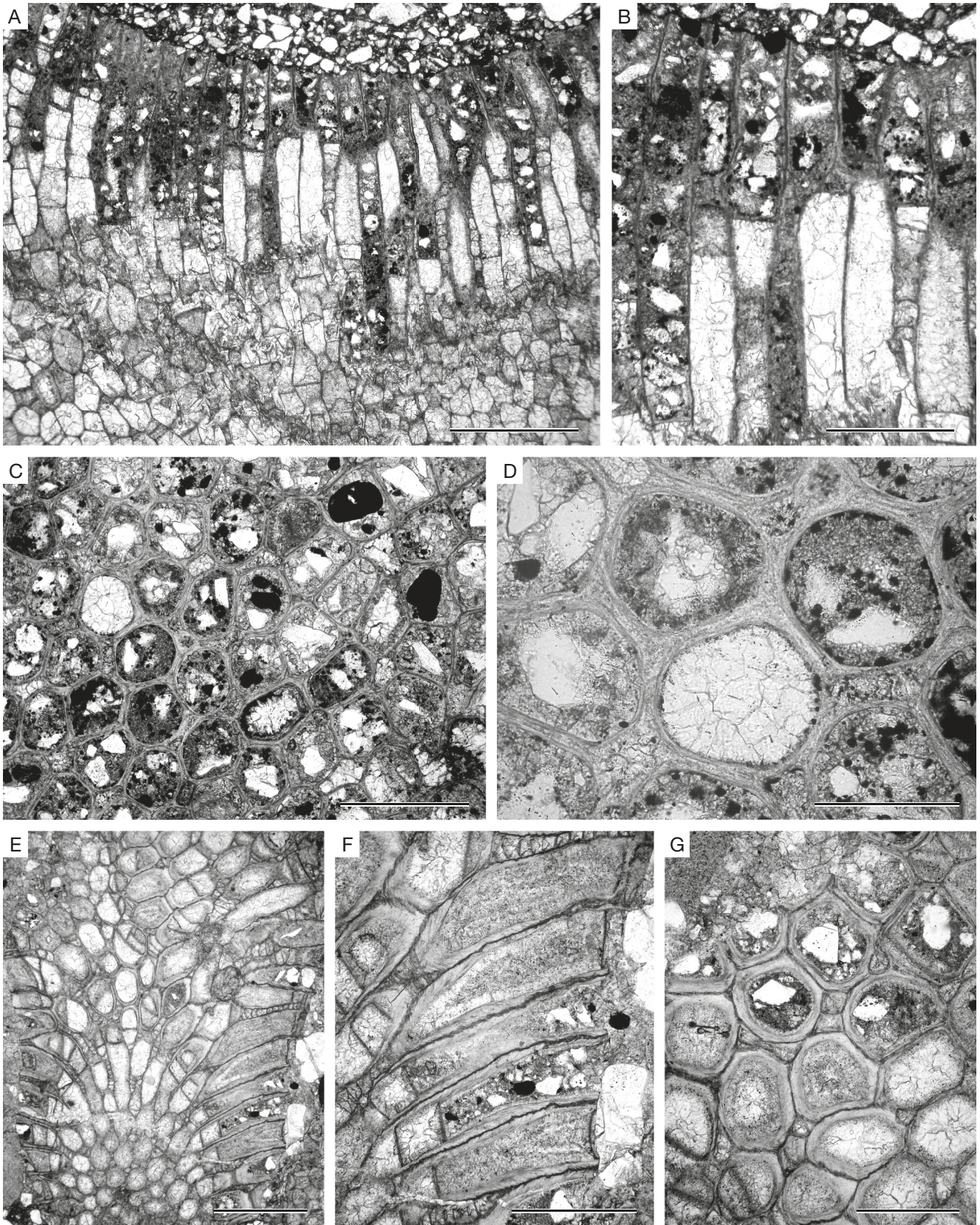


FIG. 10. — **A-D**, *Diplotrypa* sp. A, CEGH-UNC 27543 a: **A, B**, longitudinal section showing autozooeical chambers with diaphragms and mesozooeia; **C, D**, tangential thin section showing autozooeical apertures and mesozooeia; **E-G**, *Tarphophragma macrostoma* (Loeblich, 1942), CEGH-UNC 27520 d: **E**, oblique section through the colony; **F**, longitudinal section showing autozooeical chambers and mesozooeia; **G**, tangential thin section showing autozooeical apertures and mesozooeia. Scale bars: A, E, 1 mm; B, C, F, G, 0.5 mm; D, 0.2 mm.

3-7 surrounding each autozooeical aperture, originating in the early exozone, large, cystose, containing thick diaphragms; acanthostyles large, abundant, 5-8 surrounding each autozooeical aperture, originating in endozone, having wide hyaline cores and narrow laminated sheaths, often indenting autozooeica and mesozooeica; exozonal walls thickly laminated, merged, without cingulum; maculae not observed.

ETYMOLOGY. — The new genus is named after finding it in Argentina.

OCCURRENCE. — La Pola Formation, Upper Ordovician, Sandbian; Argentine Precordillera, western Argentina.

#### COMPARISON

The new genus is characterized by large acanthostyles with narrow sheaths, cystose mesozooeica and presence of cystiphragms. It shows some similarities to the Family Ralfimartitidae Gorjunova, 2005. Gorjunova (2005) introduced the term “aulozooeica” for structures characteristic for Ralfimartitidae. The “aulozooeica” represent indeed large acanthostyles filled out by a hyaline skeletal material (see also Tavener-Smith 1969). The most similar genus in the Family Ralfimartitidae is *Rozhnovites* Gorjunova, 2005 which differs from *Argentinopora* in annulated arrangement of autozooeica and mesozooeica, as well as in absence of cystiphragms.

*Argentinopora robusta* n. gen., n. sp.  
(Figs 11F-G; 12A-F; Appendix 1)

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HOLOTYPE. — CEGH-UNC 27511 a-d (one colony, four thin sections).

PARATYPES. — CEGH-UNC 27514 a-c, CEGH-UNC 27515 a, CEGH-UNC 27520 a, b.

TYPE LOCALITY. — La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

TYPE HORIZON. — La Pola Formation, Upper Ordovician, Sandbian.

DIAGNOSIS. — As for genus.

ETYMOLOGY. — The species name refers to its thick walls and large mesozooeica and acanthostyles (from Latin “*robustus*” – robust, stable, strong).

#### DESCRIPTION

Ramose colony with multiple secondary overgrowths, 3.5-11.0 mm in diameter, with 0.72-1.44 mm wide exozones. Secondary overgrowths 1.05-2.00 mm thick. Autozooeical apertures rounded-polygonal, often petaloid. Basal diaphragms abundant, straight or inclined throughout autozooeica. Cystiphragms common in exozones. Mesozooeica abundant, 3-7 surrounding each autozooeical aperture, originating in the early exozone, large, cystose, containing thick diaphragms. Acanthostyles large, abundant, 5-8 surrounding each autozooeical aperture, originating in endozone, having wide hyaline cores and narrow laminated sheaths, often indenting autozooeica and mesozooeica. Autozooeical walls laminated, 0.01-0.03 mm thick in endozones; thickly laminated, merged, without cingulum, 0.04-0.11 mm thick in exozones. Maculae not observed.

#### COMPARISON

As for genus.

#### Genus *Nicholsonella* Ulrich, 1890

TYPE SPECIES. — *Nicholsonella ponderosa* Ulrich, 1890 by original designation, Trentonian, Sandbian, Upper Ordovician, North America.

DIAGNOSIS. — Encrusting, frondose, ramose, less commonly massive colonies. Apertures rounded and irregularly petaloid. Walls structureless, very thin, irregularly thickened in different part of colonies. Diaphragms usually abundant in whole colony, more rarely – only in the exozone. Mesozooeica abundant, containing frequent diaphragms, sometimes beaded, irregularly closed by calcitic material on the colony surface. Acanthostyles usually small, abundant, short, restricted to the outermost exozone.

OCCURRENCE. — Lower Ordovician to Lower Silurian of North America and Siberia.

#### COMPARISON

*Nicholsonella* Ulrich, 1890 and some other genera (e.g. *Dianulites*) are unique among trepostome bryozoans by their re-crystallized walls which suggest a diagenetically unstable aragonitic (McKinney 1971) or high Mg calcite composition (Taylor & Wilson 1999).

*Nicholsonella spinigera* n. sp.  
(Figs 12G, H; 13A-F; Appendix 1)

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HOLOTYPE. — CEGH-UNC 27528 b, c.

PARATYPES. — CEGH-UNC 27507 a, b, CEGH-UNC 27512 a, b, CEGH-UNC 27522 a, b, CEGH-UNC 27530 e, CEGH-UNC 27533 d, CEGH-UNC 27538 a, c, CEGH-UNC 27539 g.

TYPE LOCALITY. — La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

TYPE HORIZON. — La Pola Formation, Upper Ordovician, Sandbian.

DIAGNOSIS. — Ramose colonies with distinct exozones; secondary overgrowths occurring; autozooeical apertures angular with rounded corners; basal diaphragms abundant both in endozone and exozone, straight, or inclined; mesozooeica few, containing densely spaced thick diaphragms; acanthostyles large, 4-8 surrounding each autozooeical aperture, originating in endozone, having wide hyaline cores and narrow laminated sheaths; exozonal autozooeical walls thickly laminated, merged, showing reversal U-shaped lamination, without cingulum; maculae lacking.

ETYMOLOGY. — The species name refers to large and abundant acanthostyles of the new species (from Latin “*spiniger*” – spinose).

#### DESCRIPTION

Branched colony with secondary overgrowths, 3.5-11.0 mm in diameter, with 0.45-1.30 mm wide exozones. Secondary overgrowths 1.05-2.00 mm thick. Autozooeical apertures angular with rounded corners. Basal diaphragms abundant both in endozone and exozone, straight, or inclined. Mesozooeica few,

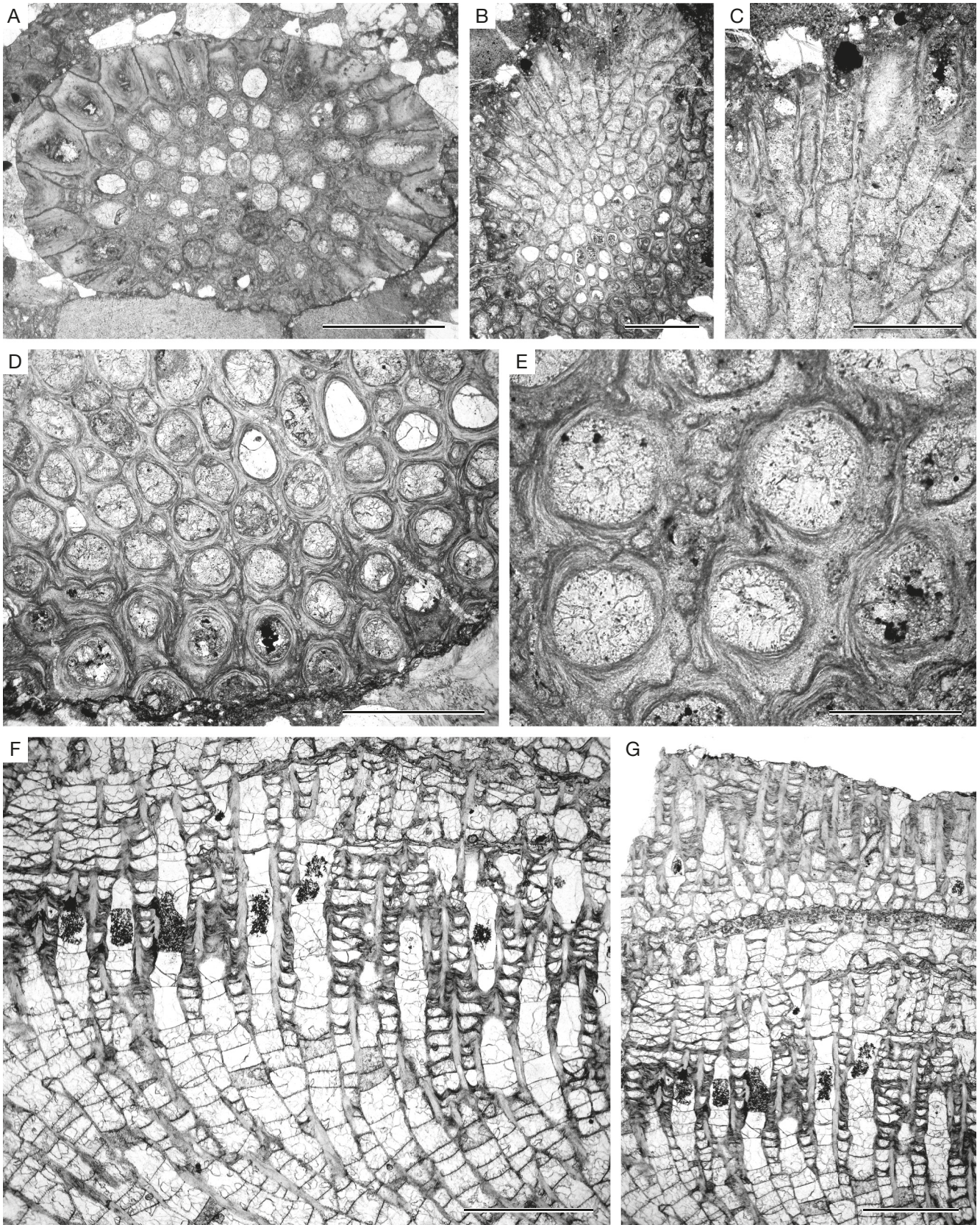


FIG. 11. — **A**, *Tarphophragma macrostoma* (Loeblich, 1942), branch transverse thin section, CEGH-UNC 27539 a; **B-E**, *Jordanopora heroensis* Ross, 1963: **B**, **C**, oblique thin section through the colony showing autozoecial chambers, CEGH-UNC 27530 f; **D**, **E**, tangential thin section showing autozoecial apertures, rare mesozooecia, and tubules in autozoecial walls, CEGH-UNC 27530 e; **F**, **G**, *Argentinopora robusta* n. gen., n. sp., holotype 27511 c, longitudinal section showing autozoecial chambers, mesozooecia, and acanthostyles. Scale bars: A, B, F, G, 1 mm; C, D, 0.5 mm; E, 0.2 mm.

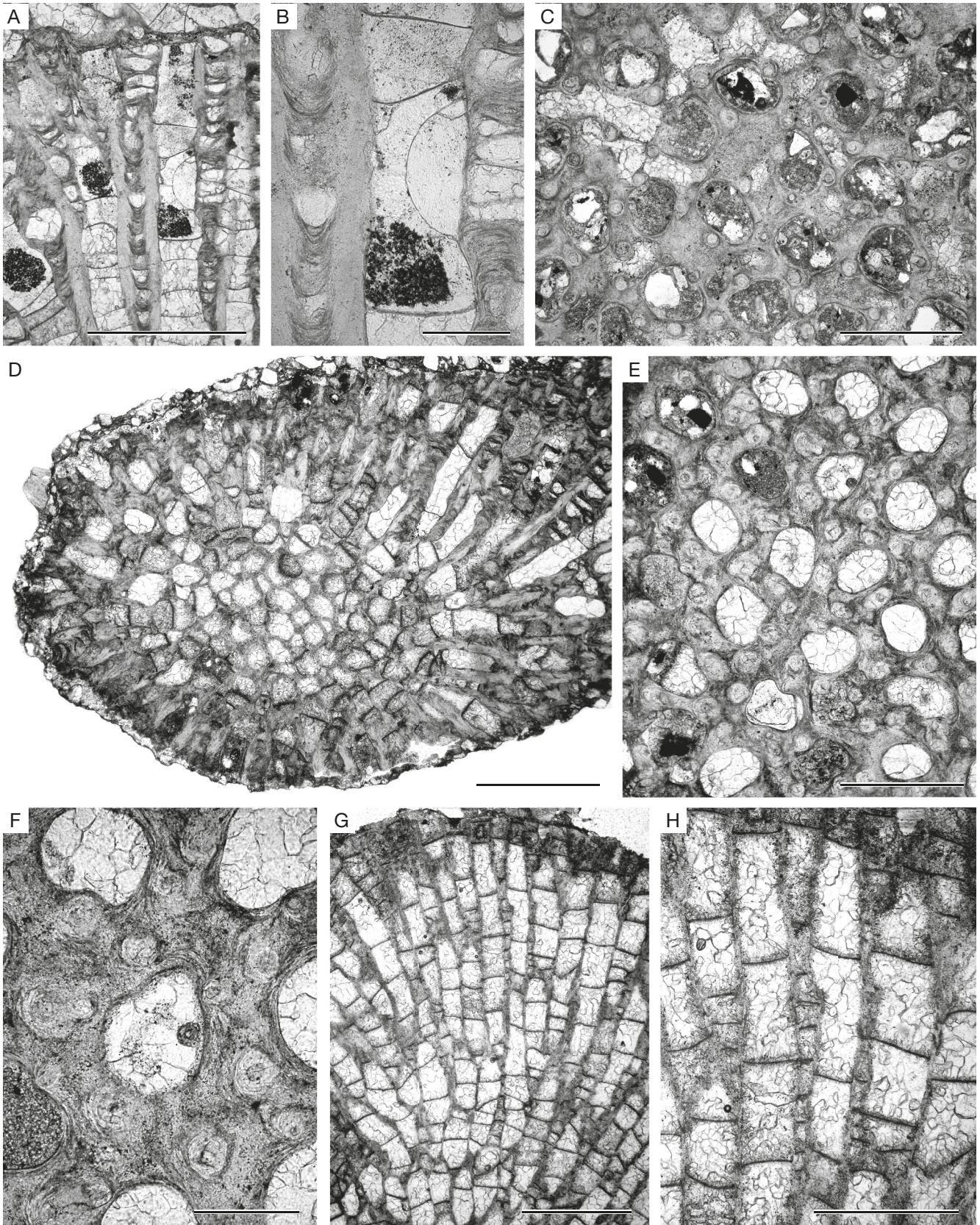


Fig. 12. — **A-F**, *Argentinopora robusta* n. gen., n. sp.: **A, B**, longitudinal thin section showing autozooeceal chambers with a cystiphragm, mesozooeceia, acanthostyles, holotype CEGH-UNC 27511 a; **C**, tangential thin section showing autozooeceal apertures, mesozooeceia, and acanthostyles, holotype CEGH-UNC 27511 d; **D**, branch transverse section, paratype CEGH-UNC 27514 b; **E, F**, tangential thin section showing autozooeceal apertures, mesozooeceia, and acanthostyles, paratype CEGH-UNC 27514 c; **G, H**, *Nicholsonella spinigera* n. sp., branch longitudinal section showing autozooeceal chambers with diaphragms, holotype CEGH-UNC 27528 c. Scale bars: A, D, G, 1 mm; B, F, 0.2 mm; C, E, H, 0.5 mm.



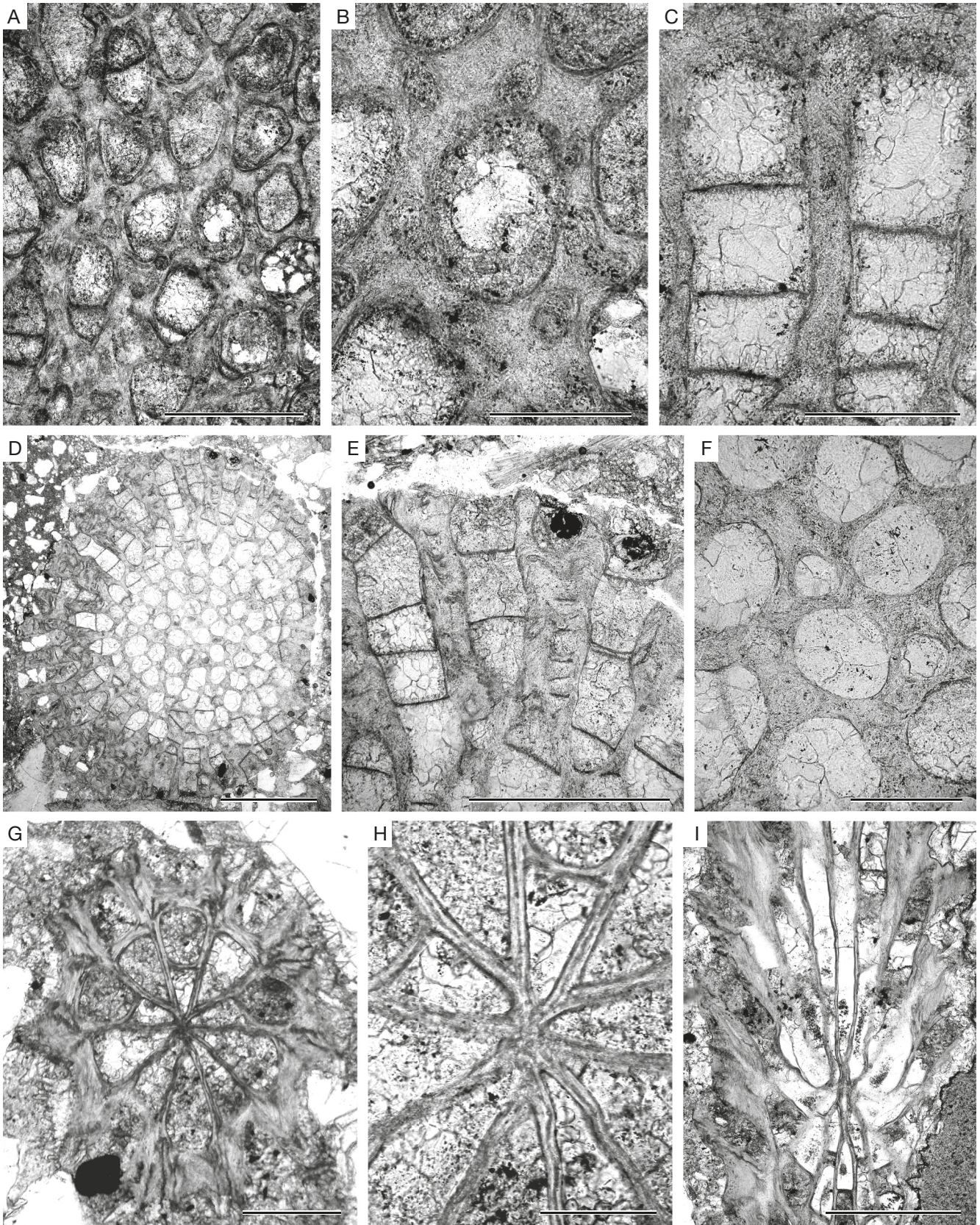


FIG. 13. — **A-F**, *Nicholsonella spinigera* n. sp.: **A, B**, tangential thin section showing autozooeical apertures, mesozooeica, and acanthostyles, holotype CEGH-UNC 27528 c; **C**, longitudinal thin section showing autozooeical chambers with diaphragms, holotype CEGH-UNC 27528 b; **D, E**, branch transverse thin section showing autozooeical chambers with diaphragms and mesozooeica, paratype CEGH-UNC 27538 a; **F**, branch transverse thin section showing autozooeical chambers and acanthostyles in endozone, paratype CEGH-UNC 27538 a; **G-I**, *Arthroclema* sp. A: **G, H**, branch transverse thin section showing autozooeical chambers, CEGH-UNC 27520 d; **I**, branch oblique thin section, CEGH-UNC 27529 b. Scale bars: A, E, I, 0.5 mm; B, C, F, G, 0.2 mm; D, 1 mm; H, 0.1 mm.

containing densely spaced thick diaphragms. Acanthostyles large, abundant, 4-8 surrounding each autozooeical aperture, originating in endozone, having wide hyaline cores and narrow laminated sheaths, often indenting autozooeica and mesozooeica. Autozooeical walls granular, 0.005-0.010 mm thick, irregularly undulating in endozones; thickly laminated, merged, showing reversal U-shaped lamination, without cingulum, 0.05-0.09 mm thick in exozones. Maculae not observed.

COMPARISON

*Nicholsonella spinigera* n. sp. is similar to *N. irregularis* Loeblich, 1942 from the Bromide Formation (Sandbian) of Oklahoma (United States), but differs from it in more abundant acanthostyles (4-8 acanthostyles per autozooeical aperture vs 5-6 in *N. irregularis*) and in more abundant autozooeical diaphragms. *Nicholsonella spinigera* n. sp. differs from *N. pulchra* Ulrich, 1893 from the Upper Ordovician of United States in less abundant mesozooeica.

Order CRYPTOSTOMATA Vine, 1884

Suborder RHABDOMESINA Astrova & Morozova, 1956

Family ARTHROSTYLIDAE Ulrich, 1882

Genus *Arthroclema* Billings, 1865

TYPE SPECIES. — *Arthroclema pulchellum* Billings, 1865 by original designation. Middle Ordovician, Trenton Limestone; Ottawa, Ontario, Canada.

DIAGNOSIS. — Colonies branched, with well defined axial stem and alternate secondary and tertiary branches. Sinuous or straight longitudinal ridges separating apertural rows often present. Axial region formed by well defined linear axis. Autozooeica attenuated to weakly inflated at their bases, having subtriangular cross-section in endozone, becoming elliptical in exozone, orientated at angles of 30-90° to colony surface. Diaphragms rare to absent. Exozonal wall material well developed, with narrow zooecial boundaries. Metazooeica absent. Paurostyles scattered to common, usually developed on ridges.

OCCURRENCE. — Middle to Upper Ordovician; North America, Europe.

COMPARISON

*Arthroclema* Billings, 1865 is similar to *Helopora* Hall in Silliman, Silliman & Dana, 1851, but differs from it in lacking metazooeica with diaphragms and acanthostyles. *Arthroclema* differs from *Ulrichostylus* Bassler, 1952 in wall structure with distinct zooecial boundaries.

*Arthroclema* sp. A

(Fig. 14A-C; Appendix 1)

MATERIAL EXAMINED. — CEGH-UNC 27525 a, CEGH-UNC 27528 b, CEGH-UNC 27529 b, CEGH-UNC 27530 e, f, CEGH-UNC 27533 c, CEGH-UNC 27538 c, CEGH-UNC 27539 a, e, f.

OCCURRENCE. — La Pola Formation, Upper Ordovician, Sandbian; La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

DESCRIPTION

Ramose colonies with well defined median axis, articulated and consisting of cylindrical segments. Segments apparently flexibly connected, 0.47-1.03 mm in diameter, with 0.10-0.26 mm wide exozones and 0.27-0.54 mm wide endozones. Autozooeica moderate in size, budding from the median axis at angles of 45-56°, bending gently to branch surface, triangular in cross-section in endozone, becoming oval in exozone. Diaphragms in autozooeica few to absent. Autozooeical apertures narrow, oval, arranged regularly in alternating rows on branch surface. Walls in endozone hyaline, 0.01-0.02 mm thick, continuing in exozone into the peristomes. Fine longitudinal striation between apertures present. Extrazooeical skeleton finely laminated, having well defined zooecial boundaries. Paurostyles abundant, irregularly arranged between autozooeical apertures, arising in the outermost exozone.

COMPARISON

*Arthroclema* sp. A is similar to *Arthroclema striatum* Ulrich, 1890 from the Middle Ordovician of United States, and to *A. pulchellum* Billings, 1865 the Middle Ordovician of Canada. It differs from the latter in larger autozooeical apertures (0.07-0.10 mm vs 0.06-0.07 mm in *A. pulchellum*; aperture width for *A. pulchellum* measured from Blake [1983: fig. 272g]).

Suborder PTILODICTYINA Astrova & Morozova, 1956  
Family RHINIDICTYIDAE Ulrich, 1893

Genus *Trigonodictya* Ulrich, 1893

*Trigonodictya* Ulrich, 1893: 160.

*Astreptodictya* Karklins, 1969: 49.

*Trigonodictya* (*Astreptodictya*) – Karklins 1983b: 513.

TYPE SPECIES. — *Pachydictya conciliatrix* Ulrich, 1886 by subsequent designation (Ulrich 1893). Decorah Shale, Middle Ordovician; United States (Minnesota).

DIAGNOSIS. — Branched colonies, sometimes with lateral ridgelike expansions. Mesotheca straight to sinuous in longitudinal section, locally zigzag in transverse section, containing median rods. Autozooeica arranged in straight rows, subrectangular to subrhomboidal in transversal section of endozone, locally separated by extrazooeical vesicles in endozone, separated by extrazooeical stereom in exozone, rectangular in deep tangential section, becoming oval on the colony surface. Basal diaphragms straight to slightly curved. Extrazooeical skeletal deposits common, consisting of laminar and vesicular portions. Vesicular structures common in inner exozones, locally in endozones. Laminar stereom commonly with dark zones, longitudinally aligned, locally with indistinct mural styles. Autozooeical boundaries distinct, delineated laterally by continuous dark zones. Monticules absent.

OCCURRENCE. — Middle Ordovician – Middle Silurian; Europe, North and South America.

COMPARISON

*Trigonodictya* Ulrich, 1893 differs from *Pachydictya* Ulrich, 1882 in regular arrangement of autozooeica in straight rows.

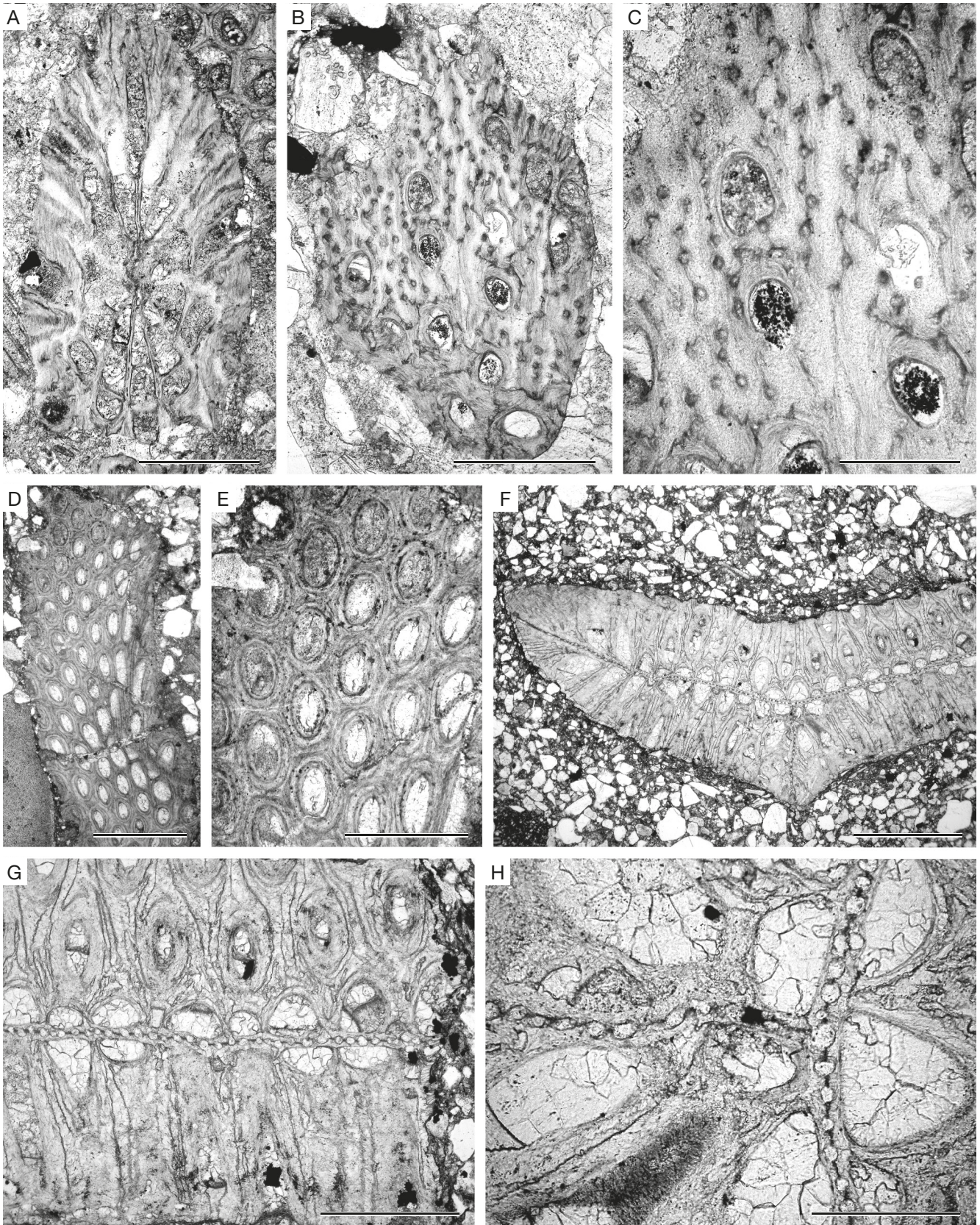


FIG. 14. — **A-C**, *Arthroclema* sp. **A**, branch oblique thin section, CEGH-UNC 27530 e; **B, C**, tangential thin section showing autozooeal apertures and paurostyles, CEGH-UNC 27529 b; **D-H**, *Trigonodictya elegans* (Ulrich, 1893): **D, E**, tangential thin section showing autozooeal apertures, CEGH-UNC 27530 c; **F-H**, branch transverse thin section showing autozooeal chambers and mesotheca with rods, CEGH-UNC 27542 b. Scale bars: A, B, E, G, 0.5 mm; C, H, 0.2 mm; D, F, 1 mm.

*Trigonodictya elegans* (Ulrich, 1893)  
(Fig. 14D-H; Appendix 1)

*Pachidictya elegans* Ulrich, 1893: 154, pl. 8, figs 18-19, pl. 9, figs 8-9. — Bassler 1911: 138, figs 62a-c. — Toots 1952: 130, pl. 8, fig. 4.

?*Pachidictya elegans* – Kieppura 1962: 408, pl. 7, fig. 3.

*Astreptodictya elegans* – Karklins 1969: 57-58, pl. 11, figs 1-4.

*Trigonodictya elegans* – Gorjunova & Lavretjeva 1993: 51.

MATERIAL EXAMINED. — CEGH-UNC 27507 b, c, CEGH-UNC 27527 b, c, CEGH-UNC 27528 a-c, CEGH-UNC 27529 b, CEGH-UNC 27530 c, e, CEGH-UNC 27539 e, CEGH-UNC 27541 a, CEGH-UNC 27542 b, CEGH-UNC 27544 b.

OCCURRENCE. — Upper Ordovician of United States and Europe. La Pola Formation, Upper Ordovician, Sandbian; La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

DESCRIPTION

Branched bifoliate, dichotomous colonies. Branches flattened, with sharp edges, 2.40-3.25 mm wide and 0.9-1.4 mm thick. Mesotheca three-layered, straight both in longitudinal and transverse sections, containing abundant median rods, 0.03-0.05 mm thick. Median rods densely spaced, 0.015-0.038 mm in diameter, continuous in dark zones separating longitudinal rows of autozoocelia. Autozoocelia regularly arranged in 10-14 alternating longitudinal rows, semicircular to trapezoid in transverse section in endozone, rectangular in deep tangential section, becoming oval on the colony surface. Autozoocelial diaphragms common, straight. Autozoocelial walls laminated, 0.015-0.025 mm thick in endozones. Autozoocelial boundaries distinct, delineated laterally by continuous dark zones. Extrazoocelial skeletal deposits well developed, consisting of laminar and vesicular portions. Laminar stereom with dark zones, longitudinally aligned, separating autozoocelia in exozones, containing abundant mural styles. Mural styles 0.02-0.04 mm in diameter. Vesicular structures small and sparse, having flat to rounded roofs, rare to common on branch edges.

COMPARISON

*Trigonodictya elegans* (Ulrich, 1893) is similar to *T. cirrita* Karklins, 1983 from the Upper Ordovician of United States and from the Las Plantas and Las Aguaditas formations (Sandbian) of Argentina, but differs from it in smaller autozoocelial apertures (average aperture width 0.11 mm vs 0.14 mm in *T. cirrita*), and in larger distances between aperture centres (at average 0.36 mm vs 0.42 mm in *T. cirrita*). *Trigonodictya elegans* is similar to *T. acuta* (Hall, 1847) from the Middle Ordovician of New York, United States, but differs from it in smaller autozoocelial apertures (aperture width 0.08-0.15 mm vs 0.10-0.16 mm in *T. acuta*).

Family STICTOPORELLIDAE Nickles & Bassler, 1900

Genus *Pseudostictoporella* Ross, 1970

TYPE SPECIES. — *Pseudostictoporella typicalis* Ross, 1970 by original designation. Rockland Formation, Selby Member (*P. bicornis* Biozone), Sandbian, Ordovician; Ontario, Canada and New York, United States.

DIAGNOSIS. — Colonies bifoliate, bifurcating. Autozoocelia subelliptical in cross section in the endozone; irregularly hexagonal in cross section in exozone; partly separated by exilazoocelia. Autozoocelial diaphragms rare to absent. Hemisepta absent. Pustules common along autozoocelial boundaries, scattered in exozonal walls. Metazoocelia polygonal to irregularly subcircular, arranged in groups, singly or in short rows. Monticules common, generally flat; consisting of metazoocelia, few autozoocelia and some skeletal material.

OCCURRENCE. — Sandbian, Upper Ordovician; Canada, United States, Argentina.

COMPARISON

The genus *Pseudostictoporella* Ross, 1970 differs from the genus *Stictoporella* Ulrich 1882 by the absence of hemisepta, from the genera *Oanduella* Männil, 1958 and *Stictoporellina* Nekhoroshev, 1956 – by bifurcating colony shape instead of reticulate one in the latter genera.

*Pseudostictoporella simplex* n. sp.  
(Fig. 15A-H; Appendix 1)

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HOLOTYPE. — CEGH-UNC 27508 a.

PARATYPES. — CEGH-UNC 27528 b, CEGH-UNC 27530 e, f, g (three thin sections of one colony), CEGH-UNC 27533 a, b, c, d (four thin sections of one colony).

TYPE LOCALITY. — La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

TYPE HORIZON. — La Pola Formation, Upper Ordovician, Sandbian.

DIAGNOSIS. — Bifoliate branched colonies; mesotheca straight, median rods absent, autozoocelia arranged in 10 to 20 regular alternating rows on branches; hemisepta absent; rare diaphragms occurring; metazoocelia and styles absent; longitudinal ridges between autozoocelial apertures.

ETYMOLOGY. — The species name reflects the simple morphology defined by lacking of metazoocelia and pustules (from Latin “*simplex*” – simple)

DESCRIPTION

Bifoliate branched colony. Branches 1.8-2.1 mm wide and 0.60-1.30 mm thick. Mesotheca straight, 0.015 to 0.045 mm thick, median rods absent. Autozoocelia short, tubular, bending sharply to branch surface, rectangular at their bases, becoming oval at branch surface, arranged in 10 to 20 regular alternating rows on branches. Hemisepta absent.

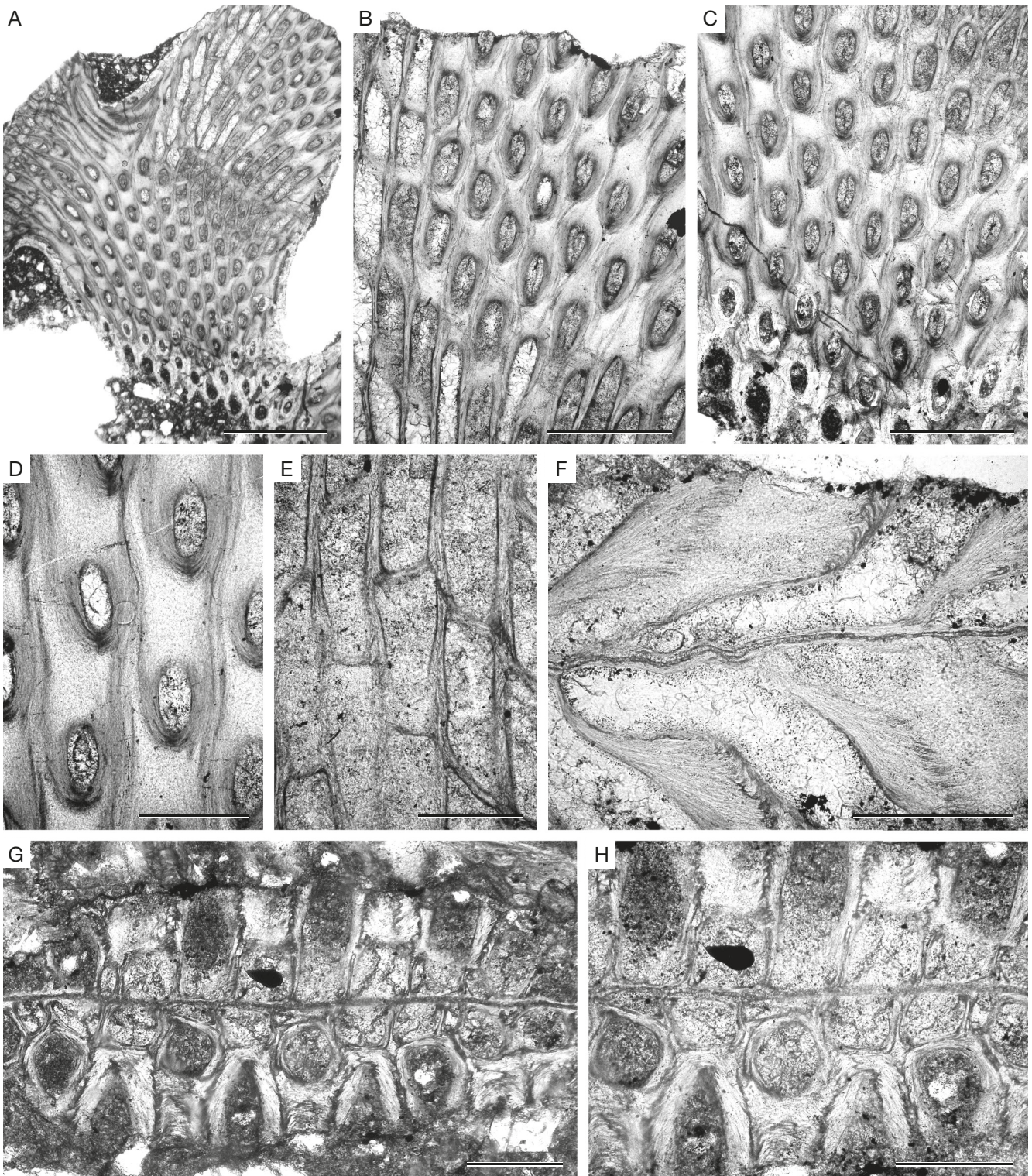


FIG. 15. — **A-H**, *Pseudostictoporella simplex* n. sp.: **A-E**, branch tangential section showing autozoecial chambers and apertures, holotype CEGH-UNC 27508 a; **F**, branch longitudinal thin section autozoecial chambers, paratype CEGH-UNC 27533 a; **G, H**, branch transverse thin section showing autozoecial chambers and mesotheca without rods, paratype CEGH-UNC 27533 d. Scale bars: A, 1 mm; B, C, 0.5 mm; D-H, 0.2 mm.

Rare diaphragms occurring. Metazooecia and styles absent. Autozoecial walls granular, 0.030 to 0.055 mm thick in endozone; thick, finely laminated in exozone. Extrazooecial skeleton well developed, consisting of laminated material. Longitudinal ridges between autozoecial apertures present.

#### COMPARISON

*Pseudostictoporella simplex* n. sp. is similar to *P. typicalis* Ross, 1970, but differs from it in absence of metazooecia and pustules. *P. iberiensis* Jiménez-Sánchez, 2009 from the Katian of Spain possesses hemisepta and may not belong to the genus *Pseudostictoporella*.

Family ESCHAROPORIDAE Karklins, 1983

Genus *Chazydictya* Ross, 1963

TYPE SPECIES. — *Chazydictya chazyensis* Ross, 1963 by original designation. Darriwilian, Ordovician; New York, United States.

DIAGNOSIS. — Bifoliate lenticular, branched colonies. Branch transverse section lens-shaped. Autozooezia short, tubular, recumbent at their bases in endozone, bending sharply to colony surface, rectangular to subrhomboidal at their bases, becoming oval at branch surface, arranged in 8 to 15 regular alternating rows on branches. Hemisepta absent. Basal diaphragms rare to common. Mesotheca straight to weakly undulating, two-layered, without median rods. Autozooezial walls granular, in endozone; thick, finely laminated in exozone. Paurostyles in the laminated skeleton abundant, arranged in up to 5 rows between autozooezial apertures, rounded to weakly stellate in tangential section. Maculae absent.

OCCURRENCE. — Darriwilian, Ordovician; United States, Canada. Sandbian, Ordovician; Argentina.

COMPARISON

*Chazydictya* Ross, 1963 differs from *Prilodictya* Lonsdale, 1839 in absence of hemisepta and presence of abundant paurostyles.

*Chazydictya ornata* n. sp.  
(Fig. 16A-F; Appendix 1)

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HOLOTYPE. — CEGH-UNC 27535 a.

PARATYPES. — CEGH-UNC 27538 a, CEGH-UNC 27539 h.

TYPE LOCALITY. — La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

TYPE HORIZON. — La Pola Formation, Upper Ordovician, Sandbian.

DIAGNOSIS. — Bifoliate lenticular, branched colony; autozooezia short, arranged in 12-15 rows on branches; few basal diaphragms occurring; paurostyles abundant, large.

ETYMOLOGY. — The species is named because of the ornamentation by abundant paurostyles (from Latin “ornatus” – adorned, decorated)

DESCRIPTION

Bifoliate lenticular, branched colony. Branches 1.4-2.0 mm wide and 0.6-1.0 mm thick. Mesotheca straight, 0.015 to 0.020 mm thick, without median rods. Autozooezia short, tubular, bending sharply to branch surface, rectangular to subrhomboidal at their bases, becoming oval at branch surface, arranged in 12 to 15 regular alternating rows on branches. Rare diaphragms occurring. Autozooezial walls granular, 0.01 to 0.02 mm thick in endozone; thick, finely laminated in exozone. Laminated skeleton well developed. Paurostyles abundant, 0.015-0.035 mm in diameter.

COMPARISON

*Chazydictya ornata* n. sp. differs from *C. chazyensis* Ross, 1963 in presence of 12-15 rows of autozooezia on branches vs 8-12 in

*C. chazyensis*, and in smaller autozooezial apertures (aperture width 0.06-0.08 mm vs 0.09-0.10 mm in *C. chazyensis*). Furthermore, *Chazydictya ornata* n. sp. has fewer diaphragms in autozooezia (none to one vs two-three in *C. chazyensis*) as well as larger paurostyles (0.015-0.035 mm vs 0.010 mm in *C. chazyensis*).

Order FENESTRATA Elias & Condra, 1957

Suborder PHYLLOPORININA Lavrentjeva, 1979

Family CHASMATOPORIDAE Schulga-Nesterenko, 1955

Genus *Parachasmatorpora* Morozova & Lavrentjeva, 1981

TYPE SPECIES. — *Parachasmatorpora maennili* Morozova & Lavrentjeva, 1981 by original designation. Sandbian, Ordovician; Estonia.

OCCURRENCE. — Middle-Upper Ordovician; United States, Estonia, Argentina.

DIAGNOSIS. — Reticulated colonies consisting of anastomosing branches. Autozooezia long, having oblong-rectangular shape in deep tangential section, having weakly developed vestibule, arranged in two-three slightly alternating rows on branches. Nodes on low keels present. Cross-section of branches rounded; their dorsal wall thin, carrying thin longitudinal ribs and microacanthostyles.

COMPARISON

*Parachasmatorpora* Morozova & Lavrentjeva, 1981 differs from *Chasmatorpora* Eichwald, 1855 in having 2-3 rows of autozooezia on branches instead of 4 in *Chasmatorpora*.

*Parachasmatorpora* sp. A  
(Figs 16G; 17A-E)

MATERIAL EXAMINED. — CEGH-UNC 27526 a, CEGH-UNC 27529 b, CEGH-UNC 27533 a, CEGH-UNC 27545 a, b.

OCCURRENCE. — La Pola Formation, Upper Ordovician, Sandbian; La Pola creek section near Albardon village, San Juan Province, Argentine Precordillera, western Argentina.

DESCRIPTION

*Exterior*

Reticulate colonies consisting of regularly anastomosing branches. Branches rounded in cross section, 0.25-0.47 mm wide and 0.30-0.50 mm thick. Fenestrules elliptical, 0.22-0.30 mm wide and 0.43-0.91 mm long. Autozooezial apertures rounded to oval, arranged in two alternating rows on branches, 3-4 in each fenestrule length, 0.05-0.09 mm in width. Low keel between autozooezial aperture rows carrying small elliptical nodes. Heterozoeezia absent. Microstylets occurring both on reverse and obverse sides of colony, 0.02-0.03 mm in diameter.

*Interior*

Autozooezia long, rectangular in deep tangential section, occasionally having abundant diaphragms. Vestibule short. Hemisepta absent. Inner granular skeleton hyaline, 0.005-0.008 mm thick. Outer lamellar skeleton usually well-developed on both obverse and reverse sides of colony, 0.075-0.040 mm thick.

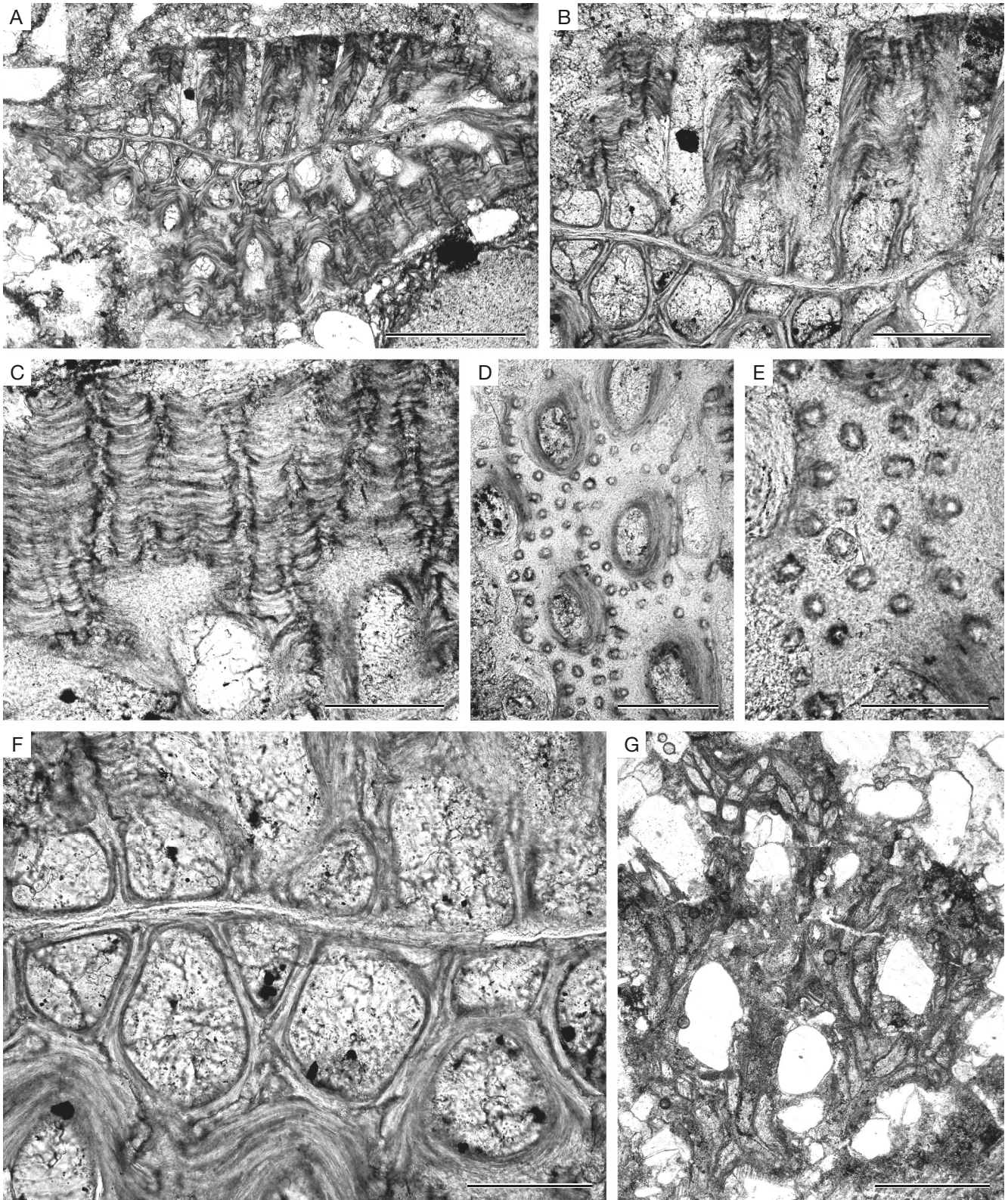


Fig. 16. — **A-F**, *Chazydictya omata* n. sp., holotype CEGH-UNC 27535 a: **A, B**, branch transverse thin section showing autozooeal chambers and mesotheca without rods; **C**, branch transverse thin section showing autozooeal walls with paurostyles; **D, E**, tangential thin section showing autozooeal apertures and paurostyles; branch transverse thin section showing autozooeal mesotheca without rods; **G**, *Parachasmatopora* sp. A, tangential section showing reticulate colony, CEGH-UNC 27526 a. Scale bars: A, G, 0.5 mm; B, D, 0.2 mm; C, E, F, 0.1 mm.

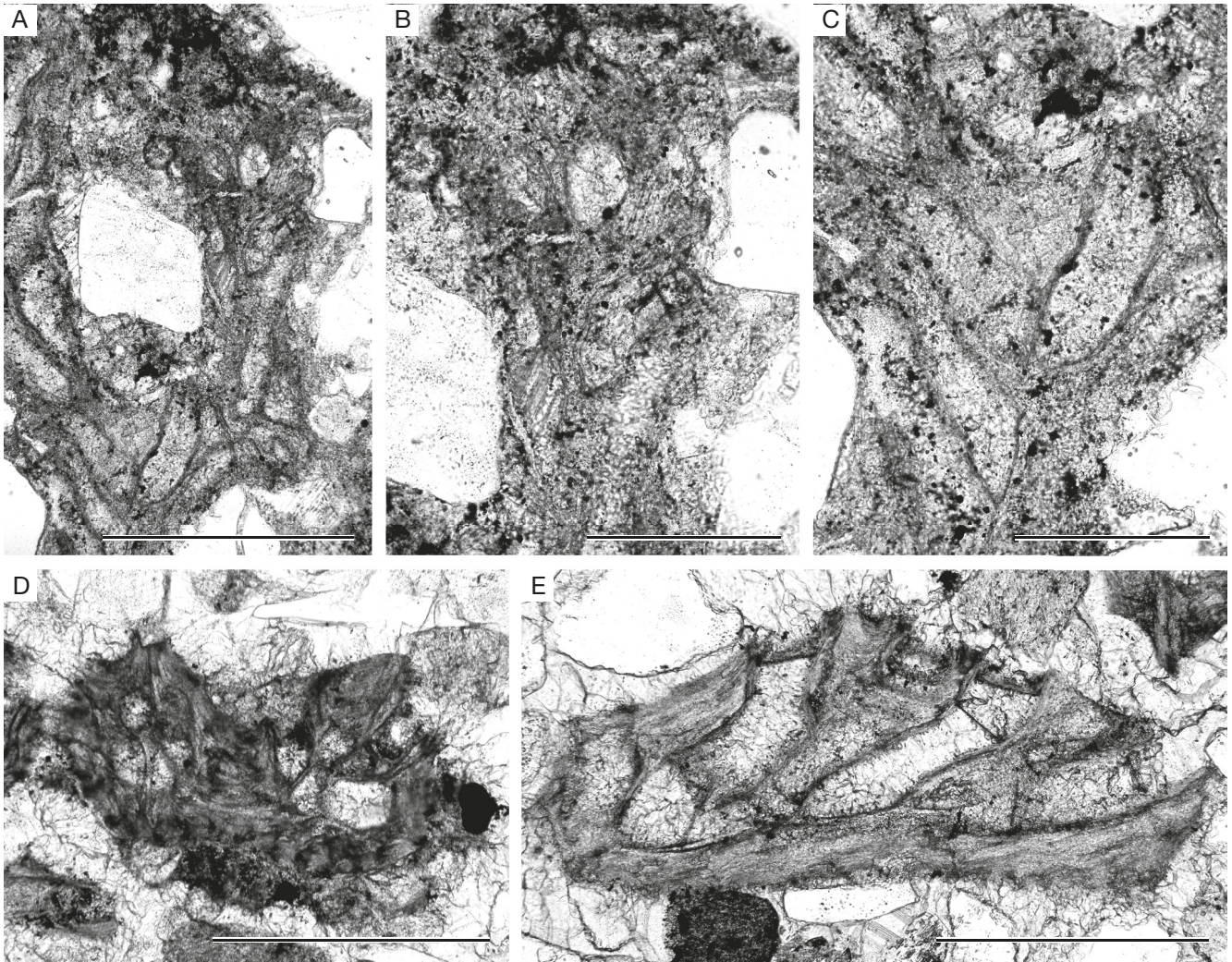


FIG. 17. — **A-E**, *Parachasmatopora* sp. **A-C**, tangential section showing branches with autozooeal apertures and chambers, CEGH-UNC 27526 a; **D**, branch transverse section showing autozooeal chambers and laminated skeleton, CEGH-UNC 27545 a; **E**, branch longitudinal section showing autozooeal chambers with diaphragms and laminated skeleton, CEGH-UNC 27545 b. Scale bars: A, D, E, 0.5 mm; B, C, 0.2 mm.

#### COMPARISON

*Parachasmatopora* sp. A species differs from *Parachasmatopora maennili* Morozova & Lavrentjeva, 1981 in smaller autozooeal apertures (0.05-0.09 mm vs 0.10-0.12 mm in *P. maennili*). Superficially, *Parachasmatopora* sp. A is similar to *Parachasmatopora typicalis* (Bassler, 1952). However, the latter species was only externally figured (Bassler 1952: figs 8-9). Therefore, a detailed comparison is impossible.

#### PALAEOBIOGEOGRAPHIC RELATIONS OF THE UPPER ORDOVICIAN BRYOZOANS FROM THE ARGENTINE PRECORDILLERA

Available data support the hypothesis of the Precordillera as an exotic terrane accreted to the Gondwana margin (Astini *et al.* 1995; Benedetto *et al.* 1999; Benedetto 2003a; Thomas & Astini 2003; Ramos 2004). The Precordillera is interpreted as a far-travelled microplate (Cuyania terrane),

rifted from the southern Appalachian margin in the Late Cambrian and accreted to the pre-Andean margin of Gondwana during the Ordovician (Astini *et al.* 1995; Benedetto 2003a; Ramos 2004 and references therein). Changes in provincialism exhibited by the Precordillera fauna, from low latitude, tropical to high latitude, peri-glacial affinities largely support this drifting history (Benedetto *et al.* 1999; Benedetto 2003a; Benedetto *et al.* 2009).

According to this scenario, the Argentine Precordillera was located as an isolated terrane in the middle of the Iapetus Ocean during the Sandbian, still with a biogeographic North American signature in their faunas, but receiving some faunal influence from Gondwana and Baltica (see Benedetto 2003b; Benedetto *et al.* 2009). The Precordillera shifted from equatorial to higher latitudes where warm-water carbonates were deposited during the Cambrian and Lower Ordovician, whereas Middle Ordovician units were deposited at mid-latitude (30-35°) locations, including the Las Aguaditas, Las Plantas and Sassito Formations (Ernst &



Carrera 2008, 2012). The Hirnantian glacial rocks of the Don Braulio Formation represent the last step in the shifting trajectory of the Precordillera terrane (Astini 1998a; Benedetto *et al.* 2009; Benedetto *et al.* 2011, Halpern & Carrera 2014).

The described bryozoan assemblage contains 19 species of which seven species were previously recorded from the Ordovician deposits of Laurentia: *Lunaferamita virginien-sis* Utgaard, 1981, *Dianulites rocklandensis* Wilson, 1921, *Orbignyella multitabulata* Coryell, 1921, *Homotrypa sub-ramosa* Ulrich, 1886, *H. vacua* McKinney, 1971, *Tarpho-phragma macrostoma* (Loeblich, 1942), and *Trigonodictya elegans* (Ulrich, 1893). These species indicate clearly the Sandbian age. One more species, *Monticulipora* aff. *mam-mulata* d'Orbigny, 1850, probably has palaeobiogeographic relations to the Upper Ordovician (Cincinnatian) of North America.

The generic association shows also strong Laurentian affinities, with only the exception of the cystoporate genus *Xenotrypa* Bassler, 1952 which was previously only known from the Lower Ordovician of Estonia and Middle Ordovician of the Russian Arctic. Trepostome genera *Heterotrypa*, *Diplotrypa*, and *Nicholsonella* are cosmopolitan taxa throughout the Ordovician. The genus *Arthroclema* is predominantly known from the Ordovician of North America (United States and Canada). Only one species, *Arthroclema vescum* Gorjunova, 1985 is known from the Lower Ordovician of Estonia. The genus *Parachasmatopora* is known predominantly from the Ordovician of Estonia, with one species recorded from the Sandbian of the United States – *P. typicalis* (Bassler, 1952). The ptilodictyine genera *Pseudostictoporella* and *Chazydictya* are both known from the Ordovician of North America. The two new genera, *Argentinopora* n. gen. and *Albardonia* n. gen. are endemic to the La Pola Formation of Argentina.

The bryozoan fauna from the Sandbian Las Aguaditas and Las Plantas formations (Ernst & Carrera 2012) shows distinct relations to the Middle-Upper Ordovician of North America. Nine species were previously reported from the Middle to Upper Ordovician of United States and Canada: *Diploplema trentonense* Ulrich, 1889, *Constellaria varia* Ulrich, 1893, *Homotrypa obliqua* Ulrich, 1882, *Bythopora dendrina* (James, 1878), *Batostoma lanensis* Ross, 1963, *Batostoma sheldonensis* Ross, 1963, *Trigonodictya cirrita* Karklins, 1983, *Orectodictya pansa* Karklins, 1983, and *Enallopora exigua* (Ulrich, 1890). *Constellaria varia* was also recorded from the Upper Ordovician (Katian) of Estonia, whereas *Bythopora dendrina* is also known from the Katian of Europe (Montagne Noire, Sicily). The genus *Argentinodictya* Ernst & Carrera, 2012, and four species established by Ernst & Carrera (2012) are endemic to the Argentine Precordillera.

According to their generic composition, Las Aguaditas and Las Plantas formations form a separated cluster mainly shown in the PCA (Fig. 18), whereas the bryozoan fauna from the La Pola Formation is closer to that of Siberia (Fig. 18). This difference may possibly be due to the slightly

older age of Las Aguaditas Formation (early Sandbian) from which several bryozoan specimens come (Ernst & Carrera 2012), considering the middle Sandbian age of the La Pola Formation. Also, a different facies composition is noted, from a clearly mixed calcareous siliciclastic composition of the Las Aguaditas-Las Plantas formations to the mostly siliciclastic quartz-rich La Pola Formation.

The bryozoan faunas of the La Pola Formation (this contribution) and the roughly coeval Las Aguaditas and Las Plantas formations take an intermediate position between the Lower Ordovician bryozoans described from the San Juan Formation (Carrera & Ernst 2010) and those from the Upper Ordovician deposits of Argentine Precordillera: Katian Sassito Formation (Ernst & Carrera 2008) and the Hirnantian Don Braulio Formation (Halpern & Carrera 2014).

In the Katian Sassito Formation, the genera *Moyerella* and *Phylloporina* were identified (Ernst & Carrera 2008). The genus *Moyerella* shows relations to Baltica proved by the presence of the species *Moyerella francisca* (Bassler, 1911) in the Sandbian-Katian of Estonia. The genus *Phylloporina* is widely distributed during the Late Ordovician, with species known from North America, Europe, and China (Lavrentjeva 1985).

Hirnantian deposits of the Precordillera, which clearly show the effects of the Late Ordovician glaciation, contain a typical Gondwana fauna (Benedetto *et al.* 1999; Benedetto 2003a) with a low diversity bryozoan fauna (Halpern & Carrera 2014) dominated by *Helopora fragilis* Hall, 1851. The genus *Helopora* shows Laurentian affinities, but it was also recorded in Estonia. It has a widespread distribution in the Silurian (Halpern & Carrera 2014).

The Sandbian bryozoan faunas of the Argentine Precordillera show quite significant level of endemism. The La Pola bryozoans contain 36.8% of endemic species (and two new genera). In the bryozoan associations of Las Aguaditas and Las Plantas formations the total proportion of endemic species reaches 25% (plus one new genus). So that, the bryozoan fauna marks high level of palaeogeographic isolation of the Precordillera terrane during the Sandbian. Globally, the generic composition of Sandbian bryozoan faunas shows relatively high endemism, as for example, Siberian faunas contain up to 50% of endemic genera (Buttler *et al.* 2013). Notwithstanding, the endemic content of Argentinean faunas appears high in relation to the size of the Precordillera, or Cuyania microcontinent, and its relative position to Laurentia, the Mediterranean province, Baltica and Gondwana within the Iapetus Ocean. The Cuyania microcontinent is estimated being no more than 1000 km long and 300 km wide (Astini *et al.* 1995; Ramos 2004).

The overall bryozoan composition of this last interval, implying Laurentian and Baltic affinities and including the presence of minor endemic elements, is in accordance with the paleogeographic scenario proposed for the Argentine Precordillera, which is also confirmed by the biogeographic signature shown by the rest of the fauna.

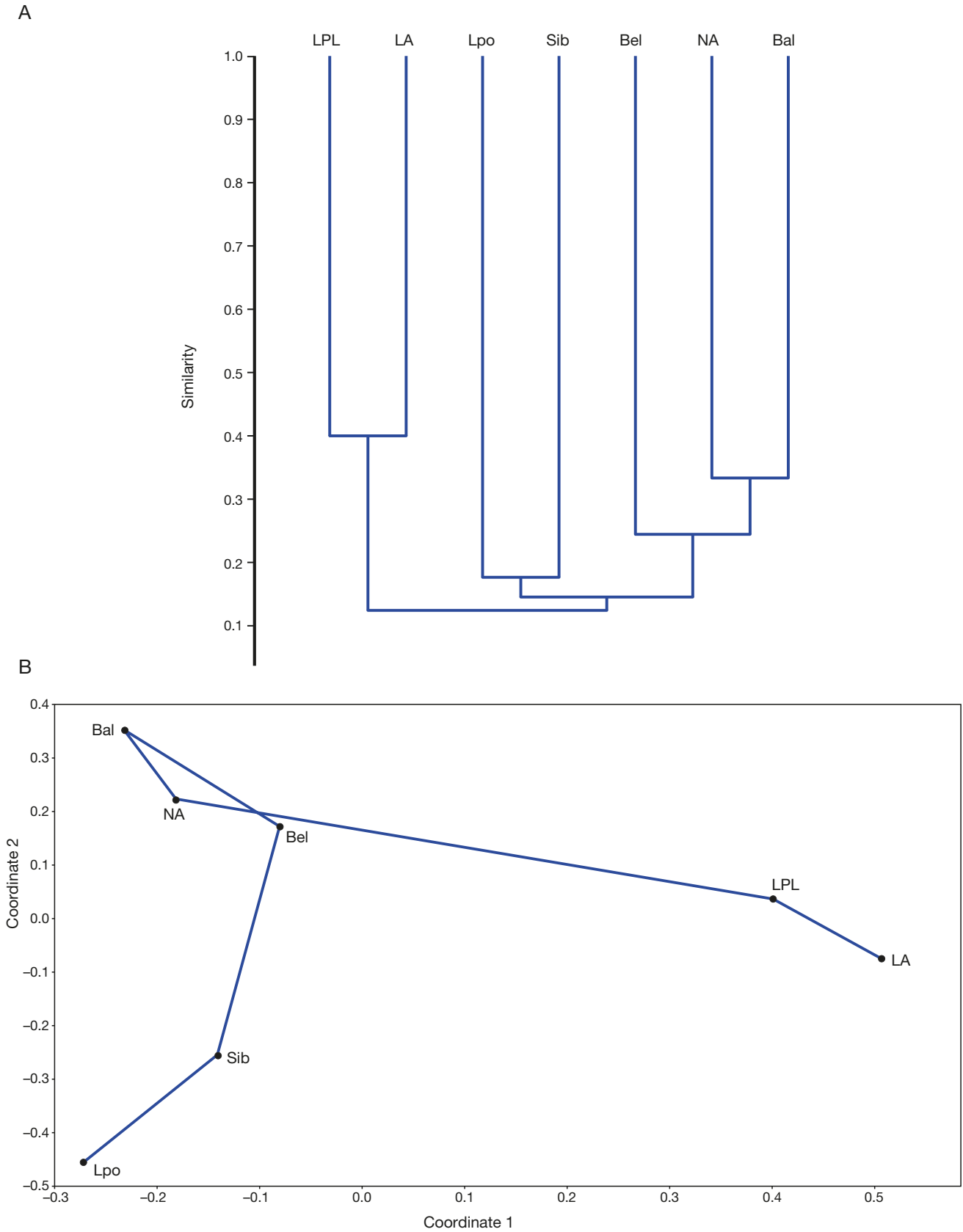


FIG. 18. — Cluster diagram (A) and principal coordinate analysis (B) showing similarities between bryozoan faunas (genus level) of different areas during the Sandbian (updated data matrix from Buttler *et al.* 2013). The cluster analysis has been performed measuring the Jaccard similarity coefficient, using the Unweighted Pair Group Algorithm with Arithmetic Mean (PAST version 1.81, Hammer *et al.* 2001). The principal coordinate analysis was performed using Jaccard's coefficient for measurement of similarities, the minimal spanning tree is based on an Euclidean distance measure of the original data points. Abbreviations: **Lpo**, La Pola Formation; **LA**, Las Aguaditas Formation; **LPL**, Las Plantas Formation; **NA**, North America; **Bal**, Baltica; **Bel**, Belarus; **Sib**, Siberia.

## ECOLOGY OF THE LA POLA BRYOZOAN FAUNA

The studied bryozoan assemblage represents mainly a para-autochthonous association deposited in siliciclastic sediments. The majority of bryozoan colonies show traces of re-deposition in form of high fragmentation rate and rounded shape of fragments (Fig. 3). Bryozoans in this assemblage display various growth forms, but massive and subramose, mainly multilayered colonies dominate here: *Lunaferamita virginienensis* Utgaard, 1981, *Xenotrypa argentinensis* n. sp., *Dianulites rocklandensis* Wilson, 1921, *Monticulipora* aff. *mammulata* d'Orbigny, 1850, *Orbignyella multitabulata* Coryell, 1921, *Homotrypa subramosa* Ulrich, 1886, and *Diplotrypa* sp. A. *Homotrypa subramosa* often produce separate unilamellar encrusting sheets. Ramose colonies are the second dominant zoarial habit represented by trepostome species: *Homotrypa vacua* McKinney, 1971, *Heterotrypa enodis* n. sp., *Jordanopora heroensis* Ross, 1963, *Tarphophragma macrostoma* (Loeblich, 1942), *Argentinopora robusta* n. gen., n. sp., and *Nicholsonella spinigera* n. sp. The third group is represented by ramose lenticular (bifoliate) growth forms and include one trepostome and three cryptostome (ptilodictyine) taxa: *Albardonia bifoliata* n. gen., n. sp., *Trigonodictya elegans* (Ulrich, 1893), *Pseudostictoporella simplex* n. sp., and *Chazydictya ornata* n. sp. The rhabdomesine cryptostome *Arthroclema* sp. A apparently forms articulated colonies consisting of flexibly connected segments. The only reticulate bryozoan is represented by *Parachasmatopora* sp. A. Such an association indicates shallow shelf conditions (e.g., Amini *et al.* 2004).

Some species from the pebbly mudstones and silty green shales appear to be autochthonous. Their colonies were found growing around or attached to pebbles or brachiopod shells without any signs of abrasion or fragmentation. The following species belong to this autochthonous association: *Lunaferamita virginienensis*, *Monticulipora* aff. *mammulata*, *Orbignyella multitabulata*, *Homotrypa subramosa*, *Argentinopora robusta*, *Albardonia bifoliata*, and *Nicholsonella spinigera*. These species developed mainly massive, encrusting, partly multilayered, or subramose colonies, as well as ramose bifoliate fronds (*Albardonia bifoliata*).

The bryozoans studied in this contribution are associated with strophomenid brachiopods, abundant *Solenopora*-like thalli, and crinoids. The composition of this association is different to the biota of the typical tropical carbonates (termed “photozoan communities” after James 1997). The combination of bryozoans, brachiopods, and red algae is rather typical for heterozoan communities of modern subtropical to temperate cool water marine platforms (“heterozoan carbonates” after James 1997; see also Mutti & Hallock 2003; Michel *et al.* 2018, and references therein). The fauna from the La Pola Formation can be defined as a cool-water bryozoan-brachiopod dominated association. Facies and biotic content for this mixed calcareous-siliciclastic deposits suggests temperate climatic conditions.

## CONCLUSIONS

The studied bryozoan fauna from the La Pola Formation (Sandbian, Upper Ordovician) of the Argentine Precordillera contains 19 species belonging to the orders Cystoporata, Trepostomata, Cryptostomata, and Fenestrata. This fauna is to 36.8% endemic at the species level, it shows some similarities to the Upper Ordovician of North America and Baltica. At the generic level, the La Pola bryozoans are close to the contemporary faunas of Las Aguaditas and Las Plantas formations of the Argentine Precordillera, as well as to Siberia. Palaeobiogeographic relations of the bryozoan fauna from the La Pola Formation support relative isolation of the Precordillera terrane during the Sandbian.

The majority of bryozoans from the La Pola Formation belong to a para-autochthonous association deposited in siliciclastic sediments. In contrast, some species from the pebbly mudstones and silty green shales appear to be autochthonous due to their in-situ position. The time interval between the deposition of para-autochthonous and autochthonous associations seems to be very short. The studied bryozoan fauna is dominated by massive and subramose, mainly multilayered colony forms, followed by ramose and lenticular (bifoliate) growth forms. Branched articulated and reticulate bryozoans are very rare in this association. The combination of these growth forms indicates shallow shelf conditions.

Facies characteristics (abundant siliciclastics) and faunal composition indicate temperate climatic conditions for the depositional environment of the La Pola Formation. A combination of bryozoans, brachiopods, red algae, and echinoderms is rather typical of cool-water heterozoan rather than of photozoan communities distributed in waters with high primary production.

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APPENDIX

APPENDIX 1. — Descriptive statistics. Abbreviations: **N**, number of measurements; **X**, mean; **SD**, sample standard deviation; **CV**, coefficient of variation; **MIN**, minimum value; **MAX**, maximum value.

**Lunaferamita virginiensis** Utgaard, 1981 (three colonies)

	N	X	SD	CV	MIN	MAX
Aperture width, mm	60	0.13	0.017	13.70	0.10	0.18
Aperture spacing, mm	60	0.18	0.018	10.04	0.14	0.21
Vesicle diameter, mm	60	0.07	0.018	27.05	0.03	0.13
Vesicles per aperture	15	5.7	0.961	16.76	4.0	8.0
Autozooeical diaphragms spacing, mm	60	0.10	0.044	45.41	0.03	0.24
Vesicle spacing, mm	60	0.07	0.022	32.56	0.03	0.13
Macrozooeia width, mm	56	0.18	0.015	8.36	0.15	0.22
Maculae width, mm	9	0.87	0.207	23.79	0.67	1.25
Maculae spacing, mm	8	1.43	0.220	15.39	1.13	1.75
Lunarium width, mm	10	0.070	0.013	18.34	0.050	0.090
Lunarium length, mm	10	0.039	0.013	33.29	0.025	0.060
Lunarium thickness, mm	10	0.028	0.006	22.29	0.018	0.035

**Xenotrypa argentinensis** n. sp. (one colony)

	N	X	SD	CV	MIN	MAX
Aperture width, mm	30	0.16	0.019	11.75	0.13	0.21
Aperture spacing, mm	30	0.31	0.041	13.11	0.25	0.40
Vesicle diameter, mm	30	0.12	0.034	29.29	0.07	0.20
Acanthostyle diameter, mm	30	0.045	0.008	17.55	0.030	0.065
Vesicles per aperture	20	5.3	0.865	16.31	4.0	7.0
Acanthostyles per aperture	20	4.6	0.826	18.14	3.0	6.0
Autozooeical diaphragms spacing, mm	30	0.17	0.055	32.41	0.09	0.31
Mesozooeical diaphragms spacing, mm	30	0.10	0.026	25.62	0.04	0.16

**Dianulites rocklandensis** Wilson, 1921 (one colony)

	N	X	SD	CV	MIN	MAX
Aperture width, mm	20	0.31	0.038	12.29	0.24	0.36
Aperture spacing, mm	20	0.34	0.044	12.77	0.25	0.42

**Monticulipora aff. mammulata** d'Orbigny, 1850 (one colony)

	N	X	SD	CV	MIN	MAX
Aperture width, mm	30	0.18	0.023	13.16	0.14	0.23
Aperture spacing, mm	30	0.19	0.025	13.55	0.14	0.23
Mesozooeia width, mm	25	0.04	0.015	34.50	0.02	0.07
Cystiphragm spacing, mm	25	0.13	0.034	27.13	0.06	0.20

**Orbignyella multitabulata** Coryell, 1921 (two colonies)

	N	X	SD	CV	MIN	MAX
Aperture width, mm	40	0.15	0.018	12.02	0.11	0.19
Aperture spacing, mm	40	0.18	0.021	12.15	0.13	0.22
Acanthostyle diameter, mm	40	0.04	0.011	28.27	0.02	0.06
Mesozooeia width, mm	40	0.053	0.017	31.45	0.025	0.088
Aperture width, mm (macular)	40	0.23	0.021	9.30	0.20	0.30
Aperture spacing, mm (macular)	40	0.27	0.030	11.01	0.22	0.35
Autozooeical diaphragms spacing, mm	40	0.17	0.050	28.91	0.10	0.31

**Homotrypa subramosa** Ulrich, 1886 (six colonies)

	N	X	SD	CV	MIN	MAX
Aperture width, mm	110	0.16	0.021	13.09	0.11	0.20
Aperture spacing, mm	110	0.18	0.028	15.39	0.13	0.26
Cystiphragm spacing, mm	80	0.10	0.041	42.44	0.04	0.25
Acanthostyle diameter, mm	45	0.04	0.009	26.54	0.02	0.06
Mesozooeia width, mm	45	0.05	0.017	33.18	0.03	0.11
Macrozooeia width, mm	8	0.21	0.012	5.48	0.20	0.23

**Homotrypa vacua** McKinney, 1971 (six colonies)

	N	X	SD	CV	MIN	MAX
Branch diameter, mm	7	1.82	0.381	20.96	1.45	2.38
Exozone width, mm	7	0.45	0.160	35.61	0.25	0.75
Endozone width, mm	7	0.92	0.281	30.47	0.60	1.45
Aperture width, mm	83	0.12	0.024	19.21	0.07	0.19
Aperture spacing, mm	84	0.17	0.023	13.66	0.10	0.22
Acanthostyle diameter, mm	30	0.033	0.007	22.62	0.025	0.055
Mesozooeia width, mm	57	0.04	0.015	34.24	0.02	0.09
Acanthostyles per aperture	11	3.6	0.924	25.42	2.0	5.0
Mesozooeia per aperture	7	4.4	0.787	17.77	3.0	5.0
Cystiphragm spacing, mm	19	0.08	0.025	30.10	0.04	0.12
Exozonal wall thickness, mm	40	0.035	0.008	23.37	0.023	0.055
Macrozooeia width, mm	26	0.18	0.018	9.96	0.15	0.22

**Heterotrypa enodis** n. sp. (two colonies)

	N	X	SD	CV	MIN	MAX
Aperture width, mm	45	0.17	0.034	20.37	0.11	0.22
Aperture spacing, mm	45	0.22	0.037	16.94	0.16	0.32
Aperture width, mm (macular)	28	0.24	0.024	9.70	0.2	0.28
Aperture spacing, mm (macular)	28	0.31	0.044	13.96	0.23	0.39
Acanthostyle diameter, mm	25	0.03	0.006	22.37	0.02	0.05
Mesozooeia width, mm	35	0.060	0.023	37.36	0.025	0.120
Autozooeical diaphragms spacing, mm	25	0.15	0.062	41.69	0.05	0.33
Mesozooeical diaphragms spacing, mm	28	0.07	0.022	32.91	0.03	0.12
Exozonal wall thickness, mm	20	0.053	0.012	23.27	0.033	0.075

**Albardonia bifoliata** n. gen., n. sp. (three colonies)

	N	X	SD	CV	MIN	MAX
Aperture width, mm	55	0.11	0.012	11.37	0.08	0.14
Aperture spacing, mm	55	0.17	0.020	11.74	0.13	0.22
Aktinostyle diameter, mm	50	0.028	0.008	27.67	0.015	0.045
Mesozooeia width, mm	55	0.05	0.015	32.88	0.02	0.11
Aktinostyles per aperture	10	6.2	0.789	12.72	5.0	7.0
Mesozooeia per aperture	20	5.2	1.196	23.01	3.0	8.0
Exozonal wall thickness, mm	10	0.03	0.011	31.96	0.02	0.05

**Diplotrypa** sp. A (one colony)

	N	X	SD	CV	MIN	MAX
Aperture width, mm	25	0.18	0.025	13.45	0.15	0.25
Aperture spacing, mm	25	0.22	0.026	11.74	0.18	0.28
Mesozooeia width, mm	25	0.07	0.018	27.37	0.03	0.11
Mesozooeical diaphragms spacing, mm	10	0.11	0.019	17.14	0.08	0.14
Exozonal wall thickness, mm	10	0.03	0.003	11.13	0.02	0.03



## APPENDIX 1. — Continuation.

***Tarphophragma macrostoma* (Loeblich, 1942) (three colonies)**

	N	X	SD	CV	MIN	MAX
Aperture width, mm	27	0.21	0.046	21.82	0.13	0.29
Aperture spacing, mm	20	0.31	0.052	17.11	0.20	0.38
Macrozoecia width, mm	4	0.33	0.036	10.97	0.30	0.38
Mesozoecia width, mm	15	0.06	0.010	16.15	0.05	0.08
Mesozoecia per aperture	10	4.3	1.160	26.97	2.0	6.0
Exozonal wall thickness, mm	13	0.08	0.021	26.41	0.04	0.12

***Jordanopora heroensis* Ross, 1963 (one colony)**

	N	X	SD	CV	MIN	MAX
Aperture width, mm	30	0.13	0.016	12.17	0.10	0.17
Aperture spacing, mm	30	0.23	0.028	12.09	0.16	0.27
Acanthostyle diameter, mm	30	0.03	0.009	29.08	0.02	0.05
Mesozoecia width, mm	20	0.048	0.013	28.11	0.025	0.065
Exozonal wall thickness, mm	10	0.075	0.018	24.52	0.045	0.110

***Argentinopora robusta* n. gen., n. sp. (two colonies)**

	N	X	SD	CV	MIN	MAX
Aperture width, mm	30	0.18	0.019	10.35	0.15	0.21
Aperture spacing, mm	30	0.31	0.028	9.32	0.25	0.4
Acanthostyle diameter, mm	30	0.07	0.018	25.46	0.03	0.10
Mesozoecia width, mm	30	0.08	0.021	24.96	0.04	0.12
Acanthostyles per aperture	30	6.2	0.874	14.18	5.0	8.0
Mesozoecia per aperture	10	4.3	1.494	34.75	3.0	7.0
Mesozoecial diaphragms spacing, mm	30	0.09	0.019	21.27	0.06	0.14
Autozoecial diaphragms spacing, mm	30	0.16	0.052	32.70	0.06	0.30

***Nicholsonella spinigera* n. sp. (five colonies)**

	N	X	SD	CV	MIN	MAX
Aperture width, mm	70	0.19	0.038	19.77	0.11	0.28
Aperture spacing, mm	70	0.26	0.030	11.44	0.19	0.35
Acanthostyle diameter, mm	70	0.052	0.011	21.32	0.025	0.075
Mesozoecia width, mm	30	0.07	0.020	30.85	0.03	0.11
Acanthostyles per aperture	30	6.3	1.124	17.75	4.0	8.0
Autozoecial diaphragms spacing, mm	20	0.23	0.088	37.93	0.12	0.52
Exozonal wall thickness, mm	20	0.07	0.012	18.18	0.05	0.09

***Arthroclema* sp. A (seven colonies)**

	N	X	SD	CV	MIN	MAX
Branch diameter, mm	9	0.75	0.191	25.44	0.47	1.03
Exozone width, mm	9	0.17	0.063	37.98	0.10	0.26
Endozone width, mm	9	0.42	0.093	22.32	0.27	0.54
Aperture width, mm	18	0.08	0.008	10.96	0.07	0.10
Aperture spacing along branch, mm	9	0.35	0.028	8.00	0.32	0.41
Aperture spacing diagonally, mm	8	0.20	0.015	7.39	0.19	0.23
Paurostyle diameter, mm	12	0.02	0.003	18.03	0.01	0.03

***Trigonodictya elegans* (Ulrich, 1893) (six colonies)**

	N	X	SD	CV	MIN	MAX
Aperture width, mm	77	0.11	0.018	16.56	0.08	0.15
Aperture spacing along branch, mm	31	0.36	0.040	11.16	0.29	0.46
Aperture spacing diagonally, mm	35	0.26	0.020	7.75	0.21	0.33

***Pseudostictoporella simplex* n. sp. (three colonies)**

	N	X	SD	CV	MIN	MAX
Aperture width, mm	50	0.09	0.033	37.14	0.05	0.14
Aperture spacing along branch, mm	50	0.30	0.059	19.98	0.18	0.49
Aperture spacing diagonally, mm	50	0.21	0.016	7.85	0.18	0.25
Maximal chamber width, mm	20	0.10	0.010	10.04	0.09	0.12

***Chazydictya ornata* n. sp. (three colonies)**

	N	X	SD	CV	MIN	MAX
Aperture width, mm	11	0.06	0.007	11.06	0.06	0.08
Aperture spacing along branch, mm	3	0.32	0.040	12.50	0.30	0.37
Aperture spacing diagonally, mm	5	0.23	0.032	14.20	0.18	0.26
Paurostyle diameter, mm	12	0.027	0.006	20.89	0.015	0.035