Description of a bryozoan fauna from mud mounds of the Lebanza Formation (Lower Devonian) in the Arauz area (Pisuerga-Carrión Province, Cantabrian Zone, NW Spain)

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ABSTRACT
A bryozoan fauna containing 16 species is described from a set of small mud mounds occurring in the Lebanza Formation (Lower Devonian) of the Arauz area, NW Spain. One genus with one species is new: the cystoporate *Petalosis clarus* n. gen., n. sp. Eleven new species are described: three cystoporates *Altshedata hispanica* n. sp., *A. gracilis* n. sp. and *Fistulipora arauzensis* n. sp.; four trepostomes: *Neotrematopora tenuis* n. sp., *Leioclema arauzensis* n. sp., *Eridotrypella validaeformis* n. sp. and *Leptotrypella armata* n. sp.; two rhabdomesine cryptostomes *Orthopora spinosa* n. sp. and *Vidronovella elegantula* n. sp.; and two fenestrates *Rectifenestella exiliformis* n. sp. and *Tectulipora tuberculata* n. sp. Two species were identified at genus and family level respectively: *Eridopora* sp. and Rhomboporidae sp. indet. Two identified species show palaeobiogeographic relations to the Lower Devonian of Altai, Mongolia, and Tajikistan respectively: *Leioclema multiacanthoporum* Astrova *in* Astrova & Yaroshinskaya, 1968 and *Hemitrypa lasutkiniae* Waschurova, 1964. The bryozoan fauna is dominated by cystoporates and trepostomes, followed by cryptostomes and fenestrates.

These species display four different growth habits: encrusting (43.75%), ramose branched/encrusting (12.5%), ramose branched (25%), and reticulate (18.75%). Encrusting and encrusting/ramose growth habits dominate in all parts of mud mounds, whereas ramose branched and reticulate bryozoans are most abundant in the lower part of mounds, being rare in the upper parts. Despite their abundance, bryozoans cannot be regarded as the principal builders of the mud mounds, which apparently were mainly built by microbial communities. Nevertheless, bryozoans played the role of sediment binders (encrusting species), stabilizing the sediment, or exerted a baffling effect (fenestrates).

KEY WORDS
Bryozoa,
Lower Devonian,
Spain,
taxonomy,
ecology,
new genus,
new species.

RÉSUMÉ
Description d'une faune de bryozoaires de type mud-mound de la Formation Lebanza (Dévonien inférieur) de la région de Arauz (province de Pisuerga-Carríon, zone cantabrique, nord-ouest de l'Espagne).
Une faune de bryozoaires contenant 16 espèces provenant des monticules de boue trouvés à la Formation Lebanza (Dévonien inférieur) de la région d'Arauz, nord-ouest de l'Espagne est décrite. Une espèce est décrite dans un nouveau genre: le cystopore *Petalosis clarus* n. gen., n. sp. Onze nouvelles espèces sont décrites dont trois cystopores (*Altshedata hispanica* n. sp., *A. gracilis* n. sp., et *Fistulipora arauzensis* n. sp.), quatre trépostomes (*Neotrematopora tenuis* n. sp., *Leioclema arauzensis* n. sp., *Eridotrypella validaeformis* n. sp., et *Leptotrypella armata* n. sp., deux cryptostomes rhabdomesines (*Orthopora spinosa* n. sp. et *Vidronovella elegantula* n. sp.) et deux fenestrés (*Rectifenestella exiliformis* n. sp. et *Tectulipora tuberculata* n. sp. Deux espèces sont déterminées aux niveaux du genre et de la famille, respectivement: *Eridopora* sp. et Rhomboporidae sp. indet. Deux des espèces identifiées montrent des relations paléobiogéographiques au Dévonien inférieur d'Altai, Mongolie et du Tajikistan, respectivement: *Leioclema multiacanthoporum* Astrova *in* Astrova & Yaroshinskaya, 1968 and *Hemitrypa lasutkiniae* Waschurova, 1964. La faune bryozoaire est dominée par les cystopores et par les trépostomes, suivis par les cryptostomes et par les fenestrés. Ces espèces présentent quatre modes de croissance: encroûtant (43.75%), rameux branchu/encroûtant (12.5%), rameux branchu (25%) et reticulé (18.75%). Les bryozoaires à types de croissance incrustant et incrustant/ramose dominent dans toutes les parties des monticules de boue, tandis que les modes rameux branchus et réticulés, abondants à leur base, sont plus rares dans leurs parties supérieures. En dépit de leur abondance, les bryozoaires ne peuvent pas être considérés comme les principaux constructeurs des monticules de boue, qui sont apparemment construits par des communautés microbiennes. Cependant, les bryozoaires ont joué un rôle de liant sédimentaire avec les espèces encroûtantes, de stabilisateur de sédiment ou ont exercé un effet déflecteur (avec les formes fenestrées).

MOTS CLÉS
Bryozoaires,
Dévonien inférieur,
Espagne,
taxonomie,
écologie,
genre nouveau,
espèces nouvelles.

INTRODUCTION

The Devonian record of the Cantabrian Zone (NW Spain) is a rather continuous and varied succession with both siliciclastic and carbonate units. The latter were mainly deposited on ramp-type platforms (Vera de la Puente 1989; Fernández *et al.* 1997, 2006; Keller 1997; Keller & Grötsch 1990; Hofmann & Keller 2006), contain a wealth of subtidal deposits with subordinate peritidal rocks, and display up to

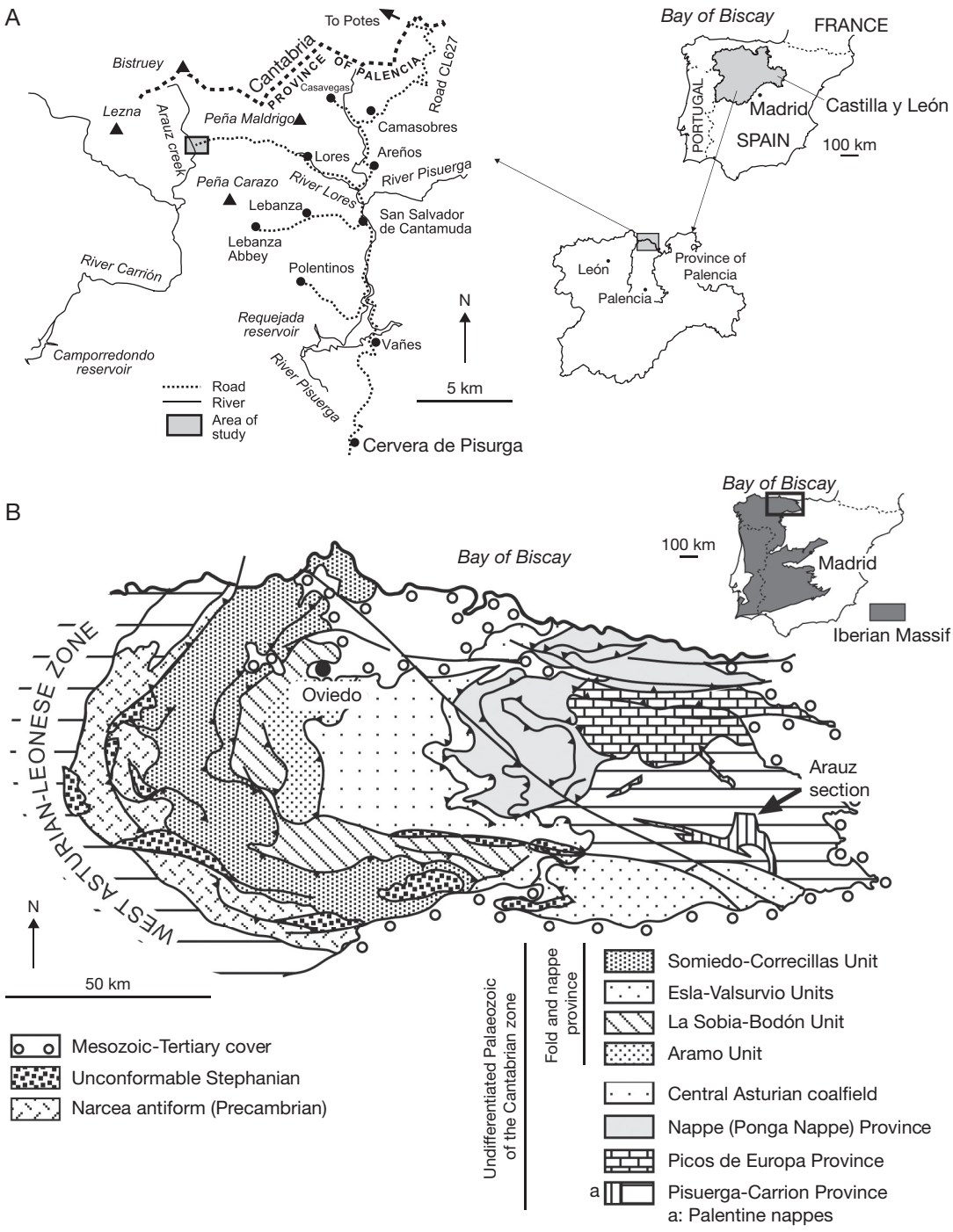

FIG. 1. — **A**, schematic map showing the location of the studied outcrops in the Arauz area (north of Palencia province, Spain); **B**, schematic geological map of the Cantabrian Zone (modified from Pérez-Estaún *et al.* 1988) showing the location of the studied outcrop in the Alto Carrión Unit.

seven coral- and stromatoporoid-dominated, reefal episodes of varying importance (see Méndez-Bedia *et al.* 1994; Fernández-Martínez *et al.* 2010). Apart from the framebuilders, these limestones contain abundant benthic faunas, chiefly brachiopods, crinoids and trilobites, which have been the subject of numerous systematic, biostratigraphic and palaeoecological studies (García-Alcalde 1996, 1998; García-Alcalde *et al.* 2002, among others).

Bryozoans are also a conspicuous element, both in the reefal and non-reefal intervals. However, despite their abundance and importance, Devonian bryozoans from NW Spain have attracted only minor attention (Arbizu *et al.* 1995; Suárez Andrés 1998, 1999a-c; Suárez Andrés & González 2000a, b). These papers contain descriptions of several bryozoan species, mainly Fenestrata, from the Moniello Formation (late Emsian-early Eifelian) of the Cantabrian Zone (NW Spain). A few recent publications have contributed to knowledge of bryozoan faunas from the Emsian-Eifelian strata of the Cantabrian Zone (Suárez Andrés & McKinney 2010; Ernst 2010, 2011; Ernst *et al.* 2012) and from elsewhere in the Iberian Massif (Central Iberian Zone, Lochkovian of the Sierra de Guadarrama: Guadalajara; Ernst & May 2012). These publications describe diverse faunas containing fenestrate, trepostome, cystoporate and cryptostome bryozoan species. Total bryozoan diversity in the Lower Devonian of Spain is estimated to be about 100 species (unpublished data).

In this paper, we examine systematically a bryozoan assemblage occurring close to the first reefal episode, in the Lower Devonian Lebanza Formation (see Fernández-Martínez *et al.* 2010). This bryozoan fauna is found in a series of recently discovered metre-size mud mounds. The mud mounds are still under study and will be dealt with in a succeeding paper.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The study locality is situated in the Arauz area (north of province of Palencia, NW Spain; Fig. 1A). Here the Lebanza Formation crops out in several fault-bounded bands, one of which contains one of the main reference sections of the formation. An exposure only a few tens of metres from this section displays a set of small mud mounds containing the bryozoan fauna described here.

The Lower Devonian (Middle Lochkovian-Lower Pragian) Lebanza Formation (Krans *et al.* 1980) is a carbonate unit that crops out in the Palentine nappes of the Pisuerga-Carrión Unit (Cantabrian Zone, Iberian Massif, Fig. 1B; see Lotze 1945; Julivert 1971; Frankenfeld 1983; Pérez-Estaún *et al.* 1988). These nappes comprise a Silurian-lower Carboniferous succession, in which the Silurian and Devonian units display, overall, a more distal character than their counterparts elsewhere in the Cantabrian Zone. This fact allowed for the distinction between the Palentine and the Astur-Leonese facies, (Brouwer 1964). The Lebanza Formation consists of 150-160 m of limestones with subordinate marlstones and shales (Fig. 2). Five members, from Member A through Member E, have been distinguished in this formation (Krans *et al.* 1980; Jahnke *et al.* 1983; García-Alcalde *et al.* 1988; see also García-López *et al.* 2002), although no agreement exists over the precise position of their boundaries. Following Krans *et al.* (1980), Jahnke *et al.* (1983) and Fernández-Martínez *et al.* (2010), members A and B consist of subtidal (shelfal and coastal) cross bedded and laminated skeletal limestones alternating with marlstones and shales and showing a shallowing upward trend. Member C comprises subtidal deposits with coated grains and dark colour suggesting a partially restricted environment. Member D is formed of peritidal limestones, and, finally, Member E is constituted by subtidal alternations of cross-bedded limestones, marlstones and shales. Reefal fauna mainly occur in the upper part of Member B, as broken and reworked colonies, and in Member C, either as broken fragments or as in situ colonies. The interval studied belongs either to the upper part of Member B or to the Member C base.

Most of the Lebanza Formation is largely arranged into metre-scale fining upward cycles (see Fernández-Martínez *et al.* 2010, Fig. 3). In the case of the upper part of Member B and of the Member C, those cycles consist of: 1) a lower interval

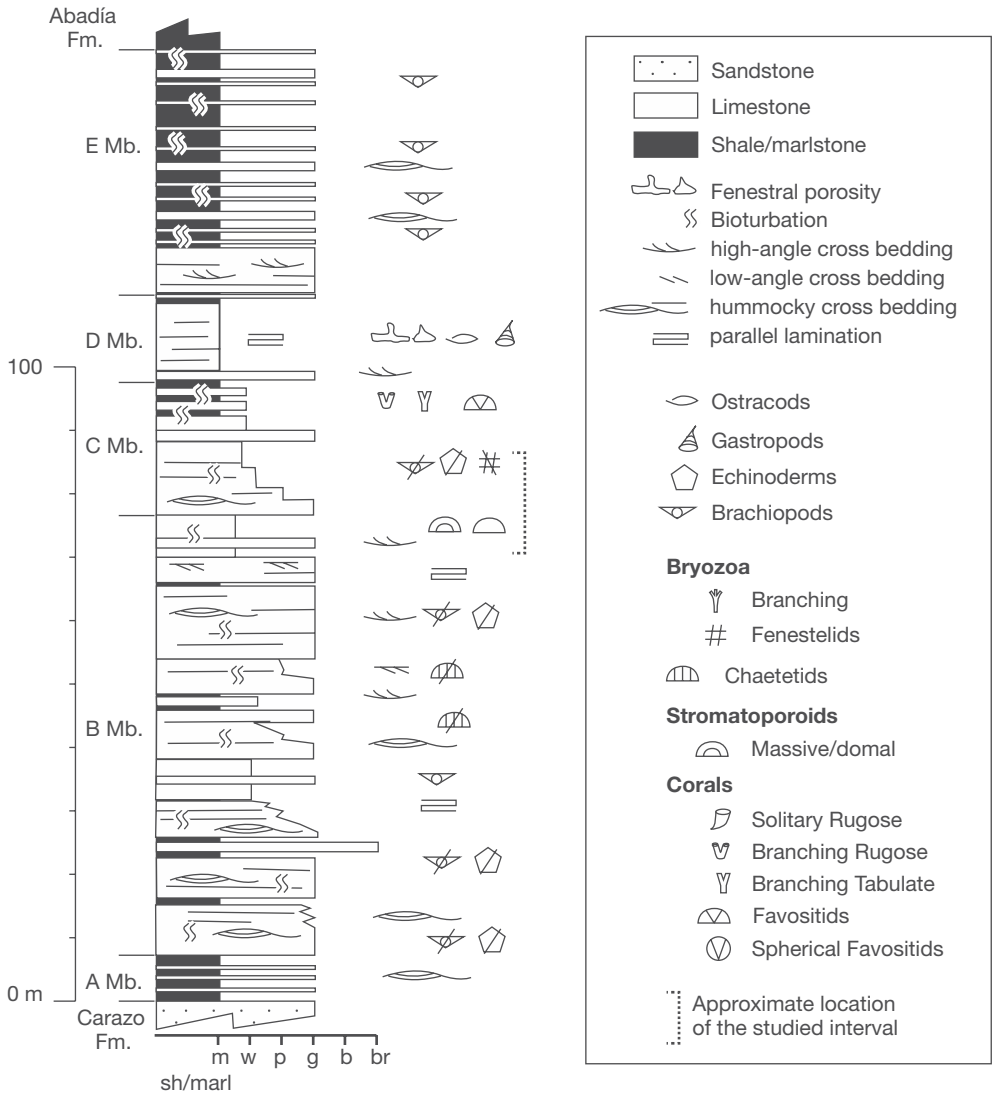

FIG. 2. — Highly generalized stratigraphical column showing the main features of the Lebanza Formation and its subdivision into members. The approximate location of the studied interval is depicted to the right of the column (adapted from Fernández-Martínez *et al.* 2010). Abbreviations: **b**, boundstone (baffle-, bind-, framestone); **br**, rudstone, floatstone; **g**, grainstone; **m**, mudstone; **p**, packstone; **w**, wackestone.

of skeletal lime grain- to packstones, which may display cross-bedding; and 2) an upper interval of burrowed limestones, marly limestones and marlstones or shales. The bryozoan-bearing mud mounds occur in the upper interval of one of these cycles, and are less than two metres thick. They directly overlie the basal package of grainstones and are interbedded with bioturbated, fine-grained grain- to packstones with irregular, laterally discontinuous marly partings.

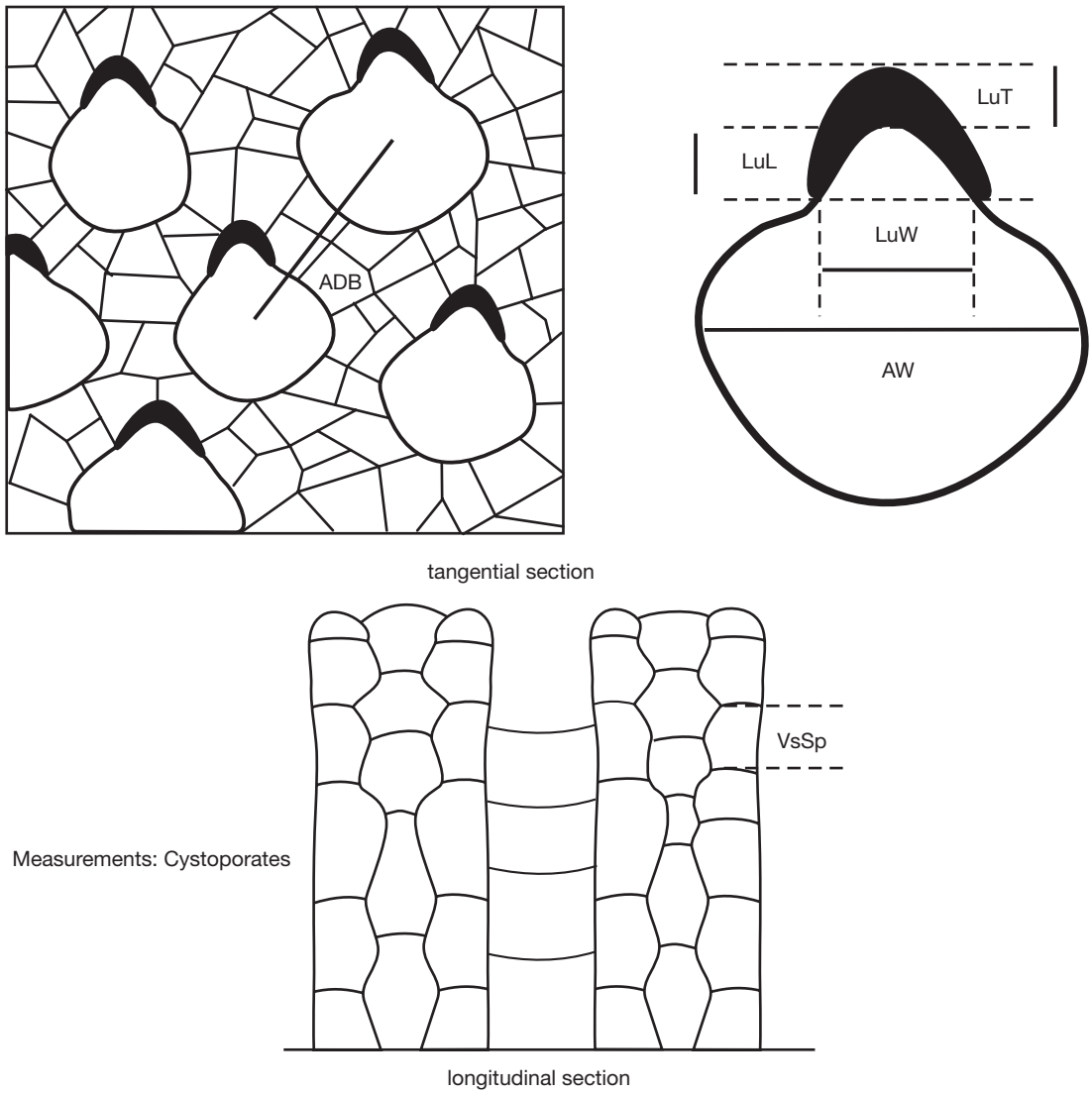

FIG. 3. — Some important measurements made on the cystoporate bryozoans. Abbreviations: **ADB**, aperture spacing; **AW**, autozooecial aperture width; **LuL**, lunarium length; **LuW**, lunarium width; **LuT**, lunarium thickness; **VsSp**, vesicle spacing.

MATERIAL AND METHODS

Bryozoan material is represent by moderately large limestone blocks, from which 70 randomly oriented thin sections were made. Studied material is housed at the Senckenberg Museum (Frankfurt am Main, Germany), numbers SMF 21.130-SMF 21.385.

Morphologic character terminology is partly adopted from Anstey & Perry (1970) and Hageman (1993). The following morphologic characters were measured and used for statistics in the studied material (Figure 3 for cystoporates and Figure 4 for fenestrates):

Branch width, branch thickness, exo- (endo-) zone width, autozooecial aperture width (non-

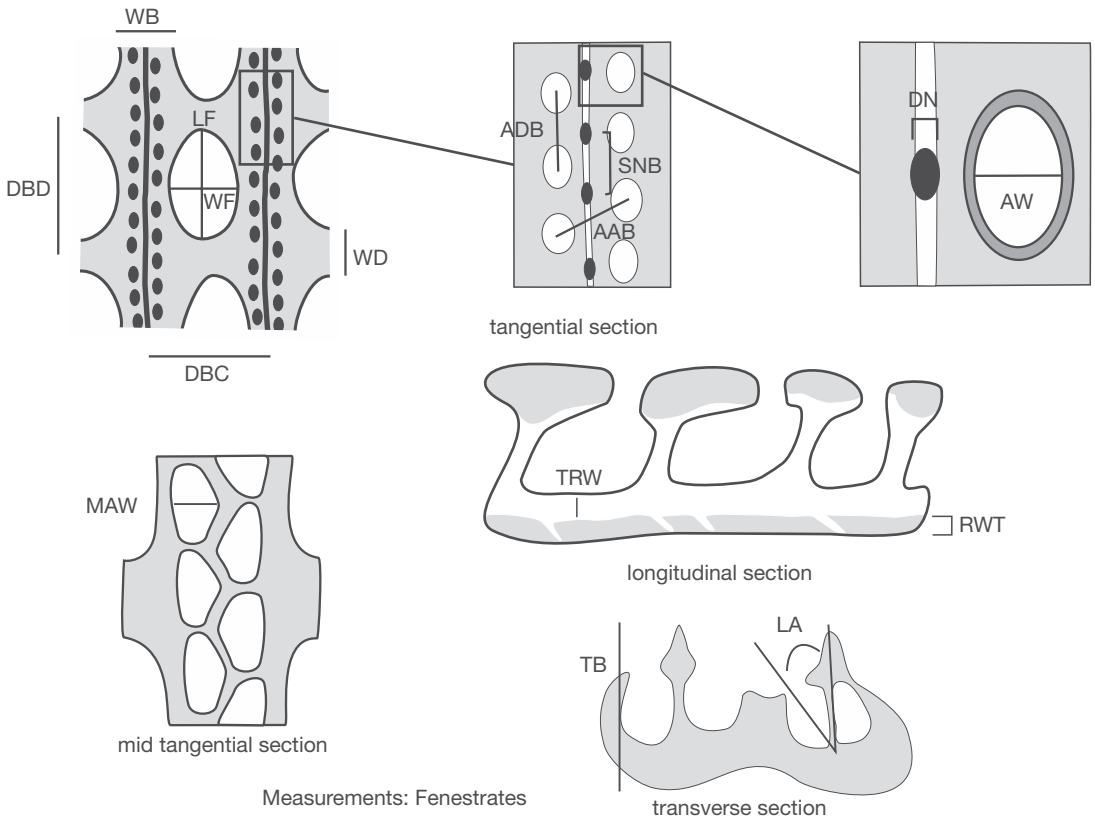

FIG. 4. — Some important measurements made on the fenestrate bryozoans. Abbreviations: **ADB**, aperture spacing along branch; **AAB**, aperture spacing diagonally; **AW**, autozooecial aperture width; **DBC**, distance between branch centres; **DBD**, distance between dissepiment centres; **DN**, node diameter; **LA**, lateral wall budding angle; **LF**, fenestrule length; **MAW**, maximum chamber width; **RWT**, thickness of reverse wall laminated layer; **SNB**, node spacing; **TB**, branch thickness; **TRW**, thickness of reverse wall granular layer; **WB**, branch width; **WD**, dissepiment width; **WF**, fenestrule width.

macular, macular), aperture spacing (non-macular, macular, along branch, diagonally) lunarium width (length, thickness), acanthostyle diameter, number of acanthostyles per aperture, mesozooecia (exilazooecia) diameter, number of mesozooecia (exilazooecia) wall thickness in exozone, vesicle diameter (spacing), number of vesicles per aperture, autozooecial budding angle in endozone (exozone), dissepiment width, fenestrule width (length), distance between branch (dissepiment) centres, apertures per fenestrule length, maximal chamber width, keel node diameter (spacing), thickness of reverse wall granular layer, thickness of reverse wall laminated layer, lateral wall budding angle.

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

SYSTEMATIC PALAEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926

Suborder FISTULIPORINA Astrova, 1964
Family ANOLOTICHIIDAE Utgaard, 1968

Genus *Altshedata* Morozova, 1959

TYPE SPECIES. — *Fistulipora belgebaschensis* Nekhoroshev, 1948, by subsequent designation (Morozova 1959). Middle Devonian (Givetian); Altai, Russia.

OCCURRENCE. — Besides the type species *Altshedata belgebaschensis* (Nekhoroshev, 1948), two species have been reported: *A. parasitica* Yang & Lu, 1983 from the Upper Carboniferous of Xinjiang (China), and *A. xiacaiyuanensis* Fan, 1993 from the Permian of Yunnan (China). However, these species may not belong to the genus *Altshedata* Morozova, 1959 because they show significant differences in their internal morphology possessing large and abundant vesicles as well as hemiphragms.

DIAGNOSIS. — Colonies encrusting or massive. Autozooecia large, living chambers subangular to subrounded in transverse section, budding from the epitheca. Lunaria moderate to large in the inner exozone, large on the colony surface, rounded, deeply indenting autozooecia. Diaphragms few to abundant. Vesicular skeleton present. Heterozooecia absent. Autozooecial walls thick, undulatory, having indistinct granular microstructure. Monticules with large zooecia and more abundant interzooecial space.

COMPARISON
Altshedata Morozova, 1959 differs from *Anolotichia* Ulrich, 1890 in having rounded lunaria indenting autozooecia and vesicular skeleton, from *Crassaluna* Utgaard, 1968 in the shape of the lunaria which are rounded in *Altshedata* but irregular with nodes and ridges in *Crassaluna*.

Altshedata hispanica n. sp.
(Figs 5A-H; 6A-C; Appendix)

HOLOTYPE. — SMF 21.130.

PARATYPES. — SMF 21.131-SMF 21.149.

ETYMOLOGY. — The species name refers to the finding of this species in Spain (from Latin "*hispanicus*" = Spanish).

TYPE LOCALITY. — Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

TYPE HORIZON. — Lebanza Formation, Lower Devonian (Pragian).

DIAGNOSIS. — Encrusting colonies; autozooecia prismatic; autozooecial diaphragms common, straight, thin; lunaria well-developed, prominent; megazooecia occurring; vesicles occasionally present, never isolating autozooecia; communication pores absent; maculae not observed.

DESCRIPTION
Encrusting colonies, 1.0-3.5 mm thick. Autozooecia prismatic, budding from the basal epitheca, hemispherical to trapezoidal at their bases, becoming then rhombic to hexagonal, recumbent in proximal parts, then bending sharply and intersecting colony surface at right angles. Autozooecial diaphragms common, straight, thin. Autozooecial apertures rounded-polygonal. Lunaria well-developed, prominent, rounded, deeply indenting autozooecial cavity, originating from bases of autozooecia, consisting of hyaline material. Ends of lunaria curved to form almost a tube. Megazooecia occurring, 0.42-0.48 mm wide. Other heterozooecia not observed. Vesicles occasionally present, irregular in shape and size, concentrated at base of exozone, never isolating autozooecia. Autozooecial walls in the endozone granular, straight, 0.005-0.010 mm thick; in exozone irregularly thickened, showing indistinct granular microstructure, 0.04-0.07 mm thick. True communication pores not observed, but deep annulations in walls giving false appearance of communication pores. Maculae not observed.

COMPARISON
Altchedata hispanica differs from the type species *A. belgebaschensis* (Nekhoroshev, 1948) in having fewer vesicles, smaller autozooecial apertures (autozooecial width 0.23-0.38 vs 0.40 mm in *A. belgebaschensis*) and larger lunaria. *Altchedata hispanica* differs from *Altchedata gracilis* in its larger autozooecia (average autozooecial width 0.3 mm vs 0.27 mm in *A. gracilis*), presence of megazooecia and absence of style-like projections in the autozooecial walls.

Altshedata gracilis n. sp.
(Figs 6D-G, 7A-D; Appendix)

HOLOTYPE. — SMF 21.150.

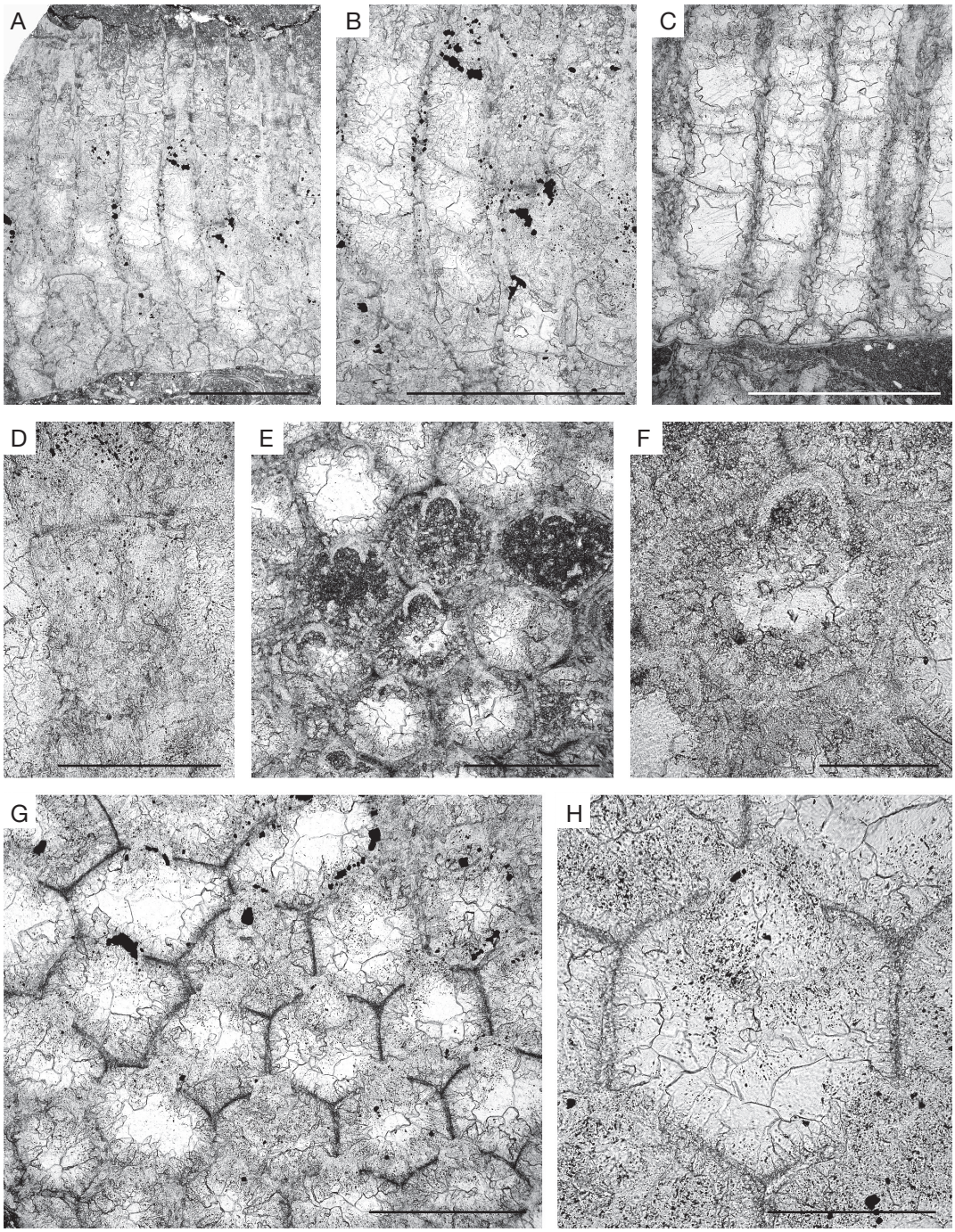

FIG. 5. — *Altshedata hispanica* n. sp.: **A**-**C**, longitudinal section showing autozooecia with abundant diaphragms, holotype SMF 21.130; **D**, longitudinal section showing microstructure of autozooecial walls, paratype SMF 21.142; **E**, **F**, tangential section showing autozooecial apertures and lunaria, holotype SMF 21.130; **G**, **H**, deep tangential section of autozooecial chambers, paratype SMF 21.142. Scale bars: A-C, 1 mm; D, 0.1 mm; E, G, 0.5 mm; F, H, 0.2 mm.

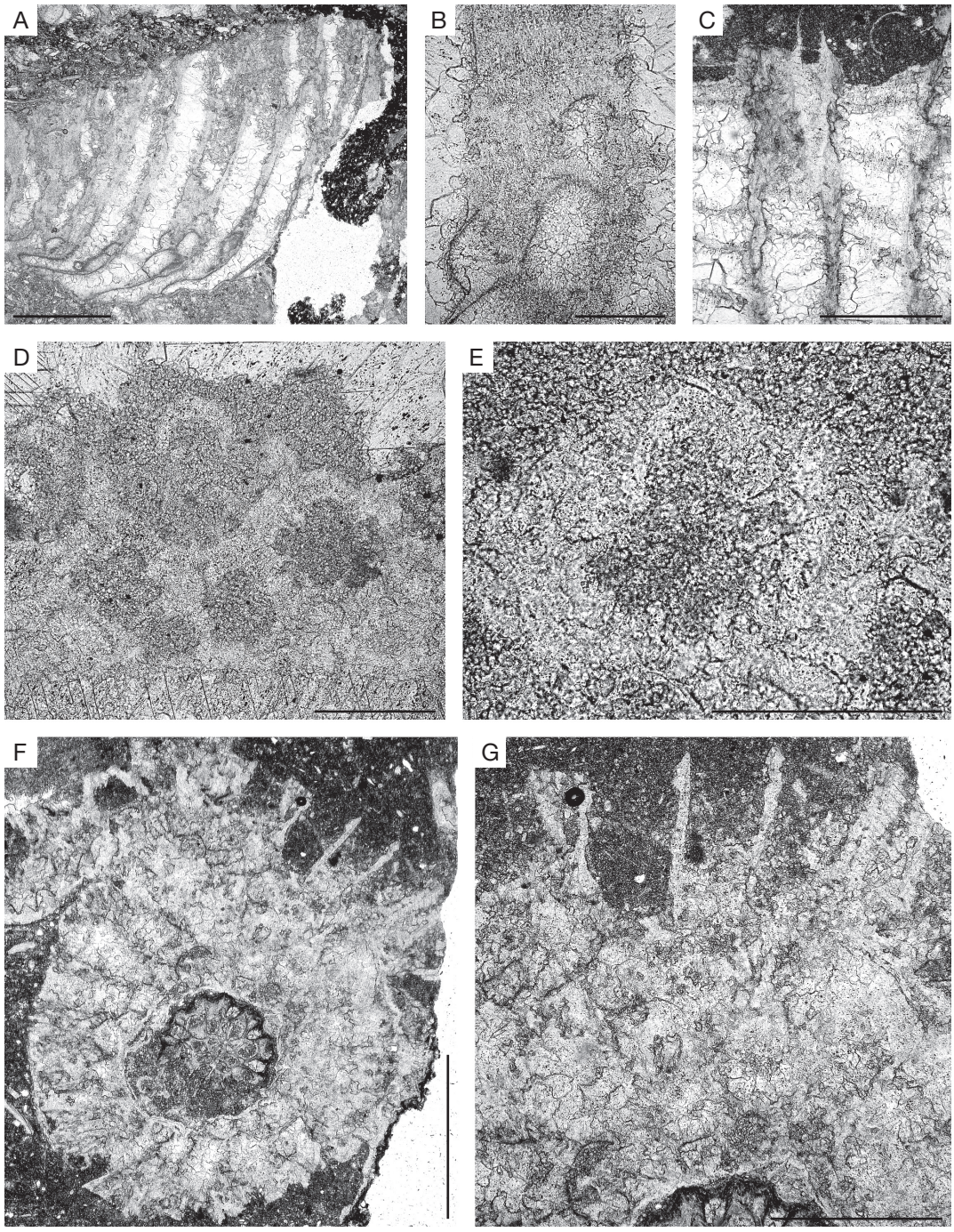

FIG. 6. — **A**-**C**, *Altshedata hispanica* n. sp.; **A**, **B**, longitudinal section showing vesicles, paratype SMF 21.144; **C**, longitudinal section showing lunarial deposits in exozone, paratype SMF 21.142; **D**-**G**, *Altshedata gracilis* n. sp.; **D**, tangential section showing autozooecial apertures, holotype SMF 21.150; **E**, tangential section, paratype SMF 21.155; **F**, **G**, longitudinal section, paratype SMF 21.163. Scale bars: A, F, 1 mm; B, D, E, 0.2 mm; C, G, 0.5 mm.

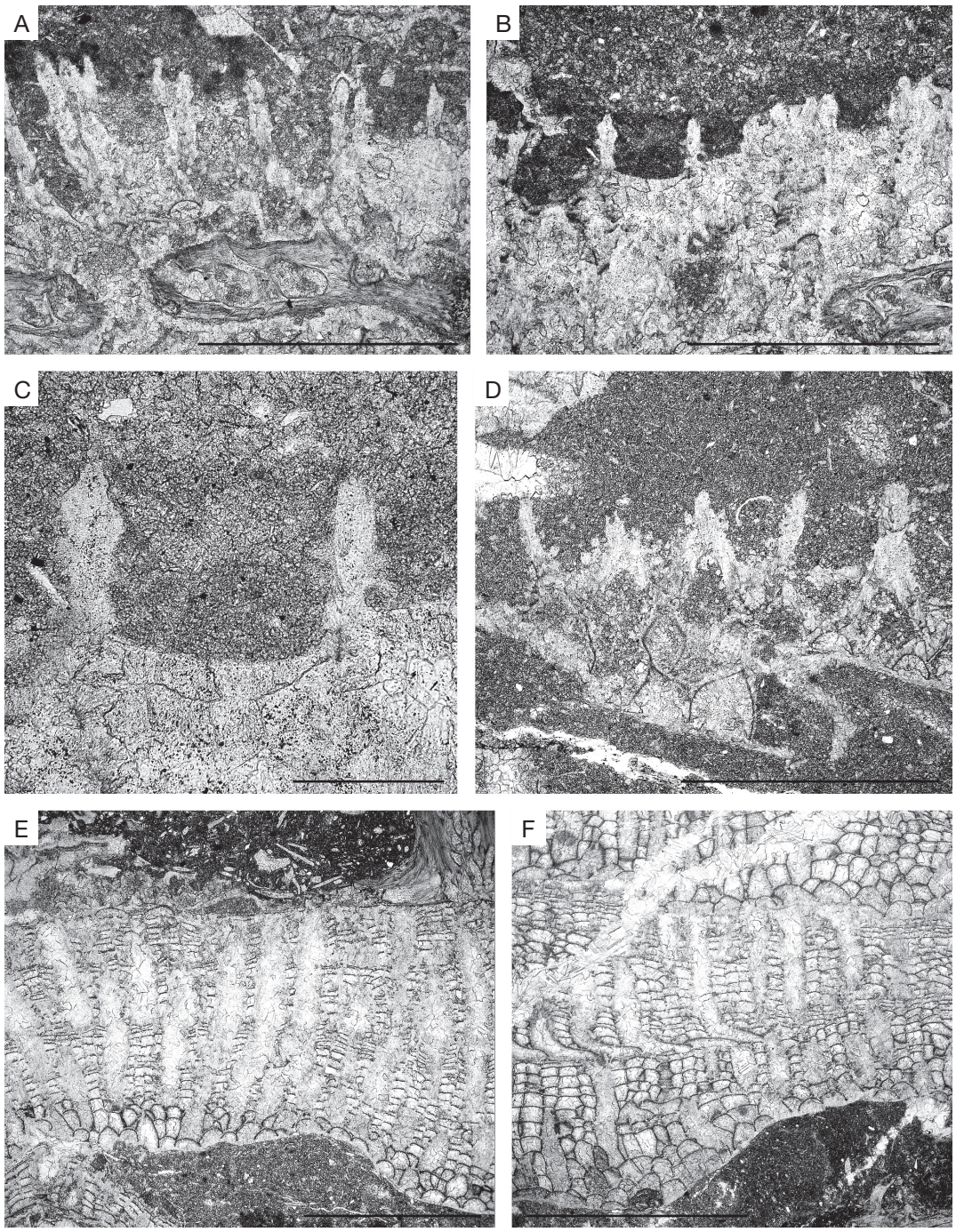

FIG. 7. — **A**-**D**, *Altshedata gracilis* n. sp.; longitudinal section autozooecia and walls, paratype SMF 21.164; **D**, longitudinal section showing autozooecia with lunaria and style-like projections, holotype SMF 21.150; **E**, **F**, *Fistulipora arauzensis* n. sp., longitudinal sections of multilayered colonies, paratype SMF 21.170. Scale bars: A, B, D, 1 mm; C, 0.2 mm; E, F, 2 mm.

PARATYPES. — SMF 21.151-SMF 21.164.

ETYMOLOGY. — The species name refers to the small sizes of colonies and autozooecia of the new species (derived from Latin "*gracilis*" = slender).

TYPE LOCALITY. — Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

TYPE HORIZON. — Lebanza Formation, Lower Devonian (Pragian).

DIAGNOSIS. — Encrusting colonies; autozooecia prismatic; autozooecial diaphragms common, straight, thin; lunaria well-developed, prominent; megazooecia or other heterozooecia not observed; vesicles occasionally present, never isolating autozooecia; communication pores absent; maculae not observed.

DESCRIPTION

Encrusting colonies, 0.9-1.2 mm thick. Autozooecia prismatic, budding from the basal epitheca, hemispherical to trapezoidal at their bases, becoming rhombic to hexagonal, recumbent in proximal parts, then bending sharply and intersecting colony surface at right angles. Autozooecial diaphragms common, straight, thin, locally absent. Autozooecial apertures rounded-polygonal. Lunaria well-developed, prominent, rounded, deeply indenting autozooecial cavity, originating from bases of autozooecia, consisting of hyaline material. Heterozooecia not observed. Vesicles rarely present, irregular in shape and size, occurring at the base of exozone. Autozooecial walls in the endozone granular, straight, 0.005-0.010 mm thick; in exozone irregularly thickened, showing indistinct granular microstructure with deep annulations, 0.03-0.05 mm thick. Short style-like projections present in autozooecial walls and in the granular skeleton on the colony surface. Communication pores not observed. Maculae not observed.

COMPARISON

Altshedata gracilis n. sp. differs from *Altshedata hispanica* n. sp. in having smaller autozooecia (average autozooecial width 0.27 vs 0.3 mm in *A. hispanica*), presence of megazooecia and the absence of style-like projections in autozooecial walls.

Family FISTULIPORIDAE Ulrich, 1882

Genus *Fistulipora* M'Coy, 1849

TYPE SPECIES. — *Fistulipora minor* M'Coy, 1849 [*Calamopora incrustans* Phillips, 1836], by subsequent designation (Milne Edwards & Haime 1850). Lower Carboniferous; England.

DIAGNOSIS. — Massive, encrusting, or branched colonies. Cylindrical autozooecia with thin walls and complete diaphragms. Apertures rounded, with horseshoe-shaped lunaria. Autozooecia separated by extrazooidal vesicular skeleton. Maculae often developed.

OCCURRENCE. — Ordovician to Permian; worldwide.

COMPARISON

Fistulipora M'Coy, 1849 differs from *Eridopora* Ulrich, 1882 in having rounded, horseshoe-shaped rather than triangular lunaria. Furthermore, *Eridopora* develops persistently encrusting colonies, whereas *Fistulipora* may also develop massive and branched colonies.

Fistulipora arauzensis n. sp.
(Figs 7E, F; 8A-E; Appendix)

HOLOTYPE. — SMF 21.165.

PARATYPES. — SMF 21.166-SMF 21.191.

ETYMOLOGY. — The species name refers to Arauz Sur, the locality where the new species was found.

TYPE LOCALITY. — Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

TYPE HORIZON. — Lebanza Formation, Lower Devonian (Pragian).

DIAGNOSIS. — Encrusting colonies with multilayered secondary overgrowths; autozooecial diaphragms few to absent, thin, planar or concave; autozooecial apertures rounded; lunaria small; vesicles abundant both in endozone and exozone, moderately large, completely isolating autozooecia in 1-2 rows, 6-12 surrounding each autozooecial aperture; maculae small, slightly depressed, consisting of vesicular skeleton, spaced widely on the colony surface.

DESCRIPTION

Encrusting colonies with multilayered secondary overgrowths. Multilayered colonies up to 4.8 mm

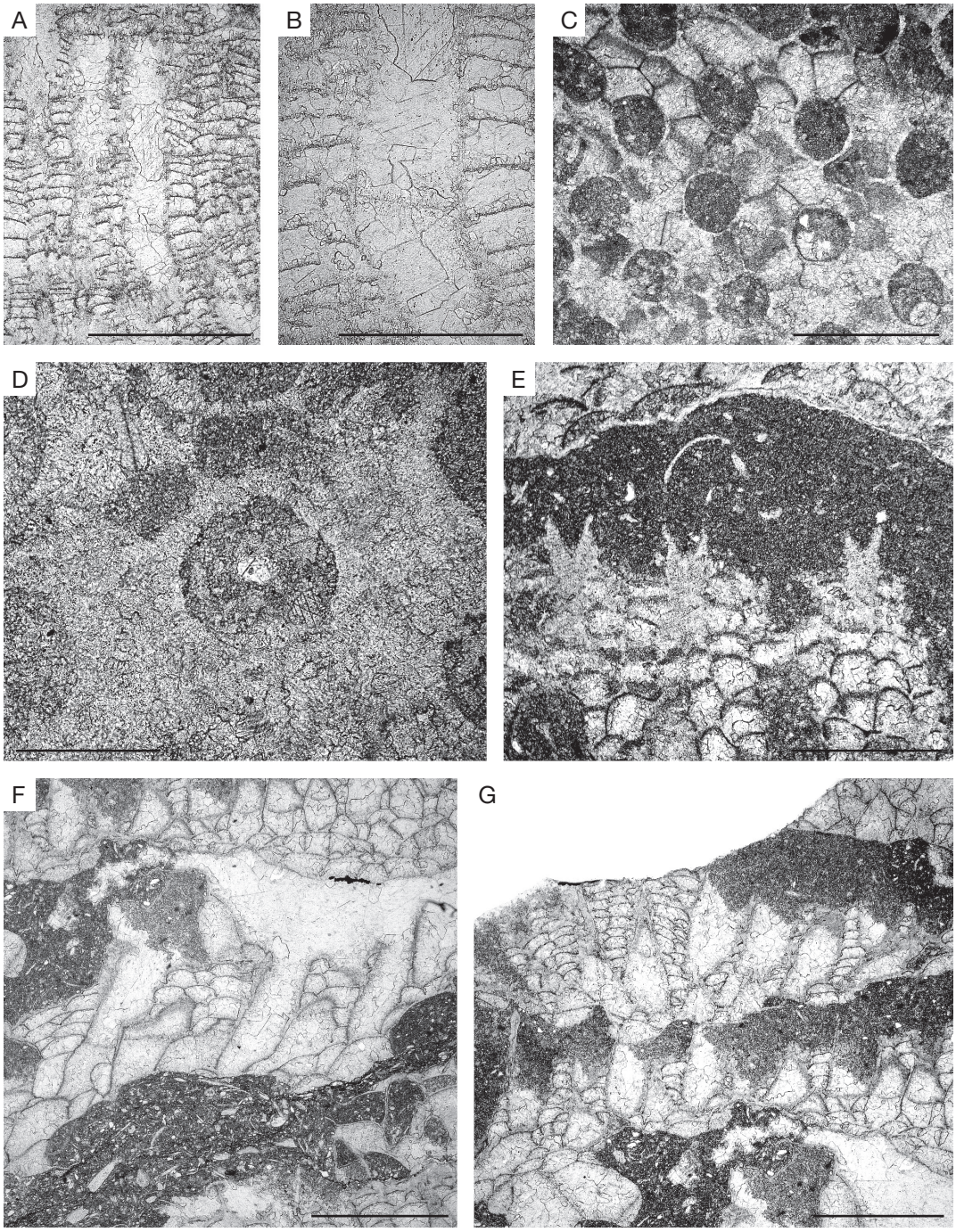

FIG. 8. — **A**-**E**, *Fistulipora arauzensis* n. sp.; **A**-**B**, longitudinal section showing autozooecial and vesicles, paratype SMF 21.170; **C**, **D**, tangential section showing autozooecial apertures and vesicles, holotype SMF 21.165; **E**, longitudinal section showing lunarial deposits in exozone, paratype SMF 21.174; **F**, **G**, *Eridopora* sp. longitudinal section showing autozooecia and large irregular vesicles, SMF 21.192. Scale bars: A, F, G, 1 mm; B, C, E, 0.5 mm; D, 0.2 mm.

thick, separate sheets 0.9-3.5 mm thick. Autozooecia growing from laminated basal layer. Autozooecial diaphragms few to absent, thin, planar or concave. Autozooecial apertures rounded. Lunaria small, horseshoe-shaped, directed to the nearest macula, consisting of hyaline material. Vesicles abundant both in endozone and exozone, moderately large, box-like, polygonal in tangential section, having flattened roofs, completely isolating autozooecia in 1-2 rows, 6-12 surrounding each autozooecial aperture; in endozone usually higher than those in exozone. Moderately thick layer of granular skeleton on colony surface often developed. Autozooecial walls thick, granular. Maculae small, slightly depressed, consisting of vesicular skeleton, 0.05-0.06 mm in diameter, spaced widely on the colony surface.

COMPARISON

Fistulipora arauzensis n. sp. is similar to *F. compacta* Astrova, 1964 from the Lower Devonian (Lochkovian) of Ukraine. The new species differs in having larger vesicles (vesicle diameter 0.07-0.018 vs 0.04-0.12 mm in *F. compacta*) and wider spaced autozooecia. *Fistulipora arauzensis* is also similar to *F. trifoliata* Schlütter, 1889 from the Middle Devonian of the Eifel but differs from it in having smaller lunaria and larger autozooecial apertures (0.14-0.24 vs 0.12-0.20 mm in *F. trifoliata*).

Genus *Eridopora* Ulrich, 1882

TYPE SPECIES. — *Eridopora macrostoma* Ulrich, 1882, by original designation. Lower Carboniferous; North America.

OCCURRENCE. — Devonian to Permian; worldwide.

DIAGNOSIS. — Thin encrusting colonies. Oval apertures with strongly developed lunaria of distinctly triangular in shape. Cylindrical autozooecia with thin walls and complete diaphragms. Vesicular skeleton consists of angular vesicles.

Eridopora sp.
(Figs 8F-G, 9A, B; Appendix)

MATERIAL. — SMF 21.192-SMF 21.193.

OCCURRENCE. — Lebanza Formation, Lower Devonian (Pragian); Arauz Sur (Arroyo section), Palencia, NW Spain (Cantabrian Mountains).

DESCRIPTION

Encrusting colonies 1.05-1.44 mm thick. Autozooecia growing from laminated basal layer. Autozooecial diaphragms few to absent, thin, planar or concave. Autozooecial apertures rounded to oval. Lunaria large, sharply triangular, consisting of hyaline material. Vesicles abundant both in endozone and exozone, moderately large, box-like, polygonal in tangential section, having flattened roofs, not completely isolating autozooecia, arranged commonly in a single row between autozooecia and 7-8 rows surrounding each autozooecial aperture. Layer of granular skeleton on colony surface thin. Autozooecial walls thin, granular. Maculae not observed.

COMPARISON

The present material is similar to *Eridopora orbiculata* (Kiepura, 1973) from the Middle Devonian of Poland and Germany, in the absence of acanthostyles skeleton but differs in having larger apertures (average autozooecial aperture width 0.31 vs 0.25 mm in *E. orbiculata*).

Petalosis n. gen.

ETYMOLOGY. — The genus name refers to the petaloid shape of autozooecial apertures due to spine-like indentions.

TYPE SPECIES. — *Petalosis clarus* n. sp. Lebanza Formation, Lower Devonian (Pragian); Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

DIAGNOSIS. — Encrusting colonies with secondary overgrowths; autozooecial apertures circular to oval; autozooecia growing from thick epitheca, bending sharply at their bases towards colony surface; basal diaphragms common to abundant; lunaria well developed, prominent, horseshoe shaped to triangular, containing 2-3 styles; one or two pairs of spine-like indentions in lateral parts of proximal ends of autozooecia; vesicles large and high, irregularly shaped, polygonal in tangential section, box-like to hemispherical, with plane or concave roofs; bands of large and irregularly shaped vesicles occurring; acanthostyles between autozooecial apertures; autozooecial walls granular in endozones and laminated in exozones; maculae not observed.

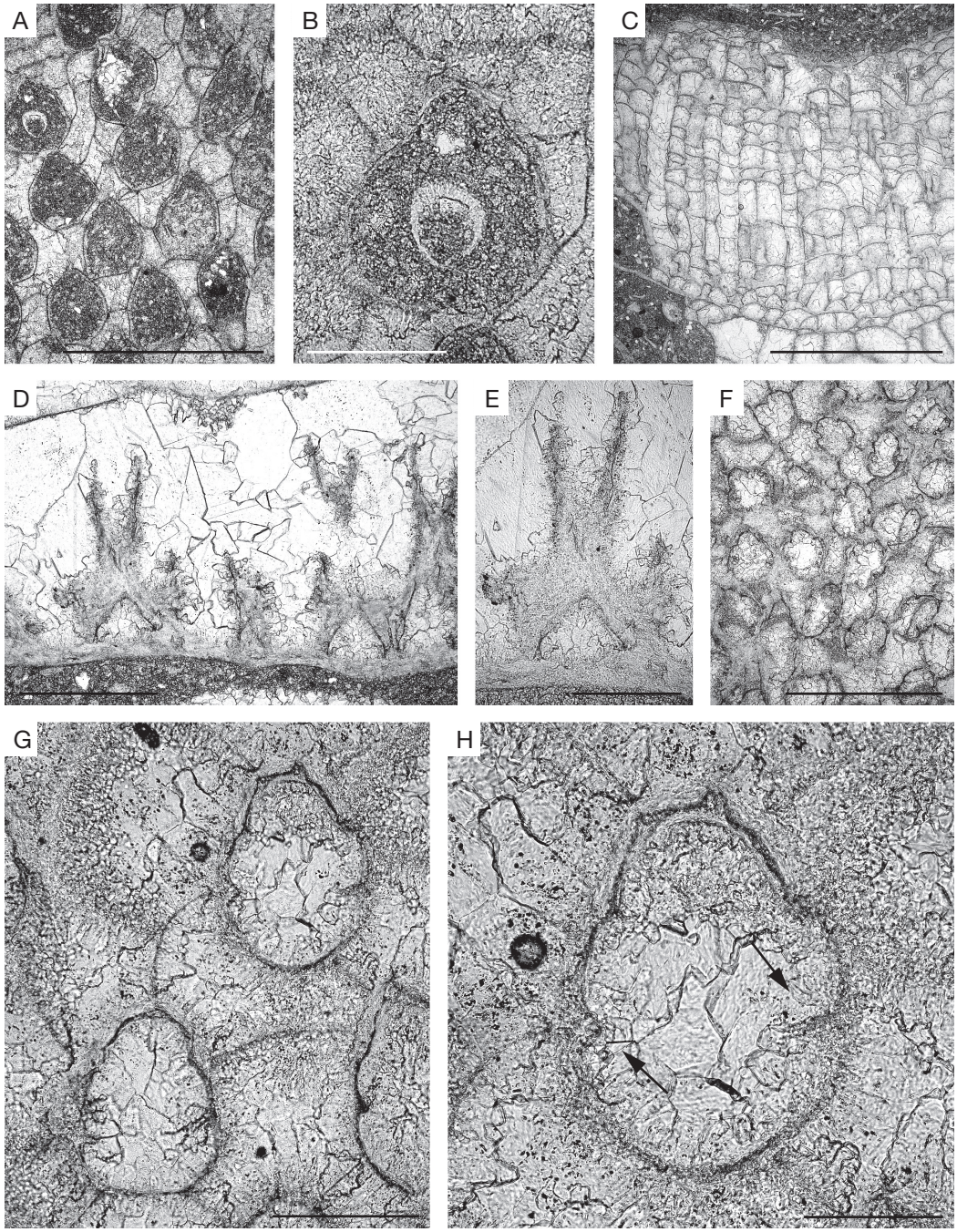

FIG. 9. — **A**, **B**, *Eridopora* sp., tangential section showing autozooecial apertures with triangular lunaria, SMF 21.193; **C**-**H**, *Petalosis clarus* n. gen. n. sp.; **C**, longitudinal section showing autozooecia and vesicles, holotype SMF 21.194; **D**, **E**, transverse section showing lunaria, paratype SMF 21.200; **F**, tangential section, holotype SMF 21.194; **G**, **H**, tangential section showing autozooecial apertures with styles (arrows), paratype SMF 21.200. Scale bars: A, F, 1 mm; B, C, G, 0.2 mm; D, 0.5 mm; E, 0.25 mm; H, 0.1 mm.

COMPARISON
Petalosis n. gen. differs from *Fistuliporella* Simpson, 1895 in having spine-like indentions in autozooecial apertures.

Petalosis clarus n. gen., n. sp.
(Figs 9C-H, 10A-C; Appendix)

ETYMOLOGY. — The species name refers to the distinct morphology of the species (derived from Latin "*clarus*" = clear, distinct).

HOLOTYPE. — SMF 21.194.

PARATYPES. — SMF 21.194-SMF 21.206.

TYPE LOCALITY. — Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

TYPE HORIZON. — Lebanza Formation, Lower Devonian (Pragian).

DIAGNOSIS. — As for genus.

DESCRIPTION
Encrusting colonies, secondary overgrowths common. Encrusting sheets 0.8 to 3.3 mm in thickness. Autozooecia growing from thick epitheca, bending sharply at their bases towards colony surface. Autozooecial apertures circular to oval. Basal diaphragms common to moderately abundant, closely spaced, thin, horizontal or inclined. Lunaria well developed, laminated, prominent, horseshoe shaped to triangular, often containing 2-3 styles. One or two pairs of spine-like indentions occurring in lateral parts of proximal ends of autozooecia. Vesicles large and high, irregularly shaped, polygonal in tangential section, box-like to hemispherical, with plane or concave roofs, 3-8 surrounding each autozooecial aperture. Bands of large and irregularly shaped vesicles present. Acanthostyles between autozooecial apertures common, 0.0.25-0.035 mm in diameter, having distinct hyaline cores and wide laminated sheaths. Autozooecial walls granular, 0.005-0.010 thick in endozones; thick, laminated in exozones. Maculae not observed.

Order TREPOSTOMATA Ulrich, 1882
Suborder HALLOPORINA Astrova, 1965
Family TREMATOPORIDAE Miller, 1889

Genus *Neotrematopora* Morozova, 1961

TYPE SPECIES. — *Neotrematopora typica* Morozova, 1961, by original designation. Middle Devonian, Givetian; Siberia, Russia.

OCCURRENCE. — Lower – Upper Devonian; Altai, Siberia, Kazakhstan, China. Lower Carboniferous; Altai and Siberia.

DIAGNOSIS. — Branched, less commonly encrusting colonies. Autozooecia with polygonal to rounded-polygonal apertures. Autozooecial diaphragms rare, restricted to exozones. Mesozooecia abundant, with abundant diaphragms, partly sealed by calcitic skeleton. Acanthostyles usually abundant. Autozooecial walls thin in endozone; laminated, regularly thickened in exozones displaying merged to serrated microstructure.

COMPARISON
Neotrematopora Morozova, 1961 differs from *Minussina* Morozova, 1961 in having partly merged autozooecial walls, which in *Minussina* are distinctly serrated with ridges on the colony surface at the zooecial boundaries.

Neotrematopora tenuis n. sp.
(Figs 10D-G; 11A; 22E, F; Appendix)

HOLOTYPE. — SMF 21.207.

PARATYPES. — SMF 21.208-SMF 21.211.

ETYMOLOGY. — The species name refers to the thin colony (derived from Latin "*tenuis*" = thin).

TYPE LOCALITY. — Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

TYPE HORIZON. — Lebanza Formation, Lower Devonian (Pragian).

DIAGNOSIS. — Encrusting colonies; autozooecial apertures rounded-polygonal; autozooecial diaphragms common to abundant; mesozooecia common, 2-5 surrounding each aperture; acanthostyles moderately large, common to abundant, 2-5 surrounding each aperture; exozonal walls distinctly laminated, often with secondary cingulum; maculae consisting larger autozooecia present.

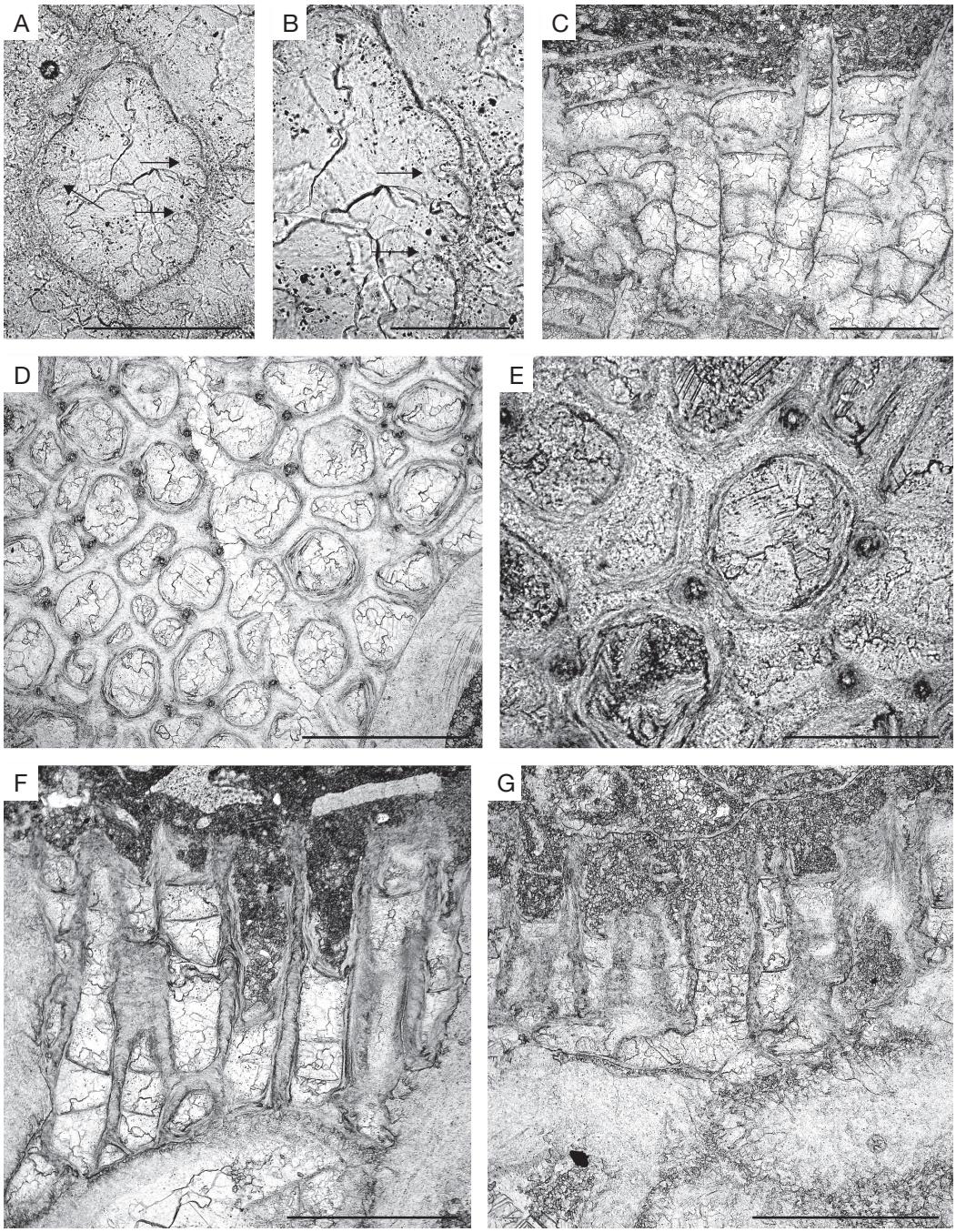

FIG. 10. — **A**-**C**, *Petalosis clarus* n. gen., n. sp.: **A**, **B**, autozooecial apertures with styles (arrows), paratype SMF 21.200; **C**, longitudinal section showing autozooecia with diaphragms and vesicles, holotype SMF 21.194; **D**-**G**, *Neotrematopora tenuis* n. sp.; **D**, **E**, tangential section showing autozooecial apertures and acanthostyles, holotype SMF 21.207; **F**, longitudinal section, holotype SMF 21.207; **G**, longitudinal section, paratype SMF 21.211. Scale bars: A, E, 0.2 mm; B, 0.1 mm; C, 1 mm; D, F, G, 0.5 mm.

DESCRIPTION
Encrusting colonies, 0.47-1.11 mm in thickness. Autozooecia budding from a thin epitheca, for a short interval oriented parallel to the substrate then bending sharply and intersecting the colony surface at right angles. Autozooecial apertures rounded-polygonal. Autozooecial diaphragms common to abundant, thick, straight or slightly deflected proximally. Mesozooecia common, 2-5 surrounding each aperture, polygonal in cross section, often beaded, irregular, containing planar diaphragms. Acanthostyles moderately large, abundant, 2-5 surrounding each aperture, originating in the distal part of exozone, sometimes indenting autozooecia, having distinct calcite cores and dark laminated sheaths. Walls in endozone granular, 0.010-0.015 mm thick; in exozone distinctly laminated; 0.03-0.08 mm thick. Cingulum often developed, 0.005-0.025 mm thick, laminated parallel to autozooecial wall surface. Maculae consisting of larger autozooecia, 0.78-0.93 mm in diameter.

COMPARISON
Neotrematopora tenuis n. sp. is similar to *N. petaloides* (Astrova, 1954) from the Lower Devonian (Lochkovian) of Ukraine. The new species differs in having encrusting colony, more abundant diaphragms and less abundant acanthostyles (2-5 around each aperture vs 4-7 in *N. petaloides*).

Family HETEROTRYPIDAE Ulrich, 1890

Genus *Leioclema* Ulrich, 1882

TYPE SPECIES. — *Callopora punctata* Hall, 1858, by subsequent designation (Ulrich 1882). Lower Carboniferous; Iowa (USA).

OCCURRENCE. — Lower Silurian to Upper Carboniferous; worldwide.

DIAGNOSIS. — Encrusting, branched, less commonly massive colonies. Autozooecia with polygonal to rounded-polygonal, sometimes petaloid apertures. Autozooecial diaphragms rare. Mesozooecia abundant, with abundant diaphragms, often beaded. Acanthostyles abundant, commonly large. Autozooecial walls thin in endozone; laminated, regularly thickened in exozones (modified from Astrova 1978).

COMPARISON
Leioclema Ulrich, 1882 differs from *Heterotrypa* Nicholson, 1879 in having rare autozooecial diaphragms and abundant acanthostyles and mesozooecia, and from *Stigmatella* Ulrich & Bassler, 1904 in having abundant mesozooecia.

Leioclema arauzensis n. sp.
(Fig. 11B-G; Appendix)

HOLOTYPE. — SMF 21.212.

PARATYPES. — SMF 21.213-SMF 21.220.

ETYMOLOGY. — The species name refers to Arauz Sur, the locality where the new species was found.

TYPE LOCALITY. — Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

TYPE HORIZON. — Lebanza Formation, Lower Devonian (Pragian).

OCCURRENCE. — Lebanza Formation, Lower Devonian (Pragian); Arauz Sur (Arroyo section), Palencia, NW-Spain (Cantabrian Mountains). Lower Devonian (Emsian); Altai Mountains, Russia. Lower Devonian (Pragian-Emsian); Mongolia.

DIAGNOSIS. — Encrusting colonies; autozooecial diaphragms few to absent; 2-5 mesozooecia surrounding each aperture; 2-6 moderately large acanthostyles surrounding each aperture.

DESCRIPTION
Encrusting colonies, 0.48-0.96 mm in thickness. Autozooecia budding from a thin epitheca, briefly oriented parallel to the substrate, then bending sharply and intersecting the colony surface at right angles. Autozooecial apertures rounded-polygonal to petaloid due to indenting acanthostyles. Autozooecial diaphragms few to absent, thin, straight or slightly deflected proximally. Mesozooecia abundant, 2-5 surrounding each aperture, polygonal in cross section, slightly beaded, containing planar diaphragms. Acanthostyles moderately large, abundant, 2-6 surrounding each aperture, originating from the base of exozone, often indenting autozooecia, having distinct calcite cores and dark laminated sheaths. Walls granular, in endozone 0.010-0.015 mm thick; in exozone 0.025-0.065 mm thick, distinctly laminated. Maculae not observed.

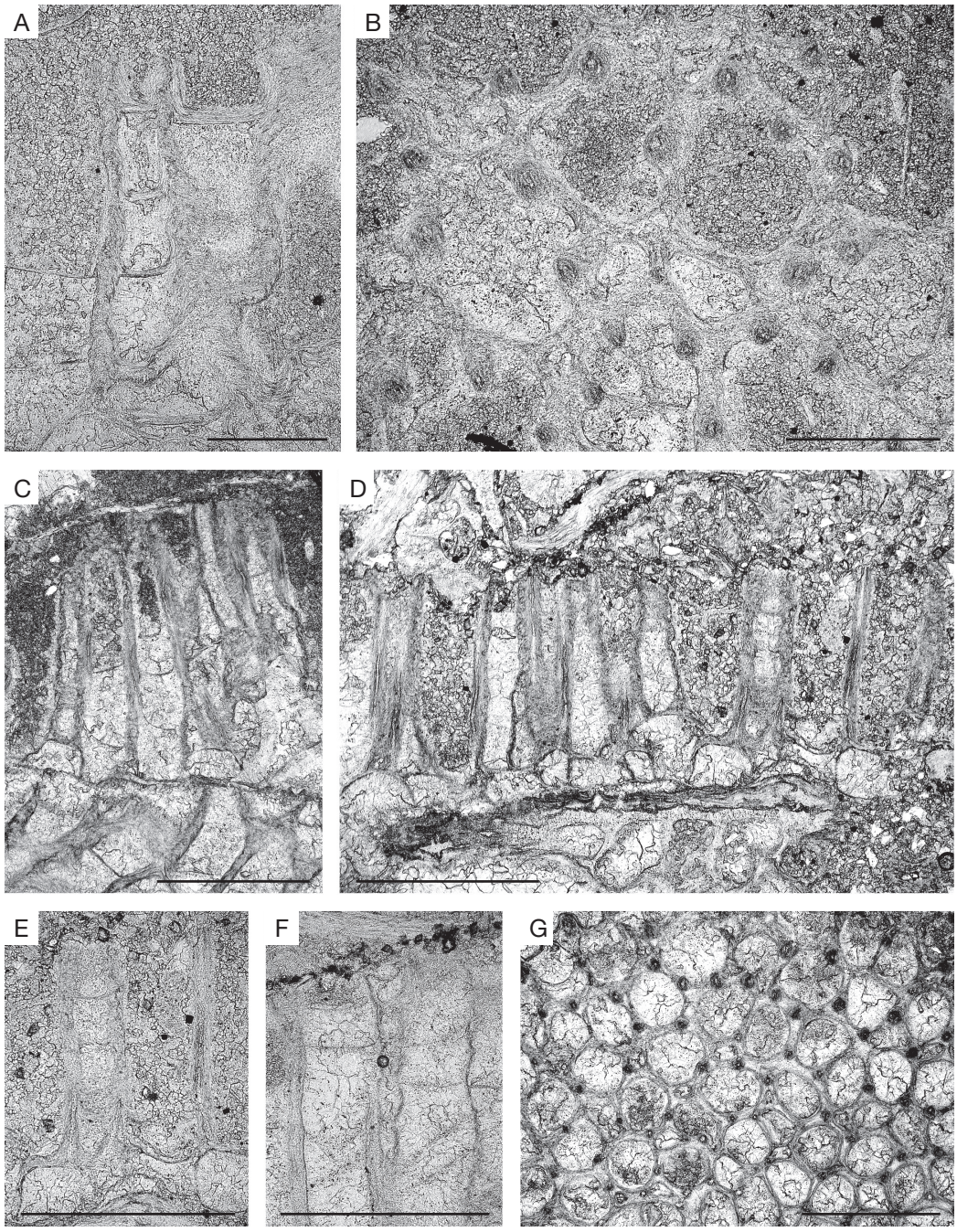

FIG. 11. — **A**, *Neotrematopora tenuis* n. sp., longitudinal section showing mesozooecium and zooecial walls, paratype SMF 21.211; **B**-**G**, *Leioclema arauzensis* n. sp.; **B**, tangential section showing autozooecial apertures, mesozooecia and abundant acanthostyles, holotype SMF 21.212; **C**, longitudinal section showing autozooecia and mesozooecia with diaphragms, holotype SMF 21.212; **D**, **E**, longitudinal section showing autozooecia with diaphragms and mesozooecia, paratype SMF 21.218; **F**, longitudinal section, paratype SMF 21.219; **G**, tangential section, paratype SMF 21.215. Scale bars: A, B, 0.2 mm; C-G, 0.5 mm.

COMPARISON
Leioclema arauzensis n. sp. is similar to *L. passitabulatum* Duncan, 1939 from the Lower-Middle Devonian of USA and Europe, but differs in having fewer mesozooecia (2-5 vs 4-10 mesozooecia around autozooecial aperture in *L. passitabulatum*).

Leioclema multiacanthoporum
(Astrova *in* Astrova & Yaroshinskaya, 1968)
(Fig. 12A-F; Appendix)

Lioclema multiacanthoporum Astrova *in* Astrova & Yaroshinskaya, 1968: 54, pl. 2, fig. 3. — Kopajevich 1984: 62, pl. 17, fig. 2.

MATERIAL. — SMF 21.221-SMF 21.226.

DESCRIPTION
Branched colonies, branches 1.8-3.1 mm in diameter, with 0.57-1.09 mm wide exozones and 0.66-0.92 mm wide endozones. Autozooecia budding from a thin epitheca, briefly oriented parallel to the substrate, then bending sharply and intersecting the colony surface at right angles. Autozooecial apertures rounded-polygonal to petaloid due to indenting acanthostyles. Autozooecial diaphragms rare to absent, thin, straight or slightly deflected proximally. Mesozooecia common, locally abundant, 2-5 surrounding each aperture, polygonal in cross section, slightly beaded, containing planar diaphragms. Acanthostyles moderately large, abundant, 4-9 surrounding each aperture, originating from the base of exozone, often indenting autozooecia, having distinct calcite cores and dark laminated sheaths. Walls granular, 0.010-0.015 mm thick in endozones; distinctly laminated, 0.025-0.065 mm thick in the exozone. Maculae not observed.

COMPARISON
Leioclema multiacanthoporum is similar to *L. elegans* Ernst, 2008 from the Lower Devonian of Prague Basin and NW-Spain (Ernst 2011), but differs from the latter in having more abundant acanthostyles (4-9 vs 3-6 in *L. elegans*) and smaller distances between aperture centres (0.20 mm vs 0.26 mm in *L. elegans* on average).

The Spanish material described here is more similar to the original description of Astrova (Astrova & Yaroshinskaya 1968) than Mongolian material which differs in having thicker stems (5-10 mm vs 2-3 mm in material from Altai and Spain). Consequently, the Mongolian representatives of this species have a larger number of mesozooecia (4-9 vs 4-7 and 2-5 in Altai and Spanish material respectively).

Suborder AMPLEXOPORINA Astrova, 1965
Family ERIDOTRYPELLIDAE Morozova, 1960

Genus *Eridotrypella* Duncan, 1939

TYPE SPECIES. — *Batostomella obliqua* Ulrich, 1890, by subsequent designation (Duncan 1939). Middle Devonian; Michigan (USA).

OCCURRENCE. — Silurian-?Carboniferous; worldwide.

DIAGNOSIS. — Branched colonies. Autozooecial apertures irregularly polygonal. Autozooecial walls laminated, without distinct zooecial boundaries, irregularly thickened, containing spherules. Diaphragms complete, varying in number. Exilazooecia rare. Acanthostyles varying in size and number.

COMPARISON
Eridotrypella Duncan, 1939 differs from *Eostenopora* Duncan, 1939 in colony form (ramose branched vs encrusting or massive colonies).

Eridotrypella validaeformis n. sp.
(Figs 12G-I; 13A-C; Appendix)

HOLOTYPE. — SMF 21.227.

PARATYPES. — SMF 21.228-SMF 21.237.

ETYMOLOGY. — The species name refers to the similarity with the species *Eridotrypella valida* Duncan, 1939.
Type locality. — Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

TYPE HORIZON. — Lebanza Formation, Lower Devonian (Pragian).

DIAGNOSIS. — Ramose branched colonies with narrow, distinctly separated exozones; autozooecial diaphragms rare; exilazooecia rare; acanthostyles rare to common, up to 3 surrounding autozooecial apertures; maculae with slightly larger autozooecia.

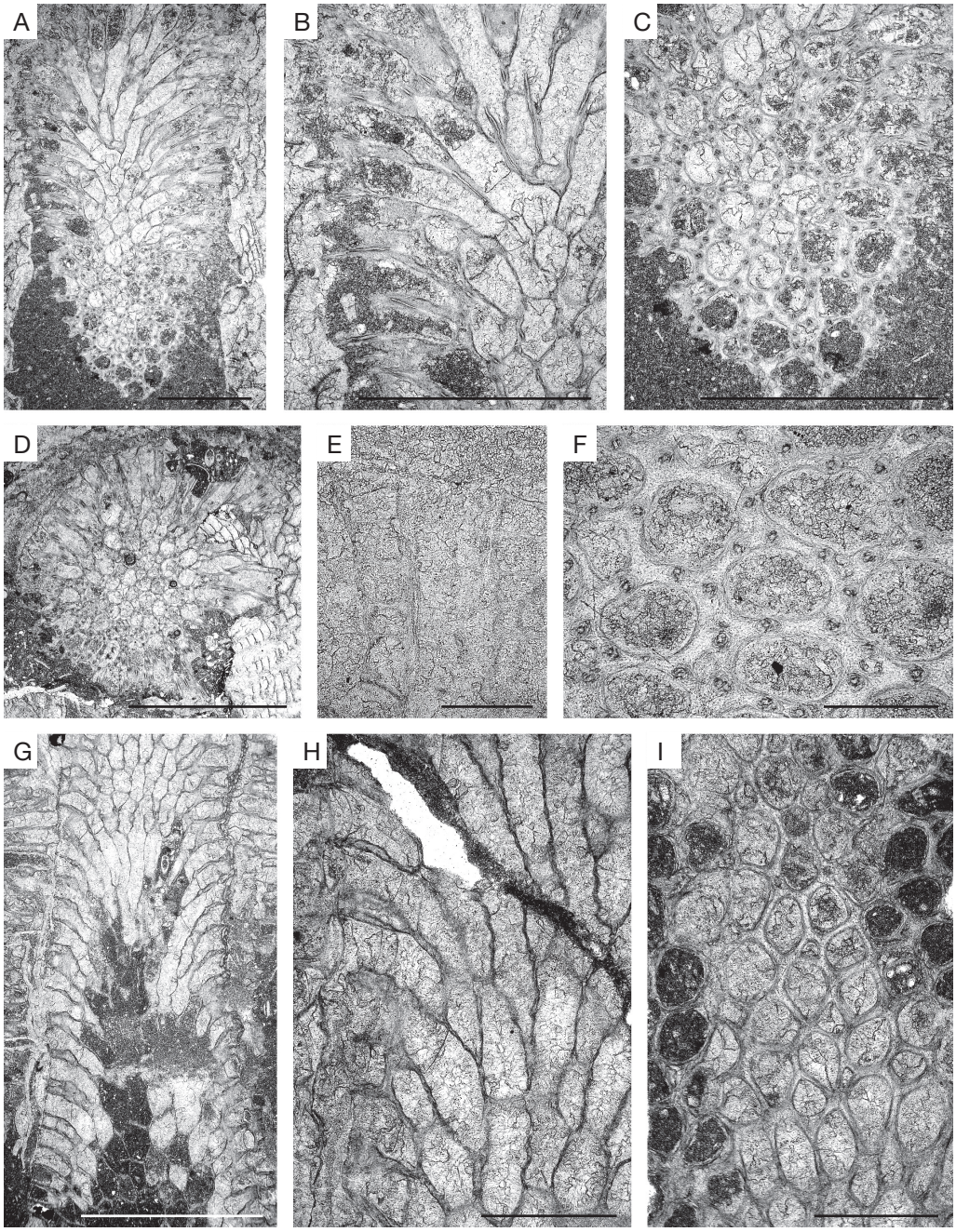

FIG. 12. — **A**-**F**, *Leioclema multiacanthoporum* (Astrova *in* Astrova & Yaroshinskaya, 1968): **A**-**C**, branch oblique section showing autozooecia, mesozooecia and acanthostyles, SMF 21.225; **D**, branch transverse section, SMF 21.221; **E**, longitudinal section showing autozooecia and mesozooecia, SMF 21.222; **F**, tangential section showing autozooecial apertures, mesozooecia and acanthostyles, SMF 21.226; **G**-**I**, *Eridotrypella validaeformis* n. sp.: **G**, branch oblique section, paratype SMF 21.385; **H**, longitudinal section showing autozooecia with diaphragms, holotype SMF 21.227; **I**, tangential section showing autozooecial apertures and rare exilazooecia, holotype SMF 21.227. Scale bars: A-C, I, 1 mm; D, G, 2 mm; E, F, 0.2 mm; H, 0.5 mm.

DESCRIPTION
Ramose branched colonies, branches 1.72-2.99 mm in diameter. Exozones 0.36-0.72 mm wide, endozones 0.88-1.94 mm wide. Exozones distinctly separated from endozones. Secondary overgrowths occurring. Autozooecia polygonal in transverse section, long in endozones, bending sharply in exozones and intersecting colony surface at angles of 77-83°. Autozooecial apertures polygonal with rounded corners. Autozooecial diaphragms rare to common, straight, thin, occurring mainly in the distal parts of autozooecia. Exilazooecia rare, short, rounded-polygonal in cross section. Acanthostyles rare to common, up to 3 surrounding autozooecial apertures, moderately large, having distinct narrow cores and laminated sheaths. Autozooecial walls in endozones granular, locally crenulated, 0.005-0.010 mm thick; in exozones finely laminated, irregularly thickened, merged, containing spherules, 0.03-0.06 mm thick. Laminated cingulum locally developed, 0.005-0.010 mm thick. Maculae consisting of slightly larger autozooecia.

COMPARISON
Eridotrypella validaeformis n. sp. differs from *E. validа* Duncan, 1939 from the Middle Devonian of Michigan, in having thinner branches and smaller autozooecia (autozooecial aperture widths 0.12-0.17 mm vs 0.21-0.25 mm in *E. valida*). *Eridotrypella validaeformis* n. sp. differs from *E. minuta* Morozova, 1961 from the Upper Devonian of Kuznetzk Basin, in having fewer acanthostyles and in the presence of maculae.

Family ATACTOTOECHIDAE Duncan, 1939

Genus *Leptotrypella* Vinassa de Regny, 1921

TYPE SPECIES. — *Chaetetes barrandei* Nicholson, 1874, by subsequent designation (Vinassa de Regny 1921). Middle Devonian; Ontario (Canada).

OCCURRENCE. — Middle Silurian to Lower Carboniferous; worldwide.

DIAGNOSIS. — Branched colonies. Autozooecia with polygonal to rounded-polygonal apertures. Autozooecial diaphragms lacking in endozones; rare to common in exozones. Exilazooecia rare. Acanthostyles long, common to abundant. Autozooecial walls granular, thin in endozones; laminated, irregularly thickened in exozones (modified after Astrova 1978).

COMPARISON
Leptotrypella Vinassa de Regny, 1921 differs from *Leptotrypa* Ulrich, 1883 in having branched colonies, and from *Anomalotoechus* Duncan, 1939 in having branched colonies and lacking diaphragms in endozones.

Leptotrypella armata n. sp.
(Figs 13D, E; 14A-F; Appendix)

ETYMOLOGY. — The species name refers to the abundant and massive acanthostyles (derived from Latin "*armata*" = armoured)

HOLOTYPE. — SMF 21.238.

PARATYPES. — SMF 21.239-SMF 21.253, SMF 21.385.

TYPE LOCALITY. — Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

TYPE HORIZON. — Lebanza Formation, Lower Devonian (Pragian).

DIAGNOSIS. — Branched colonies with distinct endozones and exozones; autozooecial diaphragms absent in endozones, common to abundant, thin and straight in exozones; exilazooecia locally common; acanthostyles moderately large, abundant, 5-12 surrounding each autozooecial aperture; mural spines abundant; maculae not observed.

DESCRIPTION
Branched colonies. Branches 0.81-1.35 mm in diameter. Exozones 0.24-0.48 mm wide, endozones 0.27-0.71 mm wide. Autozooecia long, having a polygonal shape in transverse section in endozones, bending sharply in exozones and intersecting colony surface at angles of 88-90°. Autozooecial apertures oval to slightly polygonal. Autozooecial diaphragms absent in endozones; common to abundant, thin, straight in exozones. Exilazooecia locally common, short, restricted to exozones, rounded to oval in cross section. Acanthostyles moderately large, varying in size, abundant, 5-12 surrounding each autozooecial aperture, growing from the base of the exozone, hav-

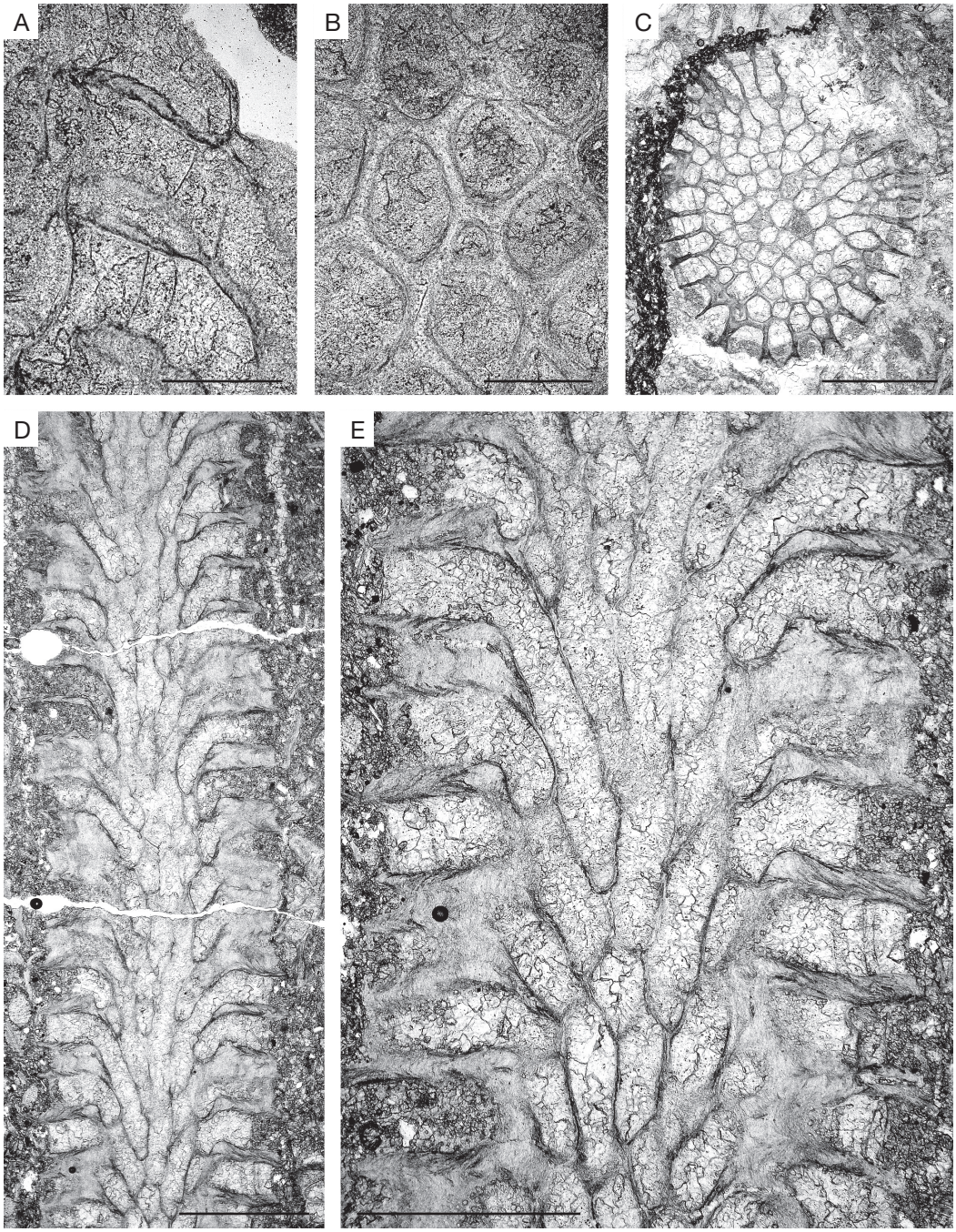

FIG. 13. — **A**-**C**, *Eridotrypella validaeformis* n. sp.: **A**, longitudinal section showing autozooecia with diaphragms and wall microstructure, holotype SMF 21.227; **B**, tangential section autozooecial apertures and an exilazooecium, holotype SMF 21.227; **C**, branch transverse section showing narrow exozone, paratype SMF 21.230; **D**, **E**, *Leptotrypella armata* n. sp., longitudinal section showing autozooecia with diaphragms, holotype SMF 21.238. Scale bars: A, B, 0.2 mm; C, D, 1 mm; E, 0.5 mm.

ing distinct cores and laminated sheaths. Autozooecial walls in endozones granular, 0.010-0.015 mm thick; in exozones laminated, merged, without distinct zooecial boundaries, 0.035-0.070 mm thick. Mural spines abundant, 0.015-0.020 mm in diameter. Maculae not observed.

COMPARISON

Leptotrypella armata n. sp. differs from *L. elliptica* Kopajevich, 1984 from the Middle-Upper Devonian of Mongolia, in having thinner branches (branch width 0.81-1.35 mm vs 2.0-2.2 mm in *L. elliptica*), and smaller apertures (aperture width 0.05-0.10 mm vs 0.07-0.13 mm in *L. elliptica*).

Order CRYPTOSTOMATA Vine, 1884
Suborder RHABDOMESINA Astrova & Morozova, 1956
Family RHABDOMESIDAE Vine, 1884

Genus *Orthopora* Hall, 1886

TYPE SPECIES. — *Trematopora regularis* Hall, 1874, by subsequent designation (Hall 1886). Lower Devonian; USA.

OCCURRENCE. — Silurian to Carboniferous of North America, Europe and China, Middle Permian of Oman.

DIAGNOSIS. — Branched colonies. Autozooecia short, budding from more or less distinct medial axis in spiral order. Autozooecial diaphragms rare to absent. Both superior and inferior hemisepta commonly present; sometimes double hemisepta occurring; rarely hemisepta absent. Autozooecial apertures oval, arranged regularly in alternating rows on the colony surface. Walls granular in the endozone; laminated in exozone. Paurostyles abundant, prominent. Acanthostyles present, less abundant than paurostyles. Heterozooecia absent.

COMPARISON

Orthopora Hall, 1886 differs from *Trematella* Hall, 1886 in lacking metazooecia and in the presence of well developed hemisepta.

Orthopora spinosa n. sp.
(Figs 14G-I; 15A-C; Appendix)

HOLOTYPE. — SMF 21.254.

PARATYPES. — SMF 21.255-SMF 21.293.

ETYMOLOGY. — The species name refers to the presence of abundant acanthostyles (derived from Latin "*spinosus*" – spiny).

TYPE LOCALITY. — Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

TYPE HORIZON. — Lebanza Formation, Lower Devonian (Pragian).

DIAGNOSIS. — Branched colonies; bifurcations common; both superior and inferior hemisepta well developed; paurostyles absent; acanthostyles abundant, arranged in single row between autozooecia, varying in size.

DESCRIPTION

Branches 0.48-0.75 mm in diameter, with 0.19-0.35 mm wide endozones and 0.14-0.22 mm wide exozones. Branch bifurcations common. Transverse sections of branches circular. Autozooecia short, growing in spiral pattern from the distinct median axis at angles of 35-51° in endozones, abruptly bending in exozones and intersecting colony surface at angles of 51-71°; having polygonal, tear-drop shape in transverse sections of endozone. Autozooecial diaphragms rare to absent. Long superior hemisepta present, curved proximally; inferior hemisepta long, positioned beneath superior hemisepta, curved distally. Autozooecial apertures oval, arranged regularly in alternating rows on the colony surface. Walls in the endozone granular, 0.005-0.010 mm thick; in exozone laminated. Acanthostyles abundant, arranged in longitudinal rows between apertures, slightly varying in size, having narrow hyaline cores and wide laminated sheaths. Heterozooecia absent.

COMPARISON

Orthopora spinosa n. sp. is similar to *O. sincera* Ernst, 2011 from the Lower to Middle Devonian of NW Spain but differs in having thinner branches (average branch width 0.62 mm vs 0.74 mm in *O. sincera*), and in the smaller and more widely spaced apertures (average aperture spacing along branch 0.28 mm vs 0.36 mm in *O. sincera*). *Orthopora spinosa* n. sp. differs from *O. tenuis* Ernst, 2008 in having smaller autozooecial apertures (average aperture width 0.050 mm vs 0.076 mm in *O. tenuis*).

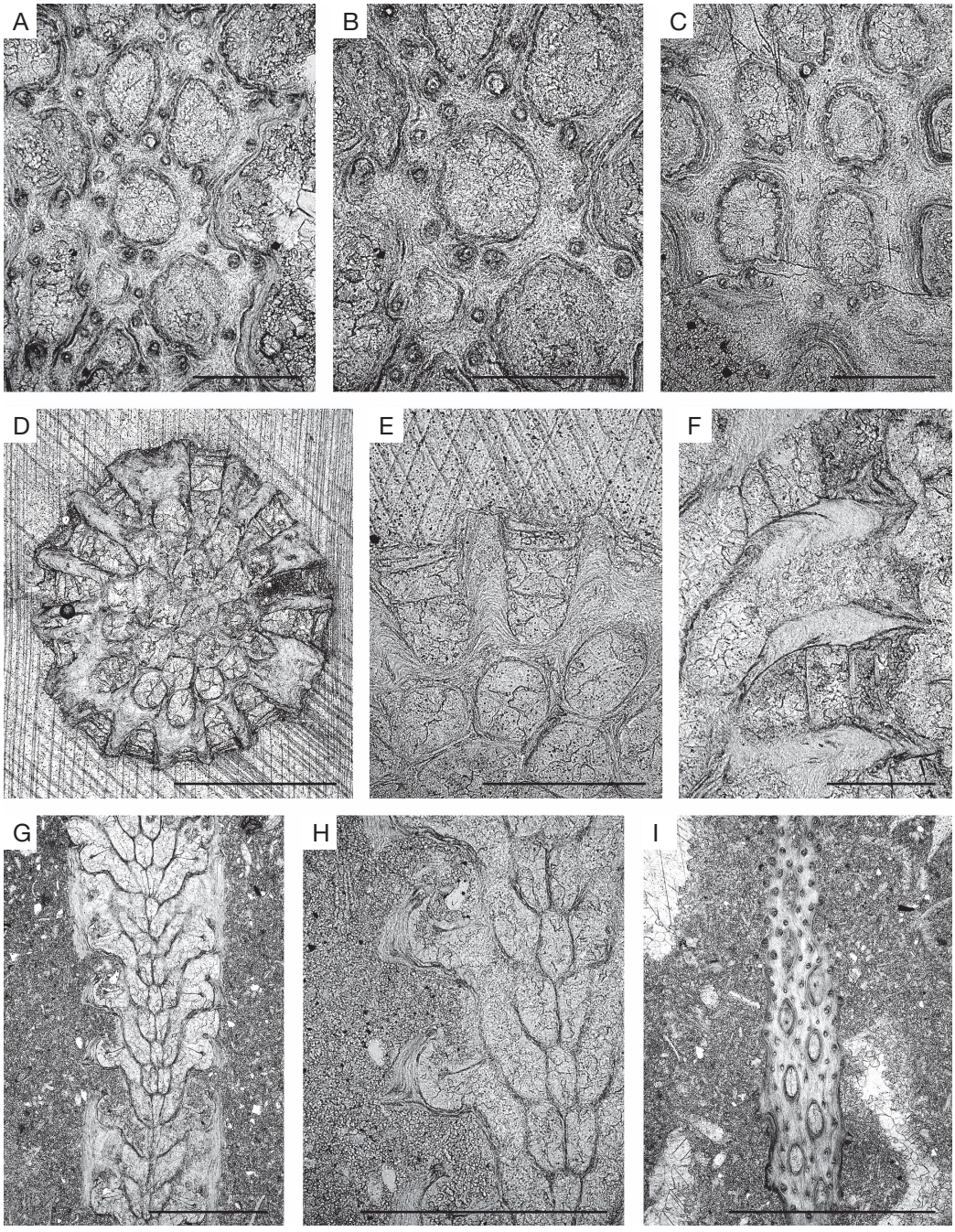

FIG. 14. — **A**-**F**, *Leptotrypella armata* n. sp.: **A**, **B**, tangential section showing autozooecial apertures and acanthostyles, holotype SMF 21.238; **C**, tangential section showing autozooecial walls with abundant mural spines, paratype SMF 21.239; **D**, **E**, transverse section showing autozooecia with abundant diaphragms and autozooecial wall with mural spines, paratype SMF 21.239; **F**, longitudinal section, paratype SMF 21.252; **G**-**I**, *Orthopora spinosa* n. sp.; **G**, **H**, longitudinal section showing autozooecia with hemisepta, holotype SMF 21.254; **I**, tangential section showing autozooecial apertures and acanthostyles, holotype SMF 21.254. Scale bars: A-C, E, F, 0.2 mm; D, G, H, 0.5 mm; I, 1 mm.

Genus *Vidronovella* Gorjunova, 2006

TYPE SPECIES. — *Vidronovella fastigiata* Gorjunova, 2006, by original designation. Late Devonian (Famennian); Afghanistan.

OCCURRENCE. — Lower Devonian of Spain, Middle Devonian of Western Sahara and Germany, Upper Devonian of Afghanistan.

DIAGNOSIS. — Colonies branched. Autozooecia tubular, short, budding from indistinct medial axis or short mesotheca in spiral order around the branch, oriented at high angles to the branch axis. Autozooecial diaphragms absent. Proximal part of autozooecia thickened in the outermost exozone ("fastigia" sensu Gorjunova 2006). Both superior and inferior hemisepta present, located in the distal part of autozooecia. Superior hemiseptum moderately long, hook-shaped, curved distally, positioned at the base of the thicken exozone ("fastigium" sensu Gorjunova 2006); inferior hemiseptum long, slender, occupying two-thirds of body cavity of autozooecia, positioned beneath superior hemisepta, curved distally. Secondary blunt hemisepta may occur, one proximally to the superior hemiseptum, and another one distally to the inferior hemiseptum. Autozooecial apertures oval to rounded-rhombic, arranged regularly in alternating rows on the colony surface. Acanthostyles large and blunt, with narrow hyaline cores and wide laminated sheaths, embedded in the skeleton. Single or two acanthostyles positioned between two longitudinally successive autozooecial apertures. Paurostyles occur in one species, irregularly distributed between acanthostyles. Heterozooecia absent. Walls granular in the endozone; laminated in exozone, becoming structureless near the colony surface. Mural spines may occur.

COMPARISON

The genus *Vidronovella* Gorjunova, 2006 is placed here in the family Rhabdomesidae Vine, 1884 because of the autozooecial shape as well as the presence of hemisepta and acanthostyles. *Vidronovella* is similar to *Orthopora* Hall, 1886, but differs from in the short autozooecia and the high budding angle of the autozooecia in the axial area.

Vidronovella elegantula n. sp.
(Figs 15D-I; 16A, B; Appendix)

ETYMOLOGY. — The species name "*elegantula*" refers to the small size and general delicate appearance of the new species (derived from Latin "elegans" = elegant).

HOLOTYPE. — SMF 21.294.

PARATYPES. — SMF 21.295-SMF 21.412.

TYPE LOCALITY. — Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

TYPE HORIZON. — Lebanza Formation, Lower Devonian (Pragian).

DIAGNOSIS. — Branched colonies; bifurcation common; single superior and single inferior hemisepta well developed; paurostyles absent; 4-6 acanthostyles surrounding each autozooecial aperture; heterozooecia absent; mural spines absent.

DESCRIPTION

Branches 0.59-0.96 mm in diameter, with 0.23-0.49 mm wide endozones and 0.16-0.26 mm wide exozones. Branch bifurcation common. Transverse sections of branches circular. Autozooecia short, budding from distinct medial axis in spiral order at angles of 45-60°. Autozooecial diaphragms absent. Superior hemiseptum moderately long, hook-shaped, curved proximally; inferior hemiseptum long, slender, occupying two-thirds of body cavity of autozooecia, positioned beneath superior hemisepta, inclined distally, widened laterally. Autozooecial apertures oval, arranged regularly in alternating rows on the colony surface. Walls in the endozone granular, 0.005-0.010 mm thick; laminated in exozone. Acanthostyles having distinct hyaline cores and wide laminated sheaths, regularly sized, single or two positioned between two longitudinally successive autozooecial apertures, 4-6 surrounding each aperture. Acanthostyles often sealed by a thick layer of laminated skeleton on the colony surface. Mural spines absent.

COMPARISON

Vidronovella elegantula n. sp. differs from *V. fastigiata* Gorjunova, 2006 in having of 4-6 instead of 4 acanthostyles surrounding each autozooecial aperture, and from *V. intricata* Ernst, 2011 in the absence of mural spines and in the presence of single hemisepta instead of the double hemisepta found in *V. intricata*.

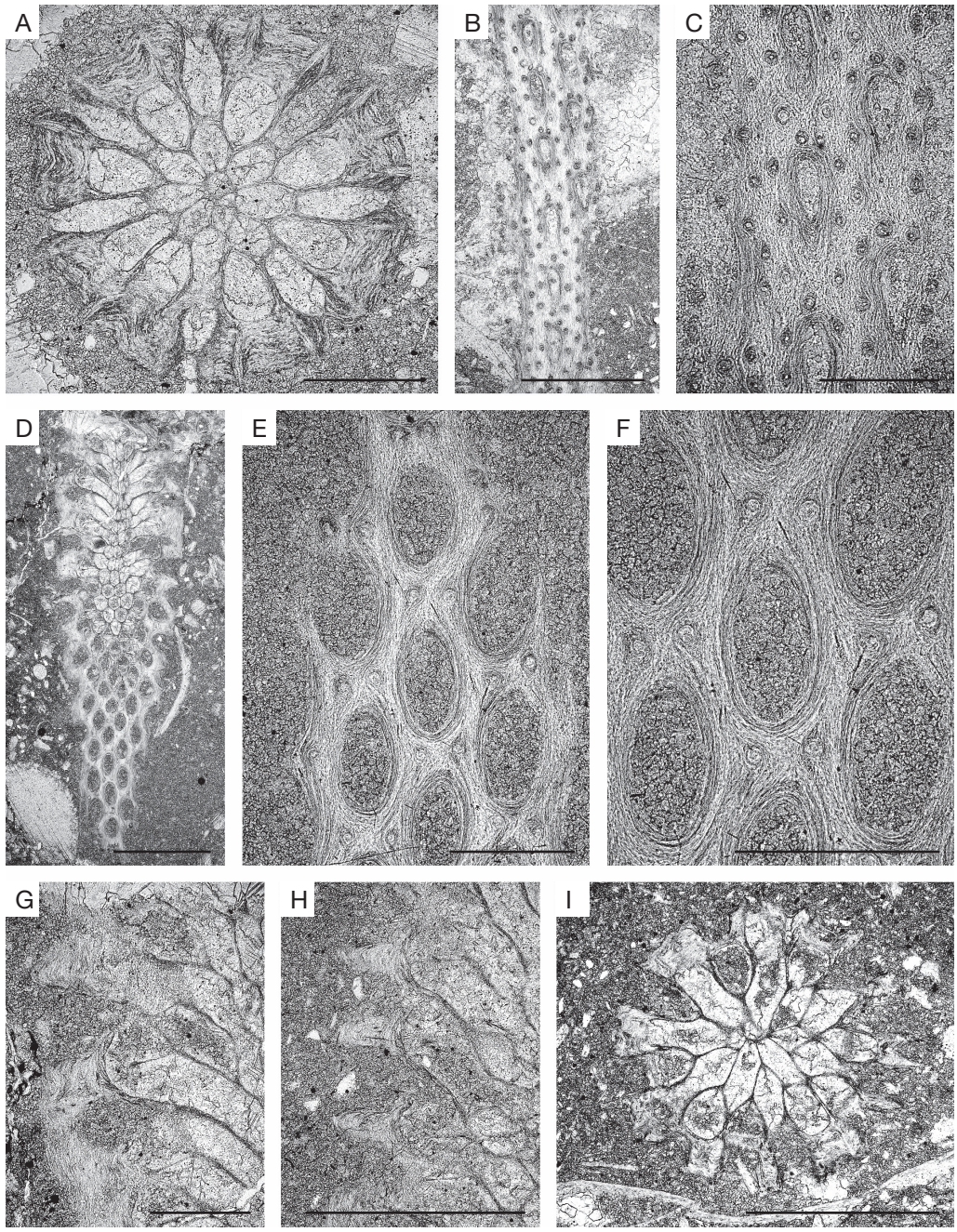

FIG. 15. — **A**-**C**, *Orthopora spinosa* n. sp.; **A**, branch transverse section showing autozooecia growing from distinct median axis, paratype SMF 21.258; **B**, **C**, tangential section showing apertures and acanthostyles, paratype SMF 21.268; **D**-**I**, *Vidronovella elegantula* n. sp.: **D**, branch oblique section, holotype SMF 21.294; **E**, **F**, tangential section showing autozooecial apertures and distribution of acanthostyles, holotype SMF 21.294; **G**, **H**, longitudinal section showing autozooecia with hemisepta, holotype SMF 21.294; **I**, branch transverse section showing autozooecia growing from distinct median axis, paratype SMF 21.312. Scale bars: A, C, E-G, 0.2 mm; B, H, I, 0.5 mm.

? Family RHOMBOPORIDAE Simpson, 1895

Rhomboporidae sp. indet.
(Figs 16C-I; Appendix)

MATERIAL. — SMF 21.313-SMF 21.314.

DESCRIPTION
Branches 0.78-0.81 mm in diameter, with 0.23-0.26 mm wide endozones and 0.25-0.30 mm wide exozones. Branch bifurcation not observed. Autozooecia short, growing in spiral pattern from the distinct median axis. Autozooecial diaphragms locally present, thin, curved. Hemisepta absent. Autozooecial apertures oval, arranged regularly in alternating rows on the colony surface. Walls in the endozone granular, 0.015-0.020 mm thick; laminated in exozone. Acanthostyles absent. Paurostyles abundant, scattered between apertures. Aktinotostyles irregularly distributed. Metazooecia present, usually one between two longitudinally successive autozooecial apertures.

COMPARISON
This species shows similarities to the family Rhomboporidae Simpson, 1895 in the presence of aktinotostyles and paurostyles and in autozooecial shape. However, metazooecia are rare in all genera of Rhomboporidae. The present material differs from *Rhombopora* Meek, 1872 in lacking acanthostyles and in the regular presence of metazooecia, and from *Saffordotaxis* in the presence of metazooecia and paurostyles (aktinotostyles are the only styles present in *Saffordotaxis*).

Order FENESTRATA Astrova & Morozova, 1956
Suborder FENESTELLINA
Astrova & Morozova, 1956
Family FENESTELLIDAE King, 1849

Genus *Rectifenestella* Morozova, 1974

TYPE SPECIES. — *Fenestella medvedkensis* Schulga-Nesterenko, 1951, by subsequent designation (Morozova 1974). Upper Carboniferous, Kasimovian-Stage; Russian Platform.

OCCURRENCE. — Lower Devonian-Upper Permian.

DIAGNOSIS. — Reticulate colonies consisting of fine to intermediately robust branches and straight dissepiments. Autozooecia triangular to pentagonal in mid tangential section. Superior hemisepta present; inferior hemisepta absent. Narrow keel with one row of intermediate nodes.

COMPARISON
Rectifenestella differs from *Laxifenestella* Morozova, 1974 in the pentagonal shape of the autozooecia in mid tangential section and the absence of inferior hemisepta. *Rectifenestella* differs from *Minilya* Crockford, 1944 in the single row of nodes on the keel whereas *Minilya* has two alternating rows of small nodes on the wide keel.

Rectifenestella exiliformis n. sp.
(Figs 17A-I; 18A-C; Appendix)

HOLOTYPE. — SMF 21.314.

PARATYPES. — SMF 21.315-SMF 21.332.

ETYMOLOGY. — The species name refers to the similarity with the species *R. exilis* (Počta, 1894) from the Lower Devonian (Pragian) of Czech Republic.

TYPE LOCALITY. — Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

TYPE HORIZON. — Lebanza Formation, Lower Devonian (Pragian).

DIAGNOSIS. — Reticulate colonies with straight branches joined by moderately wide dissepiments; autozooecia pentagonal in mid tangential section, arranged in 2 alternating rows on branches, with an additional row shortly before bifurcations, 4-7 spaced per length of a fenestrule; axial wall zigzag; peristomes containing 10-15 variously sized nodes, with 3-6 larger than the others; fenestrules oval to rectangular; keels wide, low, with widely spaced, stellate nodes; microacanthostyles abundant; large styles present on the reverse colony surface.

DESCRIPTION
Reticulate colonies with straight branches, bifurcating, joined by dissepiments. Autozooecia arranged in 2 alternating rows on branches, with additional row shortly before bifurcation, having circular apertures with moderately high peristomes,

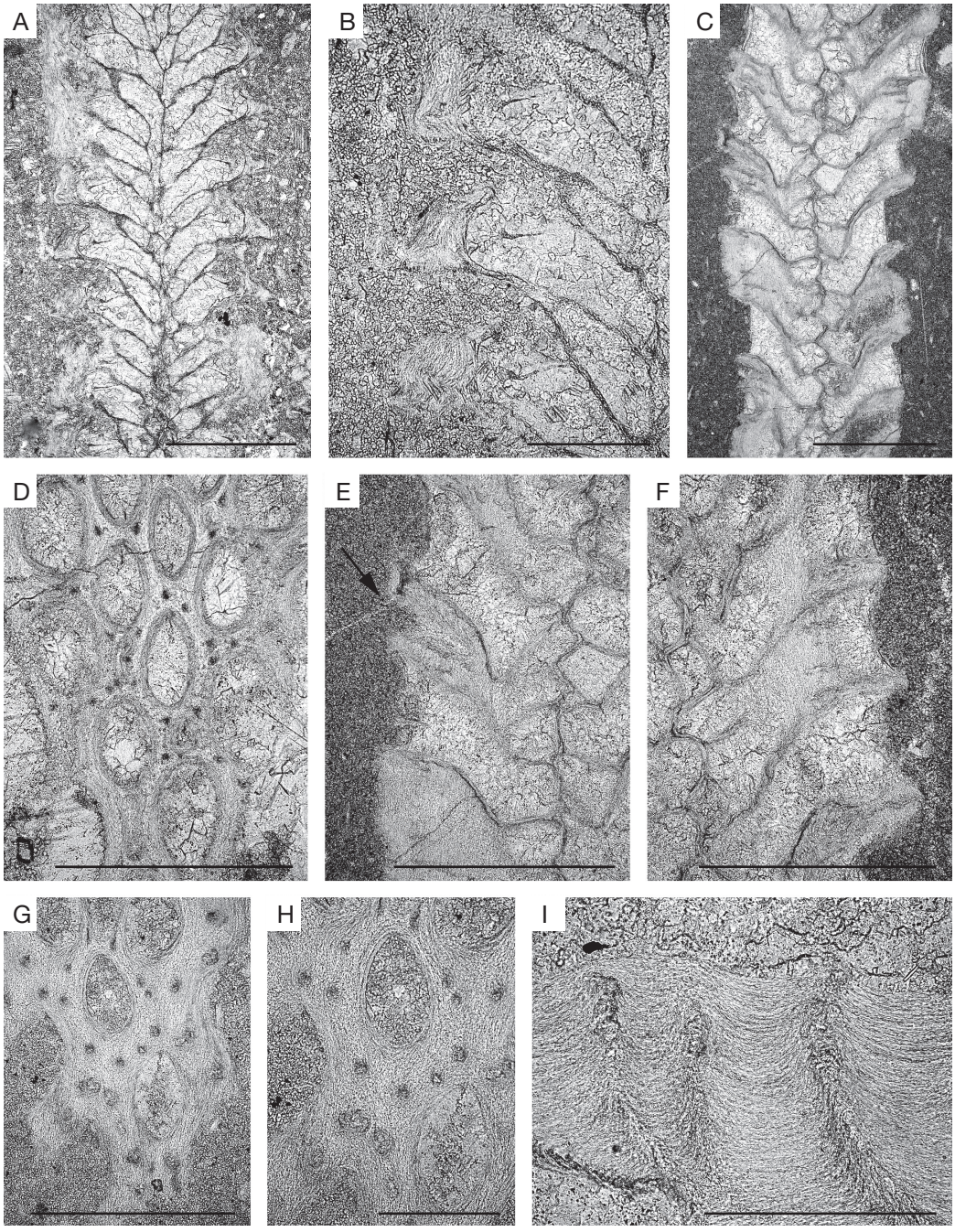

FIG. 16. — **A**, **B**, *Vidronovella elegantula* n. sp., longitudinal section showing autozooecia with long hemisepta, paratype SMF 21.296. **C**-**I**, Rhabdomesid sp. indet.; **C**, longitudinal section showing autozooecia, SMF 21.314; **D**, tangential section showing autozooecial apertures and paurostyles, SMF 21.314; **E**, **F**, longitudinal section showing autozooecia and a metazooecium (arrow), SMF 21.314; **G**, **H**, tangential section showing autozooecial apertures, aktinotostyles and paurostyles, SMF 21.313; **I**, longitudinal section showing aktinotostyles, SMF 21.313. Scale bars: A, B, I, H, 0.2 mm; C-F, G, 0.5 mm.

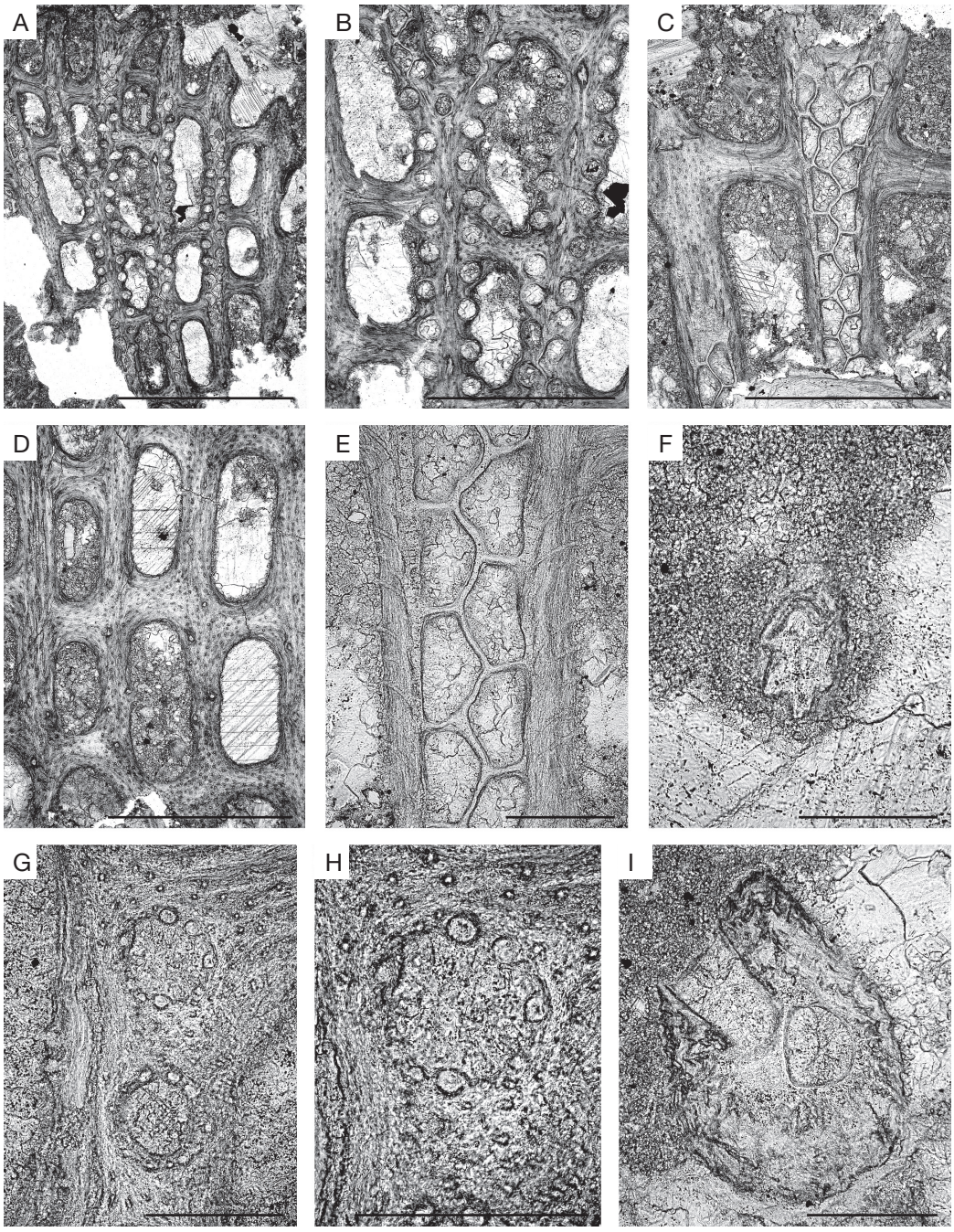

Fig. 17. — *Rectifenestella exiliformis* n. sp.: **A**, **B**, tangential section showing obverse branch surface with autozooecial apertures and nodes, holotype SMF 21.314; **C**, mid tangential section showing autozooecial chambers, paratype SMF 21.323; **D**, tangential section of reverse side showing styles, holotype SMF 21.314; **E**, mid tangential section showing autozooecial chambers, paratype SMF 21.323; **F**, tangential section of obverse side showing stellate nodes, holotype SMF 21.314; **G**, **H**, tangential section showing autozooecial apertures, paratype SMF 21.326; **I**, branch transverse section, paratype SMF 21.327. Scale bars: A, 2 mm; B-D, 1 mm; E-H, I, 0.2 mm.

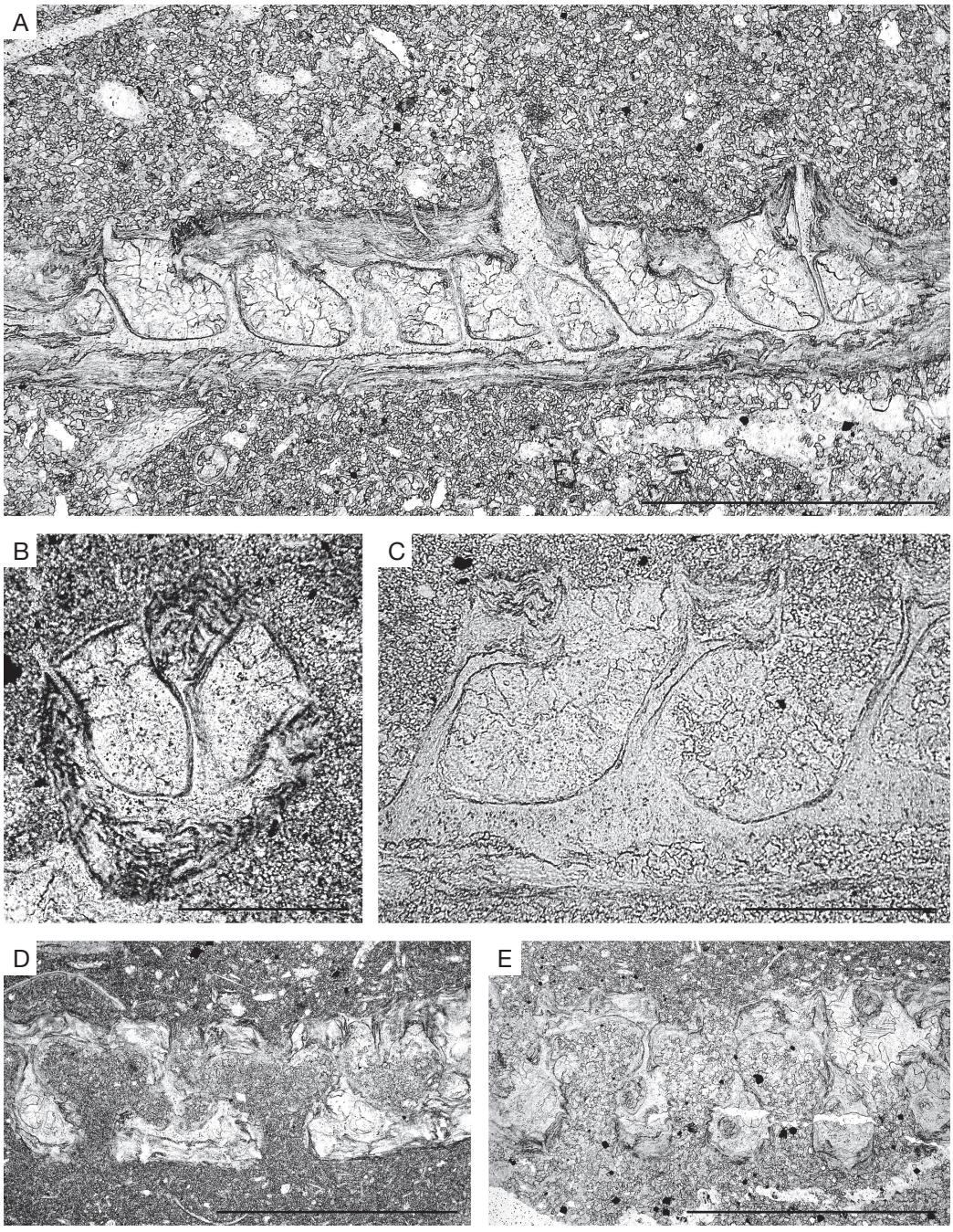

FIG. 18. — **A**-**C**, *Rectifenestella exiliformis* n. sp.; **A**, longitudinal section showing autozooecia and massive nodes, paratype SMF 21.331; **B**, branch transverse section showing autozooecia, paratype SMF 21.327; **C**, longitudinal section showing autozooecial chambers, internal granular and outer laminated skeleton, paratype SMF 21.319; **D**, **E**, *Hemitrypa lasutkiniae* Waschurova, 1964; **D**, branch transverse section showing branches and superstructure, SMF 21.353; **E**, branch transverse section, SMF 21.352. Scale bars: A, 0.5 mm; B, C, 0.2 mm; D, E, 1 mm.

4-7 spaced per length of a fenestrule. Peristomes containing 10-15 variously sized nodes, of which 3-6 are significantly larger than the others. Smaller nodes 0.010-0.015 mm in diameter, larger nodes 0.020-0.030 mm in diameter. Fenestrules oval to rectangular. Median keel wide, low. Keel nodes widely spaced, granular core stellate in shape. Microacanthostyles on the colony surface abundant, regularly spaced in longitudinal rows, 0.01-0.02 mm in diameter. Large styles irregularly spaced on the reverse colony surface, 0.03-0.06 mm in diameter.

Interior description

Autozooecia pentagonal in mid tangential section; with well-developed long vestibule; axial wall zigzag; aperture positioned at distal end of chamber. Autozooecial chambers diverging laterally at angles of 42-70°. Superior hemisepta indistinct; inferior hemisepta absent. Internal granular skeleton continuous with obverse keel, nodes, peristome and across dissepiments, 0.020-0.045 mm thick on the branch reverse wall. Outer lamellar skeleton well developed, 0.015-0.060 mm thick on the branch reverse wall. Terminal diaphragms common.

COMPARISON

Rectifenestella exiliformis n. sp. is similar to *R. exilis* (Počta, 1894) from the Lower Devonian (Pragian) of Czech Republic, but differs in having thicker branches (average branch width 0.31 mm vs 0.21 mm in *R. exilis*), more closely spaced autozooecial apertures (average distance between aperture centres 0.18 mm vs 0.23 mm in *R. exilis*), and more widely spaced branches and dissepiments. Furthermore, *R. exilis* (Počta, 1894) has a row of small nodes on the keel instead of the large stellate nodes seen in *R. exiliformis*. *Fenestella* aff. *parallela* Hall, 1881 described by Ernst *et al.* (2011: 318-320, figs 8e-g, 9a-d) has a similar peristome morphology with variously sized nodes and stellate nodes on the median keel. However, this species has rectangular shaped autozooecia in mid tangential section and a smaller number of autozooecia per fenestrule (2-4 in *Fenestella* aff. *parallela* vs 4-7 in *R. exiliformis*). *Fenestella* (*Rectifenestella*) *asterogrumosa* Waschurova, 1964 from the Lower Devonian (?Emsian) of Tajikistan has a similar peristome morphology, stellate nodes on the keel and pentagonal shaped autozooecia in mid tangential section. However, this species lacks styles on the reverse surface and has 2-3 autozooecia per fenestrule length instead of 4-7 in *R. exiliformis*. Waschurova (1964: 80) mentioned 7-20 apertural nodes 0.005-0.015 mm in diameter, without stressing variation in size. Figure 1 on Waschurova's plate 27 shows some significantly larger nodes in the aperture, however.

The present material is placed in *Rectifenestella* Morozova, 1974 because of the autozooecial chamber shape and character of the meshwork. However, the morphology of the peristome with variously sized nodes is quite unusual for *Rectifenestella*, which usually has stellate structures consisting of 8 rays in the apertures.

Genus *Hemitrypa* Phillips, 1841

TYPE SPECIES. — *Hemitrypa oculata* Phillips, 1841, by original designation. Devonian; Barton, South Devon, England.

OCCURRENCE. — Lower Devonian to Middle Permian; worldwide.

DIAGNOSIS. — Reticulate colonies, conical or fan-shaped, planar or longitudinally pleated, frontal surface exterior if conical. Branches intermediate in width, linear to moderately sinuous, closely or intermediately spaced, dichotomously divided. Two rows of autozooecia per branch, increasing to four rows proximal of branch bifurcations in some species; low straight to sinuous central keel on obverse side of branch with high nodes, composed of core of granular skeleton and sheath of laminar skeleton. Laminar wall extensions of keel nodes fused together forming a fine meshwork of polygonal openings, each opening centred over a zooecial aperture in the branch below. Axial wall between autozooecial rows zigzag in tangential sections; zooecia not strongly inflated laterally, commonly quadrangular or pentagonal in tangential section deep within endozone, less commonly elongate triangular or semicircular, pentagonal to bean-shaped in shallower endozone; maximum diameter of zooecia corresponds with either length or height; transverse walls at intermediate or high angle to reverse wall; superior hemisepta absent or weakly developed, other interior structures absent. Small- to large-diameter distal tube typically short, opening frontally or slightly inclined laterally and perhaps distally; apertural peristome present or absent; terminal diaphragms planar where present, with central boss in some species. Heterozooecia are isolated zooecia with enlarged endozonal chambers

(?gynozooecia) present in proximal parts of colonies, or spherically inflated distal tubes with diameters greater than branch width (? brood chambers). Zooecial walls of granular material that may be absent on obverse side near apertures; laminar extrazooecial skeleton traversed by small to moderate microstyles (modified after F. K. McKinney, pers. comm. 2007).

COMPARISON
Hemitrypa Phillips, 1841 is similar to *Pseudounitrypa* Nekhoroshev, 1926, but differs from it in the composition of the superstructure. The superstructure of *Hemitrypa* is produced by laminar wall extensions of keel nodes forming a meshwork of polygonal openings which are centred over zooecial apertures in the branch below, whereas openings in *Pseudounitrypa* are centred over the branches and terminate laterally over the centres of the fenestrules where the superstructural elements from adjacent branches meet and fuse.

Hemitrypa lasutkiniae Waschurova, 1964
(Figs 18D, E; 19A-F; Appendix)

Hemitrypa devonica Nekhoroshev subsp. *lasutkiniae* Waschurova, 1964: 85, pl. 27, figs 3-5.

MATERIAL. — SMF 21.333-SMF 21.360.

OCCURRENCE. — Lower Devonian (?Emsian); Tajikistan. Lebanza Formation, Lower Devonian (Pragian); Arauz Sur (Arroyo section), Palencia, NW-Spain (Cantabrian Mountains).

DESCRIPTION
Reticulate colonies with straight branches joined by dissepiments. Autozooecia arranged in two alternating rows on branches, having circular apertures with low peristomes, two spaced per length of a fenestrule. Peristomes smooth. Fenestrules oval to rectangular, varying in size. Openings in the superstructure irregularly shaped, rounded to petaloid, corresponding to positions of apertures, 0.10-0.14 mm in diameter. Superstructure containing small styles, 0.010-0.015 mm in diameter. Internal granular skeleton continuous with obverse keel, nodes, peristome and across dissepiments, 0.02-0.04 mm thick on the branch reverse wall. Outer lamellar skeleton well developed, 0.035-0.050 mm thick on the branch reverse wall. Reverse colony surface containing large, irregularly sized nodes, 0.030-0.075 mm in diameter. Heterozooecia not observed.

Interior description
Autozooecia triangular to trapezoidal or pentagonal in mid tangential section; low and elongated, with short vestibule in longitudinal section, diverging laterally at angles of 42-70°. Axial wall between autozooecial rows zigzag in tangential sections; aperture positioned at distal end of chamber. Hemisepta absent.

COMPARISON
The present material is similar to *Hemitrypa lasutkiniae* Waschurova, 1964 from the Lower Devonian (?Emsian) of Tajikistan, in having large nodes on the reverse side, the shape of the autozooecia and the size of the elements of the meshwork. *Hemitrypa lasutkinae* is similar to *H. kulalica* Waschurova, 1964 (Waschurova 1964: 83, 84, pl. 6, fig. 4) in general morphology and the presence of nodes on the reverse surface, but differs in having slightly larger fenestrules and smaller openings of the protecting superstructure (0.10-0.14 mm vs 0.17 mm in *H. kulalica*). Furthermore, *Hemitrypa lasutkinae* is similar to *H. favosa* Hall, 1881 from the upper Helderberg Group (Lower Devonian, Emsian) of Canada, but differs from the latter in the presence of nodes on the reverse side. The internal morphology of *H. favosa* is not known.

Family SEMICOSCINIIDAE Morozova, 1987

Genus *Tectulipora* Hall, 1888

TYPE SPECIES. — *Fenestella* (*Hemitrypa*) *lata* Hall, 1883, by subsequent designation (Hall 1888). Middle Devonian; Canada, Ontario.

OCCURRENCE. — Lower to Upper Devonian of North America and Eurasia.

DIAGNOSIS. — Reticulate colonies, conical or fan-shaped, planar or longitudinally pleated, frontal surface exterior if conical. Branches wide, moderately sinuous, closely or intermediately spaced, dichotomously divided. Two

rows of autozooecia per branch. Straight to sinuous, high club-shaped median keel on obverse side of branch, composed of core of granular skeleton and sheath of laminar skeleton. Axial wall between autozooecial rows straight in tangential sections, continuing unbroken in superstructure; superstructure corresponding with underlying branches and dissepiments or with autozooecial apertures, consisting of laterally expanded laths borne on continuous skeletal sheets from branches and dissepiments. Autozooecia not strongly inflated laterally, commonly rectangular in deep tangential section; transverse walls at intermediate or high angle to reverse wall; hemisepta absent. Intermediate- to large-diameter short distal tube, opening frontally or slightly inclined laterally; apertural peristome present or absent; terminal diaphragms planar where present, with central boss in some species. Laminar extrazooecial skeleton traversed by small to moderate microstyles.

COMPARISON

Unitrypa Hall, 1885 differs from *Loculipora* Hall, 1885 in having less sinuous branches which are joined by dissepiments instead of anastomoses in *Loculipora*. Transverse connections in the superstructure of *Unitrypa* do not contact with dissepiments, whereas the superstructure in *Loculipora* is produced by extensions of both median keels and dissepiments.

Tectulipora tuberculata n. sp.
(Figs 19G, H; 20A-H; Appendix)

ETYMOLOGY. — The species name refers to the presence of abundant large nodes, present both on the branches and superstructure.

HOLOTYPE. — SMF 21.361.

PARATYPES. — SMF 21.362-SMF 21.380.

TYPE LOCALITY. — Arauz Sur (Arroyo section), Province of Palencia, NW-Spain (Cantabrian Mountains).

TYPE HORIZON. — Lebanza Formation, Lower Devonian (Pragian).

DIAGNOSIS. — Reticulate colonies, conical, frontal surface exterior; autozooecia arranged in two weakly alternating rows on branches, 4-7 spaced per length of a fenestrule; autozooecial chambers rectangular in mid tangential section, short and relatively high, with moderately short vestibules; axial wall straight; hemisepta absent; terminal diaphragms planar; fenestrules oval to rectangular; superstructure produced by straight high club-shaped median keel, corresponding with underlying branches, outer lamellar skeleton well developed, traversed by small microstyles; large, irregularly sized nodes on reverse colony surface and on the protective superstructure; heterozooecia not observed.

DESCRIPTION

Reticulate colonies, conical, frontal surface exterior. Branches intermediate in width, straight, intermediately spaced, dichotomously divided, joined by straight wide dissepiments. Autozooecia arranged in two weakly alternating rows on branches, having circular apertures with low peristomes, 4-7 spaced per length of a fenestrule. Fenestrules oval to rectangular, varying in size. Straight high club-shaped median keel on obverse side of branches, composed of core of granular skeleton and sheath of laminar skeleton; superstructure corresponding with underlying branches, consisting of laterally expanded laths borne on continuous skeletal sheets from branches and dissepiments.

Internal granular skeleton continuous with obverse keel, nodes, peristome and across dissepiments, 0.015-0.055 mm thick on the branch reverse wall. Outer lamellar skeleton well developed, 0.055-0.170 mm thick on the branch reverse wall, traversed by small microstyles. Reverse colony surface containing large, irregularly sized nodes, 0.03-0.09 mm in diameter. Similar nodes occurring on the protective superstructure, 0.03-0.05 mm in diameter. Heterozooecia not observed.

Interior description

Autozooecial chambers rectangular in mid tangential section, short and relatively high, with moderately short vestibules. Axial wall between autozooecial rows straight in tangential sections, continuing unbroken in superstructure. Hemisepta absent. Terminal diaphragms planar.

COMPARISON

Tectulipora tuberculata n. sp. is similar to *T. pannosa* (Počta, 1894) from the Lower Devonian (Pragian) of Czech Republic and to *T. conjunctiva* (Hall, 1881) from the Lower Devonian of Canada in general morphology and dimensions of the meshwork, but differs from them in having large nodes

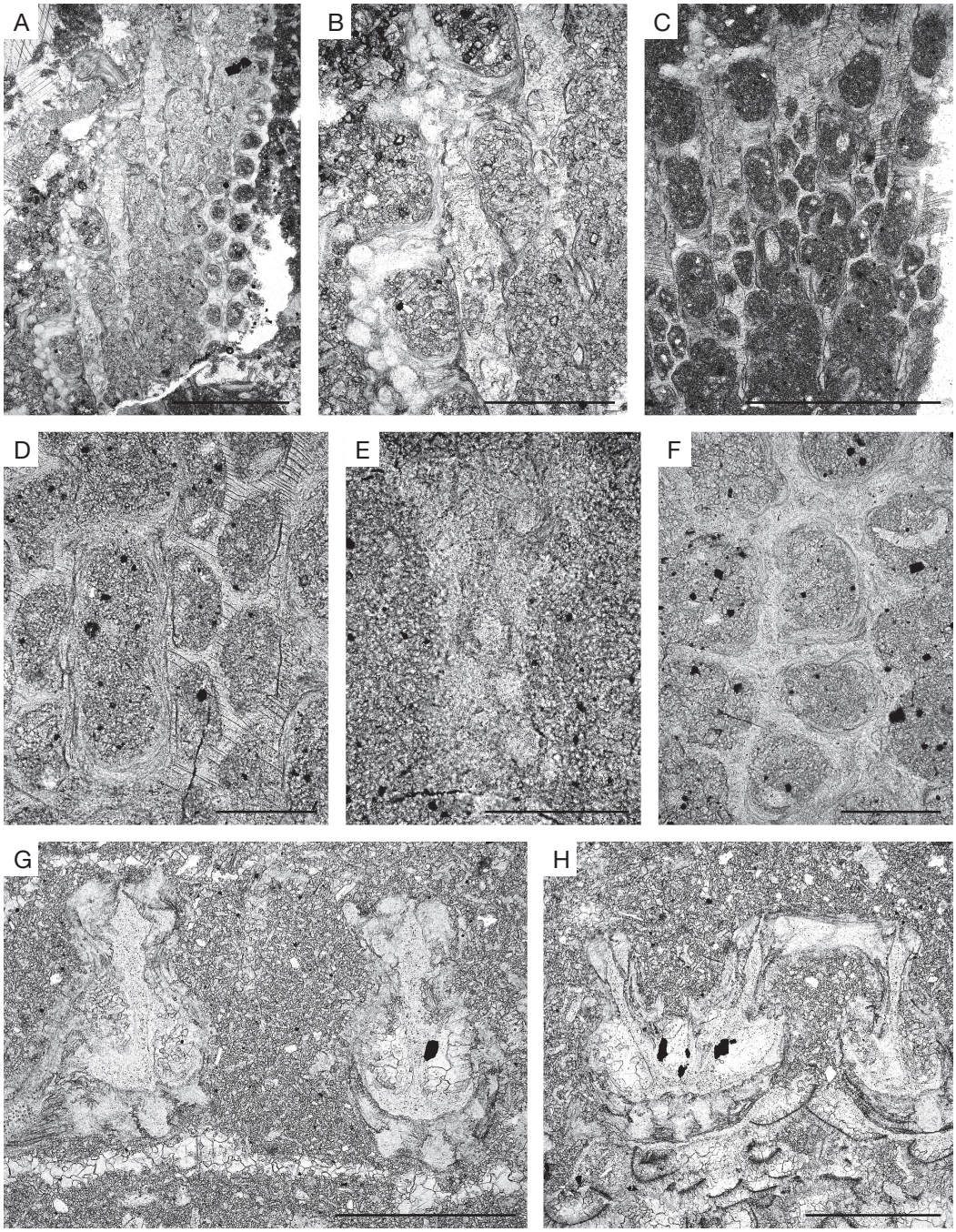

FIG. 19. — **A**-**F**, *Hemitrypa lasutkiniae* Waschurova, 1964; **A**, **B**, oblique tangential section showing protecting superstructure and nodes on the reverse surface, SMF 21.355; **C**, **D**, tangential section showing autozooecial chambers, SMF 21.358; **E**, tangential section of reverse side showing nodes, SMF 21.357; **F**, openings in superstructure, tangential section, SMF 21.358; **G**, **H**, *Tectulipora tuberculata* n. sp., branch transverse section showing branches and superstructure, paratype SMF 21.380. Scale bars: A, C, H, 1 mm; B, G, 0.5 mm; D-F, 0.2 mm.

TABLE 1. — Distribution of bryozoan species in mounds. Locations of studied samples: **1**, **2**, Level 2B (unspecified origin within bryozoan mud-mound); **3**, Bryozoan mud-mounds (upper part); **4**, Bryozoan mud-mounds (? middle part); **5**, Bryozoan mud-mounds (lower part).

	1	2	3	4	5
Altshedata hispanica n. sp.	×	×	×	×	×
Altshedata gracilis n. sp.	×	×			×
Fistulipora arauzensis n. sp.		×	×	×	×
Eridopora sp.		×			
Petalosis clarus n. gen., n. sp.	×	×		×	
Neotrematopora tenuis n. sp.			×		
Leioclema arauzensis n. sp.	×	×	×		
Leioclema multiacanthoporum Astrova *in* Astrova & Yaroshinskaya, 1968			×	×	
Eridotrypella validaeformis n. sp.	×	×	×		
Leptotrypella armata n. sp.	×	×	×		
Orthopora spinosa n. sp.	×	×	×	×	×
Vidronovella elegantula n. sp.	×	×	×		
Rhomboporidae sp. indet.		×			
Rectifenestella exiliformis n. sp.	×	×	×	×	
Hemitrypa lasutkiniae Waschurova, 1964	×	×	×	×	×
Tectulipora tuberculata n. sp.		×	×	×	

on the reverse colony surface. *Unitrypa tuberculata* n. sp. is also similar to *Isotrypa* (*Tectulipora*) *sibirica* Krasnopeeva subsp. *communis* Waschurova, 1964 (Waschurova 1964: 100, pl. 21, fig. 3) in general morphology and in the presence of nodes on the reverse colony surface and on the superstructure. However, the latter species has narrower branches (branch width 0.31 vs 0.28-0.49 mm in present material), and smaller fenestrules (fenestrule width 0.23 vs 0.20-0.42 mm and fenestrule length 0.31-0.54 vs 0.69-1.05 mm in present material).

FAUNAL COMPOSITION AND PALAEOBIOGEOGRAPHY

The studied fauna is distinctly dominated by cystoporates (5 species) and trepostomes (5 species), followed by cryptostomes (3 species) and fenestrates (3 species) (Table 1). In general, this composition is typical for the Lower Devonian (Cuffey & McKinney 1979; Bigey 1985). Palaeobiogeographical comparisons are restricted because most of the species are new. Only two species have been described earlier: *Leioclema multiacanthoporum* Astrova *in* Astrova & Yaroshinskaya, 1968 and *Hemitrypa lasutkiniae* Waschurova, 1964. *Leioclema multiacanthoporum* was recorded from the Lower Devonian (Emsian) of the Altai Mountains, Russia and the Lower Devonian (Pragian-Emsian) of Mongolia. *Hemitrypa lasutkiniae* is known from the Lower Devonian (?Emsian) of Tajikistan. The generic composition indicates relationships with the Lower Devonian of Altai (*Altshedata*, *Neotrematopora*) and Mongolia (*Neotrematopora*). Several species of *Tectulipora* are known from the Lower Devonian of the Czech Republic, USA and Tajikistan. *Vidronovella* is known from the Emsian of NW Spain. *Fistulipora*, *Leioclema*, *Eridotrypella*, *Leptotrypella*, *Orthopora*, *Rectifenestella*, and *Hemitrypa* are known from many localities worldwide (mainly North America and Eurasia).

PALAEOECOLOGY

The 16 bryozoan species display four different growth habits: encrusting (7 species): *Altshedata hispanica* n. sp., *A. gracilis* n. sp., *Fistulipora arauzensis* n. sp., *Eridopora* sp., *Petalosis clarus* n. sp., *Neotrematopora tenuis* n. sp., *Leioclema arauzensis* n. sp.; ramose branched/encrusting (2 species): *Leioclema multiacanthoporum*, *Eridotrypella validaeformis* n. sp.; ramose branched (4 species): *Leptotrypella armata* n. sp., *Orthopora spinosa* n. sp., *Vidronovella elegantula* n. sp., Rhomboporidae sp. indet.; ramose re-

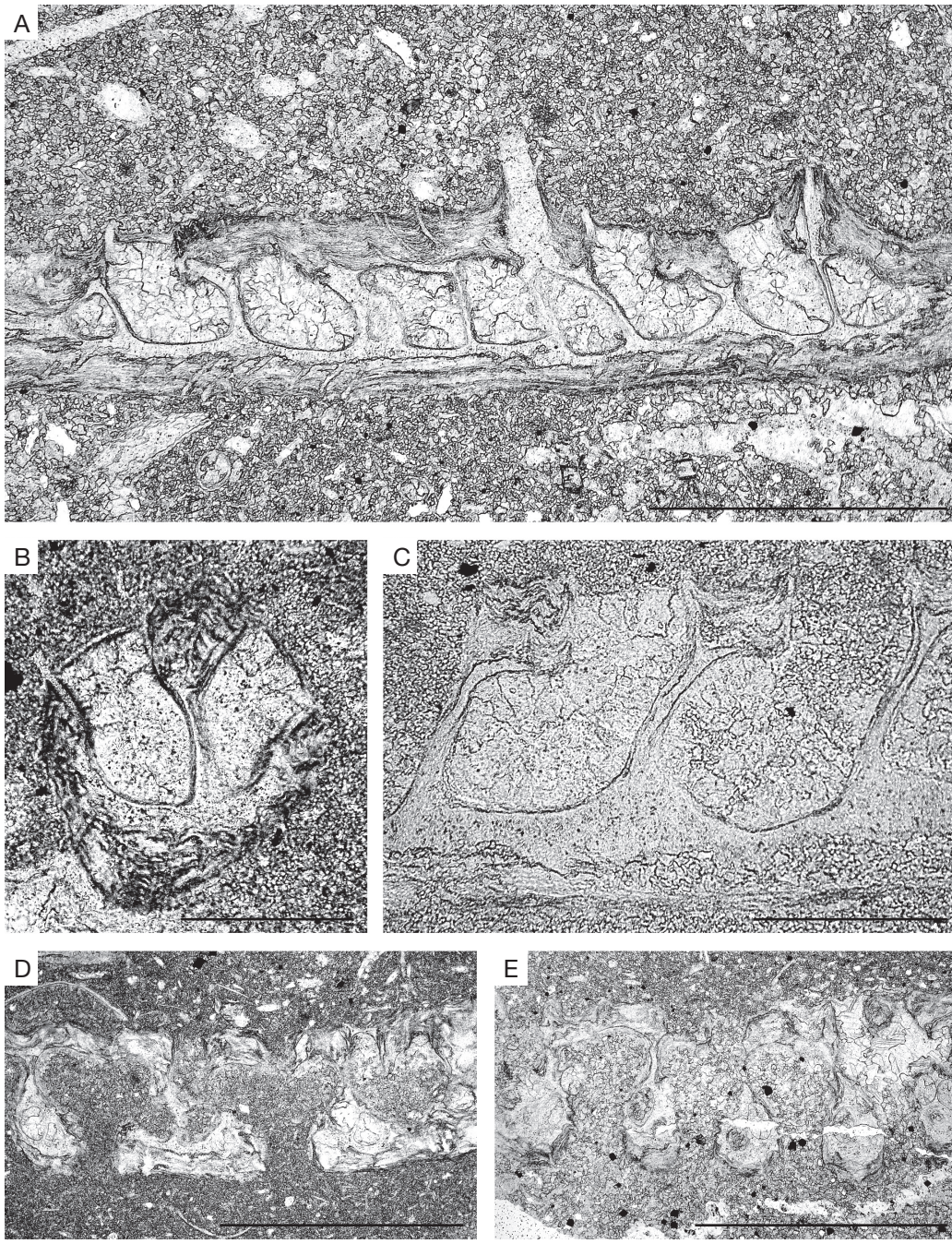

FIG. 20. — *Tectulipora tuberculata* n. sp: **A-B**, tangential section showing superstructure, holotype SMF 21.361; **C**, mid tangential section showing autozooecial chambers, apertures and wide keels, SMF 21.378; **D**, tangential section showing autozooecial apertures, holotype SMF 21.361; **E**, tangential section of reverse surface showing microacanthostyles and nodes, paratype SMF 21.377; **F**, tangential section of obverse surface showing granulated skeleton of axial wall, paratype SMF 21.371; **G**, longitudinal section, paratype SMF 21.362; **H**, transverse section of conical colony at its base, paratype SMF 21.369. Scale bars: A, B, G, H, 1 mm; C, 0.5 mm; D, 0.2 mm; E, F, 0.1 mm.

TABLE 2. — Distribution of bryozoan growth habits in mounds. Assignment of samples see Table 1.

	1	2	3	4	5
Encrusting	4	6	4	3	3
Ramose branched/encrusting	1	1	2	1	–
Ramose branched	3	4	3	1	1
Ramose reticulated	2	3	3	3	1

ticulated (3 species): *Rectifenestella exiliformis* n. sp., *Hemitrypa lasutkiniae*, *Tectulipora tuberculata* n. sp.

Encrusting growth habits dominate (43.75%), represented by five cystoporate and two trepostome species. Two trepostome species developed both encrusting and ramose branched growth habits (12.5%). One trepostome and three rhabdomesine cryptostomes developed ramose branched colonies (25%). Three fenestrates developed reticulated colonies (18.75%), most apparently conical in shape (Fig. 20H).

Regarding the distribution of growth habits in the studied Lebanza mud-mounds, the following pattern is observed. Encrusting and encrusting/ramose growth habits dominate in all parts of the mud mounds (lower, middle and upper), whereas ramose branched and reticulated bryozoans are most abundant in the lower parts of the mounds, being rare in the upper parts. Bryozoans that encrusted soft substrates, organisms such as corals and other bryozoan species produced complex multilayered aggregations (Fig. 21A-C). Similar multilayered aggregations in Devonian cystoporates and trepostomes were described by Bigey (1981). Thickness and number of layers in such aggregations were apparently regulated by exogenous (e.g., substrate type) as well as endogenous (e.g., degenerations-regenerations cycles of polypides) factors.

Ramose branched and reticulated species were apparently unable to inhabit soft unstable substrates, and their bases are often found on hard substrates, preferentially encrusting bryozoans (Fig. 21D). Encrusting bryozoans occur on small erect tabulate corals and apparently they grew on the living colonies while the coral was still alive because the coral apertures are not closed by bryozoans (Fig. 22E, F). Similar phenomenon is mentioned by McKinney *et al.* (1990) who described apparent mutualism between trepostome bryozoan *Leioclema* and tabulate coral *Aulopora* from the Lower Devonian of USA. Bryozoans used corals as substrate, and the corals profited from water currents produced by the bryozoans. Morozova (1961: 85) described the trepostome species *Leioclema minussinense* Morozova, 1961 which is encrusting an auloporal coral. She interpreted as worm grazing on bryozoans. However, the belonging of tubes to corals is obvious (Morozova 1961: pl. 12, fig. 1).

Despite their abundance, bryozoans cannot be regarded as the principal builders of the mud mounds. Judging from the texture of the rock, these were the microbial communities (see Fig 21C). Nevertheless, bryozoans played the role of sediment binders (encrusting species) that stabilized the sediment, or exerted a baffling effect (fenestrates) promoting sedimentation (McKinney *et al.* 1987).

CONCLUSIONS

A bryozoan fauna from the Lebanza Formation (Lower Devonian) of the Arauz area, NW Spain shows high diversity and abundance. This fauna contains 16 species and is dominated by cystoporates and trepostomes, followed by cryptostomes and fenestrates. The studied bryozoan fauna displays four different growth habits: encrusting, ramose branched/encrusting, ramose branched, and reticulate. Encrusting and encrusting/ramose growth habits dominate in all parts of mud mounds, whereas ramose branched and reticulate bryozoans are most abundant in the lower part of mounds, being rare in the upper parts. Bryozoans cannot be regarded as the principal builders of the mud mounds, which apparently were mainly built by microbial communities. However, bryozoans played an important role of sediment binders (encrusting species), stabilizing the sediment, or exerted a baffling effect (fenestrates). The trepostome species *Leioclema multiacanthoporum* Astrova *in* Astrova & Yaroshinskaya, 1968 shows relations to the Lower Devonian of Altai, and

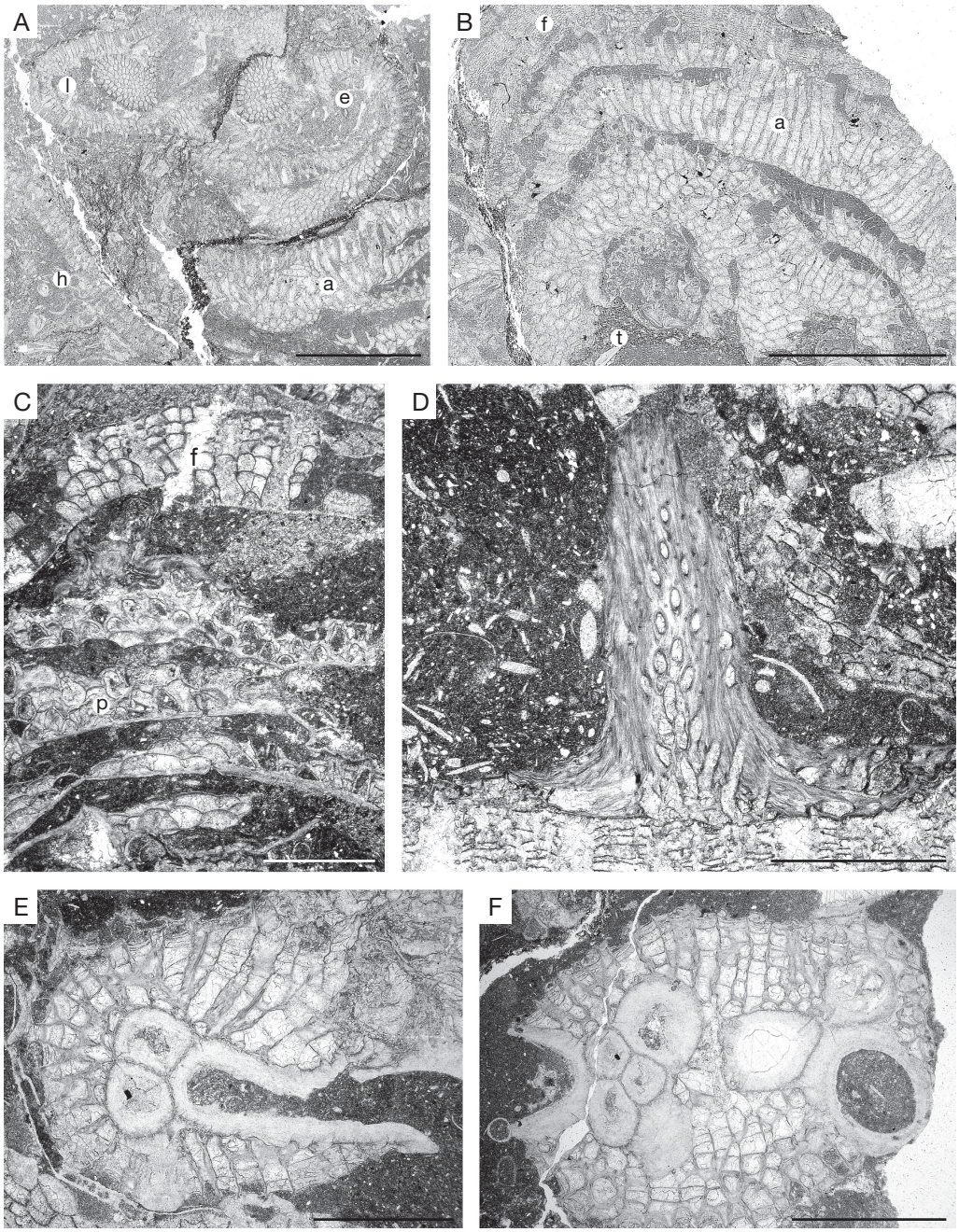

FIG. 21. — **A**, complex bryozoan community with multilayered encrusting by *Altshedata hispanica* n. sp. (**a**), *Leioclema arauzensis* n. sp. (**l**) and *Eridotrypella validaeformis* n. sp. (**e**), top of the images shows also two branches of *Eridotrypella validaeformis*.; **H**, *Hemitrypa lasutkiniae* Waschurova, 1964, SMF 21.381; **B**, complex multiple encrusting by *Altshedata hispanica* n. sp. (**a**) and *Fistulipora arauzensis* n. sp. (**f**), *Tectulipora tuberculata* n. sp. (**t**), SMF 21.382; **C**, multiple encrusting of soft substrate by thin sheets of *Petalosis clarus* n. gen. n. sp. (**p**) and *Fistulipora arauzensis* n. sp. (**f**), SMF 21.383; **D**, base of *Orthopora spinosa* n. sp. on *Fistulipora arauzensis* n. sp., SMF 21.384; **E**, **F**, *Neotrematopora tenuis* n. sp. encrusting tabulate coral; **E**, SMF 21.207; **F**, SMF 21.210. Scale bars: A, B, 5 mm; C-F, 1 mm.

Mongolia. The fenestrate species and *Hemitrypa lasutkiniae* Waschurova, 1964 is known from the Lower Devonian (Emsian) of Tajikistan.

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REFERENCES

ANSTEY R. L. & PERRY T. G. 1970. — Biometric procedures in taxonomic studies of Paleozoic bryozoans. *Journal of Paleontology* 44: 383-398.

ARBIZU M., MÉNDEZ-BEDIA I. & SOTO F. 1995. — Fossil communities in the Aguión Formation (Lower Devonian) of the Arnao Platform (Asturias, NW Spain). *Geobios* 28: 567-571.

ASTROVA G. G. 1978. — Historical development, systematics and phylogeny of Bryozoa. Order Trepostomata. [Istoriya razvitiya, sistema i filogenia mshanok: Otryad Trepostomata]. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 169: 1-240 [in Russian].

ASTROVA G. G. & YAROSHINSKAYA A. M. 1968. — [Lower Devonian and Eifelian Bryozoa of Salair and Gorno-Altai]. *Trudy Tomskogo Gosudarstvennogo Universiteta* 202: 47-62 [in Russian].

BIGEY F. P. 1981. — Overgrowths in Palaeozoic Bryozoa: Examples from Devonian forms, *in* LARWOOD G. P. & NIELSEN C. (eds), Recent and Fossil Bryozoa. Olsen & Olsen, Fredensborg, 7-17.

BIGEY F. P. 1985. — Biogeography of Devonian Bryozoa, *in* NIELSEN C. & LARWOOD G. P. (eds.), Bryozoa: Ordovician to Recent. Fredensborg, 9-23.

BROUWER A. 1964. — Devonian biostromes and bioherms of the southern Cantabrian Mountains, Northwestern Spain, *in* VAN STRAATEN L. M. J. U. (ed.), Deltaic and Shallow Marine Deposits. *Developments in Sedimentology* 1: 48-53.

CUFFEY R. J. & MCKINNEY F. K. 1979. — Devonian Bryozoa. *Special Papers in Palaeontology* 23: 307-311.

DUNCAN H. 1939. — Trepostomatous Bryozoa from the Traverse Group of Michigan. *University of Michigan Paleontology Contributions* 5 (10): 171-270.

ERNST A. 2010. — Trepostome bryozoans from the Lower-Middle Devonian of NW Spain. *Rivista Italiana di Paleontologia e Stratigrafia* 116 (3): 283-308.

ERNST A. 2011. — Cryptostome (ptilodictyine and rhabdomesine) Bryozoa from the Lower Devonian of NW Spain. *Palaeontographica A* 293 (4-6): 1-37.

ERNST A. & MAY A. 2012. — Bryozoan fauna from the Lower Devonian (Middle Lochkovian) of Sierra de Guadarrama, Spain. *Journal of Paleontology* 86 (1): 60-80.

ERNST A., MAY A. & MARKS S. 2012. — Bryozoans, corals and microfacies of Lower Eifelian (Middle Devonian) limestones at Kierspe, Germany. *Facies* 58: 727-758 .

FERNÁNDEZ L. P., FERNÁNDEZ-MARTÍNEZ E., GARCÍA-RAMOS J. C., MÉNDEZ-BEDIA I. & SOTO F. 1997. — A sequential approach to the study of reefal facies in the Candás and Portilla Formations (Middle Devonian) of the Cantabrian Zone (NW Spain). *Boletín de la Real Sociedad Española de Historia Natural (Sección Geología)* 92 (1-4): 23-33.

FERNÁNDEZ L. P., NOSE M., FERNÁNDEZ-MARTÍNEZ E., MÉNDEZ-BEDIA I., SCHRÖDER S. & SOTO F. 2006. — Reefal and mud mound facies development in the Lower Devonian La Vid Group at the Colle outcrops (León province, Cantabrian Zone, NW Spain). *Facies* 52: 307-327.

FERNÁNDEZ-MARTÍNEZ E., FERNÁNDEZ L. P., MÉNDEZ-BEDIA I., SOTO, F. & MISTIAEN B. 2010. — Earliest Pragian (Early Devonian) corals and stromatoporoids from reefal settings in the Cantabrian Zone (N Spain). *Geologica Acta* 8: 301-323.

FRANKENFELD H. 1983. — El manto de Montó-Arauz: Interpretación estructural de la Región del Pisuerga-Carrión (Zona Cantábrica, España). *Trabajos de Geología* 13: 37-47.

GARCÍA-ALCALDE J. L. 1996. — El Devónico del Dominio Astur-leonés en la Zona Cantábrica. *Revista Española de Paleontología, nº extraordinario* 1996: 58-71.

GARCÍA-ALCALDE J. L. 1998. — Devonian events in northern Spain. *Newsletter on Stratigraphy* 36: 157-175.

GARCÍA-ALCALDE J. L., MONTESINOS J. R., TRUYOLS-MASSONI M., GARCÍA-LÓPEZ S., ARBIZU M. A. & SOTO F. 1988. — El Silúrico y el Devónico del Dominio Palentino (NO de España). *Revista de la Sociedad Geológica de España* 1: 7-13.

GARCÍA-ALCALDE J. L., SOTO F. M. & TRUYOLS-MASSONI M. 2002. — Devonian of the Cantabrian Mountains, *in* GIBBONS W. & MORENO T. (eds), *The Geology of Spain*. The Geological Society of London: 68-76.

GARCÍA-LÓPEZ S., JAHNKE H. & SANZ-LÓPEZ J. 2002. — Uppermost Pridoli to Upper Emsian stratigraphy of the Alto Carrion Unit (Palentine Domain, Northwest Spain), *in* GARCÍA-LÓPEZ S. & BASTIDA F. (eds), Paleozoic conodonts from Northern Spain. *Instituto Geológico y Minero de España, serie Cuadernos del Museo Geominero* 1: 229-257.

GORJUNOVA R. V. 2006. — New bryozoans from the Devonian of Afghanistan and the Carboniferous of Iran. *Paleontologicheskii Zhurnal* 6: 43-51.

HAGEMAN S. J. 1993. — Effects of nonnormality on studies of the morphological variation of a rhabdomesine bryozoan *Streblotrypa* (*Streblascopora*) *prisca* (Gabb and Horn). The University of Kansas, Paleontological Contributions, 4: 1-13.

HALL J. 1886. — Bryozoa of the Upper Heldelberg groups; plates and explanations. *State Geologist of New York, 5th Annual Report for 1885*: 25-53.

HALL J. 1888. — Description of new species of Fenestellidae of the Lower Helderberg, with explanations of plates illustrating species of Hamilton group, described in the Report of the state Geologist for 1886. *Report of the State Geologist [of New York] for the year 1887*: 393-394, pls viii-xv.

HOFMANN M. H. & KELLER M. 2006. — Sequence stratigraphy and carbonate platform organization of the Devonian Santa Lucia Formation, Cantabrian Mountains, NW-Spain. *Facies* 52: 149-167.

JAHNKE H., HENN A., MADER H. & SCHWEINEBERG T. 1983. — Silur und Devon im Arauz-Gebiet (Provincia de Palencia, N-Spanien). *Newsletters on Stratigraphy* 13: 40-66.

JULIVERT M. 1971. — Décollement tectonics in the Variscan Cordillera of the northwest Spain. *American Journal of Science* 270: 1-29.

KELLER M. 1997. — Evolution and sequence stratigraphy of an Early Devonian carbonate ramp, Cantabrian Mountains, Northern Spain. *Journal of Sedimentary Research* 67: 638-652.

KELLER M. & GRÖTSCH J. 1990. — Depositional history and conodont biostratigraphy of the Lower Devonian La Vid Group in the Luna area (Cantabrian Mountains, NW Spain). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 3: 141-164.

KOPAJEVICH G. V. 1984. — Atlas mshanok ordovika, silura i devona Mongolii [Atlas of bryozoans from Ordovizium, Silurian and Devonian of Mongolia]. *Sovmestnaya Sovetsko-Mongolskaya Paleontologischeskaya Ekspeditsiya, Trudy* 22:1-164 [in Russian].

KRANS T. J., GUIT T. A., & VAN OFWEGEN L. P. 1980. — Facies-patterns in the Lower Devonian carbonates of the Lebanza Formation (Cantabrian Mountains, Province of Palencia, NW Spain). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 163: 192-230.

LOTZE F. 1945. — Zur Gliederung der Varisziden in der Iberischen Meseta. *Geotektonische Forschung* 6: 78-92.

MCKINNEY F. K., MCKINNEY M. J. & LISTOKIN M. R. A. 1987. — Erect bryozoans are more than baffling: Enhanced sedimentation rate by a living unilaminate branched bryozoans and possible implications for fenestrate bryozoan mudmounds. *Palaios* 2: 41-47.

MCKINNEY F. K., BROADHEAD, T. W. & GIBSON M. A. 1990. — Coral-bryozoan mutualism: Structural innovation and greater resource exploration. *Science* 248: 466-468.

MÉNDEZ-BEDIA I., SOTO F. & FERNÁNDEZ-MARTÍNEZ E. 1994. — Devonian reef types in the Cantabrian Mountains (NW Spain) and their faunal composition. *Courier Forchungsinstitut Senckenberg* 172: 161-183.

MILNE-EDWARDS H. & HAIME J. 1850-1854. — A monograph of British fossil corals. *Monographs of the Palaeontographical Society of London*: 1-322.

MOROZOVA I. P. 1959. — [New genus of the Family Fistuliporidae in Devonian in Kuznetz Basin]. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 2: 79-81 [in Russian].

MOROZOVA I. P. 1961. — [Devonian Bryozoa of the Minusinsk and Kuznetsk depressions]. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 86: 1-206 [in Russian].

MOROZOVA I. P. 1974. — Revision of the genus *Fenestella* [Reviziya roda *Fenestella*.] *Paleontologicheskij Zhurnal*, 1974 (2): 54-67 [in Russian].

PÉREZ-ESTAÚN A., BASTIDA F., ALONSO J. L., MARQUÍNEZ J., ALLER, J., ALVAREZ-MARRÓN J., MARCOS, A. & PULGAR J. A. 1988. — A thin-skinned tectonics model for an arcuate fold and thrust belt: The Cantabrian Zone (Variscan Ibero-Armorican Arc). *Tectonics* 7: 517-537.

SUÁREZ ANDRÉS J. L. 1998. — Briozoos fenestrados de la Formacion Moniello (Devonico) en el area de Arnao (Asturias, España); I, Fenestellidae. *Revista Española de Paleontologia* 13 (2): 187-196.

SUÁREZ ANDRÉS J. L. 1999a. — Briozoos fenestrados de la Formación Moniello (Devónico) en Arnao (Asturias, España). II: Septoporidae, Polyporidae y Acanthocladiidae. *Revista Española de Paleontologia, Nº Extraordinario, Homanje al Prof. J. Truyols*: 185-193.

SUÁREZ ANDRÉS J. L. 1999b. — Nuevos datos sobre los briozoos devónicos de la Zona Cantábrica. *Temas Geológico-Mineros ITGE*, 6:643-646.

SUÁREZ ANDRÉS J. L. 1999c. — Parasitismo en briozoos del Devónico de la Zona Cantábrica. *Temas Geológico-Mineros ITGE* 6: 647-650.

SUÁREZ ANDRÉS J. L. & C. GONZÁLEZ 2000a. — Consideraciones paleobiogeográficas sobre los briozoos del Devónico de la Zona Cantábrica (Asturias, NW de España), *in* DÍEZ J. B. & BALBINO A. C. (eds), *Actas I Congresso Ibérico de Paleontología-XVI Jornadas Sociedad Española de Paleontología-VIII International Meeting of IGCP* 421: 291-292.

SUÁREZ ANDRÉS J. L. & GONZÁLEZ C. 2000b. — *Fenestrapora* Hall, 1885 (Bryozoa) del Devónico de la Zona Cantábrica, *in* DÍEZ J. B. & BALBINO A. C. (eds.), *Actas i Congresso Ibérico de Paleontologia-XVI Jornadas Sociedad Española de Paleontologia-VIII International Meeting of IGCP 421*: 293, 294.

SUÁREZ ANDRÉS J. L. & MCKINNEY F. K. 2010. — Revision of the Devonian fenestrate genera *Cyclopelta* Bornemann, 1884 and *Pseudoisotrypa* Prantl, 1932, with description of a rare fenestrate growth habit. *Revista española de paleontología* 25 (2): 123-138.

ULRICH E. O. 1882. — American Paleozoic Bryozoa. *The Journal of the Cincinnati Society of Natural History* 5: 121-175, 233-257.

VERA DE LA PUENTE C. 1989. — Revisión litoestratigráfica y correlación de los Grupos Rañeces y La Vid (Devónico Inferior de la Cuenca Astur-leonesa). *Trabajos de Geología* 18: 53-65.

VINASSA DE REGNY P. 1921. — Sulla classificazione die trepostomidi. *Societa Italiana di Scienze Naturali Atti* 59:212-231.

WASCHUROVA L. I. 1964. — [Bryozoa from the Lower Devonian of the Zeravshan and Turkestan Ranges]. *Trudy Upravlenia geoligii i okhrany nedr pri Sovete Ministrov Tadzhikskoi SSSR, Paleontologia i Stratigrafia* 1: 75-168 [in Russian].

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APPENDIX

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

Altshedata hispanica n. sp.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	30	0.30	0.033	10.92	0.23	0.38
Aperture spacing, mm	30	0.34	0.029	8.43	0.29	0.40
Lunarium width, mm	15	0.147	0.017	11.28	0.120	0.180
Lunarium length, mm	15	0.141	0.031	21.95	0.100	0.200
Lunarium thickness, mm	15	0.040	0.008	20.13	0.025	0.050

Altshedata gracilis n. sp.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	25	0.27	0.041	15.23	0.20	0.36
Aperture spacing, mm	25	0.31	0.054	17.44	0.23	0.42
Lunarium width, mm	15	0.112	0.016	13.96	0.080	0.130
Lunarium length, mm	15	0.069	0.013	18.05	0.055	0.100
Lunarium thickness, mm	15	0.035	0.008	21.60	0.025	0.050

Fistulipora arauzensis n. sp.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	35	0.19	0.023	11.90	0.14	0.24
Aperture spacing, mm	35	0.35	0.042	12.04	0.28	0.44
Vesicle diameter, mm	35	0.11	0.024	21.55	0.07	0.18
Vesicles per aperture	35	8.5	1.292	15.17	6.0	12.0
Vesicle spacing, mm	35	0.14	0.038	27.01	0.06	0.24

Eridopora sp.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	20	0.31	0.041	13.28	0.25	0.38
Aperture spacing, mm	20	0.40	0.059	14.98	0.30	0.54
Vesicle diameter, mm	20	0.14	0.031	21.71	0.11	0.2
Vesicles per aperture	4	7.5	0.577	7.70	7.0	8.0
Vesicle spacing, mm	20	0.08	0.023	30.13	0.05	0.15

Petalosis clarus n. gen., n. sp.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	40	0.21	0.032	15.35	0.16	0.28
Aperture spacing, mm	40	0.35	0.039	11.21	0.26	0.42
Lunarium width, mm	30	0.120	0.013	10.96	0.095	0.145
Lunarium length, mm	30	0.076	0.012	15.09	0.055	0.105
Lunarium thickness, mm	30	0.045	0.012	26.36	0.025	0.070
Vesicle diameter, mm	40	0.20	0.047	23.41	0.12	0.30
Vesicles per aperture	20	5.2	1.182	22.95	3.0	8.0
Vesicle spacing, mm	40	0.18	0.063	35.15	0.10	0.35

Neotrematopora tenuis n. sp.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	25	0.13	0.013	9.39	0.11	0.16
Aperture spacing, mm	25	0.20	0.026	13.26	0.14	0.25
Aperture width, mm (macular)	10	0.18	0.011	6.24	0.17	0.20
Aperture spacing, mm (macular)	10	0.28	0.037	12.88	0.22	0.34
Mesozooecia width, mm	25	0.051	0.017	33.55	0.025	0.080
Acanthostyle diameter, mm	25	0.04	0.008	20.46	0.03	0.06
Acanthostyles per aperture	25	3.3	0.690	20.80	2.0	5.0
Exozonal wall thickness, mm	25	0.05	0.013	27.75	0.03	0.08

Leioclema arauzensis n. sp.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	25	0.15	0.019	12.79	0.12	0.18
Aperture spacing, mm	25	0.21	0.025	11.76	0.17	0.26
Mesozooecia width, mm	25	0.050	0.014	27.54	0.030	0.085
Acanthostyle diameter, mm	25	0.045	0.014	31.10	0.025	0.090
Acanthostyles per aperture	25	3.8	0.879	23.39	2.0	6.0
Exozonal wall thickness, mm	20	0.042	0.012	27.82	0.025	0.065

Leioclema multiacanthoporum (Astrova *in* Astrova & Yaroshinskaya, 1968)

	N	X	SD	CV	MIN	MAX
Aperture width, mm	30	0.13	0.016	11.87	0.10	0.16
Aperture spacing, mm	30	0.20	0.026	12.76	0.16	0.25
Mesozooecia width, mm	25	0.044	0.016	36.38	0.025	0.075
Acanthostyle diameter, mm	30	0.037	0.007	18.35	0.025	0.045
Acanthostyles per aperture	30	6.5	1.383	21.28	4.0	9.0

Eridotrypella validaeformis n. sp.

	N	X	SD	CV	MIN	MAX
Branch width, mm	5	2.40	0.436	18.19	1.72	2.90
Exozone width, mm	5	0.48	0.141	29.32	0.36	0.72
Endozone width, mm	5	1.44	0.440	30.62	0.88	1.94
Aperture width, mm	30	0.14	0.016	11.19	0.12	0.17
Aperture spacing, mm	30	0.20	0.021	10.51	0.17	0.24
Aperture width, mm (macular)	10	0.20	0.012	5.99	0.18	0.22
Aperture spacing, mm (macular)	10	0.25	0.017	6.63	0.24	0.28
Exilazooecia width, mm	15	0.046	0.011	23.72	0.030	0.065
Acanthostyle diameter, mm	8	0.04	0.012	29.87	0.03	0.06
Exozonal wall thickness, mm	25	0.05	0.014	25.89	0.03	0.08

Leptotrypella armata n. sp.

	N	X	SD	CV	MIN	MAX
Branch width, mm	20	1.08	0.187	17.31	0.81	1.35
Exozone width, mm	20	0.32	0.059	18.31	0.24	0.48
Endozone width, mm	20	0.43	0.125	28.81	0.27	0.71
Aperture width, mm	40	0.08	0.012	16.21	0.05	0.10
Aperture spacing, mm	40	0.17	0.026	15.11	0.13	0.24
Exilazooecia width, mm	25	0.038	0.011	27.91	0.020	0.055
Acanthostyle diameter, mm	40	0.03	0.007	21.36	0.02	0.05
Acanthostyles per aperture	30	8	1.682	21.02	5	12
Exozonal wall thickness, mm	30	0.054	0.012	22.18	0.025	0.075

Orthopora spinosa n. sp.

	N	X	SD	CV	MIN	MAX
Branch width, mm	20	0.62	0.059	9.42	0.48	0.75
Exozone width, mm	20	0.18	0.032	17.97	0.14	0.22
Endozone width, mm	20	0.27	0.051	18.75	0.19	0.35
Aperture width, mm	35	0.05	0.010	20.08	0.04	0.07
Aperture spacing along branch, mm	35	0.28	0.028	9.85	0.22	0.35
Aperture spacing diagonally, mm	35	0.18	0.014	7.692	0.12	0.20
Acanthostyle diameter, mm	35	0.031	0.005	15.670	0.020	0.045
Autozooecial budding angle in endozone	5	43.8	5.762	13.155	35.0	51.0
Autozooecial budding angle in exozone	5	66.2	8.585	12.968	51.0	71.0

Vidronovella elegantula n. sp.

	N	X	SD	CV	MIN	MAX
Branch width, mm	10	0.82	0.124	15.12	0.59	0.96
Exozone width, mm	10	0.22	0.034	15.45	0.16	0.26
Endozone width, mm	10	0.38	0.080	21.19	0.23	0.49
Aperture width, mm	35	0.10	0.012	12.56	0.07	0.12
Aperture spacing along branch, mm	35	0.22	0.018	8.12	0.19	0.25
Aperture spacing diagonally, mm	35	0.16	0.013	8.27	0.13	0.18
Acanthostyle diameter, mm	35	0.032	0.005	14.72	0.025	0.040
Autozooecial budding angle in endozone	9	52	5.172	9.95	45	60
Exozonal wall thickness, mm	15	0.04	0.005	13.65	0.03	0.05

Rhomboporidae sp. indet.

	N	X	SD	CV	MIN	MAX
Aperture width, mm	10	0.09	0.015	16.55	0.07	0.11
Aperture spacing along branch, mm	7	0.32	0.056	17.62	0.24	0.38
Aperture spacing diagonally, mm	8	0.19	0.029	15.62	0.16	0.24
Metazooecia diameter, mm	4	0.025	0.014	56.57	0.015	0.045
Paurostyle diameter, mm	10	0.022	0.003	11.74	0.020	0.025
Aktinotostyle diameter, mm	10	0.040	0.008	20.41	0.030	0.055

Rectifenestella exiliformis n. sp.

	N	X	SD	CV	MIN	MAX
Branch width, mm	12	0.31	0.016	5.08	0.28	0.32
Dissepiment width, mm	15	0.19	0.025	12.89	0.17	0.26
Fenestrule width, mm	15	0.28	0.036	12.63	0.24	0.35
Fenestrule length, mm	15	0.68	0.168	24.82	0.48	1.11
Distance between branch centres, mm	15	0.84	0.173	20.59	0.66	1.29
Distance between dissepiment centres, mm	15	0.56	0.077	13.80	0.40	0.66
Aperture width, mm	20	0.084	0.006	7.63	0.075	0.095
Aperture spacing along branch, mm	20	0.18	0.010	5.41	0.16	0.20
Aperture spacing diagonally, mm	20	0.22	0.024	10.60	0.18	0.26
Apertures per fenestrule length	10	5.1	0.994	19.50	4.0	7.0
Maximal chamber width, mm	20	0.09	0.007	7.30	0.08	0.10
Keel node diameter, mm	20	0.07	0.014	19.73	0.05	0.10
Keel node spacing, mm	20	0.47	0.069	14.91	0.35	0.60
Thickness of reverse wall granular layer, mm	6	0.028	0.010	34.70	0.020	0.045
Thickness of reverse wall laminated layer, mm	6	0.036	0.018	51.01	0.015	0.060
Lateral wall budding angle	11	54.6	9.963	18.23	42.0	70.0

Hemitrypa lasutkiniae Waschurova, 1964

	N	X	SD	CV	MIN	MAX
Branch width, mm	30	0.26	0.037	14.17	0.19	0.36
Dissepiment width, mm	30	0.14	0.025	18.84	0.10	0.18
Fenestrule width, mm	30	0.16	0.023	14.54	0.12	0.20
Fenestrule length, mm	30	0.34	0.054	15.96	0.22	0.47
Distance between branch centres, mm	30	0.37	0.045	12.17	0.29	0.48
Distance between dissepiment centres, mm	30	0.46	0.070	15.22	0.32	0.57
Aperture width, mm	9	0.08	0.007	8.10	0.07	0.09
Apertures per fenestrule length	20	2.3	0.470	20.44	2.0	3.0
Maximal chamber width, mm	20	0.10	0.009	9.31	0.09	0.12
Branch thickness, mm	20	0.55	0.074	13.52	0.47	0.75
Keel node diameter, mm	5	0.055	0.013	23.18	0.045	0.075
Keel node spacing, mm	15	0.19	0.030	15.52	0.14	0.24
Superstructure Opening Diameter, mm	20	0.12	0.010	8.42	0.10	0.14
Node diameter, mm (reverse surface)	25	0.052	0.012	22.13	0.030	0.075
Lateral wall budding angle	7	49.3	7.847	15.92	41.0	62.0

Tectulipora tuberculata n. sp.

	N	X	SD	CV	MIN	MAX
Branch width, mm	25	0.39	0.052	13.16	0.28	0.49
Dissepiment width, mm	17	0.23	0.042	18.60	0.18	0.36
Fenestrule width, mm	10	0.26	0.067	25.52	0.20	0.42
Fenestrule length, mm	10	0.86	0.128	14.88	0.69	1.05
Distance between branch centres, mm	20	0.67	0.098	14.48	0.50	0.87
Distance between dissepiment centres, mm	17	1.11	0.165	14.82	0.87	1.32
Aperture width, mm	25	0.09	0.007	7.79	0.08	0.10
Aperture spacing along branch, mm	25	0.22	0.019	8.63	0.18	0.25
Apertures per fenestrule length	6	5.8	1.169	20.04	4.0	7.0
Maximal chamber width, mm	12	0.11	0.009	7.76	0.10	0.13
Branch thickness, mm	25	0.70	0.070	9.99	0.56	0.87
Node diameter, mm (reverse surface)	25	0.05	0.015	29.21	0.03	0.09
Thickness of reverse wall granular layer, mm	20	0.032	0.010	31.19	0.015	0.055
Thickness of reverse wall laminated layer, mm	20	0.113	0.028	24.79	0.055	0.170
Lateral wall budding angle	5	33.6	5.128	15.26	28.0	41.0